Habitat Selection by Mule Deer (*Odocoileus hemionus*) in southeastern British Columbia.

Prepared for: Columbia Basin Fish and Wildlife Compensation Program

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EXECUTIVE SUMMARY

Due to their importance as a game species, mule deer (*Odocoileus hemionus*) and their habitat preferences have been extensively researched. In British Columbia (B.C.), the timber industry is regulated in order to protect designated ungulate winter ranges that are viewed as critical for population growth. Despite the importance of ungulate winter range in forest harvest planning, few empirical mule deer habitat studies have been conducted in south-central B.C., and few exist in the literature. In the West Kootenay Region of B.C., mule deer winter range is defined as having timber greater than 81 yrs of age with 20% - 40% crown closure, depending on the specific biogeoclimatic subzone. However, winter habitat use is quite literally only half the picture when it comes to mule deer habitat management, summer habitat may be just as important to population maintenance and growth. We conducted radio telemetry on mule deer in south-central B.C. from 1997 to 2001, in order to clearly delineate and evaluate seasonal habitat use of mule deer in this region. We conducted both a univariate and multivariate analysis of telemetry data. The most striking result in our study was the strong selection of Spruce/Fir forests by both sexes during summer and for mixed coniferous/deciduous habitats during winter, preservation of which may be under valued in current timber harvest practices. Canopy closure affected only female winter home range selection. At a landscape scale, females sought winter habitats with 46-65% crown closure, and fewer stands with <25% closure compared to the available landscape. These values vary slightly from the level of crown closure (≤ 40%) designated for mule deer winter range in the Kootenay region of B.C., however both sexes sought older stands in summer and younger stands in winter, contrary to current ungulate winter range designation. In summer, mule deer bucks avoided shrub habitats, possibly in response to increased predation risk. The timber industry in B.C. has both an effect on, and is affected by, ungulate habitat use. Improper delineation of winter ranges could unnecessarily restrict timber harvest, while failing to provide mule deer with the habitat protection required for the population to thrive. Summer ranges, with the forage they provide and the relative risk of predation present, are likely as important to population growth and winter survival as winter ranges and should be managed as such.
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INTRODUCTION

Due to their importance as a game species, mule deer (*Odocoileus hemionus*) and their habitat preferences have been extensively researched (e.g. Mackie et al. 1998). Mule deer are nutritionally stressed during winter and therefore winter habitat use and survival have often been thought to restrict population growth (Wallmo 1980, Unsworth et al. 1999). The principle of protecting winter ranges in order to guard ungulate populations is reflected in the British Columbia (B.C.) forest industry, where winter ranges are comprehensively mapped and preserved (protected) based on a number of habitat variables including solar duration and snow interception (Armleder et al. 1994, Mowat et al. 2003, Government of British Columbia, Victoria B.C.).

Despite the recognized role of ungulate winter range in forest harvest planning, few empirical mule deer habitat studies have been conducted in south-central B.C., and few exist in the literature (e.g. Armleder et al. 1994, D’Eon 2001, Hudson et al. 1976). Rather, past policy has been based on local knowledge, industry reports, and habitat studies conducted in other parts of North America (see Mowat et al. 2003). In the West Kootenay Region of B.C., mule deer winter range is defined as having timber stands greater than 81 yrs of age with 20% - 40% crown closure, depending on the specific biogeoclimatic subzone (Mowat et al. 2003, Braumandl and Curran 1992).

Deer are adapted to tolerate restricted distribution and high densities during winter (Mackie et al. 1998:77). Torbit et al. (1985) suggested that winter ranges will always be incapable of meeting the nutritional requirements of resident deer, and therefore should be viewed simply as holding areas until summer ranges become available. The importance of summer habitat to ungulate populations should not be overlooked and was recently demonstrated. Cook et al. (2004) found that summer-autumn nutrition had significant impacts on both cow elk and their calves. Survival of cows was found to be as affected by fat reserves at the onset of winter as it was to winter nutrition. Winter survival of calves was directly related to their size at the onset of winter, and calves born to cows nutritionally stressed in summer ceased to grow by October, significantly lowering their chance of survival. The same relationship very possibly holds true for mule deer.
does and their fawns (Reale 1997). Summer and autumn nutrition are likely as important to mule
deer doe and fawn over-winter survival as they are to cow elk and their calves. In fact, Parker et
al. (1999) concluded that to black-tailed deer (Odocoileus hemionus sitkensis), fat reserves
accumulated during summer were “critical” to winter survival. The total number of deer in a
population may reach levels dictated by the quantity and quality of available summer habitat, as
well as, or even rather than, winter maintenance.

Most habitat use studies are based on one of three methods of measuring use vs. availability
(Thomas and Taylor 1990, Manly et al. 1993). The first method uses indirect measures of use
such as tracks, pellets, or browse to identify the intensity of species use (e.g. Boulanger et al.
2000); individuals are not recognized. The second and third methods are similar in that they
both use individually marked animals, but differ based on the scale at which availability is
measured (the first at the landscape scale, the second at the scale of each individual’s home
range). In all three cases it is assumed that the availability of each habitat type is known, and use
above availability is thought to convey preference. A variety of methods have been used to
analyze selectivity, Alldredge et al. (1998), Alldredge and Ratti (1986) and White and Garrot
(1990) provide reviews of the various statistical methods, their assumptions, and the common
violations of these assumptions.

Goodness of fit chi-squared analysis (Neu et al. 1974) is likely the most common statistical
method in use vs. availability studies. One criticism of this kind of preference study is that the
proportions of all habitat types sum to 1, thus avoidance and preference of two habitat types are
explicitly linked. For this reason, Aebischer et al. (1993) proposed a multivariate method where
available habitats are determined randomly. Multivariate analysis may also reduce the chance of
Type I errors by combining many variables into a single test, rather than a series of comparisons.
Univariate studies are also limited in their transference to other landscapes as the availability of
habitat types will almost certainly vary widely across any given landscape. A multivariate
analysis may shed light on the interaction of several habitat variables making the results more
applicable to a broader area. In addition to the more traditional univariate analysis (use vs.
availability) we applied a multivariate analysis to habitat variables in an attempt to elucidate
interactions between habitat characteristics sought by mule deer. Our stepwise model selection
may provide more transferable conclusions of mule deer habitat use. The purpose of this study was to clearly delineate and evaluate seasonal habitat use by mule deer within the South Selkirk Mountains.

STUDY AREA

Our study area encompassed approximately 4000 km² in south-central B.C., northeastern Washington and northwestern Idaho. Major drainages in BC included Corn and Summit Creeks, the Salmo and South Salmo Rivers and the headwaters of the Upper Priest River. Drainages in Idaho included the Upper Priest River, Cow and Caribou Creeks and in Washington Sullivan Creek (Figure 1).

The physiography of the area is mountainous with elevations ranging from 450 m to 2,165 m. Climate is Pacific Maritime / Continental with the majority of annual precipitation falling in the form of snow (Environment Canada, Vancouver British Columbia). Weather stations maintained by Environment Canada on the east (Creston) and western (Castlegar Airport) edges of the study area provided the following data. Mean (1961 to 1990) temperatures ranged from –3.0 C° (January) to 19.3 C° (July) in Creston, and from –3.2 C° (January) to 19.9 C° (July) in Castlegar. Mean (1961 to 1990) annual snowfall was 140.6 cm in Creston (el. 597 m) and 224.6 cm in Castlegar (el. 494 m). The annual accumulated snowfall (snow depth on the ground at month’s end, January to April) from 1993 to 2003 is shown in Figure 2.

The study area is within two distinct biogeoclimatic zones; the interior cedar - hemlock (ICH), and the Engelmann spruce – subalpine fir (ESSF) (Braumandl and Curran 1992). The ICH zone extends from the lowest elevations of the study area to approximately 1,200m. Western redcedar (Thuja plicata) and western hemlock (Tsuga heterophylla) are the dominant tree species in mature forests, with black cottonwood (Populus balsamifera trichocarpa) the climax in more moist areas. Open mixed stands of Douglas-fir (Pseudotsuga menziesii) and ponderosa pine (Pinus ponderosa) are common on more xeric south facing slopes (Ketcheson et al. 1991). The ESSF zone occurs from approximately 1,200 m to 2,100 m. White and Engelmann spruce (Picea glauca and Picea engelmannii) dominates the climax forest in this zone, with subalpine fir
(Abies lasiocarpa) composing the understory, and lodgepole pine (Pinus contorta) common following fire (Coupe et al. 1991).

The combination of climate and physiography combine to create seasonally migratory deer populations (e.g., Garrott et al. 1987). Mule deer are on summer ranges from July to September, migrate between seasonal ranges during May and June and from October to December and congregate on winter ranges between December and April. Deer winter ranges are generally on south to west facing slopes and provide juxtaposition of open shrub fields and timber stands with higher canopy closure (Woods 1984, Pauley et al. 1993, Armleder et al. 1994). Higher elevation winter ranges (i.e., 900-1,200 m) are almost exclusively occupied by mule deer, whereas lower elevation ranges (i.e., ≤ 900 m) are predominantly white-tailed deer. Most winter ranges are located wholly within the ICH zone. As mentioned in the introduction, winter ranges have been extensively mapped within our study area and across British Columbia (Figure 3). Mule deer range higher into the ESSF during summer with mule deer averaging maximum elevations of 1,800 m in early October.

Fire suppression in the last 50 years has halted the main source of natural disturbance. The last major fires in the area occurred in the 1930s and have now regenerated to mixed coniferous stands (Woods 1984). Timber has been harvested in the area since the turn of the century, and is now the dominant form of disturbance.

In addition to mule deer; white-tailed deer (Odocoileus virginianus), elk (Cervus elaphus), moose (Alces alces), bighorn sheep (Ovis canadensis), and mountain caribou (Rangifer tarandus caribou), were found in the study area, roughly in that order of abundance. Common predators included coyotes (Canis latrans), black bears (Ursus americanus), bobcats (Lynx rufus), and cougars (Puma concolor). Low numbers of grizzly bears (Ursus arctos), lynx (Lynx canadensis), wolves (Canis lupus), and wolverine (Gulo gulo) were also present over the course of the study.
METHODS

Telemetry and Home Ranges

B.C. Ministry of Water, Land and Air Protection and Columbia Basin Fish and Wildlife Compensation Program (CBFWCP) personal began radio collaring mule deer in February 1997. Deer were captured using helicopter net gunning and Clover traps (Clover, 1956) between December and March. Each animal was fitted with a VHF radio collar equipped with a mortality switch on a six-hour delay (Lotek Inc., Newmarket Ontario).

Radio-collared mule deer were located by aerial telemetry from February 1997 to March 2001 by CBFWCP. Due to the rugged nature of the study area, and associated poor ground access, only aerial telemetry locations were used for habitat analysis. The use of aerial locations limits autocorrelation and any bias associated with ground access (i.e. over representation of habitat use near roads). Animal locations were marked on 1:15000 air photos during telemetry flights, then transposed onto 1:20000 forest cover maps to determine a UTM coordinate. Accuracy of aerial locations was determined through the use of know location test collars and ground-truthing of mortality locations. Aerial telemetry locations were normally within 100m of the true location.

Locations were pooled across years into two seasons; summer (July 1–Sep 20) and winter (Jan 1–Apr 30), migrational periods (May-June, and October-December) were excluded from the analysis. We used a 95% adaptive kernel (ADK; Worton 1989) to estimate seasonal home ranges for individual deer, for all males pooled, and for all females pooled.

Habitat Layers

Vegetation characteristics (cover type, crown closure, and age) were mapped by the British Columbia Ministry of Forests and the U.S. Forest Service (USFS) by interpreting aerial photographs and sampling ground plots. Polygons enclosing areas with similar characteristics were digitized using the geographic information system (GIS) ArcGIS (Environmental Systems
Research Institute, Redlands, California, USA). We classified vegetation into 12 cover types (Table 1). Crown closure was classified into 10%-intervals (i.e., 0-5, 6-15, 16-25,…, 96-100%) and age was measured in years.

Topography was derived from a 7.5-minute digital elevation model (DEM; vertical resolution = 15 m) provided by USFS and CBFWCP. We used ArcGIS to calculate slope and aspect for each 50 × 50 m grid cell in the DEM. Elevation and slope were analyzed as continuous variables. We converted aspect into a north-south index (NSI) as follows:

<table>
<thead>
<tr>
<th>Azimuth</th>
<th>NSI</th>
</tr>
</thead>
<tbody>
<tr>
<td>0°</td>
<td>0.0</td>
</tr>
<tr>
<td>1-179°</td>
<td>x / 180</td>
</tr>
<tr>
<td>180°</td>
<td>1.0</td>
</tr>
<tr>
<td>181-359°</td>
<td>(360 – x) /180</td>
</tr>
<tr>
<td>360°</td>
<td>0.0</td>
</tr>
</tbody>
</table>

and into a west-east index (WEI) as follows:

<table>
<thead>
<tr>
<th>Azimuth</th>
<th>WEI</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-89°</td>
<td>(x + 90) / 180</td>
</tr>
<tr>
<td>90°</td>
<td>1.0</td>
</tr>
<tr>
<td>91-269°</td>
<td>(270 – x) / 180</td>
</tr>
<tr>
<td>270°</td>
<td>0.0</td>
</tr>
<tr>
<td>271-359°</td>
<td>(x – 270) / 180</td>
</tr>
</tbody>
</table>

Density of elevation contour lines was be used to index topographical ruggedness (Beasom et al. 1983, Williams 1992). We used GIS to generate contour lines at 100 m intervals. A moving window then was used to calculate density of contour lines within 1 km around each grid cell. This window size was a compromise of telemetry resolution; the range, variation, and distribution (relative to normality) of the resulting ruggedness index; and an ecological scale appropriate to mule deer.
Spatial Scales

Selection was analyzed at two spatial scales; the landscape scale (location of seasonal home ranges on the landscape) and the patch scale (selective use of areas within seasonal home ranges, Figure 1). At the landscape scale, use was determined by habitat proportions within the group seasonal home range (data pooled across individuals, sexes analyzed separately). To estimate availability at the landscape scale, we first plotted the individual home ranges for each deer using all locations obtained for it (i.e., multi-year, multi-season), then merged the individual home ranges and expanded the resulting polygon by the mean radius of an average deer home range (7.2 km). We used this polygon to estimate availability at the landscape scale for both sexes and seasons (Figure 1). This availability estimate potentially was biased towards areas used by mule deer because it was defined by use pooled across deer. Such a bias could increase the chance of failing to detect selection (a type II error). The area defined as available was only 28% of the entire mapped landscape. We examined habitat distributions for the “available” area and the entire mapped landscape to assess whether the “available” area was similar to the surrounding landscape (and therefore a reasonable estimate of true availability) or biased towards the areas used by mule deer. At the patch scale, use was determined by the distribution of telemetry locations among habitats within the seasonal home range. Availability at the patch scale was the proportion of area within the home range classified by each habitat type (same as the landscape-scale use).

Univariate Analyses

For categorical variables (vegetative cover type, crown closure), we used a Chi-square goodness-of-fit test to determine whether habitat use differed from availability ($P < 0.05$). If so, we used a Bonferroni $z$-statistic to construct confidence intervals around each availability proportion, following the procedure of Neu et al. (1974), to determine which habitats were used selectively. For continuous variables (forest stand age, elevation, slope, north-south aspect, west-east aspect, ruggedness), we used a Kolmogorov goodness-of-fit procedure (Conover 1980:346-348) to test
whether cumulative distribution functions for use versus availability were different. If so, we calculated the expected value for each function to determine how use was selective. Separate univariate analyses were conducted at the landscape and patch scales.

At the landscape scale, calculating the probability that use was different from availability was problematic. Landscape-scale use was determined by pooling deer locations to obtain a composite home range for that sex and season. Therefore, even though a test statistic could be calculated, there was only one sample from the unknown distribution (use), and no way to determine the probability that the sample came from the known distribution (availability). That is, there was no sample size to evaluate whether the calculated test statistic was different from that expected just due to chance (i.e., whether the result was “significant”). The number of categorical versus continuous variables and the Chi-square versus Kolmogorov procedures used for the two variable types resulted in different solutions to this problem. For the categorical variables, we evaluated the Chi-square test statistic at the same sample size used at the patch scale (the number of telemetry locations obtained), which affected the reliability of the home range boundary estimate. To conduct the test, we distributed a hypothetical sample of \( n \) observations, where \( n \) was the number of telemetry locations obtained, across habitat categories based on the percent area of the home range in each category. This is the same procedure used to calculate the expected distribution of telemetry locations at the patch scale. As applied here to the landscape scale, it was equivalent to saying that, instead of knowing the exact distribution of habitats within the home range by summing areas in a GIS, the distribution was estimated from a sample of point observations. This was a conservative solution. An advantage of this solution was that the Neu et al. (1974) procedure could be used to assess which habitat categories were used differently than expected.

For the continuous variables, we did not attempt to evaluate the Kolmogorov statistic at any specific sample size but simply compared the magnitude of the test statistic across habitat variables to determine which influenced selection at the landscape scale the most. This solution was enabled by the larger number of continuous variables (five, vs. two categorical variables) and addressed the landscape-scale question more directly (what influences selection?) without requiring an artificial sample size.
Multivariate Analyses

Interactions among habitat variables were assessed by comparing proportions of mule deer telemetry locations (observed) versus proportions of randomly located points (random) within seasonal, group home ranges. All multivariate analyses were performed at the patch scale because of the sample size problems discussed above for the landscape scale. The number of random points in each seasonal home range was equal to the number of telemetry locations obtained for that sex during that season.

The multivariate models were constructed before conducting any univariate tests. We excluded the following pairs of variables from the models because it was unlikely they were independent: vegetative cover type (VCT) $\times$ forest stand age (FSA), VCT $\times$ aspect, VCT $\times$ elevation, slope $\times$ ruggedness, and FSA $\times$ crown closure. The following four models were tested for interactive effects:

- Vegetative Cover Type $\times$ Crown Closure $\times$ Gender $\times$ Season
- Aspect $\times$ Crown Closure $\times$ Gender $\times$ Season
- Slope $\times$ Aspect $\times$ Elevation $\times$ Gender $\times$ Season
- Forest Stand Age $\times$ Gender $\times$ Season.

The dependent variable in each model was point type (observed vs. random). For model 1, which had only categorical variables, we used a log-linear test. There were 10 categories of vegetative cover type, nine categories of crown closure and two categories each of sex and season. Models 2-4 included both categorical and continuous variables, so logistic regression was used to test for interactive effects. We used backward selection to remove terms from the full models to determine which terms contributed most to explaining variability between locations of mule deer versus random points. We plotted variable interactions graphically for terms selected as providing the best fit for each of the four models.
RESULTS

Telemetry and Home Ranges

Forty-three radio-collared mule deer (33 F, 10 M) were radiotracked in south-central British Columbia, northwestern Idaho, and northeastern Washington between February 1997 and March 2001. The average duration a single animal was monitored for was 17 months (SD = 12 mo.), resulting in an average of 53 locations (SD = 38.1), per mule deer.

Evaluation of the Area Defined as Available at the Landscape-Scale

We compared habitat distributions between the area defined as available to mule deer (landscape availability) and the surrounding landscape within which habitat was mapped (3X larger than the “available” area, Figure 1) to determine whether the available area was biased towards areas used by mule deer. For each vegetative cover type, the difference in the percent of the available area and the percent of the surrounding landscape classified as that type was $\leq 5\%$ (Figure 4). Cedar/hemlock was more abundant in the available area (13%) than in the surrounding landscape (8%), as was spruce/fir (23% vs. 18%, respectively). Douglas fir/ponderosa pine was less abundant in the available area (6%) than in the surrounding landscape (11%), as was lodgepole pine/western larch (12% vs. 16%, respectively). Compared to vegetative cover types, crown closure was most similar between the available area and the surrounding landscape (Figure 5). The greatest difference was in the 0-5% closure category (33% of the available area vs. 30% of the surrounding landscape). Mean age of forest stands was very similar between the two areas (73.9 yr available area, 83.4 yr surrounding landscape; Figure 6). Mean elevation was slightly higher in the available area (1,374 m) compared to the surrounding landscape (1,175 m; Figure 7). However, mean slope was similar between the two areas (19.3° for available area, 15.7° for surrounding area; Figure 8), as were north-south aspects and east-west aspects (Figures 9, 10). The available area was more rugged than the surrounding landscape (Figure 11).
Landscape-Scale Selection

Mule deer used vegetative cover types selectively at the landscape scale. Males were selective during both summer ($\chi^2 = 35.840, 9 \text{ df}, P < 0.001$) and winter ($\chi^2 = 115.818, 9 \text{ df}, P < 0.001$). Recall that sample size in landscape-scale tests using the chi-square procedure (i.e., for categorical variables) was subjectively set to the number of telemetry locations obtained during that season for that sex (the same sample size used to test for patch-scale selection). During summer, males spent more time in spruce/fir habitat than expected based on its availability (Figures 12, 13 and 14). During winter, males selected for mixed coniferous/deciduous habitats and avoided cedar/hemlock and spruce/fir (Figure 15 and 16). Females also used vegetative cover types selectively during both seasons ($\chi^2 \geq 64.128, 9 \text{ df}, P < 0.001$). During summer, females selected for spruce/fir, alpine, and mixed coniferous/deciduous habitats and avoided cedar/hemlock and mixed conifer forest (Figures 13, 14 and 17). Similar to males, during winter females selected for mixed coniferous/deciduous habitats and avoided cedar/hemlock and spruce/fir (Figures 15, 16 and 17).

Crown closure did not seem to influence location of mule deer group home ranges on the landscape. During both seasons, categories of crown closure were similar between the male group home range and the available landscape ($\chi^2 \leq 7.409, 10 \text{ df}, P \geq 0.686$). Females also did not respond selectively to crown closure at the landscape scale during summer ($\chi^2 = 9.300, 10 \text{ df}, P = 0.504$), but did during winter ($\chi^2 = 91.597, 10 \text{ df}, P < 0.001$). The female group home range contained more stands with 46-65% crown closure, and fewer stands with <25% closure compared to the available landscape (Figure 18).

The large number of continuous variables (forest stand age, elevation, slope, aspect, ruggedness) allowed comparison of the relative strength of landscape-scale selection across variables and between sexes and seasons. Selection was strongest for elevation (Figure 19). During summer, group home ranges of both sexes were at higher elevations than the rest of the available area, which already was at higher elevations than the surrounding landscape. In contrast, during winter both sexes used lower elevations than expected: $E(X)_{\text{males}} = 1,223 \text{ m}; E(X)_{\text{females}} = 1,161$; and $E(X)_{\text{Availability}} = 1,374 \text{ m}$. Topographical ruggedness was the second-most influential habitat.
variable. During both seasons, all deer used areas that were more rugged than the rest of the available area (Figure 19), despite that the available area already was more rugged than the surrounding landscape. Forest stand age was next in strength of selection. Again, selection was consistent between sexes but opposite between seasons. Deer used older stands during summer and younger stands during winter. Selection for slope and aspect was weak at the landscape scale (Figure 19).

**Patch-Scale Selection**

During summer, males selected against shrub habitats ($\chi^2 = 26.778$, 9 df, $P = 0.002$; Figures 13, 14, and 20). In contrast, males selected for shrub and against mixed-conifer forest and spruce/fir in winter ($\chi^2 = 133.220$, 9 df, $P < 0.001$; Figures 13, 14, and 21). Females had a different pattern of selection than males during summer. Females selected for spruce/fir and against cedar/hemlock and lodgepole pine/western larch ($\chi^2 = 86.703$, 9 df, $P < 0.001$; Figures 13, 14, and 22). However, similar to males, during winter females selected for shrub and avoided spruce/fir ($\chi^2 = 333.683$, 9 df, $P < 0.001$). Females also selected for Douglas fir/ponderosa pine and against lodgepole pine/western larch during winter (Figures 15, 16, and 23).

Mule deer also used categories of crown closure selectively at the patch scale during both seasons. During summer, males avoided stands with >55% closure ($\chi^2 = 17.439$, 8 df, $P = 0.026$; Figure 24). Males also avoided closed stands (>65% closure) during winter ($\chi^2 = 26.062$, 8 df, $P = 0.001$; Figure 25). Females showed a similar pattern during summer, avoiding stands with 56-75% closure ($\chi^2 = 39.439$, 8 df, $P < 0.001$; Figure 26). However, during winter, females avoided stands with 16-25% closure and with 56-65% closure but selected for stands with 6-15% closure ($\chi^2 = 174.373$, 8 df, $P < 0.001$; Figure 27).

Male mule deer did not use forest stands selectively relative to age during either season ($T \leq 0.115$, $n \geq 65$, $P \geq 0.201$). In contrast, females were selective during both seasons. During summer, females used older stands than expected based on the age distribution of stands within
their group home range \((T = 0.008, n = 298, P = 0.019; \text{Figure 28})\). During winter, however, females used younger stands than expected \((T = 0.118, n = 638, P < 0.001; \text{Figure 29})\).

Selection for elevation by males was close to significant during summer \((P = 0.062)\). During winter, males used lower elevations more than expected \((T = 0.323, n = 137, P < 0.001; \text{Figure 30})\). Females used higher elevations than expected during summer \((T = 0.090, n = 399, P = 0.003; \text{Figure 31})\) and, similar to males, used lower than expected elevations during winter \((T = 0.291, n = 672, P < 0.001; \text{Figure 32})\). The selection pattern was stronger for females in winter than in summer.

Neither sex used slope selectively during summer \((T \leq 0.089, n \geq 93, P \geq 0.256)\). However, both males \((T = 0.293, n = 137, P < 0.001)\) and females \((T = 0.258, n = 672, P < 0.001)\) used steeper slopes than expected during winter (Figures 33 and 34).

Males used more south-facing aspects than expected during both summer \((T = 0.192, n = 93, P = 0.002; \text{Figure 35})\) and winter \((T = 0.320, n = 137, P < 0.001; \text{Figure 36})\). Females also used more south-facing aspects than expected during both seasons \((T \geq 0.108, n \geq 418, P < 0.001; \text{Figures 37 and 38})\). For both sexes, selection for north-south aspects was stronger in winter than in summer. Males used more east-facing aspects than expected during both seasons \((T \geq 0.144, n \geq 93, P \leq 0.006; \text{Figures 39, and 40})\). Females did, too, but the selection pattern was not as strong as that of males \((T \geq 0.077, n \geq 418, P \leq 0.014; \text{Figures 41 and 42})\).

During summer, males used areas that were less rugged than expected \((T = 0.147, n = 93, P = 0.032; \text{Figure 43})\). In contrast, males selected for more rugged areas during winter \((T = 0.330, n = 137, P < 0.001; \text{Figure 44})\). Females also used areas that were more rugged than expected during both seasons, but selection was much weaker during summer \((T = 0.080, n = 418, P = 0.008; \text{Figure 45})\) compared to winter \((T = 0.259, n = 672, P < 0.001; \text{Figure 46})\).
Multivariate Analyses

Selection for vegetative cover type was influenced by gender and season, but not by crown closure. The best model was:

\[ PT = VCT + G + SN + VCT \times G + VCT \times SN, \]

where PT = point type (telemetry location vs. random point), G = gender, and SN = season (\( F = 9.146, 29 \text{ df}, P < 0.001 \)), but the model did not explain much variation between mule deer locations and random points (\( r^2 = 0.109 \)). The first main effect, VCT, indicated that mule deer used vegetative cover types selectively when gender and season were not considered. The second main effect, G, merely indicated that there were different numbers of observed and random points for males versus females. Similarly, the main effect SN indicated that numbers of observations were different between seasons. These two main effects were expected based on the study design. The first interactive term, VCT \( \times \) G, showed differences in selection between males and females (\( F = 2.739, 9 \text{ df}, P = 0.004 \)). There also were differences in selection between seasons (VCT \( \times \) SN; \( F = 8.018, 9 \text{ df}, P < 0.001 \)). To determine where selection differed between sexes and seasons, we calculated a selection ratio for each cover type as:

\[ \frac{(\text{Use} - \text{Avail})}{(\text{Use} + \text{Avail})} \]

and plotted the ratios by sex and season (Figure 47). For some cover types, selection was similar between sexes but different between seasons. Both sexes avoided alpine and cedar/hemlock more during winter than summer. Both selected for spruce/fir during summer and avoided it during winter. The opposite pattern occurred for shrub; both sexes avoided it during summer, but selected for it during winter. Some selection patterns were different between sexes. Males avoided mixed conifer forests more than females did. Males selected for lodgepole pine/western larch (LP/WL) during summer, whereas females avoided LP/WL during both seasons. Males avoided non-forested (NF) habitats (excluding shrub) during summer, whereas females selected for NF during summer.
Selection for aspect was influenced by crown closure, gender, and season. The model that fit best was:

\[ PT = SN + NSA + CC \times NSA + CC \times WEA + SN \times G \times NSA + SN \times G \times WEA + \\
+ CC \times SN \times NSA + CC \times SN \times NSA, \]

where PT = point type (telemetry location vs. random point), SN = season, NSA = north-south aspect index, CC = crown closure, WEA = west-east aspect index, and G = gender \( (F = 7.150, 44 \text{ df}, P < 0.001) \). Again, the model did not explain much of the variability in the data \( (r^2 = 0.127) \).

The mean value of the north-south index was greater at mule deer locations than at random points, indicating that deer used more south-facing aspects than expected due to chance, but the size of the difference (the strength of selection for southerly aspects) varied with crown closure \( (F = 4.612, 8 \text{ df}, P < 0.001) \). The difference was greatest at >65% crown closure and least in the 16-25% category (Figure 48). Similarly, the difference in the mean value of the west-east index between deer locations and random points varied with crown closure \( (F = 3.852, 8 \text{ df}, P < 0.001) \). Selection for easterly aspects was strongest in stands with 0-5%, 36-65%, and 76-85% crown closure (Figure 49). In contrast, deer selected for west-facing aspects in stands with 6-15%, 26-35%, and 66-75% crown closure. Selection for aspect also differed between males and females and between seasons \( (F \geq 4.706, 1 \text{ df}, P \leq 0.030) \). Selection for southerly aspects was stronger during winter for both sexes, and was stronger for female deer than for males in each season (Figure 50). Males selected for more east aspects during winter. Females showed the strongest response to west-east aspect during summer, but selected for more west aspects.

There also was an interaction between crown closure and season on selection for both north-south aspects \( (F = 6.169, 8 \text{ df}, P < 0.001) \) and west-east aspects \( (F = 2.800, 7 \text{ df}, P = 0.007) \). For north-south aspects (Figure 51), deer were less selective during summer compared to winter in stands with <65% closure, but were more selective in summer than in winter for stands with >65% closure. For west-east aspects (Figure 52), deer were most selective during summer in dense (>65% closure) stands. Selection during winter was strongest in stands with 6-15% and 26-35% closure.
There were seasonal differences in how deer responded to elevation, slope, and aspect. Males and females were analyzed together in this model. The best model was:

\[ PT = S + NSA + SN\times E + SN\times S + SN\times NSA + E\times S + E\times S\times WEA, \]

where \( PT \) = point type (mule deer locations vs. random point), \( SN \) = season (summer, winter), \( E \) = elevation, \( S \) = slope, \( NSA \) = north-south aspect index, and \( WEA \) = west-east aspect index (\( F = 56.627, 9 \text{ df}, P < 0.001 \)). The model explained 16.4% of the variability between deer locations and random points. The first main effect, slope (\( F = 112.119, 1 \text{ df}, P < 0.001 \)), reflects the results presented from the univariate analysis with mule deer selecting for steeper slopes than expected due to chance. Similarly for the second main effect, north-south aspect (\( F = 47.363, 1 \text{ df}, P < 0.001 \)), deer used more south-facing slopes than expected. Deer were more selective during winter than during summer for elevation (lower than expected; \( F = 65.058, 1 \text{ df}, P < 0.001 \); Figure 53), slope (steeper than expected; \( F = 15.165, 1 \text{ df}, P < 0.001 \); Figure 54), and aspect (more south-facing than expected; \( F = 10.385, 1 \text{ df}, P = 0.001 \); Figure 55). Slope was a confounding effect in deer selection for elevation (\( F = 49.364, 1 \text{ df}, P < 0.001 \)). A scatter-plot of elevation by slope for deer versus random points revealed no clear pattern (Figure 56); however, plotting mean elevation for different categories of slope (Figure 57) showed that the gentle slopes (<5%) used by deer were at much lower elevation than the gentle slopes where random points occurred, and that the steepest slopes (>50%) used by deer were at higher elevations than expected. Further, plotting mean slope for different categories of elevation show that selection for slope was strongest at low elevations. Deer consistently selected for steeper slopes at lower elevations, but were less selective at higher elevations (Figure 58). Aspect also was a confounding effect on deer selection for elevation (\( F = 4.776, 1 \text{ df}, P = 0.029 \)). Again, a scatter-plot of elevation by north-south aspect for deer versus random points revealed no clear pattern, but plotting mean values of the aspect index for different categories of elevation showed that although deer used more south-facing slopes than expected at all elevations, selection for south-facing slopes was strongest at the lowest (<700 m) and highest (>1,900 m) elevations (Figure 59). There was a 3-way interaction among elevation, slope, and west-east aspect that influenced selection by deer (\( F = 17.537, 1 \text{ df}, P < 0.001 \)). A plot of the three variables shows that there
were fewer deer observations on west-facing slopes at higher elevations compared to random points (Figure 60).

The final multivariate model assessed was effect of gender and season on selection for different aged forest stands. The best model was:

\[ PT = FSA + SN + FSA \times SN, \]

where PT = point type (mule deer locations vs. random point), FSA = forest stand age, and SN = season \( (F = 4.208, 3 \, df, \, P = 0.006) \). This model explained the least variability in deer locations versus random points \( (r^2 = 0.006) \). The first main effect, forest stand age, simply indicates that deer used forest stands selectively depending on the stand’s age \( (F = 7.405, 1 \, df, \, P = 0.007) \). This same effect was discussed in the univariate tests, so the results are not presented here. The second main effect, season, indicates that numbers of observations (mule deer or random) were unequal between summer and winter; an artifact of telemetry effort. The interactive effect, however, indicates that selection for forest stand age was influenced by season \( (F = 11.762, 1 \, df, \, P = 0.001) \). Deer selected for younger stands than expected during winter, but for older stands than expected during summer (Figure 61).
DISCUSSION / SUMMARY

Evaluation of the Area Defined as Available at the Landscape-Scale

A common criticism of use vs. availability studies is whether habitats considered available by biologists, are actually considered available by the animal being studied (White and Garrot, 1990:183). Interspecific competition, territoriality, and risk of predation may preclude the use of specific habitats. For instance, the “predation sensitive food” hypothesis, a synthesis of traditional models predicting habitat use based on avoidance of predators or the availability of resources, suggests that as food becomes more scarce, prey animals are willing to take greater foraging risks, perhaps using habitats they would normally avoid (Sinclair and Arcese 1995, Sweitzer 1996). It is impossible for researchers to quantify an absolute measure of available habitat and the reader is cautioned to investigate the various theories of which forces shape habitat use, and to bear in mind this limitation. However, we believe that our step-down approach to measuring available habitats, beginning at a landscape scale 3 times the size of our specific study area, to be a reasonable approximation.

Overall the portion of the landscape defined as available to mule deer (the composite home range), was similar to the surrounding landscape and therefore a reasonable estimate of availability. Crown closure, stand age, slope and aspect within the composite home range, were all very similar to the surrounding landscape, however, the composite home range was higher and more rugged. The available area (composite home range) was biased towards cedar/hemlock and spruce/fir, against Douglas fir/ponderosa pine and lodgepole pine/western larch. Therefore, landscape-scale selection results relative to those habitat types should be interpreted cautiously. Failure to find selection or finding selection contrary to these biases could be an artifact of how availability was defined. For example, if individual deer home ranges contained small proportions of cedar/hemlock relative to the available area, but the available area contained a large proportion of cedar/hemlock relative to the surrounding landscape, selection could have been masked by that greater availability (in effect, deer did not need to be selective within the available area because the available area itself was selective relative to the surrounding landscape). In contrast, finding selection in the same direction as the biases would increase the
strength of the conclusion. If deer home ranges contained large proportions of cedar/hemlock relative to the available area even though the available area already contained a large proportion relative to the surrounding landscape, this would indicate very strong selection for cedar/hemlock by deer.

**Landscape Scale**

Previous studies in this region have suggested that mule deer prefer high elevation, rugged terrain in summer, and low elevation, steep sloped, open shrub communities in winter (Hudson et al. 1976, Mowat et al. 2003). At the landscape scale (seasonal home range compared to the greater study area), both males and females selected for spruce/fir forests during summer. In winter, both sexes selected mixed coniferous/deciduous habitats while avoiding cedar/hemlock and spruce/fir. The difference in selection for spruce/fir between seasons suggests that the definition of availability, discussed in the previous section, did not bias our results. There was more spruce/fir in the available area than in the surrounding landscape, yet mule deer still selected for spruce/fir during summer indicating a strong selection for this habitat type. However, selection against cedar/hemlock during winter by males and during both seasons by females may have been an artifact of the high proportion of cedar/hemlock in the available area relative to the surrounding landscape (deer did not need to seek out cedar/hemlock because it was abundant within the available area already). The availability of cedar/hemlock may be lower on winter ranges than on summer ranges (Gwilliam, pers obs.), making selection against this habitat type more significant.

Canopy closure affected only female winter home range selection. The females, at a landscape scale, sought more stands with 46-65% crown closure, and fewer stands with <25% closure compared to the available landscape. These values are on par with the level of crown closure (≥ 40%) designated for mule deer winter range in the Kootenay region of B.C (Mowat et al. 2003). In winter, mature forest stands favoured by ungulates are thought to provide snow interception, and thermal cover (D’Eon 2001, Pauley et al. 1993, Armstrong et al. 1983). However conclusions drawn from observation can be misleading. Using captive elk and a number of
feeding and thermal cover regimes, Cook et al. (1998) found no support for the thermal cover hypothesis. Interpreting why any specific habitat is favoured goes beyond the scope of this study and caution should be taken in extrapolating the motives of study animals. In this study, both sexes chose older stands in summer, and younger stands in winter. This use is contrary to current winter range designation that calls for the preservation of stands greater than 81 years of age for snow interception/thermal cover (Mowat et al. 2003).

See Appendix 1 for a summary of our univariate analysis.

**Patch-Scale Selection**

Mule deer used vegetative cover types selectively at the patch (within seasonal home range) scale during both seasons. In summer, males selected against shrub habitats. Females selected for spruce/fir while selecting against cedar/hemlock and lodgepole pine/western larch. In winter, both males and females selected for shrub habitats and avoided spruce/fir. Females also selected for Douglas fir/ponderosa pine but against lodgepole pine/western larch. Patch-scale selection for forest stand age was different between sexes. While males did not select for a specific stand age characteristic in either season, females used older stands in summer and younger stands in winter.

Both sexes used elevation selectively at the patch scale. Both males and females used lower areas relative to what was available in their group home range. Females used areas higher in elevation than expected during summer. This preference is likely a product of doe movements to higher elevations to join bucks during the early rut. Males did not show a statistically significant selection for higher elevations in summer although selection may have been significant with only a slightly higher sample size.

Male and female mule deer responded similarly to both slope and aspect at the patch scale. Steep slopes were selected for in winter as were south facing slopes. Both sexes also used more
east facing aspects than expected during both seasons although selection was less strong for females.

Both sexes responded selectively to topographical ruggedness at the patch scale. Males chose less rugged areas in summer but in winter chose areas more rugged than what was available within the group home range. Females chose more rugged areas during both seasons although selection was weaker in summer.

See Appendix 1 for a summary of our univariate analysis.

**Multivariate Analyses**

The multivariate analysis supported the findings of our univariate analysis. Choice of vegetation cover type varied with both gender and season. For example, both sexes selected for spruce/fir forests during summer but avoided this same habitat during winter (seasonal variation). An example of gender selection was shown by males favouring lodgepole pine/western larch (LP/WL) during summer, while females avoided LP/WL during both seasons.

The multivariate analysis also showed a significant interaction between selection for aspect, crown closure, gender, and season. Selection for southerly aspects was stronger during winter for both sexes, and was stronger still for female deer than for males in each season. Males selected for more east aspects during winter. Females showed the strongest response to west aspects during summer. When the sexes were combined, deer used south-facing aspects more than expected when compared to random points, the strength of selection varying with crown closure and season. In winter, deer selected stands with 6-15% and 26-35% closure. In summer, deer selected for greater canopy closure with values higher than 65% preferred.

There were seasonal differences in how deer responded to elevation, slope, and aspect. The strongest pattern, quite simply was in winter, when deer preferred low elevation, steeply sloping, southern aspects; a traditional view of mule deer winter range.
The final multivariate model, effect of gender and season on selection for different aged forest stands, showed very little fit to our data. Deer selected for younger stands than expected during winter, but for older stands than expected during summer.
MANAGEMENT IMPLICATIONS

Studies of the effects of human induced habitat modifications on ungulate seasonal habitat use have shown mixed results, but do suggest resultant shifts in patch scale (within home range) habitat selection. Edge et al. (1985) found that logging activities did not cause elk to significantly alter their home ranges (landscape scale habitat use) but did alter habitat selection within home range (patch scale), namely by focusing use on those remaining areas that provided adequate cover. Yeo and Peek (1992) found that black-tailed deer selected for clearcuts in a mix of old growth timber, while Chang et al. (1995) found that black-tailed deer focused on the abrupt habitat edges of old growth forest and recent (<30 yr. old) clearcuts. Management at the scale of an individual deer’s home ranges is impractical, but is feasible at a landscape scale.

At the landscape level, the most striking result in our study was the strong selection of Spruce/Fir forests by both sexes during summer and for mixed coniferous/Deciduous habitats during winter. Both are likely preferred by deer due to an abundance of seasonal forage, forbs and grasses in summer and browse in winter (Kufeld et al. 1973). The preservation of these seasonal habitats may be under valued in current timber harvest prescriptions.

Across North America, mule deer populations are thought to be declining. Several regions of British Columbia (B.C.) and the Pacific northwest have also experienced seemingly sharp declines in mule deer populations throughout the 1990s (Unsworth et al. 1999). Although there is much discussion about what limits wild populations in general, and what is behind the decline of mule deer in particular, it is accepted that two contributing factors are food shortages, brought about by overpopulation or climatic conditions, and predation (McNamara and Houston 1987, and McRoberts et al. 1995).

The limiting factors of food shortages and predation can be exacerbated by human induced habitat modifications such as habitat fragmentation (e.g. interspersion of small clearcuts and intact forest). Several recent studies have shown that some species of small mammals and birds suffer increased predation in fragmented habitats (Andren et al. 1985, Oehler and Litaitis 1996).
While studies testing this hypothesis on large carnivores and their prey are few, the same principles may hold true. Van Ballenberghe and Hanley (1984) found that logging of old-growth forests caused a decline in carrying capacity for deer, which then increased predation pressure and caused a rapid decline in deer density. McNay and Voller (1995) found that non-migratory deer remaining at low elevations were more prone to predation and recommended that maintaining old intact forests at low elevations was basic to rebuilding deer populations on Vancouver Island.

Seip (1992) suggested that predation on mountain caribou in central British Columbia increased when a generalist predator (wolves) followed their primary prey (moose) into traditional caribou habitats. Kinley and Apps (2001), and Robinson et al. (2002), also suggested relevant changes in invading prey and their generalist predators (white-tailed deer and cougar) may be affecting resident animals. In our study mule deer bucks avoided shrub habitats in summer, possibly in response to increased predation risk, afforded by increased stalking cover for predators in these areas (predation sensitive foraging).

To speculate why animals use or avoid a specific habitat is great sport and the natural tendency of wildlife researchers. It is important to remember that this work was, as are most others, purely descriptive and not experimental. We can only speculate why some habitats are favoured and cannot gauge the relative importance of a specific habitat, nor can we suggest what effect it would have on the population if certain habitats were lost or modified. We found that mule deer bucks avoided shrub habitat in summer but can only speculate as to why. We found that mule deer use mixed coniferous/deciduous habitats during winter in greater proportion to their availability, but cannot say if these habitats are more important to the population than old growth conifer stands. Only through the experimental manipulation of habitat variables will research move beyond speculation and into reliable knowledge (Romesburg 1981, e.g. Cook et al. 1998).

Wildlife habitat in Southern British Columbia is becoming increasingly fragmented making sound management increasingly critical. Seasonal ungulate habitats, namely winter ranges, play an important role in British Columbia’s timber industry. Improper delineation of winter ranges, however, could unnecessarily restrict timber harvest, while failing to provide mule deer with the
habitat protection required for the population to thrive. Habitat protection should not be viewed as a single season endeavor. Summer ranges, with the forage they provide and the relative risk of predation present, are likely as important to population growth and winter survival as winter ranges and should be managed as such.
LITERATURE CITED


Williams, J. S. 1992. Population characteristics and habitat use of mountain lions in the Sun River Drainage, Montana. Montana Department of Fish, Wildlife, and Parks; Helena, Montana, USA.


Appendix 1.

**UNIVARIATE RESULT SUMMARY**

<table>
<thead>
<tr>
<th>Vegetative Cover Type</th>
<th>Landscape Scale</th>
<th>Patch Scale</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Select For</td>
<td>Select Against</td>
</tr>
<tr>
<td><strong>Female, Summer</strong></td>
<td>Alpine</td>
<td>Cedar/Hemlock</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>Mixed conifer</td>
</tr>
<tr>
<td></td>
<td>coniferous/Deciduous</td>
<td>Spruce/Fir</td>
</tr>
<tr>
<td></td>
<td>Spruce/Fir</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cedar/Hemlock</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lodgepole/Larch</td>
<td></td>
</tr>
<tr>
<td><strong>Female, Winter</strong></td>
<td>Mixed</td>
<td>Alpine</td>
</tr>
<tr>
<td></td>
<td>coniferous/Deciduous</td>
<td>Cedar/Hemlock</td>
</tr>
<tr>
<td></td>
<td>Spruce/Fir</td>
<td>Mix conifer</td>
</tr>
<tr>
<td></td>
<td>W. Pine/G. Fir</td>
<td></td>
</tr>
<tr>
<td><strong>Male, Summer</strong></td>
<td>Spruce/Fir</td>
<td></td>
</tr>
<tr>
<td><strong>Male, Winter</strong></td>
<td>Mixed</td>
<td>Cedar/Hemlock</td>
</tr>
<tr>
<td></td>
<td>coniferous/Deciduous</td>
<td>Spruce/Fir</td>
</tr>
<tr>
<td></td>
<td>Spruce/Fir</td>
<td></td>
</tr>
<tr>
<td></td>
<td>W. Pine/G. Fir</td>
<td></td>
</tr>
</tbody>
</table>

**Crown Closure**

There was no difference between whole map and study area

<table>
<thead>
<tr>
<th>Female, Summer</th>
<th>NS</th>
<th>NS</th>
<th>56-65%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>66-75%</td>
</tr>
<tr>
<td>Female, Winter</td>
<td>46-55%</td>
<td>0-15%</td>
<td>6-15%</td>
</tr>
<tr>
<td></td>
<td>56-65%</td>
<td>76-85%</td>
<td></td>
</tr>
<tr>
<td>Male, Summer</td>
<td>NS</td>
<td>NS</td>
<td>56-65%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>66-75%</td>
</tr>
<tr>
<td>Male, Winter</td>
<td>NS</td>
<td>NS</td>
<td>16-25%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>66-75%</td>
</tr>
</tbody>
</table>

**Forest Stand Age**

Whole Map vs. Study Area: $T = 0.136$, different at $n > 98$. Younger in SA (73.8 vs. 83.4)

<table>
<thead>
<tr>
<th>Female, Summer</th>
<th>No selection</th>
<th>Older forest (96.5 vs. 81.5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female, Winter</td>
<td>Younger (61.2 vs. 73.8)</td>
<td>Younger (51.4 vs. 61.2)</td>
</tr>
</tbody>
</table>
### Elevation

Elevations were higher in the study area (1,374) compared to the whole map (1,175)

<table>
<thead>
<tr>
<th>Gender, Season</th>
<th>Description</th>
<th>Selection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female, Summer</td>
<td>Higher (1,470 vs. 1,374); Less variability (1,470 vs. 1,482); strong selection</td>
<td>No selection</td>
</tr>
<tr>
<td>Female, Winter</td>
<td>Lower (1,161 vs. 1,374); Strong selection</td>
<td>No selection</td>
</tr>
<tr>
<td>Male, Summer</td>
<td>Higher (1,552 vs. 1,374); strong selection</td>
<td>Lower (1,540 vs. 1,552); Very weak selection</td>
</tr>
<tr>
<td>Male, Winter</td>
<td>Lower (1,223 vs. 1,374); weak selection</td>
<td>Lower (1,106 vs. 1,223); stronger selection</td>
</tr>
</tbody>
</table>

### Slope

Whole Map vs. Study Area: slope is greater is the study area vs. whole map (19.3 vs. 15.7)

<table>
<thead>
<tr>
<th>Gender, Season</th>
<th>Description</th>
<th>Selection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female, Summer</td>
<td>Steeper slopes (21.6 vs. 19.3), weak selection</td>
<td>No selection</td>
</tr>
<tr>
<td>Female, Winter</td>
<td>Steeper slopes (21.0 vs. 19.3), Weak selection</td>
<td>Steeper slopes (26.2 vs. 21.0)</td>
</tr>
<tr>
<td>Male, Summer</td>
<td>No selection</td>
<td>No selection</td>
</tr>
<tr>
<td>Male, Winter</td>
<td>Steeper slopes (20.9 vs. 19.3), weak selection</td>
<td>Steeper slopes (27.4 vs. 20.9)</td>
</tr>
</tbody>
</table>

### North-South Index (due north = 0, due south = 1)

Whole map and study area are not different

<table>
<thead>
<tr>
<th>Gender, Season</th>
<th>Description</th>
<th>Selection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female, Summer</td>
<td>No selection</td>
<td>Higher values (more south)</td>
</tr>
<tr>
<td>Female, Winter</td>
<td>No selection</td>
<td>Higher values (more south)</td>
</tr>
<tr>
<td>Male, Summer</td>
<td>No selection</td>
<td>Higher values (more south)</td>
</tr>
<tr>
<td>Male, Winter</td>
<td>No selection</td>
<td>Higher values (more south)</td>
</tr>
</tbody>
</table>

### West-East Index (due east = 1, due west = 0)

Whole map and study area are not different
<table>
<thead>
<tr>
<th>Gender</th>
<th>Season</th>
<th>Selection</th>
<th>Ruggedness Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>Summer</td>
<td>No selection</td>
<td>Higher values (more east)</td>
</tr>
<tr>
<td>Female</td>
<td>Winter</td>
<td>No selection</td>
<td>Higher values (more east)</td>
</tr>
<tr>
<td>Male</td>
<td>Summer</td>
<td>No selection</td>
<td>Higher values (more east)</td>
</tr>
<tr>
<td>Male</td>
<td>Winter</td>
<td>No selection</td>
<td>Higher values (more east)</td>
</tr>
</tbody>
</table>

**Ruggedness Index**

Study area is more rugged than whole map (235.6 vs. 192.0)

<table>
<thead>
<tr>
<th>Gender</th>
<th>Season</th>
<th>Selection</th>
<th>Selection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>Summer</td>
<td>Strong selection for steeper slopes (268.0 vs. 235.6)</td>
<td>Weaker selection for steeper slopes (268.0 vs. 273.6)</td>
</tr>
<tr>
<td>Female</td>
<td>Winter</td>
<td>Strong selection for steeper slopes (258.3 vs. 235.6)</td>
<td>Strong selection for steeper slopes (299.1 vs. 235.6)</td>
</tr>
<tr>
<td>Male</td>
<td>Summer</td>
<td>Weak selection for steeper slopes (246.9 vs. 235.6)</td>
<td>Selection for gentler slopes (238.1 vs. 246.9)</td>
</tr>
<tr>
<td>Male</td>
<td>Winter</td>
<td>Strong selection for steeper slopes (258.4 vs. 235.6)</td>
<td>Strong selection for steeper slopes (319.9 vs. 258.4)</td>
</tr>
</tbody>
</table>
Table 1. Description and percent for 12 vegetation cover types in mule deer study area (MSA) and extended landscape (LAND) in southeastern British Columbia, northeastern Washington, and northern Idaho.

<table>
<thead>
<tr>
<th>Vegetation Cover Type</th>
<th>MSA</th>
<th>LAND</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALPINE: crown closure ≥10%, whitebark pine (<em>Pinus albicaulis</em>) ≥50%</td>
<td>4.8</td>
<td>6.1</td>
</tr>
<tr>
<td>CEDAR / HEMLOCK (C/H): crown closure ≥10%, western redcedar (<em>Thuja plicata</em>) and western hemlock (<em>Tsuga heterophylla</em>) combined ≥50%</td>
<td>12.4</td>
<td>8.3</td>
</tr>
<tr>
<td>DOUGLAS FIR / PONDEROSA PINE (DF/PP): crown closure ≥10% with Douglas fir (<em>Pseudotsuga menziesii</em>) and ponderosa pine (<em>Pinus ponderosa</em>) combined ≥50%</td>
<td>6.1</td>
<td>10.7</td>
</tr>
<tr>
<td>HERBACEOUS (HERB): non-woody vegetative cover ≥25% with &lt;10% crown closure</td>
<td>0.7</td>
<td>1.6</td>
</tr>
<tr>
<td>LODGEPOLE PINE / WESTERN LARCH (LP/WL): crown closure ≥10%, lodgepole pine (<em>Pinus contorta</em>) and western larch (<em>larix occidentalis</em>) combined ≥50%</td>
<td>12.3</td>
<td>15.6</td>
</tr>
<tr>
<td>MIXED CONIFEROUS (MC): crown closure &gt;10%, no deciduous component and no single conifer species or conifer species pairs (C/H, DF/PP, LP/WL, ES/SF) ≥50%</td>
<td>16.7</td>
<td>14.5</td>
</tr>
<tr>
<td>NON-FORESTED (NF): &lt;25% vegetative cover</td>
<td>6.6</td>
<td>5.7</td>
</tr>
<tr>
<td>OPEN WATER (AQU)</td>
<td>2.5</td>
<td>3.7</td>
</tr>
<tr>
<td>SHRUB: woody vegetative cover ≥25% with &lt;10% crown closure</td>
<td>6.1</td>
<td>4.5</td>
</tr>
<tr>
<td>SPRUCE / FIR (ES/SF): crown closure ≥10%, Engelmann spruce (<em>Picea engelmanii</em>) and subalpine fir (<em>Abies lasiocarpa</em>) combined ≥50%</td>
<td>23.0</td>
<td>18.0</td>
</tr>
<tr>
<td>WHITE PINE / GRAND FIR (WP/GF): crown closure ≥10%, white pine (<em>Pinus monticola</em>) and grand fir (<em>Abies grandis</em>) combined ≥50%</td>
<td>0.7</td>
<td>1.3</td>
</tr>
</tbody>
</table>
Figure 1. Study Area showing three levels of habitat availability; mapped area or surrounding landscape, available landscape or available area, and within seasonal home range or patch scale (see text Spatial Scales, for explanation).
Figure 2. Annual accumulated snowfall (snow depth at months end, January to April) and ten year mean accumulated snowfall in south-central British Columbia 1993-2003.
Figure 3. Ungulate winter ranges identified/delineated by British Columbia Ministry of Environment overlain with mule deer winter telemetry locations (1997 to 2001) in southeastern British Columbia.
Figure 4. Percent of the area defined as available to mule deer (black bars; composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range) versus the surrounding landscape (white bars; 3X larger than the ‘available area’) for 13 vegetative cover type.
Figure 5. Percent of the area defined as available to mule deer (black bars; composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range) versus the surrounding landscape (white bars; 3X larger than the ‘available area’) for 11 classes of crown closure.
Figure 6. Cumulative proportion of area defined as available to mule deer (solid, thick line; composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range) versus the surrounding landscape (dashed, thin line; 3X larger than the ‘available’ area) relative to forest stand age. Expected value of the cumulative distribution function was 73.9 years for the available area versus 83.4 years for the surrounding landscape.
Figure 7. Cumulative proportion of area defined as available to mule deer (solid, thick line; composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range) versus the surrounding landscape (dashed, thin line; 3X larger than the ‘available’ area) relative to elevation.
Figure 8. Cumulative proportion of area defined as available to mule deer (solid, thick line; composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range) versus the surrounding landscape (dashed, thin line; 3X larger than the ‘available’ area) relative to slope measured in degrees. Expected value of the cumulative distribution function was 19.3° for the available area versus 15.7° for the surrounding landscape.
Figure 9. Cumulative proportion of area defined as available to mule deer (solid, thick line; composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range) versus the surrounding landscape (dashed, thin line; 3X larger than the ‘available’ area) relative to north-south aspect. The aspect index = 0.0 for due north, 1.0 for due south, and 0.5 for due east/west. Expected value of the cumulative distribution function was 0.5 for both the available area and the surrounding landscape.
Figure 10. Cumulative proportion of area defined as available to mule deer (solid, thick line; composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range) versus the surrounding landscape (dashed, thin line; 3X larger than the ‘available’ area) relative to west-east aspect. The aspect index = 0.0 for due west, 1.0 for due east, and 0.5 for due north/south. Expected value of the cumulative distribution function was 0.5 for both the available area and the surrounding landscape.
Figure 11. Cumulative proportion of area defined as available to mule deer (solid, thick line; composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range) versus the surrounding landscape (dashed, thin line; 3X larger than the ‘available’ area) relative topographical ruggedness. Ruggedness was indexed by density of elevation contour lines. Expected value of the cumulative distribution function was 235.6 for the available area and 192.0 for the surrounding landscape.
Figure 12. Landscape-scale selection for 13 vegetative cover types by male mule deer in southeastern British Columbia. Use was defined by a 95% adaptive kernel group home range (i.e., locations pooled across individuals for a given sex and season). Availability was defined by a composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range.
Figure 13. Summer telemetry locations of radio-collared mule deer in southeastern British Columbia (western portion of study area).
Figure 14. Summer telemetry locations of radio-collared mule deer in southeastern British Columbia (eastern portion of study area).
Figure 15. Winter telemetry locations of radio-collared mule deer in southeastern British Columbia (western portion of study area).
Figure 16. Winter telemetry locations of radio-collared mule deer in southeastern British Columbia (eastern portion of study area).
Figure 17. Landscape-scale selection for 13 vegetative cover types by female mule deer in southeastern British Columbia. Use was defined by a 95% adaptive kernel group home range (i.e., locations pooled across individuals for a given sex and season). Availability was defined by a composite of individual, 95% adaptive kernel home ranges expanded by the mean radius of a deer home range.
Figure 18. Selection for 11 categories of crown closure by female mule deer during winter (Jan 1-Apr 30) in southeastern British Columbia. Use (white bars) was defined by a 95% adaptive kernel group home range (i.e., locations pooled across deer). Availability (black bars) was defined by a composite of individual, 95% adaptive kernel home ranges (both sexes and seasons), expanded by the mean radius of a deer home range.
Figure 19. Relative strength of landscape-scale selection by male mule deer (grey bars) and female mule deer (white bars) during summer (July 1–Sep 20) and winter (Jan 1–Apr 30) for elevation, topographical ruggedness, forest stand age, slope, north-south aspect, and west-east aspect. Height of bars indicates strength of selection measured by the maximum difference between cumulative distribution functions (i.e., the Kolmogorov goodness-of-fit test statistic) for use (95% adaptive kernel home range from locations pooled for all deer of that sex during that season) versus availability (composite of individual, 95% adaptive kernel home ranges for all deer of both sexes during both seasons, expanded by the mean radius of a deer home range). An up-arrow above the bar indicates the expected value for the use function was greater than the expected value for the availability function. A down-arrow indicates use was less than availability.
Figure 20. Patch-scale selection for 10 vegetative cover types by male mule deer during summer (July 1–Sep 20) in southeastern British Columbia. Use was the observed distribution of telemetry locations among vegetative cover types, availability was the expected distribution based on proportions of cover types within the 95% adaptive kernel seasonal home range.
Figure 21. Patch-scale selection for 10 vegetative cover types by male mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the observed distribution of telemetry locations among vegetative cover types, availability was the expected distribution based on proportions of cover types within the 95% adaptive kernel seasonal home range.
Figure 22. Patch-scale selection for 10 vegetative cover types by female mule deer during summer (July 1–Sep 20) in southeastern British Columbia. Use was the observed distribution of telemetry locations among vegetative cover types, availability was the expected distribution based on proportions of cover types within the 95% adaptive kernel seasonal home range.
Figure 23. Patch-scale selection for 10 vegetative cover types by female mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the observed distribution of telemetry locations among vegetative cover types, availability was the expected distribution based on proportions of cover types within the 95% adaptive kernel seasonal home range.
Figure 24. Patch-scale selection for nine categories of crown closure by male mule deer during summer (July 1–Sep 20) in southeastern British Columbia. Use was the observed distribution of telemetry locations among categories. Availability was the expected distribution of locations based on category proportions within the 95% adaptive kernel seasonal home range.
Figure 25. Patch-scale selection for nine categories of crown closure by male mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the observed distribution of telemetry locations among categories. Availability was the expected distribution of locations based on category proportions within the 95% adaptive kernel seasonal home range.
Figure 26. Patch-scale selection for nine categories of crown closure by female mule deer during summer (July 1–Sep 20) in southeastern British Columbia. Use was the observed distribution of telemetry locations among categories. Availability was the expected distribution of locations based on category proportions within the 95% adaptive kernel seasonal home range.
Figure 27. Patch-scale selection for nine categories of crown closure by female mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the observed distribution of telemetry locations among categories. Availability was the expected distribution of locations based on category proportions within the 95% adaptive kernel seasonal home range.
Figure 28. Patch-scale selection for forest stand age by female mule deer during summer (July 1–Sep 20) in southeastern British Columbia. Use was the cumulative distribution function (CDF) of telemetry locations relative to forest stand age. Availability was the CDF of area within the 95% adaptive kernel relative to forest stand age. Expected values, E(X), are given for both CDFs.
Figure 29. Patch-scale selection for forest stand age by female mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the cumulative distribution function (CDF) of telemetry locations relative to forest stand age. Availability was the CDF of area within the 95% adaptive kernel relative to forest stand age. Expected values, E(X), are given for both CDFs.
Figure 30. Patch-scale selection for elevation by male mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the cumulative distribution function (CDF) of telemetry locations relative to elevation. Availability was the CDF of area within the 95% adaptive kernel relative to elevation. Expected values, E(X), are given for both CDFs.
Figure 31. Patch-scale selection for elevation by female mule deer during summer (July 1–Sep 20) in southeastern British Columbia. Use was the cumulative distribution function (CDF) of telemetry locations relative to elevation. Availability was the CDF of area within the 95% adaptive kernel relative to elevation. Expected values, $E(X)$, are given for both CDFs.
Figure 32. Patch-scale selection for elevation by female mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the cumulative distribution function (CDF) of telemetry locations relative to elevation. Availability was the CDF of area within the 95% adaptive kernel relative to elevation. Expected values, E(X), are given for both CDFs.
Figure 33. Patch-scale selection for slope by male mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the cumulative distribution function (CDF) of telemetry locations relative slope. Availability was the CDF of area within the 95% adaptive kernel relative to slope. Expected values, E(X), are given for both CDFs.
Figure 34. Patch-scale selection for slope by female mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the cumulative distribution function (CDF) of telemetry locations relative slope. Availability was the CDF of area within the 95% adaptive kernel relative to slope. Expected values, E(X), are given for both CDFs.
Figure 35. Patch-scale selection for north-south aspects by male mule deer during summer (July 1–Sep 20) in southeastern British Columbia. The index increased from due north (0.0) to due south (1.0). Use was the distribution of telemetry locations relative north-south aspect. Availability was the distribution of north-south aspects within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 36. Patch-scale selection for north-south aspects by male mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. The index increased from due north (0.0) to due south (1.0). Use was the distribution of telemetry locations relative north-south aspect. Availability was the distribution of north-south aspects within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 37. Patch-scale selection for north-south aspects by female mule deer during summer (July 1–Sep 20) in southeastern British Columbia. The index increased from due north (0.0) to due south (1.0). Use was the distribution of telemetry locations relative north-south aspect. Availability was the distribution of north-south aspects within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 38. Patch-scale selection for north-south aspects by female mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. The index increased from due north (0.0) to due south (1.0). Use was the distribution of telemetry locations relative north-south aspect. Availability was the distribution of north-south aspects within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 39. Patch-scale selection for west-east aspects by male mule deer during summer (July 1–Sep 20) in southeastern British Columbia. The index increased from due west (0.0) to due east (1.0). Use was the distribution of telemetry locations relative west-east aspect. Availability was the distribution of west-east aspects within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 40. Patch-scale selection for west-east aspects by male mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. The index increased from due west (0.0) to due east (1.0). Use was the distribution of telemetry locations relative west-east aspect. Availability was the distribution of west-east aspects within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 41. Patch-scale selection for west-east aspects by female mule deer during summer (July 1–Sep 20) in southeastern British Columbia. The index increased from due west (0.0) to due east (1.0). Use was the distribution of telemetry locations relative west-east aspect. Availability was the distribution of west-east aspects within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 42. Patch-scale selection for west-east aspects by female mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. The index increased from due west (0.0) to due east (1.0). Use was the distribution of telemetry locations relative west-east aspect. Availability was the distribution of west-east aspects within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 43. Patch-scale selection for topographical ruggedness by male mule deer during summer (July 1–Sep 20) in southeastern British Columbia. Use was the distribution of telemetry locations relative to ruggedness. Availability was the distribution of ruggedness values within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 44. Patch-scale selection for topographical ruggedness by male mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the distribution of telemetry locations relative to ruggedness. Availability was the distribution of ruggedness values within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 45. Patch-scale selection for topographical ruggedness by female mule deer during summer (July 1–Sep 20) in southeastern British Columbia. Use was the distribution of telemetry locations relative to ruggedness. Availability was the distribution of ruggedness values within the seasonal home range (95% adaptive kernel). Expected values, $E(X)$, are given for both distribution functions.
Figure 46. Patch-scale selection for topographical ruggedness by female mule deer during winter (Jan 1–Apr 30) in southeastern British Columbia. Use was the distribution of telemetry locations relative to ruggedness. Availability was the distribution of ruggedness values within the seasonal home range (95% adaptive kernel). Expected values, E(X), are given for both distribution functions.
Figure 47. Patch-scale selection for 9 vegetative cover types by mule deer during summer (July 1–Sep 20) and winter (Jan 1–Apr 30) in southeastern British Columbia. The selection index was calculated as (Use – Availability) / (Use + Availability), where use = proportion of telemetry locations in the cover type and availability = proportion of randomly located points in the cover type. The index ranged from -1.0 (no use) to 0.0 (use = availability) to +0.99 (use >> availability). Telemetry locations and randomly located points all were within the seasonal home range (a 95% adaptive kernel for telemetry locations pooled across individuals for a given sex and season).
Figure 48. Mean index of north-south aspect at telemetry locations of mule deer compared to randomly located points for nine categories of crown closure. The aspect index ranged from 0.0 (due north) to 1.0 (due south). Telemetry locations were pooled for both sexes and seasons.
Figure 49. Mean index of west-east aspect at telemetry locations of mule deer compared to randomly located points for nine categories of crown closure. The aspect index ranged from 0.0 (due east) to 1.0 (due west). Telemetry locations were pooled for both sexes and seasons.
Figure 50. Mean aspect index for mule deer telemetry locations versus randomly located points, by sex and season (Summer = July 1–Sep 20, Winter = Jan 1–Apr 30). The north-south aspect index (left side) ranged from 0.0 (due north) to 1.0 (due south). The west-east aspect index (right side) ranged from 0.0 (due west) to 1.0 (due east).
Figure 51. Mean index of north-south aspect at telemetry locations of mule deer compared to randomly located points for nine categories of crown closure by season. The aspect index ranged from 0.0 (due north) to 1.0 (due south). Telemetry locations were pooled for both sexes. Bars extending above the dashed, horizontal line indicate that more telemetry locations or random points were on south-facing slopes. Conversely, bars below the line indicate that more locations or random points were on north-facing slopes.
Figure 52. Mean index of west-east aspect at telemetry locations of mule deer compared to randomly located points for nine categories of crown closure by season. The aspect index ranged from 0.0 (due east) to 1.0 (due west). Telemetry locations were pooled for both sexes. Bars extending above the dashed, horizontal line indicate that more telemetry locations or random points were on east-facing slopes. Conversely, bars below the line indicate that more locations or random points were on west-facing slopes.
Figure 53. Cumulative proportion of mule deer telemetry locations versus random points relative to elevation during summer (Jul 1–Sep 20) and winter (Jan 1–Apr 30) in southeastern British Columbia.
Figure 54. Cumulative proportion of mule deer telemetry locations versus random points relative to slope during summer (Jul 1–Sep 20) and winter (Jan 1–Apr 30) in southeastern British Columbia.
Figure 55. Cumulative proportion of mule deer telemetry locations versus random points relative to north-south aspect during summer (Jul 1–Sep 20) and winter (Jan 1–Apr 30) in southeastern British Columbia. Value of the aspect index ranged from 0.0 (due north) to 1.0 (due south).
Figure 56. Elevation (m) versus slope (degrees) for mule deer telemetry locations and randomly located points in southeastern British Columbia.
Figure 57. Mean elevation by slope category for mule deer telemetry locations versus randomly located points in southeastern British Columbia. Deer locations were pooled across sex and season.
Figure 58. Mean slope by elevation category for mule deer telemetry locations versus randomly located points in southeastern British Columbia. Deer locations were pooled across sex and season.
Figure 59. Mean value of north-south aspect index by elevation category for mule deer telemetry locations versus randomly located points in southeastern British Columbia. Aspect values ranged from 0.0 (due north) to 1.0 (due south) Deer locations were pooled across sex and season.
Figure 60. Interactive effect of west-east aspect and slope on elevation at (A) mule deer telemetry locations versus (B) randomly located points in southeastern British Columbia. Aspect values ranged from 0.0 (due west) to 1.0 (due east). Symbol size is proportional to slope (larger circles = greater slope). Deer locations were pooled across sex and season.
Figure 61. Cumulative proportion of telemetry locations of mule deer versus randomly located points relative to forest stand age during summer (Jul 1–Sep 20) and winter (Jan 1–Apr 30) in southeastern British Columbia.