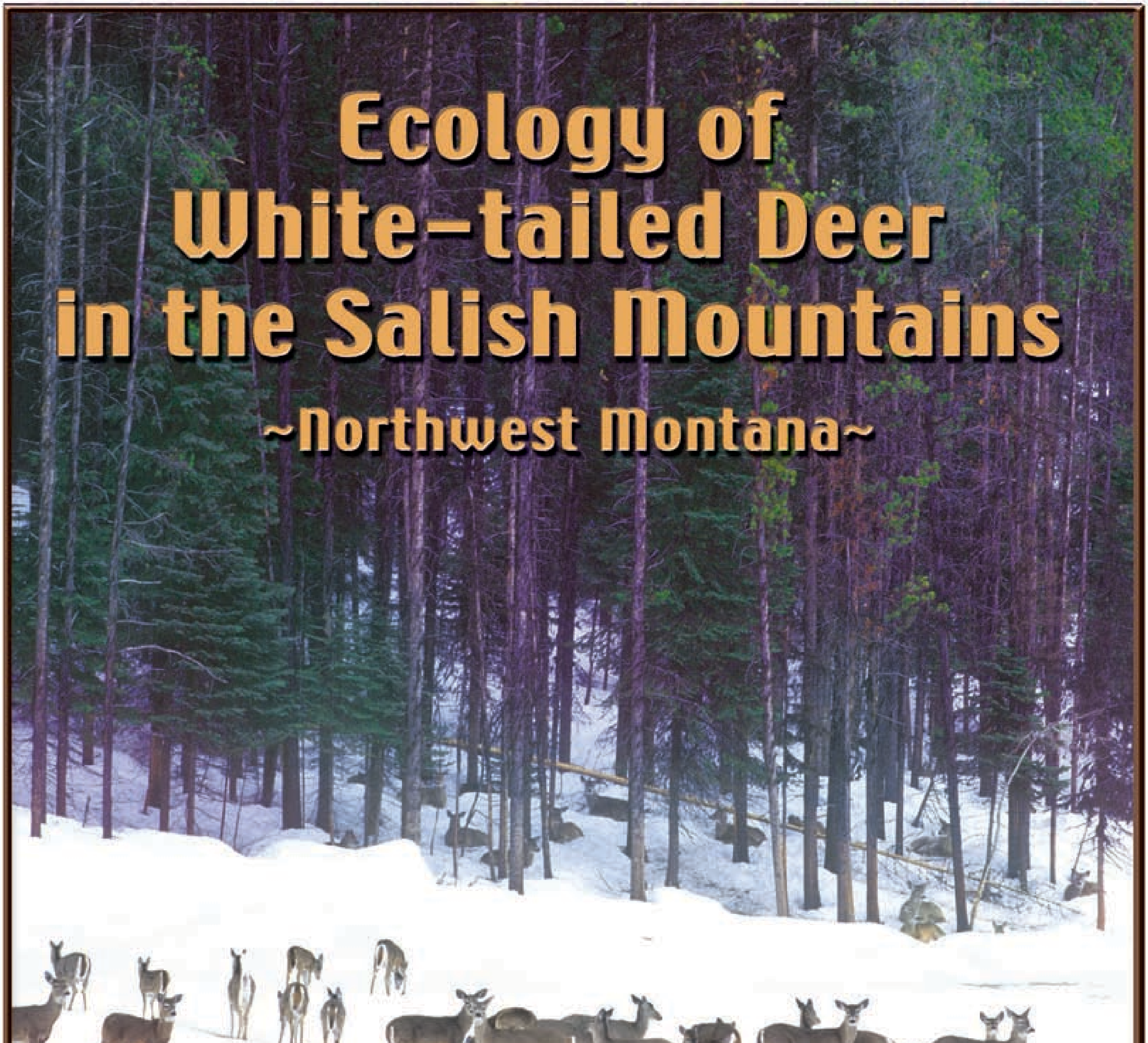
Ecology of White-tailed Deer in the Salish Mountains

~Northwest Montana~



White-tailed Deer Studies In The Salish Mountains, Northwest Montana

Montana Fish, Wildlife & Parks
Wildlife Division
Helena, Montana 59620

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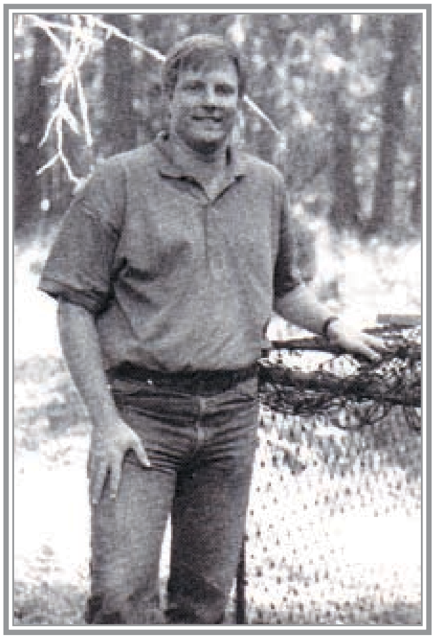
Carolyn Sime has worked for Montana Fish, Wildlife and Parks for the last 15 years. In addition to being one of the white-tailed deer project leaders she has also conducted research on sage grouse in Idaho and fire ecology on the Rocky Mountain Front. Carolyn was the primary author for Montana's Statewide Wolf Management Plan and is currently FWP' statewide Wolf Program Coordinator in Helena.



John Morgan conducted his doctoral research on white-tailed deer summer habitat use in northwest Montana as part of this research project. John is currently a program manager for the Pennsylvania Game Commission.

Photo Credits

Photos:

Gary Dusek - p. 106, 122, 165, 194, 195, 220, 231, and 240; Steve Hoekman- p. 1; Donald Jones - cover, large and lower right, p. 4, 109, 173, and 181; Louis Kiss - cover, lower center, p. 187; Brent Lonner - p. 112 and 206; Media Works stock photos - cover, lower left, p. 9, 14, 16, 19, 22, 24, 87, 91, 110, 163, 190, 191, and 199; MFWP - p. 2 (right), 21, 35, 38, 39, 42, 82, 99, 119, 126, 135, 167, 169, 171, 172, 175, 201, 207 and 233; John Morgan - p. 36; USDI Fish & Wildlife Service - p. 84 (left); Chris Peterson, Hungry Horse News - p. 115, 157, 176, 178, 188, 227, 229, and 236; Carolyn Sime - p. 2 (left); Jim Williams - p. 1, 23, 84 (right), and 186.

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Foreword

White-tailed deer have been studied more than mule deer in North America and perhaps more than any other big game animal. Most of this research has centered in the eastern and mid western regions of the United States. Conversely, white-tailed deer that reside in the snow-laden maritime forests of the northwest have been studied only at brief intervals and many questions have persisted concerning the basic ecology of these Rocky Mountain deer herds.

Most white-tailed deer in the northwestern United states reside in heavily forested regions with relatively long and cold winters and generate a high interest by local sportsmen. Whether it is annual mortality due to winter conditions or estimates of populations, local rod and gun clubs tend to review agency deer data with scrutiny and passionate involvement. Northwest Montana is no exception. Although most of Montana provides liberal deer and elk hunting opportunities for sportsmen, northwest Montana primarily features white-tailed deer hunting both in quantity and quality. Heavily forested mountains and valleys of northwest Montana also provide necessary habitat security to produce a relatively old age-class structure among antlered deer with some bucks reaching 11-12 years of age on public land and corporate timberlands that offer public hunting opportunity.

This scientific bulletin was prepared as a comprehensive summary of results from a long-term white-tailed deer research effort by Montana Fish, Wildlife and Parks (MFWP) in the Salish Mountains of northwest Montana. The project occurred during a population increase, a one hundred year winter event, and coincident with the presence of large native predators on the study area, most notably mountain lions and wolves. This intensive 12-year research effort revealed, heretofore unknown, population , habitat and predation parameters that are necessary to maintain white-tailed deer in rugged and forested mountains of northwest Montanan.

Understanding population characteristics and dynamic, including age structure of the male and female segment, patterns and rates of fawn recruitment, and rates of adult mortality are integral to managing white-tailed deer at a local level. From this study we know that the reduction or loss of one or more cohorts due to extreme winter event and winter survival linked with predation can, at times, set the stage for significant population declines and age structure changes within a deer population. Over time this may not drive long-term population trend although it generates high interest from white-tailed deer hunters and local rod and gun clubs that are immediately impacted by population declines.

Findings from this research effort challenge long-held notions that creating forest openings on white-tailed deer winter ranges automatically benefits winter survival. Rather, maintenance of a forest canopy on low level forests yield both thermal and snow intercept benefits to deer during a critical time of year. This research also reveals that white-tailed deer migration in forested habitats provides new opportunities for life history strategies that optimize resource utilization in a mountainous environment. Ultimately, white-tailed deer are tied to mature second growth forests in the foothills and lower valleys of northwest Montana.

The research presented in this report was funded and sponsored by hunters and the Federal Aid in Wildlife Restoration program. Collectively, these sources have provided major funding for scientific wildlife management since 1941. The scientific foundations and prescriptions for MFWP's white-tailed deer management program in northwest Montana presented in this final report are the result of an active MFWP research section. Montana's wildlife management programs have long been built upon the scientific investigations of and active team of MFWP research biologists. This particular research effort significantly advanced our understanding of white-tailed deer ecology and will help Montana refine deer management strategies by reducing uncertainty associated with establishing hunting seasons and managing deer habitat. Providing a scientific basis for population and habitat management prescriptions on both public and private lands remains essential to the long-term maintenance of quality white-tailed deer in northwest Montana.

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We offer our special thanks to Leonard Howke for his countless hours of help throughout the duration of fieldwork that included a lot of institutional knowledge over transition of personnel, running the hunter check station at Olney, trapping deer, keeping the snow machines and other equipment running, and for his enduring friendship. We are also greatly indebted to our families for their patience, encouragement, and support.

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Part I:
Population Ecology

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Executive Summary

White-tailed deer (*Odocoileus virginianus*) are the most abundant big game species in northwest Montana and account for more than 75% of annual deer harvests in Montana Fish, Wildlife and Parks' (FWP) Region 1. However, managers lack effective methods of monitoring population trend, recruitment, and herd response to population or habitat management actions. Whitetail winter ranges in the northern Rocky Mountains occupy second-growth stands of Douglas-fir (*Pseudotsuga menziesii*) along lower drainages and foothills. Stands typically occupied by white-tailed deer in northwest Montana today have been manipulated by fire and logging, and evidence suggests that these habitats, particularly winter ranges along the lower valleys and foothills, were subjected to human disturbance dating back 6-10 thousand years before Euro-American settlement.

From the mid 1940s through the mid 1960s, resource managers maintained that whitetails had exceeded forage-based carrying capacity on northwest Montana winter ranges as well as elsewhere. Others believed that opening forest canopies and thereby increasing availability of winter browse would benefit white-tailed deer. A common belief also held that deer would damage their range through overbrowsing, experience significant overwinter die-offs, and ultimately reduce the capacity of winter ranges to support deer. Despite efforts to liberalize and manipulate harvest regulations from the early 1950 through the mid 1970s, white-tailed deer experienced an overall upward trend in harvest in northwest Montana from the mid 1950s through the mid 1990s—traditional concepts of population dynamics of deer have failed to explain this upward trend. Aside from hunting, other factors such as fuels reduction on public forests, a change in the status of the cougar (*Puma concolor*) from a predator to a trophy game animal statewide, and management programs that promote recovery of gray wolves (*Canis lupus*) and other large carnivores in northwest Montana also have potential to affect white-tailed deer. Because of relative difficulty in surveying deer in dense, multi-storied coniferous forests, wildlife managers have relied almost entirely on harvest data to assess population status and trend.

Montana Fish, Wildlife and Parks initiated this study in 1988 in a portion of the Salish Mountains that included federal and state forests, state wildlife management areas, and adjoining private land. The goals were to better define ecological relationships of white-tailed deer occupying conifer-dominated winter ranges in northwest Montana to (1) improve an understanding of what factors regulate populations of white-tailed deer in these managed forests, (2) develop or refine techniques to estimate population size and trend; and (3) determine basic biological and ecological parameters for white-tailed deer and relate these parameters to characteristics of individual habitats to (a) physical and biological characteristics of individual habitats, (b) interactions between changing environmental conditions and population characteristics, and (c) hunting, land use practices, and other human-related factors. Data collection generally spanned the period of 1988-2000; collection of harvest records continued through 2003.

Study Area And Methods

We studied populations of white-tailed deer in a portion of the Salish Mountains in northwestern Montana that included portions of the Flathead (FNF) and Kootenai (KNF) national forests, the Stillwater State Forest, Ray Kuhns Wildlife Management Area (WMA), and private lands within and adjacent to national and state forests. The Murphy and Bowser study areas, which focused on winter ranges near Murphy and Bowser lakes, were situated primarily in Lincoln and Flathead counties, respectively. The Salish Mountains lie in a north-northwest trending glaciated intermountain basin. Elevations on the study area range from 854 to 2021 m (2802-6631 ft). Wildfire has significantly influenced vegetative cover with the last major stand replacement fires occurring in 1910 and 1926. Cutting units, which vary in age and stage of succession, dot the upland landscape.

Douglas-fir dominates the overstory among older stands of second-growth forest along the lower valley foothills. These stands also include a component of western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and to a lesser extent ponderosa pine (*P. ponderosa*). More recently altered stands consist primarily of lodgepole pine and larch. Stands of mature mixed conifers, including subalpine fir (*Abies lasiocarpa*) and Douglas-fir, large homogeneous stands of lodgepole pine, and clear-cuts of various stages of succession dominate upland portions of the Salish Mountains. Riparian sites include streams with yearlong surface flow. Wetland sites are well distributed through the uplands and include seeps, sloughs and potholes.

The climate of northwest Montana has a strong maritime influence—the area receives most of its annual precipitation during winter. Long-term records of precipitation indicate that Kalispell receives an average of 41.9 cm (16.5 in) of precipitation/year compared to 55.7 cm (21.9 in) at Whitefish and 42.9 cm (16.9 in) at Fortine. Large amounts of snow accumulate and persist through winter (Dec-Mar) during most years in northwest Montana. The most severe winter documented since climatological events have been recorded occurred during this study (1996-1997).

Harvest regulations for antlerless white-tailed deer in northwest Montana (Region 1) have been conservative compared to elsewhere in Montana. Although deer hunting has included a general firearm hunt spanning five weeks from late October through late November since the late 1960s, bag limits and the portion of the firearm season in which antlerless deer could be legally hunted have varied. During this study, antlerless deer could be legally taken only for a portion of the general season throughout much of the region. Region 1 accounted for 26% of Montana's annual harvest of white-tailed deer during 1956-1975 and 22% during 1976-2003. Hunting districts within the Salish Mountains study area accounted for 20% of the total harvest of white-tailed deer in Region 1 during 1986-2003. The highest reported combined harvest of antlered deer for hunting districts 101 and 102 from the post-hunt telephone survey occurred during 1991-1994 ($\bar{x}$ = 2183 bucks/yr) before declining to its lowest level in 1997 (1028 bucks) and increased again from 2000 to 2003 (1314 to 1894 bucks).

From January 1988 through February 1998, we equipped 390 deer (102 males, 288 females) with radio collars from which we obtained 14,741 fixes during April 1988 though May 2000 using fixed-wing aircraft. We assigned ages and collected other data relative to sex and age composition, growth and condition from 4837 white-tailed deer examined at hunter check stations during 1988-2003 and from 594 lower jaws left in barrels at the Region 1 Headquarters during 1991-1996. This provided the basis for assessing population characteristics that included population composition, condition, density, and dynamics. We used pellet group surveys, self-activating cameras, and the statewide harvest survey to assess population composition and/or population size and trend.

General Findings

- Back-dated check station records suggested only minor differences between hunting districts over all years with respect to proportion of the various sex and age classes and sex and age ratios.

- Winter severity, based on an index of winter severity (IWS) calculated for each winter range (Farnes et al. 2000), accounted for 93% of the variation in the number of days of winter range occupancy on Murphy and 66% of the variation on Bowser ($P \leq 0.002$).

- Pellet group surveys yielded an average deer density of 130/km^2 (336/mi^2) and ranged from 45 to 205 deer/km^2 (116-530/ mi^2). The lowest calculated density coincided with low long-term population numbers and a relatively mild winter in which some deer did not return to the core winter range.

- Hunting, which included documented kills and wounding losses as well as probable losses due to hunting, wounding, or poaching, accounted for 125 of 280 (45%) documented deaths of radio-collared deer older than 12 months.

- Among adult females, hunting-related mortality was the leading cause of death during most years except 1996-1997 that included a severe winter and 1998-1999 and 1999-2000 in which antlerless deer were protected from hunting.

- Predation, primarily that attributed to cougars, accounted for most nonhunting deaths among mature females (≥ 2 yrs).

- We detected an inverse linear relationship between total winter density derived from pellet group surveys at Bowser and skeletal growth through the first year of life ($R^2 = 0.69$, $P = 0.001$) based on diastema length among yearling males, i.e., total density at Bowser accounted for 69% of the variability in skeletal growth during the cohort's first winter.

- Our study suggested that regulations designed to encourage harvest of antlerless deer might reduce herds or limit population growth when rates of survival among mature females also are being influenced by other mortality factors, i.e., predation.

- Nonhunting mortality [among adult deer] was dynamic over the period of study and was additive to hunter harvest, particularly that relative to predation.

- The combined effect of population size from reconstruction of cohorts and the number of hunters afield with an 'A-tag' accounted for most of the observed annual variability in antlered harvest in both hunting districts 101 ($R^2 = 0.86$, $P < 0.001$) and 102 ($R^2 = 0.91$, $P = 0.001$). This would leave only 8-14% of the variability attributable to all other causes including random variation and any effect of weather variables on harvest trend for white-tailed deer in the Salish Mountains.

- Early post-partum losses accounted for a substantial proportion of all mortality during the first year of life. However, post-partum losses were lower than those reported in most other studies. Considering only mortality over summer (0.32) and winter-spring (0.24), we calculated a rate of survival over the first year of life of 0.52 [actually a little higher rate of survival than reported for white-tailed deer in New Brunswick and Oregon].

- Predation of which identified sources included cougars and coyotes (*C. latrans*) accounted for > 50% of deaths among fawns over winter during this study followed by losses due to malnutrition.

Findings Specific To Winter 1996-1997

- An unusually early arrival by large number of deer on both winter ranges during 1996-1997 resulted in classification of a large sample of deer during the early winter camera survey only during that one year.

- A weak yearling age class (1996 cohort) during autumn 1997 among both males and females and low recruitment among the 1997 cohort suggested that this severe winter event substantially affected two year classes; both fawns on the ground from the 1996 cohort and *in-utero* production and/or early neonatal losses from the 1997 cohort.

- Population reconstruction suggested that the lowest rate of overall survival [across all sex and age classes] occurred during 1996-1997, which included the most severe winter on record. However, only yearling recruitment rates were consistently related to winter weather patterns (critical temperature) throughout this study.

- Nonhunting mortality other than predation was markedly evident only during the severe winter of 1996-1997. Of 22 documented deaths resulting from malnutrition over the period of study, eight occurred during that winter.

- A combination of harvest regulations directed at antlerless deer on the general deer license (A-tag) and weather probably influenced the dramatic increase in antlerless harvest during autumn 1996 in both hunting districts 101 and 102.

Key Management Recommendations

- Population trend can be reliably monitored using results of the telephone harvest survey and records of harvested deer examined at check stations using population reconstruction methodology.

- Cementum analysis from all deer older than yearlings is the most accurate method of assigning ages and is necessary for population reconstruction.

- Tracking numbers of bucks examined at check stations for each hunting district yields useful trend data without the problems of time lags inherent in population reconstruction methods.

- Pellet group surveys can yield reliable population estimates during the winter in which harvest regulations are being set, providing two conditions are met: (1) pellet groups being counted reliably are from white-tailed deer; and (2) an estimate of the duration of winter range occupancy by white-tailed deer can be made consistently and reliably across years.

- Critical temperature, i.e., the cumulative number of days in which minimum daily temperature falls below –12 °C (10 °F), can be useful to setting quotas for antlerless deer harvests because of the relationship between recruitment rates and winter temperatures.

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Section 1: Introduction

White-tailed deer (*Odocoileus virginianus*) have been an important component of the Flathead and Kootenai River basins for several thousand years. Archaeologically recovered faunal and technological items suggest that humans occupied forested areas of the lower valleys and foothills in this region during late autumn through early spring and focused on deer as their primary prey (Roll 1982). Whitetails currently concentrate on localized winter ranges in these mountain valleys throughout northwest Montana (Pengelly 1963). Accounts from the fur-trapping expeditions of David Thompson and Alexander Ross in the vicinity of Hellgate, the Fisher River, and the Swan River between 1808 and 1824 (Koch 1941) also documented local abundance of deer of which many presumably were whitetails. Northwest Montana has continued as the primary domain of white-tailed deer in the state since Euro-American settlement (Allen 1971). Habitats typically occupied by white-tailed deer in northwest Montana today, particularly winter ranges along the lower valleys and foothills, have been subjected to human disturbance and manipulation dating well back into pre-historical times.

A combination of lightning- and man-caused fires probably influenced lower-elevation forests in the northern Rockies over a period pre-dating Euro-American settlement by 6-10 thousand years (Arno 1980, Barrett and Arno 1982). Human manipulation of these environments continued following Euro-American settlement. A combination of logging and fire from the 1880s to the 1930s altered the aspect of large portions of these stands to a mixture of remnant timber, second-growth timber, and shrublands. By the mid 1900s whitetail winter ranges in the northern Rocky Mountains were characterized as cutover stands of Douglas-fir (*Pseudotsuga menziesii*) along lower drainages and foothills (Pengelly 1963).

Early modern efforts to actively manage deer focused on manipulating forest cover to increase production of winter browse species. From the mid 1940s through the mid 1950s, wildlife managers interpreted from browse utilization surveys that whitetails had exceeded forage carrying capacity on many of these ranges (e.g., Cole 1959). This perception was strongly supported by timber interests. For example, Neils et al. (1955) attributed reduced regeneration of ponderosa pine (*Pinus ponderosa*) on cutover private forest to "heavy browsing on winter ranges overstocked with white-tailed deer" and recommended increased hunting pressure and season length that included harvesting both sexes of deer. Other studies from across the northern tier of the species' range speculated that opening forest canopies, and thereby creating edge and increasing availability of winter browse, would benefit habitat values for white-tailed deer (e.g., Krefting 1962, Pengelly 1963).

The perception of an overabundance of deer (mule deer [*O. hemionus*] included) on winter ranges was pervasive among resource professionals over much of Montana during the early 1950s, and a common belief held that deer would damage their range through overbrowsing, experience significant overwinter die-offs, and ultimately reduce the capacity of winter ranges to support deer (Cole 1959). Thus, the Montana Department of Fish and Game[1] liberalized hunting seasons in 1952 from "buck only" to either-sex hunts in many areas, and increased bag limits to two deer in some areas in 1955.

During the mid 1970s bag limits for both species of deer were reduced statewide in response to an unanticipated decline in mule deer harvest. From 1975 to the present time, bag limits for white-tailed deer in northwest Montana have included one deer with harvest directed primarily at antlered deer. Antlerless harvest was subjected to relatively more scrutiny from which regulations might change from year to year: (1) antlerless deer could be taken from 1-2 weeks over a 5-week general firearm season in most years, and (2) hunters also could obtain a second tag through a drawing for a limited number of antlerless white-tailed deer in some hunting districts during some years. Antlerless deer were not legally hunted in Region 1 during 1998-2000. In light of all this, annual post-hunt harvest surveys of hunters indicated that total harvest of white-tailed deer, and buck harvest in particular, increased through the mid 1990s—buck harvest reached an all-time high in 1994 (Coates et al. 2001)—after which harvests declined through the late 1990s, a period that included the severest winter on record (1996-1997).

Although harvest trends support a perception of steadily increasing populations during the mid 1970s through the mid 1990s, the most simplistic explanation for this observation is that populations had increased in light of a series of relatively mild winters combined with subtle habitat changes associated with previous forest management practices and conservative harvest regulations. Extensive timber harvest with associated road construction was a primary land use on public and corporate timberlands in northwest Montana during this time. However, short- and long-term effects of logging and improved hunter access on deer distribution and habitat selection as well as on population trend and dynamics are neither consistently defined nor well understood. Investigations relative to the influence of forested habitats and their management on the biology of white-tailed deer

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[1] The 1979 Montana Legislature changed the name of Montana Department of Fish and Game to Montana Department of Fish, Wildlife and Parks.

are replete with subjectivity and contradiction (e.g., Pengelly 1963, 1972, Mundinger 1984, Hicks 1990).

Hildebrand (1971), Leach (1982), and Mundinger (1984) in the Swan River Valley in northwest Montana and Baumeister (1992) in north-central Idaho reported a close relationship between white-tailed deer and mature, sub-climax forest. Mundinger (1981, 1984) hypothesized that population dynamics of deer, characterized by low rates of fawn recruitment and turnover among adult females, represent an adaptive strategy by which whitetails effectively exploit a stable and predictable environment. He predicted that logging as practiced in the Swan Valley at that time, would adversely impact habitats of white-tailed deer. All these studies essentially challenge a concept that categorizes white-tailed deer as an animal primarily associated with early succession.

Although Mundinger (1984) emphasized that deer make only minimal or no use of clear-cuts on seasonal ranges, several other studies in the northern Rockies document use of managed forests by deer including use of clear-cuts on summer-autumn ranges (Lyon and Jensen 1980, Morgan 2006). However, studies of wintering deer define habitat selection as influenced by an interaction of forest canopy and snow depth (Hildebrand 1971, Hicks 1990, Pauley et al. 1993) whereby deer avoid forest openings during periods of deep snow. Lyon and Jensen (1980) inferred that deer use of newly created openings is limited, but use increases substantially with forage abundance and quality and as security requirements are met.

Neither the paradigm of Cole (1959) nor that of Mundinger (1984) can explain the observed overall upward trend in harvest of white-tailed deer in northwest Montana, and that of antlered deer in particular, from the mid 1950s through the mid 1990s. Cole (1959) assumed deer throughout Montana had already exceeded carrying capacity of their winter ranges and that liberalized harvest directed at antlerless deer would yield more bucks in annual harvests by carrying smaller, ultimately more productive populations over winter. That strategy yielded promising results over the short term (Newby 1963) although long-term harvest trends in light of generally conservative harvest regulations for antlerless deer in northwest Montana tends to refute that concept. Mundinger (1981, 1984) hypothesized that a stable environment, characterized by limited annual turnover and recruitment, would maintain a relatively stable population. Thus, population increases from the 1950s into the 1990s remain unexplained.

Although fluctuating by as much as 50% over periods of a few years, whitetail harvests, particularly harvest of antlered deer, continued on an upward course for another two decades. This trend was concurrent with a harvest regime that remained more conservative than that in the portion of Montana east of the Continental Divide. A pattern of winter severity in northwest Montana over the last four decades (See Section 2) included relatively severe winters throughout, especially from the late 1950s through the mid 1980s; this would suggest that the role of "a series of mild winters" affecting long-term increases in numbers of white-tailed deer in northwest Montana might have been over-emphasized, as part of a simplistic, yet popular, explanation of an upward trend. The effect of hunting on recruitment and survival of adult deer has not been seriously tested in the northern Rockies, and like that of timber management, its effect on the biology of deer is not well understood.

Other factors also could potentially impact deer and decisions that guide their management. These include land uses and human activities on the urban interface, a change in the status of the cougar (*Puma concolor*) from a predator to a trophy game animal statewide, and recolonization of the gray wolf (*Canis lupus*) in northwest Montana. Human activities of concern include proliferation of homesite development with attendant presence of domestic dogs on deer winter ranges (Sime 1999). Management actions with the potential to impact white-tailed deer populations include fuels reduction on public forests intended to protect adjacent private holdings from the spread of wildfires and management programs that promote recovery of gray wolves and other large carnivores.

White-tailed deer carry top billing among big game species in northwest Montana due to their ubiquitous presence and popularity among local hunters. They account for more than 75% of annual deer harvests in Montana Fish, Wildlife and Parks' (FWP) Region 1, and they are by far the most abundant big game species in this portion of the state. Despite their relative importance, managers have never evaluated the effectiveness of methods used to monitor population trend, recruitment, and herd response to population or habitat management actions. Surveying deer in dense, multi-storied coniferous forests is extremely difficult. Consequently, recent management efforts have relied almost entirely on harvest data to assess population status and trend. Several studies in recent decades have focused on estimating deer numbers or evaluating various census techniques (e.g., Janke 1977, Tucker 1991, Rachael 1992); however, the short duration of individual studies confounds interpretation of results, and none were designed to relate trends in white-tailed deer harvest to long-term population trend.

Montana Fish, Wildlife and Parks (FWP) initiated this study in 1988 in a portion of the Salish Mountains that included federal and state forests, state wildlife management areas, and adjoining private land. The goal of our study was to better define ecological relationships of white-tailed deer occupying conifer-dominated winter ranges in northwest Montana. We focused on improving an understanding of what factors regulate populations of white-tailed deer in these managed forests. More specifically, we attempt to develop or refine techniques to estimate population size and trend and determine basic biological and ecological parameters for white-tailed deer and relate these parameters to characteristics of individual habitats and the following potentially limiting factors: (a) physical and biological characteristics of individual habitats, (b) interactions between changing environmental conditions and population characteristics, and (c) hunting, land use practices, and other human-related factors. Collection of field data spanned the period of 1988-2000, and collection of harvest records continued through 2003. Interim accomplishments through 1996 were reported previously (Dusek 1989, Dusek and Morgan 1990, 1991, Sime 1994, 1996). Preliminary studies were conducted in the Bowser Lake area that included the Ray Kuhns Wildlife Management Area during 1982-1984 (Mundinger and Riley 1983).

Section 2: Study Area

We studied populations of white-tailed deer in a portion of the Salish Mountains in Flathead and Lincoln Counties in northwestern Montana at 48° 30′ north latitude 114° 30′ east longitude (Fig. 2.1). The study area includes portions of the Flathead (FNF) and Kootenai (KNF) national forests, the Stillwater State Forest, Ray Kuhns Wildlife Management Area (WMA), and private lands within and adjacent to national and state forests. We defined the study area as yearlong habitat—winter, summer, and transitional ranges—for radio-collared deer monitored through May 2000 that wintered in the vicinity of Murphy and Dickey lakes in Lincoln County and Bowser and Tally lakes in Flathead County.

The study area lies in a north-northwest trending intermontane basin that has been sculpted by glaciers of the Cordilleran ice sheet (Montagne et al. 1982, Kendy and Tresch 1996). The basin occupies the southern extension of the Rocky Mountain Trench of late Paleocene to Eocene age. The Salish Mountains include metasedimentary rocks of the Middle Proterozoic Belt Supergroup made up of limestone, dolomite, siltite, quartzite, and argillite. Elevations on the study area range from 854 to 2021 m (2800-6630 ft).

With the exception of the Stillwater River and its major tributaries, second growth conifer forest dominated the vegetative cover throughout the Salish Mountains. Wildfire has significantly influenced vegetative cover with the last major stand replacement fires occurring in 1910 and 1926. A description of habitat types follows Pfister et al. (1977) although most cover types across the study area represented earlier seral communities and not necessarily climax vegetation that we list here.

Morgan (2006) provided a detailed description of transitional and summer range of white-tailed deer in the Tally Lake District. Most of the area is managed for commercial timber production and wood products. Cutting units, which vary in age and stage of succession, dot the upland landscape. The *Pseudotsuga menziesii/ Symphoricarpos albus* habitat type predominates along the lower valley foothills in which Douglas-fir dominates the overstory among older stands of second-growth forest. These stands also include a component of western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and to a lesser extent ponderosa pine. The shrub understory includes common juniper (*Juniperus communis*), snowberry (*Symphoricarpos albus*), Oregon grape (*Berberis repens*), and kinnikinnic (*Arctostaphylus uva-ursi*).

The *Abies lasiocarpa/ Clintonia uniflora* habitat type dominates upland portions of the study area although currently consists of stands of mature mixed conifers, large homogeneous stands of lodgepole pine, and clearcuts of various stages of succession. A *Pinus contorta/ Xerophyllum tenax* cover type occupies many of the upper drainages throughout the Salish Range. Timber species in older clear cuts were limited almost exclusively to lodgepole pine and western larch. The *Pseudotsuga menziesii/Calamagrostis rubescens* habitat type occupies drier, southerly exposures.

The *Picea/Clintonia uniflora* habitat type is represented along bottomlands of the Stillwater River and streams throughout the Salish Range. Deciduous trees and shrubs along riparian sites include black cottonwood (*Populus trichocarpa*), aspen (*P. tremuloides*), and willows (*Salix spp.*). Riparian sites include streams with yearlong surface flow. Wetland sites are well distributed through the uplands and include seeps, sloughs and potholes.

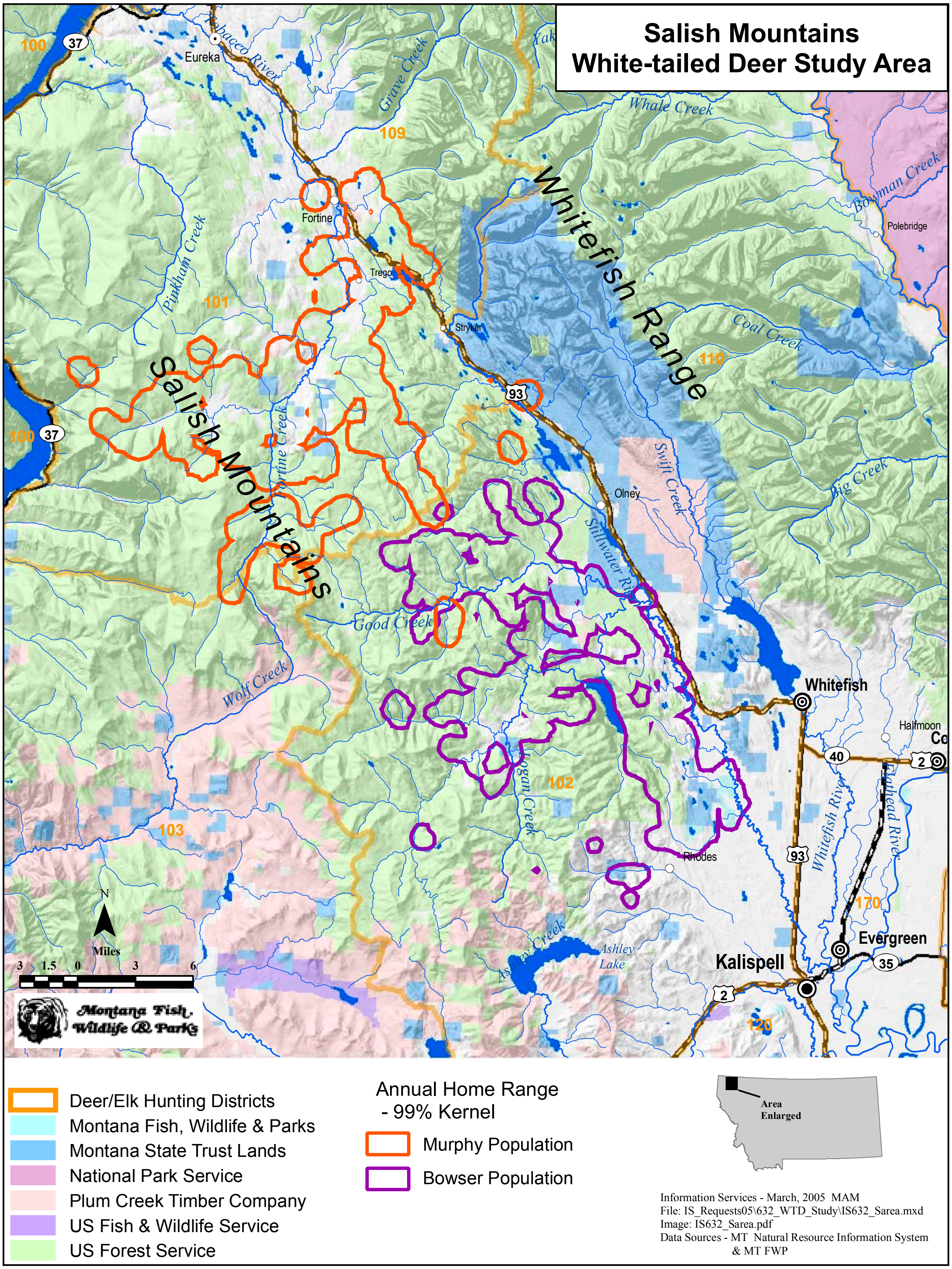

Figure 2.1. The Salish Mountains study area. Closed polygons show yearlong distribution of white-tailed deer associated with the Bowser and Murphy winter ranges.

Macroclimate and elevation influence the climate of northwest Montana (Caprio and Nielson 1992), which has a strong maritime influence—the area receives most of its annual precipitation during winter. Precipitation records from stations at Kalispell, Whitefish, and Fortine compiled for this study by Farnes et al. (2000) suggest that the vicinity of Whitefish had the wettest moisture regime (Fig. 2.2). Records over the longer term indicate that Kalispell receives an average of 41.9 cm (16.5 in) of precipitation/year compared to 55.7 cm (21.9 in) at Whitefish and 42.9 cm (16.9 in) at Fortine. The moisture regime described by Caprio and Nielson (1992) implies that large amounts of snow accumulate in northwest Montana during most years, which generally persists throughout the winter months (Dec-Mar). An index of winter severity (Picton 1979; Fig 2.3) based on long-term records of precipitation and temperature (1900-2004) suggests that the period 1959-1985, which immediately preceded this study, exhibited a markedly greater periodicity of severe winter conditions than the period 1900-1949 or the period of this study (1988-2000). However, the most severe winter documented through the entire 105-yr period occurred during this study (1996-1997).

Study Areas

Bowser-Tally Lakes

The Bowser/Tally Lakes (Bowser) study area (Fig. 2.4) included the Tally Lake Ranger District of the FNF, state forest, the Ray Kuhns WMA (see attached map in Appendix A), and surrounding private lands. The focal point of this study area was the core winter range near Bowser Lake (Mundinger and Riley 1983) that included state forest, FNF, FWP lands including Ray Kuhns WMA, and adjoining private lands. Topographical relief ranges from 900 m (2953 ft) along the Stillwater River near Ray Kuhns WMA and 1935 m (6348 ft) at the summit of Mount Swaney. The yearlong distribution of radio-collared deer associated with Bowser encompassed hunting district 102. Vegetative cover over about 77% of the hunting district (1604 km^2 or 619 mi^2) includes forested cover types.

Most deer associated with Bowser typically migrate north and northwest to summer in Good Creek and Star Meadows (Fig. 2.1). Morgan (2006) previously described the portion of the yearlong range that white-tailed deer typically occupied from early April through mid December. This includes an area of ~ 270 km^2 (~104 mi^2)

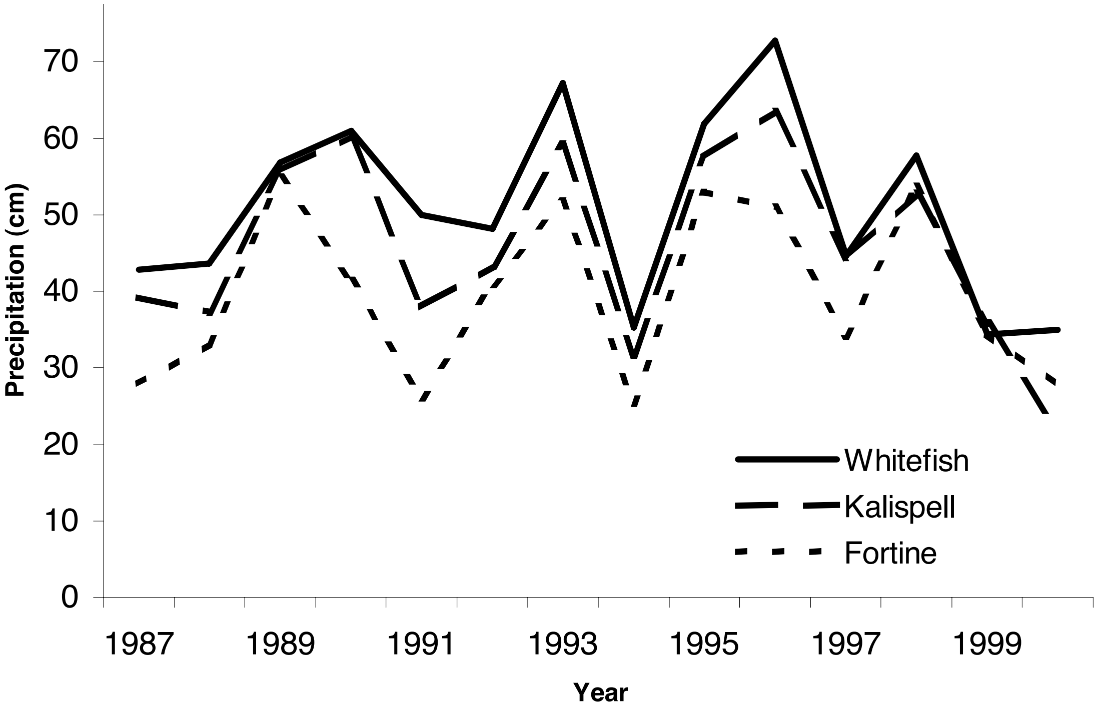

Figure 2.2. Trends in annual precipitation at three stations in and near the Salish Mountains study area.

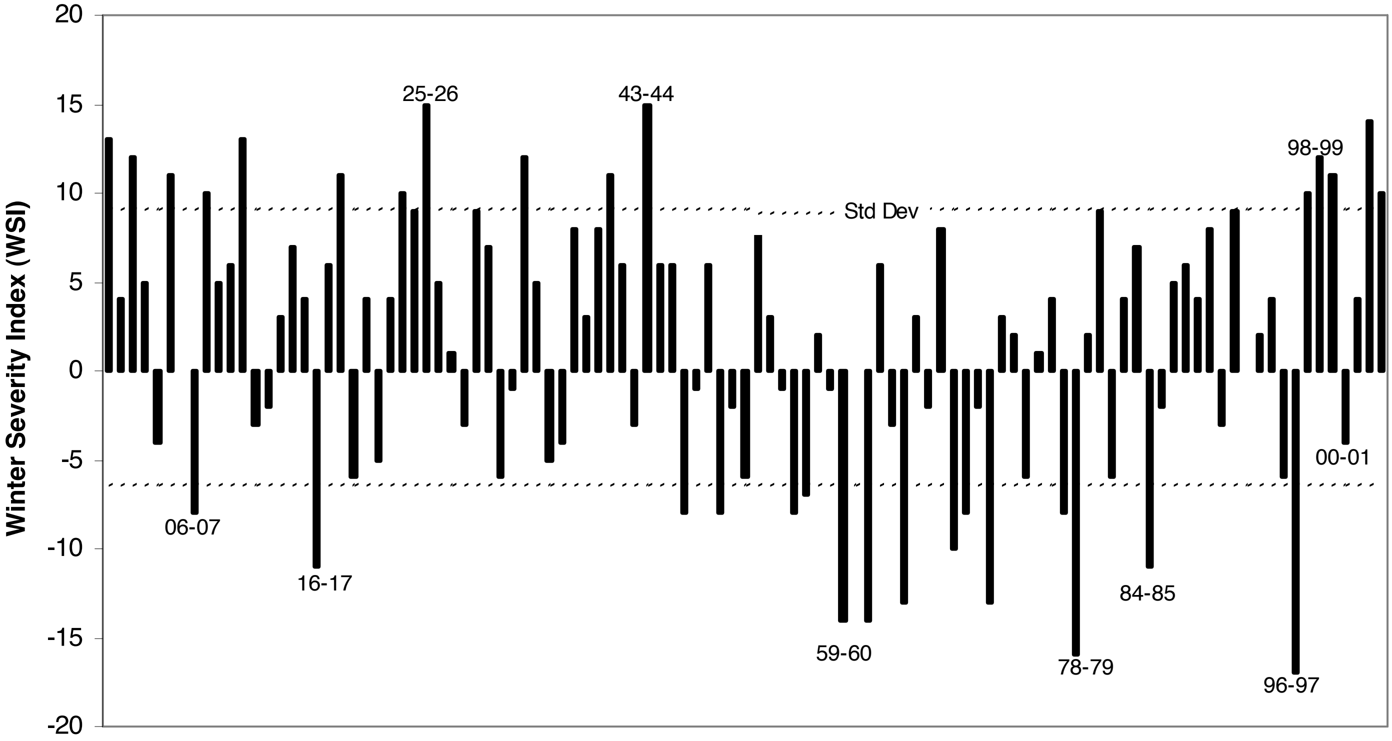

Figure 2.3. Winter severity expressed by the Lamb WSI (Picton 1979) for the years 1899-1900 through 2003-2004 based on temperature and snowfall measured at Kalispell (1899-1998) and Whitefish (1999-2004) for October through April.

with a mean elevation of 1147m (3763 ft) and range of 899-1765 m (2949-5791 ft). Wet meadow areas with which deer were associated included Star Meadows at the confluence of Sheppard, Griffin, and Logan Creeks, and Corduroy Creek a tributary of Good Creek.

Although white-tailed deer winter primarily along the eastern fringe of lower foothills from north of Pilot Knob south to Ashley Creek (Mundinger and Riley 1982), our efforts to trap and monitor deer focused primarily on ~ 32 km^2 (12 mi^2) bounded on the west and south by Lost Creek and on the east by the Stillwater River that extended north to Beaver Creek, Hansen Lake, and the northernmost extent of Pete Ridge. Pete Ridge is a prominent landmark on the western edge of the winter range. This area includes the Ray Kuhns WMA along the floodplain of the Stillwater River that also includes an area around Bowser Lake (Fig. 2.4), and a large tract of state forest. The area consists of low rolling hills and several shallow lakes of which Bowser Lake is the largest. Prior to FWP (then Department of Fish and Game) interest in the immediate area around Bowser Lake, the area had a history of logging and heavy grazing during the 1940s to an extent that resulted in agency personnel recommending corrective measures including outright acquisition and management for wildlife and aquatic resources (Couey 1948). The report also confirmed a high level of salts and minerals in the water of the lake that might attract deer to the lake during winter. The area was almost exclusively used by white-tailed deer but received minor use by elk (*Cervus elaphus*), mule deer, and moose (*Alces alces*).

Murphy-Dickey Lake

The Murphy-Dickey lake study (Murphy) area in Lincoln County (Fig. 2.5) includes the Fortine Ranger District of the KNF and encompassed the west slope of the Whitefish Range and Fortine Creek and its tributaries in the Tobacco River drainage. The only portion that occurred in the Stillwater drainage included Sunday Creek. Prior to this study, FWP had little if any baseline information on the large

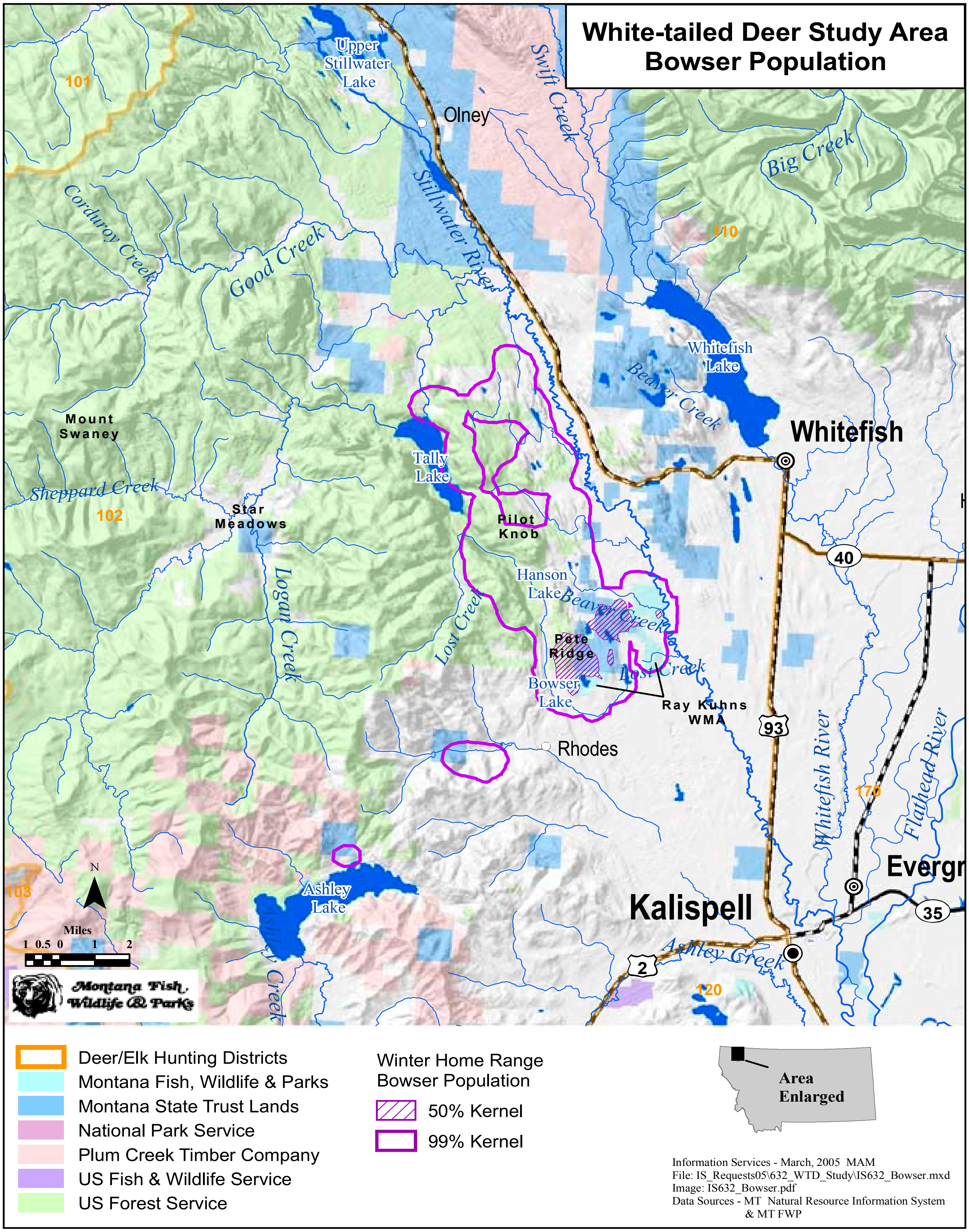

Figure 2.4. The Bowser study area showing the winter range used by white-tailed deer; the core winter range is represented by the 50% isopleth and that available during most winters is represented by the 99% isopleth..

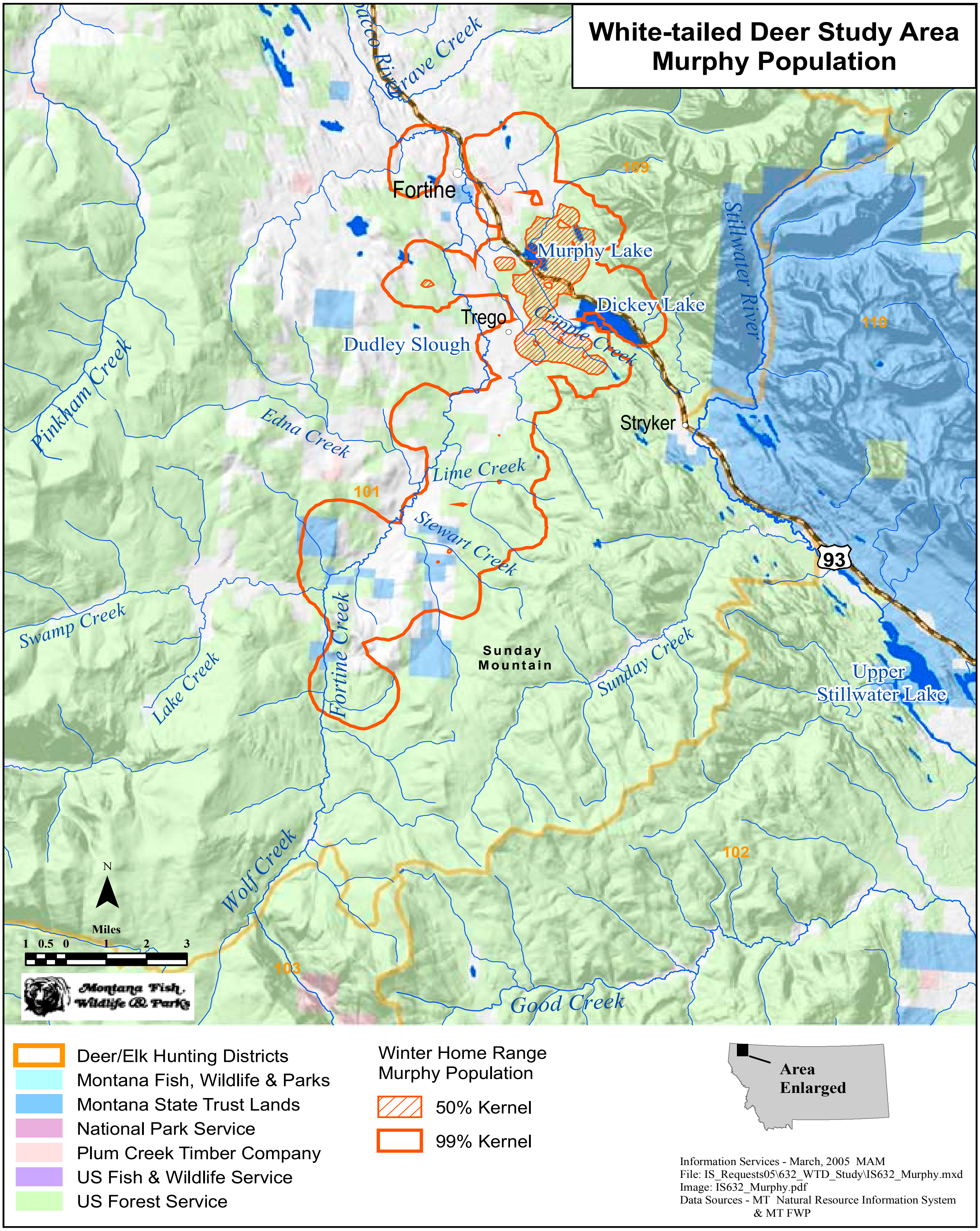

Figure 2.5. The Murphy study area showing the winter range used by white-tailed deer; the core winter range is represented by the 50% isopleth and that available during most winters is represented by the 99% isopleth.

concentration of white-tailed deer that wintered in the vicinity of Murphy and Dickey lakes referred to as the Murphy winter range.

Although white-tailed deer typically winter as far up the Fortine Creek drainage as Stewart Creek (Fig. 2.5), most of our effort to trap and mark deer centered on the area around Murphy and Dickey lakes, Ant Flat, Cripple Creek, and Dudley Slough. Significant numbers of mule deer also occupy this winter range. U.S. 93 bisects the winter range separating the portion that included Murphy Lake from that occupied by Dickey Lake, Ant Flat, and Fortine and Cripple creeks. The yearlong distribution of radio-collared deer associated with Murphy encompassed hunting district 101 (2164 km^2) of which about 82% of the vegetative cover included forest cover types. In 2002, FWP split hunting district 101 into hunting districts 101 and 109 with hunting district 109 including the portion lying northeast of U.S. 93 in the vicinity of Murphy Lake.

White-tailed deer associated with Murphy typically migrate southwest into the upper tributaries of Fortine Creek while others move due south over the divide into Sunday Creek to summer (Fig. 2.5). Wet meadow areas with which deer were associated during summer included Swamp and Lake Creeks in the upper Fortine Creek drainage.

Ancillary Areas

White-tailed deer were trapped along the north shore of Ashley Lake (Fig. 2.4) during March 1988. The area consists of national forest lands in the Tally Lake district, corporate timberlands, and private lots around the lakeshore. Most stands of mature forest had been removed on the west and north sides of the lake prior to the onset of this study. These deer either remained in the vicinity of Ashley Lake yearlong or summered in Griffin Creek just south of Star Meadows. Thus, spring migrants shared the same summer range with deer that wintered near Bowser Lake and summered in the vicinity of Star Meadows.

Radio-collared deer also wintered in McManamy and Rhodes draws that lie south and west of Bowser along a corridor of winter range generally described by Mundinger and Riley (1983). The area consists primarily of private corporate timberlands. Deer that wintered in these drainages summered in Griffin Creek near Star Meadows and thus, share a summer range with deer associated with Bowser.

Hunting Seasons And Historical Harvest

Season Structure and Harvest Regulations

Harvest regulations for antlerless white-tailed deer in northwest Montana (Region 1) have been conservative compared to elsewhere in Montana since initiation of either-sex hunting for both species of deer throughout the state in 1952. Although deer hunting included a general firearm hunt spanning five weeks from late October through late November since the late 1960s, bag limits and the portion of the firearm season in which antlerless deer could be legally hunted have varied (Appendix B). Antlerless deer could be legally taken only for a portion of the general season throughout much of the region.

Hunters could legally take two white-tailed deer of either sex throughout the entire region during the general firearm season of 1956 and during several subsequent years (Appendix B). Bag limits returned to one deer/year by the mid 1960s although a whitetail of either sex could be taken during the entire season through 1974. From 1975 through 1997, antlerless whitetails could be legally taken for 1 or 2 weeks out of a 5-wk general firearm season; there was no legal hunting of antlerless white-tailed deer in northwest Montana during 1998-2000. Periodic increases in the bag limit from 1 to 2 deer, by issuing a limited number of drawn permits, were directed at increasing antlerless harvest along with increasing hunter opportunity. Numbers of deer harvested and hunters afield are monitored via a statewide post-hunt survey.[2]

Trends in Deer Harvest

Region-wide Trends.—Region 1 accounted for 26% of Montana's annual harvest of white-tailed deer during 1956-1975 and 22% during 1976-2003. White-tailed deer steadily expanded their

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[2] Surveys were conducted through mail-in responses from hunters selected based on license sales from 1958 to 1980; after 1980 the resident portion of the survey was conducted by telephone interview (Cada 1983).

distribution east of the Continental Divide and became increasingly abundant from 1940 through 1988. They also expanded their range west of the divide but were reported to have declined in overall abundance during 1940-1970 (Allen 1971, Wood et al. 1990). Bourgeoning populations of white-tailed deer in eastern Montana along with depredations by deer on private crops during the 1980s also led to liberalization of regulations affecting antlerless harvest and consequently increased whitetail harvest in several eastern Montana regions during the mid-to-late 1980s. These factors seemingly resulted in a slight decline in Region 1's proportional contribution to the statewide white-tailed deer harvest. However, annual whitetail harvest in Region 1 continued to increase although unrelated to liberalization of harvest regulations affecting antlerless deer (Fig. 2.6).

Hunting District Trends.—Hunting districts within the Salish Mountains study area accounted for 20% of the total harvest of white-tailed deer in Region 1 (Fig. 2.6) based on the posthunt statewide telephone survey, 1986-2003. Harvest for 2002-2003 also reflects numbers of deer harvested from hunting district 109. The highest reported combined harvest of antlered deer for hunting districts 101 and 102 from the post-hunt telephone survey (Fig. 2.7) occurred during 1991-1994 ($\bar{x}$= 2183 bucks/yr) before declining to its lowest level in 1997 (1028 bucks). Antlered harvest increased from 2000 to 2003 (1314 to 1894 bucks). Reported antlered harvest tended to be higher in hunting district 102 than in hunting district 101 during most years from 1988 to 2003 (Fig. 2.7), whereas antlerless harvest in both hunting districts did not appear to differ (Fig. 2.8) except for years in which a second tag was available to hunters for hunting district 102 (1991-1996).

Northwest Montana's Socio-economic Environment

Geographically, Region 1, which encompasses roughly 9% of Montana's land area, is the smallest of FWP's administrative regions (Montana Fish, Wildlife and Parks 2000). About 64% of the region includes publicly owned forests that include FNF and KNF and several

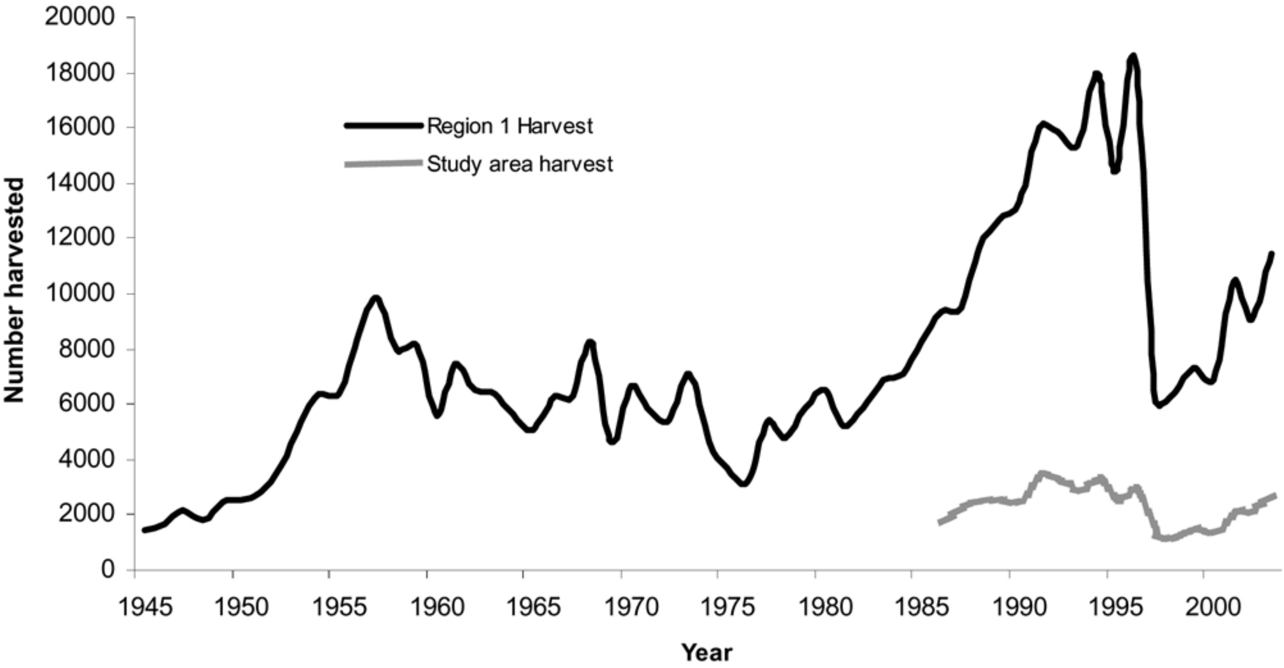

Figure 2.6. Total annual harvest of white-tailed deer in northwest Montana (Region 1) and the Salish Mountains study area (HDs 101,102 and 109), 1945-2003. Data for 1945-1971 were extrapolated from Allen (1971) and those for 1972-2003 are from the post-hunt statewide survey.

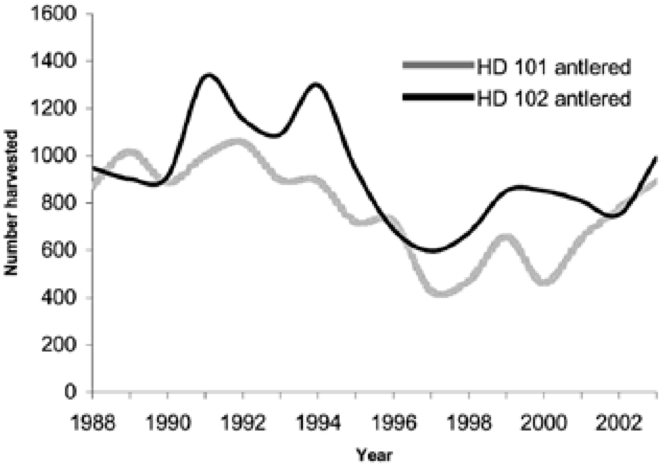

Figure 2.7. Harvest of antlered deer for hunting districts 101 and 102, 1988-2003. The total antlered harvest for hunting district 101 also includes that from hunting district 109 for 2002-2003 to make these trends comparable.

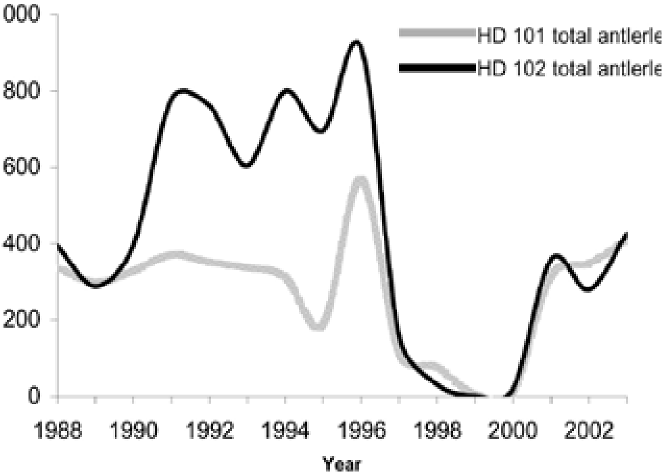

Figure 2.8. Harvest of antlerless deer for hunting districts 101 and 102, 1988-2003 from the post-hunt statewide harvest survey. The total antlerless harvest for hunting district 101 also includes that from hunting district 109 for 2002-2003 to make these trends comparable.

smaller parcels managed by Montana DNRC. USDI Fish and Wildlife Service and FWP also manage several small, scattered parcels of land. The region also includes the Flathead Indian Reservation and lies adjacent to Glacier National Park. Northwest Montana is one of the most populated (130,000 as of the 2000 U.S. Census) and fastest-growing areas in Montana.

Economically, timber-related industries, tourism and agriculture are important to the economy of northwest Montana. Large volumes of timber are harvested annually from public forests and corporate timberlands. Proximity to Glacier National Park, two scenic national forests including wilderness areas, and Flathead Lake provide the region national recognition and year-round recreational opportunity.

A relatively high human population, large public and corporate holdings of land, and large expanses of montane forest underlie several issues related to management of white-tailed deer in northwest Montana (Montana Fish, Wildlife and Parks 2000). These include defining FWP's role in recovery and management of gray wolves as well as challenges facing management of other forest carnivores. Potential loss and degradation of habitat on public and private land as a result of logging, rural housing development, and other commercial uses offers a major challenge to wildlife managers in northwest Montana.

Section 3: Methods

Field Procedures

Project personnel captured a total of 1335 white-tailed deer from January 1988 through February 1998. The sample included 779 deer on the Bowser winter range and 502 animals on the Murphy winter range. Nine additional deer were captured at Ashley Lake during March 1988. During spring and summer 1989-1991, 31 deer were captured on the Talley Lake Ranger District incidental to research that addressed summer habitat selection (Morgan 2006). Fourteen additional deer were captured during summer 1993 in Good and Sunday creeks.

We used Clover traps (Clover 1954) placed along well-traveled trails to capture deer. Traps were baited with alfalfa during winter and with salt during summer following procedures described by Morgan and Dusek (1992). Traps were distributed across the area over time to provide a representative sample of the population.

All captured deer were manually restrained from which we recorded sex and age. We assigned age based on patterns of tooth replacement and wear (Severinghaus 1949) and measured heart girth (Smart et al. 1973) to estimate whole body weight during winter. A blood sample was taken from all age classes of females during 1988-1992 to assess rates of pregnancy (Wood et al. 1986).

A numbered metal tag was affixed to each ear of all captured deer and 390 deer (102 males, 288 females) were fitted with transmitter collars (Telonics, Inc., Mesa, AZ). Beginning in January 1990, all radio collars included a mortality-sensitive transmitter package. We fitted all non-radioed deer with individually recognizable, vinyl neckbands (10 cm wide). From 1991 through 1996, we attempted to equip as many females as practical of known age rather than assigned age with transmitter collars. These included fawns or yearlings, or older recaptured females initially captured as fawns or yearlings. Because males > 1 year of age occurred in lower numbers than females of similar ages among captured deer, we fitted most bucks of ages ≥ 2 years with radio collars at least through 1994. We extracted a middle incisor (I_1) from recovered mortalities of radio-collared deer if a lower jaw was available from which an age was assigned by cementum analysis (Matson's Lab, Milltown, MT).

We located radio-collared deer using fixed-wing aircraft, i.e., PA-18 Super Cub or a Cessna 180, at intervals that varied widely throughout the period in which radio-collared deer were monitored—April 1988 though May 2000. We obtained 14,741 fixes of radio-collared deer from aerial tracking during periods of daylight (0445 and 2100 hrs). The interval between 0900 and 1600 hrs accounted for 43% of locations during late spring through early fall (Julian days 91-273) and 84% of locations during late fall through early spring. Because we did not estimate telemetry error during this study, we assume a mean error of 196 ± 72 m calculated from known vs. estimated locations of elk reported by Vore and Schmidt (2001) using the same pilot and aircraft in similar vegetation and somewhat more rugged terrain.

Hunter check stations, strategically located to optimize obtaining records of hunter participation and harvested animals, provided the primary information to evaluate age structure and condition of white-tailed deer from hunting districts 101 and 102. Records came primarily from the check stations located at Olney along U.S. 93 north of Whitefish (1988-2002), which was established in 1988 specifically to meet needs of this study but has been continued to meet regional needs. The check station at Canoe Gulch along Lake Koocanoosa provided data for this study only during 1995-2003 when a middle incisor was extracted from adult deer for assigning age by cementum analysis. FWP established the station west of Kalispell along U.S. 2 during 1996 from which data were available through 2003.

FWP personnel assigned an age based on tooth eruption and replacement and wear on the cheek teeth (Severinghaus 1949) to 4837 white-tailed deer examined at hunter check stations during 1988-2003 and from 594 lower jaws left in barrels at the Region 1 Headquarters during 1991-1996. We considered deer assigned ages of ≤ 18 months based on a sequence of eruption and replacement of mandibular teeth "known-age" deer because of minimal subjectivity in assigning ages to animals that have not attained the full complement of adult teeth. For deer assigned ages ≥ 2 years by eruption and wear patterns at check stations and jaw collection points, the first incisor (I_1) was extracted for assigning an age by cementum analysis (Gilbert 1966). We used ages assigned by cementum analysis to provide greater accuracy and consistency among animals of ages ≥ 2 years than would ages assigned by wear pattern on mandibular cheek teeth (Hamlin et al. 2000). From samples of known-age deer and those assigned an age by cementum analysis, we reconstructed cohorts in hunting districts 101 and 102 (see analytical procedures).

We estimated relative abundance of females

and males from harvested deer by assigning an individual to its respective cohort for each year that they occurred in the population. Herd composition assumed that the two sexes of fawns occurred in equal proportion during autumn because the sex ratio of fawns in the sample of harvested deer did not depart from a 50:50 ratio ($P > 0.05$). These data provided the only estimate of pre-hunt composition and sex and age ratios of the two study populations.

Check station and project personnel measured the diastema of 3374 hunter-harvested white-tailed deer from hunting districts 101 and 102 during 1988-2001. Antler measurements, including main beam length, basal diameter, and maximum inside spread, were taken from 2550 bucks ≥ 1year of age.

Self-activating cameras were used on Bowser and Murphy to estimate herd composition and sex and age ratios during early (Dec-Jan) and late winter (Feb-Mar). Early winter surveys provided estimates of post-hunt herd composition, yearly differences in timing of fall migration, and timing of activity throughout the diel period. Late winter surveys provided comparable information and also were designed to census deer on the respective winter ranges.

We used camera units that were originally developed to detect and monitor abundance of grizzly bears (*Ursus arctos horribilis*) in the South Fork of the Flathead River (Mace et al. 1990). A passive infrared sensor triggered the shutter release. Approaches to deployment and monitoring follow Dusek and Mace (1991). Units were first deployed on Bowser during mid-to-late winter 1989 to evaluate performance of cameras and accessories under winter conditions. We conducted early winter surveys (mid Dec-early Jan) on Bowser from 1989 to 1998, with the exception of 1992, and on Murphy from 1995 to 1998. Late winter census surveys were conducted on Bowser from 1989 to 1999 and on Murphy from 1990 to 1999 with the exception of 1993.

We established a 1-km^2 grid across the core winter range and used a randomized design to select quadrats for sampling. Actual camera sites within quadrats were placed along currently used trails; sites were unbaited. We checked all sites at least once throughout each survey to change film and ensure proper functioning of cameras. Our camera density on the Bowser area (32 km^2) varied from 1 camera/3.2 km^2 during late winter 1989 and 1990 to 1 camera/2.5 km^2 during all other years. Camera density on Murphy varied from 1 camera/3.3 km^2 during late winter 1991 to 1 camera/2.1 km^2 from 1995 to 1999. Jacobson et al. (1997) suggested the highest camera densities, i.e., one camera/ 0.65 and one camera/1.30 km^2 on a 40-km^2 area yielded the most reliable population estimates using mark-recapture methods. Examination of photographs from the 1989-1992 surveys suggested that 77% of exposures were triggered by animal activity (Dusek and Mace 1991). Human activity and site conditions including precipitation, wind, or a rapid change in direct sunlight in the photographic zone probably accounted for most other exposures.

We also used pellet group surveys to estimate numbers of white-tailed deer that used Bowser during 1989-1999 and on Murphy during 1991-1999. We believed Bowser especially suited to pellet group surveys because winter use consists almost entirely of white-tailed deer. However, late winter camera surveys and general reconnaissance at Murphy indicated that significant numbers of mule deer also use that winter range. We acknowledge that such dual use might confound estimates for either species since pellets deposited by mule deer could not be distinguished from those of white-tailed deer.

To estimate pellet group density we counted the number of groups within 1-milliacre (4.05-m^2) circular plots along transects within 1-km^2 quadrats. We used the small circular plot to minimize the likelihood of underestimating pellet group density in dense ground cover (Longhurst and Connolly 1982). Because transect sites were selected by random design and plots were not cleared during previous surveys, we distinguished pellet groups deposited during previous years or prior to the winter period from those deposited after by the extent of decomposition or litter accumulation. For example, pellet groups overlain by any amount of detritus from western larch would have likely been deposited prior to early November.

Initially on Bowser during 1989, we counted the number of pellet groups within 25 plots in each of 10 transects within randomly selected quadrats for a total of 250 plots. We attempted to locate a corner of each quadrat from which we oriented transects at an angle of 45° from a north-south or east-west azimuth. We determined number of paces between plots by generating random numbers. After evaluating results of the first year, we increased the number of plots sampled/transect to 50 and the number of transects to 13 in 1990 to increase precision following Davis (1982). We increased the number of transects sampled/year to 14 in 1992 that yielded a total of 700 total plots/year that was the protocol followed through the remainder of the study (1992-1999). On Murphy, nine transects of 50 plots each were sampled in 1991 and 50 plots within each of 14 transects through 1999. Survey area boundaries changed slightly at Bowser over the course of the study but most transects were within a defined 32-km^2 survey within which camera surveys also were conducted (Appendix C). The size of the area surveyed at Murphy consisted of 29 km^2.

Carcasses obtained from deer collected specifically as part of this study (Morgan 1993), trap mortalities, and other types of mortality yielded biological information pertaining to reproduction, physical condition, and food habits through March 1993. Additional carcasses from animals that died during winter 1996-1997 were collected to determine condition and fetal rates. Sex, age, location, and cause of death were noted as well as reproductive status for females during the period of January through May 1989-1993. Ages were assigned to deer following eruption and wear and cementum analysis techniques described above (Severinghaus 1949, Gilbert 1966, Hamlin et al. 2000). Kidneys and attached perirenal fat were taken from carcasses that were not badly decomposed or consumed by predators. We used a spring scale to obtain whole- and dressed-carcass weights from deer collected for study. Whole weight also was estimated from a measure of heart girth.

Analytical Procedures

Statistical procedures were consistent with Zar (1984) unless stated otherwise. We used the program *STATISTICA* (StatSoft, Inc. 2001) for individual analyses. We set the probability of a Type I error at $\alpha = 0.05$ for all statistical tests.

Estimates of Deer Abundance

Several approaches were used to estimate whitetail abundance on the study area. A mark-recapture technique using sensor-triggered cameras and pellet group transects provided estimates of numbers within herd units associated with Bowser and Murphy during winter. Autumn populations were reconstructed for hunting districts 101 and 102 from harvested deer examined at hunter check stations. We reconciled these data with results from statewide harvest telephone surveys and independent estimates of average annual wounding and nonhunting mortality to estimate deer abundance during early autumn just prior to the onset of hunting (archery).

We used a capture-resight technique using a Monte Carlo simulation (Minta and Mangel 1989) and data from late winter camera surveys on Bowser and Murphy to estimate numbers of deer on each winter range. A maximum likelihood estimate (MLE) and 95% likelihood interval were derived from 10,000 iterations of the Monte Carlo simulation. Sime (1996) investigated mark-recapture estimates of numbers of deer on the two winter ranges using different definitions of what constituted a marked sample to reduce confidence intervals of population estimates. Estimates and population trend varied depending on whether the sample included (1) surviving neck-banded deer from previous years, (2) neck-banded deer from the current year, or (3) only deer with functional radio collars. Applying the most restrictive definition of our marked sample, i.e., only those deer with functional radio collars, was perhaps the most precise way to meet the assumption of closure. This definition of the marked sample was applied to all years for which usable data were available. Thus, we treated neck-banded deer or deer with nonfunctioning radios as unmarked for the purpose estimating deer numbers on winter survey areas. We determined the number of radio-collared deer on survey areas through periodic aerial surveys and other incidental monitoring.

Remote camera surveys were conducted on Bowser and Murphy in early winter (Dec-Jan) and late winter (Feb-early Mar). A question of whether these surveys could detect deer effectively and objectively over time was raised previously (Dusek and Morgan 1991) because deer modified their behavior through the period of each survey and increasingly avoided camera stations that could reduce the efficacy of the technique for estimating population size. To address this concern Sime (1996) calculated detection rates—the number of marked individuals photographed divided by the number of marked individuals known to occur in the survey area but not photographed—for individually marked deer for each year and study area. We used detection rate to estimate the proportion of the population that was radio-collared.

Analysis of pellet group surveys to provide estimates of numbers and density of deer occupying individual winter ranges precisely followed that described by Davis (1982:353). Surveyed portions of each winter range appear in Appendix C. To facilitate that procedure we estimated the number of days that seasonal migrants occupied the winter range from routine monitoring of radio-collared deer. The number of days that each radio-collared seasonal migrant occupied the winter range was determined from the approximate dates that individual animals arrived and left the survey area. Yearlong residents of the winter range were assigned an arbitrary 121 days each year (1 Dec-1 Apr). Thus, we used the yearly average for all radio-collared winter occupants as an index to represent the span of time the population occupied the winter range each year. Our calculations also incorporated a standard defecation rate of 12.7/day (Longhurst and Connolly 1982) that is intermediate among a range reported for wintering white-tailed deer in the Midwest (Neff 1968:604-605).

Population reconstruction using harvest records from hunter check stations requires a set of sex- and age-specific data over an uninterrupted sequence of years to reconstruct numbers of individuals in specific cohorts backward through time—the number of individuals in specific cohorts present immediately preceding the period of harvest (Fryxell et al. 1991, Gilbert and Raedeke 2004). Reconstruction also requires an independent estimate of nonhunting survival rates. Fryxell et al. (1991) assumed that nonhunting survival rates were not age or density dependent and emphasized that population estimates for latter years are likely biased because younger cohorts would be incomplete. To address the bias in estimates for the latter years of the study, we

continued to collect harvest data for 3 years beyond which the final population estimates were made.

We obtained harvest records for white-tailed deer from check stations in northwest Montana during the hunting seasons of 1988 through 2003 to estimate autumn populations of deer in hunting districts 101 and 102. We chose to directly estimate numbers of antlered deer because antlered deer could be hunted through the entire general firearm season (5 wks/yr), and regulations affecting antlered harvest did not change over the period of data collection (1988-2003). Annual harvest regulations allowed hunters to take antlerless deer from 1-2 weeks during all years except 1998-2000 when most hunters could not legally take an antlerless deer. Additionally, initial evaluation of age-class composition of males and females indicated that male cohorts typically turn over within 9 years, and female cohorts turnover in about 13-16 years. Numbers of females of ages ≥ 1 year and fawns were calculated from the antlered segment (ages ≥1 year) by applying sex and age ratios resulting from backdating all harvest records as described earlier.

We determined age-class composition of all antlered deer examined at check stations from 1988 to 2003 using tooth eruption and replacement and cementum analysis as described earlier—specific age of all deer ≥ 2 years were assigned by cementum analysis. We then reconciled the proportion in each age class from check station records with estimated total antlered harvest by hunting district from the statewide harvest questionnaire. This figure was multiplied by correction figures for wounding and non-hunting mortality (e.g., Hamlin and Ross 2002) as determined from mortality among radio-collared deer to account for all males that died during a given year. Numbers for each cohort were added to estimate the original cohort size at an age of ~ 3 months, i.e., the onset of archery hunting in early September.

Population Parameters

Condition.—We estimated whole weights of deer from the study area for seasonal comparison for early autumn (pre-hunt), late autumn (hunting season), winter, and early spring. Whole weights were taken directly from animals collected for study during 1990-1991. Whole weights for late autumn (1988-2001) were estimated from field-dressed weights of 535 deer examined at check stations and from a regression of whole to dressed weight for 31 carcasses for which we obtained both whole and dressed weights. A total of 1253 live-trapped deer from both winter ranges during 1988-1998 provided estimates of whole weight from a measure of heart girth using a regression formula (Smart 1973). We report mean whole weights by sex, age, and season.

Reproduction.—We determined pregnancy rate from 16 females necropsied from 1989 to 1993 and radioimmunoassay for pregnancy-specific protein B (PSPB) from peripheral blood (Wood et al. 1986) from 316 females captured during the winters of 1988-1991, which would have included those potentially having bred during autumn 1987-1990. A sample of 23 female reproductive tracts were examined in 1997 of which an age was assigned to only 19 females; a fetal sex ratio was calculated from all these females, whereas pregnancy and fetal rates considered only those for which an age had been assigned.

Composition by sex and age.— We determined population characteristics from early and late winter camera surveys conducted on the Bowser and Murphy winter ranges following procedures described by Dusek and Mace (1991). Data from 1333 deer captured on the two winter ranges during January and February also were used to assess herd composition. We attempted to identify deer among photographs from camera surveys. Deer were classified as fawn (<12 months), adult female (≥12 months), yearling male (12-23 months), or mature male (≥24 months). During late winter we attempted to distinguish adult (≥ 1 yr) males from females by the presence of a pedicel.

Survival estimates.—We estimated survivorship from records of radio-collared deer and from reconstruction of the population. We estimated survival of deer older than fawns for the biological year 1 June-31 May and that of fawns for the period of 1 January-31 May. Animals captured during a monthly interval were included in estimates for that interval to maximize sample sizes although we acknowledge that doing so might slightly bias estimates of survival upward (Unsworth et al. 1999). We censored animals from analyses that died within

14 days of capture because of the likelihood that the death was trap related. Deer that shed transmitters or the transmitter failed and those for which the status was uncertain were censored following the time interval (month) in which the animal was known to be alive and the transmitter was attached and functioning. We estimated survival functions among radio-collared deer using the staggered-entry Kaplan-Meier procedure (Pollock et al. 1989). We tested for differences among survival rates using a general Chi-square statistic to evaluate hypotheses of homogeneity among rates (Sauer and Williams 1989) and individual contrasts using a log-rank test (Pollock et al. 1989). Survival functions were calculated for each year by age class for females of ages ≥ 1 year. Functions for males of ages ≥ 1 year and for both sexes of fawns combined were pooled across all years because of very small yearly samples.

Climate data

We obtained historical data for the Salish Mountains study area that included Bowser and Murphy under a contract with the Earth Sciences Department at Montana State University (Farnes et al. 2000). Snow pack, precipitation, and temperature were processed under this contract for correlation with soil moisture, winter severity, and other deer/climate relationships. Six snow courses, one SNOTEL site, and four climatological stations provided the primary data that were supplemented with manual snow measurements taken at 14 additional locations within the study area (Farnes et al. 2000). We used the processed weather data in regression analyses to ascertain if and how the region's climate and weather variables might influence population dynamics, body growth, antler development, and intensity of use and occupancy of winter ranges by white-tailed deer. We used two components of winter severity to evaluate these relationships. Snow water equivalent (SWE) represented the amount of water stored in the snowpack at a specific time and location. Temperature was evaluated relative to the effective critical temperature of –12 °C (10 °F) for white-tailed deer Mautz (1985)—a temperature below which deer must increase their basal metabolic rate to maintain body temperature. We also evaluated two indices of drought for their potential effect on growth and condition as well as other population parameters. These included the Keetch-Byram drought index (KBDI) as summarized by Farnes et al. (2000) and the Palmer drought severity index calculated by the National Oceanic and Atmospheric Administration (NOAA).

A Study To Test Effects Of Antlerless Harvest

Selective harvest management assumes that (1) antlerless harvest can be manipulated through specific harvest regulations, and (2) manipulating antlerless harvest can effectively influence population trend (Giles and Findlay 2004). We addressed the effects of harvest removal of antlerless deer by attempting to double the antlerless harvest in one of two distinct population units (HD 102) while using the other (HD 101) as a control. Population units associated with two distinct and separate winter ranges generally distributed themselves within the boundaries of the two hunting districts; the two areas are relatively similar in climate, vegetation, and land use. Both units had been subjected to the same harvest regulations for three years prior to treatment (1988-1990). Three years of pre-treatment monitoring suggested no measurable differences in overall survival of adult females and other population variables between the two units (Dusek and Morgan 1991).

Season length and harvest regulations for the general deer license (A-tag) were the same for hunting districts 101 and 102 throughout the study, but regulations affecting antlerless harvest varied. Throughout the pre-treatment period, hunters were allowed only one deer per year (A-tag) over a 5-wk general firearm season during which time antlerless deer could be taken during the first 15 days, and only antlered deer could be legally taken thereafter. From 1991 through 1995, hunters could legally take antlerless white-tailed deer on the A-tag during the first 15 days of the 5-wk general big game season or only an antlered buck during the remainder of the season. For the 1996 season the period in which antlerless deer could be taken was split to include the first 8 days and last 7 days of the 5-wk season. During 1997, antlerless deer could be taken on the A-tag only during the first 8 days, and antlerless deer could not be legally harvested during the hunting seasons of 1998-2000.

Under an experimental design, hunting

district 101 served as a control area during the hunting seasons of 1991-1996. That is, hunting of antlerless deer precisely followed the regulations described above in which there was no opportunity to legally harvest a second deer.

Hunting district 102 served as the treatment area. Although the same regulation package was in effect as in hunting district 101, a second license (permit) was issued via drawing for hunting district 102 in 1991 to 600 hunters through a random drawing. The permits, which allowed successful applicants an opportunity to take a second deer, were valid for the archery season that ran from early September to mid October and the entire general firearm season that ran from late October to late November. We based the initial number of permits issued on what we would expect necessary to double the harvest of antlerless deer from the number harvested in the absence of permits over a period of 8-15 days of annual general firearm seasons. Success in harvesting antlerless deer by permit holders was projected from that observed in hunting district 130 (Swan Valley) for which permits were issued in previous years (S. J. Riley, personal communication). FWP issued 700 permits/year during 1992-1994, 950 permits for 1995, and 800 permits for 1996. No permits were issued after 1996 through the end of the field effort in May 2000. Monitoring of mortality, recruitment, and growth and condition parameters followed that described previously.

Section 4: Population Characteristics

Population Structure

Sex and Age Composition During Autumn

Age structure calculated from samples of harvested deer was skewed heavily towards younger deer among both males and females with > 60% of individuals occurring in age classes ≤ 2 years during most years (Fig. 4.1). For hunting district 101, the proportion of females in these age classes ranged from a low of 48% in 1996 to a high of 70% in 1989. We observed the respective low and high for these combined age classes in hunting district 102 in 1996 (51%) and 1999 (78%). Age composition varied between hunting districts 101 and 102 within individual years although average composition across years suggested a slightly older age structure in hunting district 101. For autumn 1988-2000, age classes ≤ 2 years accounted for an average 62% of females and 77% of males in hunting district 101. These age classes averaged 64 and 80% of the respective sexes in hunting district 102. Age classes 3-5 years accounted for 23% of the female segment in hunting district 101 and 22% in hunting district 102, whereas females ≥ 6 years accounted for 15 and 14% of females in the respective hunting districts. The respective proportion of males in age classes 3-5 years was 20% in hunting district 101 and 18% in hunting district 102. Males ≥ 6 years accounted for 4% of the male segment in each hunting district. The oldest age assigned to a harvested female by cementum analysis was 15 years, whereas the oldest age assigned to a harvested male was 12 years.

An older age structure characterized white-tailed deer in the Salish Mountains than that reported for a population in a riparian river bottom in eastern Montana (Dusek et al. 1989), a difference that was particularly apparent among adult males. On the lower Yellowstone, males ≥ 4 years accounted for < 1% of the male segment (Dusek et al. 1989) compared to 13% for the Salish Mountains. Rates of removal of antlered males through hunting probably explained this difference. However, harvest regulations alone do not explain these in between-area differences among males because regulations directly affecting harvest of antlered deer were the same in both areas during the respective studies. Habitat security, as expressed by dense multi-storied cover in mountainous terrain and a dispersed distribution of deer during late autumn of most years that coincided with annual hunting seasons, (see Hoekman, et al. 2006) probably accounted for the older age structure that we documented for the Salish Mountains.

Back dating harvest records and assigning individuals to their respective cohorts provided our only estimates of pre-hunt composition and sex and age ratios. These data suggested only minor differences between hunting districts over all years with respect to proportion of the various sex and age classes and sex and age ratios (Tables 4.1 and 4.2). Although Tables 4.1 and 4.2 summarize values for individual years and hunting district, the average fawn:adult ratio was slightly higher in hunting district 102, and the average buck:doe ratio was slightly higher in hunting district 101, but these differences were not significant ($P > 0.10$). Harvested females as well as males were used to estimate composition and ratios. Consequently, incomplete female cohorts that resulted from differences in longevity between the sexes might have influenced estimates for the latter years of this study. Ratios also were probably influenced by relatively conservative regulations affecting antlerless

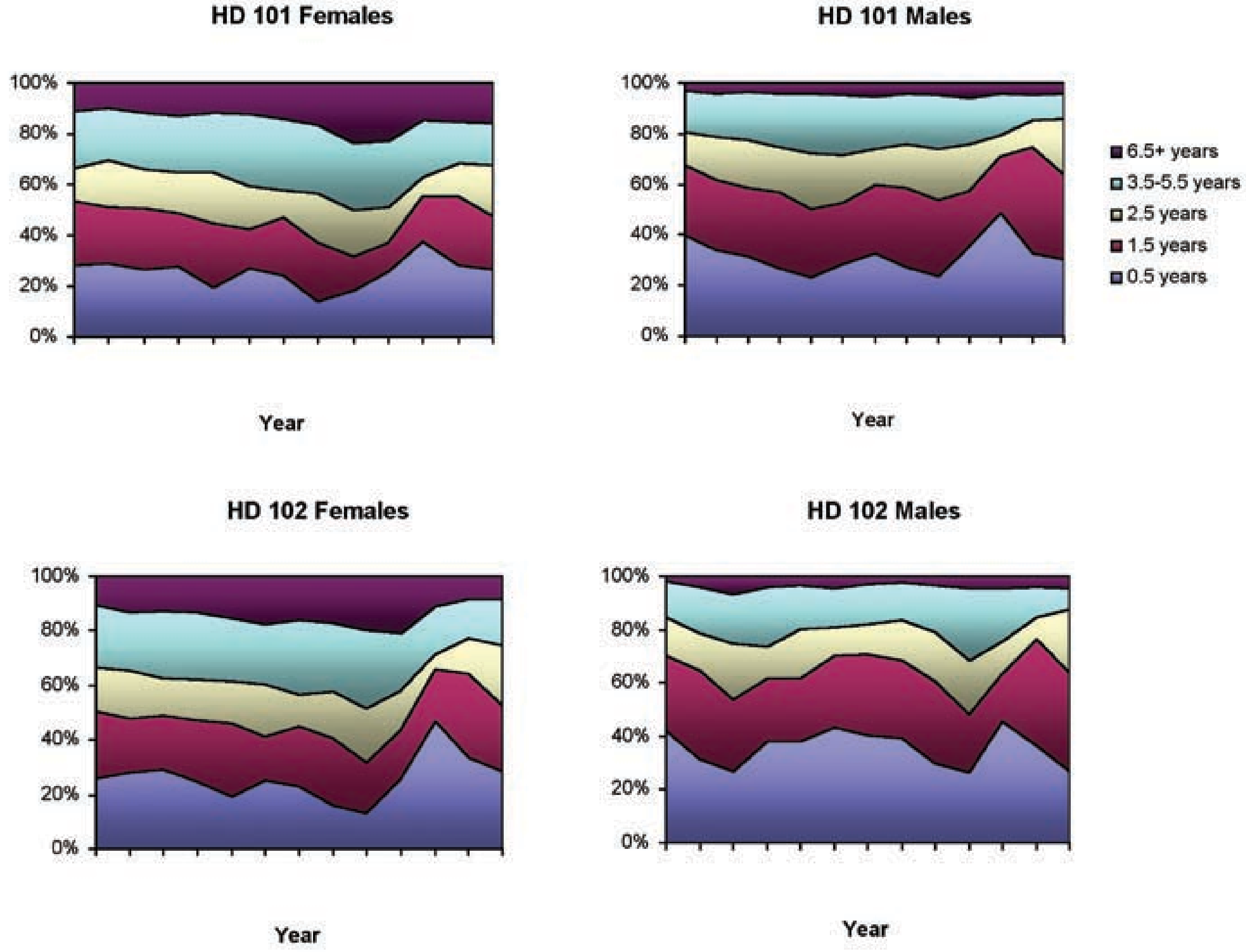

Figure 4.1. Percent composition by sex, age, and hunting district for white-tailed deer in the Salish Mountains from back-dating harvest records through 2003.

harvests and specifically that antlerless deer were not legally hunted in northwest Montana during 1998-2000. However, we believe that this broadly represented an autumn population structure among white-tailed deer in the Salish Mountains over this study that we can support with other independent sources of data in the following sections.

Sex and Age Classification

Early Winter.—Camera surveys during early winter provided a classified sample of 2234 white-tailed deer on the two winter ranges during 1989-1998 (Tables 4.3 and 4.4). Distribution of deer across seasonal ranges generally associate deer wintering at Bowser with HD 102 and those wintering at Murphy with HD 101 (Morgan 2006, Hoekman et al. 2006.). Early winter camera surveys covered a period of transition by deer from summer to winter ranges. Time and extent of arrival on the two winter ranges where cameras were placed varied among years. Consequently, samples of classified deer from early-winter surveys were substantially and consistently smaller than those from late-winter surveys that confounded interpretation and direct comparison with those of autumn and late winter. An unusually early arrival by large number of deer on both winter ranges during 1996-1997 resulted in classification of a large sample of deer only during that one year. Overall, these data show an increase in the fawn:adult ratio and decrease in the buck:doe ratio reflecting disproportionate harvest rates, i.e., buck harvest over-represented abundance of bucks in autumn

Table 4.1. Autumn population composition of white-tailed deer in Hunting District 101 (pre-hunt), 1988-2000, calculated by back dating harvest records from check stations.

	Herd composition						**Sex and age ratios**		
Year[1]	**Total[2]**	**% fawns**	**% yrlg ♂♂**	**% ♂♂ ≥ 2 years**	**% ♀♀ ≥ 1 year**	**% total adults**	**Fawns: 100 ♀♀ ≥ 1 year**	**Fawns: 100 adults ≥ 1 year**	**Ad ♂♂: 100 ♀♀ (≥ 1 year)**
1988	303	33	12	14	42	67	79	49	60
1989	321	31	13	18	38	69	81	45	79
1990	349	29	13	19	39	71	73	40	81
1991	367	27	15	22	36	73	76	37	104
1992	477	21	12	22	44	79	47	27	79
1993	359	28	12	23	37	72	75	39	93
1994	361	28	11	17	44	72	63	38	65
1995	548	18	11	14	57	82	32	22	43
1996	476	21	13	20	45	79	46	27	74
1997	345	29	9	17	45	71	65	41	58
1998	235	43	10	13	35	57	122	74	64
1999	324	31	19	12	38	69	80	45	80
2000	348	29	15	17	41	71	70	40	75
$\bar{x}$		28	13	17	42	72	70	40	74
Coeff. var.							31	32	

[1] Data for 2000-2003 included harvest in hunting district 109 that was split from "old hunting district" 101 for the 2002 hunting season.

[2] Total number of deer based on a sample of 100 fawns assuming a 1:1 sex ratio with relative abundance among age classes reconstructed from back dating ages of harvested deer examined at check stations during 1988-2003. Totals were based on the ratio calculated from 100 fawns and not the total number in the hunting district.

populations, fawns harvest under-represented abundance of fawns.

Late Winter.— Camera surveys during late winter provided a classified sample of 6569 whitetails on the two winter ranges during 1989-1998 (Tables 4.3 and 4.4). The proportion of the herd comprised of fawns generally remained similar to those from early winter surveys suggesting that annual trapping effort and camera surveys were completed prior to a period in which any significant mortality of fawns might occur. Thus, fawn:adult ratios of late winter probably overestimated recruitment to 1 year of age during most years.

Fawns accounted for 22-51% of early winter population and 21-47% of late winter populations on Bowser (Table 4.3) that averaged 34 (*n* = 6, SD = 10) and 35% (*n* = 11, SD = 7), respectively. Mean fawn:adult ratios were 56:100 (SD = 26) and 55:100 (SD = 17) for the respective time periods. Mundinger and Riley (1983) reported substantially lower estimates of fawn production on Bowser[3] during the early 1980s than those typically observed during 1989-1999. They reported fawn:adult ratios of 33 and 39:100 for the respective years of 1982 and 1983. We observed ratios < 40 fawns:100 adults only during 3 years from 1989-1999.

The proportion of unclassified adults approached 25% of deer classified by age among yearly samples during both early and late winter. This might have masked any year-to-year trend in fawn:adult female and buck:doe ratios. Fawn:

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[3] These data were obtained from routes surveyed in the vicinity of the Ray Kuhns Wildlife Management Area that lies within the Bowser/Tally Lake Winter Range. Mundinger and Riley (1983) cite these as early spring ratios but were obtained while deer occupied the winter range.

Table 4.2. Autumn population composition of white-tailed deer in Hunting District 102 (pre-hunt), 1988-2000, calculated by back dating harvest records from check stations.

	Herd composition						Sex and age ratios		
Year	Total[1]	% fawns	% yrlg ♂♂	% ♂♂ ≥ 2 years	% ♀♀ ≥ 1 year	% total adults	Fawns: 100 ♀♀ ≥ 1 year	Fawns: 100 adults ≥ 1 year	Ad ♂♂: 100 ♀♀ (≥ 1 year)
1988	313	32	11	11	46	68	70	47	48
1989	340	29	16	17	38	71	77	42	84
1990	355	28	14	24	34	72	82	39	110
1991	332	30	9	15	45	70	66	43	54
1992	390	26	8	13	54	74	48	34	39
1993	315	32	10	11	47	68	67	47	44
1994	341	29	11	11	49	71	60	41	44
1995	446	22	8	9	60	78	37	29	29
1996	549	18	9	12	60	82	30	22	35
1997	386	26	11	26	38	74	69	35	97
1998	217	46	9	18	27	54	173	86	103
1999	287	35	19	11	35	65	100	53	87
2000	357	28	19	19	35	72	81	39	108
$\bar{x}$		29	12	15	44	71	74	43	65
Coeff. var.							48	35	

[1] Total number of deer based on a sample of 100 fawns assuming a 1:1 sex ratio with relative abundance among age classes reconstructed from back dating ages of harvested deer examined at check stations during 1988-2003. Totals were based on the ratio calculated from 100 fawns and not the total number in the hunting district.

adult female ratios averaged 81:100 (SD = 28) and 84:100 (SD = 32) during early and mid-to-late winter, respectively. Average buck:doe ratios during the respective periods were 24:100 (SD = 12) and 17:100 (SD = 8). Antler drop and perhaps sexual segregation probably contributed to the decline in buck:doe ratios from early to late winter.

Estimates of fawn production from both camera surveys and trapped deer suggested lower production/survival of fawns on Murphy (Tables 4.3, 4.4, and 4.5). Relative vulnerability of fawns than older deer to trapping seemingly varied among years, which confounded year-to-year comparison. However, averages for all years reflected trends between the two winter ranges similar to camera surveys. Fawns accounted for 22-24% of early winter populations and 13-44% of late winter populations from camera surveys (Table 4.4). Fawns averaged 26 (*n* = 3, SD = 5) and 32% (*n* = 9, SD = 10) of respective early and late winter samples. Mean fawn:adult ratios were 36:100 (SD = 9) and 49:100 (SD = 21) for the respective time periods. Fawn:adult female ratios averaged 54:100 and 56:100 (SD = 27) during early and late winter, respectively. Average buck:doe ratios during the respective periods were 17:100 and 12:100 (SD = 2). These ratios suggested that samples of trapped deer underrepresented bucks during winter.

Surveys during February-March 1998 (Tables 4.3 and 4.4) yielded the lowest fawn:adult ratios observed on either winter range during this study and reflected a weak cohort born in June 1997. Comparatively low representation of fawns in samples of deer trapped during that winter also suggested low fawn production and/or survival during that biological year (Table 4.5). Age structure in Figure 4.1 clearly illustrates a weak yearling age class (1996 cohort) during autumn 1997 among both males and females. This and low recruitment among the 1997 cohort suggested that this severe winter event substantially affected two year

Table 4.3. Seasonal population composition of white-tailed deer on the Bowser winter range from 5293 individual deer classified from camera surveys, 1989-1999.

		Herd composition						Sex and age ratios		
	Total classified	% fawns	% yr ♂♂	% ♂♂ ≥2 years	% ♀♀ ≥1 years	% unclass. adults	% total adults	Fawns: 100 ♀♀ ≥1 year[1]	Fawns: 100 adults ≥1 year[2]	Ad ♂♂:100 ad ♀♀ (≥1 year)[3]
Early winter (Dec/Jan)										
1989-1990	113	36	4	4	48	9	65	76	56	17
1990-1991	35	51	3		43	3	49	120	106	7
1991-1992										
1994-1995	174	37	3	12	33	15	63	114	60	44
1995-1996	95	22	8	8	49	12	78	45	28	34
1996-1997	662	36	4	5	46	10	64	78	55	19
1997-1998										
1998-1999	134	22	3	7	43	25	78	51	29	22
$\bar{x}$		34	4	7	44	12	66	81	56	24
Late winter(Feb/Mar)										
1989	203	47				33	53		88	
1990	230	40				41	60		64	
1991	243	39		4	34	24	61	116	63	11
1992	467	26	5	7	40	22	74	65	35	30
1993	526	38				56	62		61	
1994	430	30				61	70		42	
1995	328	41	3	5	41	9	59	101	71	19
1996	389	38	3	4	31	24	62	124	61	23
1997	651	28	1	3	43	24	72	66	39	10
1998	260	21	1	5	62	11	79	34	27	10
1999	596	33					67		49	
$\bar{x}$		35	3	5	42	31	65	84	55	17
Coefficient of variation								42	33	

[1] Fawn:adult female ratios are displayed only for years in which the proportion of unclassified adults was ≤ 25% of the total classified as to adult or fawn and calculated from unadjusted numbers of adult females among the total number of adults.

[2] Fawn:adult ratios were calculated for all years using the entire classified sample.

[3] Adult male:adult female ratios are displayed only for years in which the proportion of unclassified adults was ≤25% of the total classified as to adult or fawn and calculated from unadjusted numbers of adult females and males ≥1 year of age.

Table 4.4. Seasonal population composition of white-tailed deer on the Murphy winter range from 3267 individual deer classified from camera surveys, 1990-1999.

		Herd composition		Sex and age ratios						
	Total classified	% fawns	% yr ♂♂	% ♂♂ ≥2 years	% ♀♀ ≥1 years	% unclass. adults	% total adults	Fawns: 100 ♀♀ ≥1 year[1]	Fawns: 100 adults ≥1 year[2]	Ad ♂♂: 100 ad ♀♀ (≥1 year)[3]
Early winter (Dec/Jan)										
1994-1995										
1995-1996	161	22	4	7	61	7	78	36	28	17
1996-1997	682	33	3	5	46	13	67	72	49	16
1997-1998										
1998-1999	178	24				28	76		32	
$\bar{x}$		26	4	6	54	16	74	54	36	17
Late winter (Feb/Mar)										
1990	343	37				40	63		58	
1991	170	41				32	59		70	
1992	32	44				50	56		78	
1993										
1994	65	20				69	80		25	
1995	317	35	2	3	45	3	65	76	54	10
1996	256	35	3	4	40	18	65	88	54	16
1997	571	20	1	5	50	25	80	39	24	11
1998	149	13	1	6	64	15	87	21	16	12
1999	343	39				33	61		63	
$\bar{x}$		32	2	5	50	32	68	56	49	12
Coefficient of variation								56	45	

[1] Fawn:adult female ratios are displayed only for years in which the proportion of unclassified adults was ≤25% of the total classified as to adult or fawn and calculated from unadjusted numbers of adult females among the total number of adults.

[2] Fawn:adult ratios were calculated for all years using the entire classified sample.

[3] Adult male:adult female ratios are displayed only for years in which the proportion of unclassified adults was ≤25% of the total classified as to adult or fawn and calculated from unadjusted numbers of adult females and males ≥1 year of age.

Table 4.5. Composition by sex and age of 1333 white-tailed deer captured on the Bowser and Murphy winter ranges, 1988-1998.

				Bowser					
Year	**Total**	**% fawns**	**% yr ♂♂**	**% ♂♂ ≥2 years**	**% yr ♀♀**	**% ♀♀ ≥2 years**	**Fawns: 100 ♀♀ ≥1 year**	**Fawns: 100 adults ≥1 year**	**Ad ♂♂:100 ad ♀♀ (≥1 year)**
1988[1]	45	38	2	13	7	40	81	61	33
1989	133	45	10	6	8	32	115	82	40
1990	106	41	9	8	12	30	96	68	40
1991	100	39	7	3	11	40	76	64	20
1992	85	31	9	6	7	47	57	44	28
1993	65	45	5	11	9	31	112	81	38
1994	74	42	3	4	4	47	82	72	13
1995	64	67	9	2	9	13	307	205	50
1996	69	25	7	6	7	55	40	33	21
1997	58	24	7		7	62	35	32	10
1998	29	28	3	10	7	52	47	38	24
$\bar{x}$		38	7	6	8	41	95	71	29
				Murphy					
Year	**Total**	**% fawns**	**% yr ♂♂**	**% ♂♂ ≥2 years**	**% yr ♀♀**	**% ♀♀ ≥2 years**	**Fawns: 100 ♀♀ ≥1 year**	**Fawns: 100 adults ≥1 year**	**Ad ♂♂:100 ad ♀♀ (≥1 year)**
1988	22	55		5		41	133	120	11
1989	42	48	2	7	5	38	111	91	22
1990	45	38	9	7	4	42	81	61	33
1991	49	16	6	14	14	49	26	20	32
1992	56	30	7	4	14	45	52	44	18
1993	59	34	3	5	12	46	59	51	15
1994	47	36	4	4	0	55	65	57	15
1995	61	34	7	5	7	48	64	53	21
1996	59	31	2	3	7	58	47	44	8
1997	42	36	2	7	10	45	65	56	17
1998	23	26	4		4	65	38	35	6
$\bar{x}$		35	4	6	7	48	67	57	18

[1] Fawns include the cohort born the previous calendar year.

classes; both fawns on the ground from the 1996 cohort and in-utero production and/or early neonatal losses from the 1997 cohort. Both age structure (Fig. 4.1) and late winter classifications suggested a sharp increase in per capita recruitment in 1998.

The respective ratios from back dating harvest records (Tables 4.1 and 4.2) did not reflect the extremes in rates of recruitment between autumn 1997 and 1998. However, rates fell below the mean for the entire duration of study during 1997 and substantially above the mean in 1998. Although the sex ratio of fawns did not depart from a 1:1 ratio over the duration of study, they may have departed from unity in some years.

Long-term Trends.—We detected no differences between study units in recruitment to fall or late winter as expressed by proportions of the respective populations that were fawns ($P \geq 0.16$). However, fawn:adult ratios of late winter

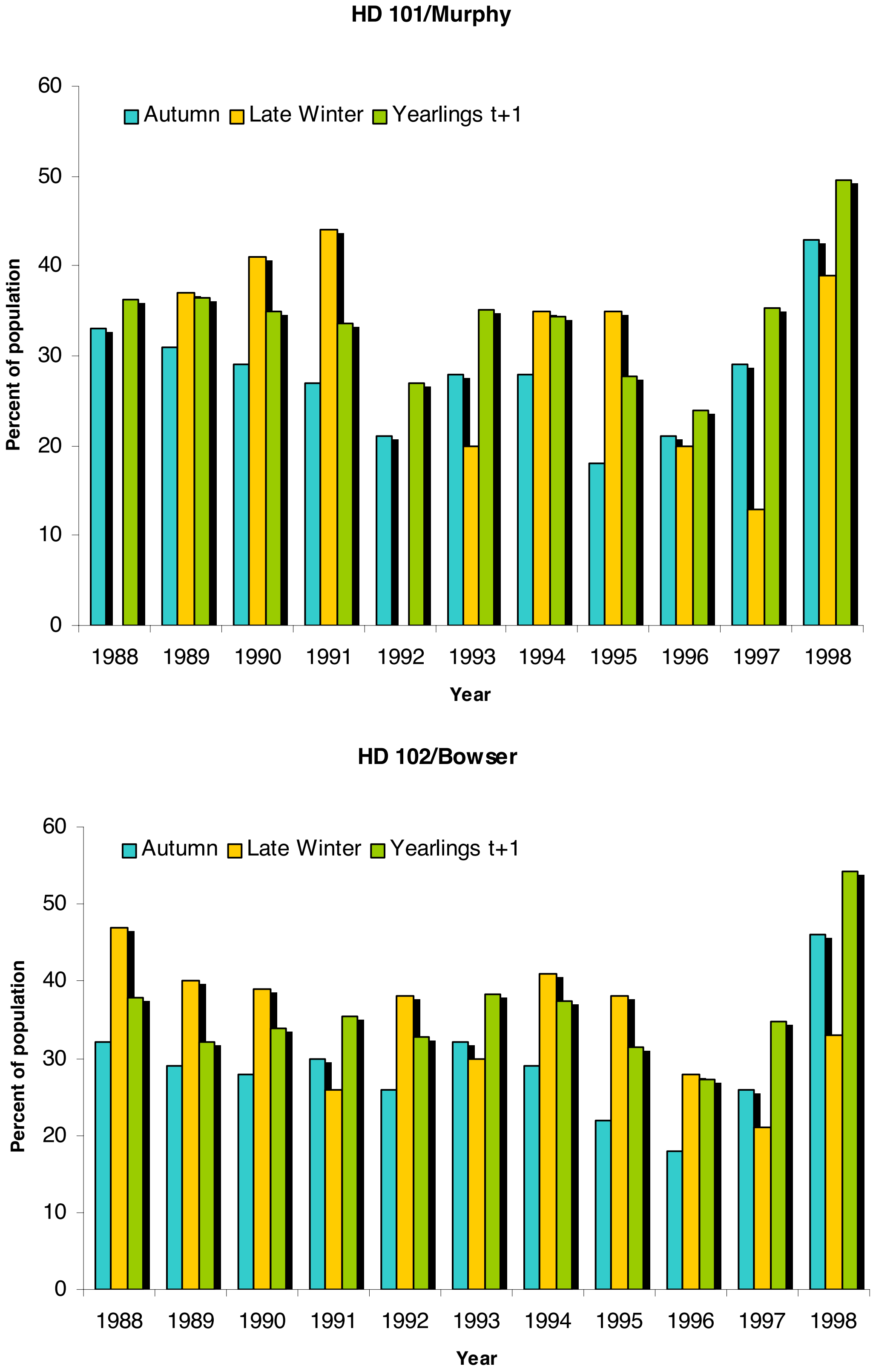

Figure 4.2. Trends in recruitment as measured by the proportion of populations consisting of deer at ages of 3 (Sept), 9 (Mar), and 15 (Sept+1) months.

might have overestimated recruitment to one year of age during most years in both study areas. Net recruitment (Fig. 4.2), which compared percent fawns from late winter camera surveys (Tables 4.3 and 4.4) to percent yearlings among all adults (≥ 1 yr) the following autumn, averaged only 2.5% lower for Bowser and 5% lower for Murphy from 1988 through 1996. After 1996, autumn estimates based on the proportion of yearlings among adults markedly exceeded estimates from camera survey (Fig. 4.2) suggested that incomplete turnover of adult females probably biased ratios based on back-dated harvest records. The general trend of markedly higher estimates in winter compared to the previous autumn could be explained largely by the preponderance of adults, primarily bucks, in annual harvests (Fig. 4.2).

Figure 4.3 summarizes fawn:adult ratios from all of FWP Region 1 for the years of 1942-2004.[4] The mean ratio over the entire period was 48 fawns:100 adults (SD = 12.7). Three obviously distinct periods emerge—1942-1970, 1971-1984, and 1986-2004—in which observed patterns of fawn production/recruitment might have differed. Mean ratios during the respective periods were 52 (SD = 9), 37 (SD = 7), and 52 fawns:100 adults (SD = 15). Although recent rates are comparable to the 1942-1970 period, there is much more variability in fawn recruitment during 1986-2004 compared to earlier years; it's noteworthy to mention that some of the variability over time might have reflected an emphasis from individual areas and observers contributing to yearly samples.

Average fawn:adult ratios from Bowser and Murphy during the period of this study (1989-1999) were comparable to those reported for white-tailed deer in eastern Montana during the 1970s and 1980s (Table 4.6). However, reproductive success in eastern Montana appeared somewhat higher than the long-term average for northwest Montana particularly that reported for the Swan Valley from the late 1970s and early 1980s. Allen (1968) reported fawn: adult ratios of 12-120:100 on bottomlands of the Missouri River in central Montana that would appear to represent the extremes in estimated productivity of white-tailed deer in Montana. Although this population exhibited very high potential in terms of in-utero productivity, Allen (1968) attributed periodic poor fawn survival to the effects of flooding along bottomlands just above Fort Peck Reservoir.

Reliability of Ratios.—We believe that any attempt to classify adult deer by sex during

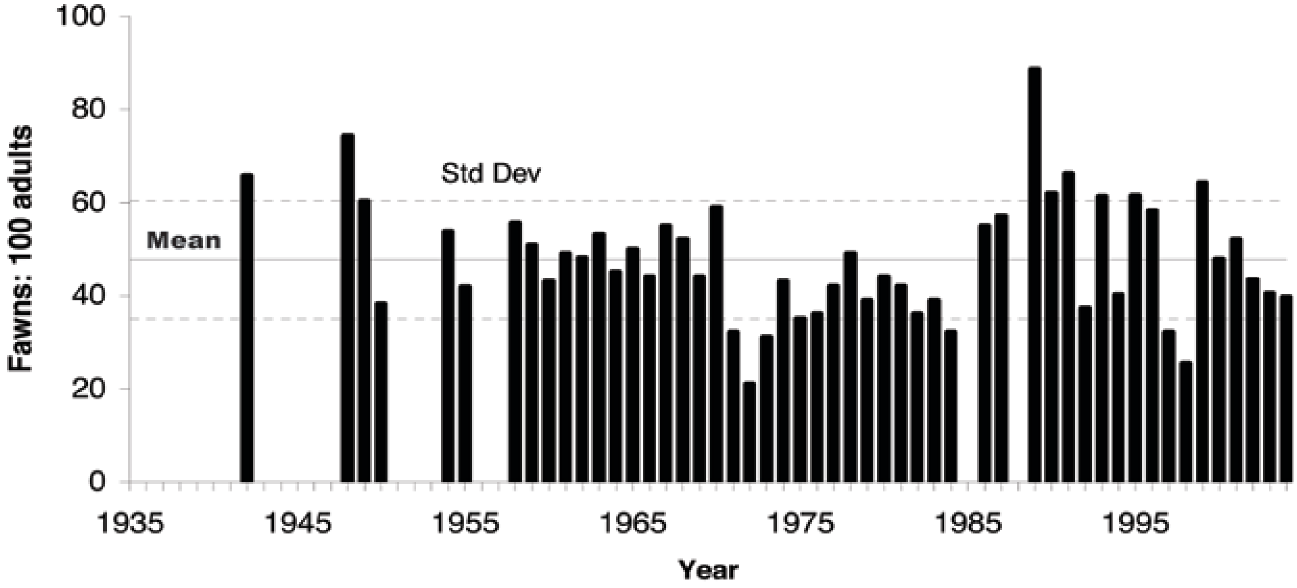

Figure 4.3. Fawn:adult ratios for 1942-2004 from late winter/early spring surveys from throughout FWP Region 1.

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[4] The period of 1942-1975 is heavily represented by data from the northwestern part of Region 1. Data for 1975 through 1982 are from the Swan Valley, most data for 1989-1996 are from this study, and data for 1997 to the present are from across the region.

Table 4.6. *Summary of white-tailed deer population characteristics for winter-spring from throughout Montana.*

Location	Years	Period	% fawns $\bar{x}$	% fawns SD	Fawns:100 ads $\bar{x}$	Fawns:100 ads SD	Source
Bowser	1982-1983	Feb-Mar	27	2	36	4	Mundinger and Riley 1982
Bowser	1989-1999	Feb-Mar	35	7	55	17	This study
Murphy	1990-1999	Feb-Mar	32	10	49	21	This study
Swan Valley	1976-1982	Jan-Apr	30	2	43	5	Mundinger and Riley 1982
Cherry Creek	1976-1987	Mar	33	11	53	26	Wood et al. 1989
Lower Yellowstone R.	1981-1986	Mar	36	7	58	18	Dusek et al. 1989

late winter, even by examining photographs, would not yield reliable results because of the subjectivity that it involves. First, males were conclusively identified by the presence of pedicels, which due to their relative size one might more readily identify mature males, e.g., ≥ 2 years, than on yearling males. Some young adult males very likely were classified as does, whereas others were listed as unclassified adults. Classification from early to late winter (Table 4.3 and 4.4) suggested that as the proportion of unclassified adults among samples increased, buck:doe ratios decreased.

Sex Ratios of Fawns.—We examined sex ratios of fawns from samples of deer trapped on the respective winter ranges and deer examined at hunter check stations from hunting districts 101 and 102 (Table 4.7). Data were pooled for all years because of relatively small samples within most years. None of the ratios departed from unity ($P > 0.10$). Thus, any analysis of population data assumes a sex ratio of 1:1 to 1 year of age.

Physical Characteristics And Condition Parameters

Condition

Body mass.—The annual weight cycle for fawns, yearlings, and adults in the Salish Mountains was consistent with that described for white-tailed deer in Montana (Dusek et al. 1989) and elsewhere (Mautz 1978, Moen and Severinghaus 1981) across the northern portion of the species' range whereby weight gain and loss corresponds to accretion and mobilization of body fat. Body weight of both sexes of adults peaked during late fall just prior to breeding and then declined (Fig. 4.4). For males weight loss leveled off by early to late winter, whereas that of adult females continued into summer during lactation.

Whole weights declined from late fall to early winter for all years combined among all age and sex classes although the greatest weight

Table 4.7. *Sex ratios of fawns among samples of white-tailed deer trapped on winter ranges and from deer examined at check stations.*

	Trapped deer		Harvested deer	
	Murphy	**Bowser**	**HD 101**	**HD102**
No. fawns (*n*)	171	327	180	102
Males:100 females	92	114	94	100
χ^2	0.14	0.68	0.10	0.00
***P*-value**	0.71	0.41	0.75	1.00

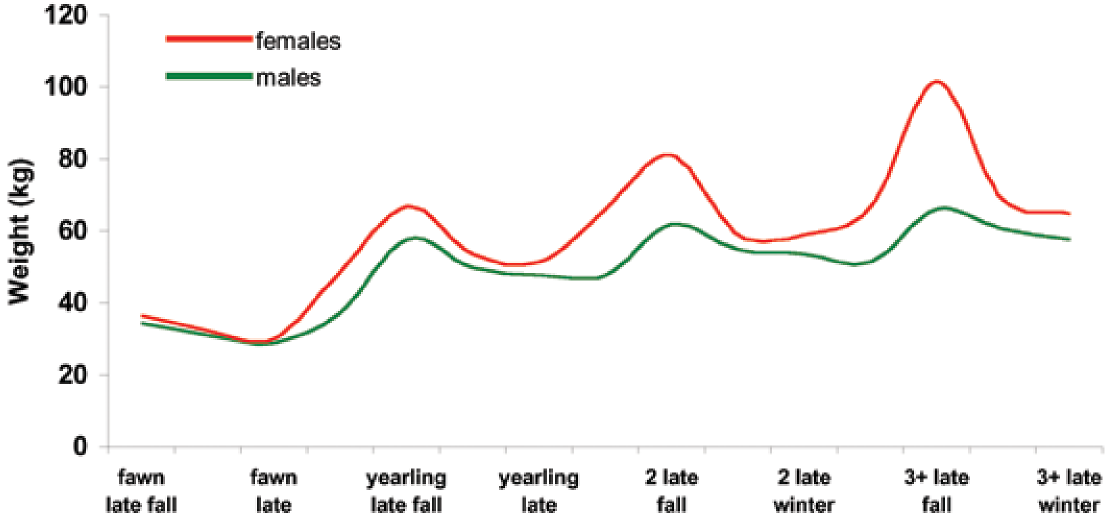


Figure 4.4. Annual weight cycle by sex and age for white-tailed deer in the Salish Mountains based on measured and estimated whole weights.

loss occurred among adult males (Table 4.8). Fawns of both sexes lost an average of 14% of late fall body weight by late winter. Females of ages 1, 2, and ≥3 years lost 18, 14, and 12% of their respective fall weights by late winter. Over the same period, males of those age classes lost 22, 27, and 36% of their respective fall weights. Dusek et al. (1989) observed similar over-winter weight losses for white-tailed deer on the lower Yellowstone River in eastern Montana.

ANOVA indicated that dressed carcass weight differed by sex, age and among years ($P < 0.01$) but did not differ between hunting districts ($P > 0.50$). Dressed carcass weight declined from 1989 to 1994, increased in 1995 and then declined and leveled off through 2001 (Fig. 4.5). For males, dressed carcass weights increased to an age of 6 years before leveling off, whereas those of females leveled off at 3 years of age (Fig. 4.6). Dressed weights for females ≥ 4 years averaged 47.4 kg (104.5 lb), and those for males ≥ 6.5 years averaged 77.3 kg (170.4 lb). This pattern closely followed that described by Knowlton et al. (1980) and Dusek et al. (1991). Dressed weights of fawns during fall averaged 24.7 kg (54.5 lb) for males and 24.3 kg (53.6 lb) for females. Average

Table 4.8. Estimated whole weights (kg) by season, sex, and age of white-tailed deer in the Salish Mountains.

Sex and age (yrs)	Summer/early fall			Late fall			Early winter			Late winter		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Females												
0				18	35	5	146	32	3	79	30	2
1	6	38	5	36	58	6	61	50	5	43	48	5
2	10	48	6	20	62	6	64	55	5	45	54	5
≥3	31	52	5	51	66	6	263	61	6	152	58	6
Males												
0				15	37	4	137	33	3	103	31	3
1	8	49	11	160	67	6	48	54	7	31	52	6
2	1	71		114	81	8	14	59	5	14	59	5
≥3	1	62		120	101	13	29	69	6	11	65	5

[1] Whole weights for summer/early fall were taken by spring scale, those of late fall were estimated from field-dressed weights, and those of early and late winter were estimated from heart-girth measurement.

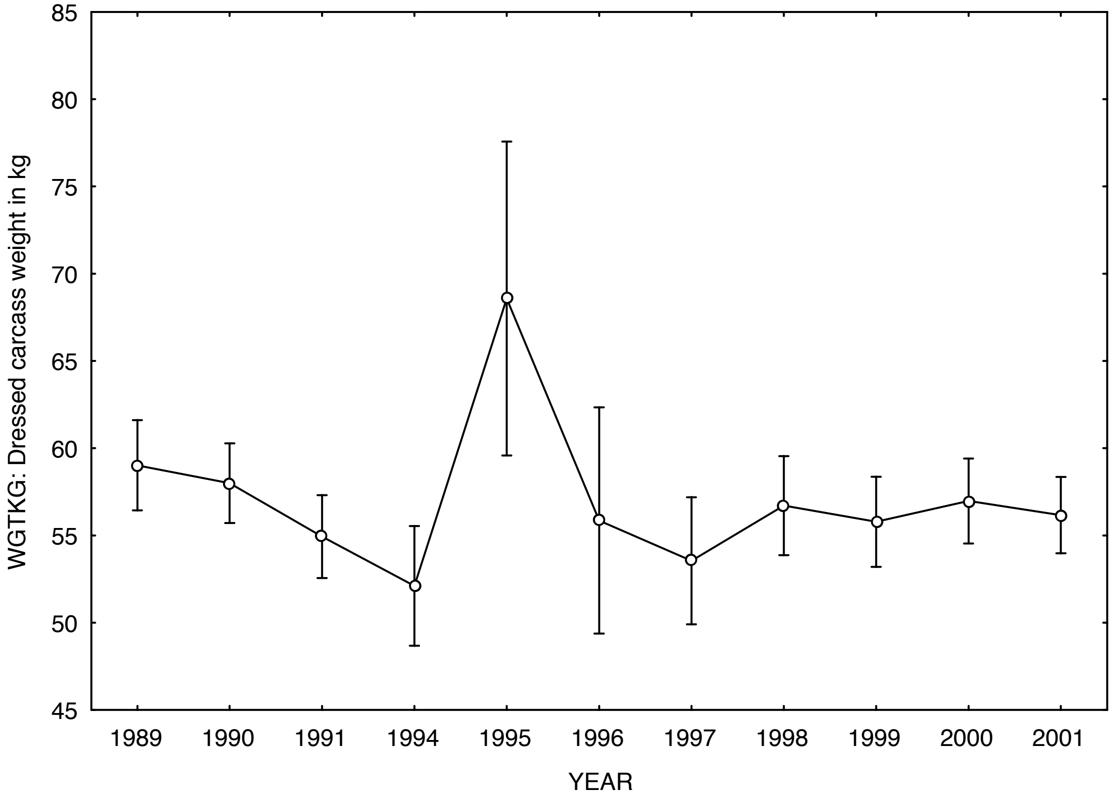


Figure 4.5. Trends in dressed carcass weight using ANOVA to control for the effects of sex and age from 536 white-tailed deer weighed at hunter check stations, 1989-2001. Data were pooled for hunting districts 101 and 102.

dressed weights for yearlings were 47.4 kg (104.5 lb) for males and 42.5 kg (93.7 lb) for females.

Kidney fat index.—The kidney fat index (KFI), as determined from a sample of 29 deer, varied seasonally (Table 4.9) in a manner similar to that of whole weights (Table 4.8). No samples were available during late October through November, a period in which we would expect deer to rapidly accumulate body fat. However, two samples for winter, both adult females collected in early January, suggested that the KFI among adult females probably peaked during the early winter period. Comparison of these data with those from the lower Yellowstone River (Dusek et al. 1989) and the Long Pines (Dusek 1987) suggested that adult females might come through winter in poorer condition than their counterparts in eastern Montana and also were slower in recovering body fat through early fall.

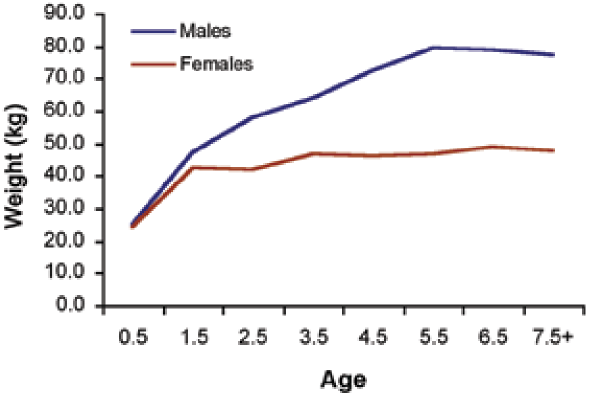


Figure 4.6. Dressed weight by age and sex for 536 white-tailed deer from hunting districts 101 and 102 weighed at hunter check stations, 1988-2001.

Skeletal Growth

We used the length of the diastema among deer examined at hunter check stations as an index of skeletal growth assuming a direct relationship between nutritional condition and skeletal growth within sex and age classes (Reimers 1972). ANOVA indicated that length of the diastema differed by sex, age, and among years ($P < 0.01$) but did not differ between hunting districts ($P > 0.050$). Diastema length declined from 1993 to 1994 then increased through 1997 (Fig. 4.7); the low point in diastema

Table 4.9. Mean seasonal kidney fat indices (KFI, %) by sex and age, of white-tailed deer from the Salish Mountains, 1989-1991, the lower Yellowstone River (LYR; Dusek et al. 1989), 1980-1986, and the Long Pines (Dusek 1987), 1976-1979.

Sex and age (yrs)	Summer		Autumn		Winter		Spring	
	n	$\bar{x}$	*n*	$\bar{x}$	*n*	$\bar{x}$	*n*	$\bar{x}$
Fawns[1]								
Salish Mts	1	10	2	23			1	10
LYR			15	56	11	58	11	23
Long Pines			6	70	2	49	15	18
Females								
1 yr								
Salish Mts	3	20					1	10
LYR	6	46	5	129	7	162	7	48
≥ 2 yrs								
Salish Mts	5	12	4	60	2	170	3	6
LYR	10	43	17	99	17	118	17	53
Long Pines[2]	4	23	9	115	12	59	13	25
Males								
1 yr								
Salish Mts	3	21	2	92			1	5
LYR	4	29	10	141	12	52	3	30
≥ 2 yrs								
Salish Mts	1	13						
LYR	1	16	6	159	6	68	2	21
Long Pines[2]	2	26	16	187	3	20	2	11

[1] Both sexes of fawns were combined.

[2] Long Pines sample includes all deer ≥ 1 yr.

length in 1994 coincided with that for dressed carcass weight.

We observed a significant correlation ($r = 0.79$, $P < 0.05$) between the diastema and field-dressed carcass weight of 483 deer from hunting districts 101 and 102 that were examined at hunter check stations. However, dressed carcass weights were highest during 1995 at a time when diastema length second lowest recorded during the study (Figs. 4.5 and 4.7). Diastema lengths increased from 1996 through 1998 when dressed carcass weights remained relatively stable.

The period of rapid skeletal growth, as with body mass, occurred during the first 18 months for both sexes (Figs. 4.6 and 4.8). Skeletal growth continued at least though 8 years of age for both sexes but at a lower rate for females. Body mass among females, as expressed by field-dressed carcass weights, appeared to level off at about 3 years of age but increased until at least 8 years of age for males. Yearly variation in diastema length among males of 2 and 3 years of age followed the pattern observed for yearling males (Fig. 4.9). For example, years of relatively low skeletal growth for yearlings were also poor growth years for 2 and 3 year-olds.

Antlers

Antler points.—The number of points/side among antlered white-tailed deer in the Salish Mountains increased with age through 7 years (Table 4.10). Without including brow tines, the proportion of males carrying antlers with ≥ 4 points/side increased from 4% for 2-year-olds to 59% for 7-year-olds. Among the sample >7 years ($n = 49$), 51% carried antlers with ≥ 4 points/side. Among males of ages ≥7 years, about 98% carried antlers with ≥3 points/side.

About half the yearling males examined

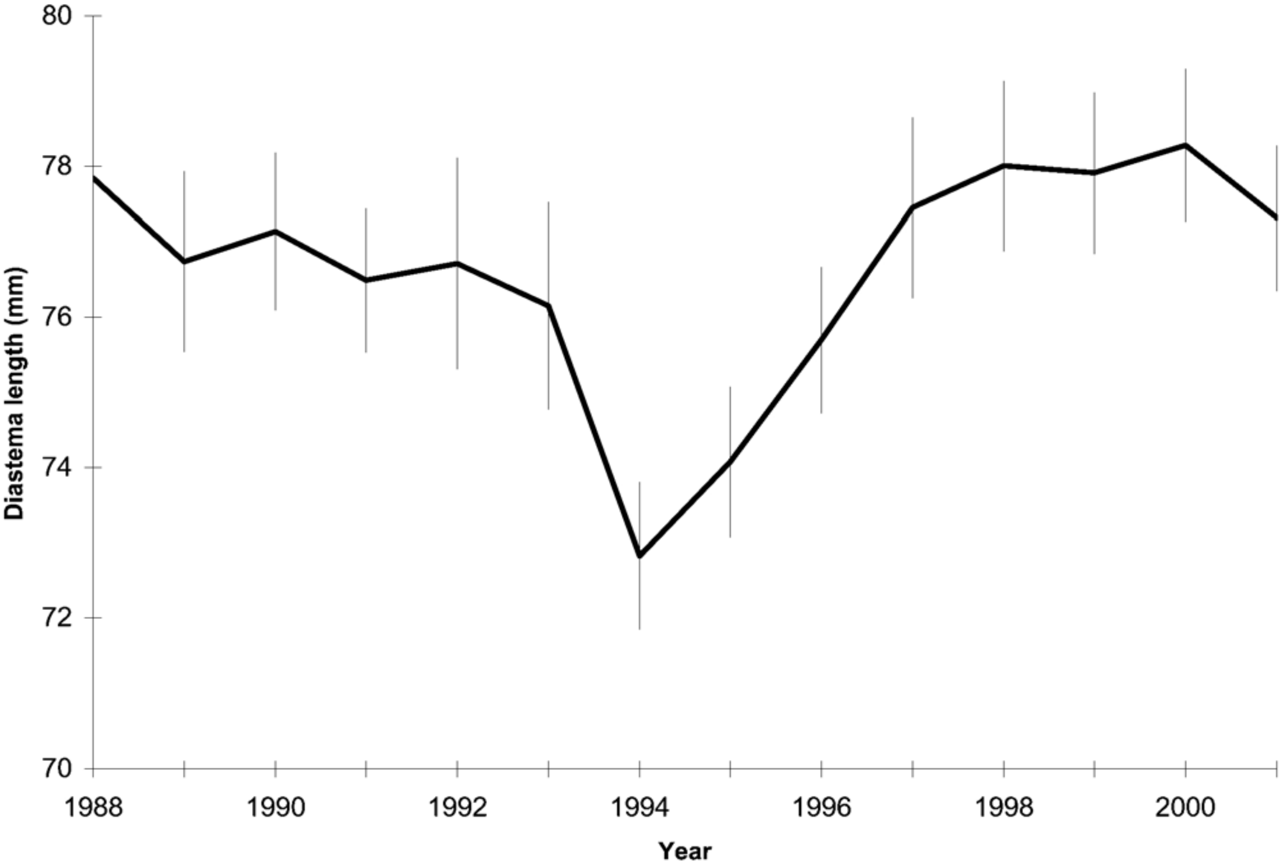


Figure 4.7. Trends in diastema measurement (mm) using ANOVA to control for the effects of sex and age from 3877 white-tailed deer examined at hunter check stations, 1988-2001. Data were pooled for hunting districts 101 and 102.

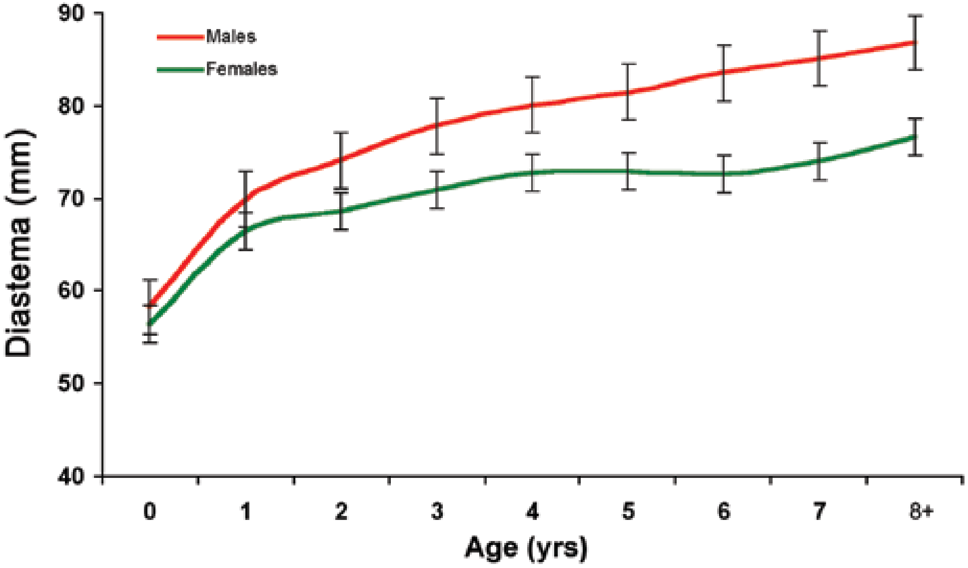


Figure 4.8. Diastema length by sex and age for 3877 white-tailed deer examined at check stations from combined hunting districts 101 and 102, 1988-2001. Vertical bars represent $\bar{x}$ ± 1 SE.

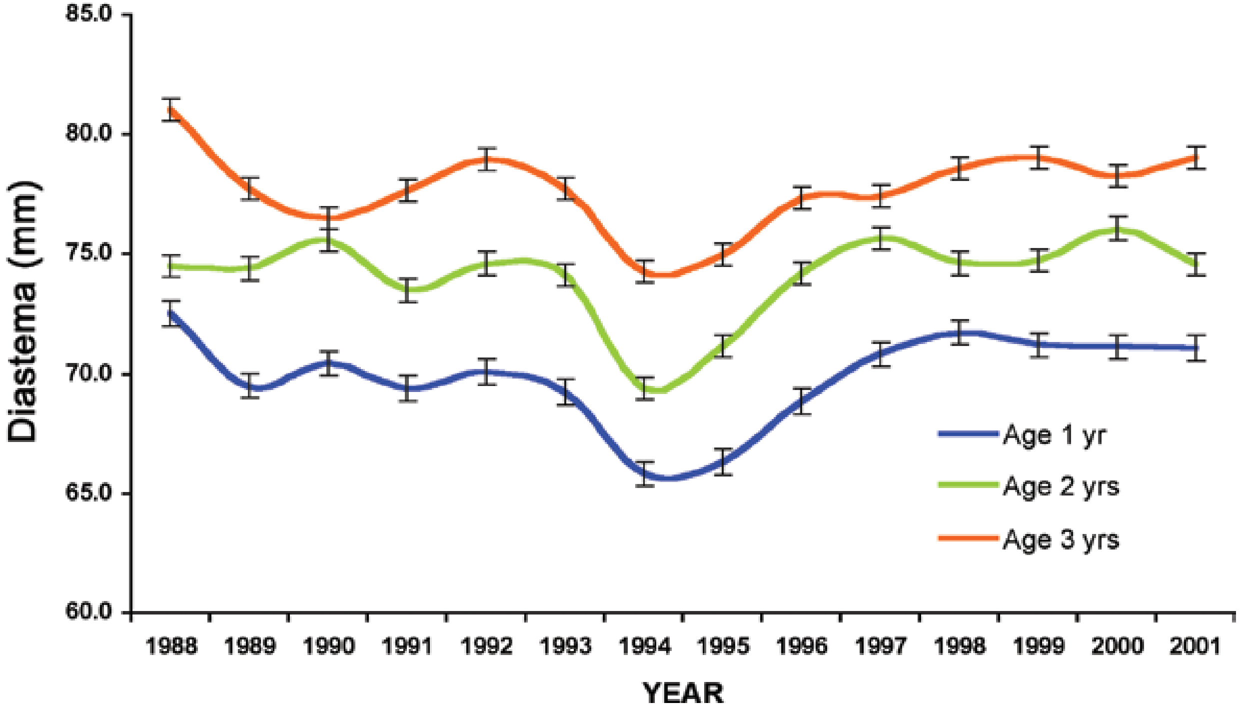


Figure 4.9. Trend in length of diastema for male white-tailed deer of ages 1 through 3 years from data pooled for hunting districts 101 and 102, 1988-2001. Vertical bars represent $\bar{x} \pm 1$ SE.

at hunter check stations were "spikes" (Table 4.10)—an unbranched main beam. The proportion of all yearling males bearing spike antlers varied (23-84%) among years with the highest percentages occurring in 1995 and 1997 and the lowest in 1998 (Table 4.11). ANOVA indicated the average number of points/side for yearling males, including brow tines, differed among years ($P < 0.01$; Fig. 4.10) but did not differ between hunting districts ($P > 0.050$). Dusek et al. (1989) reported an overall lower incidence of spike antlers among yearling males on the lower Yellowstone than that observed in the Salish Mountains

Antler measurements.—We observed a relationship between three measurements of antler growth—main beam length, maximum inside spread, and maximum beam diameter—and age (Fig. 4.11). Antler dimensions increased in a curvilinear fashion at least through 8 years of age. Reducing the model to include only animals ≥ 6 years still suggested that age accounted for >90% of the variation in antler growth. ANOVA indicated that average main beam length differed by age and among years ($P < 0.01$) but did not differ between hunting districts ($P > 0.050$). Average main beam length declined from 1988 through 1997 and increased in 1998 and 1999 (Fig. 4.12).

Aside from age, environmental factors as they affect forage availability or quality explain most observed variation in antler characteristics in white-tailed deer, particularly among yearling males (French et al. 1956, Lukefahr and Jacobson 1998). Hamlin and Mackie (1989) reported that antler characteristics accurately reflected forage conditions for mule deer during years of extreme environmental conditions. The combined effects of female density and precipitation during the immediate past autumn-spring period (Sep, Oct, Apr, and May) explained most observed variation in main beam length for yearling male white-tailed deer on the lower Yellowstone River in eastern Montana (Dusek et al. 1989).

Body mass and skeletal and antler growth.—We observed a generally consistent pattern between average main beam length number of points/antler for yearling males (Figs. 4.10 and 4.12). Those measurements were high in 1988, low from 1995 to 1997, increased sharply to 1998, and generally declined to 2001. This contrasted with body mass and diastema length of which both reached minimum observed values one year prior to antler measurements (1994). Antler measurements remained low through 1997 while diastema length and dressed carcass

Table 4.10. Antler point characteristics for 2502 antlered white-tailed deer from the Salish Mountains (HDs 101 and 102) from which both antlers were present, 1988-2001.

Antler points[1]	Age (yrs)[2]							
	1 (1004) [3]	2 (698)	3 (323)	4 (177)	5 (118)	6 (80)	7 (54)	≥ 8 (49)
1X1	50.9[4]	0.4						
1X2	14.3	2.1	0.3					
1X3	0.4	0.6	0.3					
1X4			0.3		1.7			2.0
2X2	28.4	19.3	1.5	1.1	0.8			
2X3	3.6	14.2	6.2	2.3	5.9	1.3		
2X4		0.1	0.3					
3X3	2.4	56.0	60.4	50.8	33.9	35.0	29.6	24.5
3X4		3.6	12.7	14.7	16.1	18.8	11.1	22.4
3X5			0.6	1.1	0.8			
4X4		3.3	15.5	23.7	31.4	33.8	38.9	26.5
4X5			0.3	3.4	7.6	6.3	11.1	12.2
4X6					0.8			
5X5			1.5	1.1	0.8	3.8	3.7	6.1
5X6		0.1		0.6		1.3	1.9	2.0
≥6 points/side		0.1		1.1			3.7	4.1

[1] Brow tines are excluded from number of points.

[2] Sample includes animals for which age was known or assigned by cementum analysis.

[3] Number in sample (*n*) for each age class.

[4] Expressed as a percent of *n* for each age class.

Table 4.11. Percent of spikes among yearling male white-tailed deer from the Salish Mountains examined at hunter check stations, 1988-2001.

	Year													
	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
n	31	44	72	63	57	56	66	62	66	25	64	149	150	99
Spikes w/o br tine	29.0[2]	54.5	27.8	57.1	40.4	57.1	33.3	79.0	51.5	84.0	23.4	30.2	37.3	50.5
Spikes w/ br tine	12.9	11.4	11.1	1.59	15.8	8.93	7.58	4.84	9.09	0	4.69	6.04	5.33	9.09
Total spikes	41.9	65.9	38.9	58.7	56.1	66.1	40.9	83.9	60.6	84.0	28.1	36.2	42.7	59.6

[1] The sample came from hunting districts 101 and 102.

[2] Expressed as a percent of all yearlings in any given year.

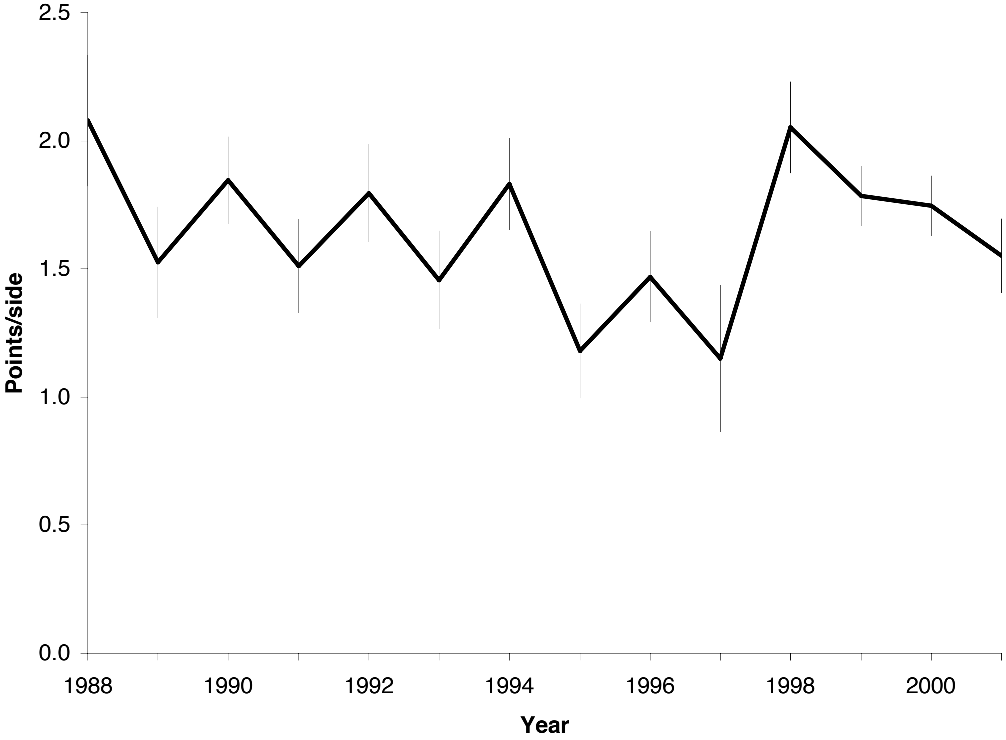


Figure 4.10. Yearly means for all points per side, including brow tines, from 1003 yearling male white-tailed deer in which both antlers were available, 1988-2001. Data were pooled for hunting districts 101 and 102.

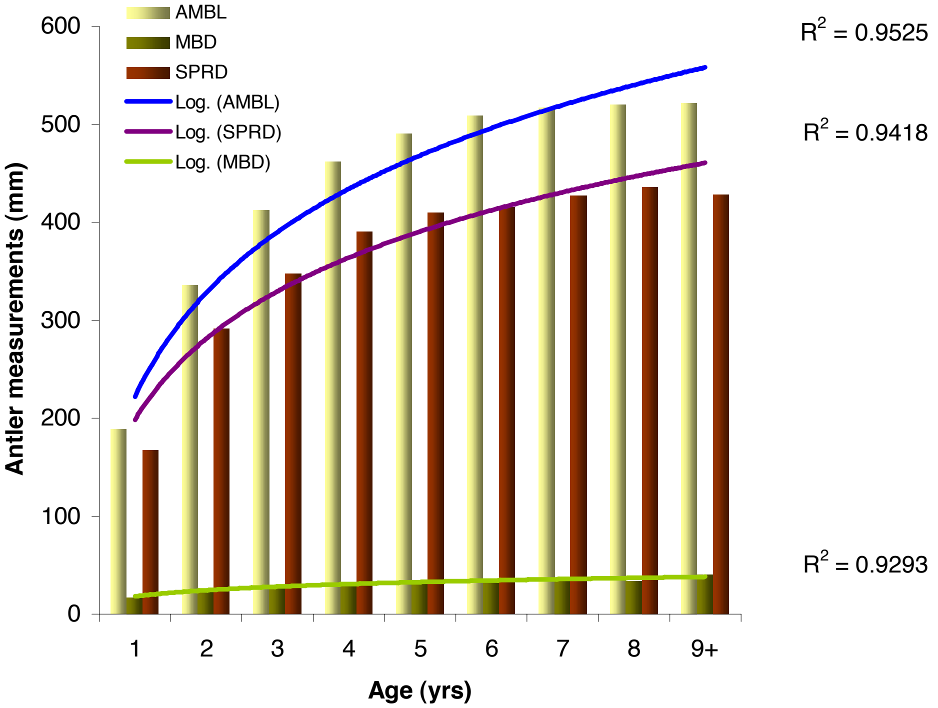


Figure 4.11. Antler measurements including average main beam length (AMBL), main beam diameter (MBD), and maximum inside spread (SPRD) for 2502 males of ages ≥ 1 year that were measured at hunter check stations from hunting districts 101 and 102, 1988-2001.

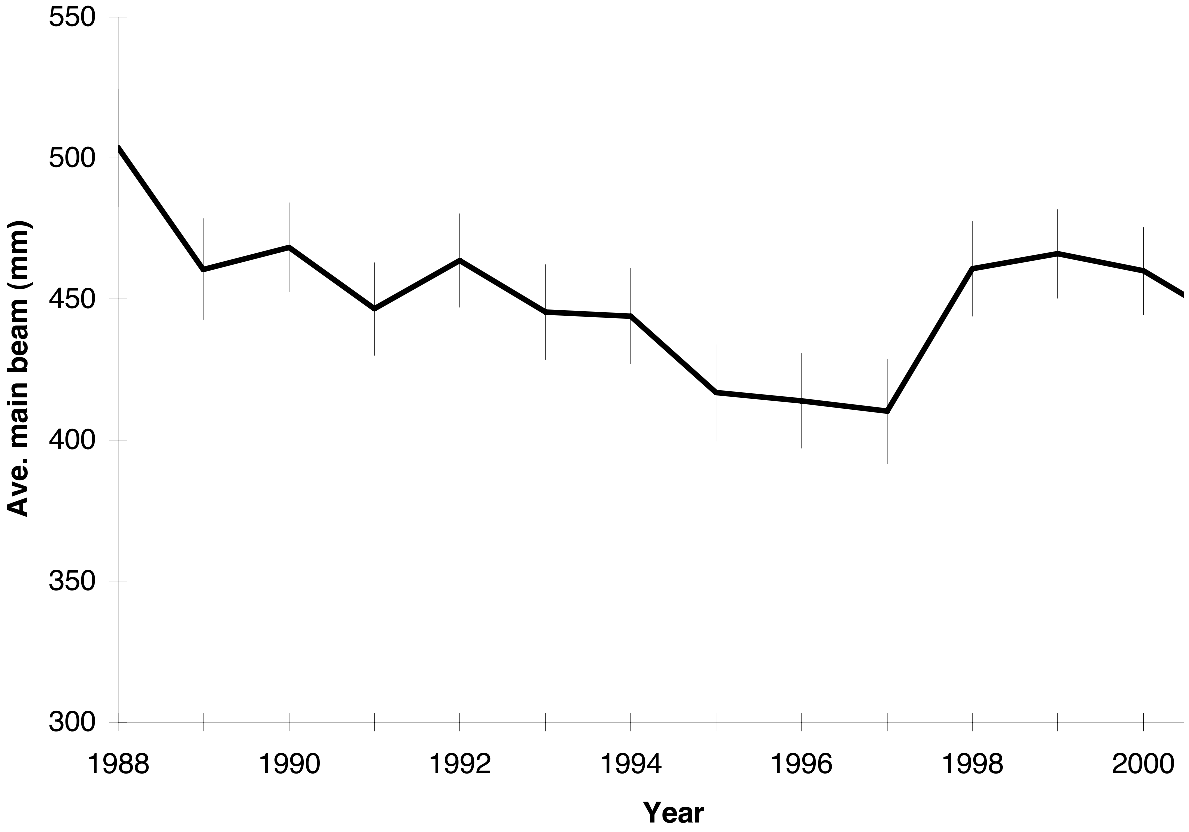


Figure 4.12. Yearly means for average main beam length using ANOVA to control for the effects of age from 2402 male white-tailed deer examined at check stations from which both antlers were available, 1988-2001. Data were pooled for hunting districts 101 and 102.

weights increased. These patterns conflict with published literature that suggests that skeletal growth takes priority over antler growth (e.g., Reimers 1972). For these populations, cumulative effects and/or time lags affecting any or all of these indices may have masked any meaningful relationship between antler and body growth.

Population Numbers And Density

Population Estimates and Trends

Population reconstruction from harvest records.— Deer numbers in hunting district 101 declined from 1988 through 1995 (β = -652.15, $t_{0.05(2),\,6}$ = -5.52, P = 0.001) and stabilized through 1999 (β = -683.98, $t_{0.05(2),\,6}$ = -1.70, P = 0.189; Fig. 4.13). Numbers of deer in hunting district 102 remained somewhat stable during 1988-1995 (β = 422.69, $t_{0.05(2),\,2}$ = 1.32, P = 0.245) and then seemingly declined from 1995 to 1999 (β = -2032.56, $t_{0.05(2),\,2}$ = -2.29, P = 0.106; Fig. 4.13). Populations in each hunting district reached a low point during autumn 1997 and appeared to increase from that point—but more so in hunting district 102.

Although dynamics of the two populations appeared to function differently through the period of study (autumn 1988 through autumn 1999; Fig. 4.13), both populations declined over the entire period. The finite rate of population change (λ) from 1988 to 1999 was 0.41 for hunting district 101 and 0.54 for hunting district 102. The observed trend in total population numbers in each hunting district mirrored that within the adult female segment ($\geq$ 1 yrs). The calculated adult sex ratios (Tables 4.1 and 4. 2) from which female numbers were estimated probably underestimated females relative to males in the respective populations during the latter years of the study because it takes the female segment 4 or more years longer than males to

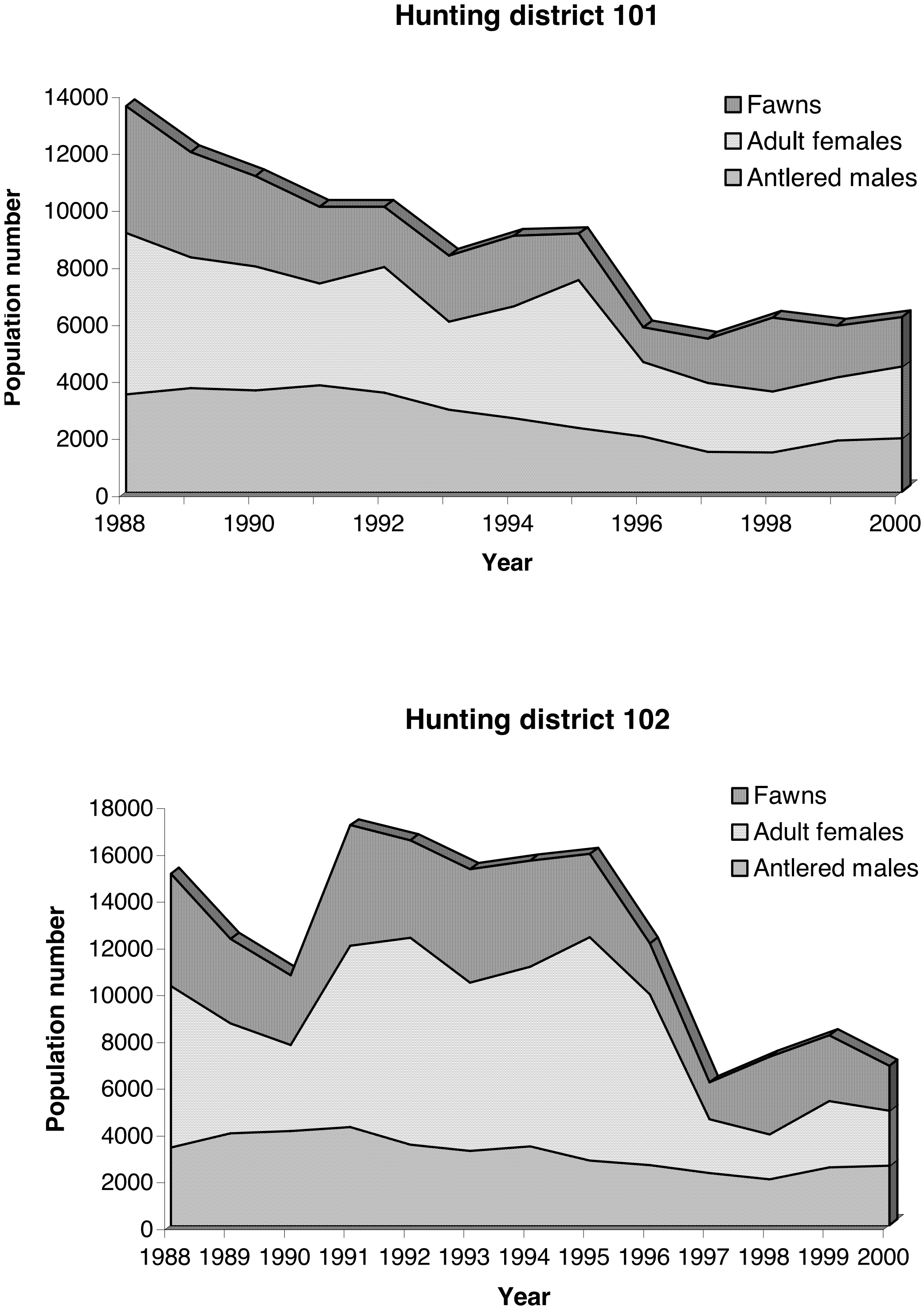


Figure 4.13. Annual estimates of white-tailed deer in hunting districts 101 and 102 by reconstructing populations from check station records and antlered harvest from the statewide hunter harvest survey, 1988-2003.

Table 4.12. Cumulative proportion that annual harvest of antlered white-tailed deer contributed to completion of each cohort. Only years beyond which at least 11 subsequent years of data were available were used—a period in which we could completely recover the entire cohort.

HD 101

	Cohort year[1]						
Age at harvest	1987	1988	1989	1990	1991	1992	$\bar{x}$
1	0.40[2]	0.29	0.30	0.30	0.32	0.37	0.33
2	0.64	0.53	0.61	0.69	0.62	0.69	0.63
3	0.79	0.71	0.75	0.85	0.78	0.90	0.80
4	0.86	0.85	0.88	0.93	0.86	0.97	0.89
5	0.92	0.90	0.96	0.95	0.92	0.97	0.94
6	0.97	0.96	0.98	0.98	0.96	0.99	0.97
7	0.99	0.99	1.00	0.98	0.97	1.00	0.99
8	0.99	1.00	1.00	0.99	0.97	1.00	0.99
9	1.00	1.00	1.00	1.00	0.99	1.00	1.00
10	1.00	1.00	1.00	1.00	0.99	1.00	1.00
11	1.00	1.00	1.00	1.00	1.00	1.00	1.00

HD 102

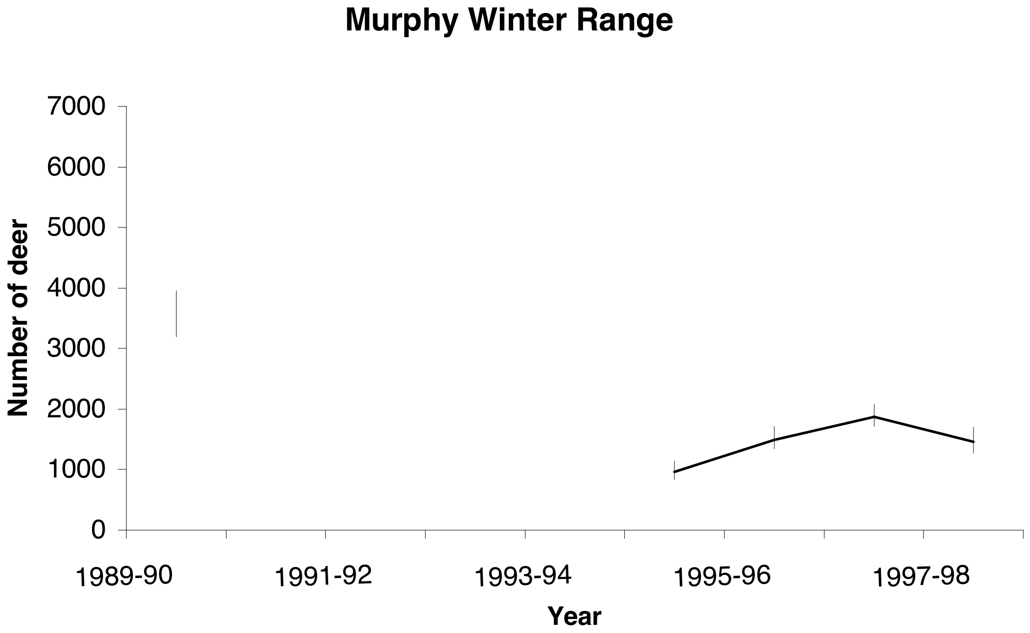
	Cohort year						
Age at harvest	1987	1988	1989	1990	1991	1992	$\bar{x}$
1	0.46	0.34	0.37	0.29	0.48	0.54	0.41
2	0.72	0.55	0.70	0.62	0.65	0.71	0.66
3	0.78	0.76	0.90	0.79	0.85	0.89	0.83
4	0.87	0.90	0.90	0.92	0.90	0.92	0.90
5	0.87	0.95	0.94	0.92	0.93	0.93	0.92
6	0.93	0.98	0.99	0.96	0.96	0.98	0.97
7	0.96	0.98	0.99	0.98	0.99	0.98	0.98
8	1.00	1.00	0.99	0.99	1.00	0.99	0.99
9	1.00	1.00	0.99	1.00	1.00	1.00	1.00
10	1.00	1.00	1.00	1.00	1.00	1.00	1.00
11	1.00	1.00	1.00	1.00	1.00	1.00	1.00

[1] Year of birth of the male cohort (year class).

[2] The proportion of all individuals (n) alive in year$_t$ estimated to have died from both hunting and nonhunting sources of mortality by year$_{t+1}$ prior to the onset of hunting.

completely turn over. For example, our estimates of female numbers for 1998 and 1999 would increase noticeably if we incorporated harvest records beyond 2003. Direct reconstruction of the male segment of both populations suggested that the total number of males present in the youngest cohort just prior to the onset of the hunting season during any given year declined by 90% in 4 years and by 99% in 7-8 years (Table 4.12; *see also* Fig. 4.21 in Survival/Mortality). Thus, we would expect these estimates to more reasonably reflect numbers of antlered deer in each hunting district through 1999 having calculated them from harvest data collected through 2003.

Camera surveys.—We computed population estimates for 9 years for Bowser and 5 years for Murphy using Monte Carlo simulations of mark-recapture data collected during remote camera surveys (Fig. 4.14). We detected no significant correlations between estimates from camera surveys and other indices of deer abundance ($P > 0.50$). Although estimates of numbers of deer on Bowser approximated those from pellet group surveys for 1990, 1997, and 1998 (Figs. 4.14 and 4.15), numbers estimated from camera surveys in 1991 and 1993-1996 averaged only 46% of estimates from pellet group surveys. During 1999,



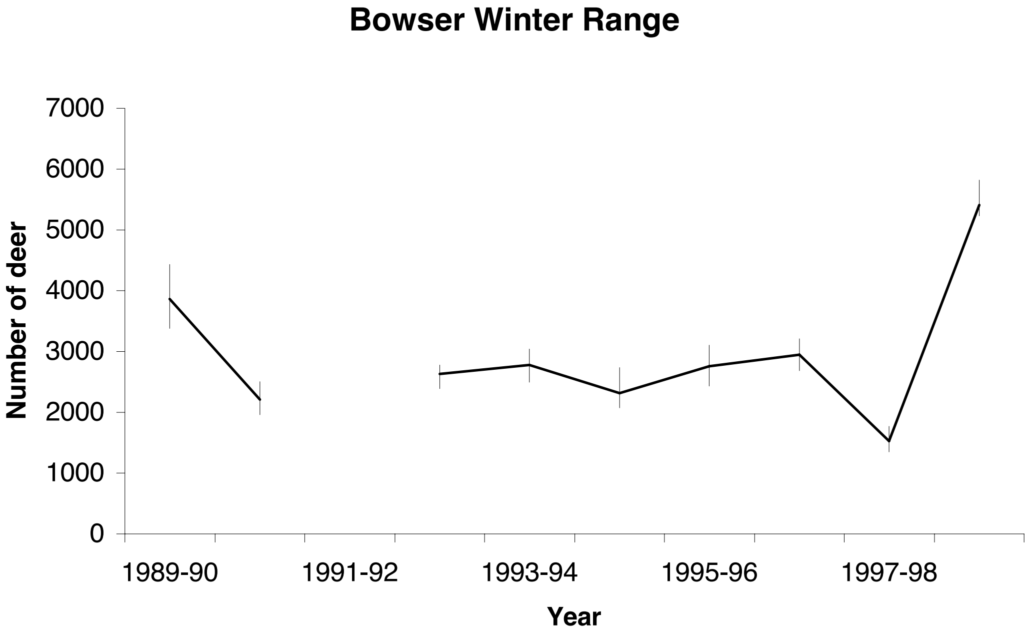
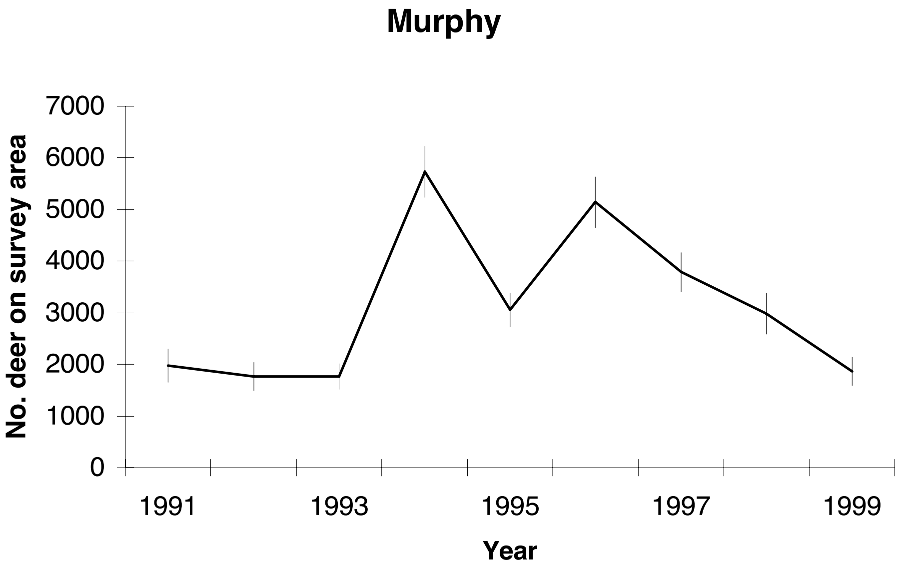


Figure 4.14. Annual estimates of white-tailed deer on the Bowser and Murphy winter ranges using mark-recapture data from camera survey (radio-collared deer) and a Monte Carlo simulation. Vertical bars represent 95% confidence limits.



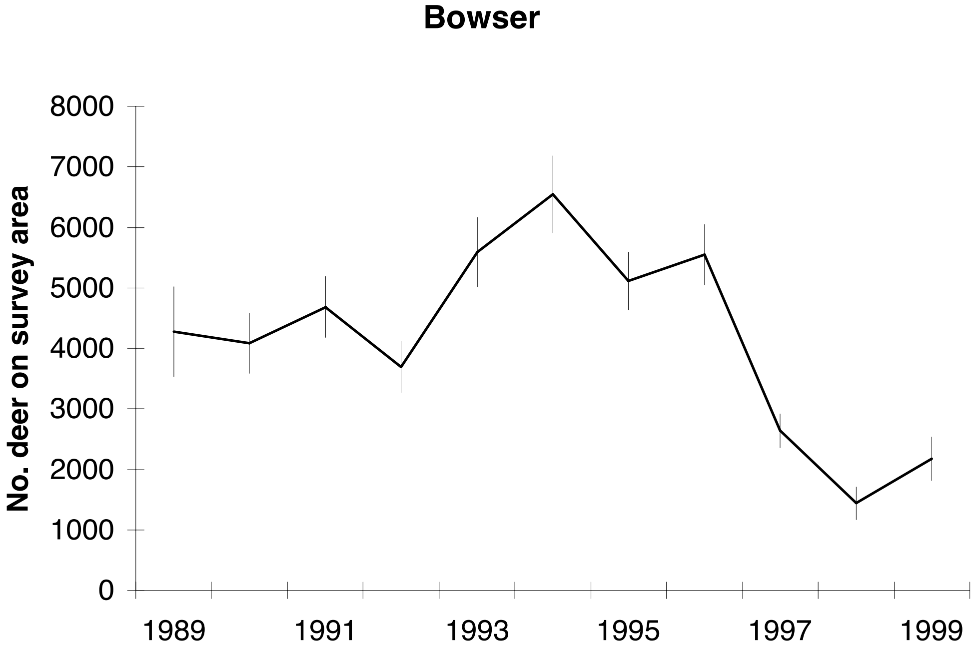


Figure 4.15. Annual estimates of white-tailed deer on the Bowser and Murphy winter ranges from spring pellet group surveys reflecting numbers of deer using the respective ranges during winter. Vertical bars represent 95% confidence limits.

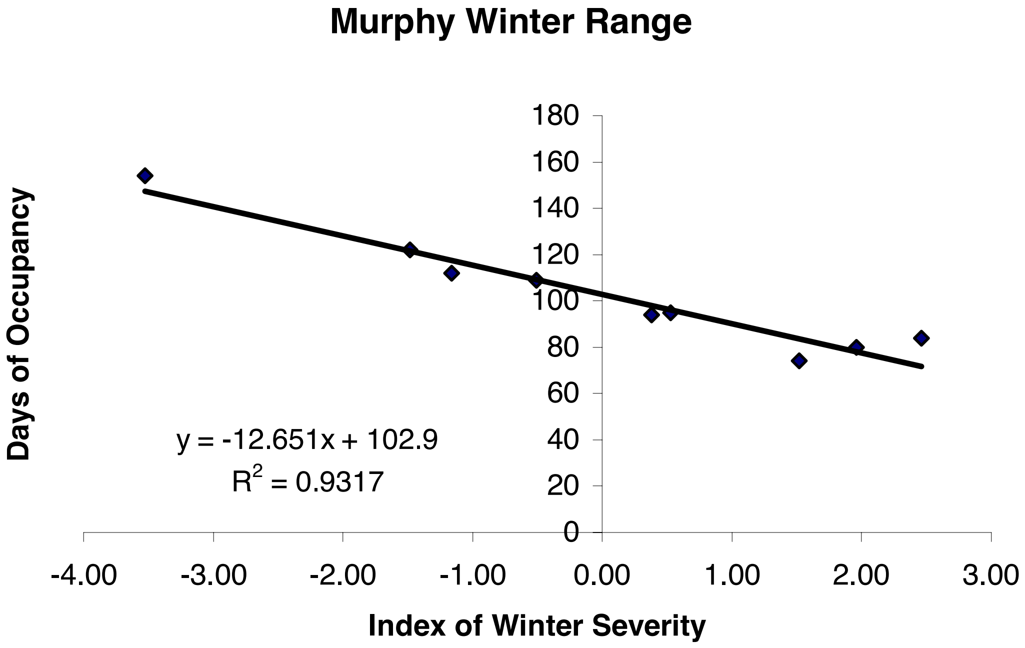
the estimate from the camera survey was 248% of that from the annual pellet group survey. For Murphy, the camera survey yielded an estimate that was 183% of the 1999 estimate from the pellet group survey and averaged 50% for the years 1996-1999.

The mark-recapture methodology we used considered multiple re-sightings that would improve precision of population estimates. However, several issues confound estimates from camera surveys to such an extent that they probably do not reflect real change in population numbers. First, we detected only a small proportion of radio-collared deer that occupied the winter ranges; an average of 15 ± 4% (95% CI) were re-sighted at Bowser and 11 ± 4% at Murphy. Second, a very low density of camera sites on our survey area (Jacobson et al. 1997) probably influenced the low rate of re-observation of available radio-collared deer. Most radio-collared deer detected by the cameras were only sighted once during any given survey. Third, analysis of data for 1990 and 1991 at Bowser (Dusek and Morgan 1991) indicated that total numbers of marked and unmarked deer detected/day by all cameras decreased with time from the beginning of the survey. Sime (1994) reported the same trend for 1993 and 1994, all of which suggests that triggering of camera units probably modified deer behavior in a way that caused most to avoid trails where cameras were located. Finally, the changes in project personnel on this study made it difficult to consistently reconcile the proportion of radio-collared deer occupying the surveyed portion of the winter range. Others (e.g., Janke 1977) have urged caution with regard to using mark-recapture techniques to estimate numbers of deer in coniferous forests of western Montana because the manner in which deer use winter ranges can make meeting the underlying assumptions difficult.

Pellet group surveys.—As with the mark-recapture estimates from camera surveys, we used pellet group surveys to estimate the number of deer that occupied the respective winter ranges (Fig. 4.15). Average pellet group density alone varies among years as demonstrated by Kunkel (1997). However, variation in mean pellet group density does not consider the length of time that seasonal migrants occupy winter ranges and therefore might not predictably reflect either the magnitude or direction of change in population size. The average number of days that radio-collared deer occupied the respective winter ranges varied from 74 to 154 days on Murphy and from 84 to 163 days on Bowser. Winter severity, based on an index (IWS) calculated for each winter range (Farnes et al. 2000), accounted for 93% of the variation in the number of days of winter range occupancy on Murphy and 66% of the variation on Bowser ($P \leq 0.002$; Fig. 4.16; see further discussion for Bowser later in this section). Thus, our estimates of deer numbers on the winter range incorporated both length of time that seasonal migrants occupied the respective winter ranges, as determined from radio-collared deer, as well as a standard defecation rate. We did not adjust these estimates to reflect the proportion of residual radio-collared deer associated with the respective winter ranges that had actually occupied it during the winter immediately preceding the survey because we lacked a reliable multiplier for some years. Thus, we emphasize that these procedures only reflect the number of deer within the respective populations that actually occupied the core winter range during a given year and underestimate the entire segment associated with these areas during winters in which some migrants did not return and occupied another part of their yearlong range. At Bowser, for example, maximum yearly occupancy increased with the IWS ($R^2 = 0.64$, $n = 9$, $P = 0.01$).

Correlations between estimates of deer numbers from pellet group surveys and other estimates of deer abundance (Fig. 4.17) either for Murphy or hunting district 101 were not significant ($P \geq 0.25$). Use of the area by mule deer for at least a portion of each winter might have masked any trend in whitetail numbers. General observations suggest that mule deer continued to use the winter range after most white-tailed deer left the area during March prior to pellet group counts in April.

Estimates of the number of deer from pellet group surveys on Bowser were significantly correlated with estimates from population reconstruction for hunting district 102 ($r = 0.77$, $n = 11$, $P < 0.01$) and with estimates of antlered harvest for hunting district 102 from the statewide harvest survey ($r = 0.69$, $n = 11$, $P = 0.02$; Fig. 4.17). A λ-value of 0.51 for estimates from pellet group surveys on Bowser suggested that a decline among numbers of deer associated with Bowser was of a magnitude similar to that observed for all of hunting district 102 (0.54) for which Bowser is a small part.



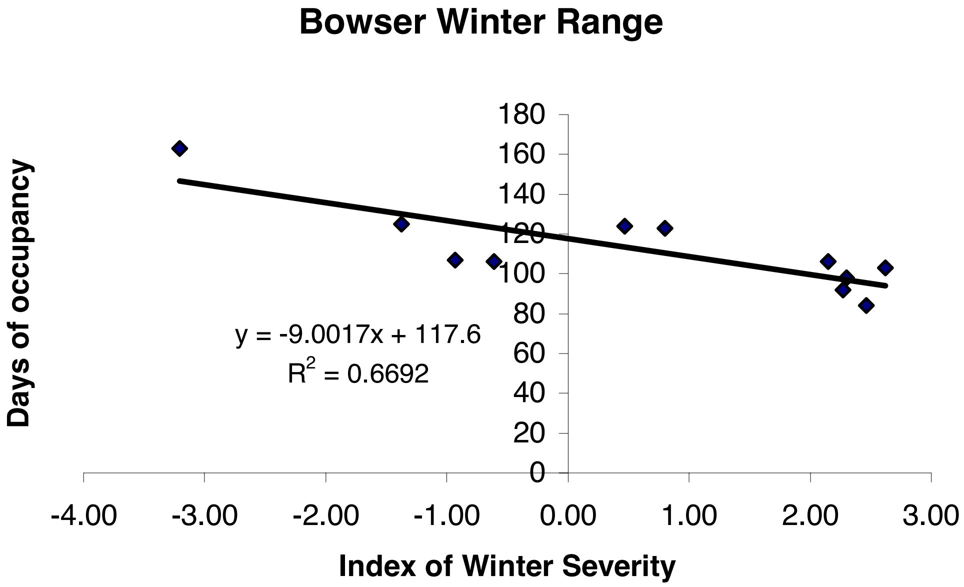
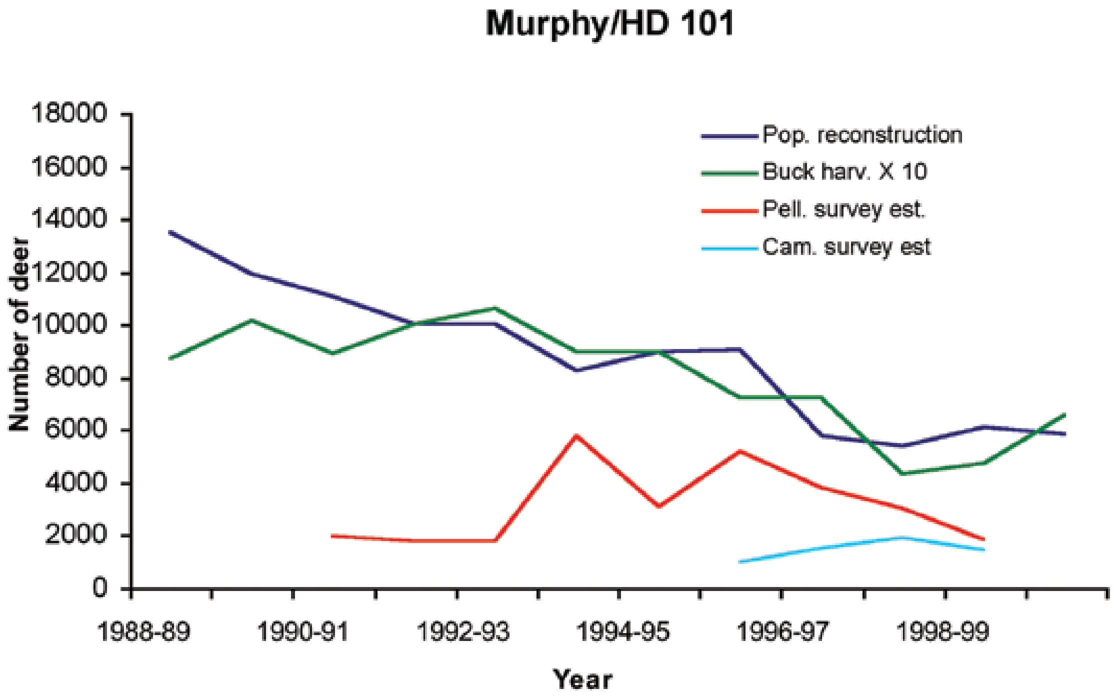


Figure 4.16. The average number of days that radio-collared deer occupied the respective winter ranges plotted against the Index of Weather Severity calculated for each winter range (Farnes et al. 2000) adjusted to utilize only temperature and snowpack.

Trends based on buck harvest.—Our results suggested that a trend in buck harvest from the statewide harvest survey reflected a general trend in total population numbers over time. Estimates of annual harvest of antlered deer in hunting districts 101 (r = 0.76, *n* = 12, *P* = 0.004) and 102 (r = 0.84, *n* = 12, *P* = 0.001; Fig. 4.17) varied directly with estimates of populations for the respective hunting districts that we calculated from population reconstruction. Additionally, estimates of buck harvest for hunting district 102 from the statewide harvest survey also varied directly with numbers of white-tailed deer occupying Bowser as



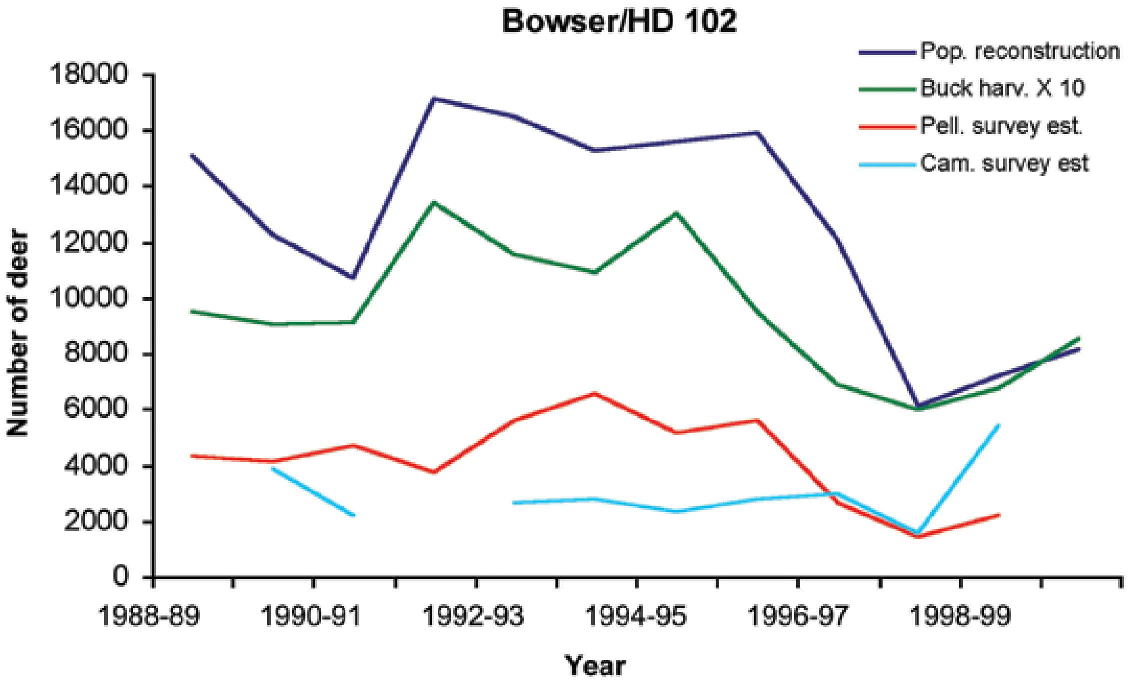
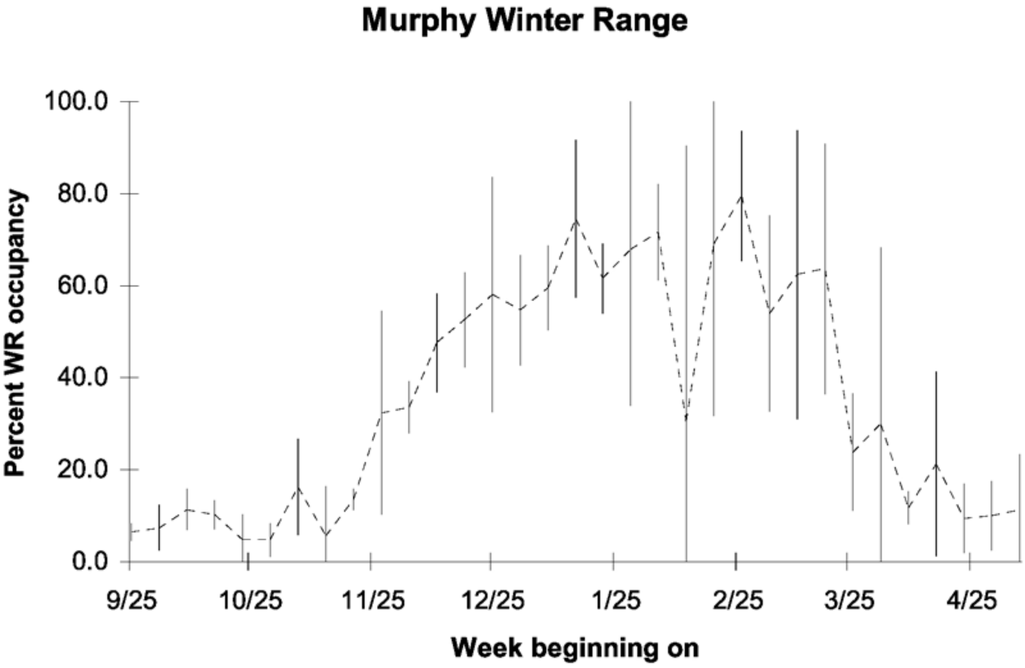


Figure 4.17. Population trend from camera and pellet group surveys, population reconstruction from harvest records, and antlered whitetail harvest from the statewide hunter harvest survey.



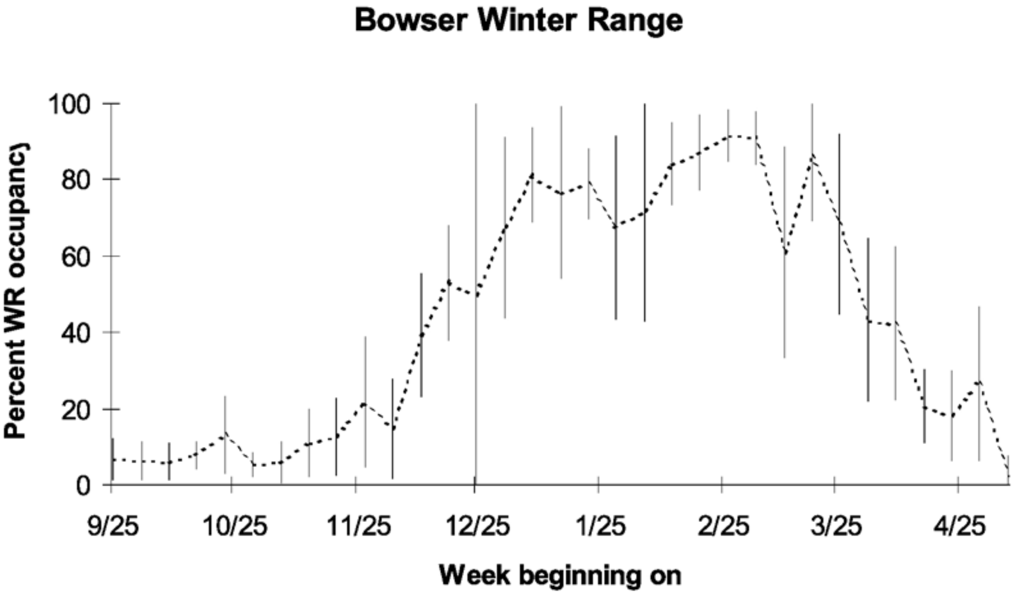


Figure 4.18. Mean weekly winter range occupancy from early October through mid May at Murphy and Bowser winter ranges, 1988-1989 through 1999-2000 with upper and lower 95% CI. Percent occupancy represents the proportion of all white-tailed deer associated with the winter range that actually occupied it during a given week as determined from radio-collared deer.

determined from pellet group surveys. Factors other than population size might affect buck harvest, and these will be discussed in another section of this report.

Use of total antlered harvest to estimate total numbers of antlered deer in each hunting district could have contributed to such a strong relationship. However, the contribution of one year's harvest to estimates of total abundance for that year would have been small because it took several years of harvest data to estimate the total number of individuals in each cohort during each year (Table 4.12). Estimating the total number of females ≥ 1 year and fawns from sex and age ratios using a separate procedure that did not consider total harvest estimates of antlered deer from the posthunt telephone survey should have further minimized opportunity for autocorrelation.

Population Density

Reconstruction of population numbers of white-tailed deer from harvest records yielded overall densities of 4 deer/km^2 (11/mi^2) in hunting district 101 and 8 deer/km^2 (21/mi^2) in hunting district 102. We calculated the amount of forest cover in each of the two hunting districts to determine if the relative amount of habitat differed in a way that might affect distribution and overall density of white-tailed deer. However, forest cover was actually greater in hunting district 101 where deer density was lowest.

Deer density across the entire hunting district 102 averaged 8 deer/km^2 (21/mi^2) and ranged from 11 to 4 deer/km^2 based on reconstructed population estimates. The winter range occupied approximately 2% of the total area within hunting district 102. However, an average of 32% (n = 11, $CI_{\alpha=0.05}$ = ± 4.5%) of estimated numbers of deer in hunting district 102 during autumn occupied Bowser during winter. Pellet group surveys yielded an average deer density of 130/km^2 (336/mi^2) and ranged from 45 to 205 deer/km^2 (116-530/ mi^2). The lowest calculated density coincided with low long-term population numbers and a relatively mild winter in which some deer did not return to the core winter range.

Effect of Winter Severity and Duration on Deer Use of Winter Ranges

Understanding how environmental variation might affect numbers of deer using winter ranges and the length of time that they occupy winter ranges are essential to using pellet group surveys to monitor population size and trend. We observed deer occupancy of winter ranges to vary both within and among years (Fig. 4.18). Movement onto each winter range was gradual beginning about the first week of December (Julian wk 49) and appeared to plateau by the 2nd to 3rd week in January. The segment of the respective populations that occupied each winter range remained there through late March (Julian wk 12). A slight increase in occupancy from January through March reflected trapping efforts on each winter range and not necessarily increases in the number of winter occupants. Exit from Bowser was steady from late March (Julian wk 12) until mid May (Julian wk 18). Deer occupancy on Bowser decreased by 50% from late March through Mid April (Julian wks 12-15). In contrast, occupancy of Murphy decreased by > 50% from the last week of March to the first week of April, whereas the remainder exited from the first week of April until mid May. Migratory deer with functioning radios spent an average of 112 days on Bowser each year (range = 84-163 days) compared to an average of 103 days at Murphy (range = 74-154 days).

Our analyses suggested that suitability of habitat composition and structure to ameliorate effects of temperature and snow accumulation were important determinants of deer use of the Bowser winter range. Annual variation in the duration and intensity of deer occupancy of the winter range varied with winter weather. The average number of days that radio-collared deer occupied the winter range reflects duration whereas average pellet group density reflects intensity of deer occupancy, i.e., proportion of all deer associated with a winter range that actually used it in a given year. This analysis only considers Bowser on which deer use consisted almost exclusively of white-tailed deer, whereas deer use on Murphy also included significant use by mule deer. Indices of duration and intensity appeared to represent independent components of winter range use because they were not correlated ($P > 0.50$) over the course of this study. The index of critical temperature (Farnes et al.

2000) varied inversely with annual average pellet group density on the winter range ($R^2 = 0.39$, $n = 11$, $P = 0.04$), but the scaled index of snow water equivalent (SWE) did not contribute to explaining annual variation of average pellet group density. Contrastingly, the average number of days spent on the winter range was only positively related to SWE ($R^2 = 0.80$, $n = 11$, $P = 0.001$) but not affected by critical temperature. However, the severe winter of 1996-1997 was the data point that resulted in these significant relationships. With that year excluded, neither temperature nor SWE were related to number of days spent on the winter range ($R^2 = 0.33$, $n = 11$, $P = 0.10$). Thus, habitat structure and composition on Bowser probably effectively ameliorated the adverse affects of snow and temperature on deer during all but the most severe winters compared to other areas that these deer used during winter throughout this study.

Population Dynamics

Reproductive Potential

Pregnancy rates.—We determined pregnancy rates from carcass collections and serum assay only during 1988-1991. Individuals that would have bred at an age of 5-6 months and would have given birth as yearlings potentially contributed only a negligible portion of annual reproduction (Table 4.13); 4 of 88 (5%) fawns for which reproductive status was determined from reproductive tracts (n = 4) and serum assay (n = 84) were pregnant. Of 244 females examined of ages ≥ 1 year (11 reproductive tracts, 232 serum samples), 235 (96%) were pregnant, a rate that Mundinger (1981) also reported for females of the same ages in the Swan Valley. Dusek et al. (1989) reported similar pregnancy rates for whitetails on the lower Yellowstone River in eastern Montana although rates varied between segments of the river bottom. We detected an age-related difference in pregnancy rates among adult (≥ 1 yr) females (Table 4.13). Pregnancy rates among females of ages 1 and 2 years at the time of breeding were lower than those of ages ≥ 3 years ($\chi^2 = 4.25$, 3df, $P = 0.039$). Of 21 carcasses from females examined during late winter and early spring 1997, 19 (90%) were pregnant.

Coefficients of variation for yearling and mature females (≥ 2 yrs) were 7 and 2%, respectively, for 1988-1991. Dusek et al. (1989) reported greater year-to-year variability in pregnancy rates among yearlings than older females for the lower Yellowstone—coefficients of variation were 16 and 5%, respectively.

Fetal rates.—Carcasses of eleven females of ages ≥ 2 years examined from 1989 to 1991 yielded a fetal rate of 142 fawns:100 pregnant females, which fell within but near the low end of the range reported for white-tailed deer across their inhabited range in North America. We observed a fetal rate/pregnant mature female in the Salish Mountains of 138 fawns:100 females during winter 1997 (Table 4.14). A sex ratio for during late winter-early spring 1997 for 25 collected fetuses (257 ♂♂ :100 ♀♀) significantly departed from a 50:50 ratio ($P = 0.028$). Research on penned deer has demonstrated that pregnancy and fetal rates reflect female condition at the time of breeding (Verme 1969). Assuming this later sample generally represented the reproductive

Table 4.13. Age-specific pregnancy rates among 332 female white-tailed deer in the Salish Mountains from serum assay and carcass collections, 1988-1991.

	Age (yrs)											
	0		**1**		**2**		**3**		**4-7**		**≥8**	
Year	% preg.	(*n*)	% preg.	(*n*)	% preg.	(*n*)	% preg.	(*n*)	% preg.	(*n*)	% preg.	(*n*)
1988	0	(11)	100	(3)	100	(3)	100	(5)	100	(4)	100	(1)
1989	11	(28)	100	(15)	89	(18)	100	(13)	94	(18)	100	(14)
1990	4	(26)	86	(14)	94	(16)	92	(12)	100	(15)	100	(9)
1991	0	(23)	95	(19)	95	(20)	100	(18)	100	(15)	100	(12)
All years	5	(88)	94	(51)	93	(57)	98	(48)	98	(52)	100	(36)

[1] Data were collected during winter and spring following the breeding season.

Table 4.14. Reproductive potential for white-tailed deer across their range in North America.

	Ovulation rate		**Pregnancy rate**		**Fetal rate**		
Geographical Location	**Yearling**	**Mature**	**Yearling**	**Mature**	**Yearling**	**Mature**	**Source**
Southeast							
Florida					1.14	1.32	Richter and Labisky (1985)
Southwest							
South Texas					1.32	1.59	Barron and Harwell (1973)
Llano Basin, Texas	1.27	1.56			0.75	1.08	Teer et a1. (1965)
Coastal Texas						1.57	White (1973)
Midwest							
Iowa	2.36	2.23			2.00	2.23	Haugen (1975)
Illinois	1.93	2.24			1.76	1.94	Roseberry & Klimstra (1970)
N. Gr. Plains							
L. Yellowst. R., Montana	1.41	2.09	0.91	0.98	1.26	1.88	Dusek et al. (1989)
Long Pines, Montana						1.80	Dusek (1987)
N. Rocky Mts.							
Idaho	1.50	2.09			1.50	1.88	Will (1973)
Swan Valley, Montana	1.30	1.95			1.25	1.64	Mundinger (1981)
Salish Mts, Montana			0.94	0.97		1.38	This study (1988-1991 and 1997)
Canada							
Ontario	1.21	1.74			0.82	1.31	Mansell (1974)

status of breeding-age females in our study areas, rates observed among this later sample would not have resulted from the severe winter of 1996-1997 but rather the growing season preceding that winter.

Fetal rates that we observed among adult females in the Salish Mountains (Table 4.14) were lower than those reported for the Swan Valley (Mundinger 1981) and Idaho (Will 1973). Given that the earlier sample coincided with a period of relatively high density for both populations and the later sample coincided with a period of population decline and low condition indices, these data might reflect reasonable estimates of fetal rates for the Salish Mountains. Comparative age-specific data indicated lower average fetal rates in the Swan Valley among the most productive age classes of females (2-6 yrs) than those for the lower Yellowstone River (Mackie et al. 1998); fetal rates of yearling and older adult females ($\geq$ 7 years) were about the same in both areas.

Survival/Mortality

General patterns of survival.—Population reconstruction yielded estimates of survival (1 Sep-31 Aug) among deer of ages > 3 months for the combined hunting districts (101 and 102) varying from 46 to 88% during years beginning in 1988-1999 (Table 4.15). This method suggested that the lowest rate of overall survival occurred during 1996-1997, which included the most severe winter on record. Reconstruction of populations from harvest records yielded average annual survival rates of 67% for hunting district 101 and 68% for hunting district 102. However, yearly trends in survival from reconstruction varied somewhat between hunting districts ($r = 0.30$, $P > 0.05$; Fig. 4.19).

Annual survival of females $\geq$ 1 year of age exceeded that of males among the same age

Table 4.15. Annual survival from population re-construction of white-tailed deer in the Salish Mountains in northwest Montana, 1988-1999.

	Year													
	1988[2]	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	$\bar{x}$	SD
Total	0.59	0.65	0.88	0.74	0.62	0.75	0.80	0.58	0.46	0.65	0.69	0.65	0.67	0.11
Fawns	0.64	0.70	1.00	0.84	0.70	0.85	0.89	0.74	0.59	0.78	0.79	0.78	0.77	0.11
Females														
1-yr	0.54	0.61	0.94	0.84	0.60	0.77	0.90	0.54	0.43	0.47	0.72	0.62	0.67	0.17
2-5 yrs	0.51	0.59	1.02	0.76	0.60	0.84	0.95	0.57	0.30	0.56	0.69	0.62	0.67	0.20
≥ 6 yrs	0.53	0.68	1.06	0.86	0.69	0.81	0.70	0.52	0.41	0.54	0.68	0.67	0.68	0.18
Males														
1-yr	0.54	0.66	0.63	0.71	0.52	0.46	0.48	0.67	0.61	0.80	0.62	0.60	0.61	0.10
2-5 yrs	0.67	0.83	0.80	0.51	0.57	0.67	0.50	0.59	0.74	0.63	0.50	0.40	0.62	0.13
≥ 6 yrs	1.00	1.00	0.33	0.00	0.75	0.45	0.28	0.39	0.51	0.46	0.52	0.47	0.51	0.29

[1] Data, from hunter check station during 1988-2003, were pooled for HDs 101 and 102 ; data represent survival from about 1 Sep to 31 August.
[2] Year representing t_0 with the following year representing t_{+1}.

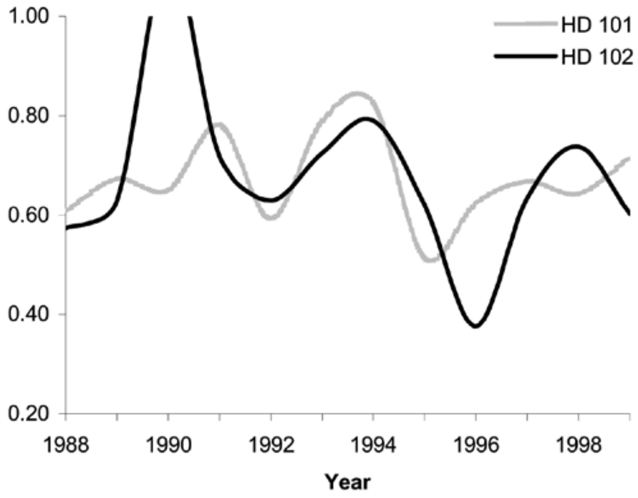


Figure 4.19. Estimates of annual survival of white-tailed deer of all sex and age classes in hunting districts 101 and 102 from reconstruction of annual populations based on harvest records, 1988-2003.

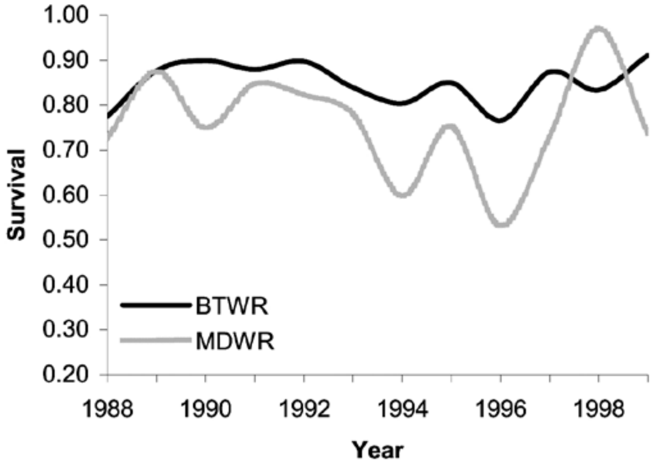


Figure 4.20. Annual survival of radio-collared mature (≥ 2 yrs) female white-tailed deer (Kaplan-Meier estimator) associated with Bowser and Murphy from 1988-1989 through 1998-1999

classes (Table 4.15) but estimates from population reconstruction demonstrated less disparity between sexes in some years and the mean for all years. Issues of longevity between the sexes and incomplete female cohorts as discussed earlier all probably contributed to underestimating female survival at least during the latter years of this study.

We observed a more stable rate of survival (June-May) among radio-collared females ≥ 2 years of age during years ending in 1989-2000 than from population reconstruction (Tables 4.15 and 4.16, Figs. 4.19 and 4.20). Coefficients of variation for females of ages ≥ 2 year among year were 8% for radio-collared deer and 27% from population reconstruction. Mean survival as determined from the Kaplan-Meier estimator for the entire period of study was higher than that resulting from population reconstruction.

Annual survival of radio-collared mature females (≥ 2 yrs) differed with respect to study area and year (Table 4.16). Chi-square

Table 4.16. Annual survival (Jun-May) of radio-collared adult female white-tailed deer associated with the Bowser and Murphy winter ranges in northwest Montana using the Kaplan-Meier estimator, 1988-1999.

		1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	$\bar{x}$	SD
								Bowser							
2-5 yr fem															
	n[1]	26	33	41	42	31	31	29	26	39	33	20	10		
	$\hat{S}(T_j)$[2]	0.857	0.968	0.921	0.897	0.887	0.880	0.804	0.906	0.757	0.749	1.000	0.771	0.866	0.082
	Var[$\hat{S}(T_j)$][3]	0.017	0.001	0.002	0.002	0.004	0.004	0.008	0.004	0.008	0.008	0.000	0.021		
≥ 6 yr fem															
	n	9	12	14	20	23	15	13	12	22	28	31	28		
	$\hat{S}(T_j)$	0.583	0.583	0.840	0.842	0.957	0.750	0.800	0.727	0.777	1.000	0.712	0.962	0.794	0.136
	Var[$\hat{S}(T_j)$]	0.063	0.025	0.011	0.007	0.002	0.017	0.032	0.018	0.014	0.000	0.008	0.001		
								Murphy							
2-5 yr fem															
	n	10	12	11	12	13	17	17	15	20	22	16	8		
	$\hat{S}(T_j)$	0.600	0.857	0.667	0.800	0.923	0.817	0.648	0.700	0.583	0.727	1.000	0.857	0.765	0.132
	Var[$\hat{S}(T_j)$]	0.048	0.017	0.025	0.016	0.005	0.009	0.020	0.021	0.020	0.018	0.000	0.017		
≥ 6 yr fem															
	n	7	10	11	11	11	9	7	6	15	21	21	22		
	$\hat{S}(T_j)$	0.857	0.889	0.818	0.900	0.500	0.667	0.500	0.800	0.514	0.728	0.950	0.697	0.735	0.162
	Var[$\hat{S}(T_j)$]	0.017	0.011	0.014	0.009	0.063	0.037	0.042	0.032	0.024	0.014	0.002	0.011		

[1] Number of radio-collared deer at risk during each time period—some individuals were in the sample ≥ 2 years.

[2] Kaplan-Meier survival estimate.

[3] Variance of the survival function—Greenwood's formula—(Pollock et al. 1989).

tests indicated that at least one of the annual survival rates differed among all mature radio-collared females ($\chi^2 = 68.99$, 47 df, $P = 0.02$) and specifically among those ≥ 6 years old ($\chi^2 = 40.16$, 23 df, $P = 0.015$). We detected no significant differences with respect to age class ($P \geq 0.092$). Differences with respect to year were not significant among ages 2-5 years for females associated with either winter range ($P \geq 0.33$). Survival rates differed slightly among females of ages ≥ 6 years at Bowser ($\chi^2 = 19.89$, 11 df, $P = 0.047$) and approached significance among females of those ages at Murphy ($\chi^2 = 18.50$, 11 df, $P = 0.07$). Though survival functions did not differ among years for females of ages 2-5 years at Bowser, we did observe an overall downward trend in survival during 1989-1997 ($\beta = -0.024$, $t_{0.05(2),8} = -4.52$, $P = 0.003$) of 2.4%/year (Table 4.16). An overall decline of 2.1%/year over the same period for the population associated with Murphy was not significant ($\beta = -0.021$, $t_{0.05(2),8} = -1.60$, $P = 0.15$). We observed comparatively low survival rates during biological year 1996-1997 for both winter ranges and both age groups of adult females (Table 4.16). Although we found no significant differences in survival estimates with respect to female age overall, our data suggest that older age classes of females may experience a more variable risk to one or more sources of mortality than younger females. For all further analyses, we pooled data for females ≥ 2 years of age.

Estimates of annual survival among years were consistently higher among females associated with Bowser than those associated with Murphy (Fig. 4.20). Survival rates for the pooled sample of all radio-collared mature (≥ 2 yrs) females associated with Bowser averaged 9% higher per year than those associated with Murphy (Fig. 4.20, paired-$t = 3.07$, $P = 0.01$). Survival rates associated with hunting (paired-$t = 1.06$) and nonhunting sources of mortality (paired-$t = 1.33$) suggested a higher rate of survival of females associated with Bowser, but the differences were not significant ($P > 0.10$). The 9% higher annual survival on Bowser was about equally attributable to hunter harvest and all other sources.

Small samples of radio-collared fawns and yearlings of both sexes and adult males (≥ 2 yrs) for all years precluded analysis inclusive of all sex and age classes. So based solely on the results of females > 2 years, we pooled data into four groups (yearlings and adults for both males and females) across study areas and all years to analyze annual and seasonal trends in survival (Table

4.17). A test for homogeneity among annual survival rates for adult deer indicated highly significant differences with respect to sex and age ($\chi^2 = 30.5$, 3 df, $P < 0.001$). Highest survivorship occurred among mature (≥ 2 yrs) females (0.83) and the lowest among mature males (0.53); yearling females were comparable to mature females and yearling males were intermediate between females and adult males (Table 4.17).

Survival among radio-collared deer was highest during summer (Jun-Aug) for all sex and age classes of females ≥ 1 year of age and for mature males pooled across study areas (Table 4.17). We observed lowest survival rates during fall (Sep-Dec), which coincided with annual hunting seasons. Based on the number of deaths by month for mature males and females (Fig. 4.21), the proportion that died during January and February was smaller, when concentration of deer on traditional winter ranges was highest, than during March and April when deer occupied transitional ranges between their summer and winter ranges and were in their poorest physical condition of the year. The survival rate for yearling males was higher during winter-spring than during summer (Table 4.17). A survival rate for fawns, based on data for 1989-1994 was lower than that observed for adults (Table 4.17). Most deaths of fawns during the winter-spring period occurred between February and March (Fig. 4.22). Our findings concurred with Kunkel (1997) who reported very low mortality rates during Aug-Sep and high rates during late winter and early spring. We found highly significant differences among survival rates with respect to season, sex, and age ($\chi^2 = 110.53$, 11 df, $P < 0.001$). The highly significant chi-square for annual survival probably reflects a differentially higher rate of removal of antlered males during autumn (Table 4.17) because among groups of seasonal estimates we detected significant differences only during autumn ($\chi^2 = 19.49$, 3 df, $P < 0.001$).

Three estimates of adult survivorship—population reconstruction, Kaplan-Meier survival functions, and MICROMORT (Heisey and Fuller 1985 functions calculated by Sime [1996] for 1988-1996)— all suggested that male cohorts turn over in 9-10 years compared to ≥ 15 years for females (Fig. 4.23). Figure 4.23 also suggested that survival estimates based on population reconstruction closely approximated survival estimates for radio-collared males. However, the

Table 4.17. Annual and seasonal survival from the Kaplan-Meier estimator among radio-collared white-tailed deer in the Salish Mountains in northwest Montana, 1988-2000.

Age/sex status	Time period	n^1	Survival	SE
Fawns	Winter/spring	67	0.764	0.053
Yearling females	Yearlong	69	0.882	0.059
	Summer	26	1.000	0.000
	Fall	26	0.920	0.054
	Winter/spring	91	0.944	0.029
Mature females	Yearlong	895	0.826	0.014
	Summer	741	0.985	0.005
	Fall	684	0.878	0.013
	Winter/spring	704	0.955	0.008
Yearling males	Yearlong	48	0.610	0.111
	Summer	19	0.836	0.087
	Fall	15	0.787	0.110
	Winter/spring	40	0.929	0.049
Mature males	Yearlong	117	0.534	0.056
	Summer	87	0.939	0.026
	Fall	73	0.625	0.058
	Winter/spring	68	0.909	0.035

[1] Number of radio-collared deer at risk during each time period pooled over all years—some individuals were in the sample ≥ 2 years.

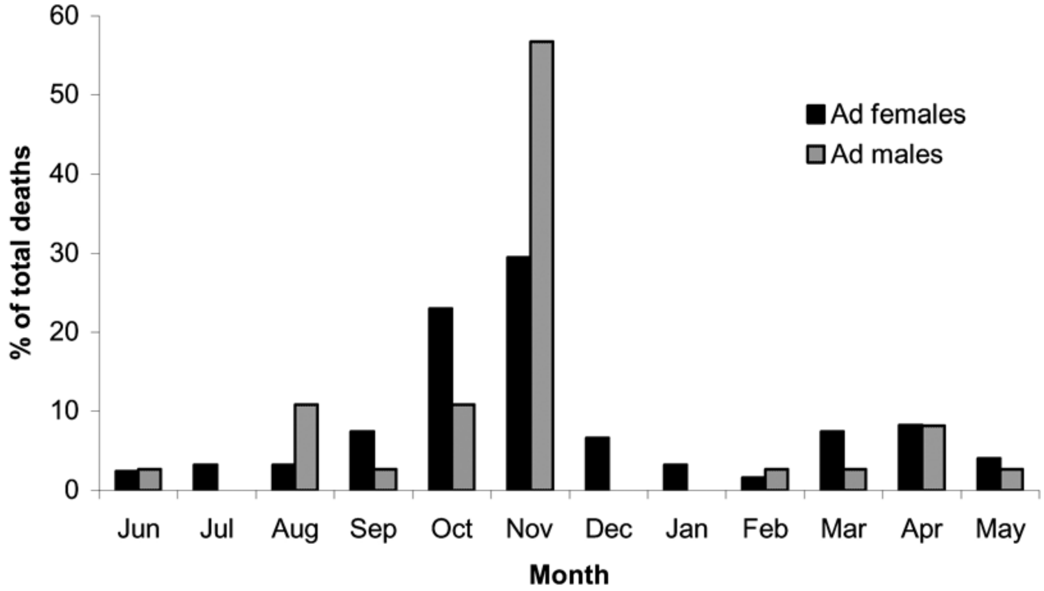


Figure 4.21. Distribution of deaths among radio-collared mature (≥ 2 yrs) white-tailed deer in the Salish Mountains by month. Data were pooled across all years.

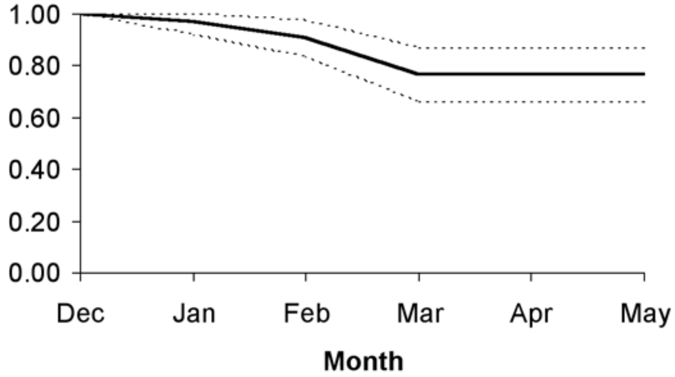


Figure 4.22. Survival of radio-collared whitetail fawns over the winter-spring period for the years 1989-1994. Dotted lines are ± 95% confidence interval.

methods we used to convert the total number of males to an estimate of the total population probably underestimated the number of females and their rate of survival.

Yearlong survival rates for adult (≥ 1 yr) females in the Salish Mountains (0.88-0.83, Table 4.17) were relatively high compared to those reported by others. Kunkel (1997) reported a yearlong survival rate of 0.74 for females (≥ 1 yr) in the North Fork of the Flathead River, an area in northwest Montana recently re-colonized by wolves. For the northern extreme of the species' distribution, Lamoureux et al. (2001) reported survival rates of 0.73 for adult females and 0.66 for adult males in a lightly hunted population in Quebec. Patterson et al. (2002) reported yearlong survival for adult females (≥ 1 yr) in Nova Scotia of 0.94 in an unhunted population and 0.80 in a lightly hunted population in which females were protected, all of which suggested that the difference in survival resulted from illegal harvest. Dusek et al. (1992) reported much lower yearlong survival (0.45-0.80) in heavily exploited populations of white-tailed deer in eastern Montana than observed for the Salish Mountains (Table 4.17).

Cause-specific mortality.—We did not ascertain the proximate or probable cause of death for 41 (15%) documented deaths because we were unable to examine the site shortly following the death. Trap-related deaths were censored from the sample prior to conducting any analyses. Hunting, which included documented kills and wounding losses as well as probable losses due to hunting, wounding, or poaching, accounted for 125 of 280 (45%) documented deaths of radio-collared deer older than 12 months. We identified deaths from wounding by an entry or exit wound and unreported harvest or suspected poaching by finding a severed belting collar either at or away

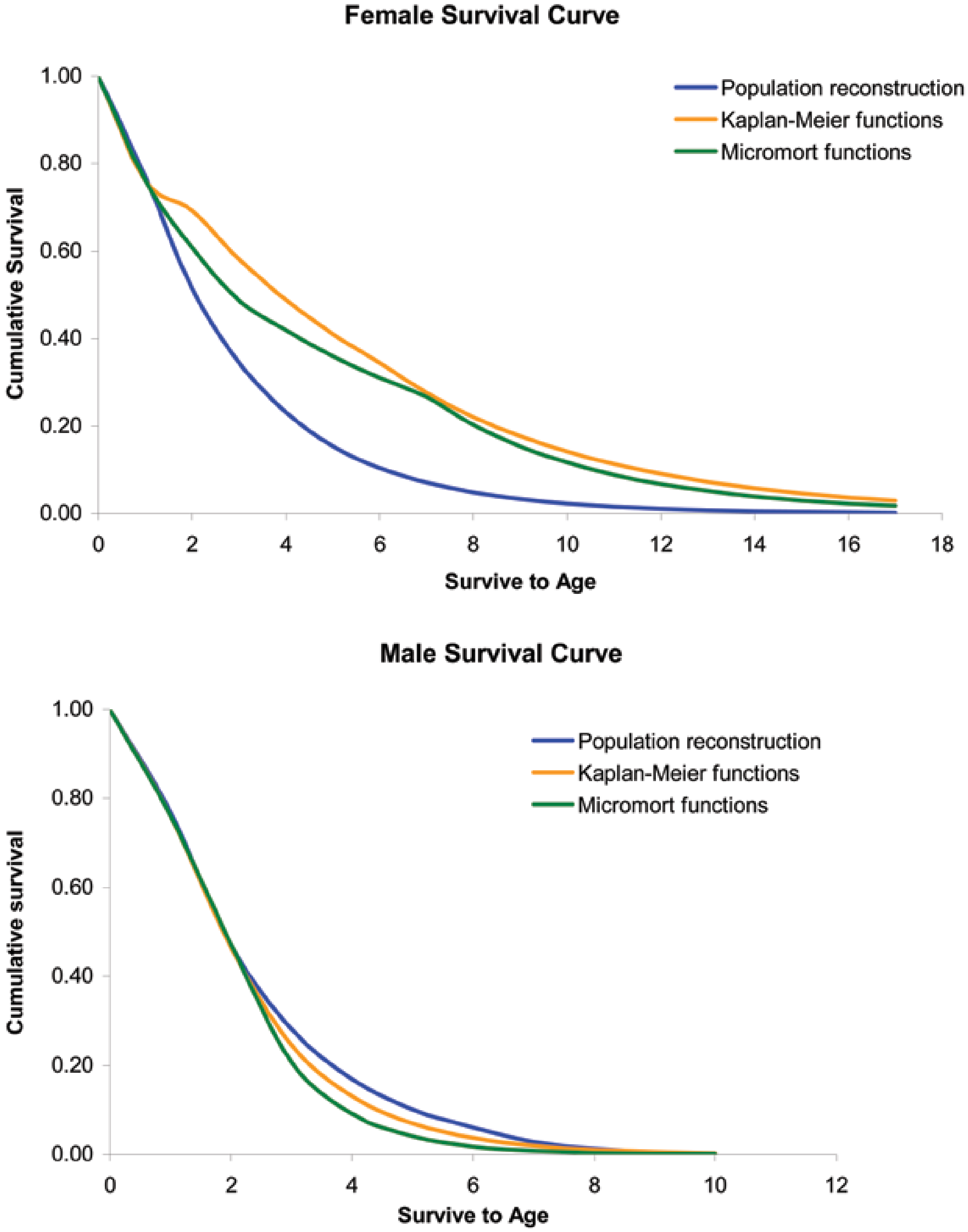


Figure 4.23. Survival curves for white-tailed deer in the Salish Mountains calculated from survival functions based population reconstruction and from survival rates of radio-collared deer. MICROMORT estimates are from Sime (1996).

from the kill site. Among adult females, hunting-related mortality was the leading cause of death during most years except 1996-1997 that included a severe winter and 1998-1999 and 1999-2000 in which antlerless deer were protected from hunting (Fig. 4.24). Tests for homogeneity among survival rates among radio-collared adult females (≥ 2 yrs) from both hunting-related and all other sources combined indicated no significant differences with respect to year and study area (P > 0.11).

Among sources of mortality other than hunting, predation (for all sex and age classes: *n* = 72, 23%) was the major proximate cause of death among radio-collared adult females yearlong and the leading cause of deaths among fawns over winter (Table 4.18). Of 29 instances in which the predator was identified, 76% involved cougars. Several studies in the Northwest reported that cougars are a major predator of deer (Williams et al. 1995, McNay and Voller 1995, Kunkel 1997). We detected a significant correlation between annual rates of deer mortality from predation from both study areas and a 1-yr lag in the number of cougars harvested in hunting districts 101 and 102 combined (*r* = 0.67, P = 0.018). Other predatory species known to have taken deer ≥ 6 months of age included wolves and coyotes (*C. latrans*). Any contribution to annual mortality by wolves was limited almost entirely to the deer population associated with Murphy/HD 101 where distribution of the wolves and white-tailed deer overlapped (Fig. 4.25). Kunkel (1997) observed that deer were less vulnerable to wolves and cougars during winter in areas of highest deer density and that severe winters appeared to increase anti-predator benefits of yarding. The trend in losses of deer to predation seemingly increased from the early to mid 1990s (Fig. 4.26). Increased predation on white-tailed deer in the Salish Mountains coincided with a peak in cougar numbers, harvest, and nonhunting deaths among cougars in Montana during the mid-to-late 1990s as suggested by Aune and Anderson (in review).

Accidents (*n* = 32, 11%) and direct losses to malnutrition (*n* = 22, 7%) followed hunting and predation in relative numbers of deaths. Most (~80%) accidental deaths resulted from deer/automobile collisions with the rest resulting from deer/train collisions or drowning. The number and relative proportion of deaths among radio-

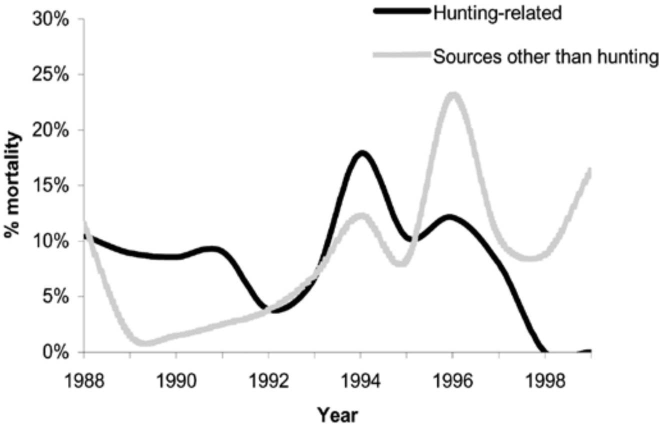


Figure 4.24. Mortality rates among radio-collared mature (≥ 2 yrs) female white-tailed deer in the Salish Mountains, pooled for hunting districts 101 and 102 from hunting-related and all other causes.

Table 4.18. Cause of mortality among radio-collared white-tailed deer in the Salish Mountains in northwest Montana, 1988-2000.

	Sources of Mortality				
Age/sex status	Hunting related[1]	Predation[2]	Accidents[3]	Winter/malnutrition[4]	Other/unknown
Fawns (winter)		8(53)[5]	2(13)	3(20)	2(13)
Ad Fem (≥ 1 yr)	98(41)	59(25)	28(12)	17(7)	34(14)
Ad males (≥ 1 yr)	27(61)	5(11)	3(7)	2(5)	7(16)

[1] Includes confirmed hunter kills and probable losses to wounding and poaching.

[2] Includes confirmed losses to predation and probable losses to predation.

[3] Includes all accidental deaths of which most were attributed to deer-vehicle collisions.

[4] Includes confirmed deaths due to malnutrition plus probable, unconfirmed losses to malnutrition.

[5] Number of deaths (% of total yearlong or seasonal deaths within sex and age classes).

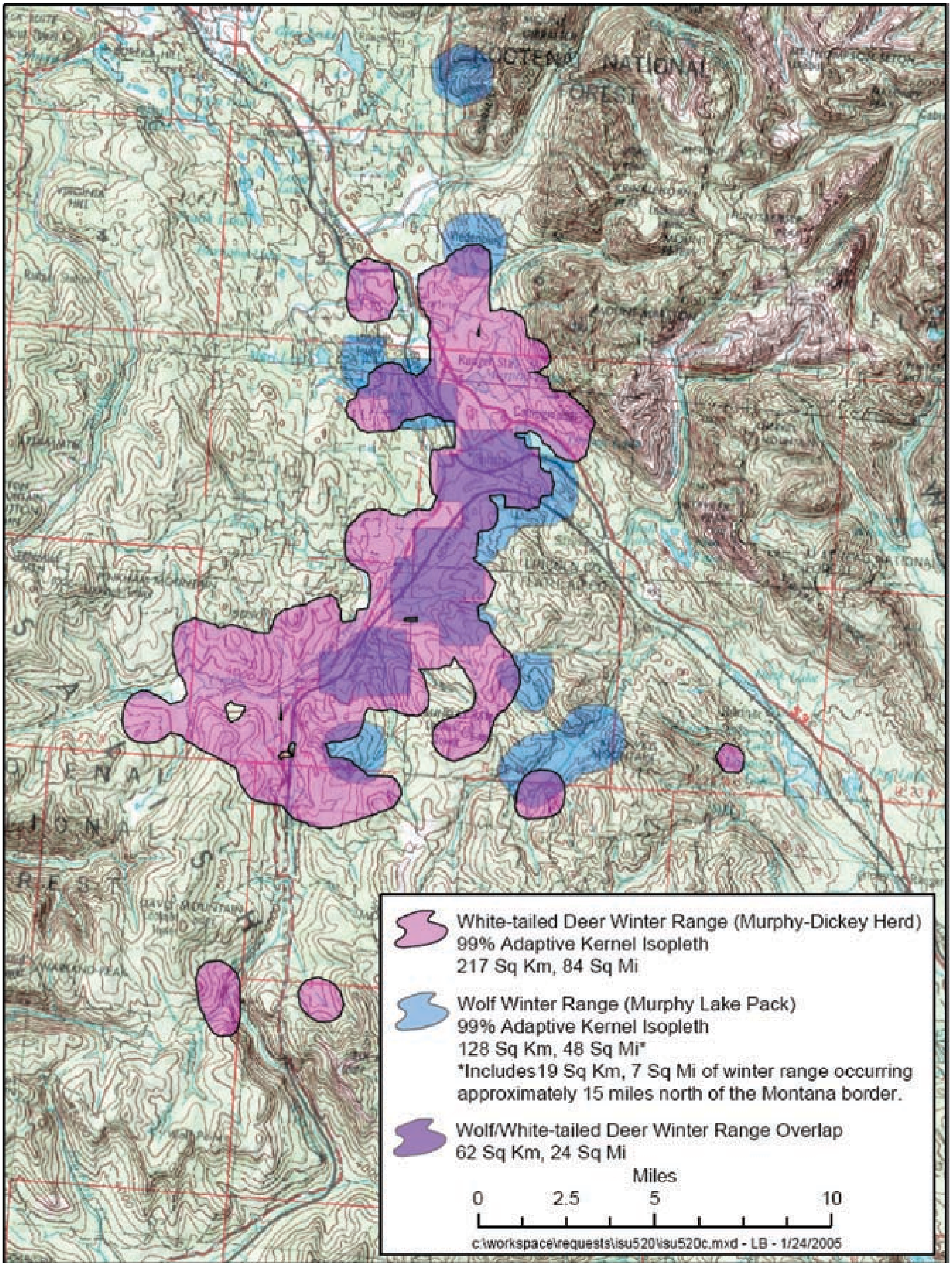


Figure 4.25. Overlap of winter distribution of wolves and white-tailed deer on the Murphy winter range based on the 99% isopleth of the adaptive kernal from radio telemetry.

collared deer attributable to these causes by sex and age appear in Table 4.18.

Nonhunting mortality other than predation was markedly evident only during the severe winter of 1996-1997. Of 22 documented deaths resulting from malnutrition over the period of study, eight occurred during that winter. Predation probably accounted for most natural mortality during all other years at least for deer older than 6 months (Table 4.18). Predation accounted for most nonhunting deaths among mature females (≥ 2 yrs; Fig. 4.26).

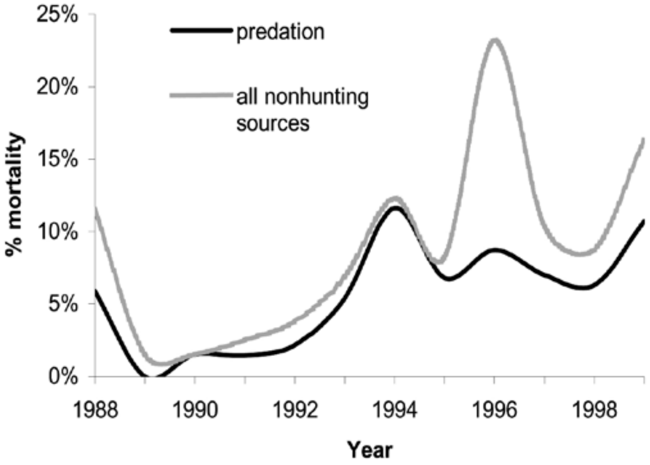


Figure 4.26. Mortality among radio-collared mature (≥ 2 yrs) female white-tailed deer in the Salish Mountains attributed to all nonhunting sources compared to that just attributed to predation. Data are pooled for hunting districts 101 and 102.

Manipulation of Antlerless Harvest Regulations.—During 1991-1996, we attempted to increase harvest of antlerless white-tailed deer to a level about twice what we would expect to occur from harvest on the general deer license (A-tag) by issuing a limited number of antlerless licenses (B-tags) through a drawing. B-tags were issued for and valid only in hunting district 102 that served as the treatment area, whereas hunting district 101 served as a control. Antlerless regulations associated with the A-tag applied to both hunting districts. Issuance of B-tags increased antlerless harvest in the treatment area (HD 102; Fig. 2.8) to a level nearly twice that of pretreatment years (1988-1990). Antlerless harvests in the control area remained relatively constant during treatment years, except during 1996 when 5 days of either-sex hunting was added to the end of the season, coinciding with a substantial increase in antlerless harvest in both areas. Record snowpack during that period also probably contributed to the relatively high antlerless harvest during that one year. Numbers and trend of antlerless deer harvested were similar between the two hunting districts during pre- and post-treatment (1997-2003, Fig. 2.8).

Despite an increased antlerless harvest in hunting district 102, effort to perturb the system fell short of a level of harvest required to decrease female survival rates. We detected no significant differences in survival among radio-collared mature females (≥ 2 yrs) from hunting-related sources for the period of September-December with regard to hunting district and treatment ($\chi^2 = 4.83$, $P = 0.19$; Table 4.19). Despite a lack of significance, survival rates during hunting seasons appeared slightly higher in the treatment area (HD 102) than in the control during both the pre-treatment and treatment periods (Table 4.19). We also compared survival of adult females from all sources of mortality occurring throughout the year (Table 4.20). Chi-square tests indicated that differences occurred among survival rates with respect to study area and treatment category ($\chi^2 = 11.24$, $P = 0.05$). Further analysis indicated that differences in survival rates among treatment categories within each hunting district were not significant ($P \geq 0.18$). However, log rank tests indicated a significant difference in overall survival between hunting districts occurred only during the period that B-tags were issued (1991-1996) for hunting district 102 ($\chi^2 = 7.19$, $P = 0.01$), but lower survival occurred in the control area rather than the treatment area (Table 4.19). Although analyzed in a slightly different way, these findings generally agree with those reported earlier that annual survival among all years was consistently higher among adult females associated with Bowser (HD 102) than Murphy (HD 101).

Table 4.19. Survival (Sep-Dec) of radio-collared mature (≥ 2 yrs) female white-tailed deer from hunting-related mortality by treatment category and hunting district, 1988-1999.

Treatment	Hunting district	n[1]	$\hat{S}(Tj)$ [2]	$Var[\hat{S}(Tj)]$[3]
Pre-treatment	101	46	0.872	0.001
Control	101	114	0.858	0.001
Pre-treatment	102	100	0.900	0.001
Treatment	102	222	0.930	0.000

[1] Number of radio-collared deer at risk during each time period—some individuals were in the sample ≥ 2 years.
[2] Kaplan-Meier survival estimate.
[3] Variance of the survival function—Greenwood's formula—(Pollock et al. 1989).

Table 4.20. Annual survival (Jun-May) of radio-collared mature (≥ 2 yrs) female white-tailed deer from all sources of mortality by treatment category and hunting district, 1988-2000.

Treatment	Hunting district	n[1]	$\hat{S}(Tj)$ [2]	$Var[\hat{S}(Tj)]$[3]
Pre-treatment	101	61	0.784	0.004
Control	101	153	0.723	0.002
Post-treatment	101	110	0.830	0.002
Pre-treatment	102	135	0.876	0.001
Treatment	102	303	0.840	0.001
Post-treatment	102	150	0.870	0.001

[1] Number of radio-collared deer at risk during each time period—some individuals were in the sample ≥ 2 years.
[2] Kaplan-Meier survival estimate.
[3] Variance of the survival function—Greenwood's formula—(Pollock et al. 1989).

Factors Affecting Population Characteristics

Effects of Environmental Variation and Population Density

Recruitment.—Both animal density and critical temperature were correlated with recruitment of deer to 1 year of age for deer associated with hunting district 102 and Bowser ($R^2 = 0.73$, $P = 0.002$). The negative effect of early autumn density of mature females (≥ 2 yrs) and the index of cumulative days in which temperatures fell below the critical temperature during the winter that the cohort were fawns strongly influenced recruitment to 1 year of age. We based our estimate of recruitment on the proportion of yearling females among the adult female segment the following autumn.

Female density and critical temperature collectively did not yield the same effect on the population associated with hunting district 101 and Murphy. There, only critical temperature during the cohort's first winter was correlated with recruitment to 1 year of age ($R^2 = 0.40$, $P = 0.027$). Observed differences in dynamics and survival among adult females in the respective populations might explain the absence of a significant influence of female density on recruitment for deer associated with hunting district 101 and Murphy. Numbers of adult females (≥ 1 yr) in hunting district 102 increased and remained at a substantially higher level than did those in hunting district 101 during 1990 through 1995 (see Population Trend Fig. 4.13). This trend also coincided with a consistently higher mean rate of survival ($\Delta = 9\%$) among mature females ($\geq$ 2 yrs) associated with Bowser than those associated with Murphy. However, white-tailed deer at Murphy shared the winter range with mule deer. The scope of data collection during this study did not allow us to determine to what extent this dual usage might have contributed to a density dependent effect, if any, on whitetails.

We detected a correlation between female density and recruitment only in the population associated with hunting district 102 and Bowser. Mature female ($\geq$ 2 years) density was negatively correlated with recruitment of fawns to autumn ($R^2 = 0.52$, $P = 0.008$). That is, female density during the autumn in which the cohort was conceived was inversely related to percent fawns in the population the following autumn (see Population Structure Table 4.2). Animal density would probably have had little if any measurable effect on pregnancy rates on females of ages $\geq$ 3 years that exhibited consistently high rates of pregnancy; nearly all had successfully bred (see Population Dynamics Table 4.13). Pregnancy rates among younger adult females (1- and 2-yr-olds) were significantly lower that allowed for more variability among years. The most likely effect of density on reproductive output the following June and survival of neonates to autumn would be an inverse effect of pre-breeding female density on fetal rates and/or birth weights that could predispose neonates to early mortality. Such a conclusion was consistent with findings of Verme (1977) and Sams et al. (1996) that related nutritional stress among adult females in deer herds at high density with lower birth weights and increased risk of mortality among newborn fawns. This study did not address mortality of neonates although fetal rates that we provide for 1988-1991 and 1997 suggest that fecundity among our study population fell well below the species potential (Table 4.14). We speculate that any density relationship would most likely manifest itself in reproductive output, particularly the youngest breeding age class(es) of females that typically exhibit the widest range of variation (see Population Dynamics Tables 4.13 and 4.14).

Adult survival.—We have no evidence to suggest that population density as measured by several sources had an effect on survival of mature female ($\geq$ 2 yrs) white-tailed deer. Hunting during autumn accounted for the greatest number of documented deaths among radio-collared deer of ages $\geq$ 1 year. Experimental evidence from elsewhere suggests that density effects are likely expressed in variable rates of juvenile rather adult survival for white-tailed deer (Dusek et al. 1989) as well as for other ungulates (Sauer and Boyce 1983, Skogland 1985, Bartman et al. 1992). Our data support that general hypothesis. Further, we detected no consistent relationship between indices of drought or winter severity and survival rates of mature females.

Growth and condition parameters.—We detected an inverse linear relationship between total winter density derived from pellet group surveys at Bowser and skeletal growth through the first year of life ($R^2 = 0.69$, $P = 0.001$) based on diastema length among yearling males examined at check stations the following autumn. Thus, total density at Bowser accounted for 69% of the variability in skeletal growth during the cohort's first winter. We could identify such a relationship only for Bowser because we did not have reliable estimates of white-tailed deer numbers occupying Murphy. Because we did not detect correlation between diastema length and total population numbers in either hunting district ($P > 0.10$), we suspect that reduced skeletal growth of fawns was a function of actual numbers of deer occupying the core winter range at Bowser and not to total numbers of deer in hunting district 102 given that a relatively large proportion of deer in hunting district 102 occupy that winter range during most years.

With the single exception documented above, we detected no meaningful relationships ($P > 0.10$) between skeletal or antler growth and factors that might affect them including drought, winter weather, or population density; we also did not detect any additional time lag effects with respect to interaction among those variables. Even considering the variation by year, sex, and/or age detected among populations in the Salish Mountains, we could not explain annual variation in body or antler growth based on various hypotheses offered in the literature (e.g., French et al 1956, Kie et al. 1983, Lukefahr and Jacobson 1998). Dusek et al. (1989) reported a 2-year effect of precipitation on skeletal growth and a 1-year effect on antler growth for yearling male white-tailed deer in eastern Montana; precipitation acted with adult female density to produce these effects. Similar patterns were not apparent for deer in the Salish Mountains. We could not relate even the extreme values for animal condition or antler growth to variation in weather indices or population density during either winter or summer. During the course of this study, factors that influenced population size operated independently of those affecting physical condition.

Effects of Hunting

Hunting-related mortality in most instances is heavily skewed toward antlered deer as evidenced by findings from this study (see Population Dynamics, Tables 4.17 and 4.18) and from elsewhere (Dusek et al. 1989, Van Deelen et al. 1997). Harvest regulations, which afford antlerless deer disproportionate protection, and hunter selection may both contribute to a harvest skewed toward antlered deer and consequently a population structure among adult deer that is skewed toward adult (≥ 1 yr) females. Even where more liberal antlerless regulations were implemented (e.g., Dusek et al. 1989), harvests were biased toward males; hunters selected antlered deer over antlerless deer and larger deer over smaller deer

Multiple regression analyses indicated that the combined effect of population size and number of hunters afield accounted for most of the observed annual variability in antlered harvest in both hunting districts 101 ($R^2 = 0.86$, $P < 0.001$) and 102 ($R^2 = 0.72$, $P = 0.001$). The hunter population for hunting district 102 included holders of antlerless permits issued through special drawings during 1991-1996. This inflated total hunter numbers during those years with hunters that would have had no effect on antlered harvest and thereby diminished the observed effect of hunters on antlered harvest. Thus, excluding those hunting on their special antlerless permits yielded a higher R^2-value ($R^2 = 0.91$, $P < 0.001$).

Manipulation of Antlerless Harvest.— Although we could not identify any measurable population response by manipulating antlerless harvest, we met one underlying assumption of selective harvest management (Giles and Findlay 2004); that is, offering a limited number of antlerless tags that allowed tag holders to take a second deer approximately doubled antlerless harvest in hunting district 102. In contrast, numbers of antlerless deer harvested in hunting district 101, serving as a control, remained relatively steady through the same period (Fig. 2.8). Numbers of tags issued by drawing during 1991-1996 averaged 730 (600-950, mean 1.6 applicants/tag issued)/ year and approached a limit of hunter interest as the number of tags offered continued to increase. For example, the ratio of applicants/issued tag was 1.9 in 1991 when only 600 tags were offered, but dropped to 1.1 when 950 tags were issued during 1995. Thus, increasing antlerless harvest further through the issuance of a limited number of B-tags would require issuing multiple tags/hunter. Allowing antlerless deer to be harvested through the entire 5-week general firearm season on the A-tag might also contribute to increased antlerless harvest. Experimental evidence suggests that hunter harvest of antlerless deer will unlikely achieve an effective herd reduction if numbers of tags and hunter interest is limited (Giles and Findlay 2004) and would be even less achievable in heavily wooded environments (Foster et al. 1997). Our study suggested that regulations designed to encourage harvest of antlerless deer might reduce herds or limit population growth when rates of survival among mature females also are being influenced by other mortality factors.

We failed to meet a second assumption underlying selective harvest management. That is, increasing antlerless harvest in hunting district 102, at least at the level that we manipulated it, did not measurably affect survival of radio-collared mature (≥ 2 yrs) females nor did it affect population size or trend. Even doubling antlerless harvest from that associated with more conservative regulations, i.e., antlerless harvest limited to 2 weeks on the A-tag, was insufficient to detect a measurable change in adult female survival. During 1988-1999, mortality for adult females from hunting-related causes (Table 4.19) varied from 7 to 10% in hunting district 102 (treatment) and 13 to 14% in hunting district 101 (control). Under comparable rates of recruitment in hunting districts 101 and 102, the 13-14% mortality rate in hunting district 101 occurred at a time of relatively continuous population decline (Fig 4.13); The 7-10% rate in hunting district 102 coincided with a somewhat different dynamic; the population in hunting district 102 didn't decline noticeably until after 1994 (Fig. 4.13) a period in which adult female mortality from nonhunting sources, of which a substantial portion probably resulted from predation, increased to a relatively higher level (4.24). Research from elsewhere also suggested that effectively influencing population dynamics through manipulation of antlerless harvest would require a slightly-to-moderately higher rate of hunting-related mortality among adult females. For example, Lamoureux et al. (2001) reported that a mortality rate from hunting-related causes of 16% in Quebec reduced female survival enough to limit population growth. A regulation package that included issuing multiple antlerless tags/hunter in southeastern Montana during the mid 1980s increased the rate of hunting-related mortality of adult females from 20 to 39% on the lower Yellowstone River and from 16 to 29% in a nearby upland prairie environment (Dusek et al. 1992); the higher rate of hunting-related mortality among adult females in these riverine and prairie environments coincided with measurable population declines (Wood et al. 1989, Dusek et al 1989).

Dynamics of the two populations in the Salish Mountains operated independently, and differed as driven by trends in numbers of adult females (Fig. 4.13; ≥ 1 yr). A consistently lower rate of survival among females associated with hunting district 101/ Murphy (Fig. 4.20) resulted in a steadily declining population. The fact that annual survival rates did not significantly differ over time in either study area did not negate important biological differences in these two populations. Nonhunting mortality was dynamic over the period of study and was additive to hunter harvest, particularly that relative to predation. Although harvest regulations increased harvest of adult females in eastern Montana (Dusek et al. 1992), harvest rates had no measurable effect on rates of nonhunting mortality in that study or in this one. Giles and Findlay (2004) documented only a mild regulatory effect on deer populations in response to increased antlerless harvest. They attributed this response to density-dependent survival having an effect on population regulation. However, they failed to identify or demonstrate a mechanism of density-dependence in survival rates among adult deer.

Influence of Weather on Harvest.—We found no meaningful relationship between snow pack on summer range (Hand Creek) or winter range (Whitefish) and the percent of the annual antlered harvest occurring within any week of the hunting season ($P > 0.20$). Antlered harvest strongly influenced trends in total whitetail harvest that probably would explain the lack of any relationship between snow pack and the percent of total annual harvest occurring within any week of the hunting season. Further, population size and hunter numbers accounted for 86-92% of the variation in harvest of antlered white-tailed deer leaving only 8-14% of the variability attributable to all other causes including random variation and any effect of weather variables on harvest trend for white-tailed deer in the Salish Mountains.

A combination of harvest regulations directed at antlerless deer on the general deer license (A-tag) and weather probably influenced the dramatic increase in antlerless harvest during autumn 1996 in both hunting districts (Fig. 2.8). That year harvest regulations allowed legal harvest of antlerless deer during the first week and the last week of the general firearm season; the last week coincided with record-setting snowpack. The last week of the general firearm season traditionally coincides with the 4th week in November (Julian week 47). During 1996 an estimated 40% of the radio-collared deer associated with Bowser occupied the winter range that week compared to an average of 13% for the years 1988-1999. Estimated winter range occupancy on Murphy for that week was 65% compared to an average of 23%. Thus, allowing legal harvest of antlerless deer during late November, which coincided with earlier than normal concentration of deer on winter ranges due to early snow pack, resulted in a very high antlerless harvest (Fig. 2.8). Results of the statewide telephone survey did not indicate a similar increase in antlered harvest during 1996. Peaks in harvest of antlered deer (1991-1994) coincided with years when total population numbers were relatively high (Figs. 2.7 and 4.13).

Effects of Predation

Adult Deer.— We observed a relationship between annual rates of deer mortality from predation and a 1-yr lag in the number of cougars harvested in the Salish Mountains. Any contribution to annual mortality of white-tailed deer by wolves was limited almost entirely to white-tailed deer associated with Murphy and hunting district 101. Although distribution of wolves and white-tailed deer closely overlapped on Murphy (Fig. 4.25), we documented only a few instances of wolves preying on adult deer. Other studies in the Northwest have also reported that cougars are a major predator of deer (Williams et al. 1995, McNay and Voller 1995, Kunkel 1997, Ruth 2004). Increased loss of deer to predation from the early-to-mid 1990s in the Salish Mountains (Fig. 4.26) also coincided with a peak in cougar numbers, harvest, and nonhunting deaths among cougars throughout Montana during the same period (Aune and Anderson in prep.). Kunkel (1997) observed that deer were less vulnerable to wolves than cougars during winter in areas of highest deer density and that anti-predator benefits of yarding increased during severe winters. A pattern of mortality that we observed for adult deer throughout this study lends support to that hypothesis.

Additionally, proliferation of domestic dogs with increased rural homesite development in the vicinity of Bowser was a concern both from the standpoint of off-leash dogs harassing wintering deer and/or as a proximate source of deer mortality (Sime 1996, 1999). However, very few deaths of individually marked deer that were not associated with winter trapping could be directly attributed to domestic dogs although stress imposed by hazing or pursuit by domestic dogs could predispose deer to other stress-related mortality especially where energy conservation is a primary strategy of overwinter survival (Sime 1999).

Fawns.—Fawns typically experience lower rates of annual survival than do older deer (Nelson and Mech 1986, Dusek et al. 1989, Patterson et al. 2002). Although this study did

not address fawn survival through 6 months of age, differences between fetal rates (Table 4.14), a reasonable estimate of production at time of fawning, and recruitment to autumn from back-dating harvest records (Tables 4.1 and 4.2) suggested that early post-partum losses accounted for a substantial proportion of all mortality during the first year of life.

To estimate the relative contribution to the following year's fawn production among the respective age classes at time of breeding, we used the pregnancy rate observed for fawns (Table 4.13) assuming 1 fetus/pregnant female for an overall fetal rate of 5 fetuses:100 female fawns. Assuming a lower fetal rate among yearlings than among mature females, we used the rate for yearlings reported for the Swan Valley (125:100) by Mundinger (1981). We calculated the contribution of mature females of ages ≥ 2 years at the time of breeding from fetal rates among 31 females. These ratios, the proportion of the female segment composed of fawn, yearling, and mature females, and autumn ratios (Table 4.3 and 4.4) yielded an estimate of summer fawn survival of 0.68 for populations associated with both hunting district 101/Murphy and hunting district 102/ Bowser. This would roughly reflect survival to an age of ~ 3 months and assumes minimal mortality among adult (≥ 1 yr) females over this period as was documented for radio-collared deer. Considering only mortality over summer (0.32) and winter-spring (0.24), we calculated a rate of survival over the first year of life of 0.52. Removal of fawns by hunting as well as losses from other sources during autumn would decrease this rate but probably by a relatively small amount.

Our estimate of neonatal fawn survival for all years combined exceeded what has been reported for white-tailed deer across the species' range. Cook et al. (1971), Nelson and Woolf (1987), Ballard et al. (1999), and Ricca et al. (2002) reported relatively high rates of mortality during the first 6 months of life of which most occurred during the first 6-8 weeks. For the respective studies, overall survival over the first 6-7 months ranged from 0.47 in New Brunswick to 0.14 in Oregon, and predation accounted for a significant proportion of documented losses. For example, losses to predation during the first 6-8 weeks postpartum accounted for about 33% of all deaths in New Brunswick (Ballard et al. 1999), 53% in Texas (Cook et al. 1971), and 77% for Columbia white-tailed deer in Oregon (Ricca et al. 2002).

Predators commonly associated with neonatal losses of fawns, such as coyotes (*Canis latrans*) bobcats (*Felis rufus*) and black bears (*Ursus Americanus*) (Beasom 1974, Ballard et al. 1999), were ubiquitous over the Salish Mountains study area. Several studies provide empirical evidence that coyotes are an effective predator of neonatal fawns (Beasom 1974, Stout 1982, Hamlin and Mackie 1989, Patterson and Messier 2003).

We documented a lower rate of survival during winter-spring among radio-collared fawns (≥ 6 mos) than for adult deer (≥ 1 yr; Table 4.17). Survival of radio-collared fawns of ages ≥ 6 months (Jan-May) for this study (0.76) fell between extremes reported for north-central Minnesota (Fuller 1990); survival of marked fawns in Minnesota was 0.89 when winter snow depth averaged 13-16 cm but only 0.60 when average snow depth was 36-44 cm. Predation accounted for > 50% of deaths among fawns over winter during this study followed by losses due to malnutrition (Table 4.18). Rates of overwinter survival of fawns from this study as well as those reported by Fuller (1990) are somewhat higher than the range reported above for the first 6 months of life. However, our estimate of overwinter fawn survival considers only winters in which radioed fawns were available (1989-1994) and does not consider the following 5 years in which cougar populations were comparatively high.

In addition to predation experienced during most years, the severe winter of 1996-1997 not only impacted recruitment of the 1996 cohort but most likely also limited survival of neonates the following summer. Nutritional stress among adult females during late winter and spring associated with an extended snowpack that delayed migration may have led to lower-than-normal birth weights of fawns. During spring 1997, 96% of deer associated with Bowser remained on the winter range during the 2nd week of April; average weekly occupancy for all years was 42%. Similarly, at Murphy 79% of radio-collared deer remained on the winter range during the 2nd week of April compared to an average of 12%.

Section 5: Conclusions And Management Implications

Recruitment

Effects on Population Dynamics

Although fetal rates observed during this study fell near the low end reported for the species (Table 4.14), net recruitment to spring was comparable to that reported for white-tailed deer elsewhere in Montana as reported by Mackie et al. (1998). That compendium reported a rate of recruitment ('spring' fawns:100 adults) for the Salish Mountains based on the first 7 years of study similar to what we observed throughout the entire 11-year period of data collection (Tables 4.3 and 4.4; 54 vs. 49-55). However, annual variability in these fawn:adult ratios as expressed by coefficients of variation suggested that the rate of annual recruitment from late winter camera surveys was characterized by greater variability than indicated from the first years of study. Additionally, variability that we detected for the Salish Mountains approached that reported for the more stochastic environments in which whitetails were studied in eastern Montana (Wood et al. 1989). Thus, variability in recruitment rates in white-tailed deer would be comparable in the mountains of northwest Montana and prairies of eastern Montana if individual studies spanned extremes in recruitment rates. For example, recruitment

rates reported for the Salish Mountains by Mackie et al. (1998) included a period when rates were consistently high.

We detected an effect of winter temperature regime on recruitment to one year of age in the Murphy and Bowser study populations and a density-related effect for the Bowser population. Some variability in annual estimates of neonatal survival also might have contributed to variability in recruitment in the Salish Mountains although we have insufficient data from which to identify the source. On the lower Yellowstone River, Dusek et al. (1989) reported an inverse relationship between the rate of recruitment to autumn and summer density of mature females; there, winter temperatures had little if any effect on long-term rates of recruitment to an age of 1 year.

Late winter-early spring classifications appeared to overestimate recruitment by as much as 2-5% because camera surveys were conducted during a seasonal peak in fawn mortality (Fig. 4.23). A difference between the actual and corrected average, however, would be quite small. Our findings conflict somewhat with Mundinger's (1981) hypothesis that various factors affecting reproduction of white-tailed deer in the Swan Valley worked to yield stable rates of net recruitment that operated interdependently with other population parameters to maintain population stability. Stability did not characterize recruitment rates in the Salish Mountains through the period of study; however we did detect an inverse relationship between female density and recruitment only for the Bowser population. Neither population remained stable through the duration of this study. Further, population fluctuation would have been evident for both populations even in the absence of the severe winter of 1996-1997.

Our findings suggest that the two study populations operated independently, and similar rates of long-term recruitment between populations yielded differing outcomes over time. Our findings suggest that population dynamics of white-tailed deer in Salish Mountains exhibited spatial variation, whereas Mundinger's (1980, 1982) work suggested a unique strategy by which deer operated in the Swan Valley, further demonstrating spatial variation. However, data collected by FWP in the Swan Valley from 1998 through 2004 demonstrated a slightly higher more variable pattern of recruitment ($\bar{x}$ = 62 fawns:100 adults, CV = 29%) than during 1976-1982 ($\bar{x}$ = 46 fawns:100 adults, CV = 25%). Given differing patterns in the Bowser, Murphy and Swan areas, annual fawn:adult ratios alone, whether from classification of deer on winter ranges or surveys following dispersal of deer from winter ranges, might be difficult to interpret without an index of population trend and/or estimate of adult female survival.

Factors Influencing Recruitment

Our analyses suggested that overwinter survival of fawns in both populations was related to the cumulative effect of days with minimum temperatures < -12 °C (10 °F; Farnes et al. 2000). We would expect the increased metabolic rate brought on by minimum daily temperatures below the critical temperature reported for white-tailed deer (-12 °C) to disproportionately impact fawns because fawns undoubtedly accumulated less body fat than older deer (Table 4.9). Although accretion and mobilization of fat by sex and age as expressed by the kidney fat index included small samples from this study, those reported for elsewhere in Montana also suggest much lower accretion of fat by fawns (Dusek 1987, Dusek et al. 1989). A late autumn to late winter weight loss among fawns of only 16% for males and 14% for females (Table 4.8) also suggested little accumulation of body fat over the first 6 months of life. From feeding experiments on deer in Michigan, Davenport (1939) reported that healthy deer could safely lose 30% of their autumn weight and survive winter. Severinghaus (1981) reported the weight loss that fawns could survive depended on shelter quality of the habitat. Estimated whole weights for < 5% of fawns captured during February for all years combined approached threshold values reported by Severinghaus (1981). A 30% loss of weight among fawns overwinter in our study populations would probably have predisposed them all to mortality from one source or another, whereas weight loss among adult males typically approached or exceeded 30%.

A pulse in overwinter mortality occurred during February and March for fawns (Fig. 4.23) and extended into April for adults (Fig. 4.22). Predation followed by malnutrition accounted for most overwinter mortality among fawns, but these estimates were documented only during the early years of the study when cougar populations were relatively low. Major overwinter losses were documented only during the severe winter of 1996-1997. Thus, high overwinter losses of fawns probably would be atypical for our study populations. The long-term climate regime and shelter quality of habitats selected by deer in winter during this study probably mitigate these losses. Although our findings indicated that cumulative effects of winter temperatures influenced annual rates of recruitment, we would expect these effects to be more pronounced and that snowpack could also become an important factor if timber harvest or natural events, such as fire, significantly altered habitat structure and composition on core winter ranges.

We found relatively little opportunity to affect recruitment through harvest management because winter temperature regime appeared to consistently drive recruitment in both study populations. Population size also might affect recruitment when populations attain threshold population levels as suggested by a relationship between density and recruitment for the Bowser population. Therefore liberalizing harvest of antlerless deer without estimates for rates of adult female survival and/or population status and trend could lead to population declines under some circumstances.

Adult Survival

Effects on Population Dynamics

We conclude that variation in female survival operated independently of recruitment to drive population trend and dynamics of white-tailed deer in the Salish Mountains. Consistent differences in survival of mature (≥ 2 yrs) females between study areas and between-year differences for older females (≥ 6 yrs) at least for the Bowser population accounted for variation within and between the two study areas. For the population associated with hunting district 101/Murphy, mature female (≥ 2 yr) survival was sufficiently low to cause the population to decline throughout most of the period of study. On Bowser, survival rates of females (ages 2-5 yrs) declined from 1989 through 1997 at an average rate of 2.4%/year. Survival rates for this group were sufficient to maintain population size until 1994. After that point a combination of harvest and predation (Table 4.16, Fig. 4.13) caused the population to decline.

On average, a 3- to 5% difference in harvest rate for mature (≥ 2 yrs) females between the population associated with Bowser/hunting district 102 and that associated with Murphy/hunting district 101 might have comprised the difference between a stable and declining population. For example, reversing the treatment and control area with respect to hunting districts 101 and 102, i.e. issuing antlerless B-tags in hunting district 101 over a 6-yr period rather than in hunting district 102, likely would have yielded a very different outcome than what we observed. Thus, room for management error could be very small, and harvest regulations designed to increase antlerless harvest could unnecessarily reduce herds or limit population growth in other areas during periods in which predation also had a marked impact on rates of adult survival.

Data from this study suggested that cougars accounted for a substantial proportion of all deaths of adult deer from causes other than hunting. Our evidence suggested that losses of adult deer to combined nonhunting causes, particularly those resulting from predation, were additive to removals by hunting. This study documented a significant relationship with a 1-year time lag between relative population size of cougars based on harvest and the rate of loss to predation suggesting that cougars were the primary predator of deer in these two areas. Thus, monitoring trends in cougar populations in northwest Montana over the long term, preferably by hunting district, might be as advantageous to managing white-tailed deer as it would be for addressing cougar management issues.

Although the dynamics of cougar numbers might explain losses of deer to predation, the extent to which other predators, including that of wolves, may have contributed to observed population declines remains unclear. Fully 60% of 72 confirmed and probable predator kills could not be assigned to a particular predator. Given that cougars accounted for 76% of that to which we identified the source, our analyses probably underestimated wolf predation because a pack of wolves is capable of completely consuming a deer carcass much more quickly than would a single cougar. The frequency of monitoring radios during this study (an average of once every 2 weeks) could have biased estimates of deaths upward for predators that take more time to consume a carcass. Kunkel et al. (1999) reported such a bias although it was limited to consumption of fawns. In relatively dense coniferous forests of northwest Montana, Kunkel et al. (1999) and Ruth (2004) found little evidence to support dichotomy in prey selection between cougars and wolves; they suggested that wolves might have adapted a strategy of stalking deer to close distances before rushing them as opposed to pursuing them over open terrain. Kunkel et al. (1999) further suggested that increases in spatial overlap between cougars and wolves occur during severe winter conditions when deer are most concentrated on winter ranges, and increased snowpack would predictably increase the percentage of deer in wolf diets. Ruth (2004) also reported that cougars and wolves killed deer of similar sex, age, and condition dispelling any differential prey selection based on hunting techniques. Thus, we cannot dismiss a significant contribution of wolf predation to declining deer numbers in hunting district 101 (currently includes a portion of hunting district 109). We also cannot dismiss the likelihood of a wolf pack establishing itself in hunting district 102 that could affect survival of white-tailed deer associated with Bowser similar to what we observed for the population associated with Murphy.

Population Monitoring

Results of this study demonstrated that population trend can be reliably monitored using results of the telephone harvest survey and records of harvested deer examined at check stations. Population reconstruction requires that a middle incisor be extracted from all deer older than yearlings for the most accurate method of assigning ages. However, estimates based on population reconstruction can only document population trend for a period from about 4 years prior to the current season. Trends in annual buck harvest from the statewide telephone survey lead to a 2-yr lag in setting harvest regulations. Despite the disadvantages related to time lags, both methods offer a reasonable estimate of long-term population trend. While buck harvest simply provides a trend, population reconstruction can identify year-to-year changes in sex and age structure. Both can be evaluated at the hunting district level. We also recommend that managers track numbers of bucks examined at check stations for each hunting district and compare those numbers to reconstructed populations. This may yield more useful trend data without the inherent problems of time lags.

Pellet group surveys can yield reliable population estimates during the winter in which harvest regulations are being set, providing two conditions are met: (1) pellet groups being counted reliably are from white-tailed deer; and (2) an estimate of the duration of winter range occupancy by white-tailed deer can be made consistently and reliably across years. The first condition could be met by surveying only those winter ranges, e.g., Bowser, in which deer occupancy from November-April is overwhelmingly that of white-tailed deer. Meeting the second condition would require a radio-collared sample of adult deer, at least initially, to establish duration of winter occupancy. Eventually, duration of occupancy could be modeled from the telemetry data and long-term trends in snow pack as measured from SWE. Pellet group surveys also offer an opportunity to evaluate relative use of key winter ranges over time that might help identify attributes to maintain these areas as crucial winter ranges for white-tailed deer.

Camera surveys employing mark-recapture techniques did not reliably yield trends in population numbers and would likely not be useful for monitoring population trend of white-tailed deer in northwest Montana. Several factors confound their usefulness for monitoring trends in population numbers: 1) our low camera density in a relatively large area probably precluded detection of a significant proportion of the marked sample including multiple re-sightings, 2) camera operation seemingly modified deer behavior and affected re-sighting of individual deer, and 3) meeting the assumption of closure was probably violated by timing of surveys and patterns of deer occupancy of the winter range.

Skeletal growth as determined from diastema measurements of yearling males provided an index of winter density for Bowser. Thus, trend in diastema length might be applied more broadly keeping in mind that winter density is a function of both population numbers and winter severity (Farnes et al. 2000). Given the complexities of these relationships, the real utility for monitoring annual variation in diastema length lies in maintenance of long-term databases that can help further clarify these relationships in the future.

Critical temperature, i.e., the cumulative number of days in which minimum daily temperature fell below –12 °C, influenced recruitment of yearlings into the adult population. Thus, monitoring daily temperatures through winter would be useful to setting quotas for antlerless deer harvests. The relationships that we identified predicted the percent of yearlings in the adult female population during autumn. Determining relationships between spring recruitment rates and critical temperature will require continuing spring classification surveys.

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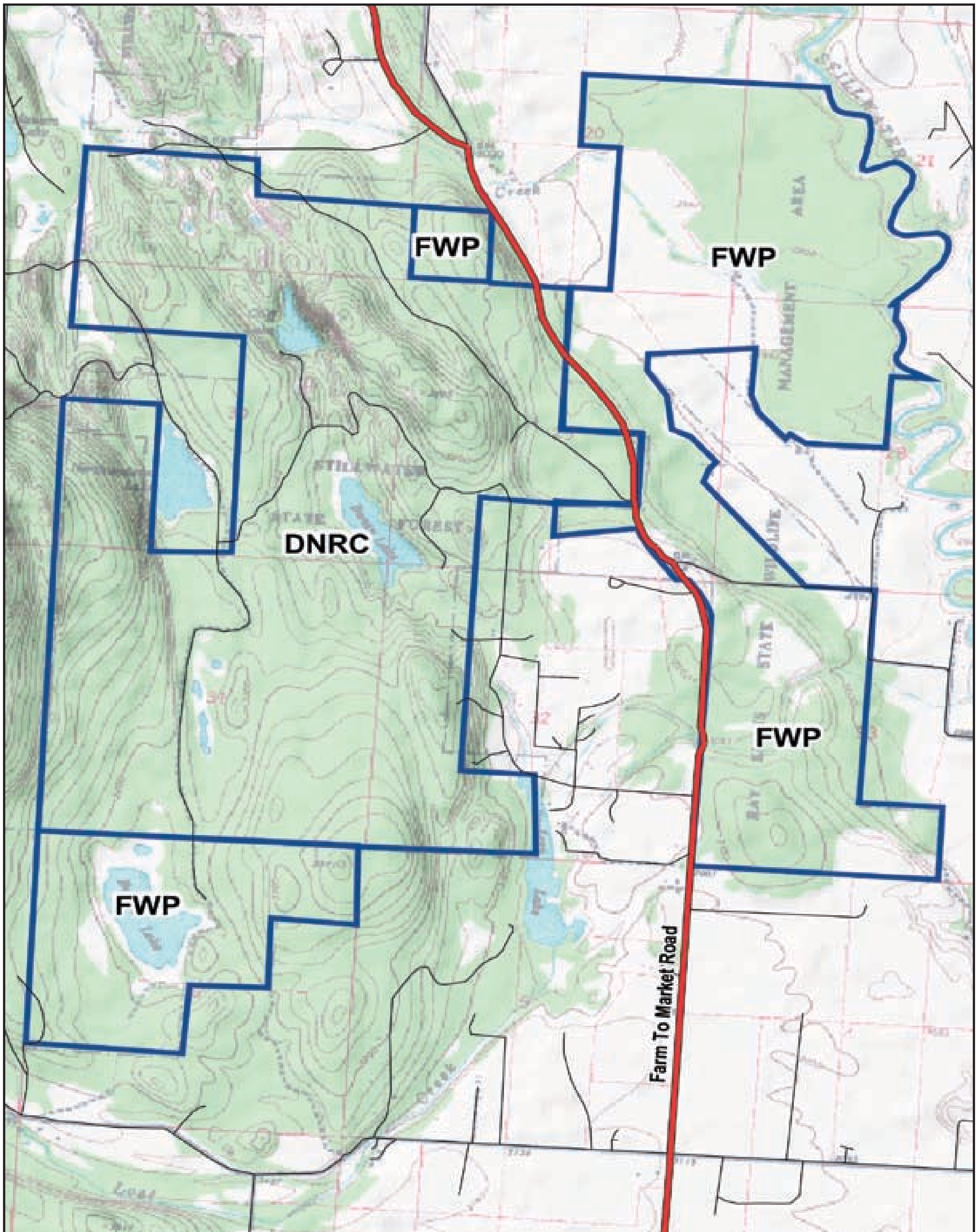
Appendices

Appendix A. Location of parcels of the Ray Kuhns Wildlife Management Area on the Bowser range with interspersed FWP and DNRC lands.



Appendix B. Deer hunting regulations, including season structure and bag limits for general firearm season in Region 1, 1951-199.

Year	General season dates	Bag limit	A-tag	B-tag	Special regulations
1951	13 Nov—15 Nov	1	Either sex deer, except for a portion of the Swan—bucks only from 15 Sep—15 Nov.		
1952	15 Oct—15 Nov	1	Bucks only with either sex hunting the last 8 days.		
1953	15 Oct—15 Nov	1	Bucks only with either sex hunting the last 3 day in Flathead Co. and last15 days in Lincoln Co		
1954	15 Oct—15 Nov	1	Bucks only with either sex hunting the last 12-16 days (wtd only in Flathead Co.).		
1955	15 Oct—15 Nov	1 with opportunity for 2nd deer in some areas as announced?	Either sex in much of Lincoln Co. season long; rest of region bucks only with either sex huntingthe last 16 days in rest of region.		
1956	15 Oct—19 Nov	2	Either sex	Either sex	Only 1 deer taken can be a mule deer.
1957	20 Oct—24 Nov	2	Either sex, either species	Either sex, mule deer only	
1958	19 Oct—23 Nov	2	Either sex, either species	Either sex, mule deer only	
1959	18 Oct—22 Nov	2	Either sex, either species	Either sex, mule deer only	
1960	02 Oct—20 Nov	2	Either sex, either species	Either sex, mule deer only	
1961	15 Oct—19 Nov	1	Either sex, either species		
1962	15 Oct—19 Nov	1	Either sex, either species		
1963	20 Oct—24 Nov	1	Either sex, either species		
1964	18 Oct—22 Nov	1	Either sex, either species		
1965		1	Either sex, either species		
1966	24 Oct—28 Nov	1	Either sex, either species	Not valid in Region 1	The upper Swan-Clearwater drainages were open from 15 Sep to 27 Nov for either sex.

Appendix B. continued.

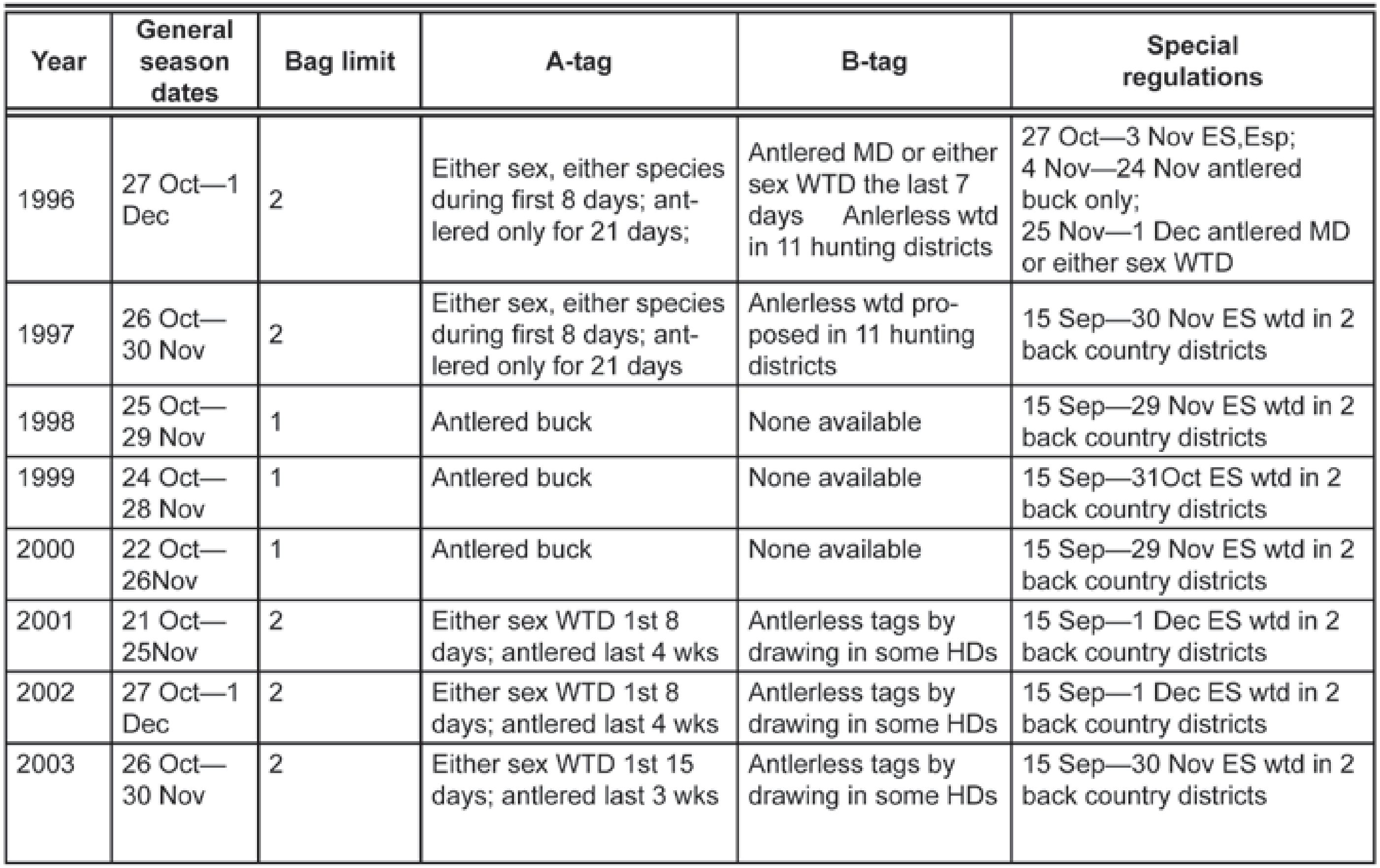
Year	General season dates	Bag limit	A-tag	B-tag	Special regulations
1967	22 Oct—19 Nov	1	Either sex, either species	Not valid in Region 1	A portion of the back country (S Fk Flathead and Swan)were open from mid-late Sep to 19 Nov for either sex.
1968	27 Oct—1 Dec	1	Either sex, either species	Not valid in Region 1	A portion of the back country (S Fk Flathead and Swan) were open similar to 1967. Season closed 17 Nov in HD 101.
1969	19 Oct—23 Nov	1	Either sex, either species	Not valid in Region 1	A portion of the back country (S Fk Flathead) opened 15 Sep.
1970	18 Oct—29 Nov	1	Either sex, either species	Not valid in Region 1	A portion of the back country (S Fk Flathead) opened 15 Sep.
1971	17 Oct—28 Nov	1	Either sex, either species	Not valid in Region 1	A portion of the back country (HD 150) opened 15 Sep.
1972	22 Oct—26 Nov	1	Either sex, either species	Not valid in Region 1	A portion of the back country (HD 150) opened 15 Sep.
1973	21 Oct—25 Nov	1	Either sex, either species	Not valid in Region 1	A portion of the back country (HD 150) opened 15 Sep.
1974	20 Oct—24 Nov	1	Either sex, either species	Not valid in Region 1	A portion of the back country (HD 150) opened 15 Sep.
1975[°]	19 Oct—23 Nov	1	E sp/E sex 1st 3 weeks	Not valid in Region 1	HD 150 open 15 Sep
1976	24 Oct—28 Nov	1	E sp/E sex 1st week	Not valid in Region 1	HD 150 open 15 Sep
1977	23 Oct—27 Nov	1	E sp/E sex 1st week	Not valid in Region 1	HD 150 open 15 Sep
1978	22 Oct—26 Nov	1	E sp/E sex 1st week	Not valid in Region 1	HD 150 open 15 Sep
1979	21 Oct—25 Nov	1	E sp/E sex 1st week	Not valid in Region 1	HD 150 open 15 Sep
1980	19 Oct—30 Nov	1	E sex, E species 1st 8 days; antlered only last 5 wks	Not valid in Region 1	
1981	25 Oct—29 Nov	1	E sex, E species 1st 8 days; antlered only last 4 wks	Not valid in Region 1	Back-country opens 15 Sep (HDs 150, 151)

[°] General season was 1 week shorter in Region 1 than in the rest of the state in 1975.

Appendix B. continued.

Year	General season dates	Bag limit	A-tag	B-tag	Special regulations
1982	24 Oct—28 Nov	1	E sex, E species 1st 8 days; antlered only last 4 wks	Not valid in Region 1	Back-country opens 15 Sep (HDs 150, 151)
1983	25 Oct—27 Nov	1	E sex, E species 1st 8 days; antlered only last 4 wks	Not valid in Region 1	Back-country opens 15 Sep (HDs 150, 151)
1984	21 Oct—25 Nov	2	E sex, E species 1st 8 days; antlered only last 4 wks	Antlerless tags by drawing in 4 HDs	Back-country opens 15 Sep (HDs 150, 151)
1985	27 Oct1 Dec 2	2	E sex, E species 1st 8 days; antlered only last 4 wks	Antlerless tags by drawing in 4 HDs	Back-country opens 15 Sep (HDs 150, 151)
1986	26 Oct—30 Nov	1	E sex, E species 1st 8 days; antlered only last 4 wks	Valid by drawing only in HD 170 for shotgun, archery of muzzle loader	Back-country opens 15 Sep (HDs 150, 151)
1987	25 Oct—29 Nov	1	E sex, E species 1st 15 days; antlered only last 3 wks	Valid by drawing only in HD 170 for shotgun, archery of muzzle loader	Back-country opens 15 Sep (HDs 150, 151)
1988	23 Oct—27 Nov	2	Either sex WTD 1st 15 days; antlered last 3 wks	Antlerless tags by drawing in 2 hunting districts: 121 and 123.	23 Oct—7 Nov ES, Esp; 8 Nov—27 Nov antlered buck only
1989	22 Oct—26 Nov	2	Either sex WTD 1st 15 days; antlered last 3 wks	Antlerless tags by drawing in 6 hunting districts	22 Oct—5 Nov ES, Esp; 6 Nov—26 Nov antlered buck only
1990	21 Oct—27 Nov	2	Either sex WTD 1st 15 days; antlered last 3 wks	Antlerless tags by drawing in 6 hunting districts	21 Oct—7 Nov ES, Esp; 8 Nov—27 Nov antlered buck only
1991	27 Oct—1 Dec	2	Either sex WTD 1st 15 days; antlered last 3 wks	Antlerless tags by drawing in 9 hunting districts	27 Oct—10 Nov ES, Esp; 11 Nov—1 Dec antlered buck only
1992	25 Oct—29 Nov	2	Either sex WTD 1st 15 days; antlered last 3 wks	Antlerless tags by drawing in 10 hunting districts	20 Oct—8 Nov ES, Esp; 9 Nov—29 Nov antlered buck only
1993	24 Oct—28 Nov	2	Either sex WTD 1st 15 days; antlered last 3 wks	Antlerless tags by drawing in 10 hunting districts drawing in	24 Oct—7 Nov ES, Esp; 8 Nov—28 Nov antlered buck only
1994	23 Oct—27 Nov	2	Either sex WTD 1st 15 days; antlered last 3 wks	Antlerless tags by drawing in 10 hunting districts	23 Oct—6 Nov ES, Esp; 7 Nov—27 Nov antlered buck only
1995	22 Oct—26 Nov	2	Either sex WTD 1st 15 days; antlered last 3 wks	Anlerless wtd in 10 hunting districts	22 Oct—5 Nov ES,Esp; 6 Nov—1 Dec antlered buck only

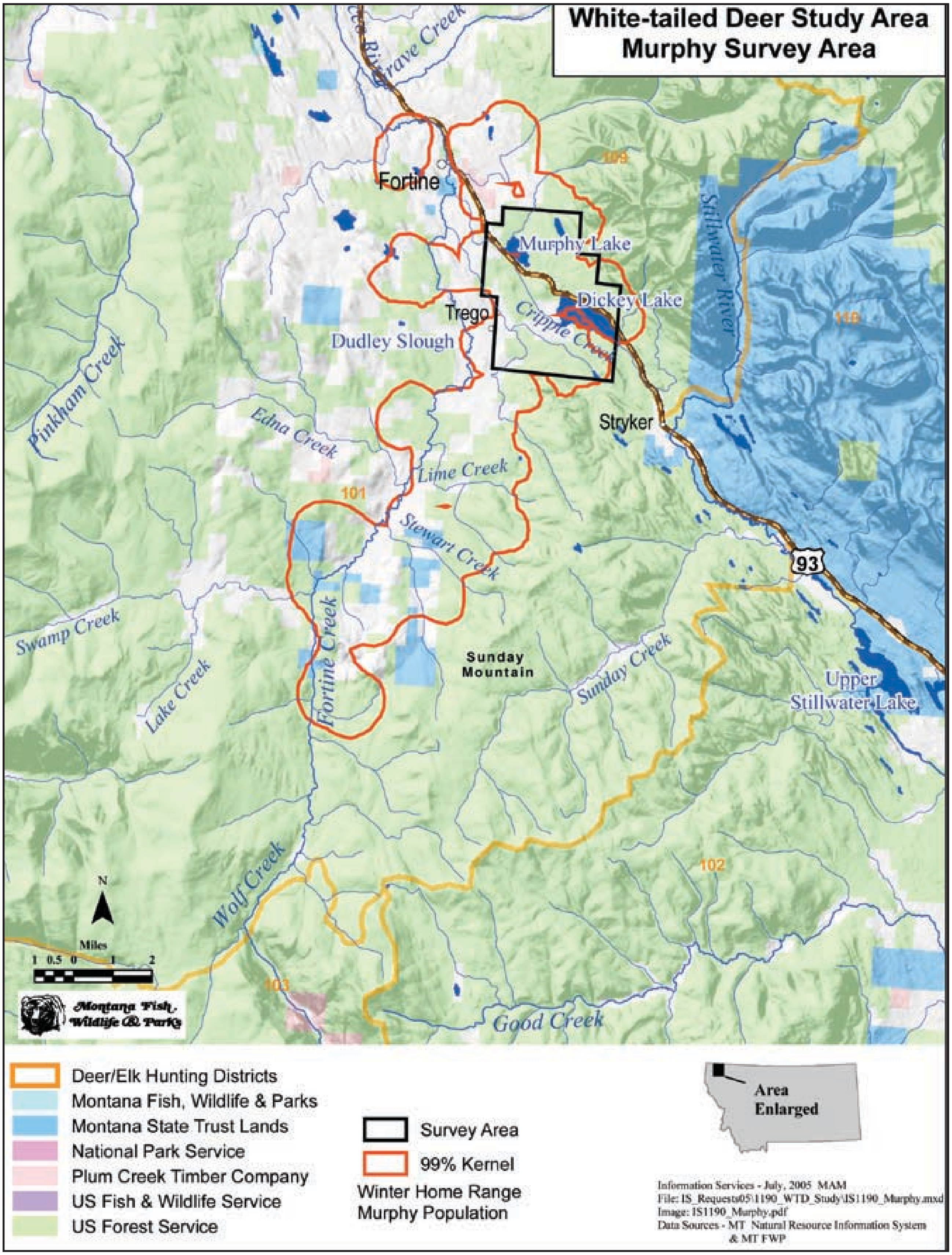
Appendix B. continued.



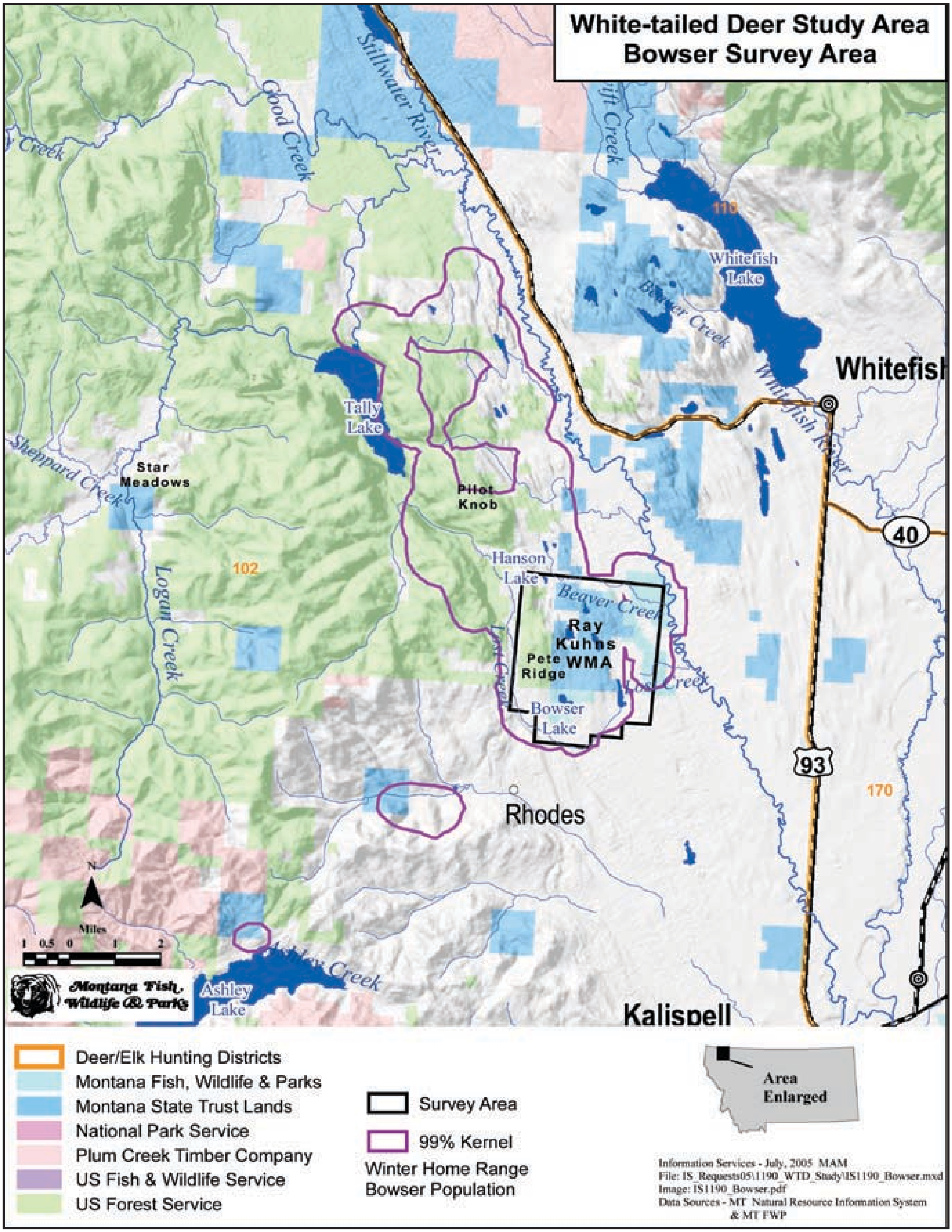
Year	General season dates	Bag limit	A-tag	B-tag	Special regulations
1996	27 Oct—1 Dec	2	Either sex, either species during first 8 days; antlered only for 21 days;	Antlered MD or either sex WTD the last 7 days Anlerless wtd in 11 hunting districts	27 Oct—3 Nov ES,Esp; 4 Nov—24 Nov antlered buck only; 25 Nov—1 Dec antlered MD or either sex WTD
1997	26 Oct—30 Nov	2	Either sex, either species during first 8 days; antlered only for 21 days	Anlerless wtd proposed in 11 hunting districts	15 Sep—30 Nov ES wtd in 2 back country districts
1998	25 Oct—29 Nov	1	Antlered buck	None available	15 Sep—29 Nov ES wtd in 2 back country districts
1999	24 Oct—28 Nov	1	Antlered buck	None available	15 Sep—31Oct ES wtd in 2 back country districts
2000	22 Oct—26Nov	1	Antlered buck	None available	15 Sep—29 Nov ES wtd in 2 back country districts
2001	21 Oct—25Nov	2	Either sex WTD 1st 8 days; antlered last 4 wks	Antlerless tags by drawing in some HDs	15 Sep—1 Dec ES wtd in 2 back country districts
2002	27 Oct—1 Dec	2	Either sex WTD 1st 8 days; antlered last 4 wks	Antlerless tags by drawing in some HDs	15 Sep—1 Dec ES wtd in 2 back country districts
2003	26 Oct—30 Nov	2	Either sex WTD 1st 15 days; antlered last 3 wks	Antlerless tags by drawing in some HDs	15 Sep—30 Nov ES wtd in 2 back country districts

Appendix C. Portions of the two winter ranges in which pellet group and camera surveys were conducted.

Appendix C-1. Murphy winter range including the surveyed portion of the winter range.



Appendix C-2. Bowser winter range including the surveyed portion of the winter range.



Part II:
Spacial Relationships and Resource Selection

Steven T. Hoekman
Gary L. Dusek
Alan K. Wood

Executive Summary

We examined fidelity to winter use areas, described migratory movement, delineated annual and winter ranges, and developed predictive models of resource use during winter relative to snow accumulation for two populations occupying the eastern Salish Mountains northwest of Whitefish, Montana. We captured deer from 1988-1998 in areas where densities during winter were greatest and equipped 409 deer with radio-collars (Bowser population, $n = 256$; Murphy population, $n = 153$), that yielded a radio-collared sample at a ratio of ~3 females: male. From March 1988 through May 2000, we monitored locations of radio-collared deer from fixed wing aircraft during daylight hours.

To assess philopatry, we compared Schoener's ratio for individuals within versus between years. We used diffusion models to estimate daily movement rates relative to date for each sex. We used Bayesian hierarchical models to compare used locations to available winter range and to estimate resource selection functions predicting relative probability of use at the individual- and population-level with respect to topography, vegetation attributes, and an index of snow accumulation. Resources within a 200-m radius buffer characterized attributes at each location. We determined mean elevation, mean slope, and an index of terrain roughness for each location using a digital elevation model. Using a LANDSAT-derived vegetation map, we characterized locations by floristics and vegetation physiognomy, i.e., tree size and tree canopy cover. For the Bowser population only, we also conducted analyses based on timber stand inventory data maintained by public land management agencies.

Slight decreases in Schoener's ratio estimated for females within versus across years ($\bar{x} \pm$ SE; Bowser, 1.75 ± 0.035 vs. 1.61 ± 0.047; Murphy 1.84 ± 0.049 vs. 1.58 ± 0.083) demonstrated that individuals showed relatively high philopatry to their winter use areas. Movement rates for both sexes and both populations peaked in late November and early April, but peaks typically were higher for males. Movement rates ebbed during midwinter and, for females, during early spring. Otherwise movement rates were much higher for males.

Resource use varied strongly relative to snow conditions. With minimal snow accumulation, use by each population was dispersed as individual preference varied widely and deer exploited a wide range of habitats and elevations. Deer extensively used both forested and non-forested habitat, but both populations tended to prefer relatively open habitats, i.e., grass, shrub, or open tree canopy. With increasing snow accumulation, deer from both populations progressively restricted their distribution and strongly avoided non-forested habitat and forest with small trees and open tree canopy cover. Instead, deer strongly preferred relatively mature forests, i.e., dominant tree DBH >10 in [25.4 cm] tree canopy cover >25% at lower elevations. Deer appeared to select these structural attributes irrespective of tree species.

High philopatry of deer to winter use areas is commonly observed in deer and likely is maintained by matrilineal inheritance of use areas by young from mothers. Such traditional use of wintering areas likely confers benefits of knowledge of local resources and social dominance of the matriarch but may limit ability to respond to habitat disturbance or colonize new areas. Segregation of populations on separate winter ranges may also create important small-scale population and genetic structure. Peak fall and spring movement rates coincided with migration, and higher fall movement rates for males likely were related to rutting behavior

rather than hunting disturbance. High energetic costs of locomotion in deep snow combined with a probable strategy of energy conservation seemingly explained low movement rates during mid-winter. A low rate of movement for females during spring coincided with fawning.

Patterns of resource use that we observed in the Salish Mountains were consistent with the hypothesis that deer enhance survival by adopting a strategy of energy conservation during most winters. Dense tree canopy intercepts snowfall and hence reduces energetic costs of movement and likely enhances ability to evade predators. With minimal snow, deer preferred relatively open habitat that may offer a somewhat wide range of forage and optimal forage availability. As snow accumulation increased, deer concentrated in mature conifer forest. Strong traditional use of winter habitat and segregation of populations during winter suggested that wintering populations can be biologically meaningful management units. However, these populations may have limited capacity to respond to disturbance on traditional wintering areas. Because mature conifer forest at lower elevations appears critical to mitigating deleterious effects of severe winter weather, we recommend management that retains effectiveness of these stands to ameliorate adverse effects of snowpack and cold temperatures on deer.

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Section 1: Introduction

White-tailed deer (*Odocoileus virginianus*) include the primary big game species harvested in northwest Montana (Dusek et al. 2006); however, guidelines for habitat management for these populations remain untested. Like other northern populations of white-tailed deer that experience a severe winter climate, populations in northwest Montana occupy coniferous forest and migrate between summer and winter ranges rather than remaining sedentary (Van Deelen et al. 1998, Sabine et al. 2002). Selective pressures on migratory populations of white-tailed deer differ by season, and migratory white-tailed deer appear to maximize forage intake outside winter but operate under a strategy that favors energy conservation during winter (Huot 1974, Dusek 1987, Nicholson et al. 1997b). Thus, the general perception that availability of browse limits white-tailed deer, and hence deer prefer open, early seral habitats (Jenkins and Wright 1988) as well as specific recommendations to open up conifer cover to improve forage production (Pengelly 1963, Lyon and Jensen 1980) may be sub-optimal for management of winter range in the northern Rocky Mountains. Instead, migratory populations during winter typically concentrate in traditional "deer yards" often characterized by mature conifer forest (Pauley et al. 1993). These habitats may mitigate detrimental effects of severe weather by minimizing snow accumulation and providing improved thermal cover. Because the cumulative effect of cold winter temperatures is negatively

related to recruitment of white-tailed deer in northwest Montana (Dusek et al. 2006) and because land management practices heavily influence vegetation physiognomy in this region, accurate predictive models of resource use during winter are critical to effective management of white-tailed deer.

We focus on the wintering ecology of two populations of white-tailed deer in northwest Montana during 1988-2000. Our overall objectives were to examine patterns of seasonal movement and distribution during winter to identify important wintering areas and to build predictive models of resource use during winter to (1) identify preferred resources, (2) increase understanding of the mechanisms driving resource selection during winter, (3) identify areas that are of high value as winter range, and (4) predict population responses to resource management. For each population we (1) examined between-year fidelity of individuals to their winter use areas, (2) estimated individual movement rates to describe migratory movements and to delineate summer versus winter periods, (3) estimated size of annual and winter ranges, and (4) developed predictive models of resource use during winter relative to topography, floristic composition, tree physiognomy, and snow accumulation.

Fidelity to Winter Use Areas

Large, terrestrial mammals that inhabit predictably changing habitats often migrate between seasonal ranges and exhibit a circannual pattern of space use with season-specific fidelity (Blanchard and Knight 1991, Linnell and Andersen 1998). Migratory behavior in ungulates can optimize use of seasonal variation in forage, facilitate escape from predators, and mitigate deleterious effects of adverse weather conditions (Seip 1992, Albon and Langvatn 1992, Nicholson et al. 1997b). White-tailed deer are sedentary across much of their range (Larson et al. 1978). However, in many northern populations where snow cover is persistent through winter, deer migrate between relatively distinct summer and winter ranges (Nelson and Mech 1981, Van Deelen et al. 1998, Lesage et al. 2000). Deer are strongly traditional in their migratory routes and seasonal ranges, which are passed from does to female offspring. Thus, matrilineal groups appear to provide a mechanism perpetuating traditional migratory movements (Tierson et al. 1985, Van Deelen et al. 1998, Nelson and Mech 1999). Individual females have consistently shown high fidelity to their previous summer use areas, but fidelity to winter use areas has been variable (Tierson et al. 1985, Dusek et al. 1989, Beier and McCullough 1990, Aycrigg and Porter 1997, Grund et al. 2002). However, strength of fidelity to winter use areas could have strong implications for population response to variable winter weather conditions (Grund et al. 2002), response to management or disturbance of winter range habitat (Hood and Inglis 1974, Tierson et al. 1985), social and genetic structure of the population (Mathews and Porter 1993, Ellsworth et al. 1994, Purdue et al. 2000), dispersal from and colonization of winter range (Purdue et al. 2000), and local population control (McNulty et al. 1997). Thus, we assessed the magnitude of fidelity of individuals to winter use areas among years.

Timing and Distance of Seasonal Movement

Most white-tailed deer in the Salish Mountains are migratory, moving ~20-30 km between summer range consisting of higher-elevation forest and meadows and winter range in lower-elevation valleys with relatively dense coniferous cover (Morgan 1993). For many white-tailed deer populations in high elevation or northern areas, decreasing temperatures and increasing snow accumulation appear to drive short-distance migrations from summer to winter areas (Nelson and Mech 1981, Tierson et al. 1985, Sabine et al. 2002). Differences in selective pressures between summer and winter periods could explain differences in behavioral patterns and resource use between these periods. Migratory white-tailed deer appear to optimize foraging opportunities on summer areas and to optimize energy conservation and minimize risk of predation on wintering areas (Huot 1974, Nelson and Mech 1981, Dusek 1987, Beier and McCullough 1990, Nicholson et al. 1997b).

Analyses of resource selection benefit from focusing on critical periods during the annual cycle and from delineating periods during which available resources and patterns of resource selection are expected to be relatively uniform (Manly et al. 2002). Morgan (1993) previously described summer movements and resource use patterns for the Bowser herd. We focus on resource selection during winter.

Defining Available Resources

Knowledge of resource requirements is necessary for effective management of wildlife populations. Studies of resource selection compare usage of resources by animals to available resources to determine preferences. Defining resources that are considered available to animals is critical to the results and interpretation of resource selection analyses (Johnson 1980, Manly et al. 2002). Considering resource components rarely or never selected as available likely will be uninformative and may influence interpretation of whether used resources are preferred or avoided (Johnson 1980). Resource selection often has been conceptualized as a hierarchical process, in which selections at larger scales delimit available resources at smaller scales, and criteria for selection likely differ among scales (Johnson 1980, Wiens and Rotenberry 1981, Manly et al. 2002). For example, selection of home range might define the total resource requirements of an animal relative to locally available resources, foraging needs may lead to disproportionate selection of specific habitat patches within the home range, and individual food items within each “foraging patch” are selected to optimize energy intake. Although all scales may be arbitrary and no single scale is “correct,” the most appropriate scale(s) are those most clearly linked to the motivation for the study (Manly et al. 2002). Multi-scale approaches to analyses of resource selection are often preferable because conclusions are less likely to depend on any one scale and because differing patterns at each scale can be identified (Levin 1992, Otis 1997). We defined available habitat at the annual range and winter range scales, using kernel density estimators to define 99% utilization distributions for each population using locations throughout the year or during the winter period.

Resource Selection Analyses

Resource use by white-tailed deer typically is explained relative to their energy budget. Although some areas of dense vegetation may be necessary to satisfy cover requirements, many studies of resource selection have emphasized that deer optimize forage intake by selecting relatively open canopy habitats that promote growth of seral shrubs and forbs (Jenkins and Wright 1988). Management recommendations for benefitting white-tailed deer populations in forested areas have focused on silviculture treatments opening tree canopy and creating habitat edge (Pengelly 1963, Krefting and Phillips 1970, Lyon and Jensen 1980). However, northern deer populations that experience severe winter climate face divergent selective pressures during summer and winter and often are migratory (Lesage et al. 2000).

Deep snow is a primary factor dictating patterns of migratory behavior and habitat selection during winter (Van Deelen et al. 1998, Sabine et al. 2002). Cold temperatures and accumulation of deep snow triggers winter migration and imposes severe energetic constraints. Decreased abundance and availability of forage diminishes potential energy intake, difficulty in locomotion and obtaining forage in deep snow increase energy expenditure, and temperatures below lower critical temperatures increase basal metabolism and hence energetic needs (Parker et al. 1984, Mautz et al. 1985). In response to severe winter climate, deer may adapt a strategy favoring energy conservation over energy intake. In addition to physiological responses depressing energy needs, deer may also migrate to lower elevations, become less mobile, select mature conifer stands that lack forage but reduce snow depth (Hoffman and Robinson 1966, Pauley et al. 1993).

We determined resource preferences for our study populations by comparing used to available resources at multiple spatial scales. We defined available at the scale of the estimated annual and winter ranges for each population. We developed predictive models of relative probability of use based on attributes of topographic, floristic, and tree physiognomic resources. Furthermore, we examined how resource selection interacted with severe winter weather as characterized by snow accumulation and minimum temperatures. Finally, we used projections from selected predictive models to identify critical habitat for these populations during winter and in particular during periods of severe weather.

Section 2: Study Areas And Field Methods

Study Areas

We studied two populations of white-tailed deer in the Salish Mountains in Flathead and Lincoln Counties in north-west Montana at latitude 48° 30' N longitude 114° 30' E (Fig. 1). The study populations primarily occupied areas northwest of Whitefish, Montana and west of the Stillwater River in the Fortine Creek, Good Creek, and Logan Creek drainages. The region inhabited by both populations lies in a north-northwest trending intermontane basin that was sculpted by glaciers of the Cordilleran ice sheet (Montagne et al. 1982, Kendy and Tresch 1996). The basin occupies the southern extension of the Rocky Mountain Trench of late Paleocene to Eocene age. The Salish Mountains include metasedimentary rocks of the Middle Proterozoic Belt Supergroup made up of limestone, dolomite, siltite, quartzite, and argillite. Elevations on the study area range from ~850 to ~2000 m.

The macroclimate has a strong maritime influence and is characterized by warm, relatively dry summers and cool, moist winters (Caprio and Nielson 1992). Most of the annual precipitation accumulates during winter as snowfall, which generally persists from December through March in most years. Local microclimates are strongly influenced by elevation and a precipitation shadow created by mountains on the west side of the valley, with lower temperatures and increased snow accumulation and persistence generally occurring with increasing elevation (Farnes et al. 2000). Precipitation records from climatological stations indicate an average of 42 cm precipitation/year at Kalispell, 56 cm at Whitefish, and >70 cm near the crest of the mountain ridges on the west side of the valley.

We trapped deer from two areas of high winter concentration. One area was focused on the population of deer that wintered on the "core" winter range near Bowser and Tally Lakes (Mundinger and Riley 1983), henceforth the "Bowser population." Although white-tailed deer winter primarily along the eastern fringe of lower foothills from north of Pilot Knob south to Ashley Creek (Mundinger and Riley 1982), our efforts to trap and monitor deer focused primarily on ~ 32 km2 bounded on the west and south by Lost Creek and on the east by the Stillwater River that extended north to Beaver Creek, Hansen Lake, and the northernmost extent of Pete Ridge. This area included the Ray Kuhns WMA along the floodplain of the Stillwater River, the Bowser Lake WMA, and a large tract of state forest. Our second trapping area was focused on the population of deer that wintered near Murphy and Dickey Lakes, henceforth the "Murphy population." Although deer may winter in the Fortine Creek drainage to areas extending above Stewart Creek, most of our effort to trap and mark deer centered on the area around Murphy and Dickey lakes, Ant Flat, Cripple Creek, and Dudley Slough.

A small number of deer were trapped along the north shore at Ashley Lake during March 1988. Because these deer showed distinct patterns of space use relative to deer trapped on the "core" Bowser winter range, the yearlong range of most of these deer ooccupied areas spatially distinct from the Bowser population and hence were excluded from analyses.

Deer in these two populations frequented portions of the Flathead (FNF) and Kootenai (KNF) national forests, the Stillwater State Forest, the Ray Kuhns WMA administered by Montana, Fish, Wildlife and Parks (FWP), and commercial and residential private lands (Fig. 1). Most land has been managed for commercial timber production and wood products. Cutting units, which vary in age and stage of succession,

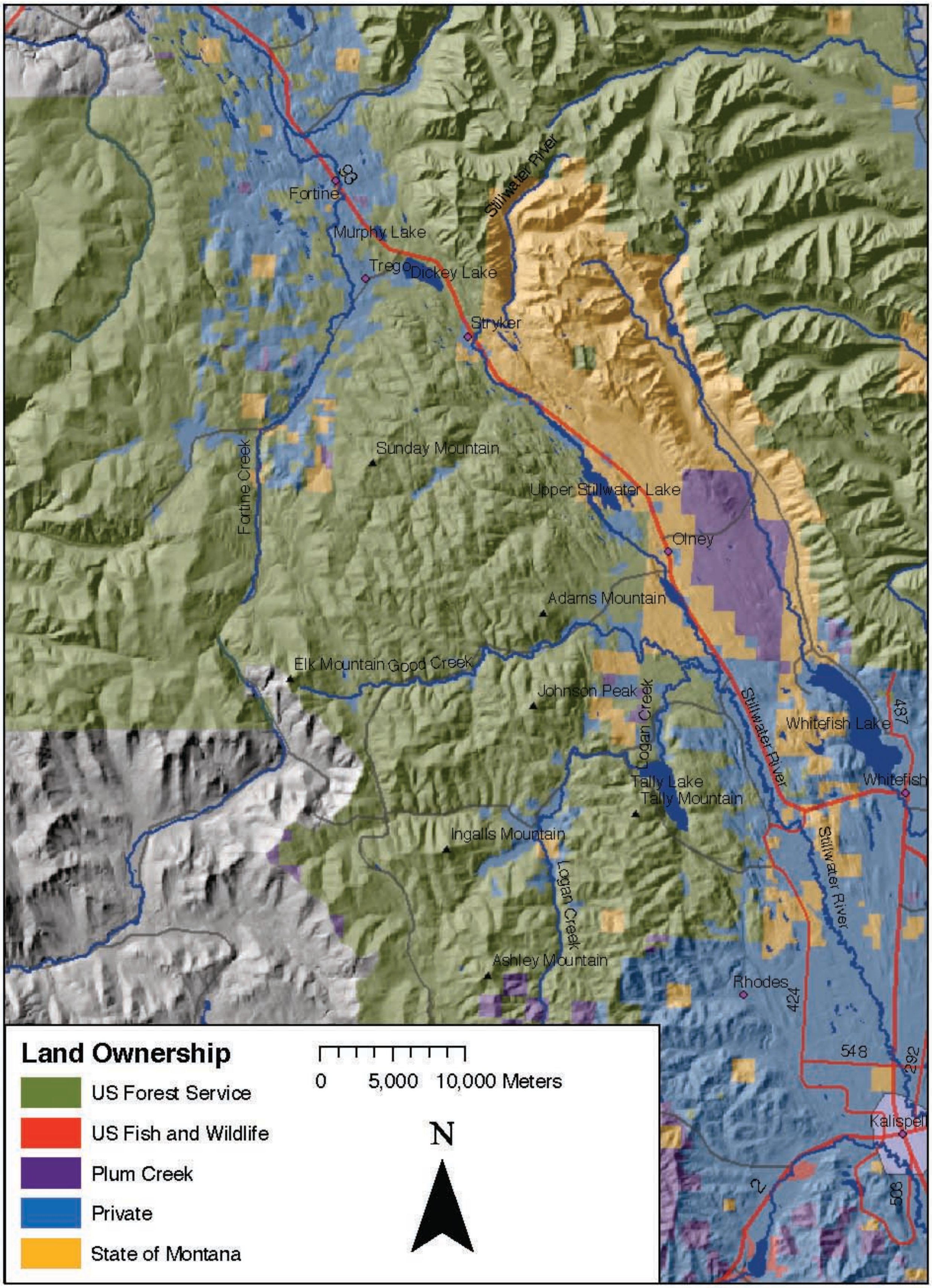


Figure 1. Land ownership in areas occupied by the Bowser and Murphy populations of white-tailed deer in north-west Montana during 1988-2000.

dot the upland landscape. With the exception of the Stillwater River and its major tributaries, second growth conifer forest dominated the vegetative cover throughout the Salish Mountains. Wildfire has significantly influenced vegetative cover with the last major stand replacement fires occurring in 1910 and 1926.

The *Pseudotsuga menziesii/Symphoricarpos albus* habitat type (habitat types defined following Pfister et al. 1977) predominated along the lower valley foothills in which Douglas-fir dominates the overstory among older stands of second-growth forest. These stands also include a component of western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and to a lesser extent ponderosa pine (*Pinus ponderosa*). The shrub understory included common juniper (*Juniperus communis*), snowberry (*Sympnoricarpos albus*), Oregon grape (*Berberis repens*), and kinnikinnic (*Arctostaphylus uva-ursi*). The *Abies lasiocarpa// Clintonia uniflora* habitat type dominated upland portions of the study area although currently consists of stands of mature mixed conifers, large homogeneous stands of lodgepole pine, and clearcuts of various stages of succession. A *Pinus contorta/ Xerophyllum tenax* cover type occupied many of the upper drainages throughout the Salish Range. Timber species regeneration in older clear cuts was limited almost exclusively to lodgepole pine and western larch. The *Pseudotsuga menziesii/ Calamagrostis rubescens* habitat type occupied drier, southerly exposures. The *Picea/ Clintonia uniflora* habitat type occurred along bottomlands of the Stillwater River and streams throughout the Salish Range. Deciduous trees and shrubs along riparian sites included black cottonwood (*Populus trichocarpa*), aspen (*P. tremuloides*), and willows (*Salix spp*.). Riparian sites included streams with yearlong surface flow. Wetland sites were well distributed through the uplands and included seeps, sloughs and potholes.

Field Methods

We used Clover traps (Clover 1954) placed along well-traveled deer trails to capture white-tailed deer on each trapping area during January and February from 1988 though 1998. Traps were baited with alfalfa following procedures described by Morgan and Dusek (1992). We altered placement of traps within each trapping area over time to attempt to evenly distribute trapping effort across space and hence to obtain a representative sample of deer from each population. All captured deer were manually restrained. We recorded sex and estimated age based on patterns of tooth replacement and wear (Severinghaus 1949). Capture and handling of deer followed protocols established by FWP. We affixed a numbered metal tag to each ear of all captured deer and fitted a sample of deer with radio-transmitter collars (Telonics, Mesa, AZ). We maintained a ratio of ~3 female/male deer in the radio-marked sample. From 1991 through 1996, we sought to radio-mark as many females of known versus estimated age as possible. Known-age females included fawns or yearlings, as well as older females that had previously been captured as fawns or yearlings. Because males >1 year of age were infrequent in the captured sample relative to females of the same age, we included most captured males >1 year of age in the radio-marked sample from 1988 through 1994. When possible, we extracted a middle incisor (I_1) from radio-marked deer after death in order to more accurately estimate age using cementum analysis (Matson's Lab, Milltown, Montana).

We relocated radio-marked deer using fixed-wing aircraft from April 1988 through May 2000. Intervals between relocations were variable, but typically ranged between 2-4 weeks. Relocations were obtained only during daylight hours, with most obtained between 0600 and 1300. We assumed that telemetry location in this study was similar to the estimate of 196 ± 72 m estimated from a study of radio-marked elk (*Cervus elaphus*) in the same region (Vore and Schmidt 2001), which was conducted in similar habitat and somewhat more rugged terrain and that used the same pilot and aircraft.

Section 3: Statistical Analyses

Fidelity to Winter Use Areas

We used comparisons of Schoener's ratio (1981) estimated within versus across years to quantitatively assess fidelity of individuals to winter use areas. Schoener's ratio provides a mathematical description of autocorrelation in movement data by comparing variation in distance among serial locations to average variation in distance among all locations. This ratio is useful for assessing site fidelity, because differences in the use of space over time lead to increased serial autocorrelation (Mauritzen et al. 2001). Use of Schoener's ratio relative to home range estimators or multiresponse permutation procedures offered substantial advantages, including avoidance of restrictive assumptions, estimates that were largely independent of sample size, and avoidance of a tendency to overestimate lack of fidelity because of serial autocorrelation or sampling error (Swihart and Slade 1985b, White and Garrott 1990, Van Dyke et al. 1998, Kernohan et al. 2001, Kernohan et al. 2002).

For our analyses, x and y coordinates described the easting and northing in meters in the 2-dimensional Universal Transverse Mercator plane. For a sample of consecutive locations $i = 1$ to n, the mean squared distance between successive locations is

$$t^2 = \frac{1}{m}\sum_{i=1}^{m}\left(x_{i+1} - x_i\right)^2 + \frac{1}{m}\sum_{i=1}^{m}\left(y_{i+1} - y_i\right)^2, \quad (1)$$

where m is the number of pairs of successive locations and $[x_i, y_i]$ are paired coordinates describing the ith location. The mean squared distance from the center of activity is

$$r^2 = \frac{1}{n-1}\sum_{i=1}^{n}\left(x_i - \bar{x}\right)^2 + \frac{1}{n-1}\sum_{i=1}^{n}\left(y_i - \bar{y}\right)^2, \quad (2)$$

where $\bar{x} = \sum x_i / n$ and $\bar{y} = \sum y_i / n.$ (3)

Schoener's ratio is defined as t^2/r^2 (Schoener 1981) and generally has an expected value of 2 when serial locations are independent and a decreasing value ≤ 2 but > 0 as correlation between serial locations increases (Swihart and Slade 1985b). Because estimates within individuals likely were non-independent, we relied on a design treating individuals as the sampling unit to make inference about the population (Manly et al. 2002). We estimated the mean and sampling variance for each population as the mean and variance of the sample of estimates for individuals. For each individual, we included in analyses only winter seasons with $m \geq 2$. The within-season estimate for an individual was the mean of estimates for each winter season. We estimated Schoener's ratio across seasons using pooled locations across all winters to calculate r^2, but using only serial locations within winters to calculate t^2. Thus, we would expect within versus across year estimates to be equal if individuals exhibited complete site fidelity, but lack of fidelity would lead to increases in r^2 and hence relatively lower estimates of Schoener's ratio across years. We conducted separate analyses for each deer population, excluding the very small samples of males and the few non-migratory individuals.

To provide a more biologically interpretable measure of the magnitude of change in use of space, we estimated the mean distance between successive centers of winter use areas for individuals. For these analyses, we used only estimated winter centers of activity estimated from ≥ 5 locations, and we considered males versus females separately. We also estimated mean distance from the center of winter use areas in each year for each individual, which provided a biologically interpretable index of the size of winter use areas. Because both distributions of distances were strongly positively skewed, we used a natural log transformation to normalize these data. To facilitate interpretation, we back-transformed estimates to original units and estimated standard errors using the Delta Method (Seber 1982).

Analyses of fidelity to winter use areas were based on locations that were previously classified as winter locations. Locations were divided into four categories (summer, winter, transitional, accessory) as described by Morgan (1993). Most locations for individuals during each year fell into distinct summer and winter groupings, characterized by dense, highly localized locations that were utilized consistently through each season. Typically, ≤ 2 transitional locations were intermediate to summer and winter locations during migration. Accessory locations were the few locations falling into none of the previous categories. These locations normally consisted of 1-3 serial locations in an area that was utilized once or not in all years.

Timing and Distance of Seasonal Movement

The linear distance between two successive locations for an individual likely increases with the length of the time interval, which must be accounted for to estimate daily movement rates (Hjermann 2000). Relationships between linear distance moved versus time interval often have been modeled as a diffusion process, where movement rates in conjunction with tortuosity, i.e., directed vs. convoluted movement paths, determine linear movement distance over a time interval (Johnson et al. 1992). We estimated linear distance *d* between successive locations using a log linear model

$$\ln(d) = k \cdot \ln(t) + \beta + e, \tag{4}$$

where *k* is an estimated constant describing tortuosity, *t* is the time interval in days between successive locations, β is the linear structure of the model, and *e* is a normally distributed error term with mean = 0 and variance = σ^2. A value of *k* = 1 describes a simple random walk (Fickian diffusion), *k* >1 indicates facilitated diffusion, and *k* < 1 indicates inhibited diffusion (Johnson et al. 1992). We initially fit this model for each population with no linear structure. Examination of residuals on predicted values showed no large outliers or evidence of trends in residuals, supporting the adequacy of this model structure in accounting for time interval on movement distance in our data.

To allow flexibility in estimation of variation in movement distance relative to date, we modeled seasonal variation in daily movement rates using a polynomial structure

$$\ln(d) = k \cdot \ln(t) + \beta_0 + \beta_1(j) + \beta_2(j)^2 + \beta_3(j)^3 + \ldots + \beta_x(j)^x, \tag{5}$$

where *j* is mid-point of each time interval, defined as days since 15 July. We chose 15 July as the start of the annual cycle because our primary interest was estimation of movement to define the wintering period and because we expected females to be relatively sedentary immediately post-fawning (Morgan 1993). Because appropriate model complexity was unknown, we selected parsimonious models by sequentially adding higher order polynomial terms until Akaike's Information Criterion adjusted for sample size (AICc) no longer decreased with additional parameters (Burnham and Anderson 2002). Analyses were conducted using PROC GLM in SAS v. 8.02 (SAS Institute 1999). Because we expected seasonal activity patterns to differ between populations and between sexes, we fit separate models for each group. Despite evidence of large inter-annual variation in patterns of seasonal movement (Morgan 1993), we pooled years in analyses to define typical, long-term patterns. Because our modeling approach assumed that movement rates were constant within each individual time interval, we restricted analyses to time intervals ≤ 20 days (> 60% of all intervals) to minimize the pooling of widely disparate movement rates within an interval and to more precisely associate movement with date. Because our location methods could not precisely estimate very short movement distances and to avoid estimation problems associated with lack of movement between locations, we considered all movement distances of < 50 m (*n* = 34) to be 50 m.

We used peak-estimated rates of daily movement for females in fall and spring to delineate the winter period for each population (Ferguson and Elkie 2004). We limited analyses to females because we were primarily interested in resource selection by females, peak movement periods were similar between sexes, and larger samples for females increased precision of estimates.

To estimate mean migratory distance for each population, we calculated the mean UTM x and y locations for summer and winter locations of each individual and then calculated the Euclidian distance between mean seasonal locations for each individual. We excluded from analyses non-migratory deer and deer for which we had <5 summer or winter locations.

Defining Available Resources

Our analyses focused on identifying attributes of resources influencing selection of winter range for the Bowser and Murphy populations and understanding how environmental factors influenced resource selection. We defined available resources at two scales: resources available to each population throughout the year and during winter. To avoid arbitrary or subjective definitions of resources available to each population, we defined the spatial extent of available resources by estimating utilization distributions (Pauley et al. 1993). We estimated distributions using a bivariate adaptive kernel density estimator, which is a non-parametric estimator that provides a probability density estimate for a two-dimensional plane (Silverman 1986). We believed an adaptive kernel density estimator superior to a parametric home range estimator for our data because it (1) made no *a priori* distributional assumptions, (2) did not assume a single center of activity, (3) provided estimates of relative densities in a true probabilistic sense, and (4) increased efficiency through use of smoothing functions (Silverman 1986, Worton 1989, Harris et al. 1990). We chose the kernel density estimator over Fourier transform methods to avoid problems associated with negative density estimates and specification of a finite plane for analyses (Worton 1989). We used 99% probability contours of the estimated utilization distribution to define the spatial range of annual and winter resources available to each population. We preferred an adaptive to fixed kernel density estimator because the adaptive kernel provides better estimates in the tails of the distribution (Worton 1989) upon which our range delineation depended. The software BIOTAS v. 1.03 (Ecological Software Solutions, Switzerland) facilitated all analyses.

For a random sample of n independent locations where the data consist of a series of paired coordinates from X_1 to X_n, the underlying probability density function $f(x)$ from which data are derived can be estimated using a bivariate adaptive kernel density estimator

$$\hat{f}(\mathbf{x}) = \frac{1}{n}\sum_{i=1}^{n}\frac{1}{(s\lambda_i)^2}K\left(\frac{\mathbf{x}-\mathbf{X}_i}{s\lambda_i}\right), \tag{6}$$

where s is a global smoothing parameter satisfying $0 \leq s \leq 1$, λ_i is the local smoothing parameter, and the kernel K is a unimodal, symmetric probability density function, which we assumed followed a normal probability density function (Silverman 1986). Density estimates generally are insensitive to choice of K, but may be sensitive to choices for smoothing parameters (Worton 1989). We used least squares cross-validation to select appropriate values for λ_i, which has received support as a reliable, objective method to select λ_i appropriate for the data (Worton 1989). To avoid estimation problems associated with non-continuous data, we added a random displacement of 20 m to our data. Theoretical and practical considerations often support using $s = 0.5$ (Silverman 1986). Decreasing s increases sensitivity of estimated densities to local detail in the data (Worton 1989). Because high sensitivity to local variation in density of locations had the adverse effect of creating numerous, small "islands" on the edges of ranges rather than a more biologically intuitive continuous distribution of available range, we used elevated values of $s = 0.75$ for range estimation, except for the annual range for the Bowser population for which we used $s = 0.5$.

Autocorrelation in locations for individuals violated the independence assumption of the estimator, which can lead to underestimation of range sizes if the range is not fully traversed during the sampling period (Swihart and Slade 1985a, Otis and White 1999). However, correlation of locations among the many individuals in each population likely was small. In addition, large samples of locations and over long periods of time likely minimized underestimation of range area because individuals were likely to fully traverse the range of each population.

From the full sample of locations for each population (Bowser $n = 9731$, Murphy $n = 4820$), we initially removed locations of any single individual that were >4 km from locations of any other individual (Bowser $n = 64$, Murphy $n = 36$) in order to remove atypical movements of individuals. The estimated cumulative 99% probability density contour for all remaining locations defined the available annual range for each population. Because resource selection analyses require that all used resources are taken from the subset of available resources (Manly et al. 2002), we dropped all animal locations falling outside the estimated annual range from subsequent analyses. We used animal locations that were within each annual range and that were collected during the winter period for each population to estimate the winter range for each population. Animal locations falling outside the estimated winter ranges were dropped from analyses of winter resource selection.

Resource Data Sources

We used 2 independent sources of data on vegetation attributes for analyses of resource selection. The first was a vegetation map created by the USDA Forest Service using LANDSAT satellite imagery. This map provided continuous coverage of both study areas and included estimates of classification error. A second source of data was timber stand inventory records collected by land management agencies to facilitate resource management. Inventory data often provided more detailed information about vegetation floristics and structure than satellite maps, but differences in data collection methods, e.g., classification by on-site observers or through aerial photograph interpretation, and in vegetation attributes recorded among agencies created challenges for combining and interpreting data. In addition, inventory data were incomplete for managed land and absent for private land, and estimates of classification error were unavailable.

Table 1. Lifeform classes from the LANDSAT vegetation map providing course-level separation in vegetation physiognomy.

Lifeform class	Definition
Tree	>10% tree canopy cover
Shrub	>10% shrub canopy cover, not in tree class
Grass-forb	>10% grass-forb canopy cover, not in tree or shrub classes
Sparsely vegetated	<10% vegetation canopy cover
Water	primarily permanent water

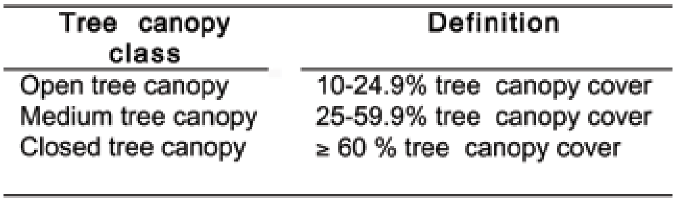
LANDSAT vegetation map.—The USDA Forest Service used LANDSAT thermatic mapping satellite imagery from 2002 to produce a vegetation map extending across northwest Montana and parts of northern Idaho. The vegetation classification followed the Federal Geographic Data Committee Vegetation Classification Standards developed for classification of vegetation based on floristic and physiognomic composition (Federal Geographic Data Committee 1996). Use of this map accrued substantial advantages: (1) consistent, continuous coverage alleviated problems stemming from differences in stand information protocols among public agencies and private timber industries as well as the lack of information for unmanaged private land; (2) large coverage area allowed greater potential for projection of our predictive models throughout the region; (3) rigorous accuracy checking of the vegetation classification enhanced our ability to assess and interpret results from our predictive models; and (4) concordance with national standards will facilitate comparison with other regions and studies.

We characterized vegetation on our study area using the four primary map products: lifeform, tree canopy cover, tree diameter, and tree dominance type. Five lifeform classes (Table 1) provided a course physiognomic separation among basic habitat types. Three tree canopy cover classes (Table 2) were based on relative canopy cover where canopy cover was >10%. Four tree size classes (Table 3) were based on mean diameter at breast height (DBH; 1.37 m) for trees forming the upper canopy layer. Tree dominance types described floristic composition of trees in the uppermost canopy layer. Where no single species dominated, types were classified as mixtures (Table 4). Classification accuracy of the vegetation map was assessed by comparison to stand classification from interpretation of aerial photos. For additional detail, see Brewer et al. (2004).

Timber stand inventory.—Timber stand inventory data from the Flathead National Forest (FNF), the Montana Department of Natural Resources and Conservation (DNRC), and the FNF Historical Range of Variability Project

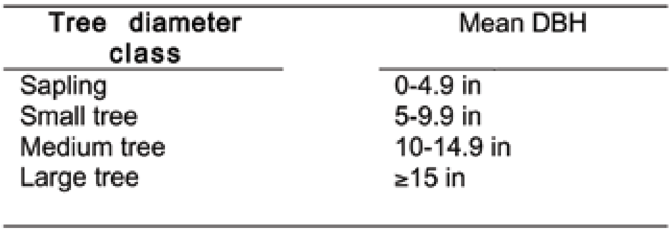
(HRV) provided an alternative, independent characterization of vegetation floristics and physiognomy. Timber stand inventory data provided poor coverage of the range of the Murphy population. Coverage of the estimated annual range of the Bowser population was also insufficient, but most of the winter range was covered. Therefore, we limited analyses to comparisons of winter use locations and available winter range falling within the inventory coverage. We obtained a small amount of additional inventory data for areas with high deer density during winter, using methods identical to the HRV Project (see Results for additional details).

Table 2. Tree canopy cover classes from the LANDSAT vegetation map based on relative canopy cover.



Tree canopy class	Definition
Open tree canopy	10-24.9% tree canopy cover
Medium tree canopy	25-59.9% tree canopy cover
Closed tree canopy	≥ 60 % tree canopy cover

Table 3. Tree diameter classes from the LANDSAT vegetation map based on mean diameter at breast height (DBH) of trees in the upper canopy layer.



Tree diameter class	Mean DBH
Sapling	0-4.9 in
Small tree	5-9.9 in
Medium tree	10-14.9 in
Large tree	≥15 in

Inventory data collected by the FNF used the same classes for tree canopy cover, tree diameter, and tree dominance type classes as the LANDSAT map (Tables 2 - 4). Sites with <10% tree canopy cover were classified as non-forested. For a portion of timber stands, a ground observer estimated vegetation attributes; stands were inventoried haphazardly over a large range of years. For unvisited stands, vegetation attributes were estimated using a variety of information sources. For stands that had been recently harvested, date and type of harvest, local knowledge, and interpretation of aerial photos were used to estimate current vegetation attributes. For unharvested stands, local knowledge and interpretation of aerial photos (including comparison of stand photo characteristics to nearby "reference" stands with known attributes) were used to estimate vegetation attributes. For all unharvested stands, vegetation attributes were projected from the time a stand was last observed to the present using a predictive model of tree growth (B. Kuropat, USDA Forest Service, personal communication).

Ground observers classified DNRC inventory data at each stand. Observers classified tree size into three categories based on the proportion of tree canopy cover within three DBH classes (Table 5). For stands with >10% tree canopy cover, the relative amount of tree canopy cover

Table 4. Tree dominance type classes from the LANDSAT vegetation map based on relative canopy cover of trees in the upper canopy layer. If no single species exceeded 60% canopy cover, relative canopy cover defined membership in 1 of 3 species mixtures.

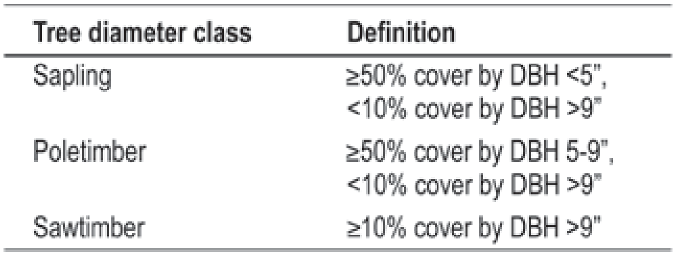
Tree dominance type class	Definition
Lodgepole pine	>60% canopy cover of lodgepole pine
Douglas fir	>60% canopy cover of douglas fir
Western larch	>60% canopy cover of western larch
Sub-alpine fir	>60% canopy cover of sub-alpine fir
Engelmann spruce	>60% canopy cover of engelmann spruce
Shade-intolerant mixture	Total canopy cover of lodgepole pine, douglas fir, and western larch > shade-tolerant mixtures 1 and 2
Shade-tolerant mixture 1	Total canopy cover of sub-alpine fir, engelmann spruce, and mountain hemlock > each of the other 2 mixtures
Shade-tolerant mixture 2	Total canopy cover of grand fir, western red cedar, and western hemlock > each of the other 2 mixtures

was divided into three categories (Table 6). Habitat type was classified as non-forested where tree canopy cover was <10%, and seven forested habitat types were defined based on the dominant tree species (Douglas fir, Douglas fir/western larch, western larch, lodgepole pine, subalpine fir, Engelmann spruce, and mixed conifer).

The HRV Project classified vegetation attributes from aerial photos from 1997. Observers estimated tree canopy cover as cover of the ground by overstory trees to the nearest 10%. Tree size was estimated as the mean DBH of overstory trees. Classes were identical to those for the LANDSAT map (Table 3), except the minimum size for the large tree class was 16 in instead of 15 in. Where tree canopy was <10%, floristic composition was classified as grass or shrub based on the lifeform with greater canopy cover. Otherwise, four tree dominance types were defined relative to dominant tree species. Recording all tree species estimated to have ≥20% of the total basal area resulted in four categories: Douglas fir, western larch, lodgepole pine, and Engelmann spruce/subalpine fir.

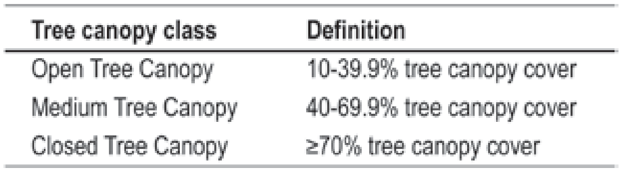
Topographic data.—Digital elevation models produced by the U. S. Geological Survey provided the basis from which we derived characterizations of topographic features, such as elevation, slope, and terrain roughness. We obtained elevation models from 7.5-min maps with a resolution of 30 m2 from the Natural Resource Information System of Montana State Library (available at <http://nris.state.mt.us/nsdi/nris/el10/dems.html>).

Table 5. Tree diameter classes from the DNRC timber stand inventory based on the proportional canopy cover of trees in different classes of diameter at breast height (DBH).



Tree diameter class	Definition
Sapling	≥50% cover by DBH <5", <10% cover by DBH >9"
Poletimber	≥50% cover by DBH 5-9", <10% cover by DBH >9"
Sawtimber	≥10% cover by DBH >9"

Table 6. Tree canopy cover classes from the DNRC timber stand inventory based on relative canopy cover.



Tree canopy class	Definition
Open Tree Canopy	10-39.9% tree canopy cover
Medium Tree Canopy	40-69.9% tree canopy cover
Closed Tree Canopy	≥70% tree canopy cover

Weather data.—We used data from one manually maintained climatological station near each study area to characterize weather conditions. Station MT3139, located near Fortine, Montana at an elevation of 923 m and latitude 48° 47' N and longitude 114° 54' E, was used to characterize the Murphy site. Station MT6218, located near Olney, Montana at an elevation of 975 m and latitude 48° 33' N and longitude 114° 34' E, was used to characterize the Bowser site. Each site was located <10 miles from and at a similar elevation to the center of the densest concentration of mid-winter deer locations. Data collected daily at these stations included minimum and maximum air temperatures, precipitation, and depth of snow on the ground. Raw data were used to estimate snow water equivalent (SWE), i.e., amount of water in the snow pack. Estimates are more accurate than direct, manual measurements for SWE because of bias inherent in manual measurements and variability in measurement error associated with variation in snow conditions, wind, and tree canopy cover. For more information on methods for estimation of SWE, see Farnes et al. (2000).

Resource Selection Analyses

Variables for analyses.—We used data sources described above to create variables for resource selection analyses that characterized resources on the study areas relative to attributes of topography, vegetation floristics and physiognomy, and weather conditions during winter. Because a large number of potential variables were available for characterizing resources, we sought to minimize the number of variables by pooling attributes that likely were functionally similar, avoiding variables describing rare attributes, and preferring continuous to categorical covariates. In addition to defining variables thought to be meaningful relative to resource selection by deer, we also included variables characterizing resource attributes that are monitored and directly manipulated by land management agencies and wood products industries. Because animals likely select resources based on attributes in their local vicinity rather than at a point location, studies of resource selection by wildlife commonly characterize used and available resources relative to a buffered area around a location. In addition, uncertainty associated with deer locations may hinder identification of resources selected by deer if those resources are not adequately represented in descriptions of "used" resources. For these reasons and also considering inherent telemetry error (Vore and Schmidt 2001), we characterized resource attributes in a 200-m circular buffer centered on used or available locations.

Topographic data.—Topographic variables were common to analyses using LANDSAT map and timber stand inventory. To calculate topographic variables (Table 7), we imported a digital elevation model for the study areas into a GIS (all GIS manipulations conducted in ArcGIS v8.3; ESRI, Inc., Redlands, California). We calculated degree of slope θ for each pixel as tangent $\theta = \Delta\text{elevation}/\Delta\text{distance}$, where Δelevation is the change in elevation between each pixel and the adjacent pixel with the greatest elevation difference and Ddistance is the distance between the center of each pixel and the center of the adjacent pixel with the greatest elevation difference. For each pixel, we calculated the standard deviation in slope among the calculated slopes for that pixel and the eight adjacent pixels. This estimate of variation in slope provided a measure of terrain "roughness" that was not directly related to slope, i.e., steep but evenly sloped terrain would have low roughness, but that would increase as terrain became more uneven or curved. For each pixel, we assigned an aspect that identified the direction with the steepest slope. For a given location, we calculated

Table 7. Variables used to characterize resources at locations used by and available to white-tailed deer during 1988-2000 in northwest Montana. See text for detailed definitions.

Variable Type	Variable	Abbreviation	Description
Topographic	Elevation	ELEV	Elevation in km
	Slope	SLP	Degree of slope
	Terrain roughness	SLPSD	SD in slope
	Aspect	ASP	Linear gradient in aspect from NW to SE.
Floristic	Grass-forb	GFB	Grass-forb dominated
	Shrub	SHR	Shrub dominated
	Shade-intolerant mixture	SIM	Upper tree canopy dominated by combination of 2 or more of following: lodgepole pine, douglas fir, and western larch
	Shade-intolerant mixture	STM	Upper tree canopy dominated by combination of 2 or more of following: sub-alpine fir, engelmann spruce, mountain hemlock, grand fir, western red cedar, and western hemlock
	Lodgepole pine	PICO	Upper tree canopy dominated primarily by lodgepole pine
	Douglas fir	PSME	Upper tree canopy dominated primarily by douglas fir
Tree Physiognomic	Sapling	DBH 0-5	Mean DBH of trees in upper canopy 0-4.9"
	Small tree	DBH 5-10	Mean DBH of trees in upper canopy 5-9.9"
	Medium tree	DBH 10-15	Mean DBH of trees in upper canopy 10-14.9"
	Large tree	DBH ≥15	Mean DBH of trees in upper canopy 15"
	Open canopy	CAN 10-25	Tree canopy cover 10-24.9%
	Moderate canopy	CAN 25-60	Tree canopy cover 25-59.9%
	Closed canopy	CAN ≥60	Tree canopy cover 60%

mean elevation, slope, standard deviation in slope, and aspect values within the 200-m buffer by including pixels whose center was inside the buffer. Transforming the mean aspect for each buffer as COSINE(aspect - 45) created a linear gradient in aspect ranged from 1 to the northeast to -1 to the southwest.

LANDSAT vegetation map.—We used the lifeform and tree dominance type classes from the USFS vegetation map to develop six floristic variables. The grass-forb and shrub lifeform classes described two broad classes of floristic composition among non-forested habitats. The sparsely vegetated (primarily developed area on <0.1% of each study area) and water (~0.5% of each study area) lifeform classes were rare and not considered suitable habitat for deer, and both classes were dropped from analyses. For the tree lifeform, we used tree dominance type classes to define floristic variables based on the dominant tree species in the upper canopy. The lodgepole pine and Douglas fir dominance types were moderately common (>8% of each study area) and were retained as variables. The western larch dominance type was relatively rare, and we pooled it with the shade-intolerant mixture. Because a variety of dominance types, e.g., sub-alpine fir, Engelmann spruce, and shade-tolerant mixture 2) containing shade-tolerant species were rare (~1% of each study area), we pooled these types with the shade-tolerant mixture 1 to create a single mixture of shade-tolerant species.

We used the tree diameter and tree canopy cover classes from the vegetation map to create seven vegetation physiognomy variables for the tree lifeform. For all floristic and physiognomic variables, we calculated for each 200-m buffer the proportional occurrence of pixels in each class relative to the total number of non-water pixels within the buffer.

Timber stand inventory.—We defined five floristic variables for these data (Table 8). We based the western larch and lodgepole pine variables on classes of the same name from each agencies inventory. The non-forested variable consisted of the pooled grass and shrub classes from the HRV and FNF inventories and the non-forested class of the DNRC. We created the sub-alpine fir variable by pooling the sub-alpine fir and Engelmann spruce classes from each inventory as well as the shade-tolerant mixture classes from the FNF. For the Douglas fir variable, we pooled the Douglas fir classes from each inventory, the shade-intolerant mixture from the FNF, and the Douglas fir-western larch and mixed conifer classes from the DNRC.

We defined four tree size variables that roughly corresponded to those for the LANDSAT map. Because cut-points separating tree classes differed slightly among inventories, DBH of 9-10 in was either included in the poletimber or medium tree variables. In addition, the DNRC inventory lumped trees of DBH ≥9 in, and we included this class in the medium tree variables because of the higher prevalence of medium (DBH 9-15 in) relative to large tree classes (DBH ≥15 in) on our study areas. Tree canopy cover classifications differed among inventories of each agency. We sought to define three variables that roughly corresponded to those for the LANDSAT map (FNF 10 to <25%, 25 to <60%, ≥60%; DNRC 10 to <40%, 40 to <70%, ≥70%; HRV 10 to 30%, 40% to 60%, ≥70%), but moderate overlap among different classes was unavoidable.

Weather data.—To characterize snow accumulation at the time of each location, we used the mean estimated SWE for that day and the two previous days. We felt a 3-day period was likely to capture large-scale movements within the study area in response to snow events. Snow accumulation varied widely across the study areas, and estimates of SWE likely were only representative of conditions on the lower portions of the winter ranges. However, we assumed that SWE estimates from climatological stations were proportional to snow accumulation at higher elevations and hence were a useful index to relative magnitude of snow accumulation across the study area.

Statistical analyses.—In this study, we used repeated observations of individually marked deer in the Bowser and Murphy populations to identify locations used during winter, and a GIS allowed us to characterize attributes of resources at used and available locations throughout each study area. Estimation of a resource selection function allows prediction of the relative probability use of locations based on their resource attributes and hence provides inference about resource preferences of animals (Manly et al. 2002). We wished to make inference about resource preferences in each population by comparing used locations to those available to these deer at three spatial scales: (1) the

Table 8. Variables used to characterize resources at locations used by and available to white-tailed deer during 1988-2000 in northwest Montana. See text for detailed definitions.

Variable Type	Variable	Abbreviation	Description
Topographic	Elevation	ELEV	Elevation in km
	Slope	SLP	Degree of slope
	SD in Slope	SLPSD	Variation in slope, terrain "roughness"
	Aspect	ASP	Linear gradient in aspect from NW to SE.
Floristic	Non-forested	NFOR	<10% tree canopy cover
	Western larch	LAOC	Upper tree canopy dominated by western larch
	Sub-alpine fir	ABLA	Upper tree canopy dominated by sub-alpine fir
	Lodgepole pine	PICO	Upper tree canopy dominated by lodgepole pine
	Douglas fir	PSME	Upper tree canopy dominated by douglas fir or douglas fir/ western larch
Tree Physiognomic	Sapling	SAPL	Tree canopy dominated by trees of DBH of <5"
	Poletimber	POLE	Tree canopy dominated by trees of DBH of ≥5" to <9-10"
	Medium tree	MED	Tree canopy dominated by trees of DBH of ≥10" to <15" or ≥9"
	Large tree	LAR	Tree canopy dominated by trees of DBH of ≥15"
	Open canopy	CCL	Tree canopy of 10 to <25-<40%
	Moderate canopy	CCM	Tree canopy of ≥25-≥40 to <59-<69%
	Closed canopy	CCH	Tree canopy of ≥60 or ≥70%

annual range available to each population, (2) the winter range available to each population, and (3) the area available to each individual based on its previous location. In addition, we sought to understand how daily fluctuations in weather conditions and attributes of individual animals influenced resource preferences. Discrete choice models were appropriate for our analyses because they allow the set of available resources to differ among individuals or over time, and probability of use can be influenced by the attributes of the selected resource as well as by attributes of the individual making the choice, e.g., age and sex of the individual, or the conditions, e.g., weather conditions, at the time when the choice is made (McCracken et al. 1998, Cooper and Millspaugh 1999).

We applied the multinomial logit discrete choice model, which has been widely used in studies of resource selection by animals. However, traditional methods of fitting these models using maximum likelihood methods treat parameters as fixed and consider the sample size to be the number of animal observations. As a result, population-level estimates are invalid because heterogeneity in preference among individuals is unaccounted for, the appropriate sample size is the number of animals rather than animal observations, and animals with higher numbers of relocations make disproportionate contributions to population-level estimates. Estimating population-level parameters as the mean of parameters estimated separately for each individual alleviates some problems by using the animal as the sample unit (Manly et al. 2002). Although improved, this approach still does not yield valid population-level estimates, it makes inefficient use of the data, overestimates individual heterogeneity in selection because of sampling error, and suffers from numerous problems arising from doing "statistics on statistics," e.g., incorrect degrees of freedom, bias in estimates.

To circumvent these problems, we fit the discrete choice model using hierarchical Bayes statistical methods. Recent increases in computer speed and development of computational techniques such as Markov Chain Monte Carlo (Gelman et al. 2004) have allowed a wide variety of generalized linear models to be fit using Bayesian methods. Bayesian approaches to discrete choice models have recently been applied to modeling human consumer preferences (Allenby and Rossi 1999, Sonnier and Train In Press) and can be readily extended to resource preferences of animals (Thomas et al. 2006). The essential feature of Bayesian approach is that parameters are normally assumed to be random rather than fixed effects, with each parameter described by a distribution rather than a point estimate.

The discrete choice model posits that animals select resource units with maximum utility to the animal from among available units. The 200-m buffered areas centered on map pixels comprised our basic resource units, and observed relocations of an animal defined selected resource units. For each animal i, we modeled the utility provided by resource unit j as

$$U_{ij} = \mathbf{B}_i \mathbf{X}_{ij} + e_{ij} = \beta_{i1} x_{i1} + \beta_{i2} x_{i2} + \ldots + \beta_{ip} x_{ip}, \tag{7}$$

where B_i is a p-dimensional vector of unknown parameters for animal i, X_{ij} is a p-dimensional vector of observed attributes for animal i and resource unit j, and e_{ij} is an error term assumed to be independent and identically distributed Type I (Gumbel) extreme value random variable. The relative probability animal i choosing resource unit j from among a set of alternative resource units A_{ir} available to animal i at the time and place of its relocation r is then

$$\Pi_{ij} = \frac{\exp(\mathbf{B}_i \mathbf{X}_{ij})}{\sum_{k \in \mathrm{A}_{ir}} \exp(\mathbf{B}_i \mathbf{X}_{ik})}. \tag{8}$$

We assumed that each of the model parameters $l = 1$ to p followed an independent normal distribution $\beta_{il} \sim N(\beta_l', \sigma_l^2)$, where β_l' is the mean for the population and σ_l^2 is the variance in estimates among individuals. We assumed that animals make selections independently of each other, that repeated observations of an individual are independent selection events, and that utility derived from one resource attribute is independent of others that is known as the assumption of independence from irrelevant alternatives (McCracken et al. 1998, Cooper and Millspaugh 1999).

The hierarchical Bayes approach provided a mechanism to appropriately weight relocations and individuals, which provides simultaneous estimates of individual- and population-level selection using valid error terms. The sample of relocations was used to estimate individual-level parameters, and the sample of individuals was used to estimate population-level parameters. Sampling variances associated with individual-level estimates were used to weight individual contributions to the population mean. In addition, estimates of variance in parameter estimates among individuals provided estimates of process variance, i.e., true variation in the population after accounting for sampling error, and a "shrinkage" estimator adjusted individual-level estimates based on process variation in the population, resulting in improved precision and accuracy of individual-level estimates. Thus, information sharing between individual- and population-levels benefited statistical inference at each level. Correlations of individual-level parameter estimates between parameters also provided insight to patterns of relative preference of different resources by individuals. For example, did individuals with relatively high preference for one resource tend to have relatively high or low preference for another resource?

For Bayesian analyses specific starting values ("prior distributions") for each parameter must be specified prior to analyses. Markov Chain Monte Carlo simulations are then used to update these distributions in light of the data to arrive at "posterior distributions," which are the parameter estimates (Gelman et al. 2004). Prior distributions can influence model results, because posterior distributions are a weighted combination of the information from the prior distributions and the data. However, because we specified "non-informative" prior distributions and because abundant data in our analyses "overwhelmed" the prior distributions, these made effectively no influence on results. In this situation, expected parameter values from our multinomial logit models are asymptotically equivalent to maximum likelihood estimates (Train 2003). Because maximum likelihood methods are computationally intractable with more than a few random effects, Bayesian methods were a convenient alternative for fitting complex models.

We fit all models in program GAUSS version 6.0 (Aptech Systems, Inc., Maple Valley, Washington) using basic code for hierarchical Bayes multinomial logit models provided by K. E. Train (algorithm described in Sonnier and Train 2005) that we modified for our analyses. We specified each β_l' to have a mean of 0 and variance sufficiently large to be flat from a numerical perspective. We specified standard diffuse priors on each σ_l^2 using an inverted Wishart distribution. All models were estimated with a full covariance matrix. Burn-in periods prior to convergence ranged from 20,000 to 200,000 iterations, depending on model complexity. After convergence, 50,000 to 150,000 posterior draws were retained for parameter estimation. Computational times for individual model simulations on Intel Pentium 4 processors ranged from 2 hrs to >2 days. We estimated the effective number of model parameters (pD) as the difference between the mean deviance across draws from the posterior distribution and the deviance at estimated parameter values (Gelman et al. 2004). We estimated the Deviance Information Criterion (DIC) as 2 · pD + the deviance at mean estimated parameter values (Spiegelhalter et al. 2002). We exported posterior draws to the Bayesian Output Analysis package (B. J. Smith; available at http://www.R-project.org) for R software (R Core Development Team 2004) to assess convergence. We initially accepted convergence of parameter means from single simulation chains if *P*-values from the convergence diagnostic of Geweke (1992) were >0.05. We then generated a second chain and accepted estimates of parameter means and variances if corrected scale reduction factors from the convergence diagnostic of Brooks, Gelman, and Rubin as modified by Brooks and Gelman (1998) were <1.2 for all parameters.

Model building and selection.—A formal approach to selection of parsimonious models from an a priori set of candidate models (e.g., Burnham and Anderson 2002) was infeasible because optimization time for all biologically plausible models would have been exorbitant. However, we believed selection of parsimonious models integral to sound statistical inference. We also believed DIC appropriate for model selection because it assesses model complexity using pD, which offers a better measure of complexity for random effects models than actual sample size (Burnham and Anderson 2002, Spiegelhalter et al. 2002). DIC is similar in interpretation to Akaike's Information Criterion to select parsimonious models (Spiegelhalter et al. 2002). Models with lower DIC values have more support, and we considered models with ΔDIC >5 relative to the best model effectively unsupported.

Our approach to model-building involved first selecting parsimonious general models of resource selection during winter; we then assessed support for more sophisticated hypotheses about effects of weather and individual attributes on resource selection. To build general resource selection models, we selected parsimonious combinations of variables in sequence from three subsets of variable types: topographic, floristic, and tree physiognomic (see Table 5). We added selected variable combinations from each subset to those from previous subsets. Except as noted below, our general approach for each subset was to enter each variable separately to determine the univariate reduction in DIC and then to add variables in a sequence of greatest to least reduction in DIC, retaining only variables that decreased the DIC by >5.

For the topographic subset, we believed quadratic specifications of ELEV, SLP, and SLPSD and a cubic specification of ELEV were biologically plausible in addition to linear effects. Because elevation was obviously fundamental to resource selection in our populations and because elevation was moderately correlated with and critical to interpretation of other topographic variables, we first selected the most parsimonious elevation model before considering other variables. To assess if the NE to SW linear trend in aspect adequately described variation in the data, we also fit models with indicator variables corresponding to four inter-cardinal categories of aspect. We considered fitting a model with a different linear trend in aspect if the categorical model suggested that a better fit was possible. For the tree physiognomic subset, strong confounding between variables made variable selection sensitive to variables already included in the model. For these models, we first entered the variable giving the greatest univariate reduction in DIC. Then, we added additional variables by assessing the reduction in DIC from adding each of the remaining variables to the current model. Because of problems encountered with model optimization and parameter estimation when strong confounding was present, we avoided simultaneously including all tree size or canopy cover variables.

We compared used locations to available locations at two spatial scales: the estimated annual and winter ranges. We obtained a systematic sample of locations by superimposing a grid with points separated by 120 m over each estimated range area, resulting in 25,438 and 16,024 locations in the Bowser annual and winter ranges and 27,030 and 14,633 locations in the Murphy annual and winter ranges. As described for deer locations above, we used a GIS to estimate resource attributes in a 200-m buffer around each available location. For each deer location and at each spatial scale, we created the choice set of available locations by randomly selecting 24 locations from the appropriate pool of available locations for each range and study area.

To examine effects of snow accumulation on resource selection, we introduced interaction terms between selected resource variables and SWE. Because SWE provided an index to relative snow conditions across the study area at a given time and hence was the same within each choice set, we could not include SWE as a main effect. Instead, entering the main effect of a resource variable and its interaction with SWE resulted in the main effect providing an estimate of response to that resource when SWE was 0 and the interaction term adjusting the slope for that resource variable for all other levels of SWE. We included interaction terms with resource variables for which we hypothesized that selection would be influenced by SWE. We hypothesized that white-tailed deer selected resources that mitigated snow accumulation, and lower elevations, mature conifer forest, and closed tree canopy are all thought to reduce snow accumulation. Therefore, we predicted that increasing SWE would result in use of lower elevations, decrease use of relatively open habitats such as grass-forb, shrub, and open canopy, and increase use of closed canopy and medium and large trees. We included SWE interactions only at the winter scale spatial scale, and we included interactions for relevant main effects previously selected in model building. We assessed support for interactions based on the magnitude of estimated coefficients for interaction terms and the ratio of estimated coefficients to their standard errors. To assess the hypothesis that habitat selection was responding to some other seasonally varying factor correlated with SWE, e.g., plant phenology, time of season, etc., we also fit a model substituting mean daily SWE over the study period for observed daily variation in SWE in the best model. To explore possible differences in selection between sexes, we examined the mean and 95% confidence interval of estimated coefficients for individuals of each sex from the best model.

Section 4: Results

We equipped 256 deer (197 females; 59 males) in the Bowser population and 153 deer (115 females; 38 males) in the Murphy population with transmitter collars during 1988-1998 (Table 9). We relocated deer continuously during March 1988-May 2000 with a median interval of 16 and 18 days between relocations for the Bowser and Murphy populations. In both populations, mean age in years at capture and marking was higher for females ($\bar{x}$ ± SD; Bowser, 3.7 ± 2.6; Murphy, 4.0 ± 2.8) than males (Bowser, 1.8 ± 1.5; Murphy 2.0 ± 2.0). Mean duration of persistence in the radio-marked sample was also longer for females (Bowser, 3.6 ± 3.9 years; Murphy, 3.3 ± 4.2) than males (Bowser, 2.1 ± 2.4; Murphy 1.8 ± 3.1) resulting in more relocations/ individual for females (Bowser, 45.0 ± 28.5; Murphy, 37.6 ± 25.2) than males (Bowser, 17.8 ± 18.1; Murphy 13.1 ± 14.9). Numbers of radio-marked individuals and hence relocations for each population peaked in 1991-1992 and again in 1998-2000 (Fig. 2). Although daily timing of relocations ranged throughout daylight hours (Fig. 3), more than 50% of the total relocations for the Bowser (n = 9731) and Murphy (n = 4820) populations were obtained between 0730-1030 hrs.

Fidelity to Winter Use Areas

Estimates of Schoener's ratio for winter use areas within the years for females in the Bowser (1.75 ± 0.035; ± SE; n = 188) and Murphy (1.84 ± 0.049; n = 95) populations were slightly less than the value of 2 expected with no serial autocorrelation, indicating that serial locations within the winter use area were nearly independent. Slight decreases in estimates of Schoener's ratio for winter use areas across years for the Bowser (1.61 ± 0.047; $\bar{x}$ ± SE; n = 113) and Murphy (1.58 ± 0.083; $\bar{x}$ ± SE; n = 53) populations indicated slight differences in winter use areas across years.

For the Bowser population, estimated mean distance between successive centers of annual winter use areas was 359 ± 35 m ($\bar{x}$ ± SE; n = 67) for females. A small sample of males yielded a similar estimate of 403 ± 55 m (n = 6). For the Murphy population, estimated mean distance between successive centers of annual winter use areas was 462 ± 89 m (n = 29) for females. For the Bowser population, estimated mean distance from the estimated center of annual winter use areas was 581 ± 32 m and 620 ± 81 m for females and males. For the Murphy population, estimated

Table 9. Samples of white-tailed deer radio-marked each year on the Bowser and Murphy study areas in northwest Montana during 1998-2000.

		Year										
Study area	**sex**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**
Bowser	F	13	36	19	19	6	15	13	13	12	34	17
	M		6	8	5	4	9	9	6	6	5	1
Murphy	F	10	10	7	7	10	10	7	7	8	20	19
	M		1		6	3	8	8	5	2	3	2

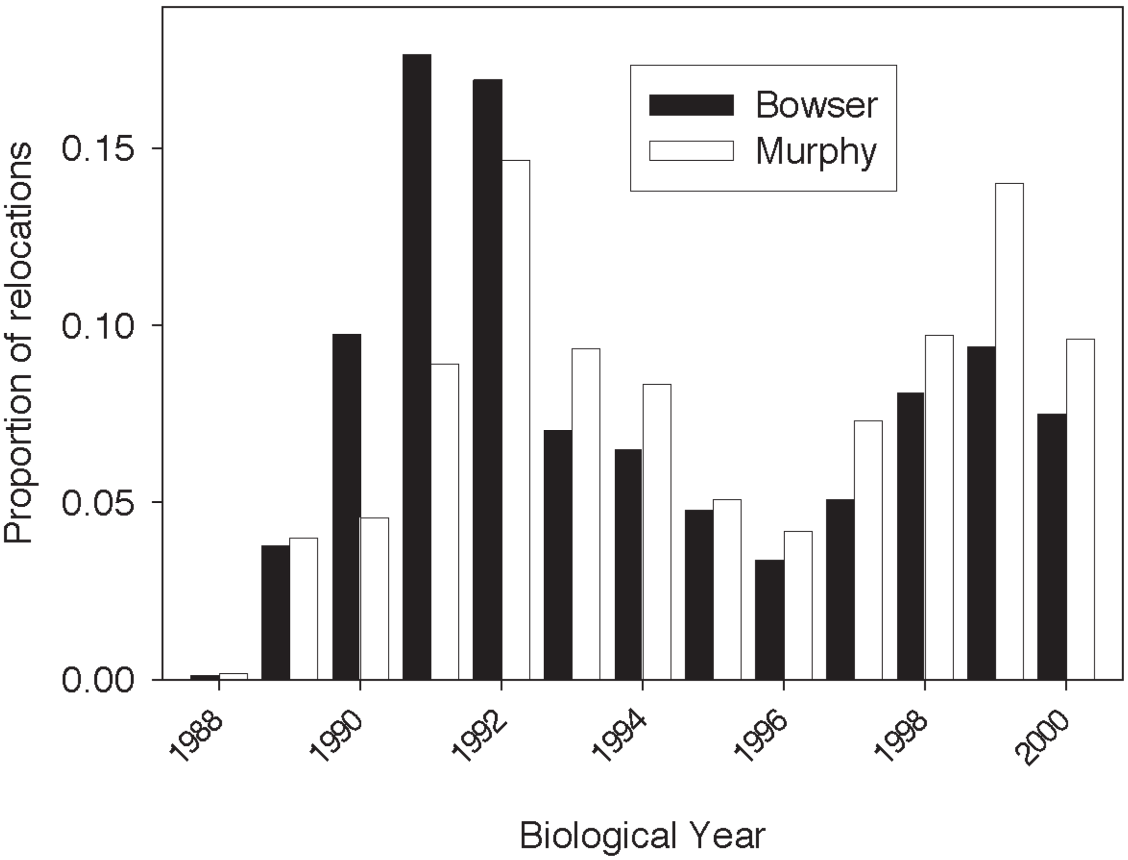


Figure 2. Proportion of total relocations of radio-marked white-tailed deer during each biological year (locations during Nov and Dec included with the following year) for 2 populations in north-west Montana.

mean distance from the estimated center of annual winter use areas was 571 ± 48 m (*n* = 95) for females.

Timing and Distance of Seasonal Movement

Little model selection uncertainty existed among candidate models of movement distance relative to season date for each population and sex (Table 10). Support for the top model in each case was overwhelming, except for males from the Murphy population, where support for the best model was >3x greater than for the second model. Estimates of *k* were far less than 1 for all best models (Table 11), suggesting movement was best described as an inhibited diffusion process, e.g., moving around a local center of activity, over short time intervals. Explanatory power was low for all models (Bowser females, $n = 5690$, $r^2 = 0.09$; Bowser males, $n = 659$, $r^2 = 0.05$; Murphy females, $n = 2495$, $r^2 = 0.06$; Murphy male, $n = 260$, $r^2 = 0.10$), indicating high variability in movement unrelated to time interval and season date. Mean intervals between locations were 13.1 ± 4.2 days (x ± SD) and 13.0 ± 4.2 days for females and males in the Bowser population and were 13.3 ± 4.0 days and 14.2 ± 3.8 days for females and males in the Murphy population.

Predicted seasonal patterns of daily movement were similar across populations and sexes (Fig. 4; projected for $t = 1$). Migratory movement peaked in November and early April, although fall movement rates were higher for males versus females. Males also had relatively high movement rates during mid-summer when females were relatively sedentary. Differences in movement by sex were inconsistent in spring; female movement was intermediate to male movement. Movement rates were depressed during mid-winter, but rates tending toward 0 near 15 July were a function of our specified model structure rather than a sharp drop in movement rates. Based on peaks of estimated

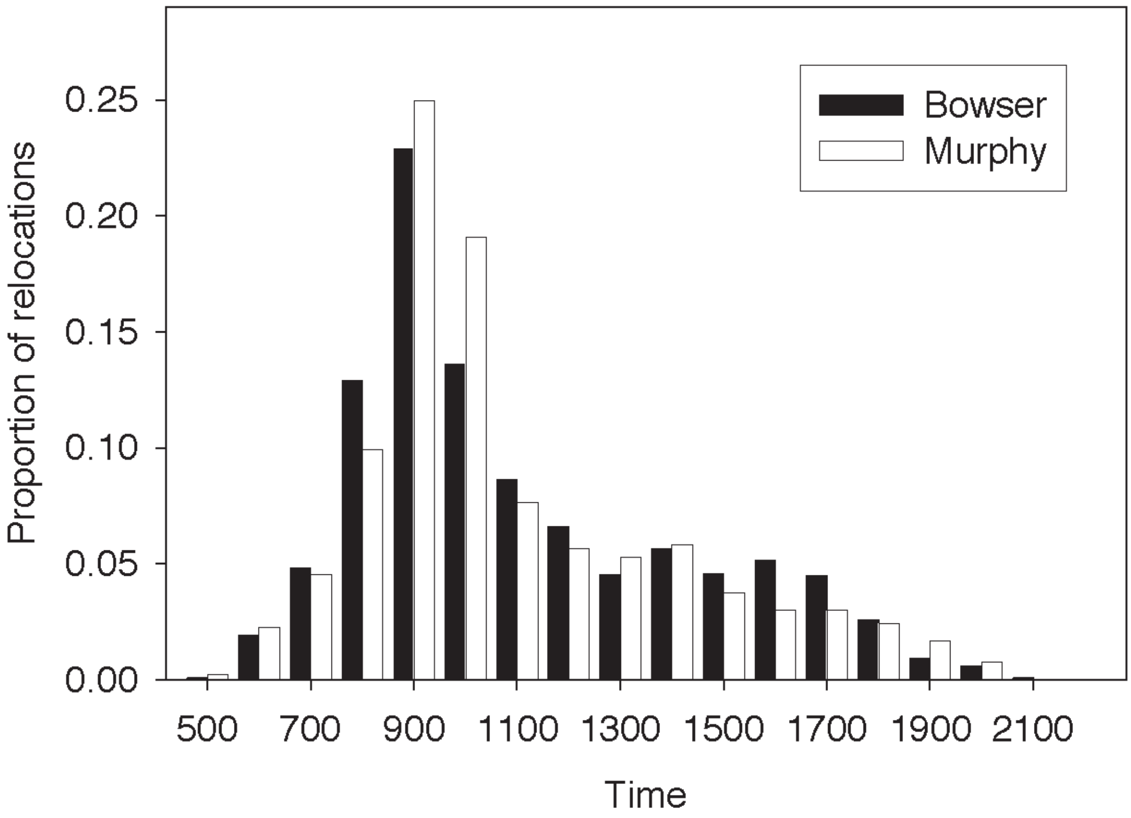


Figure 3. Proportion of total relocations of radio-marked white-tailed deer by time of day in 2 populations in north-west Montana during 1988-2000.

Table 10. Model selection results for polynomial models of seasonal variation in daily movement rates of females and males from the Bowser and Murphy populations of white-tailed deer in northwest Montana, 1988-2000. The two best models are shown for each model set.

Population	Sex	Model[a]	K[b]	-2 log(l)	$\triangle AIC_c$[c]	AIC_c weight[d]
Bowser	Female	9th order	11	2362.2	0.0	~1.000
	Female	7th order	9	2417.0	50.7	<<0.001
	Male	8th order	10	-1099.0	0.0	~1.000
	Male	7th order	9	-1053.8	25.1	<<0.001
Murphy	Female	9th order	11	939.2	0.0	0.998
	Female	8th order	10	955.1	13.8	0.001
	Male	8th order	10	-484.7	0.0	0.423
	Male	7th order	9	-480.2	2.5	0.120

[a] Models denoted by the highest order polynomial term for variable days since 15 Jul.

[b] Number of estimated parameters.

[c] Difference in AIC_c relative to the best model.

[d] Relative weight of evidence as the best approximating model.

Table 11. Parameter estimates and standard errors from AIC$_c$ selected polynomial models of daily movement rates relative to days since 15 Jul and length of time interval between successive locations for Bowser and Murphy deer populations in northwest Montana, 1988-2000.

Population	Sex	k	SE	ß$_0$	SE	ß$_1$	SE	ß$_2$	SE	ß$_3$	SE	ß$_4$	SE
Bowser	Female	0.21	0.05	-6152.3	683.3	131.6	14.9	-1.15	0.13	5.2A10^{-3}	6.4A10^{-4}	-1.1A10^{-5}	1.7A10^{-6}
	Male	0.28	0.13	-23271.7	4084.8	552.6	96.8	-5.63	0.98	3.2A10^{-2}	5.6A10^{-3}	1.1A10^{-4}	2.0A10^{-5}
Murphy	Female	0.10	0.09	-3107.3	774.8	63.5	17.2	-0.51	0.17	1.8A10^{-3}	9.2A10^{-4}	-7.5A10^{-7}	3.5A10^{-6}
	Male	-0.001	0.28	-15124.0	6244.4	356.0	147.3	-3.6	1.49	2.0A10^{-2}	8.5A10^{-3}	-7.0A10^{-5}	3.0A10^{-5}

Table 11 continued. Parameter estimates and standard errors from AIC$_c$ selected polynomial models of daily movement rates relative to days since 15 Jul and length of time interval between successive locations for Bowser and Murphy deer populations in northwest Montana, 1988-2000.

Population	Sex	ß$_5$	SE	ß$_6$	SE	ß$_7$	SE	ß$_8$	SE	ß$_9$	SE
Bowser	Female	3.4A10^{-9}	2.9A10^{-9}	4.3A10^{-11}	6.9A10^{-12}	-1.0A10^{-13}	1.3A10^{-14}	1.0A10^{-16}	1.3A10^{-17}	-3.9A10^{-20}	4.9A10^{-21}
	Male	2.5A10^{-7}	4.3A10^{-8}	-3.3A10^{-10}	5.9A10^{-11}	2.5A10^{-13}	4.5A10^{-14}	-8.3A10^{-17}	1.5A10^{-17}		
Murphy	Female	-1.7A10^{-8}	1.0A10^{-8}	6.4A10^{-11}	2.2A10^{-11}	-1.1A10^{-13}	3.0A10^{-14}	9.7A10^{-17}	2.4A10^{-17}	-3.5A10^{-20}	8.2A10^{-20}
	Male	1.5A10^{-7}	6.5A10^{-8}	-2.0A10^{-10}	8.8A10^{-11}	1.5A10^{-13}	6.7A10^{-14}	-5.0A10^{-17}	2.2A10^{-17}		

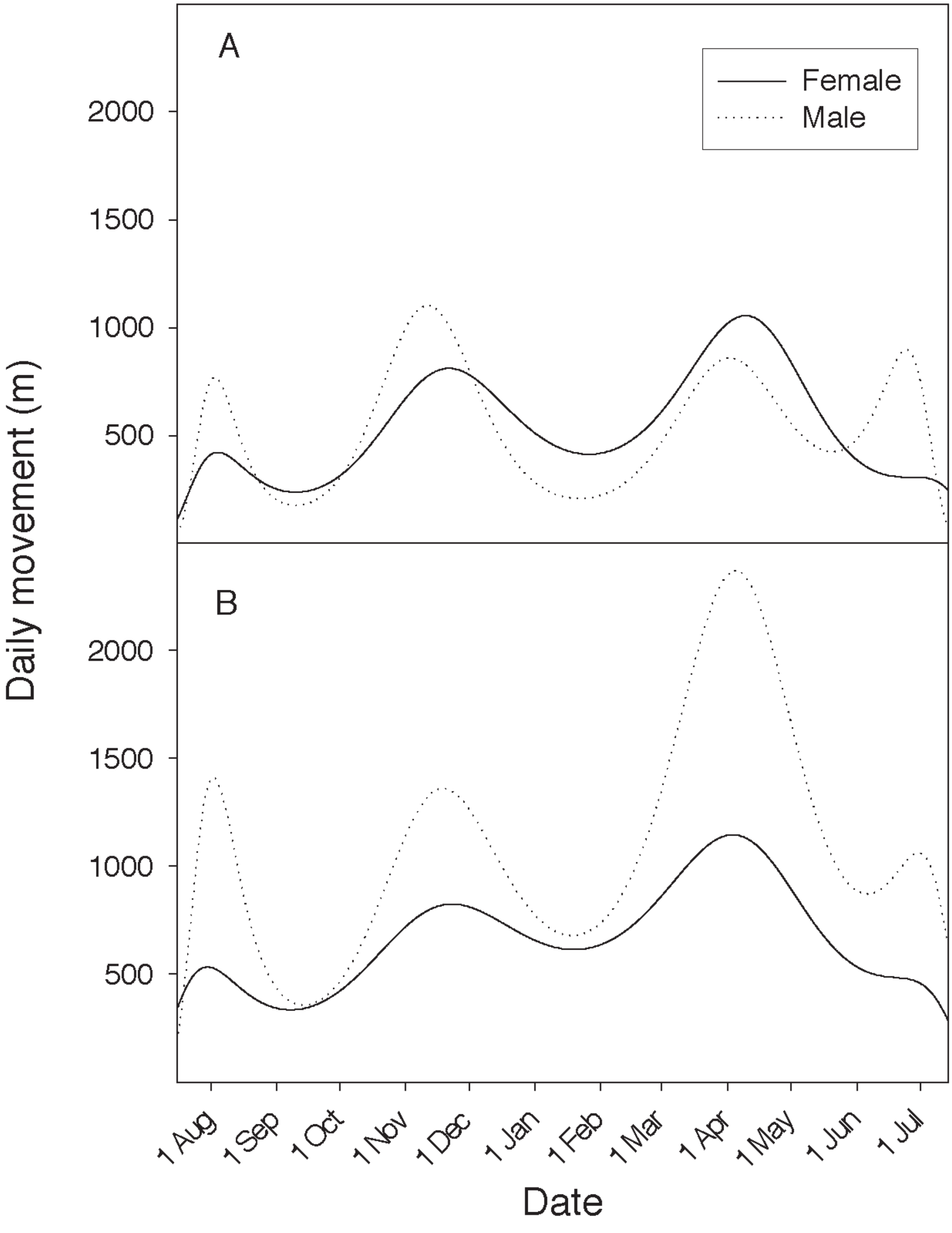


Figure 4. Estimated daily movement rates relative to date for the Bowser (A) and Murphy (B) populations of white-tailed deer in north-west Montana during 1988-2000.

movement rates of females during migration, we delineated winter periods as 22 Nov to 10 Apr for the Bowser population and 23 Nov to 4 Apr for the Murphy population.

For the Bowser population, the mean distance between summer and winter centers of activity for females and males was 23.4 ± 0.5 km (n = 123) and 23.8 ± 1.2 km (n = 16). Migratory distances ranged between 8.8 and 33.5 km. For the Murphy population, mean distance between summer and winter centers of activity was 20.1 ± 0.6 km (n = 64) for females. Migratory distances ranged between 7.2 and 32.6 km. For all individuals with ≥ 5 locations, 10% (19 of 188) and 15% (7 of 48) of females and males in the Bowser population and 9% (9 of 104) and 8% (2 of 26) of females and males in the Murphy population were classified as non-migratory during ≥ 1 year.

Defining Available Resources

The estimated 99% cumulative probability contour defining the annual range of the Bowser population (n = 9667 locations) encompassed 432 km^2 (Fig. 5). For all estimated ranges, small, relatively infrequently used travel corridors separated disjunct areas from a larger main use area. Of locations falling within the estimated annual range (n = 9399), we used those occurring during winter (n = 3663) to estimate the 99% cumulative probability contour defining the available winter range; this area encompassed 262 km^2. We retained locations during winter that fell within the winter range (n = 3583) for subsequent resource selection analyses.

The estimated 99% cumulative probability contour defining the annual range of the Murphy population (n = 4784 locations) encompassed 396 km^2 (Fig. 6). Of locations falling within the estimated annual range (n = 4588), we used those occurring during the winter period (n = 1723) to estimate the 99% cumulative probability contour defining the winter range; this area encompassed 217 km^2. Locations during the winter period falling within the winter range (n = 1655) were retained for resource selection analyses.

Resource Selection

LANDSAT vegetation map.— The number of radio-marked individuals and relocations during the winter period peaked during 1991-1992 and 1998-2000 although males were relatively sparse during the latter part of the study (Table 12). Because females persisted in the radio-marked sample longer than males, relocations/individual were greater for females ($\bar{x}$ ± SD: Bowser, 17.4 ± 11.8; Murphy, 13.1 ± 9.5) than males (Bowser, 6.9 ± 6.8; Murphy, 4.4 ± 4.4). Most relocations were constrained within the relatively short window of daylight hours (Fig. 7). A peak between 0830-1130 hrs accounted for 52% of relocations, and a smaller peak occurred between 1230-1530 hrs. Relocations appeared evenly distributed across the winter period (Fig. 8).

The study areas were generally similar in topography and floristic composition (Table 13). Both areas were dominated by shade-intolerant trees with small amounts of shade-tolerant trees most prevalent at higher elevations and small amounts of unforested habitat that occurred most prevalently along drainage bottoms. The Murphy winter range had a general southern aspect, and Bowser had a general southeast aspect. Slope and terrain roughness were somewhat higher for Bowser relative to Murphy. The two winter ranges differed in attributes of tree physiognomy. Small and large trees and moderate canopy cover dominated Bowser, but Murphy had relatively high coverage by medium trees and closed canopy. In the Bowser core winter area, large trees and moderate canopy were prevalent, but closed canopy occurred primarily in higher drainages. In contrast, closed canopy and medium trees were prevalent in the Murphy core winter area. Large trees primarily occurred in the upper Wolf Creek drainage, and moderate canopy was prevalent in upper drainages.

Correlations between resource variables were generally consistent between study areas (Table 14). As expected, strong negative correlations sometimes occurred between variables describing mutually exclusive physiognomic features, e.g., tree canopy cover and non-forested habitat. In general, increasingly large trees were strongly correlated with increasingly closed canopy cover.

Model selection for the Bowser study area showed little uncertainty within each variable set (Table 15). Substantial reductions in DIC values from adding each successive variable subset indicated dramatically improved predictive performance after controlling for previously entered variables. In the final model, β coefficients estimated resource selection at the population level, and & coefficients estimated the magnitude of individual variation in selection (Table 16). For variables which had neither quadratic nor interaction terms included,

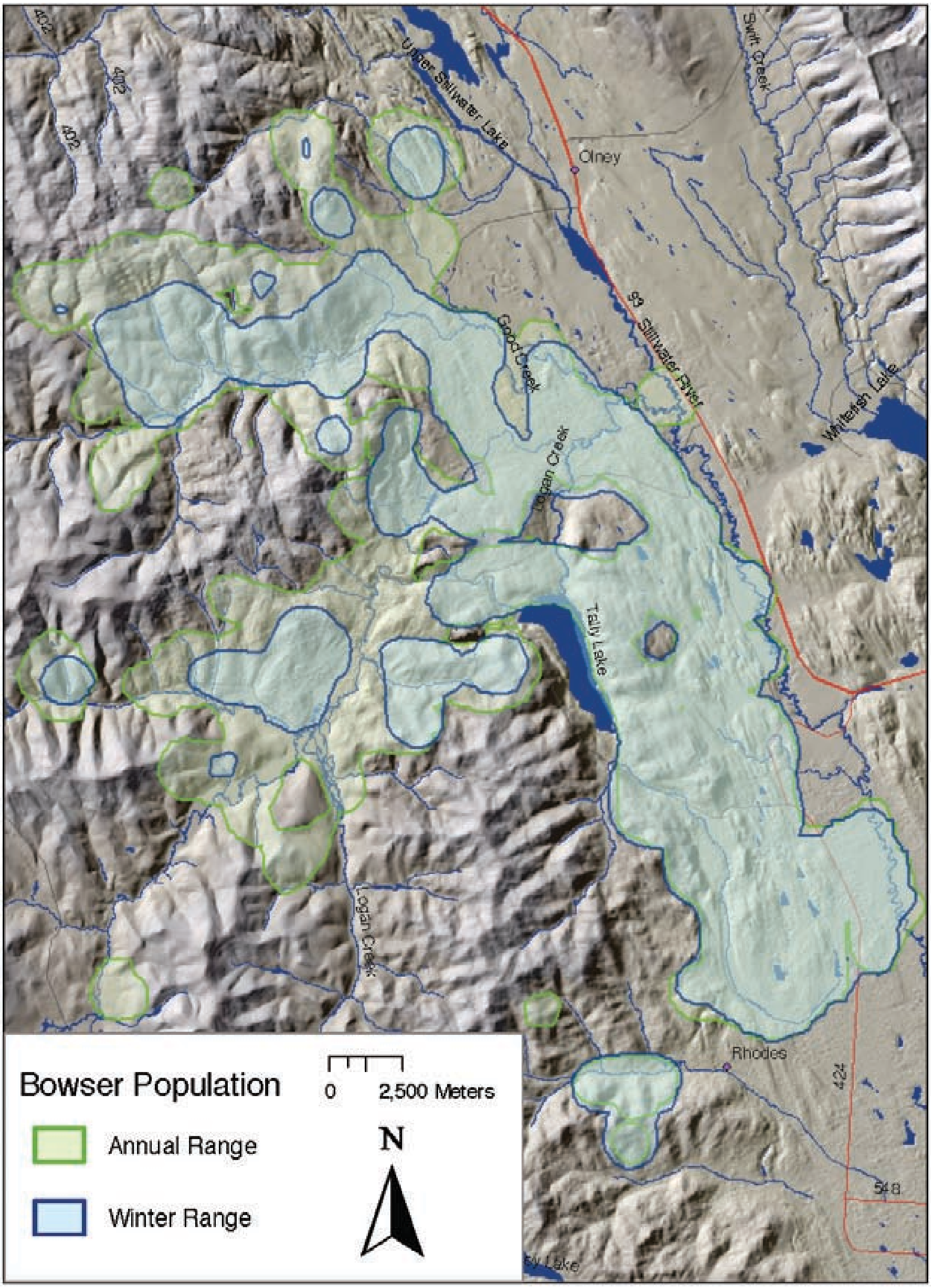


Figure 5. Estimated annual and winter (22 Nov to 10 Apr) ranges for the Bowser population of white-tailed deer in north-west Montana during 1988-2000 from bivariate adaptive kernel density estimator of utilization.

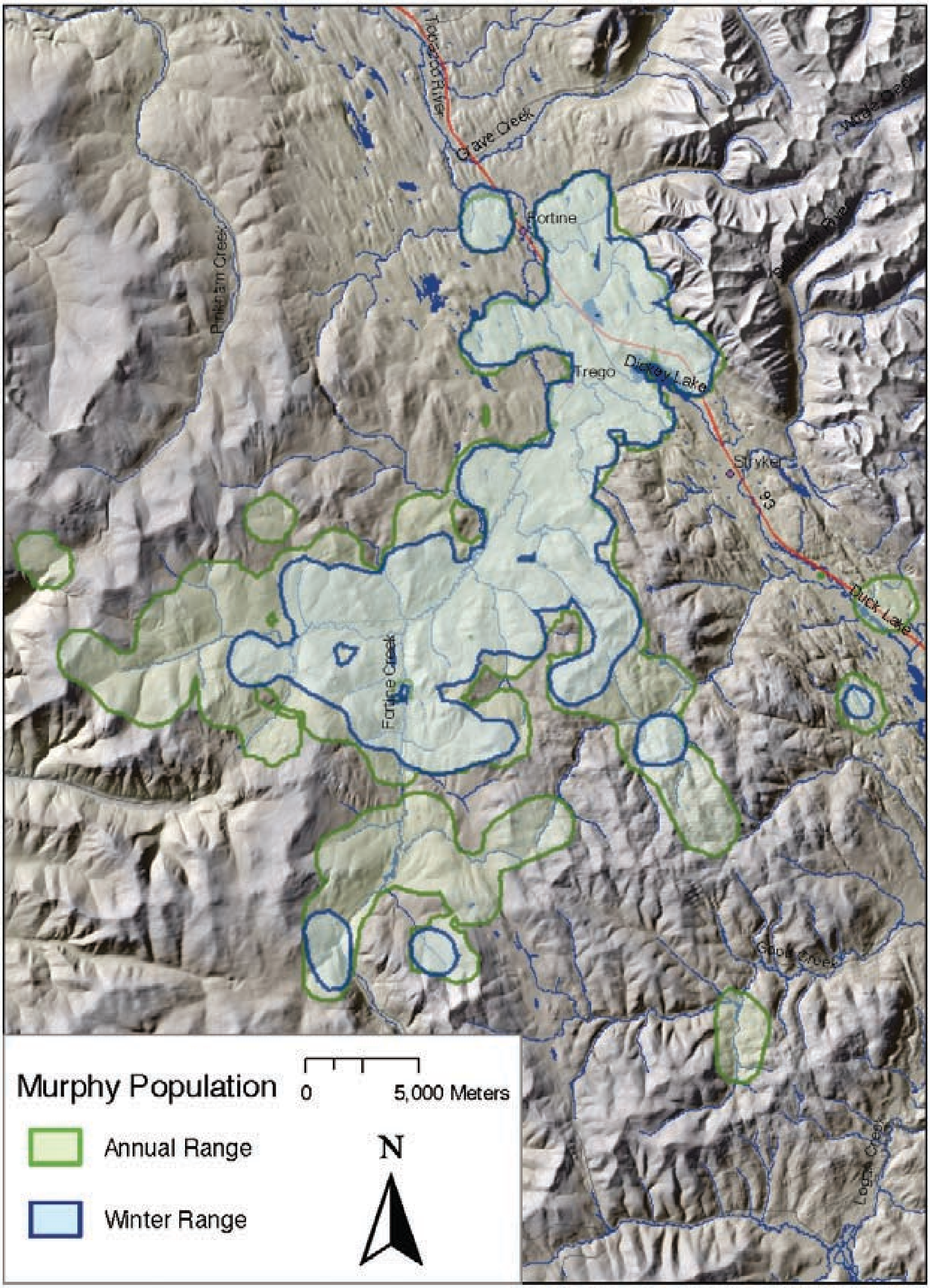


Figure 6. Estimated annual and winter (23 Nov to 4 Apr) ranges for the Murphy population of white-tailed deer in north-west Montana during 1988-2000 from bivariate adaptive kernel density estimator of utilization.

Table 12. Samples of radio-marked of white-tailed deer and relocations of individuals by sex on the winter ranges of the Bowser and Murphy study areas in northwest Montana during the winter period from 1998-2000.

Study area	**sex**	**sample**	**Biological Year**[a]												
			1988	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**
Bowser	F	relocations	10	168	266	515	521	241	167	131	37	148	290	482	316
	M			27	42	75	58	45	38	22	9	19	9	21	6
Murphy	F		6	62	83	155	198	115	115	55	16	87	148	269	180
	M			2		26	38	38	24	19	6	14	10		
Bowser	F	Individual[b]	10	40	46	56	63	43	45	41	36	59	56	44	34
	M			6	9	9	8	10	13	8	9	8	4	2	1
Murphy	F		6	18	19	24	28	24	27	20	16	34	38	32	19
	M			1		6	5	10	10	8	6	5	3		

[a] Locations during Nov and Dec in year *i* were included in biological year *i*+1.

[b] Most individuals sampled in >1 year.

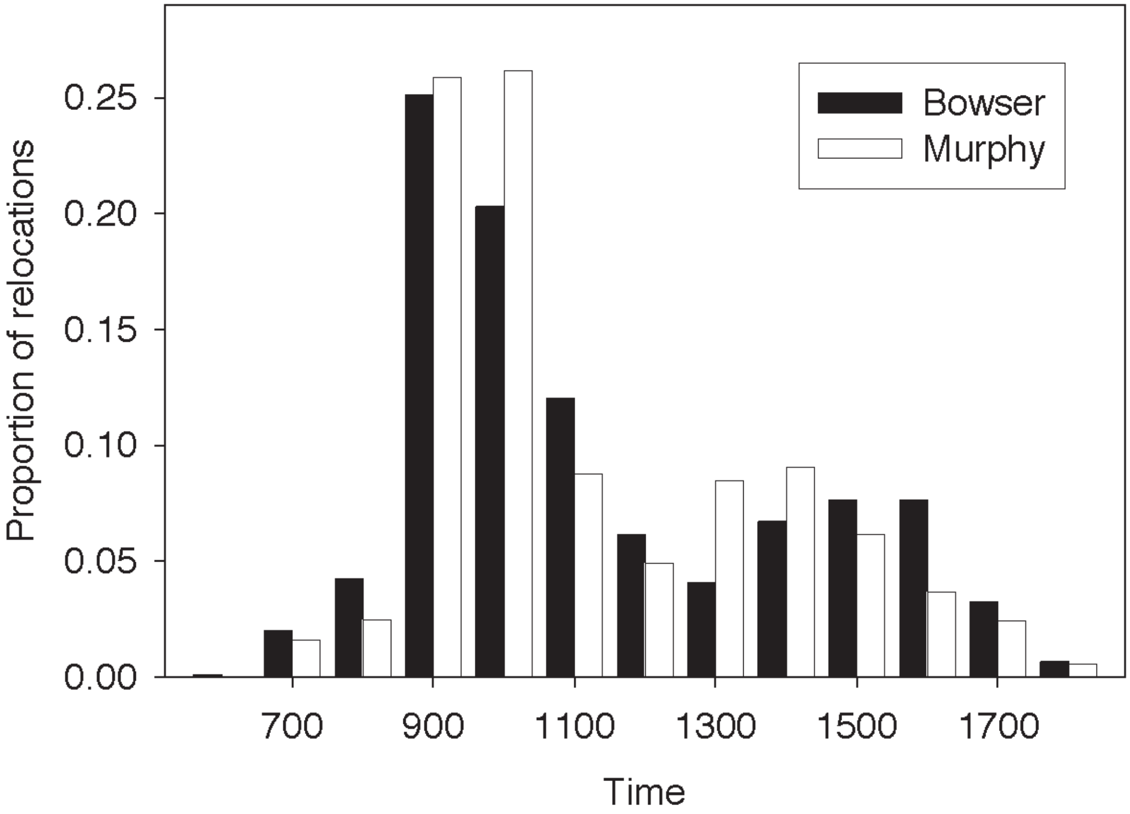


Figure 7. Proportion of total winter relocations of radio-marked white-tailed deer by time of day in 2 populations in north-west Montana during 1988-2000.

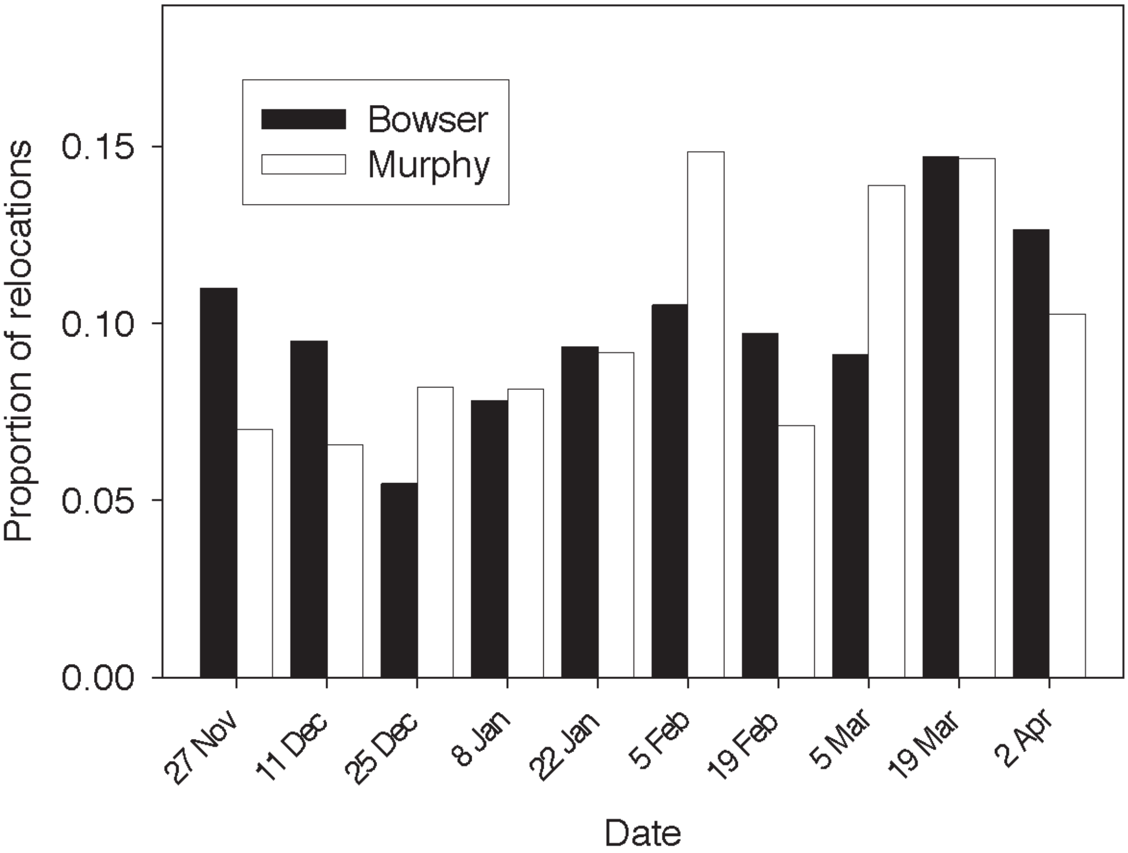


Figure 8. Proportion of total winter relocations of radio-marked white-tailed deer relative to date for 2 populations in north-west Montana during 1988-2000.

Table 13. Mean values of variables used to characterize resources for a sample of available locations in the estimated winter range of populations of white-tailed deer during 1988-2000 for the Bowser and Murphy study areas in northwest Montana.

	Topography				Floristic				
Study area	**ELEV**	**SLP**	**SLPSD**	**ASP**	**GFB**	**SHR**	**PICO**	**PSME**	**SIM**
Bowser	1.15	9.9	2.01	154	0.04	0.07	0.06	0.15	0.62
Murphy	1.16	8.7	1.40	182	0.08	0.03	0.06	0.19	0.59

Table 13 continued. Mean values of variables used to characterize resources for a sample of available locations in the estimated winter range of populations of white-tailed deer during 1988-2000 for the Bowser and Murphy study areas in northwest Montana.

	Floristic	Tree Physiognomy							
Study area	**STM**	**DBH 0-5**	**DBH 5-10**	**DBH 10-15**	**DBH $15**	**CAN 10-25**	**CAN 25-60**	**CAN $60**	**ROAD**
Bowser	0.04	0.11	0.43	0.12	0.22	0.08	0.68	0.12	162.5
Murphy	0.04	0.05	0.24	0.47	0.12	0.13	0.44	0.32	272.0

estimated β coefficients >0 or <0 indicated preference or avoidance of a resource across all levels of SWE. The population was neutral to Douglas fir, showed preference for the shade-intolerant mixture, preferred south- west to north-east aspects, and avoided the shade-tolerant mixture. However, estimated β's were > estimated ,'s in each case, indicating substantial individual heterogeneity in preference.

For linear variables for which interaction terms were included, main effects described selection when SWE was 0 cm, and interaction terms described response in selection with increasing SWE. In general, resource preferences became more specific and restricted as SWE increased. When SWE was minimal, deer were about neutral to grass-forb, medium trees, slightly preferred large trees, slightly avoided shrub and closed canopy. However, interaction terms showed a strong decrease in preference with increasing SWE for all variables except large trees, and large coefficients relative to associated standard errors provided strong support for these interactions. For most variables, increasing SWE apparently reinforced trends when SWE was minimal. For example, preference for large trees and avoidance of grass-forb became more pronounced as SWE increased (Figure 9). For

Table 14. Matrix of Pearson correlation coefficients between resource attributes from a LANDSAT vegetation map in a systematic sample of locations within the estimated winter range available to white-tailed deer in northwest Montana during 1988-2000. Coefficients to the left are for Bowser and to the right are for Murphy. To improve clarity, all coefficients are multiplied by 100, only coefficients >0.4 are reported, and negative coefficients are in bold.

Variable	ELEV	SLP	SLPSD	ASP	GFB	SHR	SIM	STM	PICO	PSME	DBH 0-5	DBH 5-10	DBH 10-15	DBH ≥15	CAN 10-25	CAN 25-60
SLP	53 • 56															
SLPSD		54 • 59														
ASP																
GFB																
SHR																
SIM						47 •										
STM																
PICO																
PSME		44 •					48 • 58									
DBH 0-5																
DBH 5-10																
DBH 10-15												• 47				
DBH ≥15+												45 •				
CAN 10-25											76 • 71					
CAN 25-60					40 •	49 •	46 •					66 • 47			• 43	
CAN ≥60													• 51	72 •		54 • 57

Table 15. Model selection results for predicting resource selection by the Bowser population of white-tailed deer in northwest Montana during 1988-2000 relative to resources available within their winter range. Analyses were based on vegetation attributes from a LANDSAT vegetation map. The top model and all other models within 20 DIC units of the top model for each variable set are included.

Variable Set	Rank[a]	Deviance	pD[b]	DIC[c]	ΔDIC[d]	Model
Topography	1	20247.0	20.2	20287.5	0.0	ELEV + $ELEV^2$ + ASP + SLPSD + $SLPSD^2$
Floristics	1	19022.9	47.3	19117.5	0.0	GFB + SHR + PSME + SIM + STM
Physiognomy	1	17944.4	67.1	18078.5	0.0	DBH 10-15 + DBH ≥15 + CAN 10-25 + CAN $60
	2	17944.9	73.5	18091.9	13.3	DBH5-10 + DBH 10-15 + DBH ≥15 + CAN 10-25 + CAN ≥60

[a] Rank of the model within each variable set relative to the model with the lowest DIC.

[b] Estimated effective number of parameters.

[c] Deviance Information Criterion.

[d] Difference in DIC relative to the model with the lowest DIC within each variable set.

Table 16. Parameter estimates from the DIC selected model predicting relative probability of use by the Bowser population of white-tailed deer in northwest Montana during 1988-200 relative to resource attributes of their winter range and interactions of selected resource attributes with snow water equivalent (SWE). Analyses were based on vegetation attributes from a LANDSAT vegetation map.

Variable	β	SE	σ^a	SE
ELEV	-2.39	1.67	12.95	1.89
ELEV^2	0.76	0.78	6.28	0.92
ASP -0.19	0.07	0.74	0.05	
SLPSD	2.82	0.24	2.18	0.22
SLPSD^2	-0.71	0.06	0.62	0.05
GFB -0.27	0.51	1.64	0.34	
SHR -0.73	0.47	1.57	0.31	
PSME	-0.01	0.36	2.03	0.29
SIM 0.64	0.29	1.36	0.19	
STM -2.74	0.48	2.94	0.57	
DBH 10-15	-0.05	0.26	1.70	0.23
DBH ≥15	0.63	0.21	1.98	0.23
CAN 10-25	0.96	0.26	1.72	0.29
CAN ≥60	-0.93	0.27	1.48	0.22
ELEV*SWE	-12.26	1.68	14.13	1.39
ELEV2*SWE	-6.68	0.81	6.47	0.67
GFB*SWE	-0.55	0.09	0.72	0.07
SHR*SWE	-0.62	0.08	0.66	0.05
DBH 10-15*SWE	-0.15	0.05	0.55	0.04
DBH ≥15*SWE	0.15	0.04	0.49	0.03
CAN 10-25*SWE	-0.68	0.10	0.83	0.07
CAN ≥60*SWE	-0.16	0.05	0.53	0.04

[a] Estimated SD in estimated βs among individuals.

all plots of utility, we would expect magnitude of difference in utility values across each function to predict relative probability of use by deer. Because only relative values on each line have meaning, it is not useful to compare utilities between lines. Open canopy was a notable exception, as it was preferred when SWE was minimal but avoided when SWE was high (Fig. 10). Negative coefficients for closed canopy appeared to occur as a result of positive coefficients for large trees and the strong positive correlation between these variables (Table 14), as models with the large tree variable omitted generally indicated a neutral or slightly positive response to closed canopy. Thus, we concluded that when SWE was high this population tended to select stands of large trees with relatively open canopy, given that large trees in general had the highest canopy closure. This pattern, combined with strong avoidance of open canopy and non-forested habitat when SWE was high, resulted in high usage of moderate canopy that greatly exceeded availability and usage of closed canopy roughly in proportion to availability.

Because quadratic effects depend on values for both coefficients, estimates for these coefficients are easiest to interpret in tandem. At the population level, deer preferred intermediate terrain roughness (Fig. 11). However, individual variation in coefficients was substantial. Viewing the utility function at ± σ, i.e., ±1 SD, around the population response shows the "average" estimated variation in preference among individuals. Because correlation between these estimated coefficients for individuals was strongly negative (Table 17), individuals with higher values for one coefficient tended to have lower values for the other, resulting in a continuum from individuals with strong preference for intermediate terrain roughness to individuals relatively neutral to terrain roughness (Fig. 11). With minimal SWE, the population was largely neutral to elevation (Fig. 12). However, increasing SWE rapidly lead to very strong preference for lower elevation. When SWE was high, deer use was largely restricted to elevations £ 1000 m. Individual heterogeneity was large (Table 16), and correlations in individual parameter estimates among elevation variables were near -/+1 (Table 17). Utility functions plotted ± ø around the population response to visualize the "average" amount of individual heterogeneity revealed a continuum of individuals whose preference ranged from low to high elevations (Fig. 13a). However, even with small increases in SWE most individuals preferred low elevation, and deer exhibited a strong preference for lower elevation with high SWE (Figs 13b,c).

For the Murphy study area, uncertainty in model selection was small for each variable set (Table 18). Reductions in DIC values for successive variable subsets indicated each improved predictive performance after controlling for previously entered variables. Because of problems with model optimization, the quadratic term on the elevation variable was dropped from the final model (Table 19). Similar to results for the Bowser population, the population showed slight preference for southwest over northeast aspects, but individual variation in preference was high. Preference for intermediate terrain roughness at the population level and patterns of individual heterogeneity (Fig. 14) were also nearly identical to those for the Bowser population (Fig. 11). However, deer at Murphy

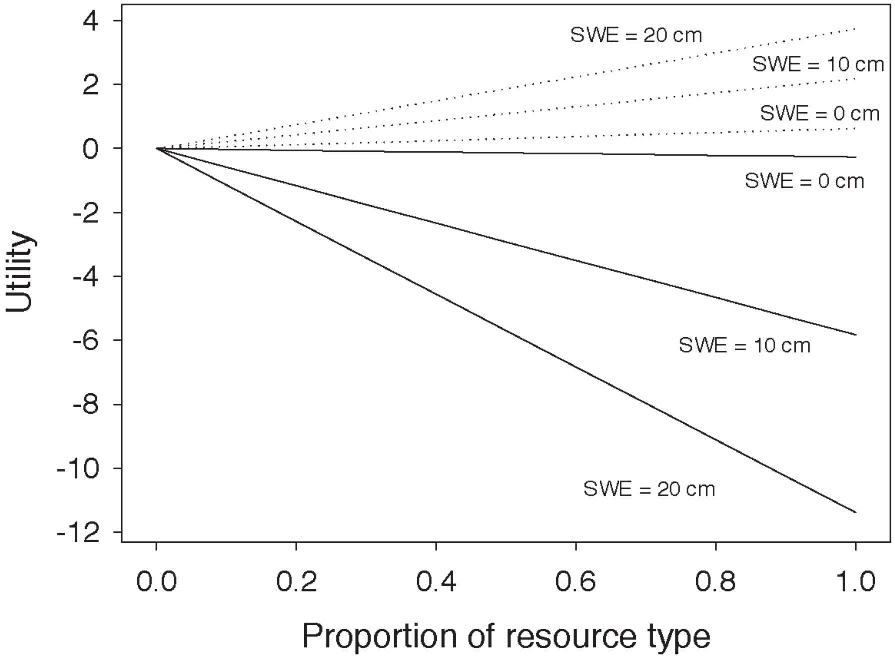


Figure 9. Estimated relative utility to white-tailed deer of the grass-forb (solid lines) and large tree (dotted lines) habitat classes on the Bowser study area in north-west Montana during winters of 1988-2000. Separate lines show relative utility for different values of snow water equivalent (SWE). Analyses were based on vegetation attributes from a LANDSAT vegetation map.

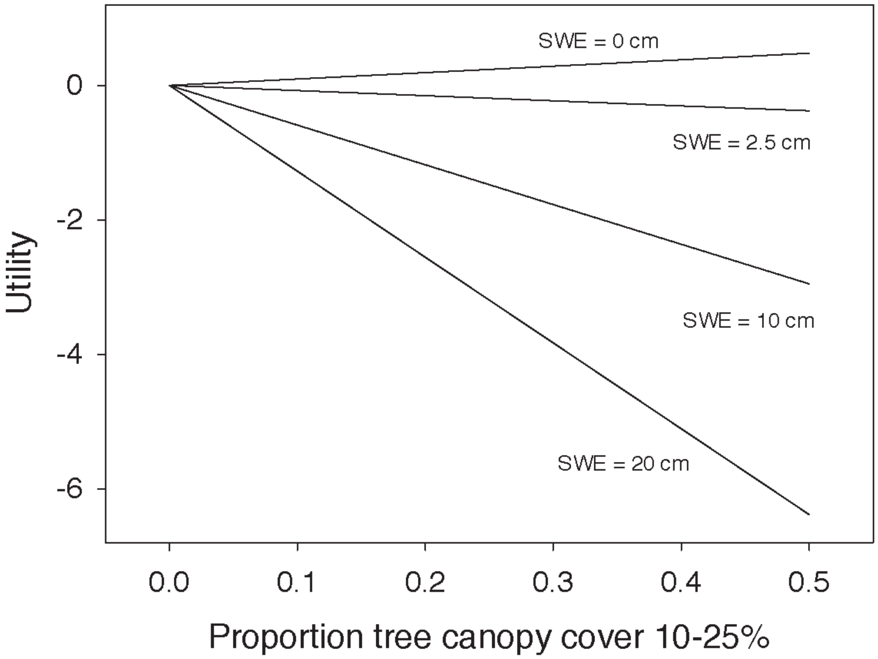


Figure 10. Estimated relative utility to white-tailed deer of proportion of open canopy cover at locations on the Bowser study area in north-west Montana during winters of 1988-2000. Separate lines show relative utility at different values of snow water equivalent (SWE). Analyses were based on vegetation attributes from a LANDSAT vegetation map.

Table 17. Correlations of estimated coefficients for individuals from the DIC selected model predicting relative probability of use by the Bowser population of white-tailed deer in northwest Montana during 1988-200 relative to resource attributes of their winter range and interactions of selected resource attributes with snow water equivalent (SWE). Analyses were based on vegetation attributes from a LANDSAT vegetation map. For clarity, only coefficients >0.45 are shown.

Variable	ELEV	ELEV^2	ASP	SLPSD	SLPSD^2	GFB	SHR	SIM	STM	PSME	DBH 10-15	DBH ≥15	CAN 10-25	CAN ≥60	ELEV *SWE	ELEV^2 *SWE	GFB *SWE	SHR *SWE	DBH 10-15 *SWE	DBH ≥15 *SWE	CAN 10-25 *SWE
ELEV^2	-0.91																				
ASP																					
SLPSD																					
SLPSD^2				-0.71																	
GFB																					
SHR																					
SIM																					
STM																					
PSME							0.48														
DBH 10-15																					
DBH ≥15																					
CAN 10-25																					
CAN ≥60																					
ELEV*SWE	0.96	-0.94																			
ELEV^2*SWE		-0.94	-0.94												-0.99						
GFB*SWE																					
SHR*SWE																					
DBH 10-15*SWE																					
DBH ≥15*SWE																					
CAN 10-25*SWE																					

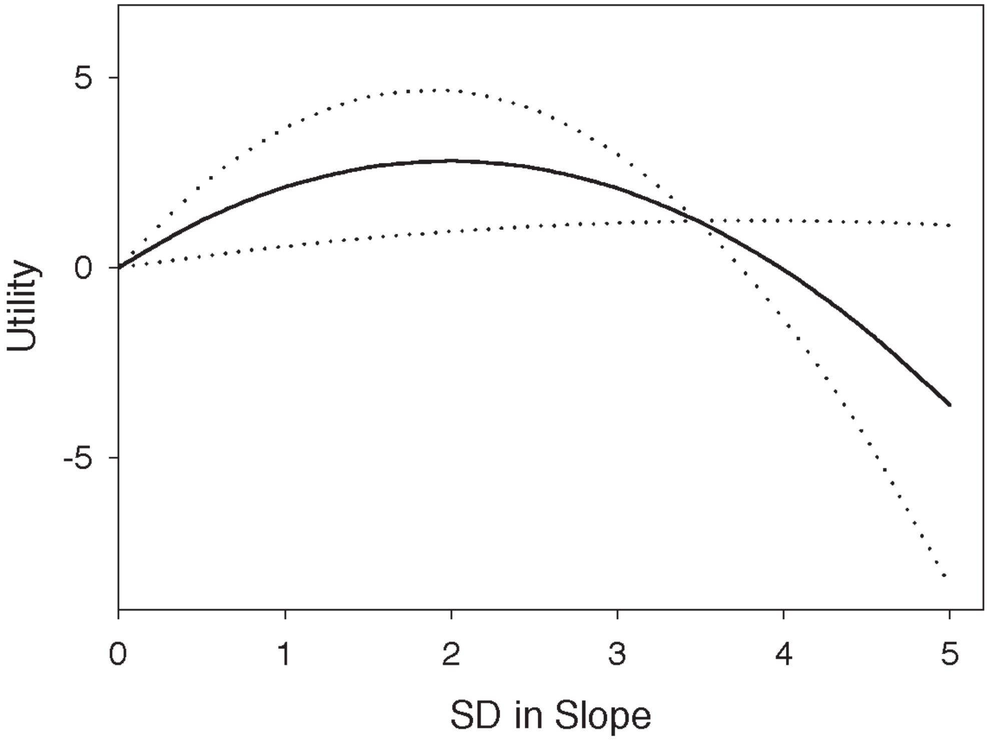


Figure 11. Estimated relative utility to white-tailed deer of SD in slope for locations in the winter range in the Bowser population in north-west Montana during 1988-2000. The solid line indicates the population mean and dotted lines indicate individual variation ±1 SD from the population mean. Analyses were based on vegetation attributes from a LANDSAT vegetation map. See text for additional detail.

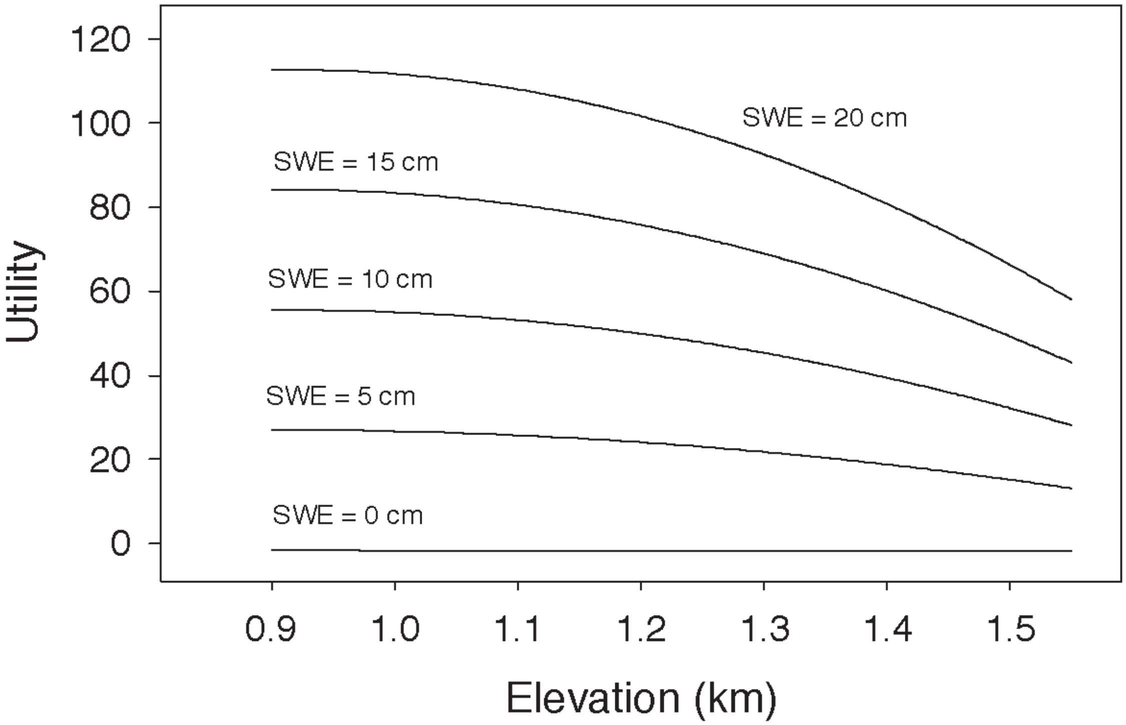


Figure 12. Estimated relative utility to white-tailed deer of elevation on the Bowser study area in north-west Montana during winters of 1988-2000. Separate lines show relative utility for different values of snow water equivalent (SWE). Analyses were based on vegetation attributes from a LANDSAT vegetation map.

were neutral to the shade-tolerant mixture in contrast to the strong avoidance observed for the Bowser population.

When SWE was minimal, deer preferred medium trees, avoided non-forest and large trees, and showed relatively weak preference for lower elevations. As SWE increased, avoidance of non-forest and higher elevations increased dramatically, preference for closed canopy increased, and preference for medium and large trees remained largely unchanged. Although an increasing avoidance of relatively open habitats was similar to results for the Bowser population, preference for medium trees and closed canopy with increasing SWE contrasted with high usage of large trees and moderate canopy at Bowser. For most variables, estimates of σ's exceeded those of an associated β*'s* that indicated relatively substantial individual variation. Correlations among selection coefficients estimated for individuals (Table 20) revealed that individuals with a strong preference for higher elevations at minimal SWE also tended to have relatively low preference for the shade-tolerant mixture and a less strong increase in preference for closed canopy with increasing SWE. In each case, deer apparently made heaviest use of floristic and physiognomic classes with higher relative prevalence at each study area.

Mean estimated SWE during the study on the Bowser study area steadily increased from near 0 at the start of the winter period to a peak of almost 15 cm in late February and then decreased rapidly to near 0 by early April (Fig. 15). Variation among years was large, with peak SWE varying by ~½ an order of magnitude. The ground remained free of snow for up to a half of the winter period in some years but had snow cover throughout the winter period in others. Because weather conditions were strongly correlated across our study areas, these patterns reflected those on the Murphy study area.

We used the best models to project predicted probability of use across available 200-m buffered locations on each winter range. To facilitate interpretation, we plotted probability of use as a ratio of predicted use to equal use for all locations. A relative value of 1 indicated predicted use equal to that expected at random. Relative use increasingly <1 and >1 indicated increasing avoidance of and preference for a location. To assess effects of typical variation in

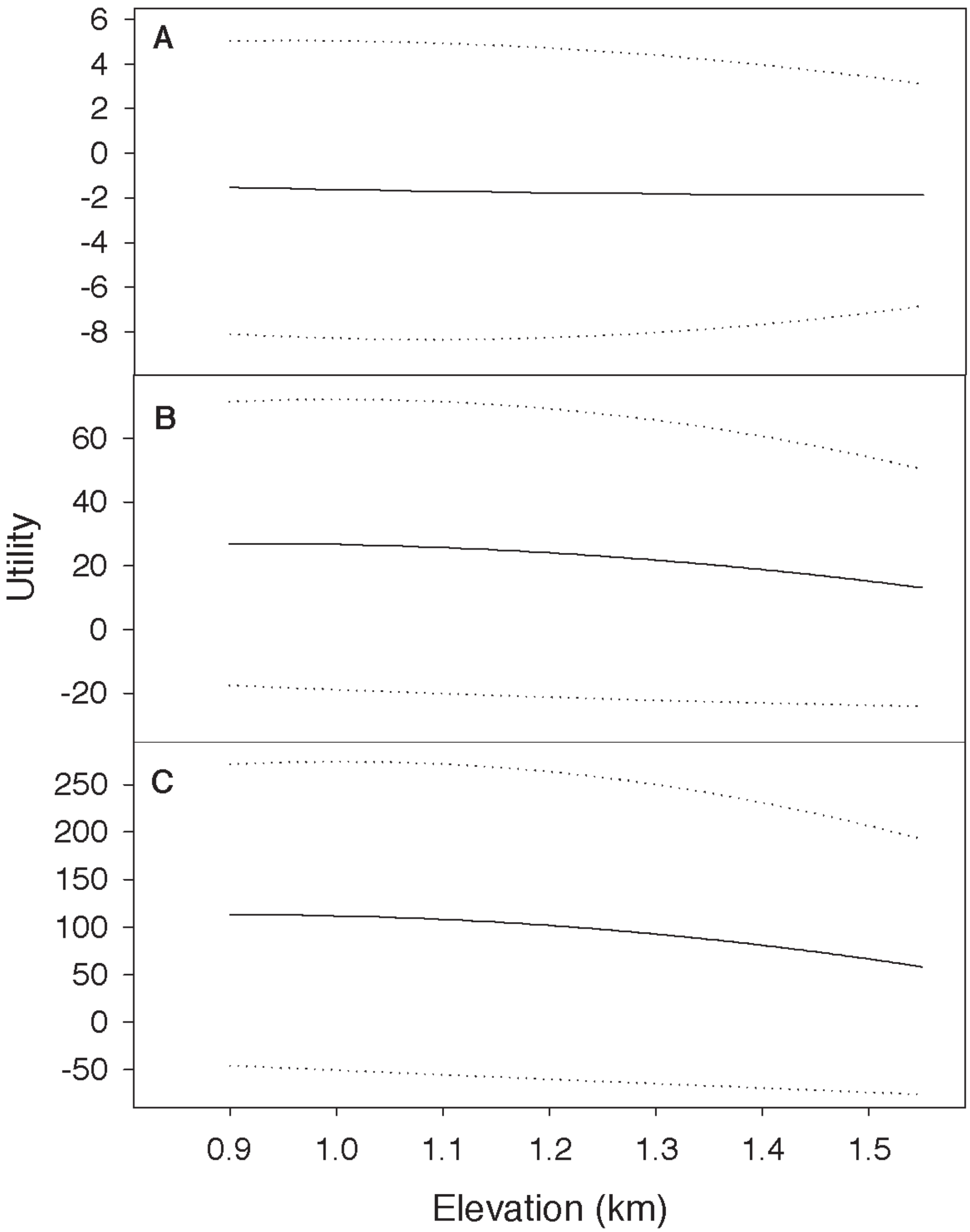


Figure 13. Estimated relative utility to white-tailed deer of elevation on the Bowser study area in north-west Montana during winters of 1988-2000 with snow water equivalent of 0 cm (A), 5 cm (B), and 20 cm (C). Analyses were based on vegetation attributes from a LANDSAT vegetation map.

Table 18. Model selection results for predicting resource selection by the Murphy population of white-tailed deer in northwest Montana during 1988-2000 relative to resources available within their winter range. The top model and all other models within 20 DIC units of the top model for each variable set are included.

Variable Set	Rank[a]	Deviance	pD[b]	DIC[c]	ΔDIC[d]	Model
Topography	1	9283.1	14.5	9312.2	0.0	ELEV + ELEV^2 + ASP + SLPSD^2
Floristics	1	8984.9	33.7	9052.3	0.0	GFB + SHR + PICO + PSME + STM
	2	9001.1	32.3	9065.7	13.4	GFB + SHR+ PSME + STM
Physiognomy	1	8830.3	57.3	8944.9	0.0	DBH 10-15 + DBH ≥15 + CAN ≥60

[a] Rank of the model within each variable set relative to the model with the lowest DIC.

[b] Estimated effective number of parameters.

[c] Deviance Information Criterion.

[d] Difference in DIC relative to the model with the lowest DIC within each variable set.

Table 19. Parameter estimates from the DIC selected model predicting relative probability of use by the Murphy population of white-tailed deer in northwest Montana during 1988-200 relative to resource attributes of their winter range and interactions of selected resource attributes with snow water equivalent (SWE).

Variable	β	SE	σ[a]	SE
ELEV	-5.28	0.51	4.06	0.48
ASP	-0.14	0.10	0.87	0.08
SLPSD	2.37	0.27	1.93	0.26
SLPSD^2	-0.79	0.09	0.67	0.07
GFB	-1.65	0.34	1.72	0.30
SHR	-2.60	0.74	2.06	0.59
PICO	0.52	0.33	1.72	0.30
PSME	0.33	0.18	1.30	0.15
STM	0.23	0.42	2.34	0.42
DBH 10-15	0.08	0.23	1.66	0.22
DBH ≥15	-0.89	0.34	2.37	0.33
CAN ≥60	0.09	0.21	1.62	0.19
ELEV*SWE	-2.66	0.30	1.59	0.22
GFB*SWE	-0.65	0.18	1.08	0.14
SHR*SWE	-0.62	0.50	1.57	0.32
DBH 10-15*SWE	0.07	0.11	0.78	0.08
DBH ≥15*SWE	0.04	0.15	0.93	0.11
CAN ≥60*SWE	0.23	0.10	0.72	0.07

[a] Estimated SD in estimated β among individuals.

snow accumulation, we projected use at three levels of SWE for each study area: A) low snow - minimal accumulation typical of early/late winter period, B) moderate snow - accumulation at mid-winter (1 Feb) during an average year, and C) high snow - accumulation at mid-winter during a severe winter (mean + 1 SD).

Projections of relative predicted use for the Bowser herd at low snow conditions (Fig 16a) showed use widely distributed across the winter range. Small patches of increased use distributed across all elevations, in response to local topography and vegetation features. The large proportion of the map covered by yellow and pale orange use classes indicated that deer use was diffuse and that preferences for resource features were relatively modest. With moderate snow accumulation, areas that were preferred were restricted primarily to low elevation locations with relatively mature timber (Fig. 16b). Small patches of preferred habitat were distributed in low-lying areas east of the Stillwater River and north to the confluence of Good and Logan Creeks, but a large block of mature timber located in the southwest portion of the winter range, i.e., the "core winter range," was strongly preferred. Deer were much more specific in resource selection, as evidenced by prevalence of deep green (strong avoidance) and red (strong preference) classes. At high snow accumulation, predicted use was severely restricted, primarily to the core winter range and a few nearby patches of mature timber to the north (Fig. 16c), and almost all other locations were strongly avoided. The strong gradient between strongly preferred and avoided locations reflected highly specific resources selected by deer.

Similar changes in predicted use with snow accumulation were evident for the Murphy area. With minimal snow accumulation (Fig. 17a), predicted use was relatively widely distributed across the winter range. Most of the low-lying areas around Murphy and Dickey Lakes showed relatively high usage, and preferred areas also extended to mid-elevations adjacent to Fortine Creek. We explain this contrast to relatively high predicted use for higher elevations at low snow accumulation for the Bowser population (Fig. 16a) by restriction of models for Murphy to linear effects of elevation, rather than by biological differences between populations. At moderate

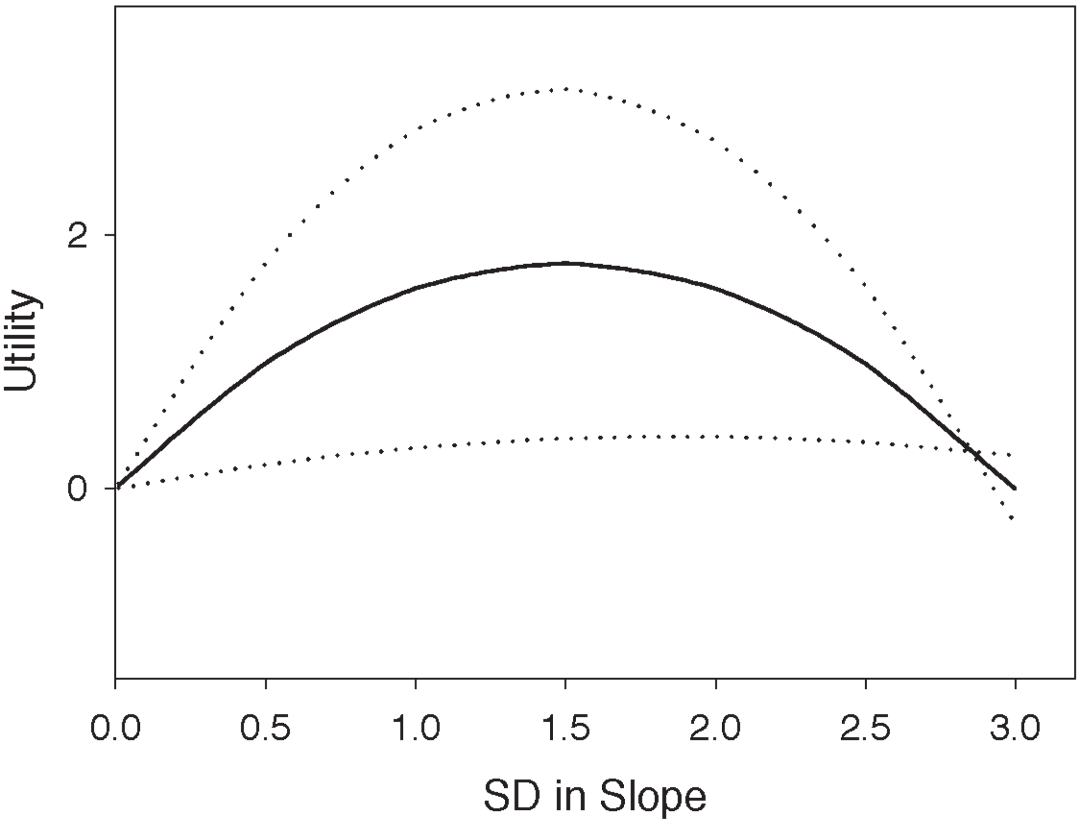


Figure 14. Estimated relative utility to white-tailed deer of SD in slope for locations in the winter range of the Bowser population in north-west Montana during 1988-2000. The solid line indicates the population mean and dotted lines indicate individual variation ±1 SD from the population mean. See text for additional detail.

Table 20. Correlation matrix of estimated coefficients for individuals from the DIC selected model predicting relative probability of use by the Murphy population of white-tailed deer in northwest Montana during 1988-200 relative to resource attributes of their winter range and interactions of selected resource attributes with snow water equivalent (SWE). For clarity, only coefficients >0.5 are shown.

Variable	ELEV	ASP	SLPSD	SLPSD^2	SHR	GFB	SHR	STM	PICO	PSME	DBH 10-15	DBH ≥15	ELEV *SWE	GFB *SWE	SHR *SWE	DBH 10-15 *SWE	DBH ≥15 *SWE
ASP																	
SLPSD																	
SLPSD^2			-0.58														
GFB																	
SHR																	
STM	-0.61																
PICO																	
PSME																	
DBH 10-15																	
DBH ≥15																	
CAN ≥60																	
ELEV*SWE																	
GFB*SWE																	
SHR*SWE																	
DBH 10-15*SWE																	
DBH ≥15*SWE																	
CAN ≥60*SWE	0.51																

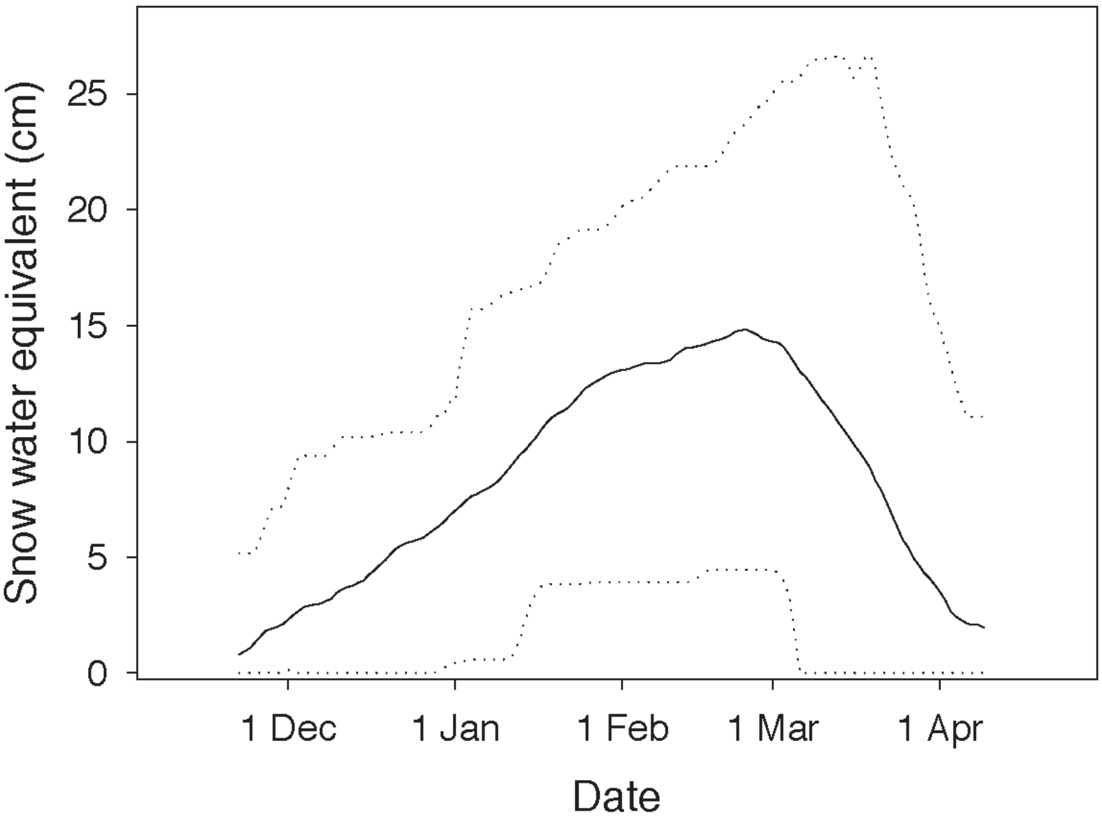


Figure 15. Mean (solid line), minimum, and maximum (dotted lines) estimated snow water equivalent on the Bowser study area in north-west Montana during winters of 1987-88 to 1999-2000.

snow conditions (Fig. 17b), preferred areas were restricted primarily to low-lying areas around Murphy and Dickey Lakes with relatively mature timber. With high snow accumulation, most use was limited to a handful of mature timber stands near Murphy and Dickey lakes and Fortine (Fig. 17c). Although more widely dispersed than at Bowser, these few strongly preferred areas constituted the core winter range for the Murphy population.

The USDA Forest Service produced classification error matrices for all resource classes in their vegetation map (Brewer et al. 2004). They determined accuracy by comparing attributes from this map to interpretation from aerial photographs, which used reference stands with known attributes and local knowledge of interpreters to optimize classification accuracy. Accuracy estimates were derived from regional vegetation maps, and hence accuracy may have differed between our study areas. We used these estimates of classification error to calculate user's classification accuracy for floristic and tree physiognomic variables used in our analyses (Table 21). Floristic classification accuracy was highest for non-forested and for the prevalent shade-intolerant mixture, but error was higher for rarer tree classes. Error rates were generally highest for tree size, and overall accuracy was highest for tree canopy. Estimates of overall "fuzzy" classification error, which includes classification in adjacent classes as accurate, for tree size (83%) and canopy (98%) classes showed that gross mis-classification was rare.

Timber stand inventory.—For the Bowser population, 2919 relocations of 239 deer (186 females, 53 males) fell within coverage of timber stand inventories. Numbers of relocations averaged 12.2/individual with a range of 1 to 41 relocations. Sixty-three percent of available locations in the winter range (10,106 of 16,024) fell within the coverage of the timber stand inventory data (Fig. 18).

Relative to the full winter range (Table 13), available habitat within the timber stand

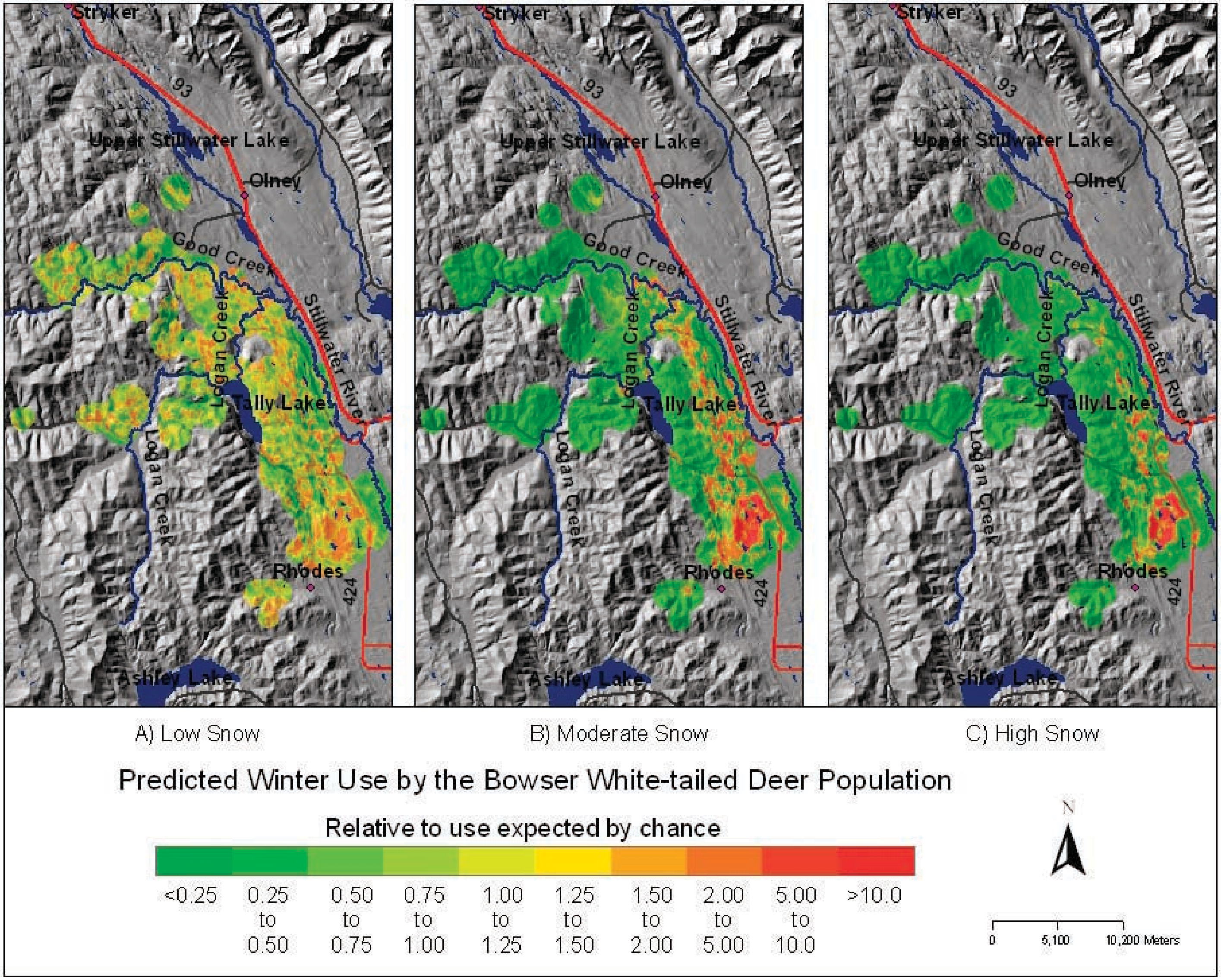


Figure 16. Predicted probability of winter use for available locations within the winter range of the Bowser population of white-tailed deer in northwest Montana during 1988-2000. Predictions are from the best model of resource selection based on a LANDSAT derived map of vegetation characteristics. Probability of use is expressed relative to expected use if all locations had equal probability of use. Relative use is projected at 3 levels of snow accumulation based on snow water equivalent (SWE) at the Olney meteorological station: A) low snow (SWE = 0) - minimal winter snow accumulation, B) moderate snow (SWE = 10 cm) - typical winter snow accumulation, and C) high snow (SWE = 20 cm) - severe winter snow accumulation.

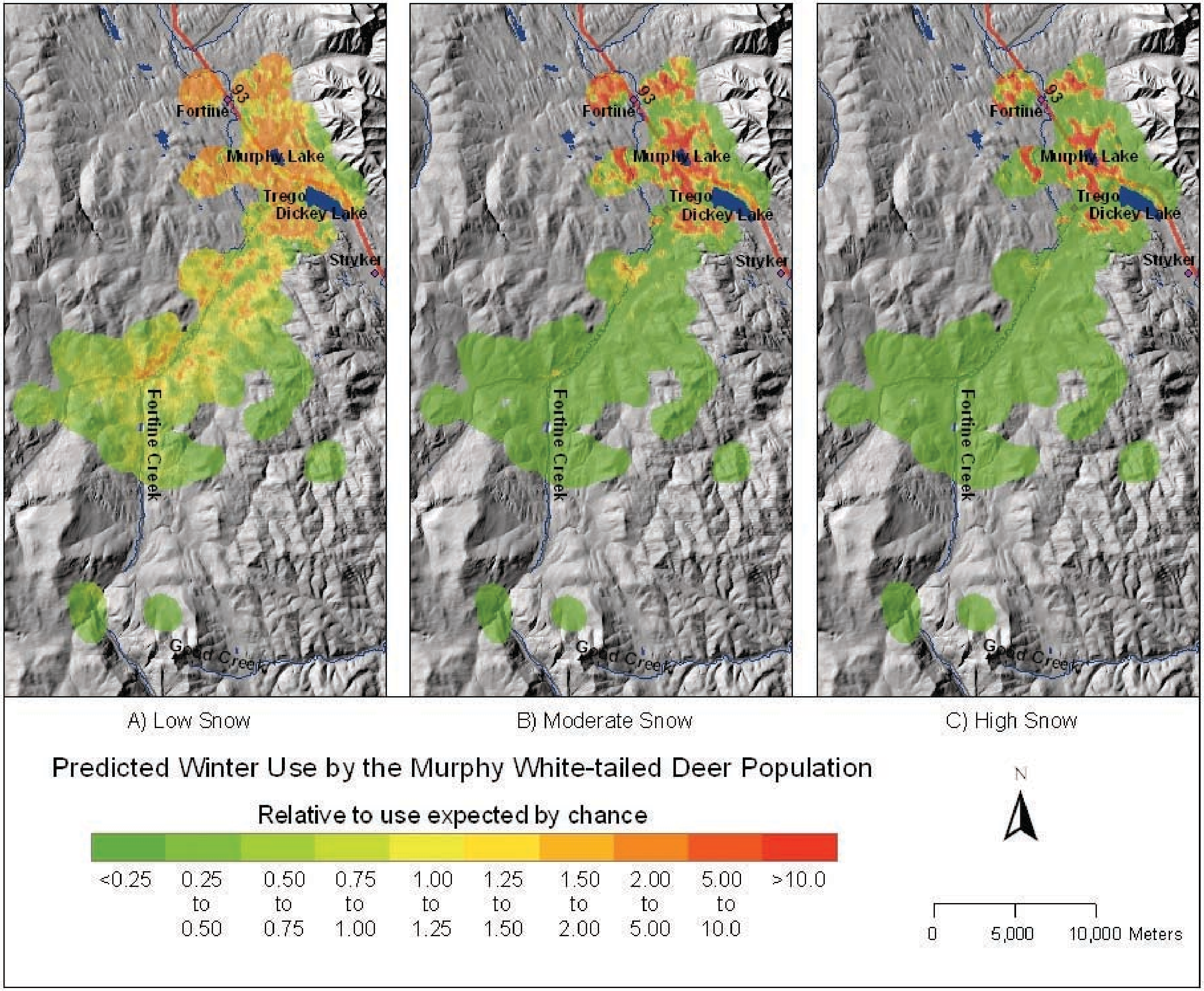


Figure 17. Predicted probability of winter use for available locations within the winter range of the Murphy population of white-tailed deer in northwest Montana during 1988-2000. Predictions are from the best model of resource selection based on a LANDSAT derived map of vegetation characteristics. Probability of use is expressed relative to expected use if all locations had equal probability of use. Relative use is projected at 3 levels of snow accumulation based on snow water equivalent (SWE) at the Fortine meteorological station: A) low snow (SWE = 0) - minimal winter snow accumulation, B) moderate snow (SWE = 7.5 cm) - typical winter snow accumulation, and C) high snow (SWE = 15 cm) - severe winter snow accumulation.

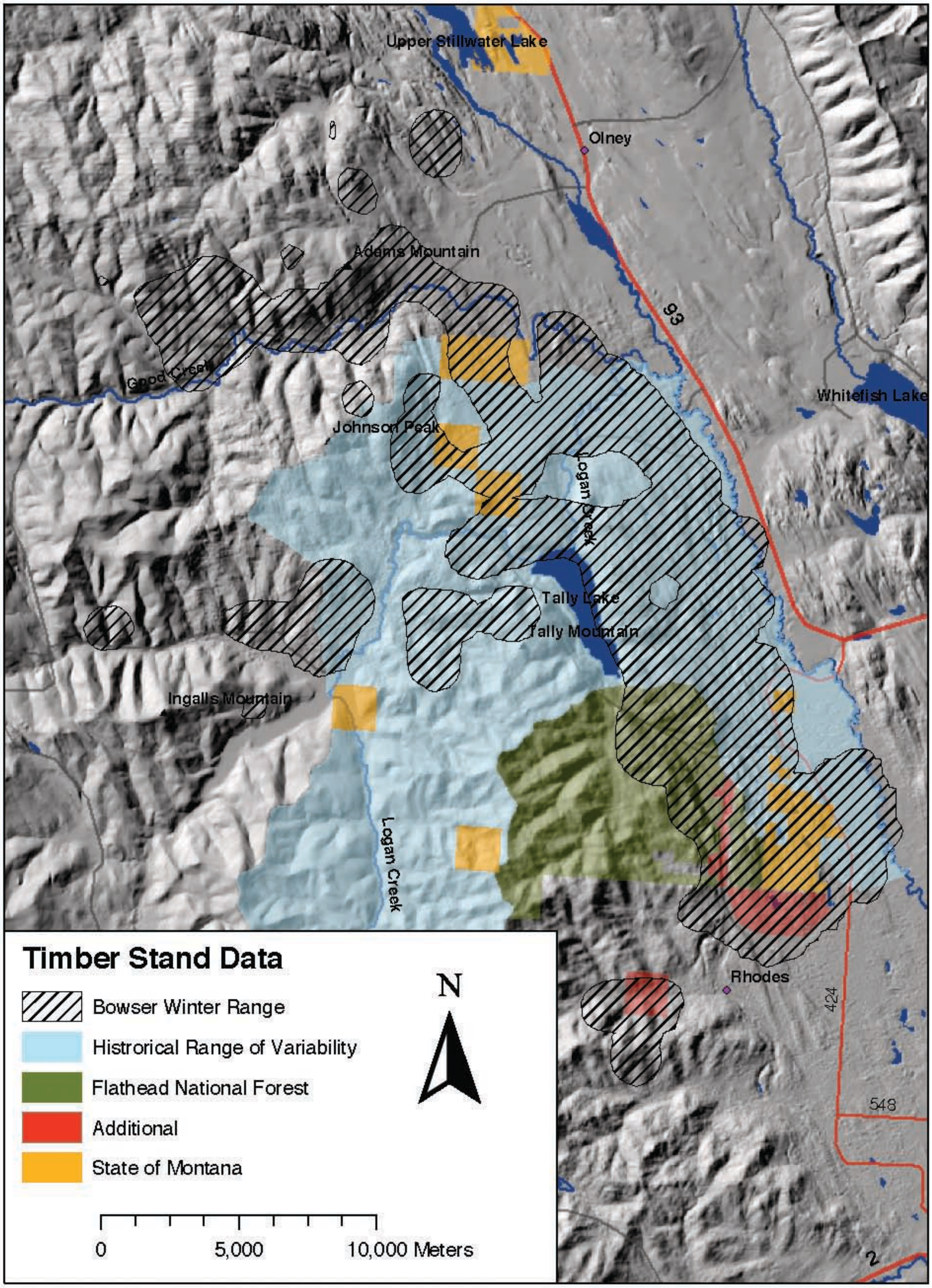


Figure 18. Estimated winter range for the Bowser population of white-tailed deer in northwest Montana during 1988-2000 relative to areal coverage of timber stand inventories maintained by public land management agencies.

inventory map coverage was slightly lower, less steep, and less rugged (Table 22). Douglas fir dominated the area, with remaining area fairly evenly spread among the western larch, lodgepole pine, and non-forest. Floristic composition was generally similar to that of the LANDSAT map. Because the shade-intolerant mixture in the LANDSAT map describes mixtures of Douglas fir and western larch, it most strongly corresponds to Douglas fir and western larch variables that were prevalent in the timber stand inventory. Similarly, subalpine fir in the timber inventory occurred in similar abundance as the comparable shade-tolerant mixture of the LANDSAT map, and the prevalence of non-forest in the timber inventory was similar to the combined grass-

Table 21. Estimated classification error rates for a resource map created from LANDSAT thermatic imaging data. We present user's classification accuracy rates, which is the probability that a map classification accurately represents that classification on the ground.

Variable Type	Variable	User's accuracy
Floristic	Grass-forb	69
	Shrub	65
	Shade-intolerant mixture	53
	Shade-tolerant mixture	38
	Lodgepole pine	35
	Douglas fir	38
	Overall	52
Tree Size	Sapling	37
	Small tree	39
	Medium tree	45
	Large tree	34
	Overall	39
Tree Canopy	Open canopy	59
	Moderate canopy	69
	Closed canopy	57
	Overall	64

Table 22. Mean values of variables derived from a timber stand inventory used to characterize resources for a sample of available locations in the estimated winter range of populations of white-tailed deer during 1988-2000 at the Bowser study area in northwest Montana.

Variable Type	Variable	Mean
Topographic	ELEV	1.11
	SLP	9.67
	SLPSD	2.05
	ASP	0.00
Habitat type	PSME	0.57
	LAOC	0.12
	PICO	0.13
	ABLA	0.04
	NFOR	0.11
Tree size	SAPL	0.08
	POLE	0.20
	MED	0.45
	LAR	0.16
Tree canopy	CCL	0.09
	CCM	0.28
	CCH	0.52

Table 23. Matrix of Pearson correlation coefficients between resource attributes in a systematic sample of locations within the annual range available to white-tailed deer in northwest Montana during 1988-2000. Vegetation attributes were from timber stand inventories. For clarity, only coefficients >0.4 are shown.

Variable	ELEV	SLP	SLPSD	ASP[a]	NFOR	LAOC	ABLA	PICO	PSME	SAPL	POLE	MED	LAR	CCL	CCM
SLP	0.50														
SLPSD		0.54													
ASP															
NFOR															
LAOC															
ABLA															
PICO															
PSME					-0.43	-0.46		-0.50							
SAPL															
POLE															
MED											-0.43				
LAR												-0.45			
CCL															
CCM															
CCH					-0.42										-0.67

forb and shrub variables in the LANDSAT map. However, medium trees and closed canopy were relatively prominent in the timber inventory, but the small trees and medium canopy were relatively prominent in the LANDSAT map.

Correlations among attributes of available resources showed few strong relationships (Table 23). As expected negative relationships existed between some mutually exclusive physiognomic variables. However, the strong relationship between tree size and canopy observed in the LANDSAT map was absent.

Little uncertainty existed in model selection (Table 24). Substantial reductions in DIC values from adding each successive variable subset indicated each dramatically improved predictive performance after controlling for previously entered variables. Because of problems with model optimization, the quadratic term on the elevation variable was dropped from the final model (Table 25). Deer showed preference for southwest aspects and Douglas fir and strong avoidance of lodgepole pine and subalpine fir. With minimal SWE, deer preferred medium trees and showed slight avoidance of higher elevations, non-forest, and relatively open tree canopy. With increasing SWE, avoidance of higher elevations, non-forest, and open tree canopy all increased, but preference for tree size remained largely unchanged. The relatively moderate change in preference for elevation with increasing SWE appeared to largely result from the exclusion of high elevation areas in the timber stand inventory coverage. The strong negative correlation of moderate and closed canopy (Table 23) showed that avoidance of moderate canopy was largely equivalent to preference for closed canopy. As usual, large estimated $\hat{U}$'s demonstrated large individual heterogeneity in preferences. Correlations among β's for individuals (Table 26) indicate that individuals showing relative preference for higher elevations also showed relatively high preference for open habitats, lodgepole pine, and subalpine fir, which were all avoided by the population in general. Also, individuals showing relative preference for higher elevation with minimal SWE showed a stronger decrease in preference for higher elevations as SWE increased.

As for models derived from LANDSAT vegetation maps, we employed our best model to project predicted probability of use relative to use expected by chance for all buffered available locations in the winter range encompassed by timber stand inventories. With low snow accumulation, areas of relatively high-predicted use were widely distributed throughout the study area (Fig. 19a). As for the Murphy models, we interpret that low predicted use of higher elevations in the west largely resulted from restriction to linear effects of elevation, rather than biological differences from predictions showing relatively higher usage of upper elevations from models using LANDSAT data (Fig. 12a). With moderate and high snow accumulation (Fig 19b, c), high use areas were relatively restricted to patches of mature timber in low-lying areas between Tally Lake and the Stillwater River and to a large block of mature timber in the southwest part of the winter range, which constituted the core winter range for these projections. Predicted areas of highest usage with high snow accumulation largely overlapped with those from models using the LANDSAT vegetation map (Fig. 12c). The core winter ranges between these models differed slightly in size, but were similar in shape and location.

For all resource selection analyses, we found that models fit using mean daily SWE received virtually no support relative to best

Table 24. Model selection results for predicting resource selection by the Bowser population of white-tailed deer in northwest Montana during 1988-2000 relative to resources available within their winter range. The top model and all other models within 20 DIC units of the top model for each variable set are included. Analyses were based on vegetation attributes from timber stand inventories.

Variable Set	Rank[a]	Deviance	pD[b]	DIC[c]	ΔDIC[d]	Model
Topography	1	17467.5	4.6	17476.7	0.0	ELEV + ELEV^2 + ASP
Floristics	1	16387.0	7.4	16401.8	0.0	NFOR + PICO + ABLA + PSME
Physiognomy	1	16193.8	9.2	16212.2	0.0	MED + CCL + CCM

[a] Rank of the model within each variable set relative to the model with the lowest DIC.

[b] Estimated effective number of parameters.

[c] Deviance Information Criterion.

[d] Difference in DIC relative to the model with the lowest DIC within each variable set.

approximating models fit with daily estimates of SWE. The predictive value of using observed SWE offered strong evidence that habitat selection responded to short-term variation in weather, rather than seasonal changes in selection that follow a similar pattern each year. Comparison of estimated individual coefficients between males and females provided no evidence of meaningful differences in resource use between sexes as 95% confidence intervals of means for each group widely overlapped in almost all cases and no differences appeared to be of biological significance.

Table 25. Parameter estimates from the DIC selected model predicting relative probability of use by the Bowser population of white-tailed deer in northwest Montana during 1988-200 relative to resource attributes of their winter range and interactions of selected resource attributes with snow water equivalent (SWE). Analyses were based on vegetation attributes from timber stand inventories.

Variable	β	SE	σ^a	SE
ELEV	-5.18	0.73	4.86	0.73
ASP	-0.43	0.05	0.50	0.04
PSME	0.39	0.10	0.73	0.07
PICO	-0.86	0.19	1.25	0.16
ABLA	-3.12	0.39	2.11	0.34
NFOR	-1.23	0.27	1.36	0.24
MED	0.49	0.16	0.95	0.13
CCL	-0.62	0.40	1.39	0.29
CCM	-0.43	0.19	0.96	0.14
ELEV*SWE	-0.43	0.08	0.61	0.06
NFOR*SWE	-0.23	0.05	0.43	0.03
MED*SWE	0.03	0.03	0.35	0.02
CCL*SWE	-0.34	0.06	0.50	0.04
CCM*SWE	-0.11	0.04	0.38	0.02

[a]Estimated SD in estimated β among individuals.

Table 26. Correlation matrix of estimated coefficients for individuals from a model predicting relative probability of use by the Bowser population of white-tailed deer in northwest Montana during 1988-200 relative to resource attributes of their winter range and interactions of selected resource attributes with snow water equivalent (SWE). Analyses were based on vegetation attributes from timber stand inventories. For clarity, only coefficients >0.45 are shown.

Variable	ELEV	ASP	PSME	PICO	ABLA	NFOR	MED	CCL	CCM	ELEV *SWE	NFOR *SWE	MED *SWE	CCL *SWE
ASP													
PSME													
PICO	0.49												
ABLA	0.77												
NFOR	0.53												
MED													
CCL	0.61				0.51								
CCM													
ELEV*SWE													
NFOR*SWE													
MED*SWE													
CCL*SWE													
CCM*SWE	-0.49												

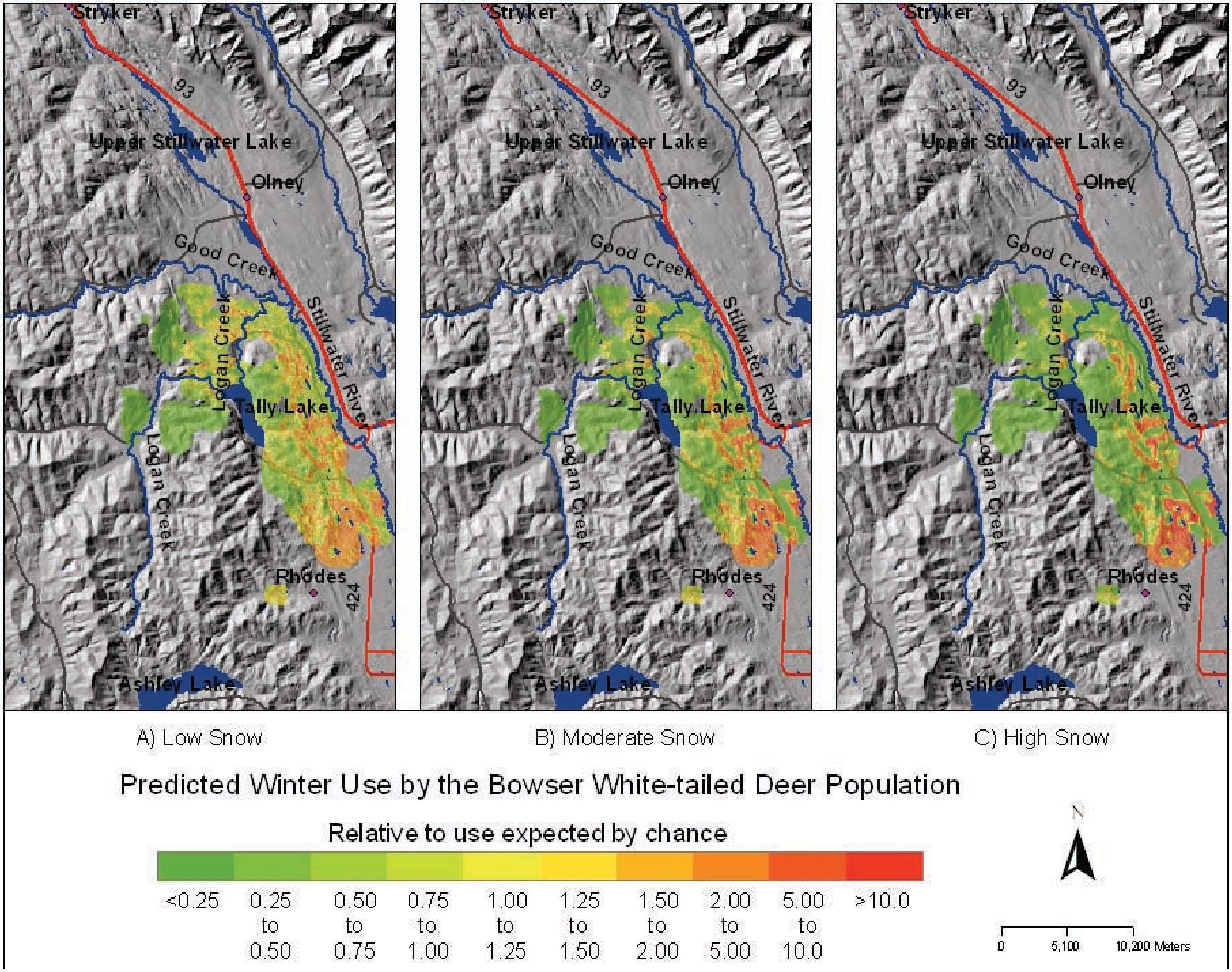


Figure 19. Predicted probability of winter use for available locations within the winter range of the Bowser population of white-tailed deer in northwest Montana during 1988-2000. Predictions are from the best model of resource selection based on a map of vegetation characteristics derived from timber stand inventories maintained by resource management agencies. Probability of use is expressed relative to expected use if all locations had equal probability of use. Relative use is projected at 3 levels of snow accumulation based on snow water equivalent (SWE) at the Olney meteorological station: A) low snow (SWE = 0) - minimal winter snow accumulation, B) moderate snow (SWE = 10 cm) - typical winter snow accumulation, and C) high snow (SWE = 20 cm) - severe winter snow accumulation.

Section 5: Discussion

Fidelity to Winter Use Areas

Serial autocorrelation in animal location data might arise because time intervals between successive locations were insufficient to allow individuals to fully traverse their seasonal home ranges, use areas shift over time, or disproportionate use of portions of seasonal home ranges. Within-year estimates of Schoener's ratio of only slightly < 2 for our populations indicated that serial autocorrelation in location of individuals was weak. Because our methods did not assume independence of locations within individuals, autocorrelation did not invalidate our statistical inference. However, autocorrelation affected precision of resource selection estimates and also provided meaningful information about fidelity in use of space. Weak autocorrelation provided evidence that the typical time interval between serial locations (~2-3 weeks) was sufficient to provide nearly independent information about an individual's use of space and resources and relatively efficient in minimizing imprecision in estimates of resource use relative to sampling effort. For a given sample of locations, stronger autocorrelation will reduce the effective sample size and hence decrease precision of individual- and population-level estimates. Thus, decreases in the sampling interval that increase autocorrelation will result in diminished returns to precision of estimates relative to sampling effort.

Weak autocorrelation in serial locations of individuals within each year also provided evidence that the winter use areas did not show much variation in use of space within each winter. Hence, once individuals reached winter use areas, we saw little support for large-scale shifts in use areas over time or in response to environmental factors. In addition, our results were consistent with proportionate use of space within use areas and provided little evidence for clustered use of trails or bedding sites. However, our ability to detect these patterns may have been limited. Locations were normally sampled during diurnal periods, typically from 0900 to 1600 hours. Thus, locations receiving disproportionate use at other times in the diel cycle, e.g., nocturnal bedding sites, were outside our inferential scope.

In addition, error in estimates of animal locations (196 ± 72 m; Vore and Schmidt 2001) inherent in our aerial telemetry methods could have obscured relatively subtle patterns in location data, such as disproportionate use of space within use areas. However, we would not expect that location error would obscure relatively large-scale patterns such as spatial changes in use areas.

Our methods of estimating fidelity to winter use areas using Schoener's ratio provided a continuous, quantitative measure of fidelity. Thus, our approach placed emphasis on assessing the statistical and biological magnitude of fidelity rather than treating fidelity as a binary outcome. Small decreases in estimates of Schoener's ratio across versus within years indicated that individuals in our populations showed some variation in winter use areas across years. However, even relatively modest movement of individuals to accessory winter use areas that did not substantially overlap with previous use areas would have caused estimates of Schoener's ratio to approach 0 (McNay and Bunnell 1994).

Although our analyses indicated differences in winter use areas across years, the magnitude of inter-annual movements generally was small with most individuals partially shifting from previous use areas rather than adopting accessory use areas. Mean distances between successive centers of winter use areas (~400 m) were rather modest relative to migratory movements of these deer (~20-30 km) and estimated area of their respective winter ranges (300-400 km^2), which suggested individuals returned to winter in relatively specific areas in the context of each population's yearlong range. In addition, small numbers of relocations/winter for individuals and large spatial error in relocations also contributed to inter-annual differences. Distances between successive use areas were also less than the mean distance of individual locations from centers of use areas within each year, which indicated that successive winter use areas tended to overlap substantially and that inter-annual movements were on average smaller than typical movements within winter use areas.

Many studies have concluded that white-tailed deer populations and individuals are strongly traditional in their circannual movements. Individuals typically show nearly complete fidelity to summer use areas but lesser fidelity to winter use areas (Tierson et al. 1985, Beier and McCullough 1990, Aycrigg and Porter 1997, Lesage et al. 2000). Although differences in sampling and statistical methods among studies preclude direct comparison, our conclusions were consistent with other assessments of fidelity to winter use areas. Using methods similar to ours, Dusek et al. (1989) reported very similar estimates of fidelity to winter use areas for white-tailed deer in eastern Montana.

Traditional use of space likely derives from the strong matrilineal family groups formed by female white-tailed deer. Young females typically establish seasonal use areas adjacent to or partially within their ancestral matriarch's use areas, and natal dispersal from the mother's use area is rare for subadult females but common for subadult males (Hawkins and Klimstra 1970, Nelson and Mech 1992, Hölzenbein and Marchinton 1992b, Rosenberry et al. 1999, Nelson and Mech 1999). Passing of use areas from older females to their offspring may confer benefits derived from familiarity with local resources and escape routes and from the social dominance of the matriarch (Beier and McCullough 1990). However, expansion of females to new winter use areas tends to be incremental and slow, leading to potentially negative consequences for populations (Nelson and Mech 1999). Strong fidelity by females suggests that populations may be slow to colonize unoccupied but suitable habitat or to refill depleted areas (Nelson and Mech 1981, Crawford 1984, McNulty et al. 1997). Furthermore, populations may be slow to respond to disturbances or changes in habitat (Hood and Inglis 1974).

Fidelity in use of space by females also appears to provide a strong mechanism for structuring local populations. Strong genetic differentiation over short distances appears common in white-tailed deer populations and has been related to fidelity by female matrilines and limited dispersal by females, and this genetic structure may be unrelated to typical boundaries used to delineate management units (Mathews and Porter 1993, Ellsworth et al. 1994, Scribner et al. 1997, Purdue et al. 2000). In addition, traditional use of winter ranges may spatially isolate groups of females during winter but not during other seasons, and such isolation may lead to genetic differentiation among groups using different winter ranges (Mathews and Porter 1993, Van Deelen et al. 1998). Thus, fidelity of use areas by females may provide population structure relevant both to population dynamics and population genetics. Hence, consideration of fidelity in use of space may be informative for delineation of biologically meaningful units for population management.

We sampled locations primarily during the diurnal period, but diel use areas might be larger than diurnal use areas and nocturnal movement patterns differ from diurnal patterns (Dusek et al. 1989, Fritzen et al. 1995). Thus, we caution that inference from our data cannot be reliably extended to crepuscular and nocturnal periods.

Timing and Distance of Seasonal Movement

Estimates of *k* much <1 from our models of movement rates indicated that an inhibited diffusion process best described daily movement of individuals. Thus, the majority of movement over the typical ~2 week interval between successive locations was concentrated around a local center of activity. Facilitated movement during migration between summer and winter use areas was exceptional and constituted only a small fraction of total annual movement. Similar to patterns observed by McNay et al. (1994) for black-tailed deer (*Odocoileus hemionus columbianus*), we found that time interval between locations was a poor predictor of movement distance.

Peak movement rates during mid-November and early April corresponded with observed migratory movements in both populations. Timing of migration was similar to those in other northern populations of white-tailed deer, although fall migration occurred earlier in this study relative to non-mountainous regions (Rongstad and Tester 1969, Hoskinson and Mech 1976, Van Deelen et al. 1998, Sabine et al. 2002). Others (Rongstad and Tester 1969, Tierson et al. 1985) have linked onset of fall migration in northern populations of white-tailed deer inhabiting mountainous areas to snow accumulation on the summer range, which was consistent with our observations.

Fall migration for the Bowser and Murphy populations also generally coincided with peak rutting behavior (late Nov) and annual hunting seasons (mid-Oct to late Nov), and these may have contributed to relatively higher movement rates and slightly earlier peak in movement by males. We believe that increased movement rates for males relative to females during fall migration most likely resulted from rutting behavior of males. Harvest typically is biased toward males, and avoidance of hunters might partially explain higher movement rates for males. Behavioral response to harvest is uncertain, but limited evidence has suggested increased movement rates for females but not males (Root et al. 1988). Increased movement rates and home range size observed for rutting males have been

proposed to maximize breeding opportunities. In contrast, females have been reported to increase activity but restrict movement to their core home range (Kammermeyer and Marchinton 1977, Nelson and Mech 1981, Ivey and Causey 1984, Holzenbein and Schwede 1989, Beier and McCullough 1990, Nixon et al. 1991). In addition, home ranges of males but not females increased during the fall in a non-migratory population (Beier and McCullough 1990).

Peak migratory movement rates in early April corresponded with snow melt and growth of new vegetation, which increased availability and quality of forage at higher elevations. Beier and McCullough (1990) proposed that increased metabolic needs during gestation led to higher activity levels of females versus males during late-winter and spring. Although slightly higher female movement rates for the Bowser population were consistent with this hypothesis, male movement rates in the Murphy population were much higher than for females, and we have no clear explanation for this contrast.

Low movement rates that we observed for females during June coincided with the onset of fawning. Others have reported decreased home range size for adult females during the fawning period (Beier and McCullough 1990) and smaller home ranges for producing than for non-producing females (Aycrigg and Porter 1997). Limited movement capabilities of young, vulnerability of young to predators, and elevated energetic needs of females during lactation likely constrained females to habitat where abundant forage and hiding cover coincided (Moen 1978, Huegel et al. 1986, Kie and Bowyer 1999). Territorial behavior by females immediately after parturition appears to spatially segregate females, which has been hypothesized to optimize survival of fawns and which would further contribute decreased home range size and movement rates (Ozoga et al. 1982, Dusek et al. 1989, Nixon et al. 1991). Previous analyses indicated that females in the Bowser population had much smaller home ranges than males during summer and that females heavily utilized dense but narrow cover along riparian areas during the early post-fawning period (Morgan 1993). High fidelity to small summer home ranges among adult females might reflect adaptation to a stable environment in which dense cover and quality forage were closely interspersed within small, familiar areas as reported elsewhere (Gavin et al. 1984, Dusek et al. 1989).

In contrast, males in both our populations exhibited a relative peak in movement rates during mid-summer, and males in the Bowser population had larger home ranges during summer than females (Morgan 1993). Morgan (1993) concluded that the Bowser population increased use of higher elevation areas as the summer progressed. Increased late-summer movement by males may have reflected movement to forage at higher elevations, which would allow exploitation of relatively new vegetation growth and could also reduce competition with breeding-age females and fawns in riparian areas (Beier and McCullough 1990). However, predator avoidance by females rather than competition may also explain differences between sexes (Kie and Bowyer 1999).

Low movement rates, low activity rates, and small use areas exhibited by both sexes that we observed during winter appear typical for northern populations of white-tailed deer (Heezen and Tester 1967, Dusek 1987, Mooty et al. 1987, Beier and McCullough 1990). Decreases in home range size and activity levels have been related to increasing snow depth and extreme cold (Progulske and Duerre 1964, Loveless 1964, Rongstad and Tester 1969, Huot 1974, Beier and McCullough 1990). White-tailed deer must increase their basal metabolic rate to maintain body temperature when air temperature falls below their effective critical temperature (-12C; Mautz et al. 1985) to maintain body temperature. In addition, availability and quality of forage decreases during winter (Short 1975, Moen 1978), and increasing snow depth increases costs of locomotion (Bell 1988). Hence, low movement rates during winter likely are part of a survival strategy that favors energy conservation by which deer cope with extreme winter conditions and forage of limited quality (Heezen and Tester 1967, Silver et al. 1969, Huot 1974, Dusek 1987, Wood 1988).

Based on peak estimated movements rates for females during fall and spring, we delineated the winter period as 22 November to 9 April for the Bowser population and 23 November to 3 April for the Murphy population. Defining the winter period using peaks in migratory movement likely resulted in inclusion of substantial migratory movement in the winter period although these dates are similar to subjectively defined winter periods reported for white-tailed deer elsewhere in the northern Rocky Mountains (Hicks 1990, Pauley et al.

1993). We used this broad definition of the winter period rather than inflection points where rates of change in movement rate were greatest because we were interested in examining factors influencing the large annual variation in timing of increased use of winter range. Peak of fall and spring movement rates captured time when some average individual was making the transition from migratory movement to local movement on seasonal use areas. Our methods assumed that movement was uniform across the interval between successive locations of an individual (mean for all analyses = 13.2 days). This assumption would be expected to flatten estimated peaks relative to true patterns.

Mean migratory distances between individual summer and winter use areas for the Bowser and Murphy populations were similar to those previously observed for the Bowser population (Morgan 1993) and for other migratory populations of white-tailed deer herds in northern areas (Sparrowe and Springer 1970, Hoskinson and Mech 1976, Lesage et al. 2000). We found considerable individual variation in migratory distance, and some non-migratory individuals remained on traditional winter range year long. Such mixed-migration strategies reported for other deer populations may be explained by variability in winter weather or by "conditional migrants" remaining on summer range during mild winters (Drolet 1976, Parker et al. 1984, Nicholson et al. 1997b, Sabine et al. 2002). However, our observed pattern of use of all the range during summer but use of only a portion of the range during winter was consistent with the "partially migratory" behavior observed by Sparrowe and Springer (1970). A plausible explanation for partial migration is that winter range contains resources throughout the year, but that resources on summer range are insufficient or inaccessible during most winters. Alternatively, social disruption resulting from mortality of adult does may cause non-migratory behavior if migration routes are not passed to orphaned offspring (Larson et al. 1978, Nixon et al. 1991, Hölzenbein and Marchinton 1992a).

Defining Available Resources

Range estimation demonstrated the Bowser and Murphy populations were largely segregated in space with overlap only along Gregg Creek near the confluence with Good Creek. Estimation of 99% probability contours provided an objective means to estimate annual and winter range available to each population. These contours define an area expected to contain 99% of locations in the target population at least during a portion of the defined winter period during some years. Hence, available ranges were

expected to encompass commonly used areas but exclude unused or infrequently used areas.

Yearlong distribution of both populations appeared strongly influenced by local drainages. Our estimate of the annual range of the Bowser population generated conclusions similar to observations by Morgan (1993) for the same population during 1989-1991. Lower elevation areas in the upper Star Meadows and Good Creek drainages generally received heavy use in summer, and low-lying areas around Lost Creek received heavy use during winter. Two primary travel corridors connected summer and winter areas: one path traversed the north-east edge of Tally Lake and the other traversed west of the Stillwater River to its confluence with Good Creek. High ground near Chinook Lake apparently separated these travel corridors. The Stillwater River appeared to bound the eastern edge of the Bowser population's range. The estimated annual range of the Murphy population showed heavy use of the upper areas of the Fortine Creek drainage during summer and heavy use of the Fortine Creek drainage near Murphy and Dickey Lakes during winter. The Fortine Creek drainage provided the primary travel corridor connecting these main summer and winter areas.

Winter ranges for each population were largely encompassed within the respective annual ranges. Winter ranges comprised 61% of the annual range for the Bowser population and 55% for the Murphy population. These large winter ranges encompassed all areas receiving use during the entire season, and our broad definition of the winter period also included migratory locations in each winter range. Use of upper drainages during winter was generally confined to drainage bottoms.

Resource Selection

Resource selection by white-tailed deer during winter responded strongly to weather conditions. When snow accumulation was minimal, the Bowser and Murphy populations utilized a wide variety of forested and non-forested habitats across a large range of elevations throughout their winter range. Strong preference for a narrow suite of resources accompanied increased snowpack, resulting in severely restricted distributions. Altitudinal migration by deer in response to heavy snow accumulation concentrated deer on small core winter areas, which were characterized by low elevations and relatively mature timber cover.

Although white-tailed deer are generally non-migratory across their range, northern populations experiencing persistent snow during winter commonly exhibit seasonal migration to winter deer "yards" (Drolet 1976, Van Deelen et al. 1998, Nelson and Mech 1999). Deer appear acutely responsive to increased movement costs resulting from accumulation of deep snow (>30-40 cm) (Kelsall 1969, Parker et al. 1984, Parker et al. 1999), and deer are thought to adopt a strategy emphasizing energy conservation in response to deep snow (Moen 1978, Dusek 1987, Pauley et al. 1993). Our results were consistent with this "energy conservation" hypothesis, as deer responded to snow accumulation by narrowing preference to resources that mitigated deleterious effects of deep snow.

Under conditions of minimal snow accumulation we observed diverse resource use; deer heavily used non-forested habitat as well as forested habitat composed of stands of poletimber to moderate-sized trees with relatively open canopy cover. Diffuse use of a wide range of habitat types was consistent with the conclusion of Dusek et al. (2005) that white-tailed deer in northwest Montana are forage generalists during winter, and low densities of deer may have served to reduce intraspecific competition for forage. Alternatively, social avoidance could also disperse deer, as observed for mule deer in Montana (Wood 1987, Hamlin and Mackie 1989).

At the largest spatial scale, the Bowser and Murphy study populations minimized deleterious effects of deep snow by restricting use to lower elevations, a typical pattern for white-tailed deer in montane habitats throughout the northern Rocky Mountains (Pengelly 1961, Berner et al. 1988, Pauley et al. 1993, Secord 1994). This behavior likely serves to reduce energetic costs associated with daily movement and also reduces predation risk resulting from decreased mobility. Prevailing westerly winds created a "precipitation shadow" west of the Salish mountains, resulting in a strong, decreasing west-to-east gradient in precipitation falling as snow across our study areas (Farnes et al. 2000). Typical snow depths during mid-winter (estimated from models in Farnes et al. 2000) at the Olney climatological station, which was similar in climate to low-lying portions of the winter ranges, typically exceeded the 25 to 40 cm threshold reported to substantially increase locomotion costs for deer.

Hence, deer had strong incentive to seek lower elevations with lesser snow accumulation but also to select resource attributes that further mitigated effects of snowpack. Avoidance of increased metabolic costs in cold temperatures likely was less important to promoting migratory behavior, as white-tailed deer in areas with low temperatures but little snow typically are non-migratory (Beier and McCullough 1990, Sabine et al. 2002). In addition, temperatures on or near our study areas did not often drop below the lower critical temperature for white-tailed deer for sustained periods. We also found that deer preferred southwest aspects in which increased insolation likely provided thermal benefits for deer as well as increasing snow melt rates (Pauley et al. 1993). Preference for moderate terrain roughness might reflect thermal benefits provided by minimizing exposure and wind speed as well as providing sites with increased solar insolation. Alternatively, gently sloping terrain may create heterogeneous snow conditions and allow deer to select movement routes minimizing movement costs (Jacobsen et al. 1976, Parker et al. 1984, Pauley et al. 1993).

As snow accumulation increased, both populations appeared to minimize energy expenditure by shifting preference from relatively open habitats to forest characterized by relatively large conifers and increased tree canopy. High use of areas with mature conifers during periods of deep snow is common (Ozoga and Gysel 1972, Euler and Thurston 1980, Peek 1984, Pauley et al. 1993) and appears to take advantage of high interception of snowfall provided by crowns of conifers (Huot 1974, Crawford 1984, Johnson 1992), resulting in reduced locomotion costs for deer and enhanced ability to evade predators (Bloom 1978, Kirchhoff and Schoen 1987, Pauley et al. 1993). Mature conifer stands may also reduce wind and moderate temperatures (Ozoga 1968, Verme 1968), and use of mature conifer forest has been related to periods of extreme cold and wind (Ozoga and Gysel 1972, Jacobsen et al. 1976).

Pauley et al. (1993) observed that increasing snowpack resulted in a shift from use of energy-rich, open habitats with abundant seral shrubs to energy-poor stands of mature conifer with depauperate understories, a transition that likely substantially reduced energy intake. However, we failed to find evidence for this pattern in the Bowser and Murphy populations. In contrast to depauperate stands of mature western red cedar and western hemlock described by Pauley et al. (1993), stands of mature conifers on our study areas contained diverse food resources in the understory that commonly included Douglas fir, Oregon grape, and arboreal lichens all of which dominated diets of the both populations throughout winter (Dusek et al. 2005). More energy-rich seral forbs and shrubs that the Bowser population preferred during spring through fall (Morgan 1993) were likely less

attractive to deer while dormant. In addition, winter snowpack appeared unrelated to adult survival, recruitment, and body condition in the Bowser and Murphy populations (Dusek et al. 2006), which suggested that mature conifer stands provided adequate energetic resources during winter use.

Lack of consistent selection patterns for different tree floristic groups in our results, coupled with relatively consistent patterns for tree physiognomy, suggested that tree structure was of primary importance to selection. Dominant tree species in conifer stands selected by white-tailed deer during winter have been diverse, including ponderosa pine, Douglas fir, Engelmann spruce, western red cedar, and western hemlock (Mundinger 1980, Jenkins and Wright 1988, Bell 1988, Pauley et al. 1993, Sabine et al. 2002). This diversity in combination with consistent selection for mature stands suggests that deer select structural features mitigating snow accumulation regardless of vegetation association. Local vegetation associations seemingly influence local forage use, which lends credence to a hypothesis that deer have become very specialized in habitat selection in these environments but very generalist in foraging patterns. However, our data may not have been well-suited to detecting floristic preferences because classes for each analysis were dominated by one floristic class, tree stands typically contained mixtures of common species, and species classification likely was subject to considerable inaccuracy.

Our results only reflected behavior during the diurnal period that we sampled. The Bowser population during winter generally showed greatest movement activity during diurnal periods, and proportions of diurnal activity increased during late winter (Dusek and Morgan 1991). Because most foraging likely occurs during active periods, our results likely encompassed resources essential to foraging during winter. In contrast to the premise that opening tree canopy will increase production of forage and attractiveness to deer, our results, in concert with observations on winter food habitats (Dusek et al. 2005), strongly suggest that deer commonly used food resources in mature forest when snowpack was heavy.

Our results demonstrated substantial individual heterogeneity in resource selection. The wide diversity in use of elevation when SWE was minimal demonstrated a mixture of migratory behaviors in the Bowser and Murphy populations. About 8-10% of the radio-marked deer were non-migratory, residing on or near

winter use areas throughout the year, with the rest migrating between distinct summer and winter use areas. In areas with consistent accumulation of deep snow each winter, deer typically migrate to and from winter use areas at consistent dates (obligate migration; Sabine et al. 2002). However, mixed migration strategies may exist in areas with more moderate or variable winter conditions, with some individuals migrating to winter use areas for only a short period or even remaining on summer use areas during some years (conditional migration; Drolet 1976, Nicholson et al. 1997). Conditional migrants appeared responsive to weather cues, migrating from summer to winter use areas only when snow depths approached a threshold thought to impede movement. Deer populations with mixed migratory behaviors have been described as containing individuals clearly segregated among obligate or conditional migration behaviors (Nelson 1995, Whitlaw et al. 1998). However, clear distinctions were not apparent for our populations as almost all individuals moved from summer use areas during fall, but not all immediately moved to winter use areas. Instead, migratory behavior fell along a continuum, with individuals distributed across elevations on the winter range when snow accumulation was minimal. As accumulation of deep snow reached progressively lower elevations, deer moved lower and concentrated on core winter use areas. However, factors that create and maintain heterogeneity in migratory behavior in populations remain unclear. When snow accumulation was low, our populations tended to select a wide range of habitats regardless of elevation, and we speculate that dispersion of deer across elevations and habitats served to minimize intra-specific competition.

We could not attribute abundant individual variation in resource selection and migratory behavior in our populations to differences between sexes, which appeared somewhat counterintuitive. However, sexes differ in energetic requirements that could lead to differences in habitat selection. Some evidence suggests that sexes may be spatially segregated on winter ranges in northern regions (McCullough 1979, Brockmann 1988). Additionally, sexes maintain exclusive social groups outside the breeding season (Hirth 1977), suggesting little opportunity to coordinate movements between sexes. Van Deelen et al. (1998) also found no differences in seasonal movements between sexes and suggested that infrequent re-association of young males with their mothers over a 2-3 year period reported by Nelson and Mech (1984) might provide a link for coordinating migratory movements between sexes.

Individual heterogeneity in resource selection was high for almost all variables included in selected models. With minimal snow accumulation, high heterogeneity was consistent with resource selection by a habitat generalist and may have also reflected dispersion to avoid intraspecific competition. Preferences became increasingly narrow as snow accumulation increased, but substantial individual heterogeneity persisted, perhaps reflecting a range of suitable habitat.

Importance of resource selection to population management depends on its consequences for demography. Heavy snowpack, cold temperatures, and minimal forage quality might be expected to cause increased adult mortality in white-tailed deer. However, hunter harvest during fall was the leading cause of adult mortality during this study (45% of all documented deaths; Dusek et al. 2006). A peak in mortality of adult females attributed to predation, primarily by cougars (*Puma concolor*) occurred during late winter (Feb/Mar), but adult survival

appeared unrelated to winter severity, with the exception of winter 1996-1997. In contrast, fawn mortality was strongly positively related with cold temperatures, with a pulse in mortality from starvation and predators occurring during late winter. Low accretion of fat prior to winter by fawns relative to adults (Dusek et al. 1989, Dusek et al. 2006) likely makes fawns more susceptible to winter mortality and more dependent on appropriate shelter during winter (Severinghaus 1981). These results are consistent with the pattern in ungulates that effects of environmental variation or density-dependence are expressed through changes in juvenile rather than adult survival (Sauer and Boyce 1983, Skogland 1985, Bartman et al. 1992, Gaillard et al. 1998).

Our analyses provided relatively consistent results concerning selection of non-forest habitat and forest stands with relatively small DBH trees and open canopy cover, but results diverged relative to mature forest stands (medium and large DBH trees, moderate and closed tree canopy cover). Qualitative differences in results from resource selection analyses most likely arose from actual differences in selection among study populations, differences in spatial scope of the two analyses for Bowser, and errors in vegetation classification.

Estimated classification error rates for the LANDSAT vegetation map (Table 21) suggested that inaccuracy contributed to inconsistent results. Error estimates were unavailable for timber stand inventories, but common use of ground observers rather than remote sensing for classification implied greater classification accuracy. However, differences among observers, long intervals between observations, errors in photo interpretation, and uncertainties inherent in projecting stand growth all likely contributed to inaccuracy, but we have no quantitative basis to compare the quality of our two data sources.

Intuitively, high classification accuracy for some vegetation classes that were relatively easy to discern, such as for non-forest classes, could in part explain consistent results for these classes as analyses would be more likely to detect true selection patterns. However, classification accuracy for LANDSAT data was also high for moderate and closed tree canopy classes, and thus, classification inaccuracy alone would seemingly not explain contrasting results for these variables. Systematic error (consistently mis-classifying a vegetation class as another, as opposed to more “random” errors) presents a more difficult problem, as true selection in these populations could give support to erroneous conclusions. Comparison of forest structure characteristics for overlapping portions of the LANDSAT and timber inventory maps on the Bowser study area revealed that large forest stands received different structural classification. These differences led to large differences in the relative proportions of different forest structure classes (consistent with differences observed for the full extent of each map as seen in Tables 13, 22), which provided strong evidence that systematic error existed in at least one map. We further concluded that differences in results between these maps relative to selection of mature forest could largely be attributed to systematic differences in classification. Examination of error matrices for LANDSAT vegetation classification (Brewer et al. 2004) failed to reveal evidence that systematic error influenced our results. However, this accuracy assessment was conducted for all of western Montana, and potential for systematic error at the level of the forest stand could not be assessed.

Despite differences in conclusions regarding selection of vegetation structure, some results appeared robust to problems with classifying forest structure. Models from both vegetation maps predicted very similar distribution in space for the Bowser population, indicating that each model was able to identify stands important to deer but that differences in how these stands were classified lead to differences in results about preferred vegetation features. In addition, all analyses concurred that mature forest was strongly preferred with increasing snow accumulation, a result consistent with previous studies of winter habitat use in areas with substantial snow (Moen 1978, Pauley et al. 1993, Secord 1994).

Management Implications

High fidelity to relatively concentrated winter use areas and a matrilineal system among deer that passes migratory traditions to offspring create populations that are more segregated in winter than summer (Van Deelen et al. 1998). Population dynamics of separate herds likely will be largely independent; hence, populations on these paired summer and winter ranges may be biologically meaningful management units (Van Deelen et al. 1998). Segregation of populations during winter makes this an appropriate time for monitoring, but large individual heterogeneity in migratory behavior complicates surveys. Because the fraction of both populations occupying core winter use areas depended on variable weather conditions, survey methods should account for the distribution of deer, e.g., stratified survey, and factors influencing their distribution.

Strong migratory traditions in white-tailed deer are maintained by matrilineal inheritance of migratory behavior and high fidelity to winter use areas. Consequently, capacity to respond to alterations to winter range habitat appears limited. When traditional winter range suffers degradation, populations show little propensity to shift use to higher quality habitat nearby (Verme 1973, Nelson and Mech 1981), and thus, loss of critical habitat can negatively affect populations. We found that deer exploited a wide range of habitats during winter, but resources selected during winters with significant snow accumulation likely are of heightened importance because (1) severe winter weather imposes energetic stress on deer (Mautz 1978, Parker et al. 1999), (2) resource requirements were narrowest and preferences strongest at this time in the Bowser and Murphy populations, (3) both populations occupied a very small portion of their yearlong range during winter, and (4) a peak of non-hunting mortality occurred during late winter in our populations (Dusek et al. 2006).

Traditional management prescriptions for white-tailed deer favor silviculture treatments to open dense forest canopy on winter ranges to increase abundance of forage (Pengelly 1963, Verme 1965, Ozoga 1968, Krefting and Phillips 1970, Lyon and Jensen 1980). Although deer may respond favorably to food resources provided by active timber harvest (Tierson et al. 1985, Van Deelen et al. 1998), clearcuts on winter ranges in areas with significant snowfall appear detrimental over the long term as snow accumulation in non-forested areas precludes use by deer (Telfer 1974, Mundinger 1981, Crawford 1984). Winter range quality can limit populations in northern areas (Pengelly 1963, Drolet 1976, Peek 1984), and sensitivity of fawn mortality to winter weather conditions would likely be exacerbated by removal of effective shelter. Therefore, we recommend promotion and retention of relatively mature forest stands, characterized by large trees (≥ 10 in [25.4 cm] DBH) and relatively closed tree canopy cover (>25%), at lower elevations, as such habitat appears critical to mitigating energetic stress imposed by snowpack. For our study areas, areas with high-predicted probability of use at moderate and high snow conditions identified critical winter range habitat. Our predictive models likely will be useful to identify potential critical winter habitat for ecologically similar white-tailed deer populations in the region, but extrapolation will benefit from further validation of these models.

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Part III:

Summer Habitat Use[1]

John T. Morgan

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[1] Adapted from a doctoral thesis submitted to the College of Graduate Studies, Montana State University, Bozeman

Abstract

Summer habitat relationships of white-tailed deer (*Odocoileus virainianus*) were studied on the Tally Lake Ranger District of the Flathead National Forest in northwestern Montana during 1989-1991. Macro-habitat selection patterns were analyzed using 2009 relocations of radio-collared deer obtained through aerial surveys while deer occupied summer ranges. An additional 463 relocations provided information on migration routes and accessory areas. Micro-habitat selection was investigated in the Star Meadows and Corduroy Creek complexes through 18 diel telemetry sessions and a remote camera survey in Corduroy Creek. The geographic information system programs ERDAS and EPPL7 were used to create eight habitat component data layers including: slope, aspect, elevation, vegetation, riparian areas, and roads (all, open, and closed).

Deer habitat selection at the macro level appeared to be influenced by locations of second- and third-order streams and associated riparian meadow complexes. Deer initially selected sites close to riparian habitat, between 1159 and 1524 m, containing naturally occurring grass/forb and shrub/hardwood vegetation. Later in the season deer preferences shifted to slightly higher elevations containing more open and closed pole/immature timber. In general, early seral and mature vegetation were avoided. Roads appeared to play little role in whitetail habitat selection except for avoidance of sites ≤ 100 m of a road. Aspect and slope also had little impact on habitat selection. Deer habitat selection at the micro level was less specific. Once deer selected their summer home range, use of individual habitat variables within this area apparently was less important.

Forest management on the Tally Lake District should aim to preserve riparian complexes, including mesic bottomlands and associated upland pole/immature timber ≤ 750 m of riparian sites cutting units occurring above 1646 or below 1159 m and/or on westerly to northerly aspects would have less impact on deer. Stands should be allowed to return to the pole/immature stage before adjacent cuts are made.

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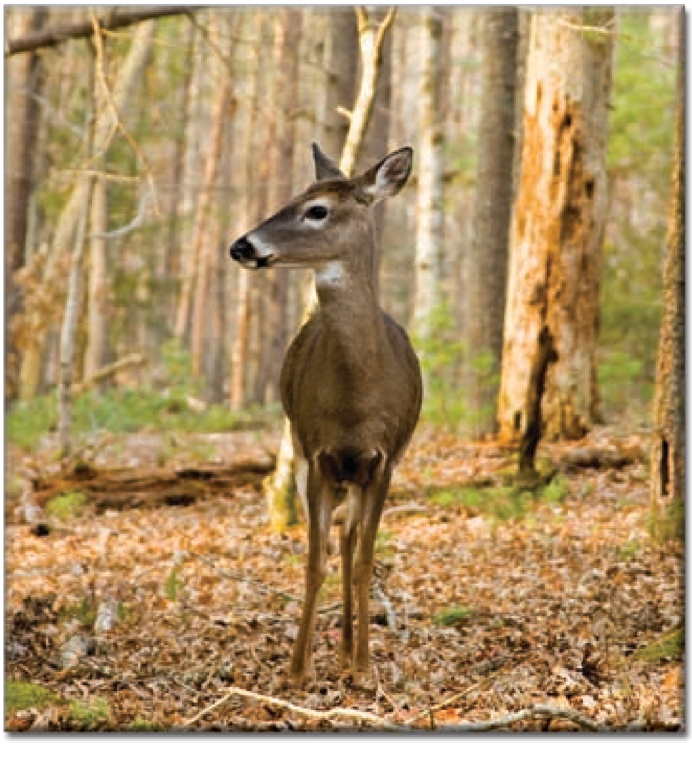

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Section 1: Introduction

White-tailed deer (*Odocoileus virginianus*) are the most widely distributed and abundant of North American big game mammals (Smith and Coggin 1984). Their ability to exist in a diversity of habitats, under a variety of conditions, and in the presence of humans has allowed whitetail populations to expand and occupy much of North America. Whitetails also are one of the most studied wildlife species in the country as indicated by the numerous texts, monographs, and journal articles on the species (Halls 1984).

Despite this abundance of information, knowledge of whitetail ecology and requirements in specific habitats is often lacking. A widely applicable and generally acceptable framework of knowledge and understanding of habitat relationships has yet to be developed. Thus, Caughley (1980) claimed white-tailed deer were one of the most studied and least understood of all animals.

In Montana, whitetail populations are distributed throughout the mountains and plains in a variety of habitats (Allen 1971). The Dakota subspecies (*O. v. dacotensis*), found east of the Continental Divide, primarily inhabits river bottoms (Dusek et al. 1989), a few isolated mountainous areas (Martinka. 1968, Kamps 1969), and to a limited extent prairie habitats (Swenson et al. 1983, Wood et al. 1989). However, whitetails reach their greatest concentrations west of the divide, particularly in the heavily timbered northwest counties (Allen 1971) where the Northwest subspecies (*O. v. ochrourus*) has been studied in the Swan River Valley (Hildebrand 1971, Leach 1982, Mundinger 1984), the Clearwater River Valley (Janke 1977, Slott 1979), the Thompson River Valley (Hicks 1990), along the North Fork of the Flathead River (Jenkins 1985, Krahmer 1989, Tucker 1991, Rachael 1992), and in the Fisher River/Wolf Creek drainages (Zajanc 1948, Schmautz 1949, Schmautz and Zajanc 1949, 1951, Blair 1954, 1955, Neils et al. 1955, Firebaugh et al. 1975). These northwest white-tailed deer populations are somewhat unique in their close yearlong association with relatively dense, often mature coniferous forest habitats.

Many whitetail studies in northwestern Montana have concentrated on winter habitat relationships. Generally, these have emphasized deer use of southerly aspects, which are often clear of snow (Firebaugh et al. 1975, Janke 1977, Slott 1979), mature timber in riparian and/or upland areas, which intercepts snow (Hildebrand 1971, Mundinger 1984, Hicks 1990), and timbered areas interspersed with small openings providing edge (Krahmer 1989).

However, whitetails in northwestern Montana are generally migratory and often spend up to 9 months of the year on summer ranges and/or transitional and accessory areas between summer and winter range. Summer habitat must not only meet the general food, water, and cover requirements for adult deer throughout the season but must also provide for specific seasonal needs. For instance, adult females require quality forage throughout this season for gestation, lactation, and recovery. Fawns need hiding cover early and quality forage later in the summer to meet their growth and survival needs. Also important is security cover from predators and during hunting season, which is ongoing while deer occupy summer ranges. And last, high quality forage in abundance is needed for maintaining physical condition and building fat reserves prior to fall migration and the onset of winter.

Summer use of coniferous forest by white-tailed deer in northwestern Montana was previously reported by Leach (1982) in the Swan River Valley, Slott (1979) along the Clearwater

River, and Krahmer (1989) and Rachael (1992) along the North Fork of the Flathead River. All studies showed an apparent preference by whitetails for riparian areas and moist habitats. In managed forests small cutting units providing a diverse vegetative structure also were noted as important to deer (Leach 1982, Krahmer 1989).

The Salish Mountains, which include the Tally Lake Ranger District of the Flathead National Forest northwest of Kalispell, also provide important whitetail summer range (Mundinger and Riley 1982, 1983). Extensive timber harvesting and road building on the district could potentially disrupt traditional patterns of whitetail activity and habitat use on summer ranges and during migration to wintering areas.

This study was initiated to investigate habitat use and selection patterns at the macro- and micro-habitat levels by whitetails on summer and transitional ranges on the Tally Lake District. Research was conducted from spring through fall 1989-1991. Specific objectives were to (1) determine use and importance of various seral stages of coniferous forest and riparian communities, (2) determine how spatial distribution and organization of these communities to form habitat complexes influences distribution and abundance of deer, and (3) determine the importance of other habitat features including topographic, climatic, and land use components.

Section 2: Study Area

The Tally Lake Ranger District (TLRD) of the Flathead National Forest (FNF) lies in the northern portion of the Salish Mountains in northwestern Montana at 48° 30′ north latitude 114° 30′ west longitude (Fig. 1). The study area, as used for macro-habitat analysis, was defined as the area within the district containing all summer and transitional relocations of radio-marked deer from January 1989 through December 1991. This included approximately that portion of the district north of Ashley Mountain, east of the Flathead/Lincoln County line, south of Martin Falls, and west of Tally Lake. The district is approximately 926 km^2 (USDA Forest Service {USFS} 1985). The study area consisted of ~ 445 km^2 of USFS land and 35 km^2 of private land within and adjacent to the district boundary.

Geologically, parent material throughout much of northwestern Montana consists of fine-grained metamorphic rocks from the Belt Super Group of the late Precambrian age (Johns 1970, Montagne et al. 1982). The northern Salish Mountains were created by faulting and folding during the late Cretaceous to early Tertiary ages and are characterized by north-northwest trending folds in the Belt sediments. The Cordilleran ice sheet covered much of northwestern Montana moving into

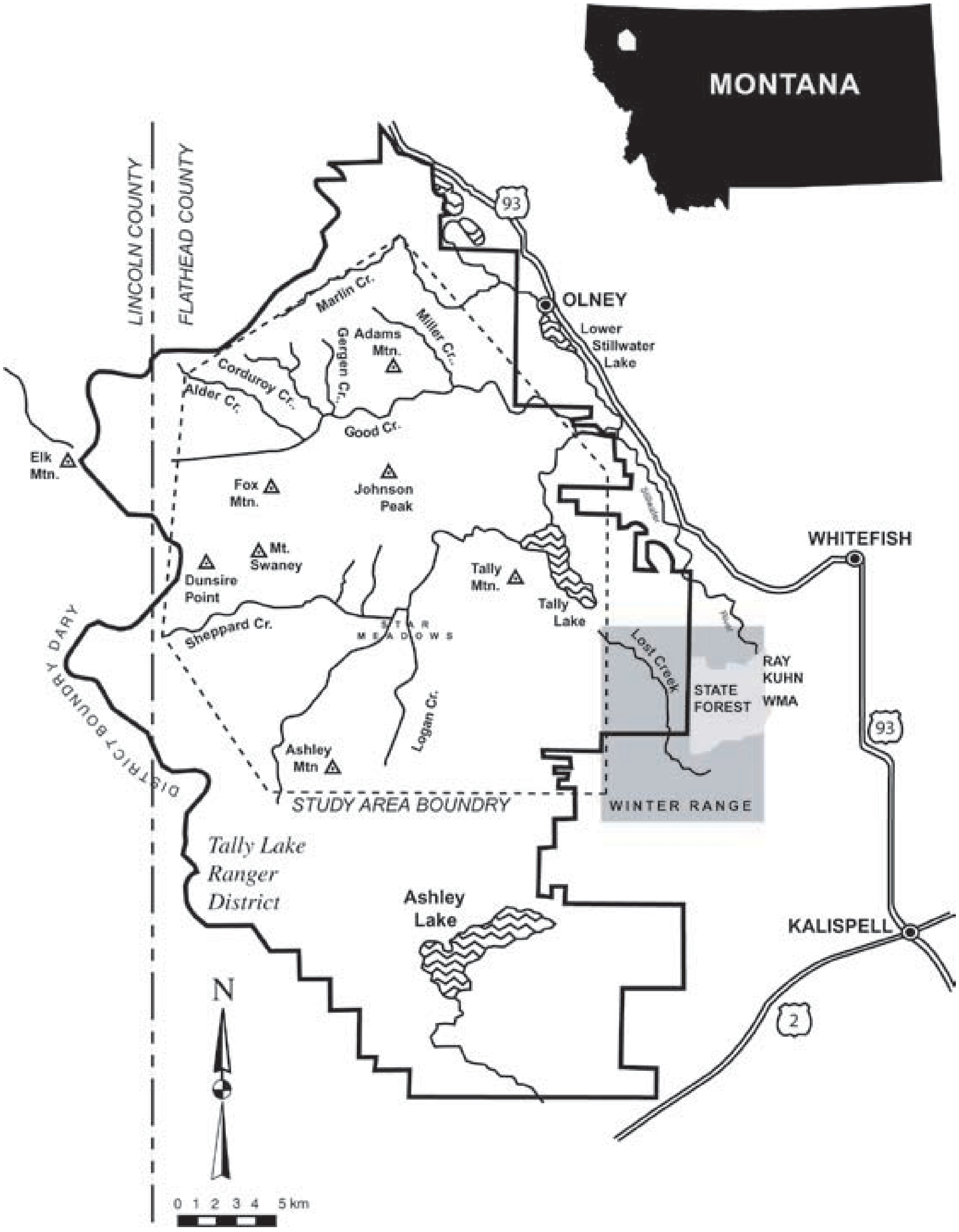


Figure 1. White-tailed deer study area within the Tally Lake Ranger District, Flathead National Forest

the northern and western portions of the Tally Lake District. Also, 30-45 cm of volcanic ash covered northwestern Montana. The metamorphic parent material, glacial till, volcanic ash, cool temperatures, and relatively high precipitation have resulted in deep fertile soils from the Alfisol and Inceptisol orders which are typically found under coniferous canopies (Montagne et al. 1982).

Topographically, the study area lies between 915 m at the confluence of Good and Logan Creeks in the northeast and 1935 m at the summit of Mount Swaney (Fig. 2). The majority of the study area (60%) lies between 1281 and 1646 m. Because the northwestern edge of the district terminates at the highest elevations, easterly and southerly aspects prevail slightly over northern and western aspects. Slope is fairly moderate throughout the study area with the majority (53.5%) falling between 6 and 25%.

The study area drains to the northeast into the Stillwater River via Martin, Good, and Logan Creeks (Fig. 1). The northern portion is characterized by relatively low ridges (10,500 m) of moderate slope (< 25%) separated by numerous first and second order drainages flowing into Martin and Good Creeks.

The central portion of the district is separated from the north by the 1585-1935 m Dunsire Point/Johnson Peak ridge line (Fig. 1). Star Meadows, at 1219 m, is the primary feature in the central portion and is formed by the confluence of Sheppard, Griffin, and Logan Creeks, with Logan Creek emptying the meadow to the northeast into Tally Lake.

Climate in northwestern Montana is strongly influenced by moisture-ladened air from the Pacific northwest. The area is characterized by cool winters and warm summers with frequent cloudy days much of the year except mid-summer.

Long-term and daily climatic data were available from the weather station at Olney, Montana, on the northern edge of the study area (Appendix Table 28). Annual precipitation averages 59.4 cm of which approximately half falls as snow averaging 323.5 cm. Maximum and minimum temperatures average 27.2 °C during July and August and -11.1 °C during January. During the 3 years of the study, annual and summer mean daily maximum and minimum temperatures, as well as mean monthly precipitation were not significantly different from long-term averages (*t*-tests, $P < 0.05$).

The area is 94% forestland with only a few natural grass and shrub openings. The *Abies lasiocarpa/Clintonia uniflora* habitat type predominates (Pfister et al. 1977). However, habitat alteration through logging, cattle grazing, and natural fires has produced a forest that is now a mosaic of mature mixed conifer, large stands of lodgepole pine (*Pinus contorta*), clearcuts in various stages of regrowth, riparian areas, and natural willow/grass meadows.

Major overstory species include lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), and western larch (*Larix occidentalis*). Common grass, forb, and shrub species include pine grass (*Calamagrostis rubescens*), timothy (*Phleum pratense*), strawberry (*Fragaria virginiana*), yarrow (*Achillea millefolium*), arnica (*Arnica spp.*), fireweed (*Epilobium angustifolium*), beargrass (*Xerophyllum tenax*), pachistima (*Pachistima myrsinites*), prince's pine (*Chimaphila umbellata*), spiraea (*Spiraea densiflora*), rose (*Rosa gymnocarpa*), Oregon grape (*Berberis repens*), twinflower (*Linnaea borealis*), buffaloberry (*Shepherdia canadensis*), alder (*Alnus spp.*), willow (*Salix spp.*), snowberry (*Symphoricarpus albus*), and huckleberry (*Vaccinium spp.*).

The study area included two specific areas, or microhabitat complexes, that supported large numbers of deer throughout summer; the Star Meadows complex and the Alder-Corduroy-Gergen-Good Creek complex located in the central and northern portions of the district, respectively. Star Meadows is approximately 65 km^2 of which one-third was riparian bottomland consisting of a mixture of large open meadowlands, willows, and scattered timber. Slopes within the complex comprised a mosaic of timber and cutover areas.

The Alder-Corduroy-Gergen-Good Creek complex was approximately 32 km in contrast to Star Meadows this area consisted primarily of large stands of 60-70 year-old lodgepole pine, a remnant of large fires, which occurred during the early part of this century. This complex lacks large meadows but small wet meadows were associated with each drainage.

Timber production was the primary land use on the study area. Road development, in association with timber production, occurred throughout the area such that over 40% of available habitat was ≤ 100 m of a road.

Cattle grazing occurred on private land around Star Meadows during snow free periods and on USFS land just north of Star Meadows

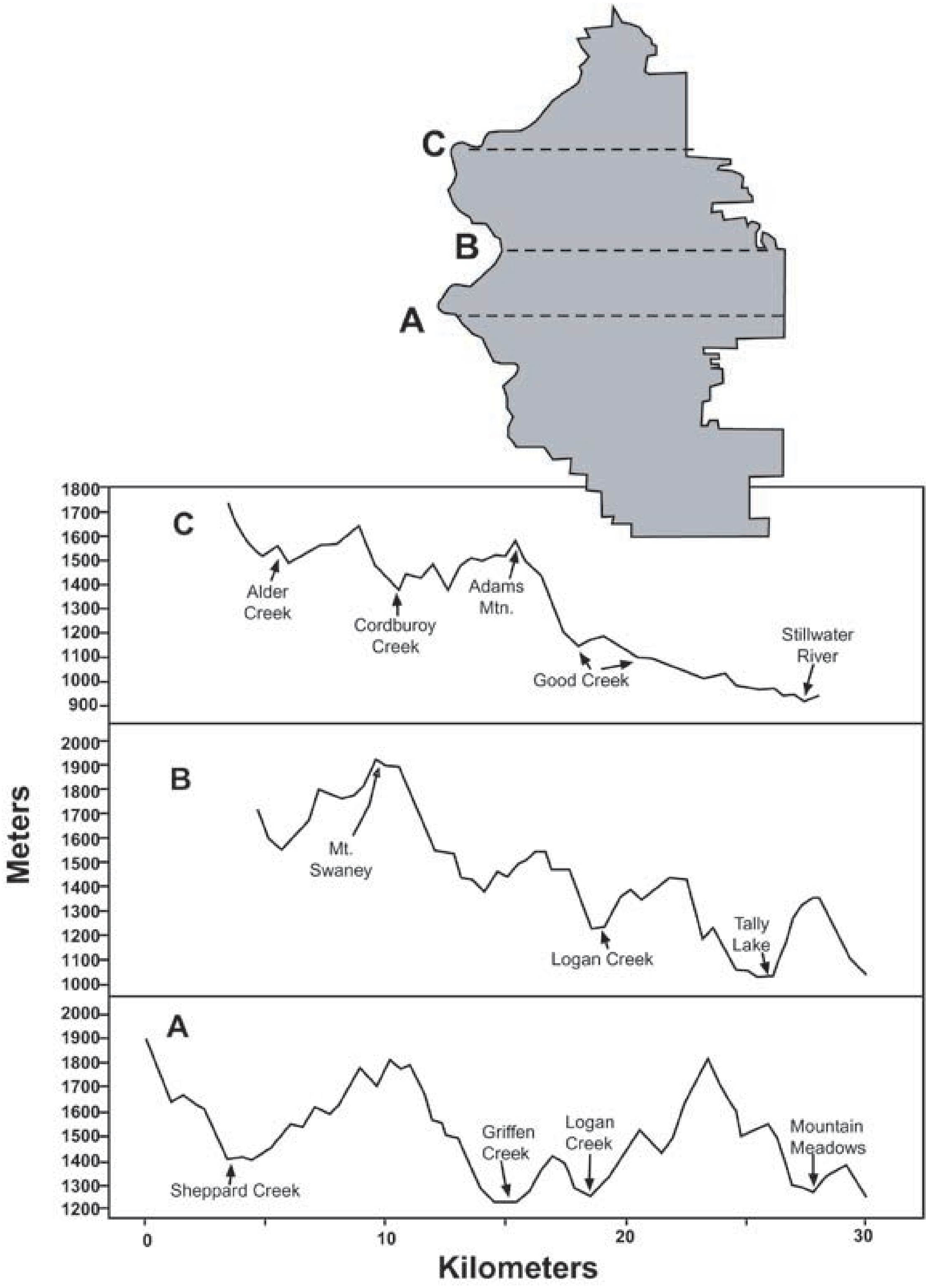


Figure 2. Cross-section of northern, central and southern portions of the study area showing elevation change

during Jul-Sep. Private residences primarily occurred around Star Meadows and along Good Creek as well as on the northern and eastern periphery of the study area.

Tally Lake was the primary recreation point on the district attracting campers, boaters, and anglers. Sylvia Lake and some of the larger streams provided additional fishing opportunities. Hiking trails were present on the district but received limited use. Firewood cutting occurred yearlong but increased during fall.

The study area lies within hunting district 102. The proximity to Kalispell and other communities, as well as abundant game, make the area popular for hunting. Although white-tailed deer were the most abundant big game species, mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose, (*Alces alces*), and black bear (*Ursus americanus*) also occurred on the area. In addition to black bear, mountain lions (Felis concolor) and coyotes (*Canis latrans*) are predators common to the area. Wolves (*Canus lupus*) are extending their range in northwest Montana and have been sighted on the Tally Lake District. There also have been a few sightings of grizzly bears (*U. arctos*); however, like wolves, this species is a rare visitor.

Section 3: Methods

Data Collection

Animal Component.—Collection of data on white-tailed deer essentially involved monitoring individually radio-collared animals which summered on the Tally Lake District. Three hundred eighty-nine deer were captured by Montana Department of Fish, Wildlife, and Parks personnel and myself using Clover traps (Clover 1954) during both winter (1988-1991) and spring-summer (1989-1991) periods. Female deer trapped included 139 adults, 38 yearlings, and 75 fawns. Male deer trapped included 22 adults, 33 yearlings, and 82 fawns.

Ninety-one percent (356) of all deer captured were on winter range. Although summer trapping contributed only a fraction of the total trapping effort, trap efficiency (number of deer captured/trap night) was similar to winter trapping. Also, summer trapping greatly added to samples of radio-collared deer available for micro-habitat analysis in the Star Meadows and Corduroy Creek complexes. Specific details on trapping techniques and the relationship between winter and summer trapping have been reported previously (Morgan and Dusek 1992).

For each deer captured, sex and age assigned through mandibular tooth wear and replacement (*Severinghaus 1949*) were recorded. Every deer was marked with an individually numbered metal ear tag and a uniquely colored neckband. One hundred deer (26% of total) were equipped with radio transmitters (about half with mortality sensors) in the 150-152 MHz range (Telonics Inc., Mesa, Ariz.).

Fifty-eight (79%) of 73 deer radio-collared on winter range migrated north and northwest to summer on the Tally Lake District. Relocations of these deer were used to assess macro-habitat use patterns. In addition, 27 deer were radio-equipped on summer range and 1 deer was trapped on Fortine Ranger District but summered on the Tally Lake District. Relocations of these deer were added to the winter-trapped sample to assess micro-habitat use patterns in the Star Meadows and Corduroy Creek areas. Hence, 86 radio-collared deer were present on the district during all or part of three field seasons and provided data for this study (Appendix Table 29).

The 86 radio-equipped deer were relocated 3299 times through aerial telemetry surveys conducted with a Cessna 180 or 182 equipped with two-element H-antennas mounted on the wing struts. Visual confirmation of specific deer was rarely attempted due to the timbered habitat of the study area and difficulty in identifying collar colors and patterns from the air. Each deer was located 2-3 times/month between 0500 and 1900 hrs mountain standard time (MST) with the majority being between 0700 and 1000 hrs. Locations were marked on topographic maps or air photos and assigned a coordinate via the Universal Transverse Mercator (UTM) System.

Locations were recorded as summer, winter, transitional, or accessory. Winter and summer range locations were easy to determine whereby a deer would generally remain in the same area for several months. Eight hundred twenty seven and 2009 winter and summer relocations were recorded, respectively. Of 2009 summer relocations, 1599 were of winter-trapped deer and were used to assess macro-habitat use. Of this same sample of summer relocations 551and 560 were from deer in the Corduroy Creek and Star Meadows complexes, respectively, that were used to assess micro-habitat use.

Transitional locations were those occurring during spring or fall migration wherein a deer usually occurred in an area from which only one relocation was obtained. Accessory areas were those in which a deer was found at least 2-3 times but included neither summer nor winter areas. Two hundred twenty and 243 transitional and accessory relocations were recorded, respectively.

Accuracy of aerial telemetry was checked through test transmitters placed at known locations by another individual familiar with the study area and through locations of dead animals or dropped transmitters. Relocations of test transmitters (n = 13) averaged 104 m from actual locations.

An additional 31 relocations were obtained through direct observations and 15 were obtained from remote camera surveys. These were used along with aerial data in calculating home ranges. Composite and individual summer home ranges and activity centers were calculated using program TELEM (Coleman and Jones 1988).

Diel monitoring by triangulation from 3 ground-based stations was conducted in the Star Meadows and Corduroy Creek areas to assess micro-habitat use patterns. Truck-mounted null antennae arrays were used to locate deer over a 24-hr period. A beacon transmitter was set in a known location. Each station recorded the azimuth of each deer in the area hourly as degrees from the beacon. After the session all relocations were adjusted to indicate degrees from true north. The program TELEM (Coleman and Jones 1988) was used to triangulate the angles and indicate the location of the deer. Accuracy of the system was checked by placing 1-3 test transmitters at known locations during each session (White and Garrott 1990).

Diel monitoring was conducted monthly in each area during July and August 1989, Jun-Sep 1990, and Jul 1991. Monitoring was conducted only in Star Meadows during Apr 1990 and only in Corduroy Creek during May 1990 and Aug and Sep 1991.

Remote camera units developed to detect and monitor grizzly bears (Mace et al. 1990) also were applied to this study. Design and use of the camera system has been described previously (Mace et al. 1990, Dusek and Mace 1991). Cameras can be used to assess whitetail population size, age and sex structure, and habitat use. However, only summer habitat use results are discussed. Cameras were placed randomly at the macro-level, i.e., drainage or quadrat. At the micro level, cameras were placed along active deer trails. All cameras were placed in operation within 1-3 days of each other and removed within 1-3 days. Hence, all cameras collected data for approximately the same time period. Sites were visited after 1 week to check film. After 2-3 weeks cameras were removed from the sites and all film was developed. Photographs were examined for animal species present, number of individuals, and sex and age class when possible. Surveys were conducted in the Star Meadows area during May 1990, in Griffin Creek alone during August and September 1990, and in the Corduroy Creek drainage during July-August 1991.

The 1990 sessions were experimental to determine if sufficient numbers of deer, dispersed on summer range, could be recorded by cameras to obtain useful data. During these sessions photographs of radio-collared deer were assigned a UTM coordinate and included in the relocation database for use in home range calculations and micro-habitat use.

The experimental design of the 1991 session at Corduroy Creek was described previously (Dusek and Morgan 1991). For this session cameras were deployed to maximize the number of radio-collared deer photographed for population estimation. It was known from aerial relocations that approximately half of the radio-collared deer in the drainage were below 1400 m, 35% were between 1400 and 1525 m, and 15% above 1525 m. Hence, the drainage was divided into 25-ha quadrats, and 20 cameras were distributed randomly in similar proportions to deer distribution.

A secondary objective was to use the camera system to compliment habitat use data obtained through radio telemetry. The deployment of cameras described above was not necessarily ideal to meet this objective. A sampling scheme distributing cameras based on area of available habitat would have been better. However, it would be difficult to distribute 20 cameras equally among the 6 habitat components described.

Food habits were investigated during 1990 and 1991. Deer collections were made twice monthly from April-October as authorized by the FWP Commission. A l-qt (0.95-l)sample of rumen material was taken from each animal and fixed with 1% formalin. Samples were rinsed and sorted macroscopically at the FWP Wildlife Research Lab in Bozeman. I identified plant taxa by comparing large fragments with known plant specimens. Percent occurrence was noted for browse and forbs to the species level when practical. Grass-like plants were simply noted as such. Percent volume was measured by water displacement in a graduated cylinder.

Habitat Component.—eight individual geographic information system (GIS) layers were developed for the study area, each containing 7-9 specific classes (Table 1). Data layers were originally created at the Flathead National Forest GIS lab (Kalispell, MT) with the aid of Landsat imagery, digitized maps, and the computer program ERDAS version 7.5 (ERDAS, Atlanta, GA 1990). Layers were modified using program EPPL7 (EPPL7, Minnesota Department of Natural Resources). All layers were created using a pixel size of 50 m.

The vegetation layer was developed using the Landsat TM image No. 041-026 from 28 Aug 1988 (EOSAT Inc., Lanham, Md.). The image recorded the district in 7 bands (3 visual, 3 near infrared, and 1 thermal infrared) with a spectral resolution of 256 classes. Many of the original 256 classes were vegetatively similar, which thus required combining spectral classes.

Initially, an unsupervised spectral classification system using spectral bands 3, 4, and 7 was employed to reduce the 256 spectral classes to 60. These 60 classes were then grouped into 10 based on crown closure, topographic position, reflectance, and general vegetative condition. However, further analysis was needed because of overlap among the 10 groups. The district landtype layer was used to group terrain features based on slope, aspect, and general substrate into nine landtype associations. The 10 spectral groups were then sorted by the nine

Table 1. Geographic information system data layers and classes.

Layer	Classes								
Elevation (m)	915-1158	1159-1280	1281-1402	1403-1524	1525-1646	1647-1768	≥ 1769		
Slope (%)	0-5	6-10	11-15	16-20	21-25	26-35	36-50	≥ 51	
Aspect	N	NE	E	SE	S	SW	W	NW	No aspect
Vegetation	Grass/forb natural	Grass/forb artificial	Shrub/ hardwood	Seedling/ sapling	Sapling/ pole	Pole/ immature/ open	Pole/ immature/ closed	Mature open	Mature closed
Riparian features, all roads, open roads, and closed roads (distance from in meters)	0-100	100-200	200-300	300-400	400-500	500-750	750-1000	> 1000	

landtypes yielding 90 classes. These 90 classes were then regrouped using information from aerial photographs, previously conducted ground surveys, or surveys that were carried out for the sole purpose of verifying GIS information.

The USFS defined vegetation classes (Hodgeboon and Long, Flathead National Forest, unpublished memo) that I modified. Basically, grass/forb and shrub/hardwood layers were lands containing < 10% coniferous trees. Timbered areas were defined according to DBH class and age: seedling = 0-2.3 cm. and/or 0-15 yrs, sapling = 2.4-12.6 cm and/or 16-30 yrs, pole/immature = 12.7-22.8 cm and/or 31-70 yrs, and mature ≥ 22.8 cm and/or ≥ 71 yrs.

Modifications to the vegetation layer for this study included combining and dividing types. Grass/forb areas were divided as either artificial or natural. Artificial grass/forb areas were those created through logging or road building. Natural grass/forb areas included riparian meadows and naturally burned sites. Some regrowth probably occurred because a 1988 satellite image was used, thus moving some stands into later seral classes. Hence, seedling/sapling and sapling/pole classes were created. Vegetation in these two classes was generally of the smaller type, i.e., seedling and sapling, respectively. However, I acknowledge that some larger plants also might have been present. Pole/immature and mature classes were split as open or closed canopy based on 70% canopy closure. Corrections were made for areas logged since 1988 by combining the GIS layer for forest activity with the completed vegetation layer. Areas on the vegetation layer within sites of recent logging activity were changed to artificial grass/forb if not already in that class.

Topographic layers were developed from the digital elevation model (DEN) created by the Geometronics; Service Center, a branch of the USFS at Salt Lake City, Utah. Topographic maps were scanned into the computer and each pixel was assigned a value for slope (%), aspect (degree), and elevation (ft converted to m).

Riparian and road layers were developed in the Flathead National Forest computer lab by digitizing from USGS 7.5´ topographic maps using a Numonics digitizing pad and the computer program JELLY (USFS Region 1, Missoula, MT). I included additional roads created since the last update by changing the GIS layer.

Habitat information also was obtained through ground truthing 50 randomly selected aerial relocations of radiocollared deer during both 1990 and 1991. Each site was identified using aerial photos and topographic maps. Topography, plant species present, an estimate of relative abundance, as well as vegetational cover were recorded for descriptive purposes and to verify GIS data layers.

GIS layers were verified by locating the UTM coordinate of the ground plot on each GIS layer and determining if the description from the ground agreed with the GIS layer. Because walking into a particular quarter-ha area (50-m pixel) was difficult, and aerial telemetry was not accurate to 50 m, an error radius of 100 m or 2 pixels was used. Also, for topographic layers, I allowed a margin of error of 2% for slope, 3° for aspect, and 61 m for elevation.

All GIS and onsite descriptions of a location were in agreement more than 80% of the time. Specifically, elevation, slope, and aspect were in agreement 99, 88, and 88% of the time, respectively. The vegetation layer agreed with ground data 90% of the time in general although open and closed canopy areas were in agreement only 82% of the time. Distances from roads and riparian areas were not measured in the field and could not be checked. However, because locations of roads and riparian areas have been checked by the USFS, I believe these layers were reasonably and accurately distinguished.

Photoplots were set up at seven sites throughout the study area during 1991 to record general phenological change. Photographs were taken monthly from May to September.

Data Analysis

The general analytical procedure used in this study follows that described by Neu et al. (1974) and Byers et al. (1984). Chi-square goodness-of-fit tests were used to determine if classes within a habitat component were used in proportion to availability. Then, 95% Bonferoni confidence intervals were calculated for each class in each component to determine if the class was used greater than, less than, or equal to availability. If deer use was statistically greater than availability the class presumably had some positive aspects for deer and could be considered a preferred class within that habitat component. Use less than availability would connotate a negative relationship or avoidance.

Habitat availability was determined by the number of pixels within each class of each GIS habitat layer. Use was determined by the number of deer relocations in each class of each layer.

Generally, one deer location would equal one pixel. However, because radiotelemetry was not accurate to 50 m (the size of a pixel), I attempted to improve confidence in estimates of deer locations and hence, habitat use. To do this, I used the BUFFER routine in EPPL7 to create a "scanning circle" (Pac et al. 1991) around each deer location. Each location was buffered by two pixels on each side and on pixel on the diagonals forming a 13-pixel star-shaped complex. Used habitat was calculated by determining the proportion of each habitat class within these complexes.

Following analysis, the technique of buffering relocations to gain greater confidence in deer locations made only a negligible difference in the results. Hence, used habitat was calculated solely on the original deer locations with no buffering. In studies with smaller sample sizes buffering, or the use or scanning circles, might give a truer picture of habitat use.

For this study, habitat analysis was conducted at two scales. Macro-habitat use involved determining general habitat preferences of deer throughout the entire study area. This involved using summer locations of only those deer captured and radio-equipped on winter range. Because deer were captured on winter range in an essentially random pattern, migration routes, summer range areas, and patterns of habitat selection were unknown prior to their first use of an area. Hence, they potentially had the opportunity to migrate off the Bowser Lake wintering area and select any part of the study area for summer range. Using locations of deer captured on summer range would bias results.

Micro-habitat use involved determining habitat preferences within areas of high deer use, i.e., star meadows and the Corduroy Creek complexes. Reasons for deer selection of these areas were determined through analysis of macro-habitat use. However, once in one of these preferred areas, analysis of micro-habitat use patterns evaluated seasonal and daily habitat use. This analysis also included all locations of summer-trapped deer, 24-hr monitoring, and camera surveys.

Macro-Habitat Use.—Use versus availability analysis was conducted first at the macro-scale based on pooled data, i.e., all summer range relocations of winter trapped deer. This allowed determination of general habitat selection patterns for deer throughout the entire period on summer range. Next, because most deer were actually using summer range through 3 seasons, data were segregated for spring (first location on summer range-30 Jun), summer (1 Jul-31 Aug), and fall (1 Sep-last location on summer range). This categorization roughly coincided with changes in plant phenology on the study area, changes in deer annual cycle, i.e., pre-fawning and fawning, early post-fawning, and hunting season, and changes in road status on the district (many roads gated all year were open during Jul and Aug).

I attempted to assess habitat use differences based on sex and age classes. In this study, deer were grouped in subadult and adult age classes. Because deer changed age halfway through a study season, early 2-year-olds were included as subadults.

After habitat preference was determined for each habitat layer individually, all layers were combined to create a deer habitat preference map of the study area (Manley and Mace In press). Chi-square values were used to weight each layer, determining the relative importance of each habitat component in deer selection. For example, if chi-square values for slope and aspect were 100 and 10, respectively, the slope layer would apparently be of greater importance to determining deer preference of an area.

Classes in each layer were then revalued using the results of the Bonferroni confidence intervals. Classes used more than available were assigned a value of 10, those used equal to availability a value of 5, and those used less than available a value of 1. The EVALUATE routine in EPPL7 was then used to combine all layers and provide a new GIS layer with values from 1-10, 10 being the most preferred areas. From these data a preference map was created.

Because vegetation is the habitat variable most influenced by humans, this component was analyzed in detail. Managed timber stands were present on the study area at various densities, e.g., 20% of a given area was cutover). Use was related to availability of various densities (occurrence/unit area) of managed timber to determine whether some degree of disturbance affected use by deer. In addition, use was related to degree of diversity whereby diversity was defined as the number of different vegetative classes/unit area.

Micro-Habitat Use.—Analysis of micro-habitat use patterns was conducted for deer inhabiting the Star Meadows and Corduroy Creek complexes in a fashion similar to macro-habitat analysis for deer use within the entire study area. Composite home ranges of deer determined boundaries of the two complexes. I determined habitat availability by the number of pixels/class/habitat component within each area and deer use by the number of locations/class/component.

Diel telemetry sessions were used to determine possible differences in use of vegetation between day and night within randomly selected 24-hr periods each season. Diel telemetry sessions involved ground-based equipment from three stations. Thus, telemetry error needed to be calculated differently than for aerial relocations. Error angles (degrees from true location) from 1-3 test transmitters put out during each session were used to calculate error arcs (distance from true location) for each deer from each station. The largest arc for each deer was used to determine the distance a deer had to move between subsequent relocations to be considered a true move. When subsequent relocations were less than 2 times the error arc, the latter relocation was eliminated from analysis. No relocations from a deer with a calculated error arc greater than 250 m were used. This generally eliminated deer that were far from a particular station because more distant deer tended to yield larger error arcs. It also eliminated all data from three 24-hr sessions that were conducted under adverse weather conditions.

Use versus availability analysis also was applied to data from the 1991 camera survey at Corduroy Creek. Habitat availability there was determined by number of camera locations/class/component, e.g., if four of 20 cameras were in mature timber, this class had a 20% availability. I determined use by the number of deer photographs recorded/class/component but not including fawns or multiple photos of the same deer taken in succession. Because deer could not be individually identified, photos of the same deer recorded on different days or

Section 4: Results

Movements, Distribution. and Home Range

As noted earlier, 79% of deer radio-collared on winter range migrated to the Tally Lake District to summer. Other deer radio-collared on winter range migrated shorter distances typically moving north along the Stillwater River but not onto the national forest. A few deer spent the entire year around the Bowser Lake winter range.

Spring migration generally commenced between the last week of March and early April although a few deer remained on winter range until late May. Departure dates were difficult to ascertain because of relatively infrequent aerial monitoring. Transitional locations were not obtained for all deer, though most were located sufficiently to assume general migration routes. There was no definitive relationship between location of deer on winter range and subsequent summer locations. Hence, I assumed that winter trapping was generally random with respect to migration routes as well as summer distribution.

Deer followed two general routes between winter range and summer ranges on the Tally Lake District (Fig. 3). Those summering in the northern portion of the study area moved from winter range northwest along the northeast side of Tally Lake toward the confluence of Good and Logan Creeks. Transitional areas included Stovepipe Canyon, Bootjack Lake, and Round Meadow. From there, deer moved up Good Creek toward its confluence with Miller Creek, where this large riparian area, and lower slopes of Adams Mountain, were used by some deer as a spring accessory area. These initial movements of ~22 km occurred relatively quickly, typically between relocation flights (7-10 days).

Deer summering further west moved from the base of Adams Mountain up Good Creek using the creek bottom and south-facing slopes as transitional areas. This movement of up to 13 km often spanned several weeks depending on snowmelt and the distance to specific summering areas. According to 1991 photoplots from the Corduroy Creek drainage, snow was still present in higher elevations during mid-May and vegetation was sparse throughout the drainage until mid-June, thus influencing deer arrival on that portion of summer range.

Deer moving from winter range to Star Meadows followed three different routes. Some traveled along the northeast side of Tally Lake then southwest across Hill Meadow toward Logan Creek. Others moved along the southwest side of the lake continuing up Logan Creek toward Star Meadows. Still a third path took deer over Reid Creek or Lost Creek Divides. Transitional areas used varied depending on the exact route. They included Stovepipe Canyon, Lost Creek, and Logan Creek above Tally Lake. The only true accessory area along these routes was Star Meadows as used by deer moving further up Griffin and Sheppard Creeks. These movements of ~22 km from winter range to Star Meadows occurred quickly, again typically between aerial relocations.

Once in Star Meadows-deer tended to use southerly slopes waiting for snowmelt and the meadow to dry out. Photoplots from around Star Meadows showed the meadow completely flooded in May and partially flooded in June.

Vegetation in the corduroy creek drainage was most succulent during July and August. While vegetation in September was still green, riparian bottoms especially meadows, began to dry out. Fall migration from the northern portion of the study area began for some deer as early as September. However, the majority of deer didn't leave summer range until November.

Migration routes from the northern portion of the study area were similar to spring. During fall, Stovepipe Canyon and Hill Meadow were used as accessory areas in which deer often spent several weeks before moving onto winter range. This apparently depended on snow conditions with an occasional deer remaining in the area the entire winter.

Plant phenology around Star Meadows tended to be slightly ahead of Corduroy Creek. Vegetation was most succulent during June and July, and deer used the meadow bottom at this time. By August the meadow began to dry out, and deer moved up slope. Although one or two deer moved completely back to winter range in August, deer more typically moved to Tally Mountain, which was used by deer as a late summer/fall accessory area for up to 3 months prior to a final move to winter range.

Among all deer monitored in 1991, approximately 35% moved off summer range prior to hunting season (last week of Oct) while approximately 15% moved completely

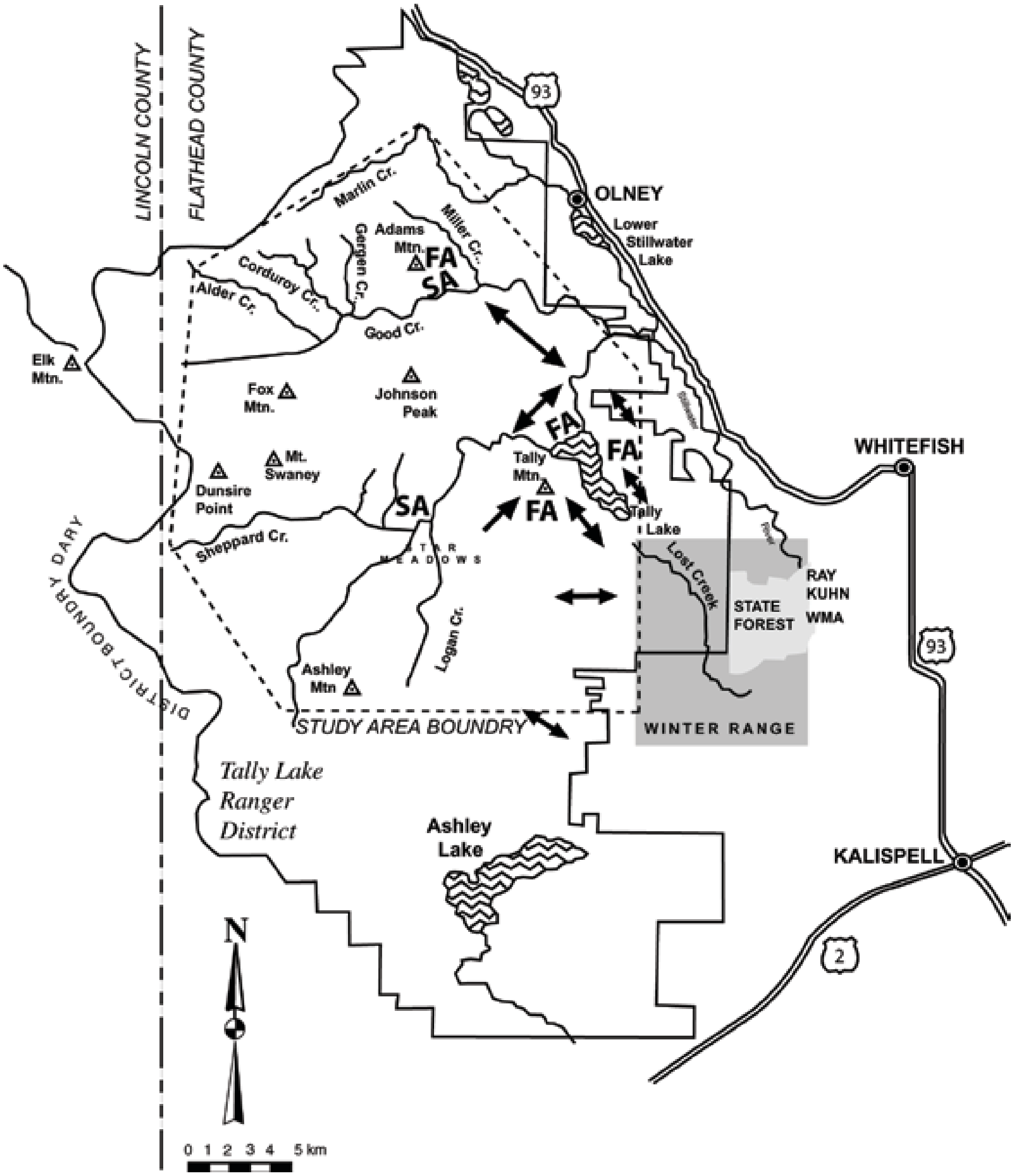


Figure 3. General migration routes and spring (SA) and fall (FA) accessory area of deer moving to and from the Bowser Lake winter range

to winter range by this time. By the end of the hunting season (last week of Nov) all deer had left summer areas although a few remained in transitional locations. Movements off summer ranges during 1991were slightly earlier than in 1989 or 1990 because of earlier than usual snowfall and cold weather.

The 58 deer migrating to the Tally Lake District were distributed throughout the study area during summer (Fig. 4). However, there appeared to be greater use of some areas than others. Summer activity centers for individual deer were tested for random distribution throughout the study area. Results indicated that in each year deer were not distributed randomly but were clumped (1989, $\chi^2 = 3.56$, $P = 0.059$; 1990, $\chi^2 = 5.93$ $P = 0.015$; 1991, $\chi 2 = 7.92$ $P = 0.005$) in three primary areas. Thirty-one deer summered in the southern portion of the study area that included 21 deer in and around Star Meadows. Twenty-seven deer summered in the northern portion of the study area; of these, 12 and 10 deer used the Corduroy Creek and Adams Mountain complexes, respectively.

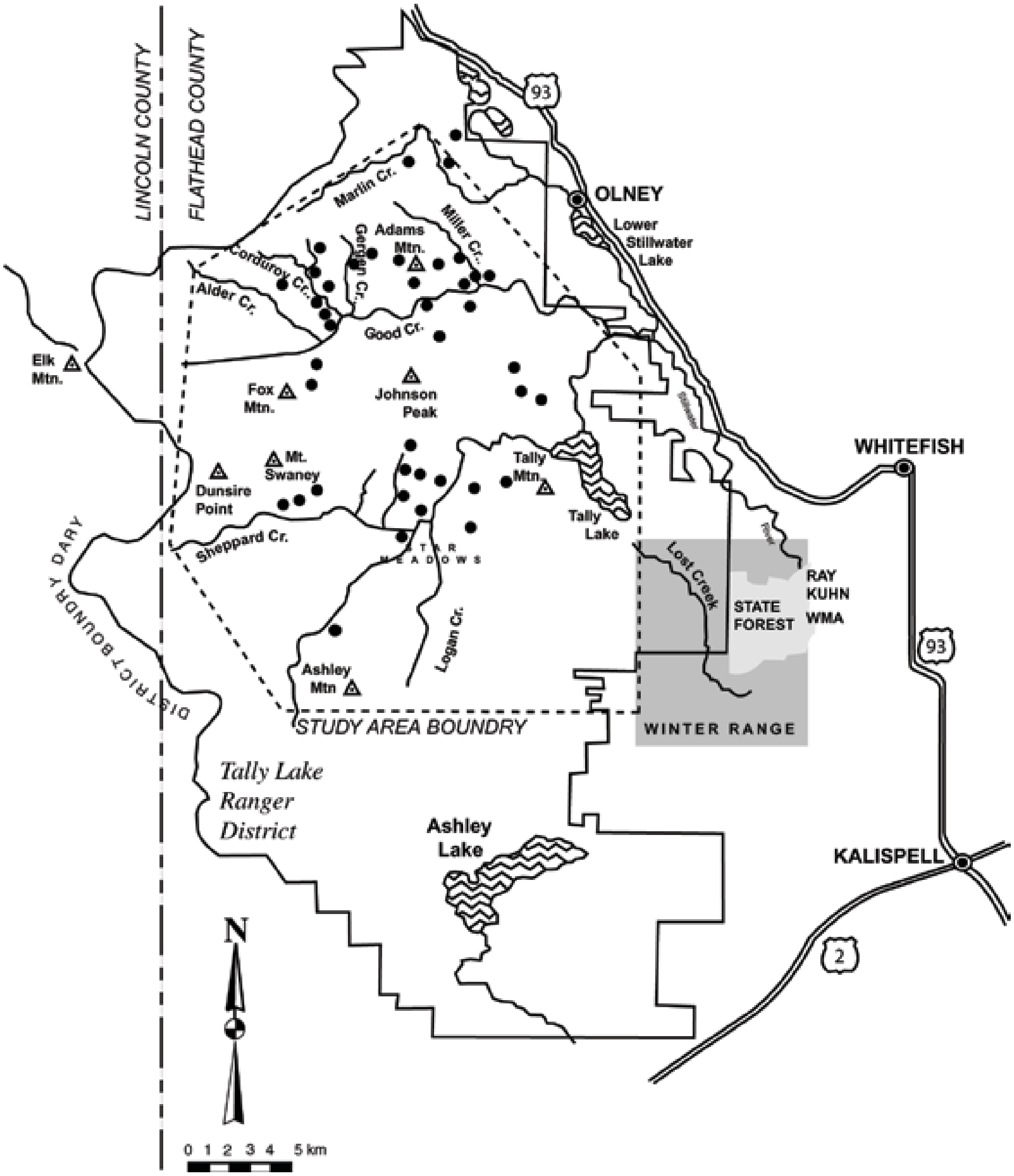


Figure 4. Deer distribution on the Tally Lake District as indicated by summer activity centers, 1991

Summer home ranges averaged 88.5 ha with male home ranges being larger than females and subadult home ranges larger than adults (Table 2).

Table 2. Average home range (convex polygon using 90% of locations) of white-tailed deer on the Tally Lake study area for all years combined.

	Adult	Subadult	Total
Female	61.6 (86)[1]	90.8 (19)	66.6 (105)
Male	235.3 (12)	268.2 (3)	241.9 (15)
Total	82.5 (98)	115.0 (22)	88.5 (120)

[1] Home range in ha (number of individuals)

Macro-Habitat Use

Pooled and Seasonal Data.—Summer habitat selection by deer migrating off the winter range was independent of availability (χ^2 tests, $P < 0.05$) for 5 of 6 habitat components considered (Table 3). This indicated deer selected particular habitat classes over others within a given habitat component.

Elevation was the most important habitat component (highest χ^2) with respect to deer selection of summer range for both pooled and seasonal data. Although its importance diminished throughout the period that deer remained on summer range, its relative weight remained well above the other components except all roads.

The vegetation and road components were about equal in importance when data were pooled although much less than elevation. When separated seasonally, vegetation remained an important factor particularly during spring and summer. When the road layer was separated seasonally, it also remained an important factor. However, when it was split between open and closed its importance to deer habitat selection lessened except for the relatively high value for closed roads during summer.

Aspect and riparian areas also were about equal in importance to deer habitat selection when data were pooled, but of even less importance than vegetation and roads. Like other layers, importance of aspect and riparian areas to habitat selection diminished during summer and fall. Slope appeared to have very little influence on deer habitat selection relative to other components regardless of season.

Elevationally, deer as a group used the 1159- to 1524-m zone more than available, 1525-1646 m equal to available, and areas >1646 and < 1159 m a less than available (Table 4). The preferred elevation zone included 48% of the study area. In the southern portion of the study area this preferred zone included Star Meadows and the Logan, Griffin, and Sheppard creek bottomlands, as well as the slopes adjacent to these areas except the highest ridges that were used equal or less than available. In the northern portion of the study area the preferred elevation zone included the Good Creek bottom above Miller Creek and the adjacent drainages and slopes, except for the higher ridges.

Seasonally, preferred elevation shifted higher from spring to fall. During spring deer preferred the 1159- to 1524-m zones of elevation;

Table 3. Values of chi-square goodness-of-fit tests (relative weights)[1] for individual habitat components, pooled and seasonal data.

	Pooled		Spring		Summer		Fall	
Slope	13.1	(1)^{NS}	15.1	(2)	7.5	(1)^{NS}	16.4	(1)
Aspect	72.3	(6)	58.2	(8)	19.1	(3)	19.3	(1)
Elevation	459.3	(35)	274.7	(37)	138.7	(18)	114.6	(7)
Vegetation	155.5	(12)	72.4	(10)	64.3	(9)	62.6	(4)
Riparian areas	89.1	(7)	52.8	(7)	32.4	(4)	20.8	(1)
All roads	161.6	(12)	40.4	(5)	56.3	(7)	104.5	(6)
Open roads			7.4	(1)^{NS}	12.9	(1)^{NS}	37.9	(2)
Closed roads			16.9	(2)	61.1	(8)	24.1	(1)

[1] Weight of chi-square value relative to lowest

^{NS} not significant, $\alpha = 0.05$

other zones were avoided. During summer, use of the next higher elevational zone, 1525-1646 m, increased from less than available to equal. During fall, use of the 1525-1646 m as the only preferred elevational zone.

Vegetatively, deer as a group used natural grass/forb, shrub/hardwood, and both open and closed pole/immature stands more than available (Table 5). Artificial grass/forb, seedling/sapling, and closed mature timber were used less than available. Sapling/pole and closed mature timber were used equal to availability.

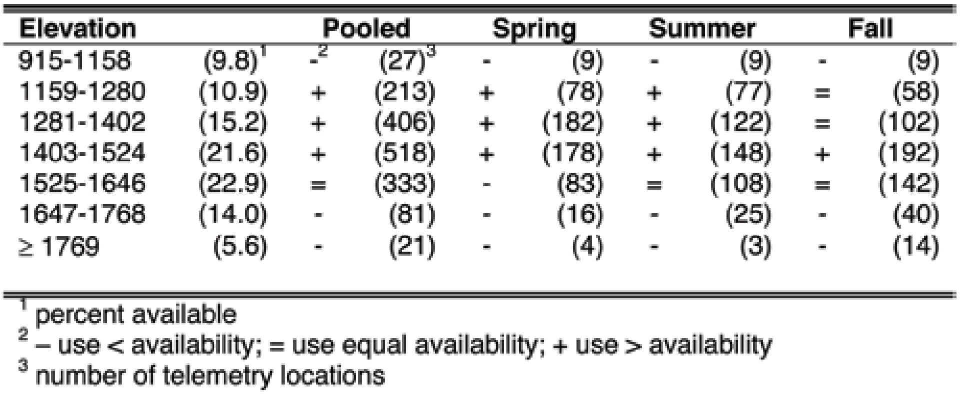
Only 35% of the study area contained preferred vegetation and unlike the distinct elevation zones preferred vegetation was interspersed with avoided and areas of equal use. However, there were some large sections of preferred vegetation, which included the Star Meadows bottom where natural grass/forb and shrub/hardwood types occurred together. Another large area of preferred vegetation included the north side Good Creek of which contained an abundance of both open and closed pole/immature timber.

Approximately one-half of the 40% of avoided vegetation included early seral coniferous stands composed of artificial grass/forb and seedling/sapling. Hence, portions of the district most affected by timber harvesting generally were avoided. The other half of the avoided vegetation included the relatively large, closed mature timber type. These areas often occurred on the south side of Good Creek and in higher portions of the district.

Seasonally, the trend was toward greater use of timbered areas and less use of open, shrubby areas from spring to fall. While use of natural grass/forb and seedling/sapling types remained the same, deer made less use of artificial grass/forb and shrub/hardwood as the summer range season progressed. At the same time, use of both open and closed pole/immature timber increased during fall.

When roads were grouped regardless of

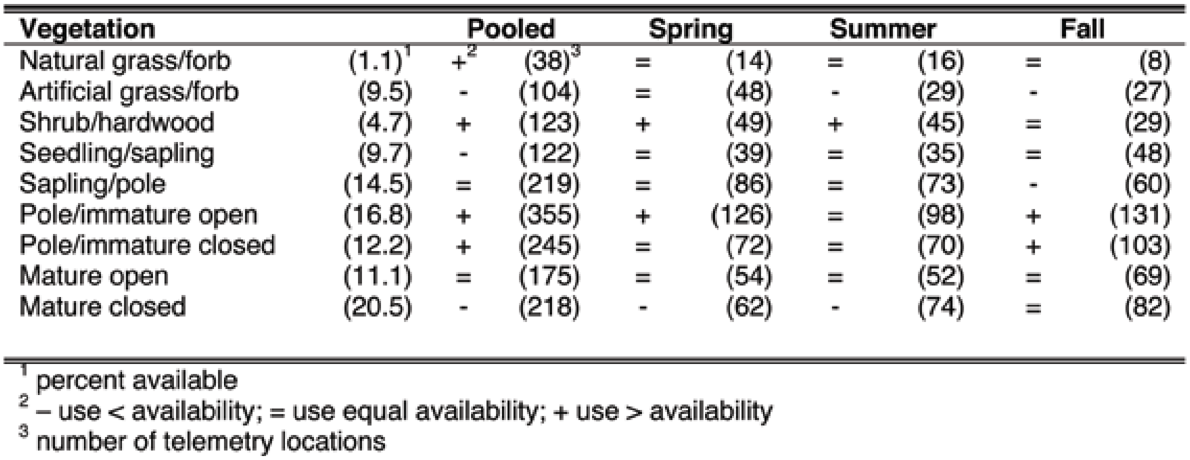
Table 4. Use versus availability of elevation (m) habitat component from pooled and seasonal data.



Elevation		Pooled		Spring		Summer		Fall	
915-1158	(9.8)[1]	-[2]	(27)[3]	-	(9)	-	(9)	-	(9)
1159-1280	(10.9)	+	(213)	+	(78)	+	(77)	=	(58)
1281-1402	(15.2)	+	(406)	+	(182)	+	(122)	=	(102)
1403-1524	(21.6)	+	(518)	+	(178)	+	(148)	+	(192)
1525-1646	(22.9)	=	(333)	-	(83)	=	(108)	=	(142)
1647-1768	(14.0)	-	(81)	-	(16)	-	(25)	-	(40)
≥ 1769	(5.6)	-	(21)	-	(4)	-	(3)	-	(14)

[1] percent available
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

Table 5. Use versus availability of vegetation habitat component from pooled and seasonal data.



Vegetation		Pooled		Spring		Summer		Fall	
Natural grass/forb	(1.1)[1]	+[2]	(38)[3]	=	(14)	=	(16)	=	(8)
Artificial grass/forb	(9.5)	-	(104)	=	(48)	-	(29)	-	(27)
Shrub/hardwood	(4.7)	+	(123)	+	(49)	+	(45)	=	(29)
Seedling/sapling	(9.7)	-	(122)	=	(39)	=	(35)	=	(48)
Sapling/pole	(14.5)	=	(219)	=	(86)	=	(73)	-	(60)
Pole/immature open	(16.8)	+	(355)	+	(126)	=	(98)	+	(131)
Pole/immature closed	(12.2)	+	(245)	=	(72)	=	(70)	+	(103)
Mature open	(11.1)	=	(175)	=	(54)	=	(52)	=	(69)
Mature closed	(20.5)	-	(218)	-	(62)	-	(74)	=	(82)

[1] percent available
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

being open or closed deer generally avoided areas closest to a road and preferred sites ≥500 m away (Table 6). While only the 0-100 m zone was avoided, this accounted for 41% of the study area. The preferred areas ≥500 m from a road accounted for only 11% of the study area. The primary roadless portions of the study area were found on top of Tally mountain, on the north side of Good Creek in Corduroy, Gergen, and Grouse creeks, and on the south side of Good Creek along the north side of Johnson Peak.

Seasonally, there was little variation in use of roads. The area closet to a road was always avoided while the furthest areas generally were preferred regardless of season.

When open and closed roads were considered separately deer generally used areas similar to availability (Tables 7 and 8). However, deer still avoided areas adjacent to closed roads; open roads were only avoided during fall.

Deer as a group used sites ≤100 m of riparian habitats more than available and avoided sites 300-400 m and > 750 m (Table 9). Deer preferred the ≤100-m zone regardless of season. However, preferences appeared to shift slightly from riparian habitats through summer and fall as indicated by change in the further zones from use less than available to equal to available.

Preferred sites made up only 21% of the study area and were found along all drainages containing water at least long enough for riparian vegetation to exist. Avoided areas accounted for 24% of the study area. Large sites lacking riparian habitat occurred on Reid and Lost Creek Divides, northwest of the head of Martin Creek, and on Fox Mountain.

Easterly and southerly aspects were selected greater than available by deer as a group whereas northerly and northwesterly aspects were avoided (Table 10). Preferred aspects accounted for 24% of the study area. Because major drainages tended to flow to the northeast many preferred

Table 6. Use versus availability of the road habitat component, regardless whether open or closed, from pooled and seasonal data.

Distance from (m)		Pooled		Spring		Summer		Fall	
0-100	(41.1)[1]	-[2]	(497)[3]	-	(181)	-	(149)	-	(167)
100-200	(21.4)	=	(320)	=	(114)	=	(103)	=	(103)
200-300	(13.1)	=	(231)	=	(80)	=	(71)	=	(80)
300-400	(7.8)	=	(151)	=	(50)	=	(44)	=	(57)
400-500	(5.4)	=	(100)	=	(44)	=	(28)	=	(28)
500-750	(6.3)	+	(132)	=	(31)	=	(43)	+	(58)
750-1000	(2.6)	+	(83)	+	(31)	+	(29)	=	(23)
≥1000	(2.3)	+	(85)	=	(19)	+	(25)	+	(41)

[1] percent available
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

Table 7. Use versus availability of the open road habitat component, regardless whether open or closed, from pooled and seasonal data.

Distance from (m)		Spring		Summer		Fall	
0-100	(20.5/30.9)[1]	=[2]	(101)[3]	=	(127)	-	(87)
100-200	(14.2/18.9)	=	(87)	=	(100)	=	(64)
200-300	(12.0/13.3)	=	(74)	=	(56)	=	(61)
300-400	(9.4/9.1)	=	(57)	=	(56)	=	(60)
400-500	(8.4/7.2)	=	(55)	=	(36)	=	(43)
500-750	(14.5/10.1)	=	(74)	=	(52)	=	(92)
750-1000	(9.3/5.4)	=	(42)	=	(36)	=	(44)
≥1000	(119/5.0)	=	(60)	=	(29)	+	(106)

[1] percent available (non-summer/summer)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

aspects occurred on the north side of Good Creek and Star Meadows and their tributaries. Aspect became less important as summer progressed; during summer and fall most aspects were used in proportion to availability.

As previously stated, slope was not an important factor in habitat selection. No slopes were preferred and only the 36-50% slope was avoided (Table 11). There was ,little seasonal change with respect to use of slope.

Sex and Age Differences.—I attempted to assess differences in habitat use between sexes and two female ages classes. Adult (≥2 yrs) accounted for a majority of radio-collared deer. Hence, 1143 (71%) of 1599 relocations were adult females, only 197 (12%) were subadult females, and 259 (16%) were males. Similar use versus availability analyses were conducted on the three groups individually. Selection by adult females was similar to the overall data presented above while subadult females and males generally used each habitat class equal to availability.

Composite Habitat Preference.—The habitat preference map developed by meshing the various layers together emphasized the importance of the elevation component in macro-site selection (Fig. 5). Because elevation had such a high weighting factor, preferred and avoided areas on the composite preference map were similar to those for elevation with the exception of areas where use equalled availability. Preferred habitat under this scenario was located along major drainages and up the adjacent slopes because these areas were located within the 1159 and 1524 m zone. Areas where use was equal to availability occurred along the next high elevation zone and where other components such as roads and vegetation played an important role.

Table 8. Use versus availability of the closed road habitat component, regardless whether open or closed, from pooled and seasonal data.

Distance from (m)		Spring		Summer		Fall	
0-100	(24.1/14.0)[1]	-[2]	(97)[3]	-	(36)	-	(96)
100-200	(16.3/11.2)	=	(84)	=	(42)	=	(88)
200-300	(13.7/11.1)	=	(86)	=	(62)	=	(82)
300-400	(10.4/9.7)	=	(58)	=	(41)	=	(69)
400-500	(9.0/9.7)	=	(58)	=	(55)	=	(48)
500-750	(13.5/18.0)	=	(88)	=	(77)	=	(92)
750-1000	(6.9/12.2)	=	(38)	=	(59)	=	(33)
≥1000	(6.2/14.0)	=	(41)	+	(120)	=	(49)

[1] percent available (non-summer/summer)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

Table 9. Use versus availability of the riparian habitat component, measured as distance from (m), from pooled and seasonal data.

Distance from (m)		Pooled		Spring		Summer		Fall	
0-100	(21.5)[1]	+[2]	(468)[3]	+	(167)	+	(150)	+	(151)
100-200	(16. 2)	=	(247)	=	(100)	=	(73)	=	(74)
200-300	(15.2)	=	(219)	=	(70)	=	(69)	=	(80)
300-400	(11.9)	-	(150)	=	(51)	=	(49)	=	(50)
400-500	(10.0)	=	(160)	=	(60)	=	(46)	=	(54)
500-750	(13.7)	=	(215)	=	(79)	=	(72)	=	(94)
750-1000	(6.1)	-	(66)	-	(14)	=	(22)	=	(30)
≥1000	(5.4)	-	(44)	-	(9)	-	(11)	=	(24)

[1] percent available
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

When elevation was removed from the equation, preferred habitat was much more interspersed (Fig. 6). Under this scenario vegetation and roads had the highest weighting factors and were most dominant with riparian areas and aspect secondary. Major preferred areas occurred.in the Star Meadows bottom and along the north side of Good-Creek in Corduroy, Gergen, and Grouse creeks.

Deer Habitat Use of Managed Timber.— Managed timber areas are those altered by humans either through cutting or prescribed burns. In this study, artificial grass/forb and seedling/sapling types were managed timber areas. Deer generally used artificial grass/forb areas equal to availability only avoiding areas containing 28%/0.9 km2 (Table 12). There was greater selection within the seedling/sapling type. Deer preferred areas with no seedling/sapling and avoided areas with 11-17 and 39%/0.9 km^2. When the two types were combined, 0-5% and ≥50% were preferred, whereas17 and 33% were avaoided.

Sapling/pole could be considered managed timber in certain instances. In the northern portion of the study area sapling/pole stands often occurred as remnants of fires in the early part of the century. However, the type also exists as a result of logging. In either case, deer again showed a preference for areas with little or no (0-5%), and relatively high (≥50%), amounts of sapling/pole (Table 12); they avoided areas with sapling/pole present on 17 and 39% of the units.

Table 10. Use versus availability of aspect habitat component from pooled and seasonal data.

Aspect			Pooled		Spring		Summer		Fall
East	(14.1)[1]	+[2]	(268)[3]	=	(101)	=	(73)	=	(94)
Northeast	(14.7)	=	(203)	-	(56)	=	(69)	=	(78)
North	(11.2)	-	(125)	-	(31)	=	(39)	=	(55)
Northwest	(9.7)	-	(104)	-	(33)	-	(31)	=	(40)
West	(9.1)	=	(123)	=	(40)	=	(41)	=	(42)
Southwest	(11.2)	=	(216)	=	(74)	=	(71)	=	(71)
South	(10.2)	+	(201)	=	(68)	=	(59)	=	(71)
Southeast	(11.9)	=	(222)	+	(90)	=	(62)	=	(70)
No Aspect	(8.0)	=	(137)	=	(57)	=	(47)	-	(33)

[1] percent available
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

Table 11. Use versus availability of the slope habitat component, regardless whether open or closed, from pooled and seasonal data.

Slope (%)			Pooled		Spring		Summer		Fall
0-5	(8.1)[1]	=[2]	(123)[3]	=	(48)	=	(45)	=	(30)
6-10	(11.3)	=	(188)	=	(72)	=	(58)	=	(58)
11-15	(13.0)	=	(240)	=	(81)	=	(80)	=	(79)
16-20	(14.3)	=	(237)	=	(97)	=	(64)	=	(76)
21-25	(14.9)	=	(246)	=	(80)	=	(73)	=	(93)
26-35	(23.6)	=	(362)	-	(104)	=	(110)	=	(148)
36-50	(12.6)	-	(166)	=	(59)	=	(53)	=	(54)
≥ 50	(2.2)	=	(37)	=	(9)	=	(9)	=	(19)

[1] percent available
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

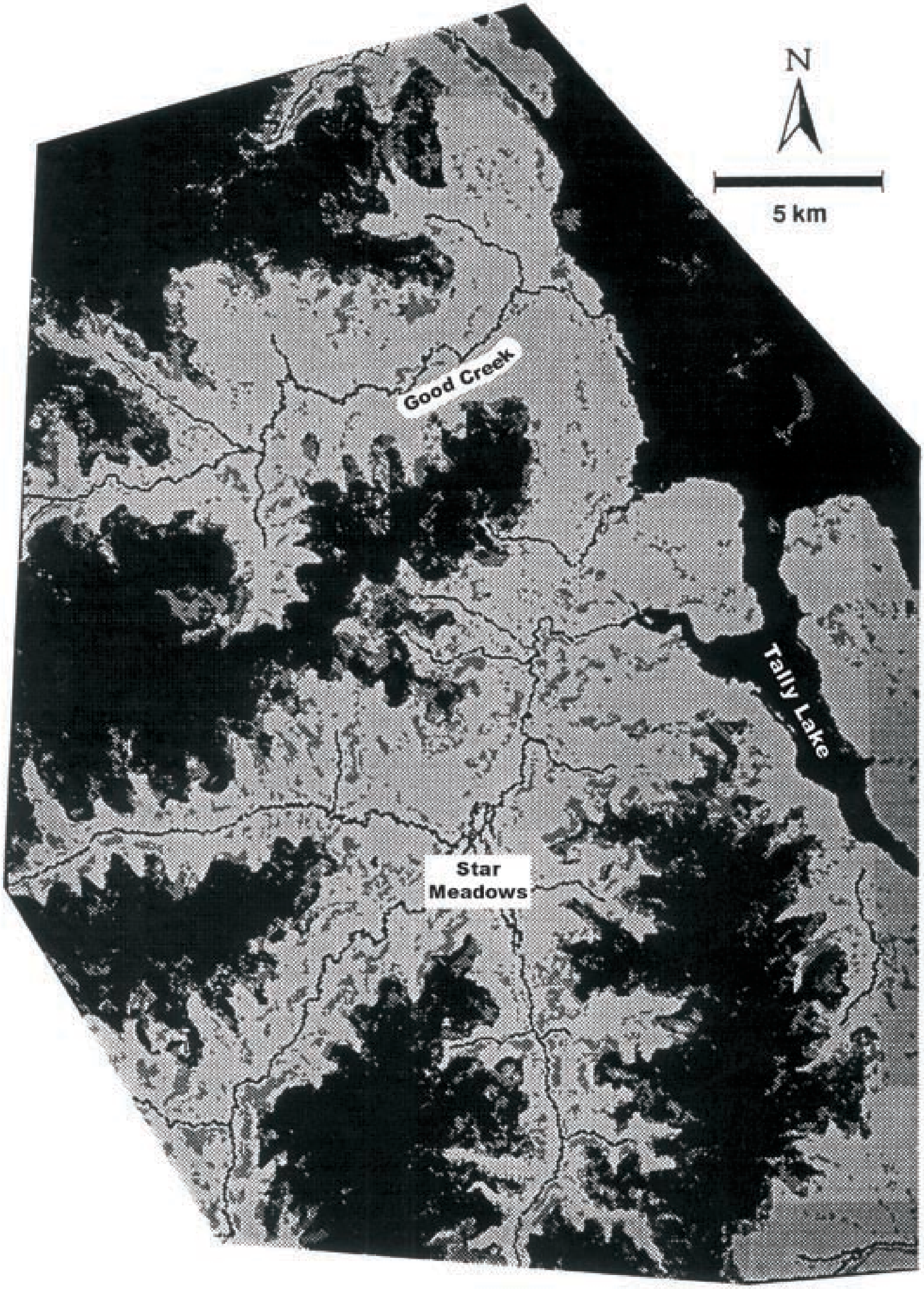


Figure 5. White-tailed deer study area habitat preference map encompassing all six habitat components (dark tone indicates use < available, light tone indicates use > available, and middle tone indicates use = available.)

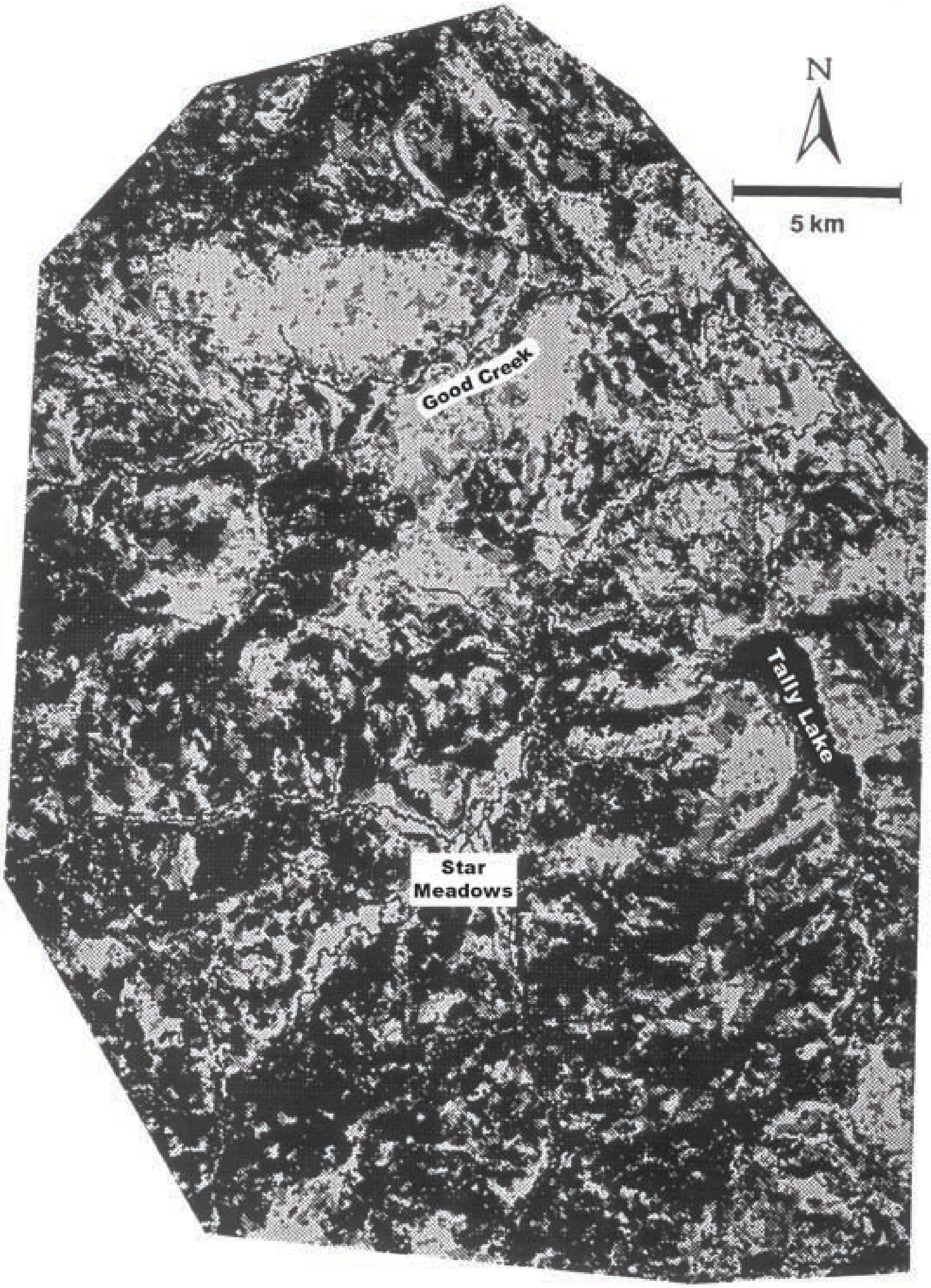


Figure 6. Modified habitat preference map with elevation removed from the equation (dark tone indicates use < available, light tone indicates use > available, and middle tone indicates use = available.)

When all 3 types were combined, deer preferred only habitat with no managed timber.

Vegetation Diversity.—An area was considered more vegetatively diverse as the number of different vegetative classes/unit area approached the maximum of 9. Three different size areas (blocks) were considered: 90, 20, and 7 ha. In general, the more immediate the surroundings, the less diversity was important (Table 13). At the large scale (90 ha), deer preferred a moderate amount of diversity (5 types) as well as the maximum amount of diversity (8-9 types). They avoided areas of intermediate diversity (7 types). At the middle level (20 ha), deer again preferred the maximum amount of diversity; however, they avoided habitats just less than maximum diversity. At the smallest scale (7 ha), diversity appeared to play a minor role in habitat selection.

Micro-Habitat Use

Pooled and Seasonal Data.—Macro-habitat analyses indicated that deer migrating off winter range selected summer areas based on elevation,

Table 12. Use versus availability of managed timber.

% cut/ 90 ha		Grass/forb artificial		Seedling/sapling		Sapling/pole		Columns 1 and 2		Columns 1, 2, and 3
0	=[1]	(33.5/564)[2]	+	(34.1/675)	+	(28.8/576)	+	(20.3/443)	+	(8.7/252)
5	=	(18.2/264)	=	(21.5/338)	+	(19.6/378)	=	(14.9/225)	=	(7.6/147)
11	=	(14.0/189)	-	(13.9/183)	=	(15.2/219)	=	(11.9/172)	=	(8.3/140)
17	=	(10.2/190)	-	(9.3/118)	-	(11.1/128)	-	(10.2.131)	=	(9.1/143)
22	=	(6.9/108)	=	(7.0/101)	-	(7.9/72)	=	(9.6/133)	-	(9.5/114)
28	-	(4.8/52)	=	(4.4/69)	-	(5.5/26)	=	(8.3/105)	-	(8.9/96)
33	=	(3.2/50)	=	(2.8/37)	-	(3.8/26)	-	(6.6/75)	-	(8.3/98)
39	=	(2.4/46)	-	(2.0/16)	-	(2.4/23)	=	(5.0/67)	-	(7.7/88)
44	=	(1.8/39)	=	(1.5/15)	=	(1.5/40)	=	(3.8/52)	=	(6.9/98)
≥50	=	(4.9/97)	=	(3.5/47)	+	(4.3/111)	+	(9.4/196)	=	(25.2/423)

[1] – use < availability; = use equal availability; + use > availability
[2] percent available/number of telemetry locations (*n*)

Table 13. Use versus availability of vegetation layer by diversity.

Number of different vegetation types/unit area	Unit area					
		90 ha		20 ha		7 ha
1		n/a		*	=	(2.5/45)
2		n/a	=	(1.2/24)	=	(11.4/165)
3		*	=	(4.1/79)	=	(22.8/397)
4	=[1]	(1.0/13)[2]	=	(13.5/233)	=	(29.4/512)
5	+	(4.4/108)	=	(22.1/376)	=	(22.2/313)
6	=	(10.9/156)	-	(31.1/419)	=	(9.8/127)
7	-	(48.2/510)	-	(23.8/331)	=	(1.9/40)
8	+	(28.0/526)	+	(4.3/137)		**
9	+	(7.5/286)		**		n/a

[1] – use < availability; = use equal availability; + use > availability
[2] percent available/number of telemetry locations
* combined with class below
**combined with class above

vegetation, roads in general, presence of riparian areas, aspect, and slope generally in that order depending on season. The two areas that supported the greatest number of radio-collared deer, Star Meadows and the Corduroy Creek complexes, occurred almost entirely within the preferred elevational zone. Thus, detailed analyses of habitat structure and use of these areas by deer should provide closer insight to the importance of various habitat components and habitat relationships in general.

Micro-habitat use for pooled data in both the Corduroy Creek and Star Meadows Complexes was independent of availability (χ^2 tests, $P < 0.05$) for each of the six habitat components considered except for vegetation at Star Meadows (Tables 14 and 15). However, unlike macro-analysis, here individual layers were closer (χ^2 values less extreme) with regard to importance in determining habitat selection. Also, when separated seasonally, habitat classes in most layers were not used differently from occurrence on the study area. Major exceptions were that elevation at both Corduroy Creek and Star Meadows and open roads at Star Meadows were important during all seasons.

In general, classes within individual habitat components were used equal to availability as would be expected when χ^2 values are not significant. Elevation showed some differential use among classes (Table 16). Even though both complexes were generally within the overall preferred elevational zone, middle elevations were preferred within each complex. At Corduroy Creek, use of elevation was similar between spring and summer but preferences shifted to higher zones during fall. Deer associated with Star Meadows shifted to slightly lower elevations from spring to summer but moved higher from summer to fall.

Table 14. Values of chi-square goodness-of-fit tests (relative weights)1 for individual habitat components for the Corduroy Creek complex from pooled and seasonal data.

	Pooled	Spring	Summer	Fall
Slope	16.6 (1)	6.9 (2)^{NS}	12.2 (3)^{NS}	10.5 (2)^{NS}
Aspect	25.5 (1)	7.7 (3)^{NS}	9.4 (2)^{NS}	22.2 (4)
Elevation	79.0 (5)	43.4 (15)	25.5 (6)	29.3 (5)
Vegetation	20.6 (1)	13.2 (3)^{NS}	10.6 (3)^{NS}	14.8 (3)^{NS}
Riparian areas	21.3 (1)	7.8 (3)^{NS}	6.2 (1)^{NS}	7.0 (1)^{NS}
All roads	22.3 (1)	11.1 (4)^{NS}	7.9 (2)^{NS}	13.6 (2)^{NS}
Open roads		2.9 (1)^{NS}	4.2 (1)^{NS}	16.7 (3)
Closed roads		9.7 (3)^{NS}	16.2 (4)	5.7 (1)^{NS}

[1] Weight of chi-square value relative to lowest

^{NS} not significant, $\alpha = 0.05$

Table 15. Values of chi-square goodness-of-fit tests (relative weights)1 for individual habitat components for the Star Meadows complex from pooled and seasonal data.

	Pooled	Spring	Summer	Fall
Slope	19.9 (1)	20.8 (3)	11.5 (2)^{NS}	6.6 (1)^{NS}
Aspect	32.7 (2)	27.4 (4)	10.4 (2)^{NS}	11.4 (2)^{NS}
Elevation	18.0 (1)	22.5 (3)	16.7 (3)	27.8 (4)
Vegetation	13.6 (1)^{NS}	12.2 (2)^{NS}	10.0 (2)^{NS}	16.2 (2)
Riparian areas	27.8 (2)	9.3 (1)^{NS}	9.3 (2)^{NS}	36.1 (5)
All roads	24.0 (3)	7.4 (1)^{NS}	6.3 (1)^{NS}	27.1 (4)
Open roads		21.3 (3)	24.9 (5)	14.2 (2)
Closed roads		12.9 (2)	5.2 (1)^{NS}	10.3 (2)^{NS}

[1] Weight of chi-square value relative to lowest

^{NS} not significant, $\alpha = 0.05$

Table 16. Use versus availability of elevation (m) habitat component for Corduroy Creek (CC) and Star Meadows (SM) from pooled and seasonal data.

Elevation		Pooled				Spring				Summer				Fall			
			CC		SM		CC		SM		CC		SM		CC		SM
1219-1280	(na/13.4)[1]		n/a	=[2]	(66)[3]		n/a	=	(24)		n/a	=	(32)		n/a	=	(10)
1281-1340	(3.7/22.8)	=	(16)	=	(122)	=	(3)	=	(61)	=	(10)	=	(46)	-	(3)	-	(15)
1341-1402	(11.0/18.7)	=	(77)	=	(122)	=	(18)	+	(63)	=	(22)	=	(43)	=	(37)	-	(16)
1403-1462	(17.4/18.4)	+	(150)	+	(131)	+	(46)	=	(46)	+	(48)	=	(50)	=	(56)	=	(35)
1463-1524	(15.0/18.4)	+	(113)	=	(60)	=	(24)	=	(21)	=	(32)	-	(15)	+	(57)	=	(24)
≥ 1525	(52.9/13.4)	-	(195)	=	(59)	-	(36)	-	(16)	-	(60)	-	(15)	-	(99)	=	(28)

[1] percent available (Corduroy Creek/Star Meadows)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

Table 17. Use versus availability of vegetation habitat component for Corduroy Creek (CC) and Star Meadows (SM) from pooled and seasonal data.

Vegetation		Pooled				Spring				Summer				Fall			
			CC		SM		CC		SM		CC		SM		CC		SM
Natural grass/forb	(0.9/6.24)[1]	=[2]	(2)[3]	=	(40)	-	(0)	=	(16)	=	(2)	=	(17)	-	(0)	=	(7)
Artificial grass/forb	(1.1/14.7)	=	(4)	=	(67)	-	(0)	=	(36)	-	(0)	-	(18)	=	(4)	=	(13)
Shrub/hardwood	(2.7/8.5)	=	(18)	=	(45)	=	(4)	=	(22)	=	(10)	=	(22)	=	(4)	-	(1)
Seedling/sapling	4.9/17.5)	=	(27)	=	(102)	=	(5)	=	(43)	=	(7)	=	(34)	=	(15)	=	(25)
Sapling/pole	(10.5/8.9)	-	(37)	=	(51)	=	(9)	=	(16)	=	(13)	=	(18)	-	(15)	=	(17)
Pole/immat. open	(27.6/13.7)	=	(178)	=	(89)	=	(45)	=	(38)	=	(50)	=	(31)	=	(83)	=	(20)
Pole/immat. closed	(25.2/13.7)	=	(140)	=	(49)	=	(35)	=	(22)	=	(40)	=	(15)	=	(65)	=	(12)
Mature open	(10.9/14.2)	=	(72)	=	(65)	=	(18)	=	(23)	=	(21)	=	(23)	=	(33)	=	(19)
Mature closed	(16.3/9.9)	=	(73)	=	(52)	-	(11)	=	(15)	=	(29)	=	(23)	=	(33)	=	(14)

[1] percent available (Corduroy Creek/Star Meadows)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

Deer generally used vegetation types equal to availability in both complexes during all seasons (Table 17). No types were used more than expected during any season or when pooled across seasons. The only type avoided in the pooled sample was sapling/pole in Corduroy Creek. Natural and artificial grass/forb types in Corduroy Creek were used less than expected during some seasons; howeve, these types occurred only in small quantities.

Among the remaining habitat components, few types were used significantly more or less than expected and there was little evidence suggesting seasonal shifts in habitat use (Tables 18-23). Those habitat classes used more or less than expected generally followed results from macro-analyses. For instance at Corduroy Creek, areas furthest from riparian habitats were avoided in spring (Table 18). Northerly and westerly aspects and steeper slopes were avoided during some seasons (Tables 19 and 20). Few significant relationships existed for the road components.

Diel Habitat Use.—Changes in habitat use between day and night periods generally consisted of movement by deer to and from cover and open areas. At Corduroy Creek, deer apparently moved out into more open areas at night as use of open timber decreased and both natural and artificial grass/forb areas increased (Table 24). However, as with aerial data the sample of relocations in the latter types was extremely low, as was the amount of habitat available. Also at Corduroy Creek, deer used both seedling/sapling and sapling/pole less than available during both day and night.

At Star Meadows, deer used all types equal to availability except for an increased use of sapling/pole at night.

Use Based on Remote Camera Survey.—Data recorded during the 1991 Jul/Aug camera survey at Corduroy Creek (Tables 25-27) did not always concur with micro-habitat data from summer aerial surveys conducted in this same area (Tables 16-23).

Topographically, camera data showed a preference by deer for steeper slopes (Table 25), contrary to aerial data. However, data from the camera survey also suggested that deer preferred the 1402- to1462- m elevation zone was and used all aspects in aproportion equal to availability (Table 25). This was similar to results based on data from aerial surveys during summer.

Another difference between the camera survey and aerial data was in use of vegetation and riparian components. Camera data indicated that open mature timber was the only preferred vegetation type, open pole/immature was avoided (Table 26). Aerial data indicated these types were used equal to availability during summer. Camera data also indicated that the zone closest to a riparian area was used less than available while the 100-200 m zone was used more than available. Data from micro-analysis indicated all zones were used equal to availability.

Camera data showed areas close to open roads were used greater than available and areas far from closed roads were used equal to availability (Table 27). Aerial data for the time showed deer used these areas equal to and greater than expected, respectively.

Food Habits

Results from rumen analysis indicated that whitetails in the study area primarily were browsers, feeding selectively on leaves, buds, and small twigs (Appendix Table 30). Browse occurred in all rumen samples at volumes comprising 47, 66, and 82% of spring, summer, and fall samples, respectively. Grass-like plants accounted for most of the additional volume in spring; forbs, including leaves and fruits, made up much of the remaining summer volume.

The most abundant species by both percent occurrence and volume was pachistima which accounted for over 25% of the total volume of rumen contents in all 3 seasons. Other browse

Table 18. Use versus availability of riparian (distance from in meters) habitat component for Corduroy Creek (CC) and Star Meadows (SM) from pooled and seasonal data.

Distance from (m)		Pooled				Spring				Summer				Fall			
			CC		SM		CC		SM		CC		SM		CC		SM
0-100	(21.1/29.3)[1]	=[2]	(132)[3]	=	(183)	=	(27)	=	(76)	=	(45)	=	(74)	=	(60)	=	(33)
100-200	(15.8/16.7)	=	(82)	=	(74)	=	(22)	=	(37)	=	(26)	=	(26)	=	(34)	-	(11)
200-300	(15.5/15.7)	=	(102)	-	(62)	=	(26)	-	(21)	=	(29)	=	(23)	=	(47)	=	(18)
300-400	(12.5/12.1)	=	(75)	=	(65)	=	(16)	=	(28)	=	(25)	=	(25)	=	(34)	=	(12)
400-500	(10.2/9.6)	=	(50)	=	(62)	=	(13)	=	(28)	=	(16)	=	(19)	=	(21)	=	(15)
500-750	(13.9/12.6)	=	(73)	+	(98)	=	(18)	=	(32)	=	(18)	=	(29)	=	(37)	+	(37)
≥ 750	(10.8/4.0)	-	(37)	=	(16)	-	(5)	=	(9)	=	(5)	=	(13)	=	(19)	=	(2)

[1] percent available (Corduroy Creek/Star Meadows)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

Table 19. Use versus availability of aspect habitat component for Corduroy Creek (CC) and Star Meadows (SM) from pooled and seasonal data.

Aspect		Pooled				Spring				Summer				Fall			
			CC		SM		CC		SM		CC		SM		CC		SM
East	(14.0/11.5)[1]	=[2]	(98)[3]	=	(67)	=	(21)	=	(25)	=	(32)	=	(23)	=	(45)	=	(19)
Northeast	(14.5/9.7)	=	(75)	=	(50)	=	(11)	=	(18)	=	(27)	=	(19)	=	(37)	=	(13)
North	(3.1/10.4)	=	(21)	=	(44)	=	(2)	-	(12)	=	(6)	=	(18)	=	(13)	=	(14)
Northwest	(2.9/11.5)	=	(8)	-	(46)	=	(3)	=	(17)	=	(2)	-	(12)	=	(3)	=	(17)
West	(7.9/10.8)	-	(20)	=	(44)	=	(8)	=	(17)	=	(6)	=	(21)	=	(6)	-	(6)
Southwest	(24.0/11.0)	=	(127)	=	(60)	=	(33)	=	(29)	=	(42)	=	(22)	=	(52)	=	(9)
South	(17.2/10.0)	=	(106)	=	(66)	=	(25)	=	(28)	=	(27)	=	(23)	=	(54)	=	(15)
Southeast	(12.8/14.1)	=	(76)	+	(113)	=	(21)	=	(48)	=	(22)	=	(39)	=	(33)	=	(26)
No Aspect	(3.7/10.9)	=	(20)	=	(74)	=	(3)	=	(37)	=	(8)	=	(24)	=	(9)	=	(13)

[1] percent available (Corduroy Creek/Star Meadows)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

species found in high occurrence

Table 20. Use versus availability of slope habitat component for Corduroy Creek (CC) and Star Meadows (SM) from pooled and seasonal data.

Slope (%)		Pooled				Spring				Summer				Fall			
		CC		SM		CC		SM		CC		SM		CC		SM	
0-5	(3.7/11.1)[1]	=[2]	(21)[3]	=	(68)	=	(5)	=	(35)	=	(10)	=	(23)	=	(6)	=	(10)
6-10	(7.3/12.5)	=	(43)	=	(79)	=	(7)	=	(36)	=	(15)	=	(25)	=	(21)	=	(18)
11-15	(11.5/13.4)	=	(76)	=	(98)	=	(19)	=	(36)	=	(29)	=	(38)	=	(28)	=	(24)
16-20	(16.2/14.2)	=	(99)	=	(84)	=	(26)	=	(43)	=	(31)	=	(22)	=	(42)	=	(19)
21-25	(19.5/14.3)	=	(119)	=	(73)	=	(27)	=	(27)	=	(34)	=	(31)	=	(58)	=	(15)
26-35	(28.8/21.9)	=	(149)	=	(114)	=	(33)	=	(41)	=	(37)	=	(47)	=	(79)	=	(26)
36-50	(12.0/11.3)	-	(42)	-	(40)	=	(10)	-	(12)	=	(15)	=	(15)	-	(17)	=	(13)
≥ 51	(1.0/1.2)	=	(2)	=	(4)	-	(0)	=	(1)	=	(10)	-	(0)	-	(1)	=	(30)

[1] percent available (Corduroy Creek/Star Meadows)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

Table 21. Use versus availability of road habitat component for Corduroy Creek (CC) and Star Meadows (SM), regardless of being open or closed, from pooled and seasonal data.

Distance from (m)		Pooled				Spring				Summer				Fall			
		CC		SM		CC		SM		CC		SM		CC		SM	
0-100	(33.6/43.5)[1]	=[2]	(163)[3]	=	(234)	=	(36)	=	(96)	=	(60)	=	(86)	=	(67)	=	(52)
100-200	(19.6/22.9)	=	(118)	=	(126)	=	(26)	=	(49)	=	(34)	=	(49)	=	(58)	=	(28)
200-300	(12.2/15.3)	=	(65)	=	(72)	=	(13)	=	(35)	=	(16)	=	(25)	=	(36)	=	(12)
300-400	(8.5/9.1)	=	(44)	=	(46)	=	(11)	=	(18)	=	(12)	=	(14)	=	(21)	=	(14)
400-500	(6.7/5.6)	=	(38)	=	(44)	=	(13)	=	(20)	=	(9)	=	(17)	=	(16)	=	(7)
500-750	(9.3/3.6)	=	(39)	+	(38)	=	(7)	=	(13)	=	(14)	=	(10)	=	(18)	=	(15)
750-1000	(6.0/*)	=	(46)	*		=	(12)	*		=	(16)	*		=	(18)	*	
≥ 1000	(4.1/na)	=	(38)	na		=	(9)	na		=	(11)	na		=	(18)	na	

[1] percent available (Corduroy Creek/Star Meadows)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations
* combined with class above

Table 22. Use versus availability of open road habitat component for Corduroy Creek (CC) and Star Meadows (SM), regardless of being open or closed, from pooled and seasonal data.

Distance from (m)			Spring				Summer				Fall			
			CC		SM		CC		SM		CC		SM	
0-100	(14.4/25.2)	(31.2/34.4)[1]	=[2]	(20)[3]	=	(43)	=	(53)	=	(64)	=	(19)	=	(31)
100-200	(10.3/18.1)	(19.7/21.9)	=	(11)	=	(39)	=	(35)	=	(42)	=	(27)	=	(15)
200-300	(8.2/15.8)	(12.5/16.6)	=	(8)	=	(44)	=	(17)	=	(24)	=	(12)	=	(23)
300-400	(6.3/11.7)	(8.2/10.9)	=	(6)	=	(24)	=	(15)	=	(17)	=	(16)	=	(12)
400-500	(5.5/9.8)	(6.9/8.1)	=	(7)	=	(28)	=	(11)	=	(25)	=	(14)	=	(12)
500-750	(10.3/11.9)	(8.8/6.8)	=	(17)	=	(43)	=	(12)	=	(21)	=	(27)	=	(26)
750-1000	(9.8/4.5)	(5.4/1.3)	=	(14)	=	(9)	=	(13)	=	(8)	=	(30)	=	(8)
≥ 1000	(35.3/3.0)	(7.3/*)	=	(44)	-	(1)	=	(16)	*		=	(107)	-	(1)

[1] percent available (Corduroy Creek/Star Meadows)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations
* combined with class above

Table 23. Use versus availability of closed road habitat component for Corduroy Creek (CC) and Star Meadows (SM), regardless of being open or closed, from pooled and seasonal data.

Distance from (m)			Spring				Summer				Fall			
			CC		SM		CC		SM		CC		SM	
0-100	(20.7/23.1)	(3.5/12.9)[1]	=[2]	(17)[3]	=	(61)	=	(12)	=	(27)	=	(49)	=	(30)
100-200	(15.1/17.0)	(4.0/11.3)	=	(24)	=	(36)	=	(4)	=	(26)	=	(44)	=	(32)
200-300	(13.4/15.7)	(5.1/12.2)	=	(19)	=	(34)	=	(7)	=	(27)	=	(35)	=	(20)
300-400	(11.5/12.2)	(6.0/10.7)	=	(14)	=	(22)	-	(4)	=	(21)	=	(24)	=	(17)
400-500	(10.6/10.5)	(7.4/10.7)	=	(12)	=	(27)	=	(15)	=	(26)	=	(23)	=	(9)
500-750	(16.3/14.1)	(15.9/19.6)	=	(19)	=	(33)	=	(24)	=	(39)	=	(40)	=	(16)
750-1000	(6.7/5.1)	(13.2/11.9)	=	(9)	=	(7)	=	(16)	=	(22)	=	(16)	=	(4)
≥ 1000	(5.7/2.1)	(44.9/10.7)	=	(13)	=	(11)	=	(90)	=	(13)	=	(21)	-	(0)

[1] percent available (Corduroy Creek/Star Meadows)
[2] – use < availability; = use equal availability; + use > availability
[3] number of telemetry locations

included various huckleberry species, spiraea, and prince's pine. Prince's pine was the only browse species other than pachistima to make up greater than 10% volume.

Typically forbs were difficult to identify and no attempt was made to identify grasses. Fireweed was the only forb making up more than 10% volume.

In contrast to the limited number of forbs (8) identified in rumen samples, 32 different species were located in vegetation plots (Appendix Table 31). Thirty-six browse species were found in vegetation plots compared to 20 found in rumen samples. However, some plants found in rumen samples could not be identified at all, others were identified only to the genus level.

Pachistima, huckleberry, and spiraea were frequently found in vegetation plots-as well as in rumen samples. However, species such as rose, buffaloberry, queen's cup beadlily, and Oregon grape occurred in over 30% of the vegetation plots, but were infrequent in rumens if at all. Arnica, strawberry, and beargrass were forbs found in over 30% of the vegetation plots but had limited if any occurrence in rumens.

Table 24. Use versus availability of vegetation habitat component for Corduroy Creek (CC) and Star Meadows (SM) complexes during day/night periods of 24-hr telemetry sessions.

		Corduroy Creek		Star Meadows	
		Day/night		Day/night	
Natural grass/forb	(0.9/11.1)[1]	-/=[2]	(0/1)[3]	=/=	(20/11)
Artificial grass/forb	(1.1/16.6)	-/=	(0/2)	=/=	(37/21)
Shrub/hardwood	(2.7/11.5)	=/=	(14/7)	=/=	(25/11)
Seedling/sapling	(4.9/18.5)	-/-	(1/0)	=/=	(21/12)
Sapling/pole	(10.6/9.9)	-/-	(11/5)	-/=	(5/9)
Pole/immature open	(27.6/13.0)	+/=	(93/47)	=/=	(19/9)
Pole/immature closed	(25.2/4.4)	-/=	(33/32)	=/=	(3/3)
Mature open	(10.9/9.7)	=/=	(24/16)	=/=	(16/5)
Mature closed	(16.3/5.3)	=/=	(34/13)	=/=	(14/6)

[1] percent available (Corduroy Creek/Star Meadows)

[2] – use < availability; = use equal availability; + use > availability

[3] number of telemetry locations

Table 25. Use versus availability of slope, aspect, and elevation habitat components1 from Jul/Aug 1991 camera survey in Corduroy Creek.

Slope (%)				Aspect				Elevation (m)			
6-10	(5)[2]	=[3]	(8)[4]	East	(35)	=	(78)	1341-1402	(25)	-	(23)
11-15	(15)	-	(16)	Northeast	(20)	=	(43)	1403-1462	(20)	+	(65)
16-20	(20)	=	(35)	Southwest	(20)	=	(29)	1463-1524	(25)	=	(42)
21-25	(15)	=	(24)	South	(5)	=	(7)	≥ 1525	(30)	=	(54)
26-35	(20)	=	(35)	Southeast	(15)	=	(19)				
36-50	(25)	+	(66)	No aspect	(5)	=	(8)				

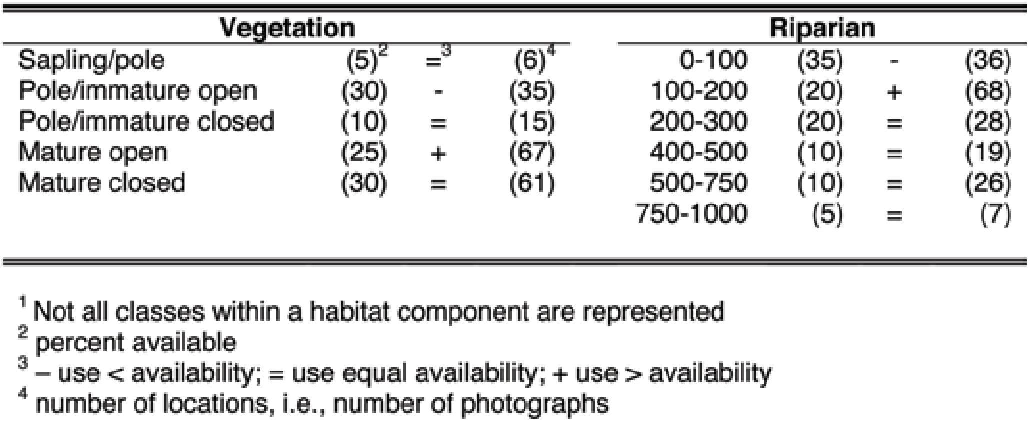
[1] Not all classes within a habitat component are represented

[2] percent available

[3] – use < availability; = use equal availability; + use > availability

[4] number of locations, i.e., number of photographs

Table 26. Use versus availability of vegetation and riparian (distance from in meters) habitat components1 from Jul/Aug 1991 camera survey in Corduroy Creek.



Vegetation				Riparian			
Sapling/pole	(5)[2]	=[3]	(6)[4]	0-100	(35)	-	(36)
Pole/immature open	(30)	-	(35)	100-200	(20)	+	(68)
Pole/immature closed	(10)	=	(15)	200-300	(20)	=	(28)
Mature open	(25)	+	(67)	400-500	(10)	=	(19)
Mature closed	(30)	=	(61)	500-750	(10)	=	(26)
				750-1000	(5)	=	(7)

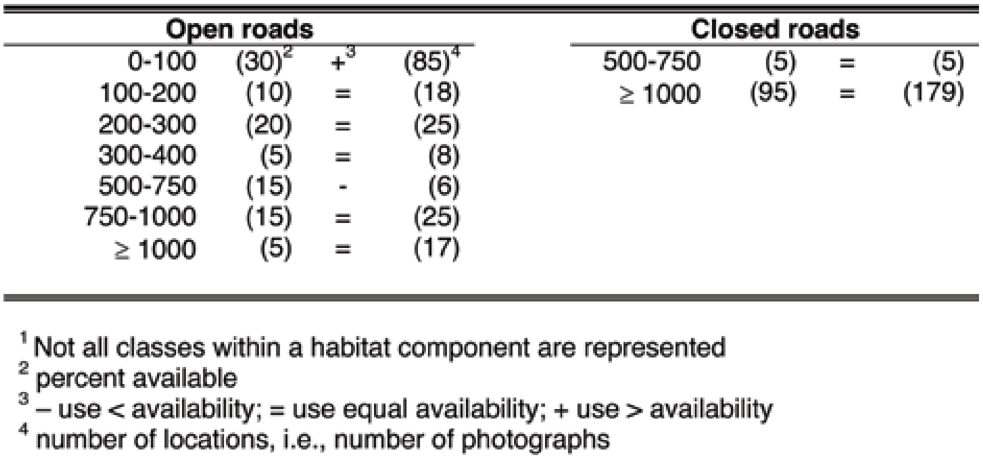
[1] Not all classes within a habitat component are represented

[2] percent available

[3] – use < availability; = use equal availability; + use > availability

[4] number of locations, i.e., number of photographs

Table 27. Use versus availability for open and closed road (distance from in meters) habitat components1 from Jul/Aug 1991 camera survey in Corduroy Creek



Open roads				Closed roads			
0-100	(30)[2]	+[3]	(85)[4]	500-750	(5)	=	(5)
100-200	(10)	=	(18)	≥ 1000	(95)	=	(179)
200-300	(20)	=	(25)				
300-400	(5)	=	(8)				
500-750	(15)	-	(6)				
750-1000	(15)	=	(25)				
≥ 1000	(5)	=	(17)				

[1] Not all classes within a habitat component are represented

[2] percent available

[3] – use < availability; = use equal availability; + use > availability

[4] number of locations, i.e., number of photographs

Section 4: Discussion

Patton (1992) defined habitat as the environment of and the specific place where an organism lives. The components that make up habitat fall into two categories: fixed-stable and dynamic-variable (Hamlin and Mackie 1989). Fixed-stable components are those in which change occurs only slowly, over long periods of time, if at all. These include the geographic location (longitude and latitude) of the site being considered as well as the general characteristics of topography, climate, soil, and vegetation associated with that location. The fixed-stable components determine how well an area meets the morphological, physiological, and behavioral constraints or requirements of deer.

Dynamic-variable components are those that change more frequently, annually, and/or over periods of years. These include weather and forage variability, predation and hunting pressure, land use, and inter- and intra-specific competition. The dynamic-variable components influence seasonal and annual habitat suitability. The dynamic-variable component of greatest concern in this study was land use, i.e., the influence of human activities such as timber harvesting and road building.

Although fixed-stable habitat components associated with a particular environment or place may not change very rapidly over time, they can vary dramatically in space. For instance, the location of the Tally Lake District is obviously fixed as are general topographic, climatic, edaphic, and vegetative features associated with the area (see Study Area section). However, each of these components varies locally throughout the district and deer need to seek out and exploit the most beneficial set, or complex, of habitat components to meet their survival, growth, and reproductive needs. Also, deer needs vary by season and sex and age; hence, use of habitat components will vary accordingly.

While selecting the best combination of fixed-stable components, deer also must contend with the ever-changing dynamic-variable components. Deer that return to the same summer range every year may find that the previous winter's heavy snowfall has left fawning areas flooded, or an overwinter cutting operation may have eliminated hiding cover or reproductive habitat. Thus, while deer tend to exhibit strong fidelity to specific summer ranges and resources, at least some adaptability is necessary for longterm survival.

Movements and Distribution

White-tailed deer wintering on the Bowser Lake area followed a migration pattern similar to that described for mule deer both in the Bridger Mountains of southwest Montana (Pac et al. 1991) and the Salish Mountains west of my study area (Stansberry 1991). Some deer remain on the winter range yearlong. These would include deer which made occasional small movements off the winter range. Others, including deer that migrated off the winter range but did not summer on the Tally Lake District, migrated relatively short distances. Still others, including deer that spent at least part of the summer on the district, migrated long distances. This study considered habitat use patterns only for those deer that summered on the district; however, some deer wintering in the same area summered at lower elevations near the Stillwater River.

Migration routes of deer summering in the northern and southern portion of the study area had some similarities although I noted important differences regarding distances travelled and terrain traversed. For the Clearwater River area of northern Idaho, Baumeister (1992) suggested that topography along the migration route influenced timing of migration. There, deer followed two major migration routes. Those crossing higher ridges and greater travel distance left summer range earlier to avoid deep snow. Deer following a shorter route along the river migrated later.

Differences in timing and pattern of migration in relation to topography and other habitat features also have been reported for mule deer in the northern Rocky Mountains (Pac et al. 1989, Pac et al. 1991). In the Missouri River Breaks of northcentral Montana, occurrence and patterns of migration in mule deer were related to topography and other environmental characteristics of areas individual deer inhabited (Hamlin and Mackie 1989).

Deer summering in the northern portion of the Tally Lake District traveled further but over a somewhat easier route than deer summering in the southern portion. Individuals summering in the Corduroy Creek complex traveled along bottomland and south facing slopes adjacent to Good Creek and a wide area of low elevation between Logan and Good Creeks. This lower-elevation route allowed deer to remain on summer range longer as deep snow was less likely to impede migration although use of this route may carry some ultimate cost. The Good Creek bottom is a relatively narrow corridor, essentially a bottleneck for deer migrating to and from summering areas to the west. Development and logging might easily disrupt this corridor and thus, force deer to migrate through more open terrain or higher ridges subject to greater accumulation of snow.

Deer migrating to and from Star Meadows often traversed a shorter distance although the route crossed higher ridges. Some deer traveled along Logan Creek and around Tally Lake over terrain similar to that followed by deer from Good Creek. However, most moved across the higher ridges (1525 m) of Lost Creek and Reid Divides. These deer left summer range earlier than other deer before heavy snowfall (again similar to the Clearwater River study). The benefit of this movement pattern to deer was that, while the ridgetops had been extensively cutover, it is a broad area wherein, unlike the Good Creek bottom, deer can alter their movements to select secure cover. Also, many deer migrated over the relatively undisturbed Tally Mountain.

White-tailed deer distribution on the district coincided with the location of major streams. Few deer were found greater than 1 km from a perennial creek. Only one radioed deer summered in the higher elevations in the center of the study area; Fox Mountain. Similarly, no deer summered on the high western and northwestern edge of the study area between the Tally Lake and Fortine and Fisher River Ranger Districts, possibly a result of the extended distance from the Bowser Lake wintering area. However, four deer trapped on summer range in the Corduroy Creek drainage migrated across these higher elevation ranges to other winter ranges.

Macro-Habitat Use

Habitat selection on the Tally Lake District appeared driven by the need to maximize use of high quality forage and hiding cover. Sites that offer both forage and cover together typically are preferred over sites which meet these needs individually (Surling and Vohs 1979, Baumeister 1992). Seasonal change in behavior, including distribution, movements, and habitat types selected, allow deer to take advantage of changes in forage and cover availability (Kohn and Mooty 1971). On the Tally Lake study area, the best strategy to simultaneously meet food and cover needs was through use of major riparian complexes initially, and a variety of sites, particularly uplands, later in the season. Use of specific elevations, slopes, aspects, and preference or avoidance for roads was largely a result of the relationship with riparian areas.

Elevation was by far the strongest component affecting habitat selection in all seasons. However, elevational classes were arbitrary divisions. Other studies in the northern Rockies have documented whitetail use of similar elevations (Kamps 1969, Slott 1979, Leach 1982, Baumeister 1992). What changed from one elevation zone to the next was the complex of specific habitat components, especially the proximity of riparian areas and the type and abundance of certain vegetation classes.

The majority of relocations of radio-collared deer occurred in the Star Meadows and the Corduroy Creek complexes. These complexes were associated with 2nd and 3rd order drainages and contained wet meadow areas composed primarily of natural grass/forb and shrub/hardwood vegetation. Major 2nd and 3rd order drainages coincidentally were located within the 1159- to 1524-m elevation zone on the Tally Lake District. Elsewhere in the northern Rockies, wet meadow complexes may occur at higher or lower elevations and yet be attractive to deer depending on local environmental features. Higher elevations were not necessarily poor deer habitat in this study because of elevation alone; they were simply further from riparian—preferred—vegetation complexes.

A relationship between elevation, riparian sites, and vegetation is further highlighted by

seasonal movement patterns. The greatest use of riparian complexes occurred during spring when these sites provided an abundant source of high-quality forage; higher elevations lagged phenologically, perhaps because of delayed snowmelt. Food habits data showed that grass, typically found in greater abundance in riparian areas, made up a substantial portion of the diet of deer only in spring. White-tailed deer use of more open habitats in spring has been documented in other studies. White-tailed deer in Minnesota used fields more in spring/early summer and late summer when grass was most succulent (Kohn and Mooty 1971). Whitetails in northcentral Montana also used open, bunchgrass vegetation types most during spring (Martinka 1968).

During early summer, deer were able to make greater use of the Star Meadows bottom as flooding subsided. However, in late summer the meadow bottom and other low elevation sites began to dry up and deer began to move to higher elevations and farther from riparian foraging areas. Food habits at this time shifted from a browse/grass to a browse/forb diet.

A shift in habitat selection from wet bottomlands to higher-elevation mesic timbered areas continued during fall. Rumen analysis indicated that many whitetail food items, including pachistima, spiraea, prince's pine, and vaccinium were more prevalent in fall, concurrent with movement by deer to higher timbered habitats. Similarly other studies of whitetail food habits during summer and fall, particularly in non-agricultural areas, typically show a high proportion of use of understory shrubs. Forage species commonly utilized by deer on the Tally Lake District, e.g., pachistima, snowberry, serviceberry, red-osier dogwood, and rose, also have been reported to be important in other studies from the northern Rockies (Roberts 1956, Thilenius 1960, Martinka 1968, Kamps 1969).

Niche separation by sex and age classes has been demonstrated to occur in whitetail populations for a variety of physiological and behavioral reasons (Beier and McCullough 1990). In my study, adult females accounted for three-fourths of the relocations and hence they dictated patterns of habitat use. Males and subadult females, with much smaller sample sizes, generally used the various habitat components equal to availability. This indicated adult females, more typically those with fawns, were more selective in habitat use.

Riparian areas provided spatial isolation and fawning cover as well as succulent high-quality forage needed by does dispersed throughout each meadow complex in late spring. Although no fawns (< 6 mos) were equipped with radio transmitters, residents around Star Meadows often reported sightings of newborn fawns in and around the willow/grass ecotone. Studies documenting fawn habitat selection indicate that deer prefer dense shrubby cover for bedding and nursing (Black et al. 1976, Dood 1978, Huegel et al. 1986, Ozoga and Verme 1986). Riparian complexes on my study area were generally comprised of a combination of dense shrubby cover and open grass/forb meadows and thus provided primary reproductive sites for adult females.

In summer adult females need high quality forage for lactation (Verme and Ullrey 1984) and hiding cover for fawns (Huegel et al. 1986). At this time adult females would be more prone to continue using lower-elevation riparian areas. Males and subadult females with other physiological and behavioral needs could tend to use sites more distant from riparian areas in summer. In fall as riparian areas became more desiccated, adult females with fewer restrictions from nursing fawns also would tend to select habitats further from riparian areas and at higher elevations. Hence, although not shown statistically, movement from riparian bottomlands to higher-elevation timbered sites probably began and subadult females with adult females following later in the season.

Two composite habitat preference maps (Figs. 5 and 6) further highlight the importance of riparian areas to deer. In the first, elevation overshadows the importance of riparian habitat. Deer clearly preferred the area between elevations of 1159 and 1524 m. The only evidence of any influence from other components occurred where vegetation, roads, aspect, or riparian habitat had strong enough influence to change an over- or under-used area to equal. Stronger evidence for riparian habitats appeared when elevation was removed as in the second figure. As a result, preferred areas occurred along many major streams and in large tracts of pole/immature timber away from roads. Deer selection of major streams occurred because of the preference for sites within 100 m of riparian habitat and natural grass/forb and shrub/hardwood vegetation often found in association with riparian areas.

A close association between white-tailed deer and riparian areas typified summer habitat selection by the species in northwestern Montana and perhaps elsewhere in the northern Rocky Mountains and Great Plains. Leach (1982) determined that whitetail does in the Swan and Clearwater Valleys selected for riparian areas. She did not discuss preference for specific elevational zones although her study area ranged in elevation from 1060 to 1575 m, similar to the Tally Lake area. Krahmer (1989) noted that whitetail home ranges in the North Fork of the Flathead River were closer to water, and hence riparian areas, than random points. Although he too noted no particular preference for elevational zone by deer, his study area was located between elevations of 1067 and 1289 m, only slightly lower than the Tally Lake study area.

In addition to natural grass/forb and shrub/hardwood, two other vegetation classes, deer selected open and closed pole/immature timber on the study area. The occurrence of these was not necessarily related to either elevation or riparian areas, but rather, they possessed characteristics that might help meet food and cover needs of deer at certain times of the year. Small natural openings in both, along with the more open canopy of the open pole/immature timber type potentially allowed enough light for shrub growth. open timber frequently included thick patches of large shrubs, primarily alder and buffaloberry, for hiding cover. Krahmer (1989), Pauley (1990), and Baumeister (1992) documented pole timber as a preferred type elsewhere in the northern Rocky Mountains and attributed this preference to improved availability of forage and cover.

Seasonal use of pole/immature timber stands followed the logic discussed earlier. That is, as riparian meadows became desiccated, deer moved to higher elevations seeking higher quality forage and cover. Pole/immature stands apparently met these needs as deer selected them more during summer and fall than during spring.

Three of four avoided vegetation classes, i,e, artificial grass/forb, seedling/sapling, and sapling/pole, typically resulted from timber harvest on upland sites, which were not generally associated with riparian habitats. Hence, one would expect deer selecting for riparian areas to avoid these classes.

However, I noted some seasonal differences. For instance, in spring when open forage areas were most lush, deer used artificial grass/forb and seedling/sapling types equal to availability.

Sapling/pole, a potential source of cover, was used equal to availability in spring and summer. Seedling/sapling, although generally avoided, was used equal to availability during all three seasons. Thus, whereas deer avoided all three managed timber types at some point, a more detailed analysis suggested that in certain circumstances they were used and provided some forage and/or cover.

Deer use of three managed timber types at various percentages of occurrence within 90-ha habitat blocks also suggested that under certain conditions or levels of occurrence deer may use or select them. However, this analysis did not consider deer use of specific types but use of complexes within a 90-ha area. Thus, detecting or prescribing specific levels of occurrence of each or all three relative to selection or avoidance of an area was not possible.

Among the three managed timber classes, deer apparently used, or at least showed less avoidance of areas interspersed with grass/forb vegetation more than areas characterized by the other two types or classes. Deer more often avoided or only preferred seedling/sapling and sapling/pole classes when present at low densities although deer also preferred sapling/pole at high densities. When these classes were combined, deer exhibited even less preference for managed timber areas. This analysis suggested that deer did make use of areas containing interspersed small amounts of managed timber, especially where units were spatially separated. These data generally support Baumeister's (1992) suggestion that whitetails in the northwest are not early successional animals, at least in terms of traditional interpretation of deer-habitat relationships

Closed mature timber, the fourth vegetation class avoided by deer, often occurred near riparian areas. However, unlike the pole/immature timber class where sufficient light penetrated for understory growth, the dense closed canopy of mature stands precluded understory growth in many areas. As a result, the type provided very limited forage or cover for deer.

Old growth timber as designated by the USFS was very limited on the study area (R. Kuennen, USFS, personal communication). Hence, this type was combined with mature timber. Deer possibly used old growth portions of mature timber differently, but availability of old growth and limited number of relocations by deer in the type would make any assessment difficult.

Deer use of early seral and mature timber stages has been widely debated. Clearcutting enhances habitat for deer by increasing edge areas has often been suggested (Kirchhoff et al. 1983) and provides deer with a fresh, productive forage source not available under the dense canopy of mature timber (Wallmo and Schoen 1980). However, these conclusions vary by specific location and season.

In the Oregon Coastal Range, Crouch (1974) observed that black-tailed deer (*O. hemionus columbianus*) use of an area peaked shortly after clearcutting and declined thereafter. He suggested that deer use of new clearcuts was so strong that sustained clearcutting was the best way to maintain deer numbers. On my study area, deer made some use of new clearcuts, but either natural forage and cover areas were sufficiently available to satisfy deer or other habitat needs consistent with the behavior and physiology of whitetails using the area were overriding of the increased forage alone. Also, clearcut vegetation in the Salish Mountains possibly matures, or becomes dry and of low quality, sooner than other areas.

Krahmer (1989), noted that whitetail home ranges in the North Fork of the Flathead River contained more early seral conifer than did random areas. However, his analysis involved random locations within home ranges and could have included areas of unused habitat. Home ranges of deer on my study area often included islands of early seral stages that were unused.

Other studies have suggested that deer use of clearcuts occurs mainly around the edge. In New Brunswick, whitetail use of a clearcut declined with distances from the cover along the edge (Drolet 1978). Smaller cutting units lessened this effect.

Black-tailed deer in southeast Alaska used old growth areas more than neighboring clearcuts with no increase in use of edge along the clearcut (Wallmo and Schoen 1980, Kirchhoff et al. 1983). However these studies were based solely on winter habitat use.

Generally, white-tailed deer on the Tally Lake area failed to use early seral conifers more than available, and clearcutting appeared to offer little benefit. In my study, the use of early seral conifers was low although deer apparently tolerated and occasionally utilized those stands when interspersed with other preferred vegetation classes. Indeed, in some areas where natural foraging sites and hiding cover were lacking, early seral managed stands may have attracted and benefitted deer depending on location, size, and perhaps other attributes of the cutover and adjoining uncut areas.

One common suggestion for improving or maintaining whitetail habitat is creating diversity through interspersion of vegetation types. Kohn and Mooty (1971) recommended a good distribution of disturbed and young deciduous stands. Data from my study indicated that deer responded positively to diversity within a 20-90 ha area. The fact that complexes of five and 8-9 different vegetative classes in a given area were preferred corroborates the concept that whitetails usually will not do well in large tracts of undisturbed timber. However, this does not necessarily indicate that deer need or will greatly benefit from interspersion of various age clearcuts or disturbed sites with uncut timber. My analyses indicated that stands of open and closed immature timber interspersed with riparian habitat containing natural grass/forb and shrub/hardwood openings would be preferred deer habitat.

Although interrelationships among elevation, riparian habitat, and vegetation were primary in habitat use and selection, other physical factors including aspect, slope, and roads also were involved, though more indirectly.

For example, the lowest and highest elevations on the study area were creek bottoms and ridgetops, respectively. These areas naturally are relatively flat and lack aspect except in general orientation of the topography of which they are part. Steeper slopes were more characteristic of midslope areas at moderate elevations. Northerly aspects tended to be relatively mesic and capable of supporting denser canopy mature timber, whereas the drier southerly aspects generally were more open.

As noted earlier, deer tended to use lower elevations in spring and move higher in fall in association with phenological changes in vegetation. Concomitantly, deer moved from lesser to steeper slopes. Cooler, northerly aspects were avoided during spring probably due to residual snow and slower greenup of vegetation. However, beyond spring aspects generally were used equal to availability.

The combined road component was a strong factor in habitat selection during all seasons. However, when considered as open or closed, deer generally showed no preference or avoidance for roads except within the first 100 m.

Micro-Habitat Use

Patterns of habitat selection at the micro-level were less specific. Once deer selected their summer home range, use of individual habitat classes within components apparently was less important. However, it should be noted that because only deer using specific areas were considered in analyses, the sample of relocations was smaller, and hence wider Bonferroni confidence intervals were obtained yielding fewer significant results (clear differences).

While at the macro-level deer were drawn to riparian complexes, such as Star meadows and Corduroy Creek, once in these areas deer did not select specific habitats close to the riparian feature itself. For instance, the zone 0-100 m from riparian areas, which was preferred during all seasons in macro-analysis, was used equal to availability once deer were within the complex. Natural grass/forb and shrub/hardwood vegetation types, which generally make up riparian bottoms, were not preferred at either complex. Deer used even the lower elevations that encompass the riparian bottoms equal to availability.

Although deer exhibited little preference or avoidance of habitat classes within composite home ranges in my study, others have documented some significant results. Krahmer's (1989) combined group model for micro-habitat use within core areas indicated that deer selected areas with higher pole densities, farther from trails, and had more edge and gentler slopes.

Micro-habitat use analyses included diel use of the vegetation components. Habitat use studies only rarely have included diel telemetry surveys. In eastern Montana, whitetails on the Yellowstone River bottomlands moved from the security of riparian tree and shrub cover during the day to open alfalfa fields at night (Dusek et al. 1989). The only significant difference between day and night at Star Meadows was an increased deer use of sapling/pole vegetation at night. This was a somewhat curious result as sapling/pole is a type that might provide dense cover but one would expect it to receive more use during the day.

At Corduroy Creek, deer followed a pattern similar to that found along the Yellowstone River (Dusek et al. 1989). Open pole/immature was used less at night while use of open foraging areas increased. However, the sample size for use of both grass/forb classes was very small.

Data from the camera survey at Corduroy Creek showed some differences in habitat use compared with traditional radiotelemetry techniques. Most obvious was the deer preference shown by the camera survey for open mature timber and avoidance of open pole/immature. These types were both used equal to availability based on aerial surveys. One reason for this possibly was camera placement along active deer trails where most deer were moving when recorded. Aerial radio-locations were recorded only during the day when deer were probably bedded in dense cover.

Section 6: Management Implications And Recommendations

The Multiple Use-Sustained Yield Act of 1960 states, "It is the policy of Congress that the national forests be administered for outdoor recreation, range, timber, watershed, and wildlife and fish purposes." Additional laws have strengthened the role of fish and wildlife in the planning process on national forests, e.g., The Sikes Act Extension of 1974, The Forest and Rangeland Renewable Resources Planning Act of 1974, The National Forest Management Act of 1976. The Tally Lake Ranger District of the Flathead National Forest is thus mandated to be managed for both timber production and white-tailed deer habitat.

Results of this study indicated that while deer are relatively widely distributed and adaptable, there are portions of the district and habitat variables that are significantly more important to deer than other areas and variables. Unfortunately, without strong population data it is difficult to determine the present status of the deer population on the district and what effect any habitat alteration may have on the population. However, based on findings from this study, some general conclusions and recommendations are possible.

The most important general conclusions to forest management regarding deer habitat selection on the Tally Lake District are that early seral coniferous forest vegetation was of little benefit to deer generally although riparian areas and adjacent uplands containing pole/immature timber were very important. These riparian complexes are core habitats or centers of spatial distribution for whitetailed deer in northwest Montana. Not all riparian areas are critical or at least were not critical at the time of this study. Many creeks on the district are used very little by deer, perhaps because the total habitat/environment complex (including hunting) with which they were associated prohibited deer from becoming established. Deer and habitat management should involve identifying and protecting those important riparian complexes which contain the preferred topographic, climatic, vegetative, and land use components discussed.

Deer showed such a strong preference for riparian areas and the vegetation types associated with them that these sites should be disturbed as little as possible. At least a 100-m buffer of vegetation, including natural grass/forb, shrub/hardwood, and mixed timber should be maintained around riparian areas. Timber harvests, except perhaps limited selective cutting, should not occur within this buffer.

As deer moved from riparian areas in late summer and fall, they often selected pole/immature uplands. While this vegetation is highly productive for timber and often cut, it can be of great benefit to deer and should be maintained, particularly when found near riparian complexes, such as Star Meadows and the corduroy Creek areas.

While deer appeared to benefit little from early seral vegetation, they also made very little use of closed mature timber. Focusing cutting in this type would be less disturbing to deer than logging in pole/immature typed which were preferred.

White-tailed deer distribution was heavily centered at elevations between 1159 and 1646 m and on aspects from east to southwest. These topographic features, although not inherently important to deer, provided the habitat complexes that were important. However, not every location within these elevational and aspect zones need be preserved. Rather, special attention should be paid to riparian areas, pole/immature uplands, and possibly some mature timber areas as travel corridors. Locating timber sale boundaries away from zones of particular importance to deer use would be less disturbing.

In general, roads apparently did not negatively effect deer distribution and use except immediately adjacent to the road. Thus, while limiting, or closing, roads in the most preferred areas could be beneficial to deer in the immediate vicinity, its effect on deer over a wider area appears limited. Also, closing roads could prohibit distribution of hunters and lead to heavier deer harvests in areas with greater access.

In general, sites within the study area where cutting would have minimal effect on white-tailed deer include (1) elevations above 1646 m and below 1159 m, (2) northerly and westerly aspects, (3) ridgetops and other sites more than 750 m from riparian habitat, (4) areas where previous cuts have returned to the pole/immature stage, and (5) large blocks of mature timber.

Future Research Needs

This study compared to many others had a rather large sample of radio-collared deer and relocations over three field seasons. However, because the majority of radio-marked deer were adult females, limited information was available on habitat use by males and subadult females, as well as differences between the three groups. Continuation of the study with more emphasis on males and subadult females could provide more information on niche separation and yield a more complete picture of habitat use on the Tally Lake District.

Another shortfall of this and most habitat studies is that it took place over a relatively short period of time when few habitat changes occurred. Deer use of timbered habitat was compared to use of cutover areas in different parts of the district. A better assessment of timber harvesting effects on deer would be obtained by monitoring deer use of an area before, during, and after a major timber operation. Such an opportunity exists on the Tally Lake District. The Corduroy Creek drainage was relatively free of cutting units during the time I monitored deer there. However, major portions of the drainage are scheduled to be harvested by 1994. Continuation of this study during and well after timber harvesting in this area should yield some significant results and provide a better picture of the effect of timber harvesting on whitetails.

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Appendix

Table 28. Longterm and yearly climate data from Olney, MT, 48° 33' north longitude, 114° 34' west latitude, elevation 967 m

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Year: 1962-1989													
Average daily maximum temp. (C)	-1.7	2.8	7.2	13.3	18.9	23.3	27.2	27.2	20.0	12.8	3.3	-2.2	12.7
Average daily minimum temp (C)	-11.1	-9.4	-6.1	-2.8	1.1	4.4	6.1	5.6	1.1	-2.8	-5.6	-10.0	-2.5
Total monthly precip. (cm)	7.3	5.7	4.1	3.2	5.0	7.4	3.9	3.7	3.7	3.3	6	6.1	59.4
Total monthly snowfall (cm)	83.8	63.0	39.1	7.2	0	0	0	0	0.2	3.0	41.7	85.5	323.5
Year: 1989													
Average daily maximum temp. (C)	-0.5	-4.4	4.4	15.0	17.8	24.4	28.9	24.4	21.1	12.2	3.9	-1.7	12.1
Average daily minimum temp (C)	-10.5	-17.8	-6.7	-3.3	1.7	5.5	7.2	6.7	1.1	-2.8	-3.3	-7.2	-2.5
Total monthly precip. (cm)	4.9	3.8	6.2	5.3	6.2	8.1	8.4	10.9	4.2	2.4	10.1	6.5	77.0
Total monthly snowfall (cm)	99.1	89.0	149.9	27.9	0	0	0	0	0	0.8	20.3	53.3	440.3
Year: 1990													
Average daily maximum temp. (C)	0.2	1.1	8.2	15.2	16.3	21.7	27.6	27.2	26.4	10.3	3.5	-6.2	12.6
Average daily minimum temp (C)	-7.4	-11.9	-6.9	-1.8	1.8	4.7	7.3	7.4	1.3	-2.3	-4.1	-15.6	-2.3
Total monthly precip. (cm)	10.7	5.9	0.9	4.9	13.7	5.4	6.0	4.8	0.1	7.1	10.6	12.8	82.9
Total monthly snowfall (cm)	149.9	20.3	7.6	na[1]	0	0	0	0	0	7.6	Na	262.9	Na
Year 1991													
Average daily maximum temp. (C)	-5.2	6.2	4.8	13.6	17.4	20.4	28.1	29.6	23.6	13.8	1.5	-1.1	12.7
Average daily minimum temp (C)	-13.3	-6.0	-6.8	-3.2	2.1	4.8	6.8	6.2	0.2	-6.4	-7.1	-7.5	-2.5
Total monthly precip. (cm)	6.9	1.2	1.0	1.2	7.9	7.7	2.2	1.1	1.3	1.5	7.6	2.9	42.5
Total monthly snowfall (cm)	243.8	4.3	22.9	Na	0	0	0	0	0	15.2	104.1	30.5	Na

[1] na=data missing or incomplete

Table 29. Radio-collared white-tailed deer monitored on the Tally Lake Ranger District, Flathead National Forest, summers 1989-1991

Deer no.	Frequency	Sex	Age when radioed	Date radioed	Summer Location	Status-cause of death
88001	150.875	F	4	01/28/88	Listle/Sheppard Creeks	Died 11/01/90 unknown
88010	151.340	F	3	01/29/88	Gergen/Good Creeks	Lost Signal 07/14/89
88014	151.160	F	3	02/02/88	Good/Miller Creeks	Alive
88016	150.730	F	1	02/02/88	Good Crk/Adams Mountain	Alive
88019	150.690	F	3	02/03/88	Good Creek	Alive
88020	150.915	F	1	12/21/88	Martin Creek	Died 11/01/91 Harvest
88021	151.760	F	2	02/03/88	Martin Creek	Lost signal 05/03/91
88045	151.175	F	4	02/14/91	Star Face	Alive
88063	151.579	F	7	03/07/88	Griffin Creek	Died 10/20/90 Unknown
89070	150.275	F	2	12/20/88	Corduroy Creek	Alive
89083	150.150	F	4	12/22/88	Good Creek/Adams Mountain	Alive
89084	150.430	F	3	12/22/88	Corduroy Creek	Died 11/28/91 Harvest
89087	150.035	F	3	12/29/88	Logan Creek	Alive
89089	151.739	M	2	12/29/88	Alder/Corduroy Creeks	Alive
89090	151.190	M	1	12/29/88	Sheppard Creek	Died 11/16/89 Harvest
89092	150.210	F	7	12/29/88	Alder Creek	Alive
89095	151.273	M	1	12/30/88	Fox Mountain	Alive
89096	150.170	F	1	12/30/88	Alder/Corduroy Creeks	Alive
89097	150.060	F	8	12/30/88	Corduroy Creek	Died 04/15/89 Unknown
89098	150.495	F	4	01/05/89	Miller/Good Creeks	Alive
89099	150.219	M	3	01/05/89	Listle Creek	Died 08/20/90 Unknown
89100	150.570	F	2	01/05/89	Fox Mountain	Alive
89117	150.510	F	1	01/16/89	Nelson Creek/Adams Mtn	Alive
89119	150.650	F	3	01/16/89	Corduroy Creek	Alive
89124	150.670	F	1	01/17/89	Miller Crk/Adams Mtn	Alive
89134	150.410	F	8	01/18/89	Corduroy Creek	Died 08/05/90 Unknown
89148	150.585	F	3	01/26/89	Logan Creek	Alive
89149	150.450	F	1	01/26/89	North Evers Creek	Alive
89157	150.010	F	2	01/27/89	Evers Creek	Died 11/08/89 Unknown
89163	150.995	F	2	02/07/89	Logan Creek	Alive
89180	150.712	F	3	02/05/91	Reid Creek	Dropped Collar 9/91
89188	150.360	F	2	02/15/89	Griffin Creek	Alive
89189	150.260	F	3	02/15/89	Martin Lakes	Died 11/09/91 Harvest
89195	151.525	F	3	02/16/89	Alder Creek	Alive

Table 29. continued

Deer no.	Frequency	Sex	Age when radioed	Date radioed	Summer Location	Status-cause of death
89197	150.115	F	6	02/17/89	Sheppard Creek	Alive
89224	150.240	F	5	02/28/89	Good Creek	Alive
89230	150.420	F	6	03/01/89	Star Face	Died 11/04/89 Harvest
89237	150.760	F	1	03/02/89	Star Face	Alive
90243	150.320	F	4	08/09/89	Griffin Creek	Alive
90244	150.060	F	6	08/13/89	Star Face	Died 11/26/89 Unknown
90245	150.390	F	3	08/17/89	Griffin Creek	Alive
90246	151.349	F	1	08/26/89	Griffin Creek	Alive
90252	150.640	F	2	01/09/90	Logan Creek	Alive
90255	151.375	M	1	01/10/90	Griffin Creek	Died 11/22/90 Harvest
90257	150.070	M	2	01/10/90	Sheppard Creek	Alive
90263	150.540	F	1	01/12/90	Star Face	Dropped Collar 5/91
90271	150.660	F	1	01/13/90	Star Face	Alive
90304	150.599	F	1	01/26/90	Sanko Creek	Died 10/25/90 Harvest
90310	151.462	M	2	01/31/90	Alder Creek	Died 11/18/91 Harvest
90314	150.780	F	9	01/31/90	Logan Creek	Alive
90326	150.890	M	1	02/02/90	Reid Creek	Died 11/13/90 Harvest
90331	150.750	F	4	02/02/90	Good Creek	Alive
90381	150.230	F	3	01/23/91	Martin Creek	Alive
90388	150.800	F	9	02/24/90	Good/Nelson Creeks	Died 06/14/90 Mt Lion
90389	151.190	M	1	05/26/90	Sheppard Creek	Died 10/29/90 Harvest
90390	150.830	F	1	05/26/90	Star Face	Alive
90392	150.570	M	0	05/28/90	Sheppard Creek	Dropped Collar 6/90
91393	150.280	F	1	06/19/90	Griffin Creek	Alive
91394	150.800	F	6	06/21/90	Griffin Creek	Dropped Collar 8/90
91395	150.010	F	9	06/24/90	Griffin Creek	Alive
91396	150.620	F	2	07/19/90	Star Face	Alive
91397	150.770	F	3	07/19/90	Upper Martin Creek	Alive
91398	151.610	F	3	07/19/90	Corduroy Creek	Died 10/22/90 Harvest
91399	150.850	F	9	07/20/90	Corduroy Creek	Alive
91400	150.980	F	4	08/01/90	Upper Martin Creek	Alive
91401	150.800	F	3	08/06/90	Gergen/Corduroy Creeks	Alive
91403	150.310	F	0	01/03/91	Gergen Creek	Alive

Table 29. continued

Deer no.	Frequency	Sex	Age when radioed	Date radioed	Summer Location	Status-cause of death
91406	150.865	M	3	01/03/91	Evers Creek	Alive
91420	151.570	M	1	01/09/91	Shorts Meadow	Dropped Collar 7/91
91425	150.890	F	1	01/10/91	Tally Mountain	Alive
91427	150.599	F	1	01/10/91	Star Face	Alive
91429	150.935	F	0	01/10/91	Logan Creek	Alive
91433	151.609	F	1	01/15/91	Sheppard Creek	Died 10/28/91 Harvest
91435	450.100	F	1	01/15/91	Good/Nelson Creeks	Alive
91437	150.925	M	1	01/15/91	Swanson Creek	Dropped Collar 9/91
92527	151.540	F	2	06/25/91	Corduroy Creek	Alive
92542	150.460	F	3	06/17/91	Gergen/Corduroy Crks	Alive
92543	150.420	F	1	06/18/91	Corduroy/Good Crks	Alive
92544	150.540	F	2	06/19/91	Corduroy Creek	Alive
92546	150.890	M	4	06/20/91	Corduroy/Good Creeks	Lost Signal 8/91
92547	150.250	F	2	06/21/91	Corduroy Creek	Alive
92548	150.900	F	3	06/25/91	Corduroy Creek	Alive
92549	150.630	F	6	06/25/91	Corduroy Creek	Alive
92552	150.480	F	5	07/15/91	Gergen/Fortine Crks	Alive
92553	150.160	F	4	07/18/91	Corduroy Creek	Alive
92554	150.875	F	2	07/18/91	Good/Corduroy Creeks	Alive

Table 30. Percent occurrence (O) and volume (V) of forage species found in rumen samples.

	Spring (*n* = 13)		Summer (*n*= 9)		Fall (*n* = 9)	
Browse	O	V	O	V	O	V
Pachistima myrsintes	69	21	78	28	100	49
Artostaphylos uva-ursi	38	2			11	tr
Vaccinium spp.	54	2	22	2	44	6
Pseudotsuga menziesii	31	2	33	2	78	3
Spiraea densiflora	54	2				
Chimaphila umbellate	54	3	22	1	33	16
Linnaea borealis	15	tr	11	tr		
Unknown browse	31	2	22	4	33	2
Cornus spp.	8	2	22	2		
Amalanchier anifolia	15	1	33	6	22	1
Ceanothus spp.	23	2				
Symphoricarpus spp.	8	tr	22	4	22	2
Salix spp.	15	5	22	8		
Betula glandulosa			11	tr		
Rosa spp.			33	3	11	1
Alnus spp.	8	1	22	3	11	1
Pinus contorta	23	1	11	1	22	tr
Shepherdia canadensis					11	tr
Ribes spp.	8	1	11	1		
Brioria spp.	8	tr				
Juniperus communis			22	1		
Berberis repens					11	1
Total Browse	100	47	100	66	100	82
Forbs						
Unknown forbs	46	12	33	5	22	2
Trifolium spp.			11	tr		
Epilobium angustifolium			33	14	11	2
Xerophyllum tenax			11	3		
Antennaria racemosa			11	1		
Arnica spp.			11	1		
Senicio spp.			11	4	11	4
Clintonia uniflora					11	tr
Viola spp.	8	tr				
Total Forbs	46	12	100	28	44	8
Grass	100	39	67	5	67	9
Mushrooms			22	tr	33	tr

Table 31. Species present and percent occurrence in 100 vegetation plots centered on randomly selected deer locations.

Species	Common Name	% 0ccurrence
	Trees	
Psuetosuga menziesii	Douglas fir	45/47[1]
Pinus contorta	lodgepole pine	63/28
Abies lasiocarpa	subalpine fir	28/16
Larix occidentalis	western larch	45/6
Picea englemannii	Engleman spruce	7/34
Thuja plicata	western redcedar	3/3
Tsuga heterophylla	western hemlock	2/2
Abies grandis	grand fir	2/0
Populus tremuloides	quaking aspen	2/2
Populus trichocarpa	black cottonwood	1/2
	Small trees/large shrubs	
Alnus tenuifolia	thinleaf alder	26
Alnus sinuata	Sitka alder	*
Acer glabrum	Rocky Mountain maple	11
Amelanchier alnifolia	serviceberry	15
Salix spp.	willow	21
Rhamnus alnifolia	buckhorn	4
Cornus stolonifera	red-osier dogwood	9
Betula glandulosa	bog birch	2
Taxus brevifolia	Pacific yew	2
Prunus virginiana	common chokecherry	1
	Shrubs	
Vaccinium spp.	huckleberry	66
Rosa spp.	rose	37
Spiraea betulifolia	spiraea	48
Pachistima myrsinites	pachistima	42
Potentilla fruiticosa	shrubby cinquefoil	3
Juniperus communis	common juniper	13
Symphoricarpus albus	common snowberry	25
Ribes lacustre	prickly currant	10
Shepherdia canadensis	buffaloberry	31
Lonicera involucrate	bearberry honeysuckle	6
Menziesia ferruginea	mock azalea	4
Arctostaphylos uva-ursi	kinnikinnick	23
Chimaphila embellata	prince’s pine	28
Linaea borealis	twinflower	48
Rubus parviflorus	western thimbleberry	4
Berberis repens	creeping Oregon grape	37
	Herbaceous plants	
Achillea millefolium	Ccommon yarrow	25
Actaea rubra	baneberry	1
Anaphalis margaritacea	pearly everlasting	5
Antennaria racemosa	pussy-toes	6
Aralia nudicaulis	wild sarsaparilla	1
Arnica cordifolia	heartleaf arnica	38
Arnica latifolia	broadleaf arnica	*
Aster spp.	aster	2
Clintonia uniflora	queen cup beadlily	10

Table 31. continued.

Herbaceous plants continued		
CornuscCanadensis	bunchberry dogwood	20
Epilobium angustilolium	fireweed	6
Fragaria vesca	woods strawberry	45
Fragaria virginiana	strawberry	*
Galium triflorum	sweetscented bedstraw	6
Geranium viscosissimum	sticky purple geranium	2
Heracleum lanatum	cow parsnip	4
Hieracium albertinum	western hawkweed	22
Hieracium albiflorum	white-flowered hawkweed	*
Osmorhiza chilensis	mountain sweet-cicely	5
Smilacina racemosa	false Solomon's seal	2
Smilacina stellata	starry Solomon's seal	11
Thalictrum occidentale	western meadowrue	16
Trillium ovatum	white trillium	1
Vicia americana	American vetch	1
Viola spp.	violet	17
Lupinus spp.	lupine	24
Campunula rotundifolia	harebells	10
Taraxacum officinale	dandelion	2
Calochortus spp.	mariposa	1
Carduusspp.	thistle	3
Xerophyllum tenax	beargrass	37
Trifolium spp.	clover	3
Equisetum spp.	joint grass	2
Bromus spp.	brome	67
Calamagrostis rubescens	pinegrass	*
Dactylis glomerata	orchard grass	*
Phleum pretense	timothy	*
Festuca spp.	fescue	*
Equisetum spp.	horsetails	2
Carex spp.	sedge	2

[1] overstory/understory

*trace

Addendum

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Acute Nutritional Stress in White-tailed Deer During the 1996/97 Winter in Northwest Montana^{TWS}

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Once every 200-300 years, maximum snow depth at Kalispell Airport reaches that recorded during, the 1996/97 winter. Once every 33 years, an equal number of consecutive snow cover days would be recorded. Ungulate overwinter survival depends on many factors, including winter severity and possessing the necessary fat reserves to meet increased thermoregulatory demands and offset nutritional stress caused by low quality forage. To assess the timing and degree of acute nutritional stress in white-tailed deer (Odocoileus virginianus), the percent (%) marrow fat content was determined using the oven-drying; technique for femurs collected from carcasses encountered during field work and along roadways from December 1996 to June 1997. We recorded sex and age, location, cause of death, and death date estimated to julian week. Cause of death was categorized as vehicle, predation, unknown, or natural (accidents and winter-kill). Percent marrow fat in adult females declined significantly through the winter for vehicle-kills (p = 0.000 1) but did not decline for those adult females dying of natural causes (p = 0. 19). In fawns, % marrow fat declined significantly through time for vehicle kills (P = 0.008) but not for natural deaths (p = 0.66). Fawn natural mortality commenced in late January whereas adult female natural mortality commenced in mid-February. Of those deer which died of natural causes, the marrow fat content averaged 72.4% (95% C.I. 65.7 - 79. 1) for fawns and 66.9% (95% C.I. 58.1 - 75.8) for adult females. Mean % marrow fat for fawns dying of natural causes was significantly less than for predator-kills (p = 0.02), but the difference was insignificant for adult females (p = 0. 10 8).

The Winter of 1996/97: What Did it Mean to Northwest Montana White-tailed Deer Populations?^{TWS}

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The most notable attributes of the 1996/97 winter were its duration and the record snow depths at all elevations. The collective success of individual ungulates in surviving the winter has important implications for population dynamics and herd management. We assess the role that winter 1996/97 played in shaping population dynamics for white-tailed deer (Odocoileus virginianus) using data from an ongoing research project in the Salish Mountains. Fawns began dying of natural, winter-related causes in late January. The monthly observed fawn: 100 adult ratio declined

significantly from. December to March (p = 0.02). The predicted fawn: 100 adult ratio in May was 1: 100 (S.E. 7.4). The number of fawns per 100 adults estimated from remote camera surveys declined 44% in the same period, likely declining, further because deer remained on winter range for another 7 weeks post survey. Adult female natural mortality began in mid-February. Of the radio-collared adult females which survived the hunting season and entered the winter, 26% died by June 1, 1997. Fifty nine percent of the adult female mortality occurred in animals cementum-aged 6.5 or younger. Migrant radio-collared deer confined themselves to winter range an average of 159 days (range 126-185), or 8 weeks longer than the average of all previous years. Most deer entered winter range on November 23, 1996 and some stayed until May 27, 1997. Additional results and observations are discussed. Under the most ideal future conditions, it could take 3-5 years for populations in the Salish Mountains to rebound to levels prior to the severe winter event, even longer in areas which experienced harsher winter conditions.

OFF-SITE IMPACTS OF RURAL SUBDIVISION ON WINTERING WHITE-TAILED DEER IN NORTHWEST MONTANA: COULD MAN'S BEST FRIEND BE WILDLIFE'S WORST ADVERSARY?^TWS

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Impacts of rural subdivision are often considered at the project scale rather than in the greater context of the landscape. Impacts to wildlife and wildlife habitat extend beyond the boundaries of the actual development site. We demonstrate that off-site impacts to wintering white-tailed deer (Odocoileus virginianus) increase as the number of home sites increases. Between 1988- 97, white-tailed deer were systematically surveyed on public land using remotely-triggered cameras in a 29 km^2 grid. Incidental photographs of free-ranging domestic dogs (Canis familiaris) were obtained, starting in 1991. The number of septic permits, reflecting occupied home sites in a buffer of private land surrounding the survey area, was summarized for the

years 1974-1997. The number of permits issued varied annually, but the cumulative total increased significantly through time ($P < 0.000$). The average number issued per year increased from 3.2 in 1989-92 to 9.4 in 1993-97 ($P = 0.014$). Concurrently, the number of unique dogs photographed per unit effort (x100) increased from 0.21 in the period 1989-92 to 1.3 in 1993-97 ($P = 0.027$). Linear regression demonstrated that the total number of unique dogs photographed per year (TDOG) was significantly related to the cumulative number of septic permits in the buffer ($P < 0.029$). Dogs were photographed up to 2.5 km from the nearest home site. Some dogs were explicitly photographed chasing deer. Individual dogs were photographed in multiple years and on multiple occasions within a single year. One in particular was photographed on 6 occasions at 5 different sites in 15 days. Two of those sites were 3 km apart. The majority of dogs wore collars (88.5%) and were photographed during daylight (65.9%). Implications will be discussed.

ADULT FEMALE WHITE-TAILED DEER IN MONTANE ENVIRONMENTS: WHAT ARE WE MANAGING AND WHAT ARE WE COUNTING? TWS

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Despite their popularity as a big game animal and prevalence in the hunter bag, comparatively little is known about white-tailed deer response to various hunter harvest strategies in montane environments. Prior to developing an adaptive management protocol for white-tailed deer, it is important to evaluate the regulation packages and validate their anticipated outcomes. In addition, it is important to validate a monitoring protocol. One objective of the Northwest Montana Deer Research Project is to investigate the effects of various regulation types and variable harvest opportunities for antlerless deer. Telemetry was used to determine adult female harvest rates in each of two hunting districts (HD) under various regulation packages and variable antlerless harvest opportunity through time. Whereas the regulations pertaining to the general deer "A" license were consistent for each district, they did change through the 1988-2000 period of study. Antlerless harvest opportunity also changed during the period, though the changes were systematically adopted in only one HD during the hunting seasons 1991-1996, while the other HD served as a control. This permitted comparisons through space and time. Biologists frequently utilize results from the annual telephone harvest survey to monitor trends in total deer harvest for various age and sex categories. Estimates for antlerless harvest (number of deer harvested) were compared to estimated harvest rates of telemetered does. Abiotic factors were also considered. The presentation will summarize preliminary results.

Forage Use By White-tailed Deer In Northwest Montana From An Historical Perspective

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Abstract

We evaluated forage use by white-tailed deer (*Odocoileus virginianus*) that occupy montane forests of northwest Montana over a period spanning the 1940s through the 1990s. Several studies provided food habit information, but most came from the Thompson River, Swan Valley, Kootenai River, and Salish Mountains. Use of Douglas-fir (*Pseudotsuga menziesii*) and Oregon grape (*Berberis repens*) by deer during winter was consistent over the 60-year period despite habitat alteration or loss due to construction of large hydroelectric facilities, logging and other silvicultural treatments, and fire suppression. The relative importance of conifer browse and low-growing species such as Oregon grape probably varied with amount of winter snowpack. Douglas-fir and Oregon grape probably have not represented emergency or starvation forage as traditionally believed but rather a very important dietary component on deer winter ranges in northwest Montana. Availability and use of arboreal lichens by deer might also increase digestibility and importance of browse available to deer during winter. Further, the observed pattern of forage use over time was consistent with a strategy of overwinter survival that favors energy conservation whereby value of overhead cover might override that of forage in winter resource selection.

Key words: forage use, northwest Montana, *Odocoileus virginianus*, white-tailed deer

Introduction

White-tailed deer in the northern Rocky Mountains occupy winter ranges consisting of cutover stands of Douglas-fir along lower valleys and foothills. Human manipulation of these lower-valley montane forests by fire dates back some 6-10 thousand years before Euro-American settlement (Arno 1980, Barrett and Arno 1982). However, a combination of logging and fire from the 1880s to the 1930s altered a large portion of these stands to a mixture of remnant old conifers and second-growth timber dominated by shade tolerant species such as Douglas-fir and shrublands (Pengelly 1963). Additionally, increasingly effective fire suppression through the 1990s probably influenced structure and composition of traditional winter ranges used by white-tailed deer.

Timber harvest with associated road construction has been a primary use of public and corporate timberlands in northwest Montana. From the mid-1940s through the mid-1950s, private and public resource managers maintained that whitetails had exceeded forage carrying capacity on many of these ranges (e.g., Cole 1959) and cited heavy use of conifers as a symptom of overbrowsing (e.g., Adams 1949, Neils et al. 1955). During the 1960s, a common belief held that opening up the forest canopy across the northern tier of the species' range would increase winter browse for white-tailed deer by increasing abundance of shade-intolerant seral shrubs (Krefting 1962, Pengelly 1963). However, short- and long-term effects that logging might have on deer distribution and resource selection were left largely to speculation and an assumption that white-tailed deer depended heavily on early seral communities to meet yearlong forage needs. For example, efforts to mitigate habitat loss resulting from construction of Libby Dam in the early 1970s (Campbell 1971, 1972, Campbell and Knoche 1973) included treating alternative winter ranges to stimulate growth of deciduous shrubs such as serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginianus*), and bitterbrush (*Purshia tridentata*) to make these sites more attractive to both white-tailed and mule deer (*O. hemionus*).

Hildebrand (1971), Leach (1982), and Mundinger (1984) in the Swan River Valley in northwest Montana and Baumeister (1992) in north-central Idaho reported a close relationship between white-tailed deer and mature, late seral forest. All these studies essentially challenged a concept that categorized white-tailed deer as an animal primarily associated with early succession; these studies and that of Morgan (1993) on summer range in the Salish Mountains suggested that deer preferred mature forests that provided both cover and forage to those that provided either forage or cover alone. In contrast, Hicks (1990) reported that deer preferentially used younger pole-sized timber stands under severe winter conditions in the Thompson River Valley in northwest Montana.

This paper documents forage use by white-tailed deer throughout northwest Montana to determine if such use might have changed in the past 60 years related to (1) a combination of forest management practices and fire suppression policies, and (2) a perceived upward trend in white-tailed deer populations in northwest Montana.

Study Area And Methods

Descriptions of the respective areas and food habit information were previously reported for the Swan-Clearwater by Hildebrand (1971), Janke (1977), and Mundinger (1980) and for the Kootenai in the vicinity of Libby Dam by Campbell (1972). Dusek et al. (2005) described two winter ranges in the Salish Moutains for which Morgan (1993) reported food habits of deer on one of the associated summer ranges.

The early work from the Thompson River included examination of rumen contents of deer found dead in the field, and forage composition was based on weight of consumed material (Montana Fish and Game Department, unpublished). Later analyses of forage use by white-tailed deer, except those for winter in the Salish Mountains, were based on rumen samples collected incidental to the various studies; relative abundance of individual items was determined by an aggregate volume method (Martin et al. 1946).

Winter food habits of white-tailed deer from the Salish Mountains were evaluated from microhistological analysis of fecal composite (Department of Natural Resource Sciences, Washington State University, Pullman) collected on the Bowser and Murphy winter ranges (Dusek et al. 2005) during 1998 and 1999. A sample consisted of three pellets from each of 20 pellet groups. Eight samples were collected, one each during January and February, during 1998 and 1999, from both winter ranges.

Results

The 1940s and 1950s

The earliest known documentation of forage use by white-tailed deer in northwest Montana came from the Thompson River in the early 1940s (Montana Department of Fish and Game, unpubl. data). Douglas-fir occurred in all four rumens examined from the Thompson River during February and March 1942 and was the most abundant item in the diet by average weight (21%). An interpretation of these data hinted at overbrowsing of deciduous shrubs, such as bitterbrush and serviceberry, which managers at that time typically expected to be available to deer during periods of deep snow; this work also reported heavy use of "black lichen" as it became available through blow-down and cuttings. Browsing of conifers by deer was widely documented in northwest Montana by the late 1940s, and managers widely regarded such a foraging pattern indicative of degraded deer range (Adams 1949).

Weckworth (1959) reported consistent use of conifer browse in the Swan Valley from October 1957 through April 1958; among conifer species, deer used Douglas-fir most consistently and most prominently during January and February. He noted that

Oregon grape was the most abundant item in the diet (Table 1) and attributed this to mild winter conditions with relatively light snowfall.

The 1960s and 1970s

Douglas-fir and Oregon grape were major items in the winter diet during the period (Table 1) as reported from rumen analyses of white-tailed deer in the Kootenai drainage following construction of Libby Dam (Campbell 1972) and in the Swan Valley (Mundinger 1980). The relative volume of Douglas-fir in rumens was greatest during periods of heavy snowpack, whereas Oregon grape received its greatest use during years when winter and spring were relatively snow-free.

Managers believed that deer would respond favorably to an increase in shrub production following large-scale timber harvests, but undesirable shrubs would begin to reduce production of “good” browse species within 10-15 years following logging (Pengelly 1961). Treatment of forested communities to stimulate increased abundance and nutritional quality of seral shrubs considered to be important to deer dominated early efforts to mitigate loss of winter range along the Kootenai although Campbell (1972) noted that deer continued to rely primarily on Douglas-fir, other conifers, and other taxa that retained chorophyll through winter, e.g., Oregon grape and horsetail (*Equisetum* spp.).

The 1980s and 1990s

Winter.—Foods used by white-tailed deer on the Bowser and Murphy winter ranges during the relatively mild winters of 1998 and 1999 (determined from micro-histological analysis) are summarized in Table 2. Browse, including both conifers and deciduous species, accounted for about 91 percent of the winter diet (Table 2). Oregon grape and Douglas-fir were by far the most abundant items occurring among samples across both areas during both years. Their combined use accounted for an average of 79 percent among all winter samples (Table 2). Abundance of other browse species was low although willow (*Salix* spp.) and lodgepole pine (*Pinus contorta*) consistently occurred in the diet both spatially and temporally. Grasses and grass-like plants accounted for about 5 percent of the winter diet. Lichens occurred among samples for both years and from both winter ranges. These most likely represented two genera of lichens occurring in the *Pseudotsuga menziesii* Series (Eversman, personal communication 2004): *Bryoria* spp. and *Usnea* spp. Project personnel observed deer using Bryoria either from camera surveys or by direct observation. Periodic winds seemingly increased availability of this taxon through blow down.

Spring/summer/autumn.—Food habits of white-tailed deer for spring-autumn 1989 and 1990 were previously reported by Morgan (1993) for a portion of the Salish Mountains that included the Tally Lake District of the Flathead National Forest (Fig. 1). These findings offer additional evidence that browse dominated the yearlong diet of white-tailed deer in northwest Montana. Based on forage items used by deer during this period, these data further emphasized that deer foraged consistently under the forest canopy even during spring-autumn and probably made less use of early seral deciduous shrubs than one might expect.

Browse received less use during spring than in other seasons but still accounted for nearly half of the spring diet. During spring, grasses received their only significant use and accounted for most of the remaining volume among rumen samples (Fig. 1). The average volume of forbs among rumens increased from spring to summer and then declined from summer to autumn. Rumen samples for the autumn period were taken prior to 15 October; as such, these data reflect forage use only during early autumn and not that of late autumn when deer would probably increase their use of taxa that typically occur in the winter diet.

Among shrubs that contributed to the spring-autumn diet of deer in the Salish Mountains (Morgan 1993), pachistima (*Pachistima myrsintes*) accounted for ≥ 21 percent by volume among rumen samples collected during spring, summer, and autumn.

Table 1. Summary of winter food habits of white-tailed deer in Northwestern Montana from rumen analysis.

Study	Forage Class Composition (% of diet)				Top 5 species in the diet ranked by volume				
	Browse	Grasses	Forbs	Nonvascular	1	2	3	4	5
MDF&G 1942 (*n* = 3)[1]	71	9	0	13	Kinnikinnick	Douglas-fir	Lichen	Lodgepole pine	Other conifers
Weckwerth 1959 (*n* = 23)	91	2	7	0	Oregon grape	Twin -flower	Douglas-fir	Kinnikinnick	Pachistima
MDF&G 1950-70 (*n* = 62)	78	9	10	1	Oregon grape	Douglas-fir	Serviceberry	Equisitium	Lodgepole pine
Hildebrand 1971 (*n* = 23)	84	7	7	1	Oregon grape	Douglas -fir	Lodgepole pine	Ponderosa pine	Snowbrush ceanothus
Campbell 1972 (*n* = 16)	72	18	9	1	Douglas-fir	Oregon grape	Ponderosa pine	Cottonwood	Western larch
MDF&G 1970-75 (*n* = 91)	48	37	10	1	Equisitium	Douglas-fir	Oregon grape	Ponderosa pine	Serviceberry
Mundinger 1980 (*n* = 106)	91	2	5	2	Douglas-fir	Oregon grape	Lodgepole pine	Spruce	Common juniper
This Study[2]	91	5	2	2	Oregon grape	Douglas-fir	Willow	Lodgepole pine	Lichen

[1] Number of rumen samples collected

[2] Winter food habits from this study were from microhistological analysis (see Table 2).

Its use increased during spring through mid autumn. Other browse species used consistently throughout the spring-autumn period but accounted for ≤ 1 percent of the average volume for each season included huckleberry (*Vaccinium* spp.), Douglas-fir, princes-pine (*Chimaphila umbellata*), and serviceberry. Princes-pine and huckleberry received their greatest use during summer compared to spring and autumn.

Discussion

Our examination of forage use by white-tailed deer throughout northwest Montana over the past six decades leaves little doubt that second growth Douglas-fir in the foothills and lower drainages has provided key winter range for white-tailed deer in western Montana as suggested early on by Pengelly (1963). It is important to note that the predominance of Douglas-fir and Oregon grape in the winter diets of white-tailed deer was consistent in food habit studies from the 1940s through the 1990s (Tables 1 and 2). This time frame transcends a period of significant change in the forests of northwestern Montana including marked habitat loss resulting from construction of several large hydroelectric dams. Harvest patterns and fire exclusion have converted much of the late-seral forest communities to mid-seral forest communities, while invasion of noxious weeds has rapidly displaced native species throughout the

Table 2. Winter foods of white-tailed deer in the Salish Mountains, 1998-1999, from microhistological analysis of pellets from four sites across each winter range.

Deer Diets **Plant species**[1]	**BTWR** **1998**	**BTWR** **1999**	**MDWR** **1998**	**MDWR** **1999**	**Overall** **Mean**	**Rank**
Berberis repens (leaf)	58.10	33.43	52.23	53.28	47.29	1
Pseudotsuga menziesii	26.18	43.89	30.45	22.13	31.44	2
Salix spp. (stem)	0.85	2.30	0.83	2.23	1.79	3
Pinus contorta	0.83	1.45	3.80	1.23	1.66	4
Lichen	1.85	1.88	1.83	1.00	1.57	5
Poa spp.	0.63	1.73	0.08	2.40	1.49	6
Amelanchier alnifolia (stem)	0.00	1.01	0.75	1.60	1.00	7
Shepherdia canadensis	0.00	1.60	0.75	0.99	0.99	8
Vaccinium spp. (leaf)	0.28	0.40	0.48	1.83	0.87	9
Carex spp.	0.75	0.73	0.20	1.40	0.87	9
Salix spp. (leaf)	1.50	0.14	0.23	1.29	0.76	11
Moss	0.55	0.70	0.00	1.21	0.73	12
Juniperus spp.	0.98	1.23	0.08	0.33	0.69	13
Cornus stolonifera (leaf)	0.45	0.19	1.05	0.98	0.64	14
Other Shrub (stem)	0.08	0.98	0.63	0.55	0.63	15
Other grasses	0.83	0.83	0.23	0.29	0.55	16
Other forbs	0.60	0.36	0.78	0.51	0.52	17
Total	100.00	100.00	100.00	100.00	100.00	
Forage Class						
Total Conifers	28.60	48.38	34.55	23.74	34.56	
Total Shrub	61.78	42.53	60.78	64.85	56.22	
Total Grass	4.43	4.93	0.50	5.18	4.19	
Total Sedge/Rush	0.75	0.83	0.20	1.40	0.90	
Total Forb	1.75	0.73	1.63	2.09	1.50	
Total Ferns	0.10	0.00	0.43	0.04	0.10	
Nonvascular plants	2.40	2.58	1.83	2.21	2.30	

[1] Includes only those plants that comprise ≥ 0.5 % of the overall winter diet.

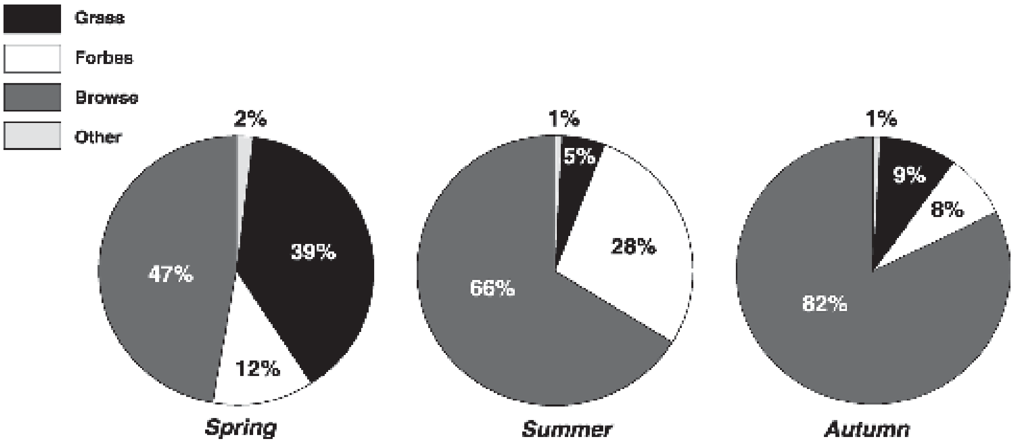

Figure 1. Use among forage classes by white-tailed deer in the Tally Lake District during Spring-Autumn based on data reported by Morgan (1993). Relative use of each forage class is expressed as a percent of the average total volume.

Pacific northwest (USDA Forest Service 1996). Douglas-fir and Oregon grape continue to dominate winter diets of deer, despite the extensive changes in forest structure and composition over the last 60 years. This, together with an upward trend in deer harvests (Dusek et al. 2005) over the same period suggests that these forage species do not and probably never represented emergency or starvation rations, but probably represented an important dietary component available to deer on winter ranges in this region.

Although early efforts to increase browse production through timber harvest, low-intensity burns, or other silvicultural treatments were based on a premise that deer would respond favorably to fragmenting continuity of forest canopy on winter ranges, such practices may have only reduced the shelter value of the habitat. For example, in Ontario deer did not noticeably respond to increased availability of browse following opening the canopy to develop cottage sites suggesting that shelter quality probably outweighed browse availability (Armstrong et al. 1983). Pauley et al. (1993) explained and predicted winter habitat selection in the context of energy budget for white-tailed deer in northern Idaho. Thus, when snow depth was < 30 cm deer strongly selected for lodgepole pine and Douglas-fir pole stands that provide relatively minimal snow interception and an abundance of 'preferred' forage (Pauley et al. 1993); however, during mid winter when snow depths often exceeded 40 cm, deer avoided openings and early successional stands and selected advanced forest age classes that provided more optimal snow conditions. Under such conditions we would expect white-tailed deer to increase their use of Douglas-fir and other browse that was readily available.

Although lichens occurred only as a small proportion of the total winter diet, they were a disproportionately important component of the winter food supply because of the synergistic effect they have on rumen function. High levels of digestible energy found in lichens increases the concentration of rumen protozoa many-fold, which results in an increased net utilization of nitrogen from other forage species (Ullrey et al. 1971). Studies of penned deer also found that a combination of energy and nitrogen supplements to a browse diet, although not changing overall digestibility of native forage species, significantly increased total forage intake when the supplement comprised as low as 10 percent of total dry matter intake (Ullrey et al. 1975). Thus, consumption of lichen likely increases nutritional status of wintering deer by increasing overall rumen function. Lichens also might be typically under-represented in dietary studies such as those reported in Table 1 because of their high and rapid digestibility (Bergerud et al. 1964). They are of disproportionate value in the winter diet of white-tailed deer relative to their composition in overall forage consumption.

Oregon grape and/or Douglas-fir are major winter food items for white-tailed deer in northwest Montana (Tables 1 and 2) and have been so for at least the last 60 years. Similar dietary patterns have been documented in the lower Clearwater-Blackfoot drainages of western Montana (Janke 1977, Slott 1980). Campbell (1972), Janke (1977) and Mundinger (1980) reported predominance of Oregon grape in the diet of deer in the Kootenai and Swan valleys during either mild winters with below-average snowfall or the portion of individual winters in which snowpack was minimal or absent; Douglas-fir dominated deer diets during periods of heavier snow accumulation. Thus, we conclude that the effect of winter snowpack on availability of Oregon grape determines forage selection between two primary forage species. These studies all point to a strategy of overwinter survival of white-tailed deer in northwest Montana that favors energy conservation whereby deer tend to be habitat specialists and forage generalists.

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