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Research Article

Grizzly Bear Selection of Avalanche Chutes: Testing the Effectiveness of Forest Buffer Retention

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ABSTRACT In mountainous areas with sufficient snowfall, avalanche chutes are an important component of grizzly bear (*Ursus arctos*) habitat. Therefore, regional land-use plans have recommended retaining adjacent forest buffers to maintain security and thus reduce potential impacts of clearcut forest harvesting. Our objective was to determine if forest buffers affected selection of avalanche chutes by grizzly bears, while accounting for factors such as vegetation composition and other physical attributes. We used radio-location data from 61 grizzly bears collected between 1994 and 2000 in southern British Columbia, mapped a sample of avalanche chutes (1,045), and quantified the amount of forb, shrub, tree, and non-vegetated cover within each chute. We also measured forested buffer width on each side of the chute, solar radiation, chute size, chute frequency (no. of chutes/km), and the area of clearcut logging adjacent to chutes. Each avalanche chute was the sample unit and the number of grizzly bear radiolocations was the dependent variable. We found that natural biophysical attributes were the strongest factors predicting the level of avalanche chute use by bears. Frequency of large chutes (>100 m wide), chute area, forb content, and solar radiation all positively affected use by bears. Larger avalanche chutes had a higher proportion of forb cover than smaller chutes, and more of these large chutes per unit area provided increased forage opportunities. Based on multivariate analyses, forested buffer width or the amount of clearcut logging were not strong factors predicting the level of use. However, a post hoc univariate analysis revealed that clearcut logging reduced the amount of bear use of the best avalanche chutes (large and abundant chutes). Furthermore, because a portion of our study area contained logging but no vehicle traffic, we concluded that it was the removal of tree cover, rather than displacement by vehicles, that caused the observed pattern. Although our multivariate models did not perform well using independent validation in a different geographic area, 4 factors were consistently important (large and abundant chutes, forb content, with a negative but weaker influence of clearcutting), suggesting broad applicability of these factors in mountainous ecosystems.

KEY WORDS avalanche chutes, British Columbia, cover, forage, forested buffers, grizzly bear, habitat, model validation, *Ursus arctos*.

While foraging, animals are confronted with trading off maximizing nutritional gain against minimizing predation risk (Lima and Dill 1990, Sih 1992, Wirsing et al. 2007). To benefit target species, habitat managers sometimes strive for the optimal mix of high-quality foraging sites with security cover or escape terrain (Thomas 1979). When preferred foraging areas are naturally occurring openings in forested landscapes, managers often try maintaining adjacent cover to encourage continued use by the focal species and other species that benefit from naturally occurring interspersion of habitat types.

In mountainous areas with sufficient snowfall, avalanches, which are the sudden and rapid movement of large volumes of snow down slope, are common. Avalanches often start high in the alpine and flow through a gullied path. They remove trees, loosen rocks and soil, and deposit the debris within a valley-bottom run-out zone. Because little snow remains over most of the avalanche track after a slide, plants emerge early in spring. Within the run-out zone, however, the deeply piled snow gradually melts, prolonging the period of vegetation emergence for months. The result of these actions are open habitats, usually with seasonally flowing water, that widen at the bottom where soils can be rich and moist (Ballantyne 1989, Korol 1994). A variety of shrubs, forbs, and grasses grow vigorously in many avalanche chutes.

Where vegetatively productive avalanche chutes occur in grizzly bear (*Ursus arctos*) range, they are consistently selected by these animals (Zager et al. 1983, Schoen et al. 1994, Waller and Mace 1997, Ramcharita 2000, McLellan and Hovey 2001). Many avalanche chutes not only produce a diversity and abundance of bear forage, but also, within various portions of the chute, produce bear foods from early spring, when bears emerge from their dens, to autumn. At a regional scale, Apps et al. (2004) used DNA extracted from

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hairs collected across a systematic hair-trap grid (Woods et al. 1999) and determined that grizzly bear abundance was positively associated with remote, rugged mountains, avalanche chutes, and un-roaded areas. In our study area, Munro (1999) found approximately half the locations of both male and female radiocollared grizzly bears to be in avalanche chutes in spring and about a third in summer and fall, although this habitat covered only 15% of the study area. At finer scales, Ramcharita (2000) used telemetry and field investigations to determine that bears selected avalanche chutes with high forb and grass content, whereas those dominated by shrubs were avoided. South-facing chutes also received the highest level of use. Logging roads did not appear to affect the level of bear use, and presence of cutblocks near chutes did not conclusively affect the level of bear use (Ramcharita 2000).

In many regions of North America, grizzly bears are restricted to mountainous areas with little human presence. Grizzly bears are listed as threatened in portions of the United States, and they are of special concern in Canada (Committee on the Status of Endangered Wildlife in Canada 2002). There is ongoing concern about the potential degradation of grizzly bear habitat through various human activities. In response, guidelines have been established in some areas to retain forested buffers (unlogged forest) around avalanche chutes for the protection of grizzly bear habitats (Revelstoke Minister's Advisory Committee 1999, Kootenay-Boundary Higher Level Plan Order 2002, Lillooet Land and Resources Management Plan 2004). The goal of retaining these forested buffers was to maintain security and thermal cover so bears would continue using avalanche chutes for foraging. However, the effectiveness of these habitat protection measures has not been tested.

Our underlying objective was to determine if forest buffers affected the use of avalanche chutes by grizzly bears, by contrasting natural versus anthropogenic factors that may affect levels of use. If forested buffers influence bear use of avalanche chutes, then we would expect a positive relationship between buffer width and level of use by bears. Conversely, we predicted a negative relationship between the amount of clearcut logging adjacent to an avalanche chute and the level of bear use of the chute. In testing these predictions, we controlled for other factors that likely influence grizzly bear use of avalanche chutes such as the size of the chute, density of avalanche chutes over a larger area, and vegetation composition of the chute.

STUDY AREA

The initial study area was previously described by Woods et al. (1999) and Apps et al. (2004). It was centered on the town of Golden, British Columbia (BC; N 51.3°, W 117.0°), with the Selkirk Mountains to the west and the Rocky Mountains to the east (Fig. 1). Both ranges are rugged with steep, narrow valleys. Elevations range from 600 m to approximately 3,500 m. Annual average precipitation in the Selkirk Mountains was 1,547 mm, and in the Rocky Mountains it was 884 mm, and fell mostly in winter as snow. Because of the steep terrain and deep snowpacks, avalanche chutes were common. In the valleys, climax overstory species included Douglas-fir (*Pseudotsuga menziesii*) and white

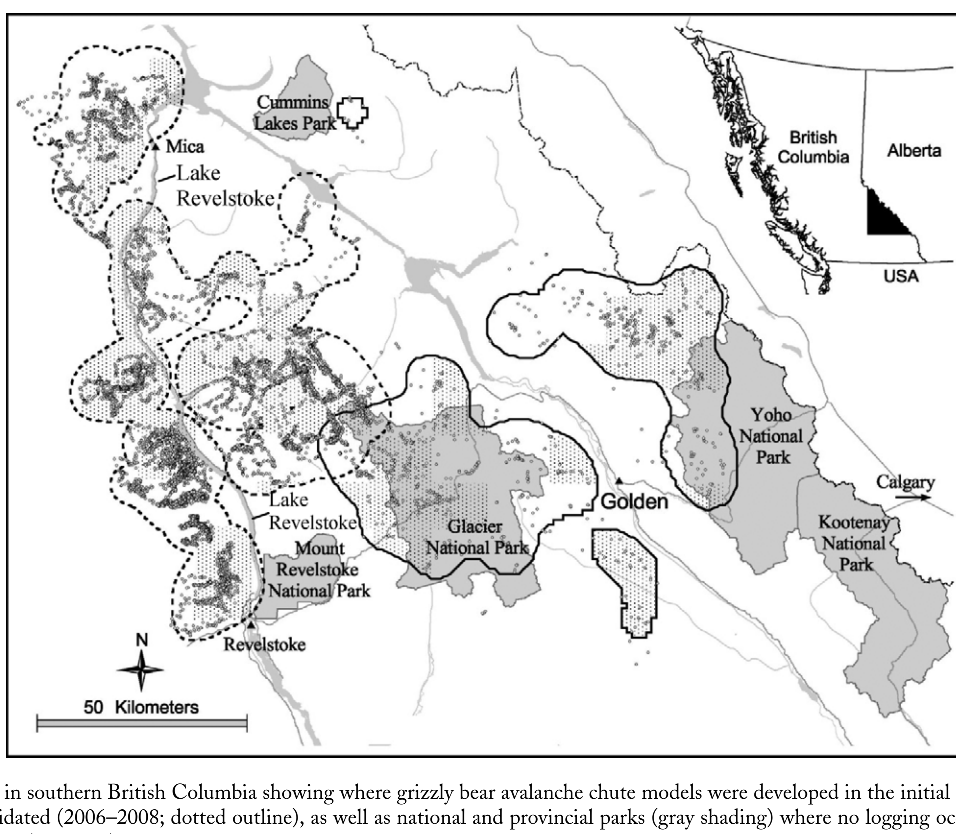

Figure 1. Study area in southern British Columbia showing where grizzly bear avalanche chute models were developed in the initial study area (1994–2000; solid outline) and validated (2006–2008; dotted outline), as well as national and provincial parks (gray shading) where no logging occurred. Dotted shading shows which mapsheets (grid cells) we typed for avalanche chutes and plant communities within them, and dots show telemetry locations.

spruce (*Picea glauca*) on drier sites and western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) on wetter sites. At intermediate elevations, Englemann spruce (*Picea englemannii*) and subalpine fir (*Abies lasiocarpa*) were usually dominant. Alpine tundra, glaciers, and exposed bedrock occurs at high elevations. Seral stands of lodgepole pine (*Pinus contorta*) were common in the Rocky Mountains.

The study area included 2 main land jurisdictions with different mandates: Yoho and Glacier national parks, where there was little or no resource extraction, and British Columbia provincial lands, where forest harvesting was common. Virtually all forest management in our study area consisted of clearcutting with replanting. In provincial lands, 33% of the forested, harvestable landbase (where logging was permitted and economically viable) had been logged and was generally <30-yr-old plantations, whereas 46% was primary (old growth, >140 yr) forest, and 12% was mid-seral to mature forests (30–140 yr old). The remaining portions were natural openings such as wetlands or shrubfields. The contrast between national parks and provincial lands provided a broad range in variation of logging intensity within and around grizzly bear habitats. Forestry roads in the study area had little human use (<2 vehicles/day on average; Ramcharita 2000). Mean grizzly bear density across the initial study area was 25 bears/1,000 km^2 (Boulanger et al. 2004).

We tested the geographic extrapolation of our results to an adjacent area to the west of the initial study area. This area included the western side of the Selkirk Mountains and the Monashee Mountains, between which was the Revelstoke reservoir. Terrain and climate were similar to the initial study area to the east (Fig. 1) and were previously detailed by Apps et al. (2001).

METHODS

There were 2 components to our study design. We first developed multivariate resource selection models and univariate selection indices using radiotelemetry locations from our initial study area. We then tested these relationships using an independent data set collected in an adjacent area that we termed the validation area (Fig. 1). Within the initial study area, we captured grizzly bears using foot snares or by darting from a helicopter. We fitted study animals with conventional very high frequency (VHF) radiocollars (Lotek Wireless, Newmarket, ON, Canada) and located them from 1994 to 2000 using weekly aerial telemetry flights between April and November. In the validation area, we darted bears from a helicopter between 2006 and 2008. Here we deployed Global Positioning System (GPS) collars programmed to obtain fixes each hour. We conducted our research under a provincial animal care capture permit (no. VI07-40505).

We initially used the VHF data, as they were collected first and because they were from more bears, even though there were fewer locations per bear than from the GPS locations in the validation area. As omnivores living in complex, mountainous terrain, there was great variation in habitats used among individual bears (McLellan and Hovey 2001), so it was preferable to use the earlier data to build models to derive inference representing the whole population.

We mapped avalanche chutes within both study areas. However, because of cost limitations, we restricted our analyses to 38% of the initial study area where we mapped avalanche chute habitats (Fig. 1). We based our sampling design on the British Columbia 1:20,000 map index grid with cells of 11 km × 14 km in our study area. We randomly selected grid cells within 2 strata, in and out of national parks, to ensure that a maximum range of clearcut logging intensity was represented. When a grid cell was selected, we mapped all avalanche chutes within the 95% utilization distribution (UD) of pooled bear locations within that cell.

We delineated the outer boundaries of avalanche chutes using digital orthophotos (computerized high-resolution aerial photos), and we divided and further delineated plant communities within these avalanche chutes into 5 vegetation classes: forb, shrub–forb complex, shrub, tree, and non-vegetated (Table 1). We mapped at 1:2,500 (0.1-ha minimum mapping unit) resolution with field verification. We independently assessed accuracy of vegetation mapping within the avalanche chutes from a helicopter using a real-time GPS-Geographic Information System (GIS) interface. For 48 polygons within 36 avalanche chutes, 41 were correctly classified. Highest misclassification was for shrub (27%) followed by shrub–forb (18%), forb (6%), and non-vegetated (0%).

For each avalanche chute we calculated the mean solar radiation value (Kumar et al. 1997), measured as hours of

Table 1. Factors we used to consider the selection of avalanche chutes by grizzly bears in southern British Columbia, 1994–2008.

Variable	Description
SOLAR	Solar radiation hitting each pixel, accounting for shading (hr)
FREQ_ALL	Frequency of chutes within 1 km on either side of the focal chute (no./2 km)
FREQ_BIG	Frequency of large (>100-m wide) chutes within 1 km on either side of the focal chute (no./2 km)
FORB	Area of forbs within a chute (ha)
FORB_SHRB	Area of forb–shrub complex within a chute (ha)
SHRUB	Area of shrubs within a chute (ha)
TREE	Treed area within a chute (ha)
NONVEG	Non-vegetated area within a chute (ha)
CHUTE_WIDTH	Average width in the run-out zone of the chute (m)
BUFFER_WIDTH	Width of forested buffer adjacent to chute (minimum; m)
PROP	Proportion of forested buffer on either side of the chute (0–1; 0 indicates evenly distributed, 1 indicates skewed entirely to 1 side)
CUT	Minimum buffer width on either side[a] (m), including only buffers that were reduced by clearcutting
CUT_HA	Clearcut area: area clearcut within a 300-m buffer of chute edge (ha)

[a] For example, if a chute was logged on both sides and one side was logged to 30 m from the chute edge, and the other side to 50 m, the value would be 30 m.

solar radiation at each pixel for a 2-month period in spring, accounting for shading of adjacent mountains. We calculated avalanche chute frequency as the number of chutes within 1 km on either side of the focal chute. We measured forested buffer width on either side of the avalanche chute, distinguishing between natural and logged buffers (buffers that had trees removed using clearcutting). We calculated the proportion of buffer that occurred on either side of the avalanche chute as

$$Sk = |PB_R - PB_L| \quad (1)$$

where Sk = skewness of the buffer, PB = proportion of the total buffer width either the right (R) or left (L) side of the avalanche chute. Skewness values range from 0 to 1, where a value of 0 indicates that buffers were evenly distributed on both sides, whereas a value of 1 indicates that the buffer was skewed entirely to one side. We calculated the area clearcut within 300 m on either side of each avalanche chute boundary, which we termed the clearcut area (Table 1). We chose this distance because it incorporated 95% of all avalanche chute buffer widths, or 97% of natural (i.e., unlogged) buffer widths. We did not use roads in our analysis because roads accessed each logged area and were thus highly correlated with clearcut area (Spearman $r = 0.65$). Plus, we were specifically interested in the effectiveness of guideline stipulation of forest retention compared to logging the buffers so we focused on buffer widths and clearcut areas. Traffic volume was low in our study areas (averaging <2 vehicles/day) but representative of most grizzly bear habitat in mountainous areas of British Columbia. However, the west side of Lake Revelstoke (Fig. 1) in our validation study area was logged and roaded but only accessible by private ferry and thus access was severely restricted. When these validation data were collected there was no traffic for months at a time (K. Huettmeyer, BC Ministry of Forests, personal communication). This contrast provided an opportunity to test whether patterns we observed were caused by the clearcut logging alone or whether the limited road traffic present elsewhere was a contributing factor (see the Independent Validation Section).

In our analyses, each avalanche chute was the sample unit and the number of bear locations in each chute was the dependent variable. We considered avalanche chutes with ≥1 location used and the rest we considered available. Within a few days of the telemetry flight, Ramcharita (2000) field checked 49 of these VHF locations in separate chutes in the initial study area and found sign of fresh bear activity in 47 of them (96%). This field validation suggests that bears estimated from the air to be in avalanche chutes were using them for feeding, bedding, or both, even though most used chutes had few locations (see the Results Section). However, to account for larger avalanche chutes containing more locations simply because of their size, we divided the number of locations by the area of the avalanche chute to obtain location density. Preliminary analyses suggested that avalanche chute size was one of the factors that greatly affected bear use, therefore we stratified most univariate analyses by avalanche chute size based on width (i.e., all chutes vs. those >100 m wide). For all univariate analyses, the dependent variable was the number of locations per area of avalanche chute. We inferred the degree of univariate selection from Ivlev's electivity index (Ivlev 1961). Positive values indicated preference and negative values indicate avoidance (i.e., more or less use than expected from random chance). The index is based on proportions used and available within categories, so the number of locations in each chute was directly proportional to the weighting of that chute in the analyses. We obtained error bars (95% CI) from bootstrapping sample units 1,000 times (Efron and Tibshirani 1993). We calculated Ivlev's scores across the range of variation for each factor considered including forest buffer width (natural and logged), avalanche chute size, solar radiation, composition of vegetation classes, avalanche chute frequency, and clearcut area. Category intervals for univariate analyses were not always equal in size but were sometimes narrower at the lower range to help determine thresholds in selection, and to more evenly distribute sample sizes within categories. We stratified each analysis by sex and pooled data if there were no differences.

Multivariate Modeling

Because we intensely sampled (>50% radiocollared) grizzly bears in the initial study area and monitored them for 7 yr, we expected that actual use by grizzly bears of avalanche chutes where we did not locate bears would be so low that their use would not bias our results. We therefore analyzed receiver operating characteristic (ROC) curves and plots of predicted versus observed data to assess model fit (Haefner 2005:154), that is, simultaneously testing for a slope of 1 and intercept of zero. Thus, a lower F-value indicates a better model fit because it is less likely that the null hypothesis (perfect fit) will be rejected (Haefner 2005). We derived 19 candidate models based on 9 natural and 4 human-caused variables that we expected to influence the use of avalanche chutes (Table 1). Some of these models contained interactions or squared terms suggested by preliminary results from the univariate analyses. Our dependent variable had a high proportion of zero use in the sample, so we were unable to use normally distributed models. We conducted exploratory analyses using the negative binomial (PROC GENMOD in SAS; SAS Institute, Inc., Cary, NC), the zero-inflated negative binomial model (PROC NLMIXED), and logistic regression (PROC LOGISTIC). The benefits of the 2 negative binomial models include the ability to account for different intensity of use across chutes (rather than zero or ≥1 location), whereas the logistic model treated all avalanche chutes with ≥1 location as equal. After preliminary analyses, we determined that the zero-inflated negative binomial model provided similar parameter estimates as the negative binomial model. We used the standard negative binomial model because it is less complex. We ranked models using Akaike Information Criteria (AIC) following Burnham and Anderson (1998). From the top-ranked models (0–2 ΔAIC), we ranked variables across all models to determine individual factors that had the greatest influence on grizzly bear use (Burnham and Anderson 1998). We put more emphasis on this latter approach for interpretation because it focuses on individual factors. No models included highly correlated variables ($r > 0.5$).

Independent Validation

To provide a robust test of our findings, we compared results from the initial study area to the adjacent validation study area (Fig. 1). To validate the multivariate models, we applied the top-ranked averaged models from the initial area to the validation area. Validation data were from GPS collars, but we subsampled these to match the location frequency of the VHF data of the initial study area by selecting 2 GPS locations randomly within each week. We attempted to use all the GPS data using mixed-effects models (e.g., Gillies et al. 2006), but the sampling intensity was different enough from the initial data set that models were difficult to compare. We applied a correction factor developed in the same mountain range (D'Eon et al. 2002) to GPS data to account for missed locations because of terrain or forest cover, but the effect was minimal because avalanche chutes, by definition, are open areas. If averaged top models from the initial data set performed poorly on the validation data set, we ran all candidate models against the validation data set to determine if there were major changes in factors affecting the use of avalanche chutes by grizzly bears between the 2 study areas. As an additional test, we compared the Ivlev selection indices from both study areas, but in this case it was appropriate to use all the GPS data from the validation area, not the subsample that we used to match the VHF location frequency. We used all GPS data because, unlike logistic regression, Ivlev's index is not based on a binary response but on relative use within categories (compared to relative available). We restricted these comparisons to variables present in the top multivariate models of both study areas because these were the most important for comparisons. As a final comparison, we analyzed the validation data where there was virtually no vehicle traffic (west side of Lake Revelstoke, Fig. 1) separately to determine if patterns were consistent, enabling us to isolate potential effects of clearcutting relative to potential displacement by vehicles.

RESULTS

Within the initial study area, we captured 61 grizzly bears and located them 2,022 times from aircraft. Average VHF position error was 133 m (SD = 71 m, $n = 15$; Ramcharita 2000). In the validation area, we collected data on 13 grizzly bears with GPS collars. Based on classifications made from the aircraft, 37% ($N = 752$) of VHF radiolocations were in avalanche chutes and most of these were during spring and summer. Using pooled locations among bears in the initial study area, a 95% UD (Hooge and Eichenlaub 2000) defined a 3,956-km^2 area that we considered to be collectively available to study animals. Given estimated bear density (Boulanger et al. 2004), this area contained approximately 100 bears.

We mapped 1,045 avalanche chutes in the initial study area and they were within the composite 95% UD of radiolocations of 43 grizzly bears (21 F, 22 M). Most (51%) of the

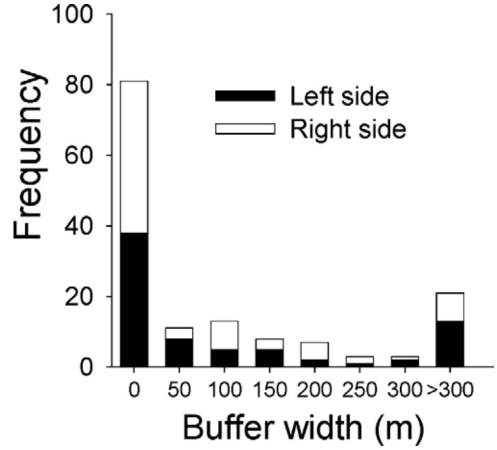

Figure 2. Frequency distribution of the number of avalanche chutes of differing buffer width classes, where the buffers were subjected to clearcutting (i.e., no unlogged buffers are included; right and left side of chutes are distinguished because mean values would misrepresent widths that were different on either side of the chute). Data are from a grizzly bear study of avalanche chute use in southern British Columbia, 1994–2000.

chutes were narrow (<100 m wide), with only 8% of chutes >300 m wide. Radiocollared bears were located at least once in 123 avalanche chutes (mean number of locations per used chutes was 1.5, median = 1, lower and upper fifth percentiles = 1–4, range 1–7). Use of chutes by individual bears ranged from 20% to 90%. For all variables, the pattern of selection was similar for male and female bears, and all bootstrapped error bars overlapped substantially, so we pooled sexes for all analyses. Of all mapped chutes, 243 (23%) had some adjacent logging. Of these avalanche chutes with logging, 63 (26%) had logging right to the edge on at least 1 side (Fig. 2). With the number of locations in each avalanche chute as the dependent variable, larger avalanche chutes were strongly favored by grizzly bears over smaller chutes (Fig. 3) and the relationship remained when the number of locations was divided by the chute area.

Avalanche chute frequency (number/km) did not influence grizzly bear selection (Fig. 4A). However, when we constrained this variable to include only larger avalanche

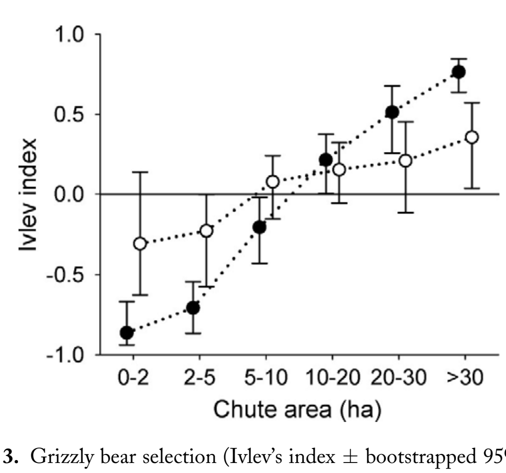

Figure 3. Grizzly bear selection (Ivlev's index ± bootstrapped 95% CI) of avalanche chutes of different size classes using the raw number of locations per chute (closed circles) and number of locations per chute corrected for chute area (open circles). $N = 1,045$. Data were collected in southern British Columbia, 1994–2000.

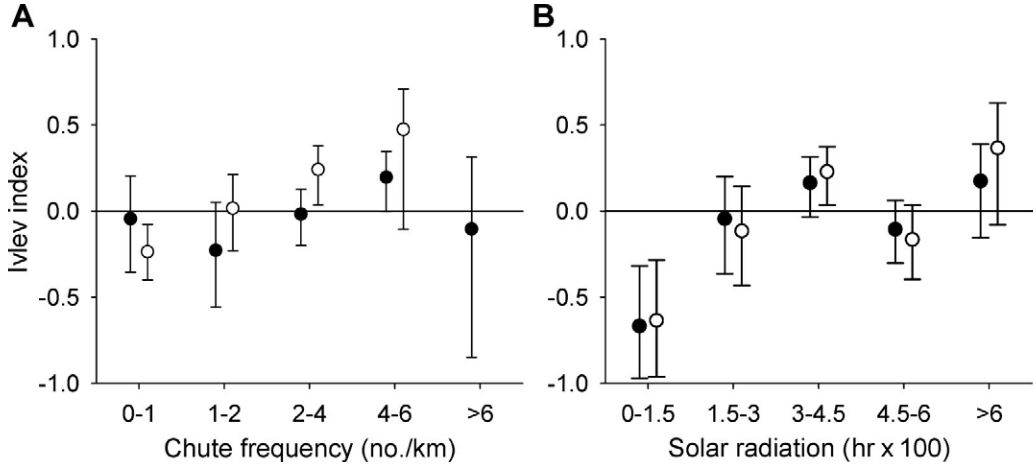

Figure 4. Grizzly bear selection (Ivlev's index ± bootstrapped 95% CI) for (A) the frequency of avalanche chutes and (B) the mean solar radiation value hitting each chute. Closed circles depict all chutes ($N = 1{,}045$) and open circles depict only large (>100-m wide; $N = 518$) chutes. Data were collected in southern British Columbia, 1994–2000.

chutes (>100 m wide; $N = 518$), preference for areas with more large avalanche chutes became apparent. Solar radiation only affected grizzly bears use of avalanche chutes at the coolest portion of the spectrum and these cool chutes were avoided by bears (Fig. 4B). Avalanche chutes that lacked any forb or shrub–forb complexes were avoided by grizzly bears, but abundance of shrubs had little influence on the selection of avalanche chutes by bears (Fig. 5).

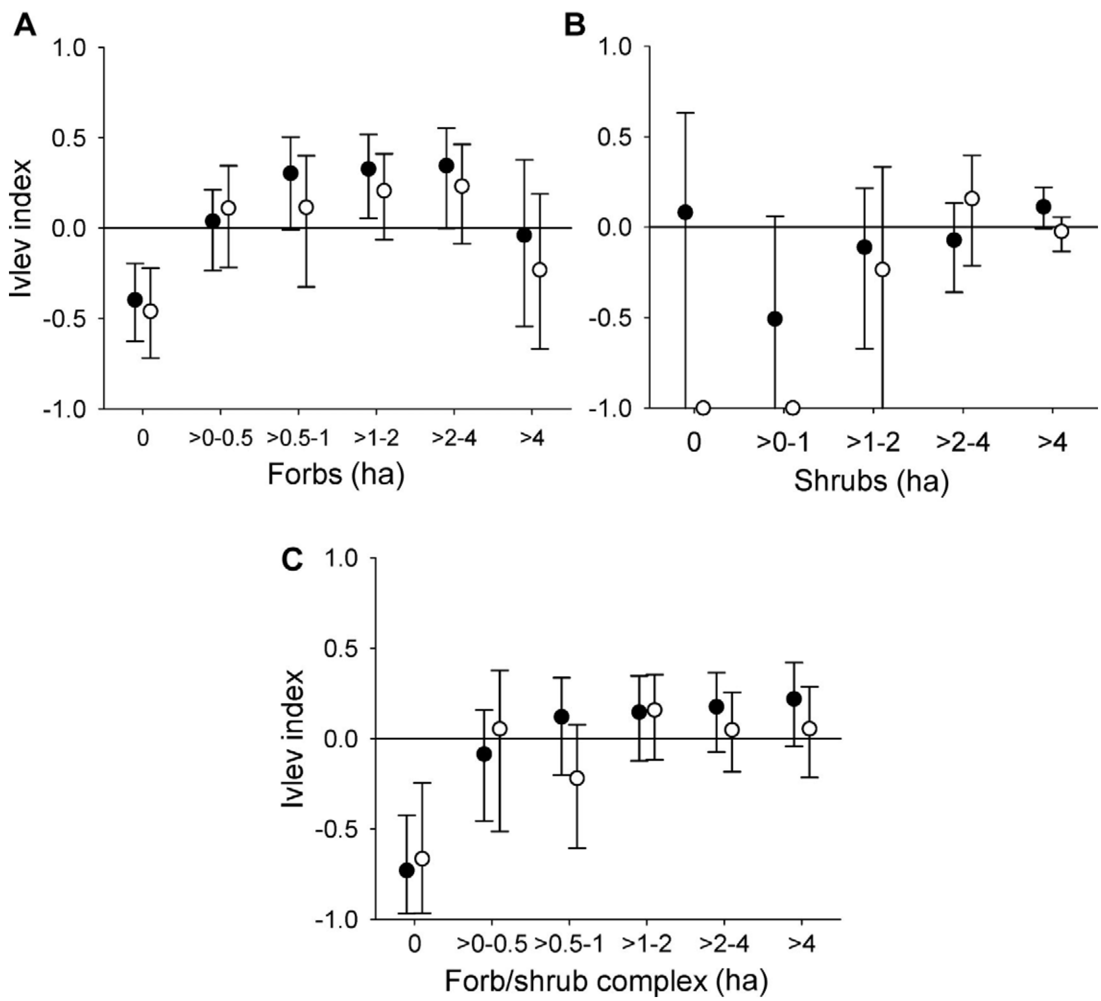

Figure 5. Grizzly bear selection for the abundance of (A) forbs (B) shrubs, and (C) a complex of shrubs and forbs. Selection indexed by Ivlev's electivity (error bars are bootstrapped 95% CI). Closed circles depict all chutes ($N = 1{,}045$) and open circles depict only large (>100-m wide; $N = 518$) chutes. Data were collected in southern British Columbia, 1994–2000.

When we considered both natural and human-affected (logged) buffers, avalanche chutes with narrow forested buffers were preferred, and this pattern held on both the left and right side of the chute (Fig. 6A). Clearcut area within a 300-m buffer of the chute edge did not seem to affect avalanche chute use (Fig. 6B), as indicated by the flat Ivlev index. However, when we restricted the analysis only to large (>100-m wide) avalanche chutes, those with no adjacent logging appeared to be preferred, whereas those with >0–5 ha of adjacent logging were avoided (Fig. 6B). There was no clear pattern for selection of how buffers were distributed (skewed) on the sides of the chute (Fig. 6C).

Initial Study Area Multivariate Analyses

For the initial data set, logistic regression models fit the data better than the negative binomial ($F_{2,19} = 0.39$, $P = 0.68$ vs. $F_{2,1043} = 41.4$, $P < 0.001$, respectively; Fig. 7A vs. 7B), even though both approaches had identical variables in the best model (Table 2; negative binomial models are not shown). The logistic regression model is simpler, having only to predict a binary response as opposed to actual counts. Furthermore, most avalanche chutes that were used contained only 1 location (73.2%), so the response was essentially binary. Thus, we conducted subsequent analyses only using logistic regression. Receiver operating characteristic values for the top models were 0.81 (Table 2). Model averaged parameter estimates were negative for the squared term, the interaction term, and clearcut area, whereas the rest were positive (Table 3). The negative interaction suggested that the positive effect of avalanche chute width was less important for warmer chutes than for cooler chutes. The negative squared term represents a concave down parabola, meaning a positive changing to negative effect of increasing forb abundance on bear use of chutes. By using all candidate models to rank the importance of individual variables (Burnham and Anderson 1998), natural biophysical factors dominated the models in their ability to predict the use of avalanche chutes by grizzly bears. The interaction term had an AIC weight of 0.73, and all other natural features were 0.99. The only anthropogenic factor with an AIC weight >0.01 was clearcut area, which had 23–32% of the weight of the natural biophysical variables (Table 3).

Validation of Multivariate Models and Univariate Selection

In the model validation area, we mapped 1,001 avalanche chutes and sampled 104 GPS locations within these avalanche chutes. Locations from 12 (5 F, 7 M) grizzly bears

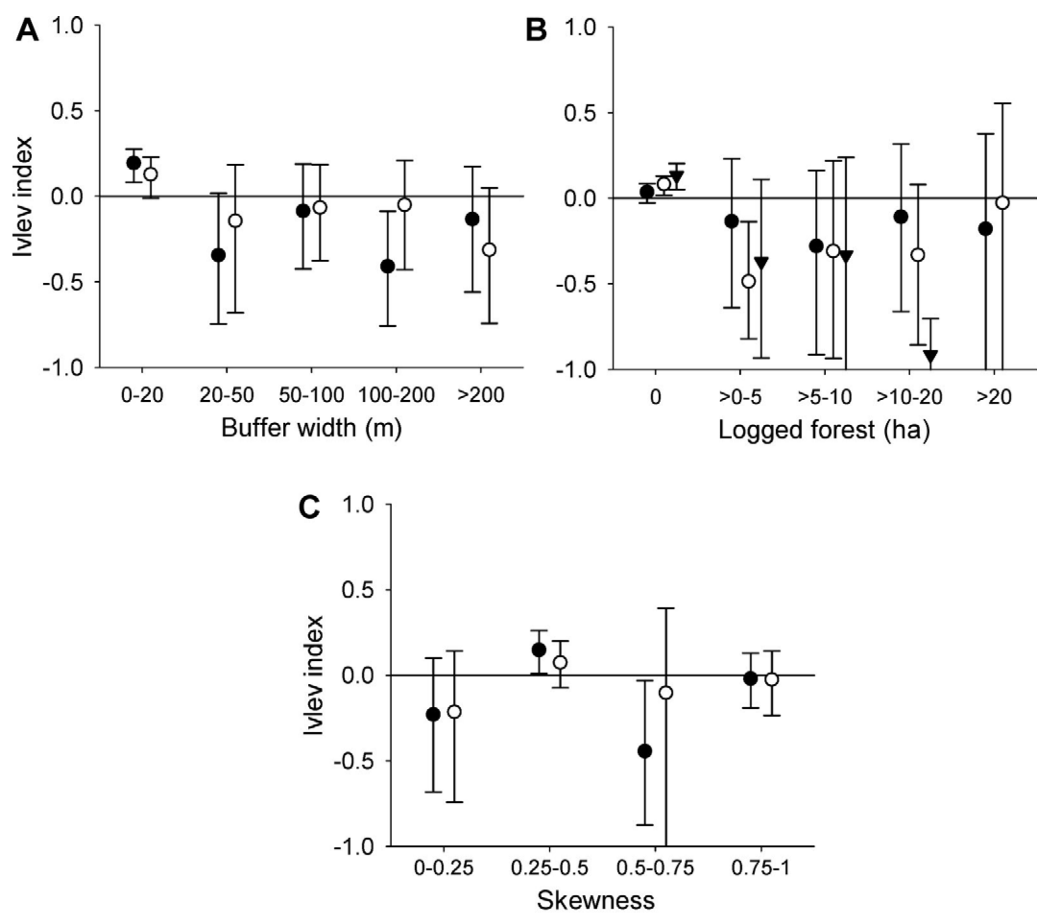

Figure 6. Grizzly bear selection for (A) forested buffer width adjacent to avalanche chutes (solid circles, right side, open circles left side), (B) amount of logging within a 300-m buffer (solid circle all chutes [$N = 1,045$], open circles large chutes [$N = 518$], triangles large and frequent [>2 chutes/km; $N = 356$] chutes), (C) skewness of buffers on either side of the chute (solid circles = all chutes and open circles = large chutes). Values range between 0 (evenly distributed) and 1 (completely skewed to one side). Data were collected in southern British Columbia, 1994–2000.

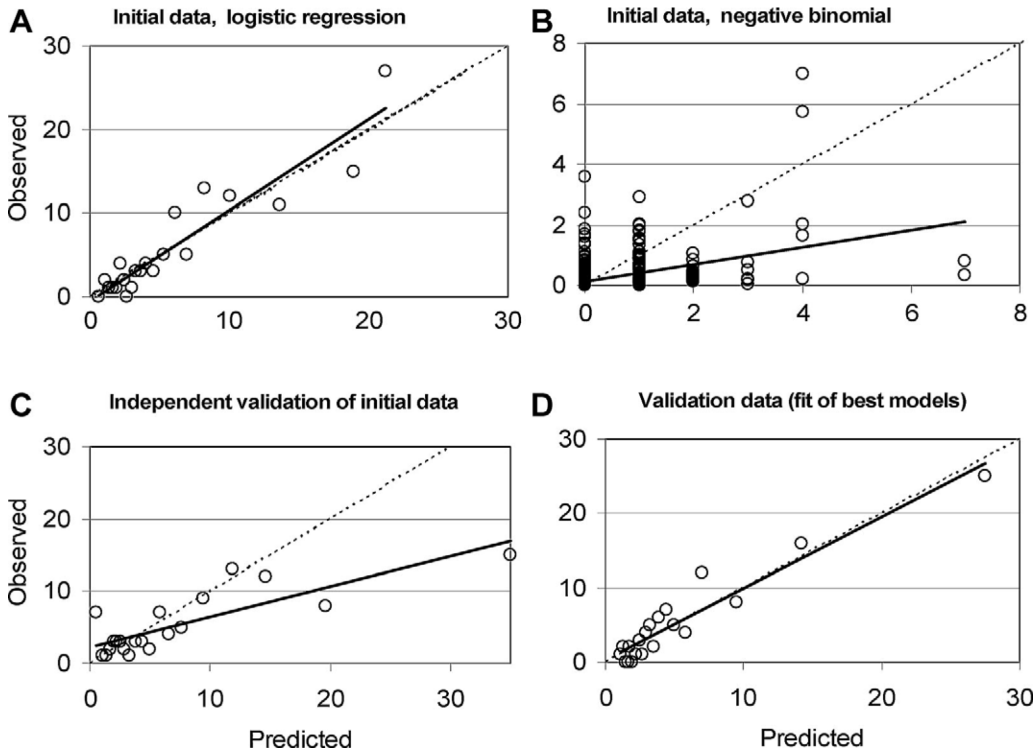

Figure 7. Goodness-of-fit plots for averaged top models representing grizzly bear selection of avalanche chutes in the initial area using (A) logistic regression or (B) the negative binomial model. When we applied the averaged top models (using logistic regression) of the initial area (1994–2000) to the validation area (2006–2008), the predictive success was more variable (shown in C). When we re-ran all candidate models on the validation area, the new averaged top models of the validation area was a better fit (D) than applying the best initial models to the validation area (C). Dotted line represents best-fit 1:1 line, and solid line represents actual fit between predicted and observed values. For the logistic regression models (A,C,D), we binned data into 20 near-equal categories of records, similar to the Hosmer and Lemeshow (1989) Goodness-of-fit test. For the negative binomial model (B), predicted versus observed counts are shown.

Table 2. Top models (0–2 Akaike Information Criteria [AIC] units) using logistic regression to predict grizzly bear use of avalanche chutes, from the initial study area in southern British Columbia, 1994–2000. We sorted models by increasing AIC, with the area under the receiver operating characteristic (ROC) curve, number of parameters (*k*), the log likelihood (LogL), the difference in AIC value (ΔAIC), and the AIC weights (*w*).

	Model structure[a]	ROC	AIC	*k*	LogL	ΔAIC	*w*
1	FREQ_BIG FORB^2 CHUTE_WIDTH SOLAR SOLAR × WIDTH	0.81	625.5	7	−305.7	0.0	0.50
2	FREQ_BIG FORB^2 CHUTE_WIDTH SOLAR	0.81	626.7	6	−307.3	1.2	0.27
3	FREQ_BIG FORB^2 CHUTE_WIDTH SOLAR SOLAR × WIDTH CUT_HA	0.81	627.0	8	−305.5	1.5	0.23

[a] If squared term is present then linear term is included by default. Variable names are provided in Table 1.

were within the area of mapped avalanche chutes. When we applied the top averaged model from the initial area to the validation data set, the fit was poor (Fig. 7C vs. 7A) and the ROC score was 0.77. The *F*-statistic for the validation area was 39.7, which is considerably higher than for the initial area ($F = 0.39$), and the null hypothesis (i.e., perfect fit) was rejected ($P < 0.001$, $F_{2,18} = 39.7$).

Table 3. Model-averaged parameter estimates and SEs using logistic regression to predict grizzly bear use of avalanche chutes, from the initial study area in southern British Columbia, 1994–2000

Variable[a]	Estimate	SE	*w*
Intercept	−5.90	0.82	1.00
FREQ_BIG	0.13	0.041	1.00
SOLAR	0.40	0.16	1.00
CHUTE_WIDTH	0.01	0.004	1.00
FORB	0.56	0.18	1.00
FORB^2	−0.12	0.03	1.00
SOLAR × WIDTH	−0.001	0.0006	0.73
CUT_HA	−0.003	0.004	0.23

[a] Variable names are provided in Table 1.

The top models from the validation data set had 3–6 parameters (Table 4), with ROC scores of 0.78–0.80. The average of these top models had a better model fit (Fig. 7D) than the averaged models derived using the initial study area data but applied to the validation area (Fig. 7C). The $F_{2,18}$-statistic was 0.12, and *P*-value was 0.88, meaning that we could not reject the null hypothesis of perfect fit, thus the observed data appeared well represented by the predictions of the validation area models. Comparing the strength of individual variables from the 2 study areas (Table 3 vs. Table 5) indicates many of the same biophysical factors ranked highly and that clearcut area was again less influential. However, comparing the sign of the parameter estimates between the 2 study areas reveals that avalanche chute width, solar

Table 4. Top models (0–2 Akaike Information Criteria [AIC] units) using logistic regression to predict grizzly bear use of avalanche chutes for the validation study area in southern British Columbia, 2006–2008. We sorted models by AIC, with the area under the receiver operating characteristic (ROC) curve, number of parameters (*k*), the log likelihood (LogL), the difference in AIC value (ΔAIC), and the AIC weights (*w*).

	Model structure[a]	ROC	AIC	*k*	LogL	ΔAIC	*w*
1	FREQ_BIG FORB_SHRB^2 CHUTE_WIDTH SOLAR SOLAR × WIDTH	0.80	565.1	7	−275.5	0.0	0.34
2	FREQ_BIG FORB_SHRB^2	0.78	565.5	4	−278.8	0.5	0.26
3	FREQ_BIG FORB_SHRB^2 CHUTE_WIDTH SOLAR SOLAR × WIDTH CUT_HA	0.80	566.1	8	−275.1	1.1	0.20
4	FREQ_BIG FORB_SHRB^2 CUT_HA	0.78	566.6	5	−278.3	1.5	0.16

[a] If squared term is present then linear term is included by default. Variable names are provided in Table 1.

radiation, and the interaction term had opposite signs with the validation data set compared to the initial data set, although the AIC weight for these 3 factors were lower in the validation area (approx. 0.57; Table 3 vs. Table 5). For the validation data set, the interpretation of the sign of the parameter estimates is more complicated than for the initial area and reflects interacting, nonlinear relationships. Avalanche chute width again positively influenced probability of bear use, except for the coolest avalanche chutes (approx. <100 hr) where it was negative, and solar radiation was negatively associated with bear use. In both data sets clearcut area was negatively associated with bear use, but its effect was not significant (e.g., validation area model 3: $\beta = -0.02$, SE = 0.02, $P = 0.36$; initial area model 3: $\beta = -0.01$, SE = 0.02, $P = 0.52$), although it was present in some models within 2 AIC units of the top model (Tables 2 and 4).

Comparing univariate selection patterns between study areas revealed similar trends, despite differences in sampling approaches. Using all of the hourly GPS data in the validation area ($n = 7{,}526$ locations) we found 325 of the 1,001 chutes had some locations, whereas 676 had no recorded use. Mean number of locations per used chutes was 23.2 (median = 4, lower and upper fifth percentiles = 1–91, range 1–1,065), indicating zero-inflated distribution with a long right tail (as with the VHF data, initial area). In all but 2 classes, the direction of the selection index was the same, and in all but 1 class the error bars of the 2 areas overlapped (Fig. 8, closed vs. open circles). Large chutes were preferred in both areas (Fig. 8A), as were chutes in areas where large chutes were common (Fig. 8B), but bears avoided chutes with no forbs (Fig. 8C). Chutes with no adjacent clearcutting were slightly preferred in both study areas over chutes adjacent to clearcut areas, and there was some evidence of increasing avoidance as the amount of clearcutting increased. The degree of avoidance related to logging differed among the study areas with bears in the validation area showing stronger avoidance where clearcutting exceeded 5 ha within 300 m of chute edges (Fig. 8D). The response by bears in the validation area where there was virtually no vehicle traffic was similar to those from the broader study area, but sampling variation was greater because this analysis was based on a more restricted sample size (reduced from 1,001 to 353 chutes; Fig. 8, triangles). This result suggests that the level of traffic found throughout our study area had little effect on which avalanche chutes bears used.

Table 5. Model-averaged parameter estimates and SEs using logistic regression to predict grizzly bear use of avalanche chutes, from the validation study area in southern British Columbia, 2006–2008.

Variable[a]	Estimate	SE	*w*
Intercept	−3.27	0.56	1.00
FORB_SHRB	0.66	0.099	1.00
FREQ_BIG	0.11	0.039	1.00
FORB_SHRB^2	−0.02	0.0080	0.96
SOLAR	−0.12	0.086	0.57
CHUTE_WIDTH	−0.0002	0.001	0.57
SOLAR × WIDTH	0.0003	0.0004	0.57
CUT_HA	−0.01	0.0087	0.36

[a] Variable names are provided in Table 1.

The area clearcut was present in the top models of both the initial and validation area, but it was a relatively weak factor based on AIC weights and non-significant parameters (Tables 3 and 5). However, we revisited the Ivlev index for the initial area to investigate the influence of forest harvesting adjacent to avalanche chutes preferred by grizzly bears, which were both large and in areas with an abundance of other large chutes. When we constrained the analysis to these avalanche chutes we found those with <10 ha of adjacent logging were frequently used by bears but those with 10–20 ha of adjacent logging were avoided by bears (Fig. 6B, triangles).

DISCUSSION

To test the effectiveness of leaving unlogged forests adjacent to avalanche chutes for grizzly bears, our sample covered a variety of avalanche chute characteristics and in areas with a broad range of clearcut harvesting. Given the range of conditions in our sample, natural biophysical factors were the strongest predictors of avalanche chute selection by grizzly bears. Grizzly bears preferred large avalanche chutes, particularly when these were in areas where other large chutes were common. Grizzly bears also preferred avalanche chutes with narrower forested buffers (natural and logged buffers combined). This result is related to bears' preference of areas with a higher density of avalanche chutes, because a higher density of chutes implicitly means that forested buffers between them will be narrow. Finally, bears avoided avalanche chutes without forb communities, yet preferred those with intermediate levels of forbs. Presumably the selection of large avalanche chutes with a mix of forbs and shrubs, in areas with many large avalanche chutes, maximized foraging

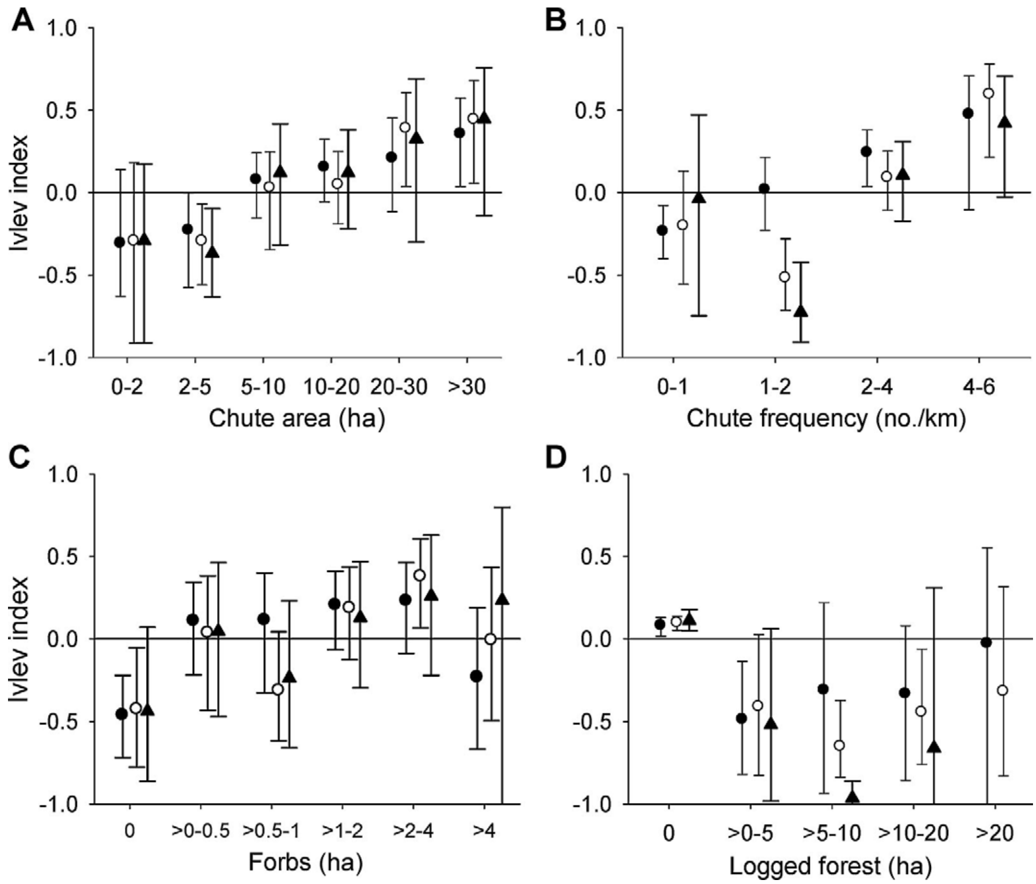

Figure 8. Comparison of Ivlev index between initial (closed circles) and validation (open circles) study areas for 4 variables: (A) chute area, (B) frequency of large (>100-m wide) chutes, (C) abundance of forbs in large avalanche chutes, and (D) amount of clearcutting within a 300-m buffer of large chutes. The initial data are based on weekly locations of 43 grizzly bears from 1994 to 2000 ($N = 1{,}045$ chutes, 123 with and 922 without locations; mean number of locations per used chutes was 1.5, median = 1, lower and upper fifth percentiles = 1–4, range 1–7), whereas the validation data was based on hourly Global Positioning System locations of 12 grizzly bears from 2006 to 2008 ($N = 1{,}001$ chutes, 325 with and 676 without locations; mean number of locations per used chutes was 23.2, median = 4, lower and upper fifth percentiles = 1–91, range 1–1,065). The avalanche chute was the sample unit and number of locations per chute (corrected for chute area) was the dependent variable. Triangles depict chutes from the validation area but restricted to the west side of Lake Revelstoke (Fig. 1) where there were roads and clearcuts but virtually no vehicle traffic ($N = 353$ chutes). Error bars are bootstrapped 95% CIs.

efficiency by concentrating quality foraging areas. During field investigations in the initial study area, Ramcharita (2000) found that most telemetry locations (84%) within chutes were associated with foraging activities. These locations also had high forage value (based on caloric content of selected bear foods) and low visual cover, relative to random plots within avalanche chutes.

When assessing the effect of timber harvesting, neither logged buffer width or area clearcut explained grizzly bear selection of avalanche chutes to a strong degree, particularly in comparison to natural factors. The multivariate modeling revealed that clearcut area was approximately 33% as important as chute density, forb content, and chute width. Ramcharita (2000) also found forest harvesting to be a weak factor influencing bear use. However, our post hoc investigation of the implications of heavy logging (>10 ha adjacent to the chute) near large avalanche chutes and in areas with many avalanche chutes, suggests that clearcutting resulted in less bear use in these instances. Our analysis of the area with very little vehicle traffic (west side of Lake Revelstoke) provided similar results to the overall study area, suggesting it was the loss of trees, not the light vehicle traffic across our study area, that caused avoidance by bears. However, if logging adjacent to avalanche chutes leads to increased access into a once roadless drainage, then the effect of the logging could have significant implications for bear conservation by facilitating an increase in bear mortality (McLellan 1989, McLellan et al. 1999, Nielsen et al. 2004).

We acknowledge that we did not have data on bear use before logging and our analysis used spatial instead of temporal variation. However, undertaking a before-during-after study would take decades to cover an appropriate area that included several bear home ranges through a logging rotation, potentially introducing many other confounding factors. By using a spatial control (i.e., national parks) with no logging we were able to incorporate a broad range of harvest intensity, which helps extend the applicability of our findings.

The models developed with data collected in our initial study area performed well (Fig. 7A) but were not robust to extrapolation in our verification study area, even though the 2 areas were adjacent and portions of each study area were in the same mountain range. However, the effects of chute width, frequency of large avalanche chutes, and area clearcut were consistent across both study areas. Plus, factors associated with forage (either forbs or shrub–forb complexes) were also important in both areas. The main difference was that in the validation area bears preferred avalanche chutes on cooler aspects. Preference for cooler aspects occurred even though the orientation of valleys in the validation area meant that more north-facing chutes were available to bears (R. Serrouya, University of Alberta, unpublished data). The discrepancy between the 2 areas does not change the general conclusion that use of avalanche chutes by grizzly bears was dominated by natural biophysical factors and that logging appeared to be less important, but with a negative influence, particularly for the best-quality avalanche chutes.

Our effort to verify the initial results in an adjacent study area highlights the problem of extrapolating habitat models without understanding and accounting for underlying mechanisms. It has been suggested that researchers are logistically constrained and are therefore unlikely to have independent data for prospective sample evaluations, so are limited to within-study area verification using withheld data (Boyce et al. 2002). Because all large mammals and other vertebrates in North America have been studied in numerous places, verification from other areas is possible and we encourage the use of independent data as a stronger test of ecological models, particularly if these are to be extrapolated.

MANAGEMENT IMPLICATIONS

Our results suggest grizzly bear habitat managers should prioritize the use of forested buffers for avalanche chutes >5 ha or >100 m wide, at a frequency >2 avalanche chutes/km, with >150 hr of solar radiation, and at least some forb or shrub–forb content. Because most chutes do not meet these criteria (i.e., are narrow and shrub dominated) and were not preferred by bears, more protection could be focused on chutes of the highest value. However, the above values depend on the risk tolerance of natural resource management agencies. Some may choose more conservative values, especially when thresholds are not obvious.

Given that the best chutes were used less than expected if there was adjacent forest harvesting, we do not recommend eliminating the forested buffer guidelines for these types of chutes. If, in the future, forest harvesting or human use of grizzly bear habitat were to increase greatly, these factors would be beyond our sampling range and our inferences may not hold. Decisions to modify guidelines for the retention of forested buffers should be made in a broader context of risk tolerance to grizzly bear–human interactions. What is more certain is that forest harvesting activities can negatively affect grizzly bear populations by providing access to formerly remote areas, thus increasing encounters with humans with firearms and causing direct mortality (McLellan 1989, McLellan et al. 1999, Nielsen et al. 2004).

In some jurisdictions land use plans have resulted in an agreement to not harvest a finite area of primary forest to help grizzly bear conservation but the location of these reserves has yet to be specified (Revelstoke Minister's Advisory Committee 1999, Kootenay-Boundary Higher Level Plan Order 2002, Lillooet Land and Resources Management Plan 2004). We suggest that in many cases where grizzly bears are a priority, the forest stands to be retained should be those towards the top end of drainages and particularly stands that are interspersed among the large avalanche chute complexes that are often common in these areas. Because roads are needed for forest harvesting and always enter drainages from the lower ends, selecting reserves at the top end over those lower in the drainage will buffer what are often the most important chutes. This approach will also increase the amount of roadless areas, which will help grizzly bear conservation and reduce road cost for the forest industry.

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