# Grizzly bears and forestry
# II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada

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## Abstract

We assessed the occurrence and fruit production of 13 grizzly bear foods in west-central Alberta, Canada, to better understand use of clearcuts by grizzly bears. Comparisons were made between clearcuts and upland forest stands, while specific models describing food or fruit occurrence within clearcuts were developed from canopy, clearcut age, scarification, and terrain-related variables using logistic regression. Ants, *Equisetum* spp., *Hedysarum* spp., *Taraxacum officinale*, *Trifolium* spp., and *Vaccinium myrtilloides* occurred with greater frequency in clearcuts, while *V. caespitosum*, *V. membranaceum*, and *V. vitis-idaea* were more likely to occur in upland forests. No differences were evident for *Arctostaphylos uva-ursi*, *Heracleum lanatum*, *Shepherdia canadensis*, and ungulate pellets, an indicator of ungulate abundance. Mechanical scarification negatively impacted the occurrence of *A. uva-ursi*, *Hedysarum* spp., and *S. canadensis*, while weaker effects were apparent for ants and ungulate pellets. In contrast, the occurrence of *Taraxacum officinale* and *Trifolium* spp. were greater in scarified clearcuts. Age of clearcut or canopy cover was well correlated with the occurrence of most foods. For some species, however, terrain-derived variables predicted occurrence best. Fit and model classification accuracy using independent data proved good for most species.

Patterns of fruit occurrence were related to canopy cover, with little support for other environmental covariates. In total, average fruit production for six fruit-bearing species was estimated at 22.9 kg/ha for clearcuts and 32.3 kg/ha for forests, a non-significant difference and generally less than that reported elsewhere in grizzly bear range. *V. caespitosum* and *V. membranaceum* complex had higher fruit production in clearcuts, while *V. vitis-idaea* had greater fruit production in forests. No difference in fruit production between clearcuts and forests was evident for the remaining species. Overall, we found that clearcuts provided a diverse array of food resources for grizzly bears, particularly roots and tubers, herbaceous materials, and ants. Although fruit production was similar between clearcuts and forests, the occurrence of other food resources likely explains the seasonal use of clearcuts by grizzly bears. We suggest that forest design and silviculture consider strategies that maximize grizzly bear food abundance, while minimizing human access. Further enhancement of foods negatively impacted by silvicultural treatments may be required.

*Keywords:* Alberta; Grizzly bear; Good; Forestry; Fruit; Logistic regression

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## 1. Introduction

Understanding the potential impacts of forest management on rare or threatened species is a primary topic of forest ecology and conservation biology. In the Rocky Mountain ecosystems of the northern United States and southern Canada industrial resource extraction activities, including forestry, threaten the persistence of grizzly bear (*Ursus arctos*) populations (Banci et al., 1994; Clark et al., 1996; McLellan, 1998). Much of this threat relates to risk of human-caused mortality from increases in human access (McLellan and Shackleton, 1988; Benn and Herrero, 2002; Nielsen et al., 2004a). Forestry activities can further impact grizzly bears through changes in landscape composition, configuration, and structure (Reed et al., 1996; Tinker et al., 1998; Popplewell et al., 2003).

Optimal grizzly bear habitat has generally been considered a blend of forested and non-forested habitats (Herrero, 1972). One might therefore expect certain forest disturbances to be beneficial to bears, especially in fire-adapted forest ecosystems with a history of fire suppression (Tande, 1979; Andison, 1998; Rhemtulla, 1999). As young fire-regenerated stands mature and effective fire suppression continues, timber harvesting provides a consistent mechanism of disturbance and forest renewal required for early seral specialists.

Despite a potential for habitat improvement, many studies have shown a pervasive avoidance of clearcuts by grizzly bears (Zager et al., 1983; Waller, 1992; McLellan and Hovey, 2001). Wielgus and Vernier (2003) and Nielsen et al. (2004b), however, observed use of clearcuts by grizzly bears in forest-managed landscapes. Nielsen et al. (2004b) suggested that differences between avoidance and selection of clearcuts were likely due to landscape and temporal contexts. The foothills of west-central Alberta lacked extensive natural openings, early seral fire-regenerated forests, and alpine meadows, which contrasted with other studies located in mountainous terrain where such habitats were common. As secure (free of human disturbance) high-quality habitats were readily available, there was little reason for selection of the non-secure alternative (i.e., clearcuts). Previous studies have also been based on VHF radiotelemetry data, where daylight locations are typical and seasonal data pooled. Nielsen et al. (2004b) found seasonal differences in selection of clearcuts, as well as greater use during the crepuscular and nighttime periods. Clearcuts appeared to provide an alternate habitat resource for certain landscape and temporal contexts, albeit a potentially risky one at that (Benn and Herrero, 2002; Nielsen et al., 2004a).

Loss of early seral forests and natural openings has the potential to cause population declines in bears (Beecham, 1980, 1983; Irwin and Hammond, 1985; Lindzey et al., 1986; Noyce and Coy, 1989; McLellan and Hovey, 2001). Young regenerating forests contain greater abundances of most critical bear foods including fruits, ants, ungulates, green herbaceous vegetation, roots, and other subterranean foods (Martin, 1983; Zager et al., 1983; Irwin and Hammond, 1985; Knight, 1999). Availability of consistent high-quality foods shapes individual nutritional level and ultimately population size (Craighead et al., 1995). However, a general sense of how specific environmental factors and past management actions influence distribution patterns of food resources, especially within successional clearcuts, is lacking. Previous food modeling efforts have focused on protected mountainous ecosystems like Yellowstone (Mattson, 2000) or Jasper (Nielsen et al., 2003) National Parks, where forest harvesting does not occur and populations are generally considered secure. Given the potential for habitat and population change outside of protected areas, an examination of food resource availability and abundance for forest management areas is a conservation priority. Identification of food patches within forest management stands provides opportunities for protection, maintenance, and enhancement of grizzly bear habitats. Moreover, specific assessments of food resource availability allow for fine-level interpretations of selection and inferences of mechanism (Morrison, 2001). Ultimately the understanding of critical food resources will allow for better grizzly bear management and conservation.

Here we explore the distribution of grizzly bear foods in an attempt to better understand the observed behavior of grizzly bears in west-central Alberta, Canada (Nielsen et al., 2004b). Specifically, we investigated how scarification, canopy cover, clearcut age, and terrain characteristics influenced the occurrence of 13 grizzly bear foods, while further examining how fruit occurrence and production varied for six

fruit-bearing species. Our objectives were three-fold: (1) determine whether differences in grizzly bear foods occurred between upland forests, our reference condition, and clearcuts; (2) develop local models describing grizzly bear food occurrence within clearcuts; and (3) describe patterns reflecting fruit and non-fruit producing clearcuts, together with an overall comparison of fruit production between clearcuts and upland forest sites. We hypothesized that forest disturbance through clearcut harvesting enhances the occurrence and diversity of grizzly bear foods. Food resources were expected, however, to be patchy and responding to local environmental gradients and management history, thereby requiring additional environmental covariates. Relationships between food resources and clearcut harvesting should help explain patterns in grizzly bear habitat use as well as provide on-the-ground management solutions to conservation problems.

## 2. Methods

### 2.1. Study area and field sampling

The environmental characteristics of the study area are described fully in Nielsen et al. (2004b). During the growing seasons (June–August) of 2001–2002, we established 355 sample plots within clearcuts and 183 sample plots within reference forest stands. All reference forest stands used were in upland sites dominated by coniferous tree species having a minimum composition of 20% lodgepole pine and not disturbed by anthropogenic activities. Upland conifer stands are one of the primary targets for local clearcut harvesting. Based on geographical information system (GIS) fire history maps, reference forest plots averaged 105 ($\pm$37 S.D.) years of age. Sampling procedures were the same for both clearcuts and forest stands. We used a GIS to identify random coordinates stratified within clearcut and upland forest sites based on a landcover classification provided by Franklin et al. (2001). To ensure an approximately equal proportion of plots within different aged clearcuts, we used a stratified random design to assign random clearcut locations to 5-year age classes. Age was not considered as a stratum for upland forest sites. A small number of randomly selected grizzly bear locations identified

from global position system (GPS) radiotelemetry data were added as additional plots to increase sample size. We navigated to all field coordinates using a hand-held Garmin GPS III plus unit, attempting to locate the plot center to within no more than 10 m of the coordinates.

At each field plot, we established a 20-m transect running south-to-north with the 10 m location being the plot center. Five 0.5 m$^2$ (70.7 mm $\times$ 70.7 mm) herbaceous quadrats were established along each transect at 5 m intervals. Within these quadrats, we recorded the presence of 10 grizzly bear food items. The presence of *Shepherdia canadensis* was measured in the shrub-layer (plants >0.5 m in height) along a belt transect 1 m $\times$ 20 m (20 m$^2$) in size. At each plot, we estimated fruit production for *Arctostaphylos uva-ursi*, *S. canadensis*, and all *Vaccinium* species. Berries were counted within herbaceous quadrats (*A. uva-ursi* and *Vaccinium* spp.) or belt transects (*S. canadensis*) using hand-held tally counters and standardized to a per hectare basis. A sub-sample of ripe fruit was weighed and used to estimate average fresh weight productivity (kg/ha) for each species. Given that berries were not present for the entire sampling period, we considered only those plots visited on or after 15 July and before 1 September to be available for characterizing fruit presence and productivity. Finally, we recorded the presence of ants (in mounds and/or woody debris) and ungulate pellets using meander searches within 10 m of either side of the established transect (20 m $\times$ 20 m; 400 m$^2$). We consider ungulate pellets as an index of animal use and not a directly scalable measure of biomass or ungulate density. Caution should be given to interpretation of forest and non-forest occurrence of pellets, as biases are known to occur (Collins and Urness, 1979). All analyses reported here were at the level of the plot and thus all five herbaceous quadrats were combined. Taxonomy of vascular plants follows that of Voss (1994).

### 2.2. Predictor variables

We dummy coded each plot to identify whether it was in a clearcut (1) or forest stand (0). For models specifically examining food occurrence within clearcuts, we queried age and silvicultural history of sites using a GIS forestry database provided by Weldwood

of Canada Ltd. (Hinton, Alberta). However, given the small sample of clearcuts visited relative to the availability of different silvicultural (site preparation) treatments, we were forced to dissolve silvicultural history into either scarified (1) or non-scarified (0) treatments, again using dummy coding.

To assess terrain-influenced conditions, we used a 26.7-m digital elevation model (DEM) that described the elevation and local micro-site conditions. From this DEM, we estimated elevation (km) for each plot. We further derived two terrain-related variables from the DEM. First, we calculated an index of soil wetness commonly referred to as the compound topographic index (CTI). CTI has previously been found to correlate with several soil attributes including horizon depth, silt percentage, organic matter, and phosphorous (Moore et al., 1993; Gessler et al., 1995). We used CTI as a surrogate for soil conditions, since a soil survey was not available for the entire area. CTI was calculated from the DEM using the spatial analyst extension in ArcView 3.2 and a CTI script from Rho (2002). Our second DEM-derived variable was a slope-aspect index (SAI) from Nielsen and Haney (1998), modified from the Beer's aspect transformation (Beers et al., 1966) and having the following form:

$$SAI = \sin(\text{aspect} + 225) \times \left(\frac{\text{slope}}{45}\right) \qquad (1)$$

where aspect and slope were derived from the DEM and measured in degrees. Slopes for all sites were $\leq 45°$, thus the sine wave was scaled from a flat line at a $0°$ slope to that of $-1$ (mesic northeast aspect) or $+1$ (xeric southwest aspect) at a $45°$ slope. Our final predictor variable was average canopy cover, estimated for each plot using a spherical densiometer (Lemon, 1956). Spherical densiometer readings were taken above each herbaceous quadrat facing the four cardinal directions (north, east, south, and west) and averaged over the entire plot (all five quadrats). Quadratic terms were fit for age, canopy, CTI and elevation given that nonlinear relationships were likely (Vaughan and Ormerod, 2003).

## 2.3. Model building strategies and statistical methods

### 2.3.1. Grizzly bear food occurrence for clearcuts versus reference forests

We used logistic regression to contrast the occurrence of 13 grizzly bear foods (Table 1) for clearcuts (1) and upland forests (0). Important food resources were based on locally reported food habits (Hamer and Herrero, 1987; Nagy et al., 1989; Hamer et al., 1991; McLellan and Hovey, 1995). We report all logistic regression results as odds ratios (Hosmer and Lemeshow, 1989) with the reference category being forest plots. These odds ratios were interpreted as the odds that grizzly bear foods were occurring in clearcuts compared with that of reference upland forest stands. We used a likelihood ratio $\chi^2$-test to determine the significance of individual food models.

Table 1
List of grizzly bear foods examined in clearcuts and upland forest stands of west-central Alberta, Canada

| Grizzly bear food | Food item number | Type of food or feeding activity | Season of use |
|---|---|---|---|
| Ants | 1 | Myremocaphagy | Summer |
| *A. uva-ursi* | 2 | Fruits | Spring and late summer |
| *Equisetum* spp. | 3 | Herbaceous | Summer |
| *Hedysarum* spp. | 4 | Roots/tuber digging | Spring and fall |
| *H. lanatum* | 5 | Herbaceous | Summer |
| *S. canadensis* | 6 | Fruits | Late summer and fall |
| *T. officinale* | 7 | Herbaceous | Spring and summer |
| *Trifolium* spp. | 8 | Herbaceous | Spring and summer |
| Ungulates (pellets) | 9 | Carnivorous | Spring to early summer |
| *V. caespitosum* | 10 | Fruits | Late summer and fall |
| *V. membranaceum* | 11 | Fruits | Late summer and fall |
| *V. myrtilloides* | 12 | Fruits | Late summer and fall |
| *V. vitis-idaea* | 13 | Fruits | Late summer and fall |

### 2.3.2. Distribution of grizzly bear foods in clearcuts

We examined grizzly bear food distribution for clearcuts by modeling their occurrence as a function of canopy, age, scarification, elevation, CTI, and SAI. Clearcut plots were divided into two groups following a random sample test set validation. The first group, the model-training group, represented a random 85% sub-sample of plots used for model development, while the remaining sub-sample (15%), the model-testing group, were used for assessing model performance by independent validation. Using model-training data and explanatory variables (Table 2), we developed logistic regression models describing the occurrence of each grizzly bear food item. Linear explanatory variables were assessed for collinearity prior to modeling through Pearson correlation ($r$) tests and variance inflator function (VIF) diagnostics. All variables with correlations ($r$) >|0.6|, individual VIF scores >10, or the mean of all VIF scores considerably larger than 1 (Chatterjee et al., 2000) were assumed to be collinear and not included within the same model structure. Using these guidelines, we found that age and canopy were strongly correlated ($r = 0.66$) and therefore were not considered for inclusion in the same candidate model. No further evidence of collinearity was evident.

Using these predictor variables, we generated six a priori candidate models (Table 3). We evaluated model selection using Akaike's information criteria (Burnham and Anderson, 1998; Anderson et al., 2000) with a small sample size correction (AIC$_c$). Akaike weights ($w_i$) were used to determine the approximate 'best' model given the data and candidate models tested for each bear food. We assessed fit and predictive accuracy of training data using Hosmer and Lemeshow (1980, 1989) goodness-of-fit $\chi^2$-tests ($\hat{C}$) and receiver operator characteristic (ROC) area under the curve estimates. Significant $\hat{C}$-values indicated poor fit between the model and data, while ROC scores were assessed based on their value falling into one of three categories. Those ranging from 0.5 to 0.7 were taken to represent 'low' model accuracy, while values between 0.7 and 0.9 were considered 'good', and finally those above 0.9 were considered to have 'high' model accuracy (Swets, 1988; Manel et al., 2001).

We used our withheld model-testing data to further assess the fit ($\hat{C}$) and predictive performance (ROC) as model verification. Finally, as an additional validation, we assessed the predictive capacity of individual

Table 2
Environmental variables used to predict the occurrence of grizzly bear foods within west-central Alberta clearcuts

| Variable code | Variable description | Units and range | Data source |
| --- | --- | --- | --- |
| Age | Age | Years (0–46) | GIS forest polygons |
| Canopy | Canopy | % Canopy (0–100) | Field measurements |
| CTI | Compound topographic index | Index (8–21) | GIS model from DEM |
| Elev | Elevation | Metres (957–1596) | DEM |
| Scar | Scarification | Yes (1) or no (0) | GIS forest polygons |
| SAI | Slope-aspect index | Index (−1 to 1) | GIS model from DEM |

Table 3
A priori candidate models used for assessing distribution of grizzly bear foods within clearcuts of west-central Alberta

| Model | Model structure | Model name | $K$ |
| --- | --- | --- | --- |
| 1 | Scar + age + age$^2$ | Scarification-age | 4 |
| 2 | Scar + canopy + canopy$^2$ | Scarification-canopy | 4 |
| 3 | CTI + CTI$^2$ + elev + elev$^2$ + SAI | Terrain | 7 |
| 4 | Canopy + canopy$^2$ | Canopy | 3 |
| 5 | Scar + age + age$^2$ + CTI + CTI$^2$ + elev + elev$^2$ + SAI | Mixed-age | 9 |
| 6 | Scar + canopy + canopy$^2$ + CTI + CTI$^2$ + elev + elev$^2$ + SAI | Mixed-canopy | 9 |

Model number, parameter structure (variables), name, and total number of parameters (including constant) used for calculating Akaike weights ($w_i$) for model selection.

AIC$_c$-selected grizzly bear food models for 136 independent field plots collected for separate purposes within the same study area in 2002. Although these independent plots were collected at a different scale (5 quadrats of 1 m$^2$ size), we felt that a general secondary validation was worthwhile. To determine the predictive capacity of our models for these data, we chose a probability cut-off point for AIC$_c$-selected grizzly bear food models that maximized both specificity and sensitivity curves simultaneously (Swets, 1988). Using AIC$_c$-selected model coefficients, we estimated the probability of occurrence for each grizzly bear food item and predicted either a presence ($\geq$cut-off point) or absence (<cut-off point) for each of the 136 independent plots. We estimated the percent correctly classified (PCC) for each species by determining the proportion of total plots correctly predicted. We considered models with a PCC of $\geq$70% to be reasonably predictive. Finally, using the AIC$_c$-selected model structure we estimated probabilities of occurrence for each variable and food item by exploring the range of predictions for that factor (within the observed range, Table 2), while holding all other variables in the model at their mean level. We plotted these predictions to provide visual interpretation of responses and estimated optima.

### 2.3.3. Distribution of fruit in clearcuts

To examine factors influencing the occurrence of fruit production within clearcuts, we again used logistic regression and the six a priori candidate models described in the previous section. A total of six species were examined for fruit production: four species of *Vaccinium*, *A. uva-ursi*, and *S. canadensis*. We used a conditional modeling strategy including only those locations where the species was present to examine fruit occurrence. At these species presence sites, we compared plots that lacked fruit production (0) with those where fruit production was present (1) during the fruiting period (15 July–31 August). Failure to discriminate the two events was interpreted to mean that berry production was random with respect to the examined variables and candidate models and thus simply mimicking the distribution of the species. Due to relatively low sample sizes resulting from the absence of species and/or berry-producing sites, along with our limited berry season, we combined both 2001 and 2002 field seasons. Similarly, *Vaccinium caespi-*

*tosum* and *V. membranaceum* were too uncommon to model individually. Instead, we combined the two species into a *V. caespitosum–membranaceum* complex. We report the general frequency of fruit, given the presence of the species, while further estimating the position at which fruit occurrence was maximized for individual AIC$_c$-selected variables.

### 2.3.4. Fruit productivity for clearcuts and reference forests

Average productivity of *A. uva-ursi*, *S. canadensis*, and 4 species of *Vaccinium* were estimated for clearcut and upland forest stands on a per hectare basis. We examined fruit production for two separate conditions during the fruiting period: (1) presence-only sites, where average fruit production was estimated for only those plots where that species was initially present and (2) all sites where, regardless of a conditional presence of the species, fruit production was estimated. Finally, we compared the difference in estimated average fruit production for all sites within clearcuts and forests for each species or species complex, along with the total fruit production, by using Mann–Whitney *U*-tests.

## 3. Results

### 3.1. Grizzly bear food occurrence in clearcuts versus reference forests

Ants, *Equisetum* spp., *Hedysarum* spp., *T. officinale*, *Trifolium* spp., and *V. myrtilloides* had significantly higher occurrence in clearcuts than upland forest sites (Table 4). *T. officinale* had the largest odds ratio at 13.9, with an observed difference in plot frequency of 38.9% for clearcuts and only 4.4% for upland forests. Although not as substantial, *Trifolium* spp., ants, and *Hedysarum* spp. also had high odds ratios of 6.7, 5.4, and 4.3, respectively, while *Equisetum* spp. and *V. myrtilloides* had smaller, but still significant odds ratios of 2.4 and 1.8.

In contrast to those grizzly bear foods positively associated with clearcuts, three species, *V. caespitosum*, *V. membranaceum*, and *V. vitis-idaea*, were more likely to occur in upland forests (Table 4). Although *V. membranaceum* and *V. vitis-idaea* had similar odds ratios at 0.2, their observed frequency was substantially different. *V. membranaceum* occurred at a 6.2

Table 4
Frequency of occurrence for 13 grizzly bear foods within clearcut ($n = 355$) and reference forest ($n = 183$) plots

| Grizzly bear food item | Clearcut frequency | Forest frequency | Odds ratio | S.E. | Model LR $\chi^2$ | $P$ |
|---|---|---|---|---|---|---|
| Ants | 65.9 | 26.2 | 5.44 | 1.098 | 78.42 | <0.001 |
| *A. uva-ursi* | 21.7 | 19.1 | 1.17 | 0.267 | 0.49 | 0.485 |
| *Equisetum* spp. | 43.9 | 24.6 | 2.40 | 0.486 | 20.01 | <0.001 |
| *Hedysarum* spp. | 10.7 | 2.7 | 4.27 | 2.069 | 12.29 | 0.001 |
| *H. lanatum* | 4.2 | 5.5 | 0.76 | 0.320 | 0.41 | 0.523 |
| *S. canadensis* | 17.8 | 14.2 | 1.30 | 0.330 | 1.12 | 0.290 |
| *T. officinale* | 38.9 | 4.4 | 13.92 | 5.253 | 88.92 | <0.001 |
| *Trifolium* spp. | 23.4 | 4.4 | 6.67 | 2.554 | 37.23 | <0.001 |
| Ungulates (pellets) | 36.1 | 39.9 | 0.85 | 0.159 | 0.76 | 0.385 |
| *V. caespitosum* | 37.8 | 49.7 | 0.61 | 0.113 | 7.09 | 0.008 |
| *V. membranaceum* | 6.2 | 22.4 | 0.23 | 0.229 | 28.87 | <0.001 |
| *V. myrtilloides* | 14.7 | 8.7 | 1.79 | 0.540 | 4.02 | 0.045 |
| *V. vitis-idaea* | 51.0 | 81.4 | 0.24 | 0.517 | 50.22 | <0.001 |

Odds ratio ($\pm$S.E.) of finding grizzly bear foods within clearcuts of west-central Alberta when compared with reference upland forest stands are reported from logistic regression models. Model likelihood ratio (LR) $\chi^2$-test and associated significance ($P$) levels are reported.

and 22.4% frequency for clearcuts and upland forest stands, respectively, while *V. vitis-idaea* was much more common with a frequency of 51.0% for clearcuts and 81.4% for upland forests. *V. caespitosum* occurrence was more similar between clearcuts and forests with an odds ratio of 0.6, but still significantly more likely to occur in upland forests. Finally, four grizzly bear foods lacked any significant difference in occurrence between clearcuts and forests. These included *A. uva-ursi*, *Heracleum lanatum*, *S. canadensis*, and ungulate pellets (Table 4).

### 3.2. Distribution of grizzly bear foods in clearcuts

Based on $AIC_c$ weights ($w_i$) there was large variation in support for the six a priori candidate models tested (Table 5). Only the scarification-canopy model had little to no support for any one grizzly bear food. Excluding three species of *Vaccinium* that all had support for the terrain model, no obvious patterns were evident between candidate models and food groups. Using likelihood ratio (LR) $\chi^2$-tests, we found all $AIC_c$-selected models to be significant (Table 5), although the proportion of deviance explained varied from a low of 2.8% for *Trifolium* spp. to a high of 31.3% for *Hedysarum* spp. There were no significant differences in fit between training data and selected models for any individual grizzly bear food using Hosmer and Lemeshow goodness-of-fit tests. Testing

data, however, revealed poor fit for four species: *Equisetum* spp., *Hedysarum* spp., *V. membranaceum*, and *V. vitis-idaea* (Table 5). Classification accuracy (ROC) for model training data proved poor (0.5–0.7) for 5 of 13 grizzly bear foods and good (0.7–0.9) for the remaining 8 food items. Decreasing model accuracy was evident for testing data on all four species that revealed poor fit. Using independent sample data, we found 6 of the 11 food items tested to have reasonably good (>70% PCC) prediction (Table 5). Overall, we found that ants, *A. uva-ursi*, *S. canadensis*, and *V. myrtilloides* had consistently good fit, classification accuracy, and predictive capacity for both training and testing data. Other food items proved to be either inconsistent between training and testing data or low in classification accuracy suggesting that further examination and modeling was required.

The scarification variable emerged in 7 of 13 $AIC_c$-selected models, having strong negative effects on the occurrence of *A. uva-ursi*, *Hedysarum* spp., and *S. canadensis*, while weaker negative effects on ants and ungulate pellets (Table 6; Fig. 1). In contrast, *Equisetum* spp. appeared to respond positively to scarification. Age or overstorey canopy was represented in 10 of 13 $AIC_c$-selected models (Table 6). Nonlinear response, with maximum occurrence at intermediate levels of overstorey canopy or age, was evident for seven foods: ants, *A. uva-ursi*, *Equisetum* spp., *Hedysarum* spp., *S. canadensis*, ungulate pellets, and

*V. vitis-idaea* (Fig. 2a and b). *T. officinale* and *Trifolium* spp. decreased in occurrence as canopy increased, while occurrence of *H. lanatum* increased with increasing canopy (Fig. 2b).

Terrain-derived variables of compound topographic index, elevation, and slope-aspect index were selected in 9 of 13 grizzly bear food models (Table 6). Nonlinear responses for CTI and elevation were useful in describing ant, *A. uva-ursi*, and *Equisetum* spp. occurrence. Most other foods responded in a more linear manner, occurring with greater frequency in areas with low or high soil moisture, low or high elevation, or xeric or mesic slopes (Fig. 2c–e).

### 3.3. Distribution of fruit in clearcuts

For all six species, the canopy model was selected as the most parsimonious model describing fruit occurrence. Little to no support was evident for other factors influencing fruit occurrence, once the presence of the species was fixed. *A. uva-ursi*, *V. caespitosum–membranaceum* complex, and *V. vitis-idaea* were predicted to occur with maximum fruit occurrence at intermediate canopy levels, 34, 34, and 64%, respectively (Table 7; Fig. 3). In contrast, *S. canadensis* and *V. myrtilloides* responded in a linear manner with

maximum fruit occurrence predicted at 0 and 100% overstorey canopy, respectively. Overall, *A. uva-ursi* fruit occurred in 45% of clearcut sites, *V. caespitosum–membranaceum* in 20% of sites, *V. vitis-idaea* in 36% of sites, *S. canadensis* in 68% of sites, and finally *V. myrtilloides* in 46% of sites (Table 7). In some cases, maximum occurrence of fruit differed from that of species occurrence. Fruit occurrence of *S. canadensis* was optimal at low to negligible overstorey canopy levels, while the maximum predicted occurrence for the species in clearcuts was at more intermediate canopy levels.

### 3.4. Fruit productivity for clearcuts versus reference forests

For clearcut locations where fruiting species were present, average fruit production ranged from 22,700 berries/ha for *A. uva-ursi* to 200,400 berries/ha for *S. canadensis* (Table 8). In comparison, when disregarding the conditional presence of the species (all sites), these estimates dropped to 6000 berries/ha for *A. uva-ursi* to 36,900 berries/ha for *S. canadensis*. Total fruit production for clearcuts (all sites) was estimated at 127,300 berries/ha or an estimated fresh weight production of 22.9 kg/ha. In upland forest

Table 5

AIC$_c$-selected models and Akaike weights ($w_i$) with corresponding metrics of overall model significance, fit, and classification accuracy using training and testing data

| Grizzly bear food item | AIC$_c$-selected model | AIC$_c$ | $w_i$ Model LR $\chi^2$ | % Dev. Explained | Training data | | Testing data | | Optimal cut-off | Independent PCC |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | $P\hat{C}$ | ROC | $P\hat{C}$ | ROC | | |
| Ants | Mixed-age | 0.977 | 62.33 | 16.0 | 0.338 | 0.755 | 0.631 | 0.742 | 0.5452 | – |
| *A. uva-ursi* | Mixed-canopy | 0.892 | 78.81 | 24.1 | 0.063 | 0.825 | 0.342 | 0.705 | 0.3120 | 72.79 |
| *Equisetum* spp. | Mixed-canopy | 0.935 | 44.58 | 10.8 | 0.919 | 0.719 | 0.031 | 0.547 | 0.4838 | 87.50 |
| *Hedysarum* spp. | Mixed-canopy | 0.997 | 62.59 | 31.3 | 0.442 | 0.860 | <0.001 | 0.640 | 0.0934 | 91.18 |
| *H. lanatum* | Canopy | 0.690 | 6.11 | 5.7 | 0.545 | 0.667 | 0.151 | 0.378 | 0.0275 | 47.06 |
| *S. canadensis* | Mixed-age | 0.692 | 80.96 | 28.9 | 0.960 | 0.862 | 0.470 | 0.814 | 0.2115 | 83.82 |
| *T. officinale* | Canopy | 0.515 | 26.18 | 6.6 | 0.174 | 0.660 | 0.236 | 0.643 | 0.3522 | 64.71 |
| *Trifolium* spp. | Canopy | 0.623 | 9.21 | 2.8 | 0.662 | 0.615 | 0.793 | 0.670 | 0.2569 | 58.09 |
| Ungulates (pellets) | Scarification-age | 0.548 | 18.25 | 4.6 | 0.958 | 0.644 | 0.564 | 0.604 | 0.4212 | – |
| *V. caespitosum* | Terrain | 0.512 | 12.42 | 3.1 | 0.325 | 0.617 | 0.596 | 0.616 | 0.3840 | 47.06 |
| *V. membranaceum* | Terrain | 0.608 | 14.58 | 10.7 | 0.151 | 0.716 | 0.027 | 0.612 | 0.0527 | 84.56 |
| *V. myrtilloides* | Terrain | 0.681 | 51.31 | 19.4 | 0.306 | 0.806 | 0.722 | 0.750 | 0.1547 | 67.65 |
| *V. vitis-idaea* | Mixed-age | 0.388 | 17.74 | 4.3 | 0.424 | 0.632 | 0.012 | 0.487 | 0.5231 | 86.03 |

All model likelihood ratio (LR) $\chi^2$-tests were significant at $P < 0.05$. Percent deviance (Dev.) explained represented the reduction in the log-likelihood from the null model. Probabilities for Hosmer and Lemeshow (1980) goodness-of-fit $\chi^2$-statistic ($P\hat{C}$) were reported for model and data fit, while receiver operating characteristic curves were used to assess model classification accuracy. Independent data from a concurrent study were used to assess the percent correctly classified based on optimal probability cut-off levels.

Table 6
Estimated coefficients ($\beta_i$) and standard errors (in parentheses) for $AIC_c$-selected models describing the probability of occurrence for grizzly bear foods within clearcuts of west-central Alberta, Canada

| Grizzly bear food item | Scarify | Age | Age²[a] | Canopy | Canopy²[a] | CTI | CTI² | Elev | Elev²[a] | SAI | Constant |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ants | −0.579 (0.582) | 0.303 (0.048) | −0.561 (0.100) | | | 0.816 (0.666) | −0.027(0.028) | −0.021 (0.017) | 0.074(0.065) | 3.149 (1.197) | 6.890(11.259) |
| *A. uva-ursi* | −0.836 (0.596) | | | 0.033 (0.020) | −0.582 (0.255) | 1.691 (0.859) | −0.064 (0.036) | 0.030 (0.027) | −0.156 (0.111) | 6.677 (1.895) | −23.496 (17.123) |
| *Equisetum* spp. | 0.768 (0.566) | | | 0.005 (0.015) | −0.249 (0.184) | −0.296 (0.794) | 0.025 (0.035) | 0.044 (0.016) | −0.173 (0.065) | −1.862 (1.082) | −28.222 (11.501) |
| *Hedysarum* spp. | −2.113 (0.858) | | | 0.138 (0.040) | −2.648 (0.731) | −0.393 (1.000) | 0.022 (0.040) | 0.082 (0.045) | −0.367 (0.187) | −1.928 (2.733) | −44.268 (27.005) |
| *H. lanatum* | | | | −0.008 (0.033) | 0.304 (0.344) | | | | | | −3.618 (0.611) |
| *S. canadensis* | −1.246 (0.627) | 0.228 (0.094) | −0.348 (0.167) | | | −0.469 (0.766) | 0.011 (0.031) | 0.055 (0.045) | −0.264 (0.185) | 2.848 (1.991) | −26.675 (27.218) |
| *T. officinale* | | | | −0.031 (0.015) | 0.119 (0.179) | | | | | | 0.189 (0.203) |
| *Trifolium* spp. | | | | −0.012 (0.017) | −0.035 (2.077) | | | | | | −0.816 (0.222) |
| Ungulates (pellets) | −0.295 (0.476) | 0.143 (0.045) | −0.234 (0.091) | | | −0.008 (0.595) | 0.0002 (0.025) | 0.039 (0.017) | −0.154 (0.066) | 2.490 (1.049) | −1.950 (0.640) |
| *V. caespitosum* | | | | | | 1.819 (2.700) | −0.092 (0.128) | −0.068 (0.023) | 0.264 (0.089) | −3.831 (2.212) | −25.035 (11.228) |
| *V. membranaceum* | | | | | | 1.070 (1.234) | −0.050 (0.055) | −0.020 (0.027) | 0.045 (0.110) | 1.357 (1.863) | 30.785 (20.154) |
| *V. myrtilloides* | | | | | | | | | | | 10.587 (17.696) |
| *V. vitis-idaea* | 0.647 (0.501) | 0.094 (0.041) | −0.243 (0.087) | | | −0.049 (0.586) | −0.0002 (0.025) | −0.041 (0.015) | 0.154 (0.060) | 0.235 (0.995) | 26.136 (10.423) |

[a] Coefficients for age² are 100, for canopy² 1000, and for elev² 10,000 times their actual size.

stands, fruit production for sites where the species was present was estimated to range from 26,000 berries/ha for *V. myrtilloides* to 150,200 berries/ha for *V. vitis-idaea* (Table 8). Disregarding the conditional presence of the species (all sites), fruit production dropped from an estimated abundance of 2500 berries/ha for *V. myrtilloides* to 116,200 berries/ha for *V. vitis-idaea*. Total fruit production for upland forests was estimated at 177,100 berries/ha, the majority of which were from *V. vitis-idaea*, or an estimated fresh weight production of 32.3 kg/ha. Mann–Whitney *U*-tests revealed that only *V. myrtilloides* and *V. vitis-idaea* fruit production differed for clearcut and upland forest sites (Table 8). *V. myrtilloides* had significantly greater production in clearcuts ($U = 2.22$, $P = 0.026$), while *V. vitis-idaea* had significantly greater production in upland forests ($U = -4.72$, $P < 0.001$). Although species-specific differences existed, total fruit production (berries/ha) was not found to significantly differ between clearcut and upland forest sites.

## 4. Discussion

Ants, *Equisetum* spp., *Hedysarum* spp., *T. officinale*, *Trifolium* spp., and *V. myrtilloides* had higher frequencies of occurrence in clearcuts compared with upland forest stands. Clearcut harvesting appeared to benefit these species through the disturbance of overstorey canopy structure, supporting our initial hypothesis. As would be expected and previously reported, the exotic species, *T. officinale* and *Trifolium* spp., responded favorably to clearcutting and mechanical disturbance (Haeussler et al., 1999; Roberts and Zhu, 2002). Unlike these exotics, however, *V. cespitosum*, *V. membranaceum*, and *V. vitis-idaea* were all more likely to occur in upland forests, suggesting that clearcut harvesting was negatively impacting their occurrence. We found no evidence that *A. uva-ursi*, *H. lanatum*, *S. canadensis*, and ungulate pellets occurred at different frequencies of occurrence for clearcuts and upland forest sites, although ungulate pellets have the potential for bias in distribution (Collins and Urness, 1979). Frequencies of *A. uva-ursi* and *S. canadensis* should also be interpreted with caution, as previous work suggests greater occurrence for early seral or open forests (Hamer, 1996; del Barrio et al., 1999). The lack of a difference suggests that clearcut harvesting may
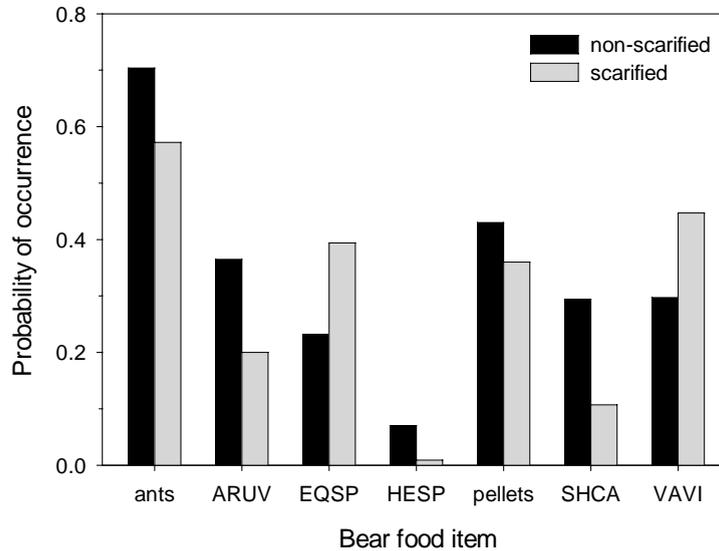
Fig. 1. Predicted probability of occurrence for $AIC_c$-selected grizzly bear food items in scarified and non-scarified clearcuts. All other environmental factors included in the selected $AIC_c$ model were held at their mean level.

be impacting occurrence. Comparisons with similar open or naturally disturbed early seral forests would be required to more fully assess these differences.

Of the six a priori candidate models evaluated, only the scarification-canopy model had little to no support for any one grizzly bear food item. The remaining five candidate models that included the variables canopy cover, scarification, clearcut age, CTI, SAI, and elevation proved useful in describing local patterns of grizzly bear food occurrence for clearcuts. Goodness-of-fit ($\hat{C}$) and model accuracy (ROC) generally revealed model fit and predictive accuracy, while model validation revealed reasonable accuracy of predictions for the majority of grizzly bear foods.

This suggests that maps describing food occurrence could be derived from the models presented here. Modeling efforts of nearby areas have already revealed the utility of using food-based models for predicting grizzly bear habitat (Nielsen et al., 2003). The same methods could be used to derive habitat quality maps for clearcuts.

Canopy cover and age of clearcut were strong predictors of food occurrence with most species peaking at intermediate canopy and age levels. The scarification variable, emerging in most $AIC_c$-selected models, had negative impacts on the occurrence of *A. uva-ursi*, *Hedysarum* spp., and *S. canadensis*, while weaker effects on ant and ungulate pellet occurrence.

Table 7

Percent frequency of fruit, given the presence of the species, for clearcuts in west-central Alberta

| Fruit species/group | % frequency of fruit | Canopy | | Canopy$^2$ | | Constant | | Predicted optima |
|---|---|---|---|---|---|---|---|---|
| | | $\beta$ | S.E. | $\beta$ | S.E. | $\beta$ | S.E. | |
| *A. uva-ursi* | 45.0 | 0.122 | 0.063 | −0.194 | 0.101 | −1.016 | 0.700 | 34 |
| *S. canadensis* | 67.9 | −0.003 | 0.052 | −0.019 | 0.060 | 1.317 | 1.009 | 0 |
| *V. caespitosum–membranaceum* | 20.0 | 0.068 | 0.037 | −0.101 | 0.050 | −1.778 | 0.525 | 34 |
| *V. myrtilloides* | 45.5 | 0.008 | 0.047 | 0.020 | 0.061 | −0.491 | 0.677 | 100 |
| *V. vitis-idaea* | 35.5 | 0.093 | 0.030 | −0.073 | 0.032 | −2.579 | 0.609 | 64 |

Estimated coefficients ($\beta_i$) for $AIC_c$-selected models describe the probability of fruit occurrence (given food item presence). Predicted optima (highest probability of occurrence) for fruit occurrence are reported. Coefficients for canopy$^2$ are 100 times their actual value.

Number and food item:

1-ants
2-*Arctostaphylos uva-ursi*
3-*Equisetum* spp.
4-*Hedysarum* spp.
5-*Heracleum lanatum*
6-*Shepherdia canadensis*
7-*Taraxacum officinale*
8-*Trifolium* spp.
9-ungulates (pellets)
10-*Vaccinium caespitosum*
11-*Vaccinium membranaceum*
12-*Vaccinium myrtilloides*
13-*Vaccinium vitis-idaea*
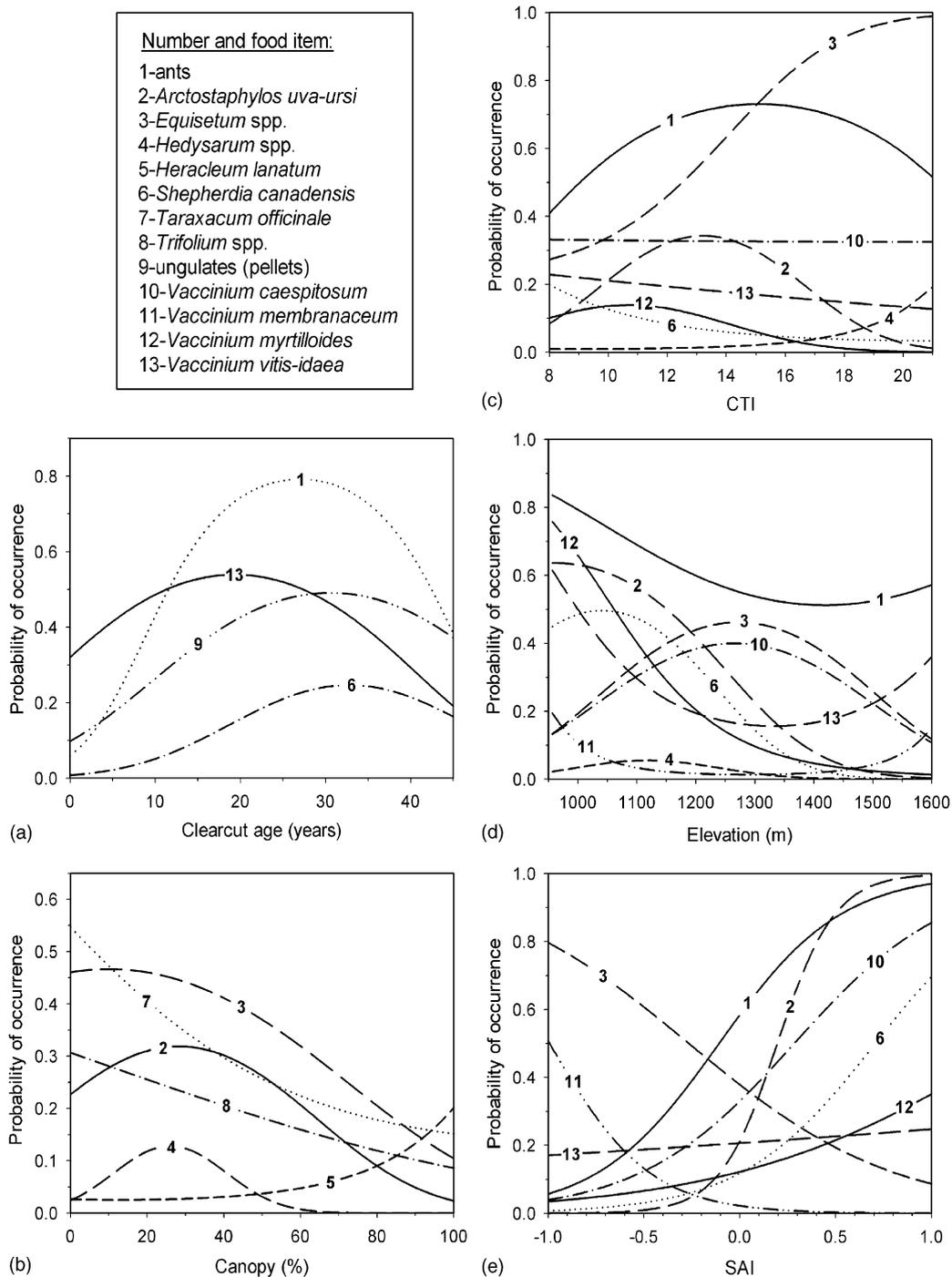
Fig. 2. Predicted probability of occurrence for AIC$_c$-selected grizzly bear food items in each of the five environmental gradients used for describing food occurrence. For each individual gradient (a–e), remaining environmental factors included in the selected AIC$_c$ model were held at their mean level. Numbers adjacent to each line correspond to the identification of grizzly bear food items defined in the upper left of the graph and in Table 1.
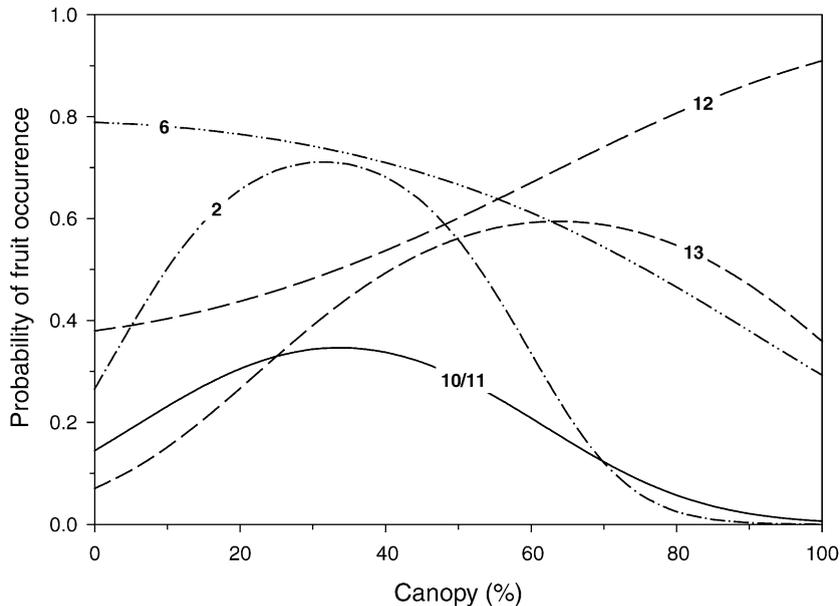
Fig. 3. Predicted probability of fruit occurrence within clearcuts of west-central Alberta for sites where the fruit-bearing species was conditionally present. Numbers along each predicted line correspond to a bear food (2—*A. uva-ursi*, 6—*S. canadensis*, 10/11—*V. caespitosum* and *V. membranaceum*, 12—*V. myrtilloides*, and 13—*V. vitis-idaea*).

In contrast, *Equisetum* spp. and *V. vitis-idaea* appeared to respond positively to scarification. Previous work has shown negative affects from mechanical scarification of Ericaceae shrubs, suggesting that the destruction of rhizomes were to blame (Zager et al., 1983;

Haeussler et al., 1999; Roberts and Zhu, 2002). Scarification has also been suggested for declines in *S. canadensis* abundance (Knight, 1999). Root and rhizome structure were likely to have been disturbed, preventing vegetative re-sprouting (Noste and Bushey,

Table 8
Average (±S.E.) fruit production (reported by thousands of berries) per hectare (ha) for five grizzly bear food groups in clearcuts and reference upland forest stands of west-central Alberta

| Grizzly bear food item | Average berry weight (g) | Clearcuts | | | Reference upland forest stands | | |
|---|---|---|---|---|---|---|---|
| | | Presence-only | All sites[a] | kg/ha | Presence-only | All sites[a] | kg/ha |
| *A. uva-ursi* | 0.186 | 22.7 ± 6.2 | 6.0 ± 6.2 | 1.11 | 30.0 ± 11.1 | 5.7 ± 2.3 | 1.05 |
| *S. canadensis* | 0.180 | 200.4 ± 117.4 | 36.9 ± 22.2 | 6.65 | 98.0 ± 34.4 | 19.4 ± 7.7 | 3.49 |
| *V. caespitosum–membranaceum* | 0.242 | 38.8 ± 15.9 | 23.7 ± 9.5 | 5.73 | 48.6 ± 18.3 | 33.4 ± 12.6 | 8.08 |
| *V. myrtilloides* | 0.142 | 124.6 ± 45.4 | 27.1 ± 10.6[*] | 3.84 | 26.0 ± 17.6 | 2.5 ± 1.8[*] | 0.35 |
| *V. vitis-idaea* | 0.165 | 47.9 ± 14.1 | 33.7 ± 10.1[***] | 5.56 | 150.2 ± 26.9 | 116.2 ± 21.7[***] | 19.18 |
| Total | | | 127.4 | 22.9 | | 177.2 | 32.3 |

Reported are estimates of berry production for sites where the species was present (presence-only) and for all sites regardless of its presence ($n = 180$) for only those plots occurring after 14 July when fruits are available. Estimated fresh weight production (kg/ha) for each food item is reported for all sites (an average clearcut or reference forest stand) based on an average berry field weight.

[a] Test of difference in fruit production for each species between clearcuts and reference forest stands (Mann–Whitney *U*-test).
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

1987). Methods to reduce the severity of mechanical scarification or implementation of post-scarification remediation activities may be necessary. Terrain variables, including elevation, compound topographic index, and slope-aspect index, were all found to be important predictors of food occurrence. Location of species optima varied from low-elevation sites to xeric or mesic soils. Small-scale changes in terrain therefore had the potential to influence food occurrence within individual clearcuts. Remediation should recognize favorable resource niches when planning actions to enhance grizzly bear habitat. Enhancing habitats near human access, however, may result in increasing the risk of human-caused mortality for grizzly bears (Nielsen et al., 2004a). Therefore, human access will need to be managed for sites where active remediation is occurring.

Responses in fruit occurrence sometimes differed from that of plant occurrence. For the six fruit species examined, canopy cover was the only variable that was found to be useful for predicting fruit occurrence, once the species was present. *S. canadensis*, for instance, was most likely to occur at intermediate canopy levels, while fruit production peaked in open sites. Hamer (1996) found similar patterns between canopy and fruit production for *S. canadensis*. Fruit production was generally stable until canopy cover reached more than 50%, causing precipitous declines. Fruit occurrence for the other five species maximized at either intermediate or high canopy levels. Maintenance of canopy levels below or near 50% through silvicultural thinning of selected micro-sites favorable for fruit-bearing species could provide attractive seasonal grizzly bear habitat through enhancement of fruit production if human access is managed.

For all fruit-bearing species, the average estimated fresh weight production of clearcuts was 22.9 kg/ha, while upland forests averaged 32.3 kg/ha. However, no significant difference in total fruit production was evident, although *V. myrtilloides* and *V. vitis-idaea* were found to differ at the individual species level. *V. myrtilloides* had greater fruit production in clearcuts, while *V. vitis-idaea* had high fruit production in upland forests. Total fruit production for *Vaccinium* species was estimated at 15.1 and 27.6 kg/ha for clearcut and upland forest stands, respectively. These productivity levels were more similar to those reported by Noyce and Coy (1989) for conifer stands in

Minnesota (9 kg/ha), rather than for Russia at 188 kg/ha (Cherkasov, 1974) and 296 kg/ha (Kolupaeva, 1980) or Alaska at 270 kg/ha (Hatler, 1967). Higher productivity levels from Russia and Alaska may reflect historical artifacts from previous forest fires or other nutrient inputs necessary for large crops (Penney et al., 1997). Comparisons of fruit production for regenerating burns and clearcuts support this conclusion (Martin, 1983; Zager et al., 1983). Although silvicultural management of clearcuts rarely involves treatment with fire, such actions may be necessary to fulfill the natural functions missing in mechanical treatments. Although total fruit production was slightly greater for upland forest stands, availability of herbaceous foods, roots and tubers, and ants were greater in clearcuts. Food habit studies have shown the importance of these items in grizzly bear diets (Hamer and Herrero, 1987; Edge et al., 1990; Hamer et al., 1991; McLellan and Hovey, 1995; Elgmork and Unander, 1999; Knight, 1999; Swenson et al., 1999).

## 5. Conclusion

Despite management implications, little information is currently available regarding specific patterns of grizzly bear foods in clearcuts. We found that clearcuts in the foothills of west-central Alberta provided a diverse array of grizzly bear foods. Use of clearcuts by grizzly bears in the study area was greatest during the mid-summer period (early hyperphagia) when green herbaceous and ant feeding was at its greatest and lowest for the late-summer period (late hyperphagia) when foraging for fruit was at its highest (Nielsen et al., 2004b). This supports our food modeling results, as herbaceous material and ants were more diverse and abundant in clearcuts than forests, while fruit production was lower in clearcuts than forests. We suggest that for forested areas lacking extensive natural openings or recent fires (e.g., extensive fire suppression), clearcut harvesting provides a potential habitat surrogate if control of human access is addressed. Terrain, clearcut age, canopy cover, and scarification characteristics influenced local patterns of food occurrence, while canopy cover alone influenced fruit occurrence. Consistent with our hypothesis, a number of grizzly bear foods increased in occurrence following clearcut harvesting. Not all

foods responded favorably, however, and thus methods of promoting grizzly bear food availability through forest management, including scarification and site preparation techniques, may be required. Active management, such as the planting of fruit-producing shrubs like *S. canadensis*, may further mitigate negative effects observed from mechanical scarification. Terrain-related micro-sites, however, should be identified for potential food plantings prior to application. Despite the maintenance and/or enhancement of grizzly bear foods in clearcuts, further control and/or management of human access will be required. If human access is not controlled, we suggest that food remediation activities occur in locations that are relatively secure from human access to avoid attractive sinks or ecological traps (Delibes et al., 2001; Nielsen et al., 2004a).

## Acknowledgements

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