

# The influence of forest cover on mule deer habitat selection, diet, and nutrition during winter in a deep-snow ecosystem

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## ARTICLE INFO

### Article history:

Received 14 January 2008

Received in revised form 24 April 2008

Accepted 24 April 2008

### Keywords:

Mule deer

Winter range

Forest management

Deciduous cover

Coniferous cover

Diet

Nutrition

## ABSTRACT

Recent research in western North America suggests that open forage areas are a greater limiting factor to mule deer abundance than closed conifer forests. However, much of this work was conducted in ecosystems prone to fire and low snow depths compared to the limits of mule deer range such as the Columbia Mountains, British Columbia, where snow is deep and fires are rare. We used snow track surveys as a measure of habitat use and fecal nitrogen as an index of dietary quality to compare the relative value to mule deer of open deciduous canopies to closed coniferous canopies in a wet ecosystem with deep snow and few fires. Deciduous canopies contain higher levels of understory forage compared to dense coniferous canopies, which are better at intercepting snow. We also evaluated food habits across landscapes with contrasting forest canopies. Results corroborated previous work in that foraging areas such as deciduous stands were strongly selected by deer, despite deeper snow relative to closed coniferous stands. Deer consumed fewer understory shrubs in coniferous-dominated stands, suggesting lower nutritional intake in these stands. Finally, deer appeared to derive a nutritional benefit in landscapes that had a higher proportion of open deciduous canopies, as indexed by fecal nitrogen. However, not all open canopy stands were of equal value to deer – deciduous-dominated stands were selected, whereas clearcuts were avoided. Similarly, not all closed coniferous stands were equally selected: cedar–hemlock stands were avoided whereas Douglas–fir stands were selected and indeed contained the highest proportion of deer tracks. We suggest that winter foraging areas have been underrepresented in management policy in British Columbia, but that snow-interception cover provided by coniferous stands still plays a role in winter deer ecology in deep-snow ecosystems.

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## 1. Introduction

Managing ungulate winter habitat in areas with deep snow is challenging because older trees with large crowns capable of intercepting snow are important to ungulates (Harestad, 1985; Armleder et al., 1994) and are also valuable to the forest industry. Lower snow depth underneath large crowns reduces energy used for ungulate movements (Parker et al., 1984), which is important for foraging and predator avoidance (Wickstrom et al., 1984; Huggard, 1993). In addition, browse under forest crowns is less likely to be buried by snow (Harestad, 1985), and some conifers such as Douglas–fir (*Pseudotsuga menziesii*) and western redcedar (*Thuja plicata*) are fed on by ungulates as are the arboreal lichens attached to their boles and canopy (Dawson et al., 1990; Pauley et al., 1993; Armleder et al., 1994; D'Eon, 2001). Overall, however,

there is far less browse under canopies than open habitats (Jameson, 1967; Thomas, 1979; Peek et al., 2001; Sullivan et al., 2007). Ungulates, therefore, must weight the varied benefits of a forest canopy against the costs of an overall lower abundance of browse under dense canopies (Jameson, 1967; Thomas, 1979; Peek et al., 2001; Sullivan et al., 2006, 2007).

The amount of snowfall will be a major factor in the trade-off between costs and benefits of a conifer canopy. In areas with relatively little snow the value of a canopy is less and deer are relatively abundant. Most research and recommendations for forest management have been in ecosystems with low snowfall (Parker et al., 1996; Peek et al., 2002; Cook et al., 2004; Sullivan et al., 2006, 2007). Thus, uncertainty remains regarding the relative value to ungulates of open versus closed stands in deep-snow ecosystems.

In our study, we estimated the importance of coniferous forest cover compared to open and deciduous cover to wintering mule deer in a region where snow depths are high. Coniferous stands are characterized by lower snow depth, but less forage value, whereas

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stands dominated by deciduous trees (e.g., paper Birch [*Betula papyrifera*] and aspen [*Populus* sp.]) or clearcuts contain more understory forage, but more snow. We also contrasted the value of these vegetation factors, which change over time and forest management regimes, to static factors such as elevation and solar radiation. We assessed the importance of these factors using track transects in snow at 3 spatial scales: (1) the selection of forest overstory composition, estimated by GIS basemaps; (2) the selection of forest understory vegetation, based on field measurements; and (3) diet selection and how this related to availability of field-based understory vegetation estimates. Multi-scaled investigations often reveal relationships that are missed because lack of selection at 1 scale may be due to the abundance of an attribute because of selection at a broader scale (McLellan, 1986). We transcend the spatial scales (Johnson et al., 2004) by relating the broad-scale selection of overstory composition to fine-scale nutritional intake by using fecal nitrogen as an index of dietary quality. This level of analysis goes beyond traditional habitat selection studies by attempting to determine if the organism actually derives a nutritional benefit from the broader-scale pattern of selection.

## 2. Methods

### 2.1. Study area

The study took place in the Columbia Mountains, and was centered on Revelstoke, British Columbia. It was bounded by Downie creek in the north, south to the town of Beaton, covering a linear distance of approximately 100 km. The weather is characterized by high precipitation (100–250 cm/year; Environment Canada, 2005) with most of this falling as snow. Annual average snowfall for the city of Revelstoke (450 m elevation a.s.l.) was 360 cm (S.E. = 26.6) from 1988 to 2007. February temperature averages  $-2.5^{\circ}\text{C}$ , and  $18.2^{\circ}\text{C}$  in July (Environment Canada, 2005).

Valley bottom elevation ranges from 450 to 575 m, and surrounding peaks reach 2900 m. Below 1400 m elevation, the interior cedar–hemlock (ICH) is the main biogeoclimatic ecosystem classification (BEC) zone (Ketcheson et al., 1991). This zone is subdivided into three “subzones and variants”, which are the ICHmw(moist-warm)2, the ICHmw3, and the ICHwk(wet-cool)1. Douglas-fir is dominant in the ICHmw2 and 3, followed by cedar and hemlock. In the ICHwk1, cedar and hemlock are dominant, followed by Douglas-fir. Western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), paper birch, trembling aspen (*Populus tremuloides*), and black cottonwood (*P. balsamifera*) all occur in these zones, although larch is absent outside the ICH mw2. Above 1400 m elevation, the Engelmann spruce-subalpine fir (ESSFwc [wet cold]) BEC zone occurs, which contains mainly Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*).

Shrubs in the ICHmw2 and 3 include falsebox (*Paxistima myrsinites*), thimbleberry (*Rubus parviflorus*), Douglas-maple (*Acer glabrum*), western yew (*Taxus brevifolia*), Utah honeysuckle (*Lonicera utahensis*), black huckleberry (*Vaccinium membranaceum*), devil's club (*Oplanax horridus*), and ocean spray (*Holodiscus discolor*). Most of these shrubs are also present in the ICHwk1, although willow (*Salix* spp.) replaces Utah honeysuckle, and yew and devil's club dominate. Shrubs in the ESSFwc1 include white-flowered rhododendron (*Rhododendron albiflorum*), black huckleberry, and false azalea (*Menziesia ferruginea*).

The most abundant wintering ungulates in the area are mule deer, elk, moose, and small pockets of white-tailed deer (*O. virginianus*). Mountain caribou (*Rangifer tarandus caribou*) also occur, but they migrate to high elevations (1800 m) during late

winter (Apps et al., 2001). Winter predators include wolves (*Canis lupus*), cougars (*Puma concolor*), and wolverines (*Gulo gulo*).

### 2.2. Study design

Previous deer research has indicated that solar aspect and elevation are important determinants of winter habitat use (D'Eon, 2001; D'Eon and Serrouya, 2005; Poole and Mowat, 2005). We therefore divided the study area into the four cardinal aspect classes nested within two elevation classes (<650 m, and 650–1300 m), for a total of eight ecologically based strata. To ensure samples were taken across a broad range of ecological conditions, transects were allocated proportionally within each of these eight strata, at random start locations.

We confined all sampling to late winter (February) because this period is most constraining to ungulate distributions (D'Eon, 2001). Variance partitioning from pilot data indicated that between-transect variability was 2.5 times higher than between-sampling session variability (Serrouya and D'Eon, unpublished data), meaning that effort should be focussed on sampling more transects instead of repeating the same transects within a winter season. We therefore sampled transects once per winter and dispersed field crews throughout the study area to minimize spatial and temporal biases.

### 2.3. Field methods

From start locations we established straight-line transects oriented perpendicular to contour lines. At 100-m intervals along these transects we collected data that were used to gauge habitat “availability”, which was quantified using the following biophysical variables: global positioning system (GPS) location, three snow depths, four estimates of canopy cover using spherical densimeters, visual estimates of tree species composition within a 20-m radius, general habitat type (riparian/wetland, clearcut [logged within 20 years], logging road, deciduous dominated [i.e., trembling aspen, paper birch, black cottonwood], cedar–hemlock dominated, Douglas-fir dominated, and Engelmann spruce/subalpine fir dominated). These same variables were collected each time we encountered an ungulate track, and were the “use” plots. We recorded the number of tracks by species at each use plot. We could not differentiate between mule deer and white-tailed deer. If a transect intersected a trail so that the number of individuals could not be determined, it was recorded as a trail and counted as 5 tracks (Thompson et al., 1989; Poole and Mowat, 2005). If there were >1 tracks within a 10-m portion of a transect, all tracks were recorded, but only one use plot was done. To increase the chance of encountering tracks, we waited a minimum of 36 h after a snowfall ended before field sampling, and recorded the amount of time since the previous snowfall to standardize track occurrences (Thompson et al., 1989).

Along transects we collected deer pellets when they were encountered. Because pellets were on top of the snow, we are confident that they were deposited since the previous snowfall and represented food eaten recently (a few days at the latest). Pellet samples were sent to the Washington State University Wildlife Habitat Laboratory (Pullman, Washington) for laboratory analyses. Twelve samples from independent pellet groups collected at least one transect apart were prepared to determine the amount of fecal nitrogen in each sample (in this case, each sample represented an individual deer). Fecal nitrogen is commonly used as an index of diet quality in wild ungulates (e.g., Leslie and Starkey, 1985; Wehausen, 1995; Osborn and Ginnett, 2001). As well, we made seven composite samples based on a high or low deciduous forest cover stratification, to help ensure that a broad range of forest

cover types were analyzed for regressions. Uncorrected diet composition analyses were performed on these seven samples using microhistological plant identification techniques (Dearden et al., 1975; level B, 50 views). Composite sampling is an accepted technique and commonly applied to obtain more representative samples (Jenks et al., 1989).

During winter sampling we flagged each plot to relocate them in the spring, after snowmelt. The purpose was to conduct browse surveys by recording the presence of browse sign for each shrub species. We also recorded the percent cover of each shrub species and lichen abundance class (Armleder et al., 1992) to determine if those factors influenced habitat selection. For certain shrubs, e.g., falsebox, availability would be impossible to determine during the winter because of snow burial, but deer frequently crater through the snow to locate these shrubs. Measuring their availability in the spring was the only way to gauge selection for these shrub species.

#### 2.4. Data analysis

We imported the Universal Transverse Mercator coordinates of each GPS location into Arcview (ESRI), a GIS package. For each location we extracted elevation, percent slope, aspect in degrees, and solar radiation. Elevation was obtained from a digital elevation model (DEM), which was created from 1:20,000-scale Terrain Resource Inventory Mapping (TRIM). Slope and aspect were derived from the DEM, at a resolution of 25-m pixels. Aspect was treated categorically, using the four vegetation resource inventory (Resources Inventory Committee, 1999) aspect classes (north = 286–59°, east = 60–135°, south = 136–240°, west = 241–285°), plus a fifth class called flat (slopes <10%).

We used a model of “direct” solar radiation created from the DEM (Kumar et al., 1997). This model estimates the solar radiation for each pixel (50 m × 50 m) in kW/m<sup>2</sup>, and hence accounts for hillside shading. Each pixel represented the mean measurements that were taken once every 2 h for a 24-h period each week from 11 January to 31 March. For all analyses, we distinguished between temporally static variables (elevation, slope, aspect, solar radiation, and BEC) and temporally dynamic variables (percent tree composition, crown closure, shrub cover, stand age).

We also extracted GIS-based remotely-sensed forest cover information for each GPS location to determine how this affected selection. Forest cover variables were stand age, tree species composition, crown closure, and disturbance history. We converted crown closure to ‘evergreen crown closure’ by accounting for the proportion of deciduous trees in the stand, to more accurately reflect the ability of the stand to intercept snow.

Our first analyses were univariate comparisons between the proportion of used habitat and what was available in the environment. Proportional use was calculated by dividing the number of tracks within the category of a variable by the total number of tracks. The same was done with the availability plots. We placed little emphasis on the statistical significance between use and availability, because we were more interested in the magnitude of the differences (Johnson, 1999, 2002; Anderson et al., 2000), and how precisely the parameters were estimated. Precision was evaluated by bootstrapping the dataset 1000 times, and presenting 95% confidence intervals (CI; Efron and Tibshirani, 1993; Johnson, 1999), which results in more robust confidence limits and helps account for potential spatial relatedness among transects. We present selection trends across the range of each habitat variable to help determine thresholds. To gauge selection, we present Ivlev’s electivity index (Ivlev, 1961). Selection indices are often criticized because of arbitrary definitions of availability (Garshelis, 2000) so we also present the proportions of habitats used to help alleviate this problem.

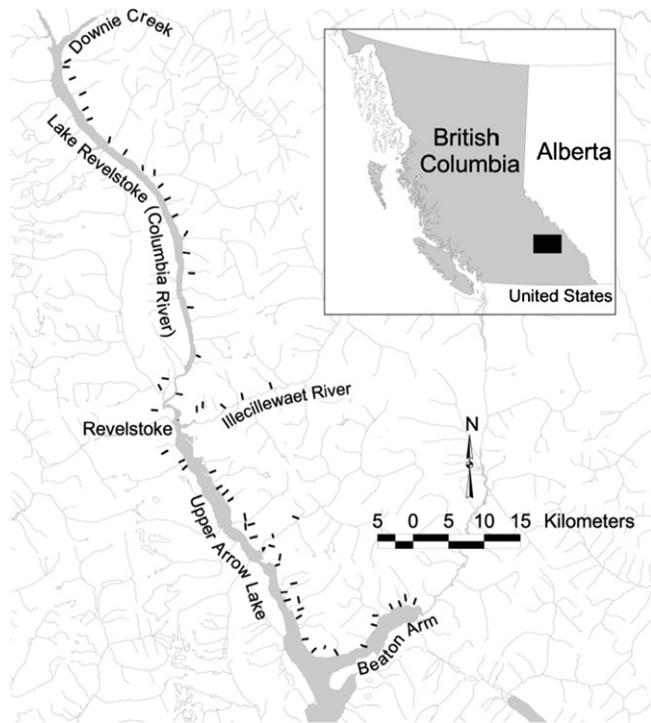
Multivariate analyses were done using logistic regression using the broad-scale (GIS) data, by converting tracks to presence/absence and predicting the probability of detecting a deer. We used an information–theoretic approach to guide the selection of competing multivariate models (Burnham and Anderson, 1998). We developed an *a priori* set of candidate models to explain mule deer habitat selection, based on information from the literature (Pauley et al., 1993; D'Eon, 2001; D'Eon and Serrouya, 2005; Poole and Mowat, 2005). These models included exclusively static factors (i.e. topography), dynamic factors (vegetation), and combinations of the two. We structured models to test competing hypotheses of the importance of areas dominated by coniferous cover, and areas dominated by forage. Forage areas included deciduous stands (measured as percent deciduous tree cover) clearcuts and natural openings (avalanche chutes, shrub fields).

Variables that were highly correlated ( $r > 0.7$ ) were not included in the same models. We selected the “best” candidate model(s) using Akaike information criteria (AIC) (Anderson et al., 2000), and tested for overdispersion (Anderson et al., 1994). If necessary, we corrected for overdispersion using quasi-likelihood methods (QAIC) when  $\hat{c}$  (the ratio of deviance to degrees of freedom) was  $>1$  (Anderson et al., 1994). For each model we present AIC values, the maximized log likelihood ( $\log L$ ), the number of parameters ( $k$ ) and  $AIC\omega$ , and report model fit statistics for the most parameterized model (Anderson and Burnham, 2002). BEC subzone was treated by assigning ordinal values of 1–3 for the ICHmw, ICHwk1, and ESSFwc, respectively. Those zones progress to cooler, moister ecosystems. We present the results of top models (0–4  $\Delta AIC$ ) and the best static-only, and dynamic-only models to evaluate the relative strength of these.

To investigate relationships between deer diets and landscape composition, we regressed fecal nitrogen and diet composition (percent shrubs and percent conifers in diet) against three landscape-level variables: amount of deciduous tree cover, amount of Douglas-fir cover, and amount of coniferous tree cover. We calculated values for these three variables for every location in our study area by using a moving window technique within a GIS. To achieve this, we converted forest cover polygon information to a 25-m × 25-m raster grid. We assigned the amount of deciduous, Douglas-fir, and total coniferous content to each 25-m × 25-m pixel based on forest cover composition information. We then calculated an average value of each variable within a 20 × 20-pixel moving window (i.e., 500 m × 500 m), which represented 25 ha on the ground. This value was assigned to the central pixel within the 25-ha window. In this way we obtained a measure of deciduous, Douglas-fir, and conifer content for each 25-m pixel in the study area – each value for each pixel representing a broader average of the surrounding landscape. This was done, in part, to account for potential spatial differences that occur between where an ungulate ingests a food item to where it defecates.

#### 2.5. Additional sampling during deep-snow year (2004)

Because our sampling took place over two winters, one which was 5% above average (2001; 378 cm total accumulation in Revelstoke) while the other was 7.2% below (2002; 334 cm), we repeated a small portion of our study in February 2004, which was a year where snow depths were 35.7% more than average (489 cm). We did this to determine whether during a deep-snow year, deer would continue to use similar amounts of deciduous versus coniferous cover. Funding was limited so we could only survey eight transects. Thus, we shifted the design such that transects were evenly split among deciduous versus coniferous-dominated stands (randomly assigning transects based on the original criteria may not have resulted in an appropriate split among the two stand

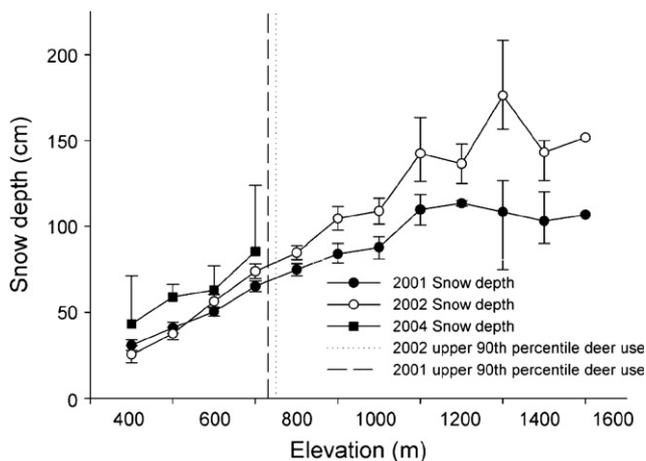


**Fig. 1.** Study area and track encounter transects (black dashes) for a mule deer winter range study in southeastern British Columbia, February 2001 and 2002.

types). The eight transects were each 1100 m long, on similar aspects and bounded by the same elevation. The primary difference was that four transects were in deciduous dominated stands ( $\bar{x} = 61.1\%$  deciduous tree cover, S.E. = 3.3), and the remainder were in coniferous-dominated stands ( $\bar{x} = 86.7\%$  coniferous cover, S.E. = 4.7). We restricted the comparison to GIS (broad scale), and tested differences in track abundance between the two treatments using a *T*-test.

### 3. Results

We surveyed 60 transects during February, 2001; the same transects were surveyed in February, 2002, with an additional transect 6 km N of Revelstoke (Fig. 1). Transects averaged 974 m



**Fig. 2.** Snow depth by elevation class (a.s.l.) for an ungulate winter range study in southeastern British Columbia, February 2001, 2002, and 2004. Also shown is the 90th percentile upper elevation use by deer for 2001 and 2002. Error bars are bootstrapped 95% CI, but lower CIs are removed for clarity (they are approximately symmetrical with upper CIs).

long (slope distance), and a total of 1198 100-m segments were sampled across both years. We counted 529 deer tracks in 2001, compared to 657 in 2002. Track encounter rates (tracks/100 m/days since snowfall [dss]) did not differ markedly between the two years (0.34 in 2001 versus 0.36 in 2002). Some of these tracks may have been white-tailed deer, but all deer ( $n = 24$ ) we observed during the study were mule deer, and 80% of the deer hunted in the area during the study ( $n = 95$ ; harvest policy is identical for both species) were mule deer. There was substantial spatial overlap of deer tracks between the two years. Eighty-nine 100-m transect segments had tracks in 2001, whereas 96 had tracks in 2002, and 53 of those segments shared tracks both years.

Snow depths differed between the two years of study. However, snow depths from 2001 and 2002 began to diverge substantially above 900 m (Fig. 2). This divergence was above where 95% of the deer tracks were located, both in 2001 and 2002. For this reason, we combined both years' data in subsequent analyses.

#### 3.1. Univariate analyses

##### 3.1.1. Temporally static variables

The mean elevation that deer used was 625 m, and 95% of deer use was below 892 m. Deer avoided elevations above 700 m, and preferred steeper slopes, up to 70% (Fig. 3). Deer selection dropped off substantially when slopes exceeded 70% (Fig. 3). Deer displayed a similar pattern for direct solar radiation, with selection dropping off above an apparent threshold of 120,000 kW/m<sup>2</sup> (Fig. 3). South and west aspects were preferred, whereas north, east, and flat aspects were avoided. Deer selection decreased as BEC subzones progressed to cooler, wetter ecosystems (Fig. 3).

##### 3.1.2. Temporally dynamic variables

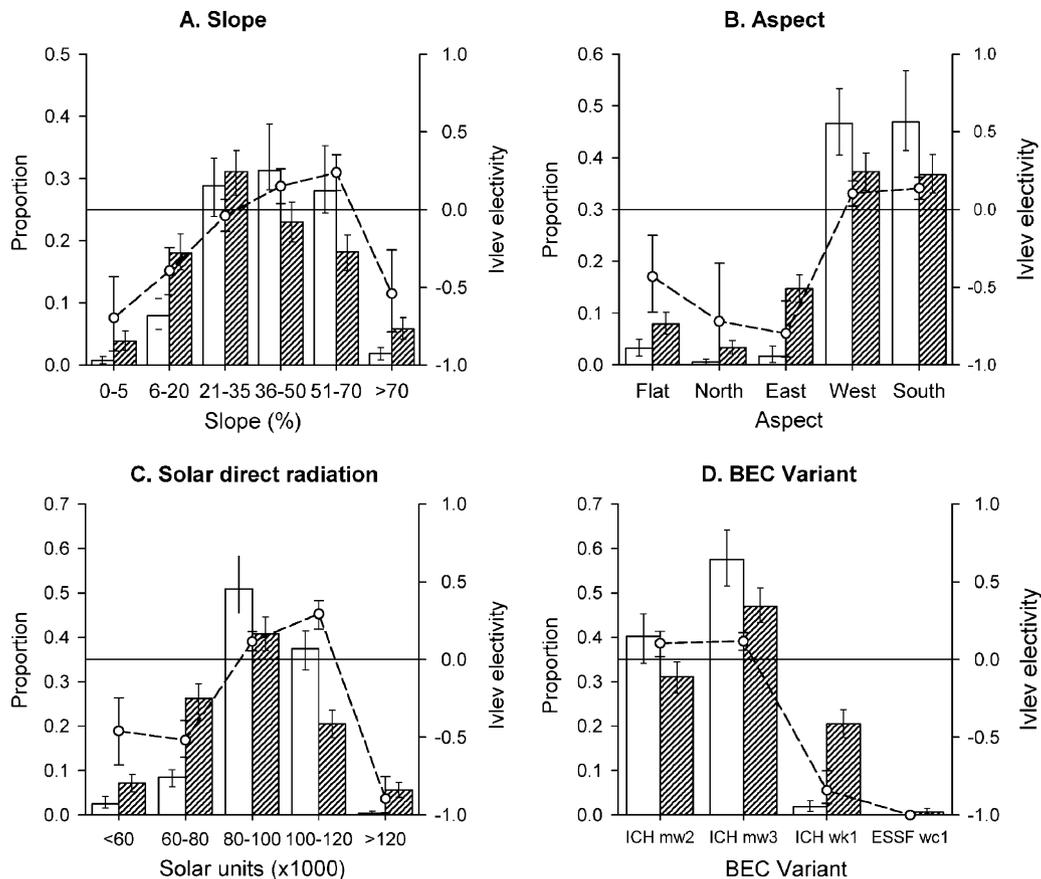
Deer avoided snow depths greater than 50 cm (Fig. 4). They also preferred stands with intermediate levels of crown closure (Fig. 4). Thirty-two percent ( $\pm 4.5\%$ ) of deer tracks were located in "open" habitats (stands with less than 30% evergreen crown closure). Stands with 41–60% Douglas-fir were selected, but stands with very high Douglas-fir composition were avoided (Fig. 4). Deer increasingly selected stands with higher levels of deciduous tree composition (Fig. 4). Deer selected stands of intermediate ages (61–100 years old) when all tree species were analyzed together but selected older stands (101–140 years old) when the analysis was restricted to stands with >60% conifers (Fig. 4).

Deer avoided clearcut stands. They comprised 5% of the study area, but only 0.2% of deer tracks were found in those stands (Fig. 5). Snow depths averaged 114.8 cm in clearcut stands and 71.8 cm in unlogged stands. The dominant habitat type available in the study area was cedar-hemlock stands, accounting for 44.4% of the area, but receiving only 11.2% of deer use (Fig. 5). Deciduous and Douglas-fir dominated stands received disproportionate use relative to what was available (Fig. 5).

Sampling during the 2004 deep-snow year revealed that deer use of deciduous stands (no. tracks/100 m/dss = 2.13, S.E. = 1.54) was >3 times higher compared to those found in coniferous stands ( $\bar{x} = 0.55$ , S.E. = 0.35), but this difference was not significant (*T*-test  $P = 0.36$ ,  $n = 4$ ).

#### 3.2. Multivariate analyses

None of the multivariate models showed signs of overdispersion ( $\hat{c} = 0.97$ ). The most parsimonious model included slope, direct solar radiation, BEC subzone, snow depth, percent deciduous tree cover, percent Douglas-fir tree cover, stand age, and an interaction of age with Douglas-fir (Table 1). Snow depth, BEC subzone, and the interaction term were negatively correlated with



**Fig. 3.** Deer use (clear bars) and availability (shaded bars) of (A) slope, (B) aspect, (C) solar radiation, and (D) BEC variant for winter range study in southeastern British Columbia, February 2001 and 2002. Also shown is Ivlev's electivity index (dashed line). Error bars are bootstrapped 95% CI.

deer presence, whereas the other variables were positively associated with deer presence. The  $R^2$  for the global model was 0.47 and the area under the receiver operating characteristic curve (ROC) was 0.85. Removing BEC subzone from the best model did not greatly affect the model's ability to represent the system ( $AIC\omega_{1/3} = 0.37/0.29 = 1.3$ ; Table 1). However, removing the interaction term yielded a model that was much less likely to represent the system ( $AIC\omega_{1/6} > 10,000$ ).

Models that contain only static variables (model 13) appear to represent deer habitat selection better than models containing only dynamic vegetation-based variables (model 15), but models that contained both types of variables were much stronger (i.e., models 1–12; models 3–12 and 14 are not shown, for brevity; Table 1). All else being equal, the model that included deciduous tree cover (model 5) was much better than the model that included Douglas-fir tree cover (model 7) or coniferous cover (model 9). The model that included both deciduous and Douglas-fir tree cover (model 3) was better than models that included each variable independently.

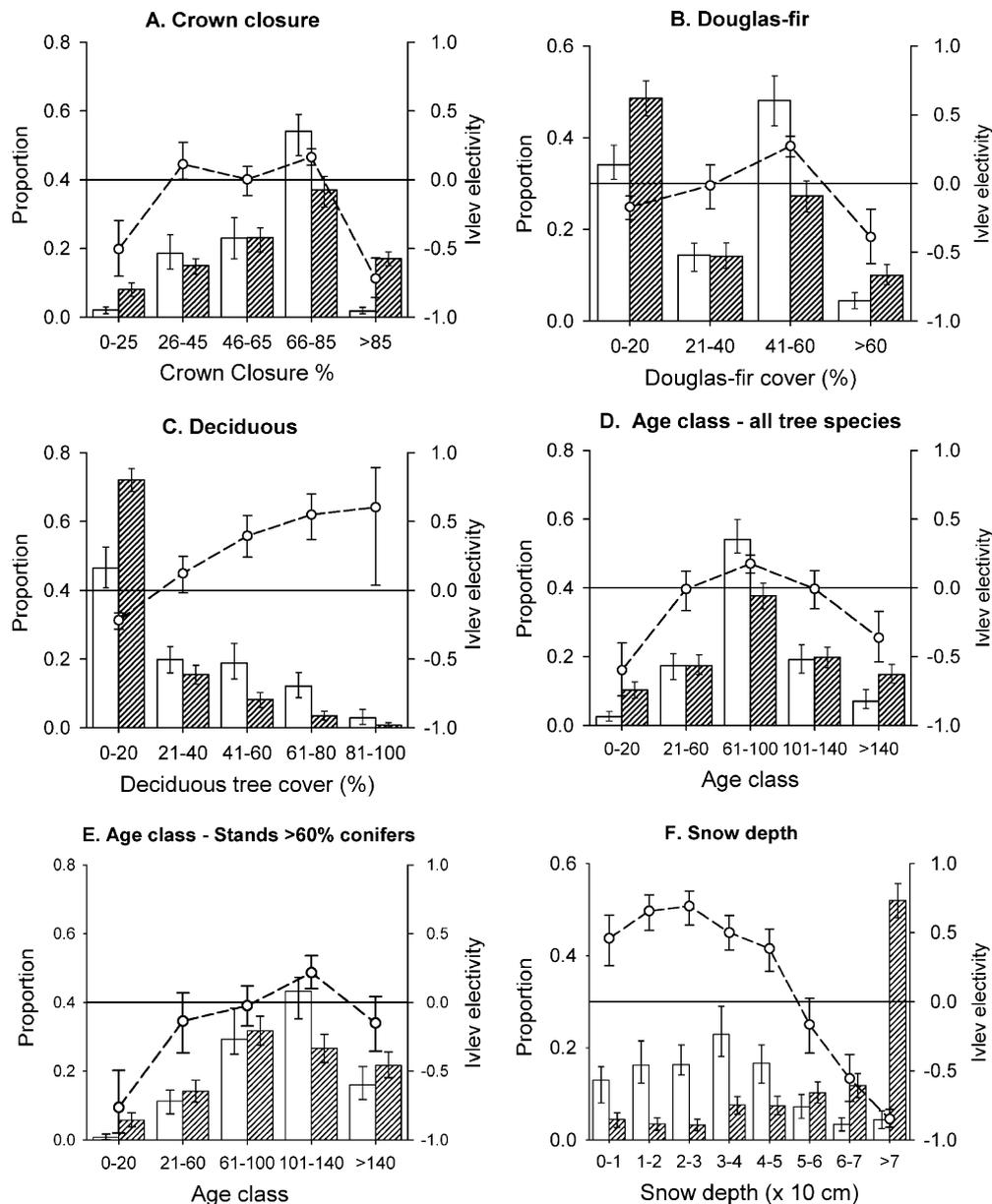
### 3.3. Diet and nutrition

From microhistological pellet analyses, conifer tissue made up the majority of deer diets in 4 of 7 composite samples and made up 55% of deer diets when averaged (S.E. = 10.8, range = 22–94%). Shrub tissue made up the majority of deer diets in 3 of 7 composite samples and made up 35% of deer diets when averaged (S.E. = 8.8, range = 3–64%). The remaining elements in diets consisted of relatively minor amounts of forbs, grasses, ferns, lichens, and mosses. Individual plant species identified as large constituents

(>5%) in diets were western redcedar, western hemlock, willow, western yew, Oregon grape (*Mahonia aquifolium*), and Douglas-maple.

From browse survey data, 33 species of deciduous and coniferous shrubs and trees were recorded within 322 sample plots (all available plant species within 2.5 m from the ground included in browse surveys and therefore included lower tree branches). Fourteen species were present in >5% of plots (Fig. 6). Several species were heavily browsed when present, but contributed relatively little to overall abundance (e.g., red-osier dogwood [*Cornus stolonifera*], western yew; Fig. 6). When browse extent was combined with overall abundance (therefore providing an index of relative importance in deer diets), western redcedar (available in 47% of plots and browsed in 75% of cases) and Douglas-maple (available in 36% of plots and browsed in 97% of cases) were most prominent in deer diets on this basis (Fig. 6). Other important species were white birch, beaked hazelnut (*Corylus cornuta*), thimbleberry, and willow, in descending order.

Fecal nitrogen among 12 pellet group samples was positively related to the amount of deciduous forest cover in the landscape ( $b = 0.0085$ , S.E. = 0.0035,  $R^2 = 0.37$ ,  $P = 0.034$ ; Fig. 7). Fecal nitrogen was negatively related to the amount of coniferous forest cover ( $b = -0.0037$ , S.E. = 0.0032,  $R^2 = 0.12$ ,  $P = 0.28$ ) in the landscape (Fig. 7), but this relationship was not significant. However, amount of shrubs in diets was negatively associated with amount of Douglas-fir ( $b = -1.51$ , S.E. = 0.44,  $R^2 = 0.70$ ,  $P = 0.019$ ) in the landscape (Fig. 8). Consistently, the amount of conifers in diets was positively associated with amount of Douglas-fir ( $b = 1.81$ , S.E. = 0.56,  $R^2 = 0.68$ ,  $P = 0.023$ ) in the landscape (Fig. 8). No significant relationship existed between the proportion of



**Fig. 4.** Deer use (clear bars) and availability (shaded bars) of (A) crown closure, (B) % Douglas-fir tree cover, (C) % deciduous tree cover, (D) age class and (E) age class for coniferous-dominated stands, and (F) snow depth for a winter range study in southeastern British Columbia, February 2001 and 2002. Also shown is Ivlev's electivity index (dashed line). Error bars are bootstrapped 95% CI.

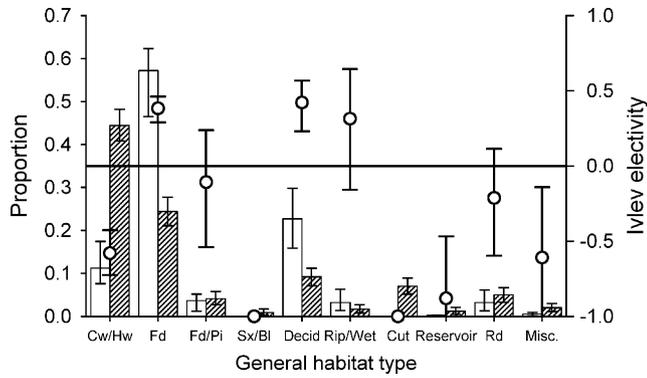
deciduous cover and shrubs ( $b = 0.32$ , S.E. = 0.50,  $R^2 = 0.08$ ,  $P = 0.55$ ) or conifers ( $b = -0.57$ , S.E. = 0.58,  $R^2 = 0.16$ ,  $P = 0.38$ ) in the diet (Fig. 8).

#### 4. Discussion

Deciduous stands and associated understory species were consistently important to wintering deer at all scales and processes investigated in this study. They were used disproportionately at the broadest scale using GIS basemaps, were ranked highly in diet selection using both scat and browse indices, and were weakly associated with higher nutritional value as indicated by fecal nitrogen content. We note that the magnitude of the fecal nitrogen relationship is likely conservative because tannin-rich plants result in disproportionately elevated nitrogen levels in feces despite being less nutritious (Mould and Robbins, 1981), and conifers are

substantially higher in tannins compared to other ungulate foods (Cook, 2002).

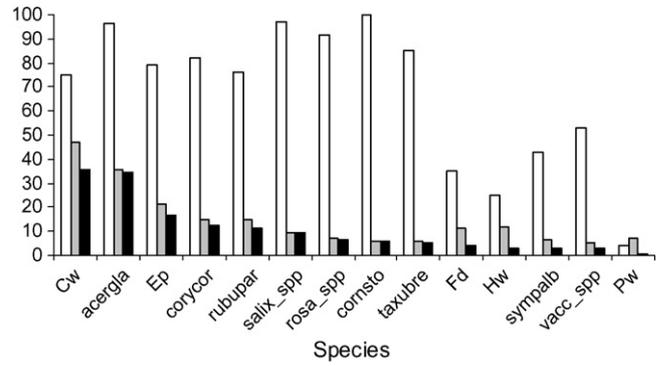
At the broadest scale we studied, even high levels (>80% cover) of deciduous stands were selected. This result is in contrast to Douglas-fir stands, which were preferred only at intermediate levels (40–60%). Predictably though, Douglas-fir stands were associated with higher coniferous foliage and lower shrub content in the diet. Coniferous foliage tends to be of lower nutritional quality than deciduous trees and shrubs (Longhurst et al., 1968; Torgerson and Pfander, 1971), although we did not quantify this in our study area. As well, there was no nutritional benefit to having increased coniferous cover in the landscape, which is in contrast to the deciduous forest cover type. Indeed, the meta-analysis done by Kie et al. (2002) showed that mule deer living in areas dominated by conifers had larger home ranges relative to areas dominated by hardwoods, suggesting that deer had to forage across larger areas to meet their energy requirements in coniferous habitats.



**Fig. 5.** Deer selection of habitat types based on field data. Cw/Hw, western redcedar/western hemlock dominated stands; Fd, Douglas-fir dominated stands; Fd/Pi, a mixture of white pine, yellow pine and Douglas-fir stands; Sx/Bl, Engelmann spruce/subalpine fir dominated stands; Decid, broadleaf deciduous dominated stands; Rip/Wet, riparian or wetland areas; cut, logged stands <20 year old, reservoir is the Columbia River drawdown area; Rd, logging road; Misc. are unclassified habitat categories. Clear bars represent use, shaded bars availability, and open circles represent Ivlev's electivity index. Error bars are bootstrapped 95% CI.

Deer responded to static topographic variables more than dynamic vegetation-based variables. The topographic variables they selected combined to favour low snow depths: lower elevations, warmer aspects and steeper slopes. Specifically, deer avoided snow depths >50 cm. These results are consistent with the findings of other studies in the Columbia Mountains (D'Eon, 2001; D'Eon and Serrouya, 2005; Poole and Mowat, 2005) and elsewhere (Pauley et al., 1993; Mysterud et al., 1997).

Despite the importance of static topographic variables, our modeling also indicated that dynamic vegetation-based variables were necessary to explain deer selection, because models that contained both types of variables fared much better than models that examined the two groups of variables independently. Among vegetation-based variables at the landscape level, deciduous tree stands were the most influential. Deciduous stands were probably preferred because they contain a high proportion of understory shrubs, particularly when compared to dense coniferous stands of similar age or structure (Bunnell et al., 1999; Serrouya and D'Eon, unpublished data). That deciduous stands were at least as valuable to deer as coniferous stands is an important result because it challenges the notion of managing ungulates primarily based on coniferous cover. The idea that coniferous cover limits deer populations has dominated UWR management in BC (e.g., KBLUP, 1997; MAC, 1999; Sullivan et al., 2007), possibly at the expense of investigating the importance of forage areas in winter and during other times of the year (e.g. Parker et al., 1996). This does not mean that



**Fig. 6.** Species frequency of occurrence within 322 sampled plots (grey bars), browse frequency of occurrence within species (i.e., proportion of species occurrences where species was browsed; light bars), and a combined ranking of browsed species occurrence (i.e. proportion of all plots where species was found and browsed; solid bars) in a deer winter track study in Upper Arrow Lake/Lake Revelstoke, British Columbia. Cw, western redcedar; Ep, paper birch; Fd, Douglas fir; Hw, western hemlock; Pw, western white pine; acer gla, *Acer glabrum*; cornsto, *Cornus stolonifera*; corycor, *Corylus cornuta*; rubupar, *Rubus parviflorus*; sympalb, *Symphoricarpos albus*; taxubre, *Taxus brevifolia*; vacc\_spp, *Vaccinium* spp.; Salix, *Salix* spp.; rosa\_spp., *Rosa* spp. Only species with >5% frequency of occurrence within all plots were included.

coniferous cover is unimportant; our modeling reinforced the notion that Douglas-fir stands are valuable to deer, although this factor was not as strong as deciduous stands based on landscape-level models. Nonetheless, Douglas-fir stands contained the highest proportion of deer tracks (Fig. 7). However, our results suggest that open habitats play an important role even in deep-snow ecosystems, based on indices of habitat selection, diet and nutrition. This result likely holds even in deeper snow years based on our sampling from 2004.

Clearcut stands, another potential source of forage, were strongly avoided by deer during this late-winter study, which is consistent with other work (Mysterud et al., 1997; Poole and Mowat, 2005). This result was probably because clearcut stands had on average 43 cm more snow compared to unlogged stands, which likely covered food and restricted movement. On Vancouver Island, Harestad et al. (1982) estimated that 50 cm of snow would bury 50% of the forage in mature forests compared to 80% in young seral stands. Parker et al. (1984) noted that a fresh 50 cm snowfall would result in increased energy expenditure of 498% in clearcuts compared to only 10% in forests, where there is less snow. It is important to note that deciduous stands also had deeper snow relative to mature coniferous stands. However, deciduous stands were used much more than clearcuts, probably because the abundant food supply in deciduous stands partially offset added costs of locomotion (*sensu* Wickstrom et al., 1984).

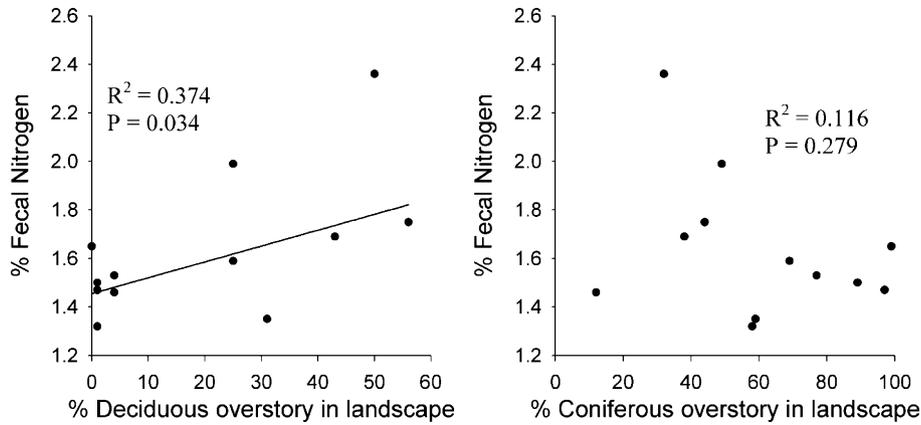
**Table 1**  
Landscape models used to predict the probability of detecting a deer track in the Lake Revelstoke Valley, BC, using logistic regression

No.	Model structure <sup>a,b</sup>	AIC	k	log L	ΔAIC	AICω <sub>i</sub>
1	snow(-) <b>slope(+)</b> <b>solar(+)</b> <b>bec(-)</b> decidbio(+) fdbio(+) age(+) ageXfdbio(-)	1150.41	9	-566.21	0.00	0.37
2	snow <b>solar bec</b> decidbio fdbio age age × fdbio	1150.58	8	-567.29	0.17	0.34
3	snow <b>slope solar</b> decidbio fdbio age age × fdbio	1150.94	8	-567.47	0.53	0.29
13	<b>elev slope solar bec</b>	1391.98	5	-690.99	241.57	1.31 × 10 <sup>-53</sup>
15	decidbio fdbio age age × fdbio clogreen	1481.48	6	-734.74	331.07	4.79 × 10 <sup>-73</sup>

Models included GIS-based variables only, except snow depth. AIC values are a relative indication of model parsimony (lower values indicate more parsimony), k is the number of parameters in the model, log L is the maximized log-likelihood, ΔAIC is the difference in AIC values between the any model and the most parsimonious model, and AICω<sub>i</sub> is the relative influence of each model. R<sup>2</sup> for the global model (no. 1) = 0.47, and ROC = 0.85. Direction of parameter (+ve or -ve) is given in brackets for the global model. n = 1843.

<sup>a</sup> Variables are elev: elevation; slope: % slope; solar: direct solar radiation; bec: biogeoclimatic subzone; fdbio, conifbio, decidbio: an index of overstory biomass of Douglas-fir, conifers, and deciduous trees, respectively; snow: snow depth; clogreen: evergreen crown closure; age: stand age.

<sup>b</sup> Bold font: static topographic variables; regular font: dynamic variables.

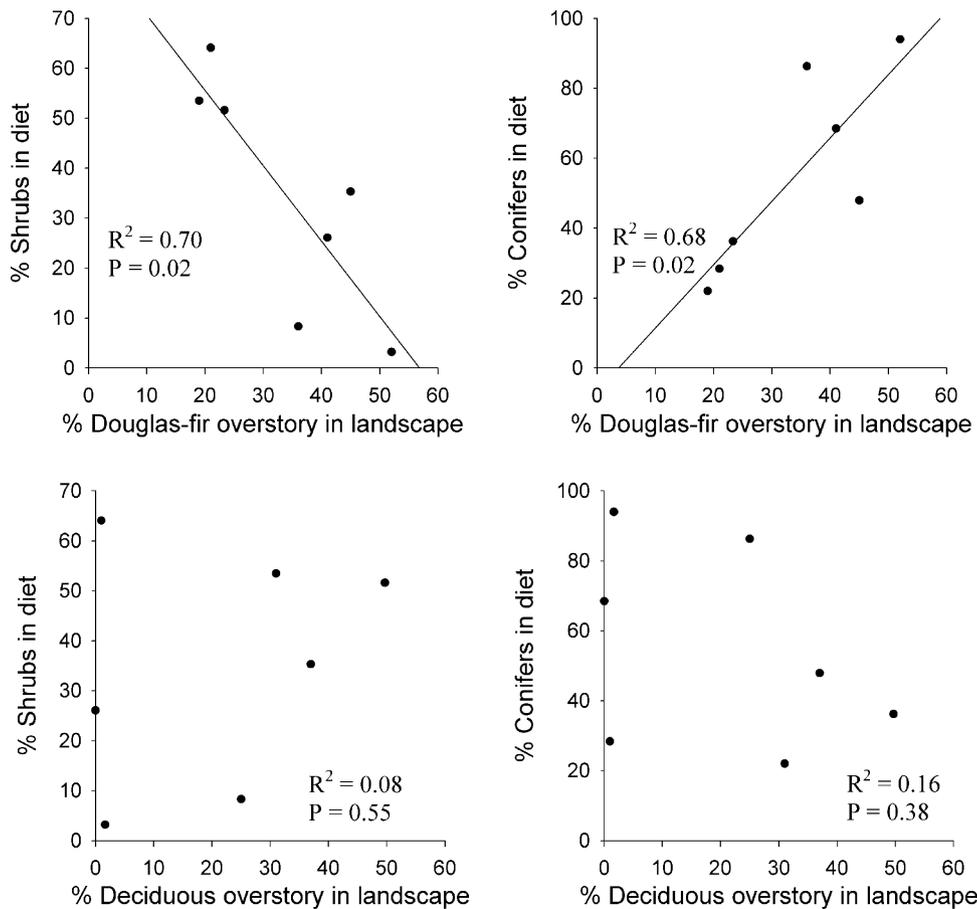


**Fig. 7.** Amount of fecal nitrogen in 12 deer pellet samples versus amounts of deciduous and conifer forest cover in the landscape in Upper Arrow Lake/Lake Revelstoke, British Columbia. Landscape variables derived from a moving window analysis of forest cover data.

**5. Conclusion**

In our study, we found the most important vegetation-based factor to be deciduous stands that originated from fires about 90 years ago. Currently, these stands have little economic value, so protecting them should pose little conflict with forest management. Pursuing such a strategy would also be beneficial to broader biodiversity objectives with no added effort because deciduous stands are important to many other organisms, including insects, birds and lichens (Bunnell et al., 1999).

Eventually though, conifers will regenerate in these areas and shrub production will decrease. If managing for mule deer is a desired goal, then maintaining the value of these stands will require fires of similar intensity to those that created them, removing conifers by mechanical methods, or learning to use silvicultural practices that accommodate deciduous stands and the forage species they contain. Other landscape-level prescriptions can include favouring forest harvesting on cooler aspects (i.e., <80,000 kW/m<sup>2</sup>), and removing coniferous species other than Douglas-fir. Retention of mature conifers could be focussed



**Fig. 8.** Amount of shrub and conifer diet content versus amount of deciduous and conifer forest cover in the landscape for seven composite deer samples in Upper Arrow Lake/Lake Revelstoke, British Columbia. Diets derived from microhistological fecal analyses; landscape variables derived from a moving window analyses of forest cover data.

on patches of Douglas-fir within or adjacent to deciduous stands, or Douglas-maple shrub fields.

Although Peek et al. (2002) presented compelling evidence that increasing Douglas-fir cover over time negatively affected mule deer populations, their ecosystems contain substantially less snow and are fire driven, unlike the ecosystems within our study area where snow is deeper and fires rare. Our work corroborates Peek et al.'s (and see Sullivan et al., 2007) to a certain degree, by demonstrating that deciduous stands (i.e. forage areas) are selected by deer. In British Columbia, the value of these stands has not been fully recognized to date in research or management plans (Poole and Mowat, 2005; Sullivan et al., 2007). However, in deep-snow zones there is likely value in maintaining Douglas-fir cover (Armleder et al., 1994), as suggested by the selection of intermediate levels of Douglas-fir cover in our study area. Broad-scale management experiments that manipulate the amount and configuration (Kie et al., 2002) of coniferous versus deciduous cover and measure deer abundance as a response would be an efficient strategy to determine ultimate factors that limit mule deer populations in deep-snow zones.

### Acknowledgements

J.T. Croston, R. Duncan, J. Herbers, M. Howard, D. Karassovitch, J. Kernohan, K. Lessard, T. Lloyd, T. Merriman, G. Pavan, B. Sinclair, and S. Stotyn provided field assistance. V. Van Tongeren provided skilled GIS assistance. C. Pike of Bell Pole Company and B. King of Kokanee Forests Consulting assisted with logistics. Funding was provided by Bell Pole Company, through Forest Renewal BC and the Forest Investment Account, and by the Columbia Forest District's Small Business Forest Enterprise Program. L. Harding provided comments on earlier drafts of this report. Finally, we would like to thank Jack Wierzchowski for deriving the solar model.

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