MOOSE CALVING STRATEGIES IN INTERIOR MONTANE ECOSYSTEMS

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Parturient ungulates are relatively more sensitive to predation risk than other individuals and during other times of the year. Selection of calving areas by ungulates may be ultimately related to trade-offs between minimizing risk of predation and meeting nutritional needs for lactation. We used digital and field data to examine selection of calving areas by 31 global positioning system–collared moose (*Alces alces*) in southeastern British Columbia. We examined movements 12 days before and after calving, and analyzed habitat selection at 2 scales of comparison: the immediate calving area to the extended calving area (100 ha), and the extended calving area to the surrounding home range. Maternal moose exhibited 1 of 2 distinct elevational strategies for calving area selection during the days leading up to calving: 16 moose were climbers and 15 were nonclimbers. Climbers moved a mean of 310 m higher in elevation to calve, whereas nonclimbers showed little change in elevation. Hourly movements by all maternal females increased 2- to 3-fold in the 1–4 days before calving and were generally directional, such that all calving areas were outside of areas used during the 12 days before calving. At the broad scale, elevation was the strongest predictor of the extended calving area within the home range. At the fine scale, climbers selected areas with reduced tree density, reduced forage, and increased distance from water, whereas nonclimbers selected areas with increased forage, decreased distance from water, and decreased slope. Beyond the obvious elevation difference between climbers and nonclimbers, moose appeared to exhibit 2 distinct calving strategies in mountainous ecosystems. A functional explanation for the 2 strategies may be that climbers moved into areas where forage quantity and quality were relatively low, but where risk of predation (mainly by grizzly bears [*Ursus arctos*]) also was reduced. Nonclimber moose calved in areas with higher forage values, and appeared to select areas at the finer scale to reduce predation risk (e.g., association with water and reduced tree density for visibility).

Key words: *Alces alces*, British Columbia, calving, habitat use, moose, movements

Female ungulates may select birth sites for a number of reasons, ultimately related to trade-offs between minimizing risk of predation of neonates and meeting nutritional needs for lactation (Bergerud 1992; Bowyer et al. 1999; Carl and Robbins 1988; Edwards 1983; Lent 1974; Stephens and Peterson 1984). Predation on young is often greatest during parturition and in the 1st weeks after birth (Ballard 1992; Ballard et al. 2001; Bowyer et al. 1998). To minimize predation risk, woodland caribou (*Rangifer tarandus*) in northern British Columbia used high-elevation slopes with poor forage for calving to space themselves from wolves (*Canis lupus*) and bears (*Ursus* spp.—Bergerud et al. 1984), and bighorn sheep (*Ovis canadensis*) moved to lambing areas before the onset of

most new plant growth, avoiding areas of high predation risk and high-quality food (Festa-Bianchet 1988).

For moose (*Alces alces*), existing data on calving area selection are conflicting. The need for secluded areas has often been described (Addison et al. 1990; Bailey and Bangs 1980; Chekchak et al. 1998; Langley and Pletscher 1994; MacCracken et al. 1997; Markgren 1969; Peterson 1955; Welch 2000), but habitat preferences are highly variable both among and within studies, with selection both for and against hiding cover, forage availability, distance to water, islands, and slope steepness and position (Addison et al. 1990; Altmann 1963; Bailey and Bangs 1980; Bowyer et al. 1999; Chekchak et al. 1998; Jackson et al. 1991; Langley and Pletscher 1994; Leptich and Gilbert 1986; Stringham 1974; Welch 2000; Wilton and Garner 1991). Some moose move higher in elevation for calving (Addison et al. 1990; Bowyer et al. 1999; Chekchak et al. 1998; Langley and Pletscher 1994; Wilton and Garner 1991), which is one option in montane environments.

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Limited data are available on moose calving area selection within interior mountain ecosystems in western North America (Altmann 1963; Langley and Pletscher 1994). In southeastern British Columbia, moose appear to calve within managed forests at a range of low to high elevation (Poole and Stuart-Smith 2004), and thus are exposed to disturbance and habitat modification from forestry activities, and the effects these modifications may have on predation risk. Logging generally enhances habitat carrying capacity for moose (Peek 1997), and does not appear to affect the vulnerability of moose to predation by wolves during winter (Kunkel and Pletscher 2000). If the habitat or topographic characteristics moose use for calving can be identified, they could be incorporated into forestry development planning to minimize disturbance during this critical period.

We examined selection of calving areas by moose in southeastern British Columbia using a multiscale approach based on remote sensing and field data. We used location data obtained during a 2-year study of late-winter habitat selection by moose in interior montane forests (Poole and Stuart-Smith 2007). Previous work in the southern part of our study area suggested that maternal moose used 2 different elevational strategies for predator avoidance (Langley and Pletscher 1994); however, these authors were unable to explore these differences. We investigated this idea with the objective of quantifying and contrasting selection of calving areas between moose that climbed to higher elevations before calving, and those that did not. We stratified moose into groups based on their movements before calving, and examined habitat selection between these 2 groups at broad and fine scales.

MATERIALS AND METHODS

Study area.—We collared adult cow moose in 3 valleys of southeastern British Columbia: the Flathead, Upper Elk, and Spillimacheen (Fig. 1). Montane Spruce and Engelmann Spruce–Subalpine Fir biogeoclimatic zones are predominant in all areas, with some Interior Cedar–Hemlock and Interior Douglas-Fir, especially in the Spillimacheen Valley (Braumandl and Curran 1992; Meidinger and Pojar 1991). The Interior Douglas-Fir zone occurs in valley bottoms and lower slopes (800–1,200 m elevation), and typically has pure Douglas-fir (*Pseudotsuga menziesii*) or mixed seral stands of Douglas-fir, western larch (*Larix occidentalis*), and lodgepole pine (*Pinus contorta*). The Interior Cedar–Hemlock zone also occurs at lower elevations (750–1,550 m) in wetter areas, and includes a wide variety of conifer tree species, including western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*), as well as larch and Douglas-fir. The Montane Spruce zone is found at moderate-elevation valley bottoms and slopes (1,200–1,650 m), and commonly has western larch, Engelmann spruce (*Picea engelmannii*), and Douglas-fir, with extensive seral stands of lodgepole pine because of past wildfires. The Engelmann Spruce–Subalpine Fir zone occurs at higher elevations (1,650–2,100 m), and is dominated by closed-canopy forests of spruce and subalpine fir (*Abies lasiocarpa*), and seral lodgepole pine stands. On high moun-
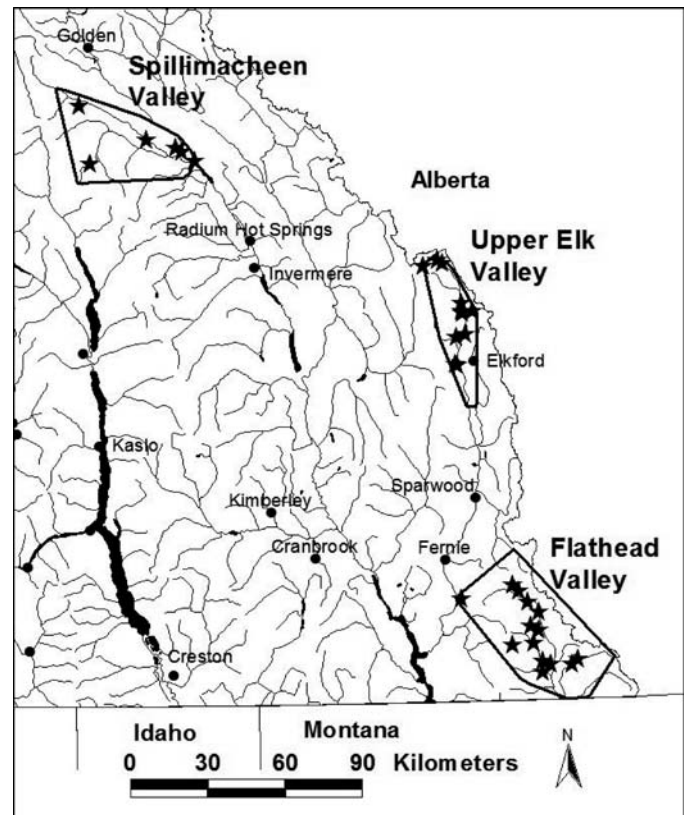

FIG. 1.—Map of southeastern British Columbia, showing study areas and moose calving areas (stars; $n = 31$).

tains, the Alpine Tundra zone occurs above the Engelmann Spruce–Subalpine Fir zone. Aspen (*Populus tremuloides*), black cottonwood (*P. balsamifera*), and paper birch (*Betula papyrifera*) occur infrequently in all zones except the Engelmann Spruce–Subalpine Fir zone and the Alpine Tundra zone, where they are very rare.

Each of the 3 areas has a wide diversity of topography and vegetation accessible to moose. All have experienced significant industrial timber harvesting over the past 50 years, and had moderate to high densities of wolves (Hayes and Gunson 1995), grizzly bears (*U. arctos*, Flathead Valley ~44/1,000 km^2; Upper Elk Valley and Spillimacheen Valley: ~24/1,000 km^2—Mowat et al. 2005), and likely black bears (*U. americanus*).

Capture of moose and identification of calving areas.—We captured and placed global positioning system radiocollars (Advanced Telemetry Systems Inc., Isanti, Minnesota) on adult female moose by net gunning from a helicopter during winters 2001–2002 and 2002–2003. Capture and handling protocols followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Collars were deployed in December–January on animals scattered throughout our study areas, and were removed in August–September each year. Global positioning system collars were programmed to obtain locations at 4-h intervals during the calving period. Accuracy of global positioning system collar locations was likely <5–30 m (50% and 95% of locations,
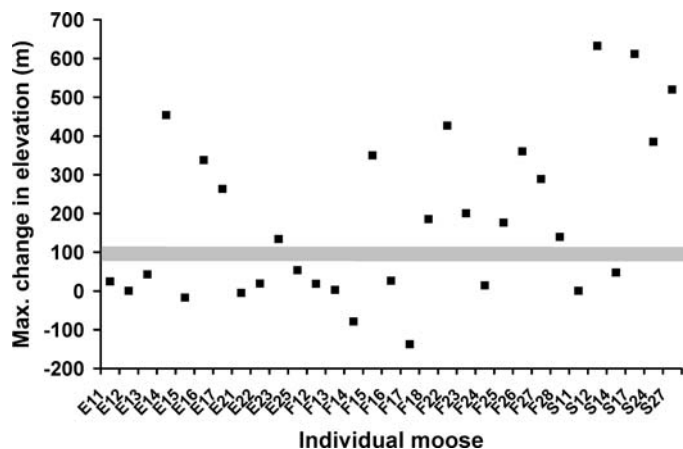
FIG. 2.—Maximum change in elevation compared to the three 4-day time periods before calving by female moose in southeastern British Columbia, 2003–2003. Gray band is the border between climbers and nonclimbers. E = Upper Elk Valley, F = Flathead Valley; S = Spillimacheen Valley.

respectively—Adrados et al. 2001; D'Eon et al. 2002). At capture we measured total contour body length and chest girth to the nearest centimeter, and subjectively scored condition to estimate body weight following the techniques and regression equation of Hundertmark and Schwartz (1998). Thirty-nine female moose were monitored during the calving period; 31 of these moose were pregnant at the time of capture (as determined by blood serum progesterone levels—Haigh et al. 1982) and appeared to localize (i.e., stay in one spot) for calving. One additional female moose was pregnant according to progesterone levels, but did not localize, and was removed from analysis. Based on previous studies, we assumed calving would occur between mid-May and mid-June (Schwartz 1997).

We used the techniques of Testa et al. (2000) and Vore and Schmidt (2001) to identify individual calving areas. Vore and Schmidt (2001) observed a significant increase then decrease in daily movements by maternal female elk (*Cervus elaphus*), coupled with fidelity to a small area, as evidence of parturition. A similar pattern was observed with moose in Alaska (Testa et al. 2000). Here we define "calving site" as the actual location of parturition, and "calving area" as the minimum convex polygon (Mohr 1947) encompassing locations of the maternal female during and in the 1st approximately 4–9 days after parturition (Langley and Pletscher 1994; Vore and Schmidt 2001). To ensure that our designation of calving areas was as small as possible, outliers during the calving period were subjectively removed (6% of locations; mainly single locations distant from all others) before calculation of calving area minimum convex polygons.

Movement.—We treated each animal as a sampling unit. Because of sample sizes, we combined analyses between years and among areas. To facilitate analysis of movements relative to the calving period, we examined 3 consecutive 4-day periods before and after the calving period. For barren females ($n = 7$) we assigned the "calving period" as the 4 days beginning on 28 May, the median date of initiation of calving. For each of

the 7 time periods we calculated the mean value of the variable in question. We compared moose movements, both between barren and maternal females, and between maternal moose showing different reproductive strategies. For maternal moose, we examined the maximum elevation change between calving and the 3 time periods before calving, and observed that moose fell into 2 distinct groups, those that moved >134 m higher in elevation compared with their lowest mean elevation before calving, and those that moved <54 m (Fig. 2). We separated these 2 groups into climbers and nonclimbers, respectively. For each of the 3 reproductive categories (barren, climbers, and nonclimbers) we examined mean elevations among time periods (scaled to 0 m for each moose at the first 4-day period to facilitate comparisons among areas). We also examined differences in hourly movement rates (m/h) between global positioning system locations obtained at 4-h intervals among time periods. To examine movement patterns, we determined the mean distance from the centroid of locations in the time periods before and after the calving period to the centroid of the calving area. Finally, we examined absolute elevations at calving between strategies for the Flathead valley because data on grizzly bear distribution were available for that area (McLellan and Hovey 2001).

Habitat selection.—We examined 2 scales of selection within each calving area: broad scale, use of a 100-ha (~565-m-radius) window (extended calving area [CAEXT]), centered on the calving area within the 95% fixed kernel home range for each animal; and fine scale, use of the calving area within the CAEXT. Comparisons were matched by animal. We used digital data for the broad-scale comparison, rationalizing that landscape- or home-range–level processes drive the 1st level of selection, and that the accuracy of the digital data would be limited at the finer scale. We used field data to examine the fine-scale comparison (see below).

We obtained digital 1:20,000 scale topographic files (Geographic Data BC 1992), forest inventory planning files (Forest Cover—Resources Inventory Branch 1995), and 1:50,000 scale British Columbia Watershed Atlas files (British Columbia Ministry of Sustainable Resource Management, Victoria, British Columbia, Canada), and conducted analyses using ArcInfo (Environmental Systems Research Institute, Redlands, California) geographic information system–and wildlife-based extensions (Hooge and Eichenlaub 2000).

For the broad-scale analysis, a 100-m (CAEXT window) or 250-m (home-range window) grid was generated, topographic and distance values were derived for each point on the grid, and mean values for the 100-ha (CAEXT) and home-range areas were obtained. For variables derived from Forest Cover data, the weighted composition of area coverage or the mean across grid points was obtained.

We included variables in the analysis based on a review of the literature for potentially important factors influencing calving area selection. We also included digital variables that might act as surrogates for more causative factors (e.g., crown closure or stand age for hiding cover or forage availability; Table 1). In lieu of aspect, we used solar duration, which is the number of hours per day that the sun illuminates a pixel based

TABLE 1.—Description of digital variables examined in broad-scale modeling of moose calving area habitat selection, southeastern British Columbia, 2002–2003.[a]

Acronym	Description
Elev	Elevation (m)
Slope	Slope (%)
Elev*Slope	Interaction term of elevation and slope, always includes individual terms
Solar	Solar duration value (h)
DistRoad	Distance to nearest road (m)
DistWater	Distance to lake or stream/river in the British Columbia Watershed Atlas (m)
DistSeral	Distance to early seral edge $\leq$ 30 years of age (m)
Decid	Weighted composition of deciduous species (%)
Pine	Weighted composition of pine species (%)
Fd	Weighted composition of Douglas-fir (%)
Spruce	Weighted composition of spruce species (%)
Subfir	Weighted composition of subalpine fir (%)
Riparian	Weighted composition of riparian cover type; swamps, wet meadows, and river edges (%)
Open	Weighted composition of open cover type; shrub, brush, meadows, and alpine (%)
Logged	Weighted composition of logged cover type; generally <40 years of age (%)
Age	Projected overstory stand age (years)
CC	Overstory crown closure (%)

[a] Overstory species were derived from species or species group, including only those Forest Cover polygons with overstory data.

TABLE 2.—Description of field variables examined in fine-scale modeling of moose calving area habitat selection, southeastern British Columbia, 2005.

Acronym	Description
Elev	Elevation (m)
Slope	Slope (%)
Solar	Solar duration value (h; obtained from digital data)
DistWater	Distance to water (m)
DensTrees	Density of all trees $\geq$ 7.5 cm dbh and > 1.3 m tall (no./ha)
DensSnags	Density of snags $\geq$ 7.5 cm dbh and > 1.3 m tall (no./ha)
Meandbh	Mean dbh of tress $\geq$ 7.5 cm dbh (cm)
Smalltrees	Density of small trees < 7.5 cm dbh and > 1.3 m tall (no./ha)
Sumshrub	Coverage of all shrubs (%)
Mooseshrub	Coverage of shrubs rated as moderate to high forage preference (%)
Greenup	Categorical variable from 1 (nonbuds; winter condition) to 5 (full leaf-out)
Browsing	Categorical variable from 1 (no browsing observed) to 5 (all shrubs heavily browsed)
CCfield	Overstory crown closure as measured with a moosehorn (%)
Visibility	Horizontal visibility measured as proportion visible (%)

on latitude and the shading effects of nearby topography (Kumar et al. 1997). We calculated means for solar duration for 11 January to 31 March to match work completed elsewhere in the region (Poole and Mowat 2005). Although this period does not include the calving period, we assumed that most areas would have the same directional bias in derived solar values. Habitats with no overstory data in the digital databases were classified into 3 cover types: riparian (swamps, wet meadows, gravel bars, and river edges), open (shrub, brush, meadows, and alpine), and logged (logged areas generally <40 years of age).

To examine fine-scale habitat selection we conducted fieldwork primarily between 15 May and 24 June 2005. A portion of the fieldwork on 4 calving areas was conducted between 17 July and 17 August 2005 because high water levels restricted access during spring. For each moose, we placed 3 plots in the calving area (at center point and in each direction half way between center point and long edge of the calving area polygon), and randomly placed 5 plots in the CAEXT, spaced apart at a minimum of 100 m. When the calving area was too small to fit 3 plots without overlap we placed 1 or 2 plots. At each plot we measured variables (Table 2) within a 5.65-m radius (0.01 ha) and within an 11.3-m radius (0.04 ha) of the center point. Within each plot we recorded elevation, slope, and aspect; estimated distance to nearest significant water body (e.g., creek, river, marsh, pond, or lake); estimated stand composition and age class; and identified vegetation type. We used solar values for each plot center (derived from digital data) to better represent the interaction between aspect and slope. We measured canopy cover at plot center and 3 m east

and west of plot center using a moosehorn (Cook et al. 1995), and averaged the readings for the plot. We measured concealment cover (also termed hiding cover or horizontal visibility) using a 2-m cover pole segmented every 10 cm (Griffith and Youtie 1988). With the observer at plot center (eye height ~ 1.7 m) and the pole held vertical 10 m away in each of 4 cardinal directions, we recorded the number of segments (to the nearest half segment) not obscured by vegetation or topography within four 50-cm classes from the ground (0–50 cm) to pole top (150–200 cm). Values were converted to percent visible, and were summed for each plot for analysis.

Within the 5.65-m plot we measured the diameter at breast height (dbh) of all trees $\geq$ 7.5 cm dbh and > 1.3 m tall by species and decay class (Thomas 1979), and within the 11.3-m-radius plot we did the same for all trees $\geq$ 30 cm dbh. Within the 5.65-m plot, trees < 7.5 cm dbh (but > 1.3 m tall) were tallied by species, and we estimated the coverage in square meters for each shrub species and small trees (< 1.3 m tall). We classified shrubs into moose forage shrubs, defined as all shrubs and small trees providing preferred moose forage (Blower 1982; Poole and Stuart-Smith 2005; Singleton 1976). We subjectively estimated plant green-up on a scale of 1 (no buds; winter condition) to 5 (full leaf-out), and estimated browse intensity, also on a scale of 1 (no browsing observed) to 5 (all shrubs heavily browsed).

Statistical analysis.—We developed an a priori set of candidate models based on the literature and field observations to explain selection of calving areas by moose using climbing and nonclimbing strategies. Candidate models for broad ($n = $ 20) and fine ($n = $ 32) scales were examined separately because the resolution and accuracy differed significantly. To account for the matched design, we used conditional logistic regression fit to a Cox-proportional hazards model to compare selection at both scales (Hosmer and Lemeshow 1989). Following suggestions by Anderson and Burnham (2002), we assessed
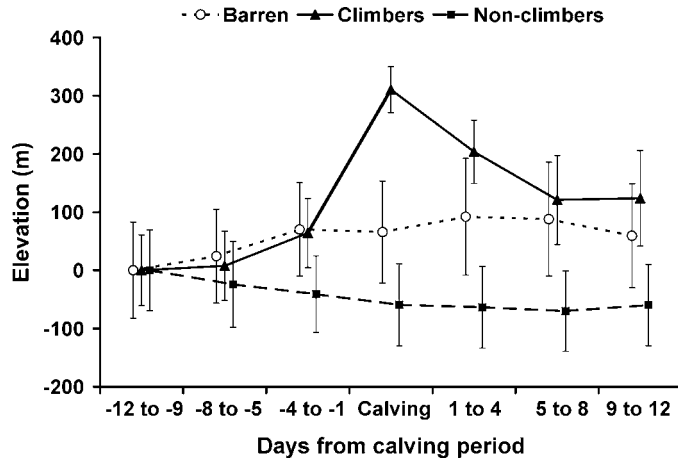
Fig. 3.—Mean elevational change (± *SE*) of barren, climber, and nonclimber female moose during 7 time periods relative to the period 9–12 days before parturition in southeastern British Columbia, 2003–2003. The "calving area" for barren females was the mean location during the 4-day period beginning on 28 May, the median date of calving.
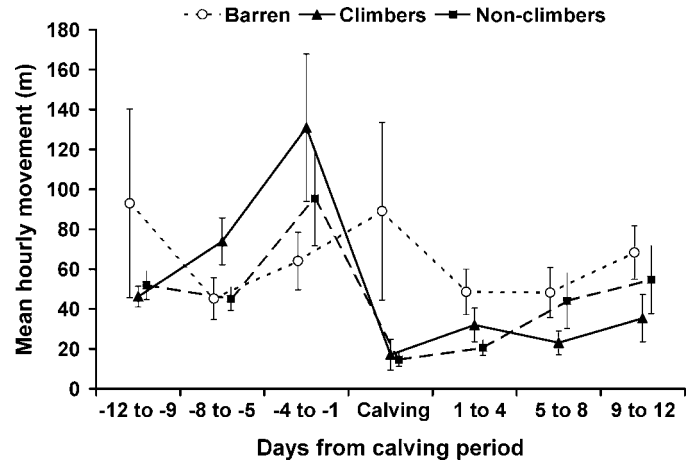

Fig. 4.—Mean hourly movements (± *SE*) of barren, climber, and nonclimber female moose during 7 time periods relative to parturition in southeastern British Columbia, 2003–2003. The "calving period" for barren females was the 4-day period beginning on 28 May, the median date of calving.

the strength of competing models using Akaike's information criterion values corrected for small sample sizes (AIC_c—Anderson et al. 2000), differences in AIC_c values (ΔAIC_c), and Akaike weights (ω). We also calculated AIC_c weights for each variable to compare relative strength among variables (Burnham and Anderson 1998). We tested for multicolinearity among variables using Spearman rank correlation analysis to avoid including highly correlated variables in the same model ($r_s > 0.7$—Tabachnick and Fidell 1996). Models that failed to converge were removed from analysis. We examined likelihood ratio chi-square statistics for assessment of goodness-of-fit for the most highly parameterized among the top models within each analysis. We used receiver operating characteristic (ROC) curves to assess model fit at the fine scale. We were unable to calculate ROC model fit for a matched case design (which lacks an intercept) with single input values for each match (broad scale). Only the top-rated models (within ~2 AIC_c units of the best model) and for comparison the null model (no covariates) are presented.

We also performed 2-tailed *t*-tests for unequal variance on individual variables between strategies for calving areas. We examined differences in use of 6 vegetation types for calving areas compared with random sites within the CAEXT using likelihood ratio chi-square statistics. Because of sample size restrictions and almost equal weighting between climbers and nonclimbers, we pooled all moose for habitat type comparisons. We conducted data analyses using SAS software (SAS Institute Inc. 1997).

RESULTS

Mean and median dates of calving were 27 May and 28 May, respectively (range 14 May–9 June). Calving areas averaged 0.8 ha in size (± 0.17 *SE,* range 0.1–4.2 ha). The length of stay in the calving area averaged 6.5 days (± 0.43

SE, range 3–12 days). Average number of locations for each moose during the calving period was 20 (± 1.5 *SE,* range 7–36 locations). Average estimated weight at capture of climbers (427 kg ± 13.9 *SE, n* = 15) tended to be lower than that of nonclimbers (461 ± 11.4 kg, *n* = 14; *t* = 1.57, *d.f.* = 27, *P* = 0.06).

Movements.—Relative elevation of barren females did not change appreciably among time periods, with a mean average increase of <92 m (Fig. 3). Nonclimbers also showed little change in elevation during the calving period, although there was a slow trend in decreasing elevation over time. Climbers moved higher in elevation ($\bar{X}$ = 310 m) for calving, compared to 9–12 days before calving, with the greatest change in movement occurring immediately before calving.

Hourly movements by barren females did not differ before, during, and after the normal calving period (Fig. 4). Both climbers and nonclimbers moved more during the 4-day period before calving (131 and 95 m/h, respectively), and to a lesser extent during the 4-day period before that (74 and 45 m/h, respectively), compared with the calving period (17 and 15 m/h, respectively). Movement rates by all maternal females increased slowly postcalving.

All females averaged >2,900 m from their calving areas until the last 4 days before calving (Fig. 5). Climbers were the greatest distance away from their calving areas, even within the last 4 days before calving ($\bar{X}$ = 4,800 m), whereas nonclimbers were roughly 40% closer to their calving areas ($\bar{X}$ = 2,900 m) before calving compared with climbers. Examination of these data suggests that the final movements to calving areas occurred immediately before the onset of calving. All calving areas were outside of areas used by maternal moose during the 12 days before calving.

Climbers in the Flathead Valley (*n* = 8) calved on average 310 m higher than did nonclimbers (*n* = 6; $\bar{X}$ = 1,680 m ± 52 *SE,* range 1,480–1,880 m, and 1,370 ± 86 m, range 1,010–1,630, respectively; *t* = 3.2, *d.f.* = 12, *P* = 0.007).

Habitat selection.—Of the 16 climbers, 4 calved in the Montane Spruce biogeoclimatic zone, 10 in the Engelmann Spruce–Subalpine Fir zone, 1 in the Alpine Tundra zone, and 1 in an area on the border between Montane Spruce and Engelmann Spruce–Subalpine Fir. Of the 15 nonclimbers, 1 calved in the Interior Cedar–Hemlock zone, 2 in the Interior Douglas-Fir zone, 5 in the Montane Spruce zone, and 7 in the Engelmann Spruce–Subalpine Fir zone.

Female moose did not select vegetation types for calving ($\chi^2 = 6.63$, $d.f. = 5$, $P = 0.25$; Table 3; Fig. 6). Only 1 calving area was in a cutblock, consisting of relatively dense 35-year-old spruce–subalpine fir regeneration. When only forested habitats were considered and pooled to immature versus mature and old estimated age classes, there was no difference in the distribution of calving areas ($n = 20$) and random sites within the extended calving area ($n = 110$; $\chi^2 = 0.53$, $d.f. = 1$, $P = 0.47$).

On average, calving areas used by climbers were 325 m higher in elevation ($t = 4.04$, $d.f. = 29$, $P = 0.0005$), on 6.7 times greater slopes ($t = 5.65$, $d.f. = 29$, $P < 0.0001$), 380 m further from water ($t = 5.26$, $d.f. = 29$, $P < 0.0001$), and in areas with 42% of the coverage of moose forage shrubs ($t = 2.42$, $d.f. = 29$, $P = 0.025$) than areas used by nonclimbers (Table 4). Although not significant, in calving areas the density of trees in areas used by climbers was 23% greater than in areas used by nonclimbers ($t = 0.62$, $d.f. = 29$, $P = 0.54$), and had 13% less green-up index than areas used by nonclimbers ($t = 1.10$, $d.f. = 29$, $P = 0.28$). Our index of green-up was negatively correlated with elevation ($r = -0.63$). Horizontal visibility did not differ between calving strategies ($t = 0.38$, $d.f. = 29$, $P = 0.70$), but for nonclimbers there tended to be greater visibility at each of the 50-cm height intervals compared with available plots in the extended calving areas for climbers (Fig. 7).
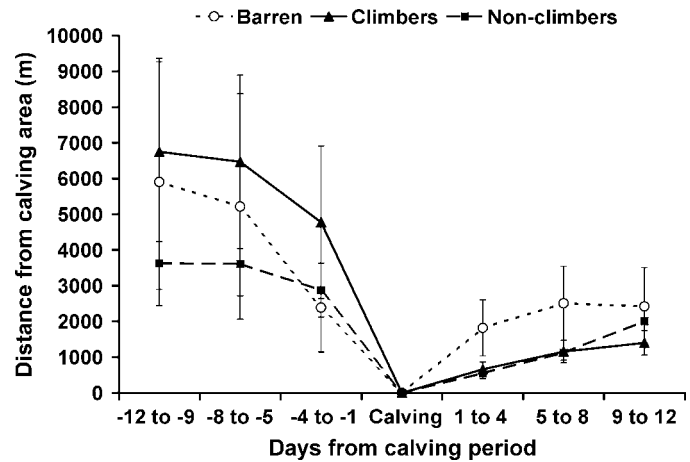

Fig. 5.—Mean distance ($\pm$ SE) of barren, climber, and nonclimber female moose from their calving area during 7 time periods relative to parturition in southeastern British Columbia, 2003–2003. The "calving area" for barren females was the mean location during the 4-day period beginning on 28 May, the median date of calving.

Climbing strategy.—At the broad scale for moose following the climbing strategy, elevation (positive coefficient) was the most probable model ($\chi^2 = 18.6$, $d.f. = 1$, $P < 0.0001$), a vast improvement over the null model (Table 5). Models including riparian (negative), and elevation and logged (negative) were weakly supported by the data. Elevation ($\omega = 0.71$), had ≥ 3 times greater variable weight than riparian cover type (0.24), and logged cover type (0.14).

At the fine scale, the model including terms for density of trees (negative), moose shrub coverage (negative), and distance to water (positive) was the most supported ($\chi^2 = 12.4$, $d.f. = 3$, $P = 0.006$), with an ROC of 0.68 (Table 5). Models with density of trees alone, density of trees and moose shrub

Table 3.—Summary statistics for digitally derived habitat characteristics of moose extended calving areas (CAEXTs; 100-ha area) and home ranges (HRs) between climber and nonclimber strategies in maternal moose in southeastern British Columbia, 2002–2003. Variable descriptions are provided in Table 1.

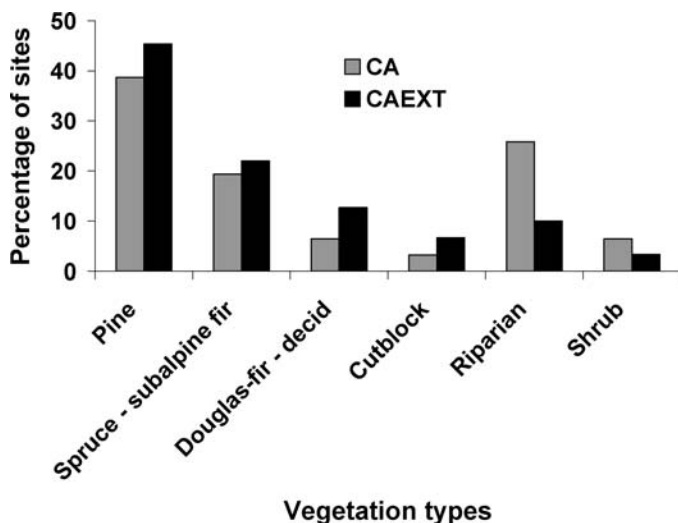|	Climbers ($n = 16$)				Nonclimbers ($n = 15$)			
	CAEXT		HR		CAEXT		HR	
Variable	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Elev (m)	1,707	45.3	1,426	70.2	1,413	71.7	1,504	65.6
Slope (%)	40	2.8	26	2.4	15	3.2	24	2.7
Solar (h)	560	29	580	14	580	32	590	14
DistRoad (m)	640	160	500	69	550	279	470	70
DistWater (m)	510	60	370	28	220	33	300	18
DistSeral (m)	160	26	280	53	190	35	300	76
Decid (%)	1	0.9	3	0.7	12	7.6	5	2.3
Pine (%)	70	7.3	62	3.6	59	9.7	61	2.9
Fd (%)	8	3.8	9	3.1	8	4.6	9	3.6
Spruce (%)	12	4.8	13	2.0	18	6.4	21	3.2
Subfir (%)	8	4.6	8	2.2	4	3.1	3	1.3
Riparian (%)	0	0.1	4	1.1	12	6.1	6	1.9
Open (%)	5	1.7	7	1.3	5	1.8	8	1.2
Logged (%)	8	3.9	17	3.3	12	6.0	15	3.6
Age (years)	79	10.3	62	2.8	70	9.1	58	2.5
CC (%)	36	3.6	31	1.4	36	4.0	33	1.6

Fig. 6.—Frequency distribution of vegetation types used at calving areas (CA; $n = 31$) compared with random sites within the extended calving areas (100 ha surrounding the calving area; CAEXT, $n = 150$) by moose in southeastern British Columbia, 2002–2003.

coverage, and distance to water alone also were more weakly supported by the data. The relatively low weight of the top model (0.224) suggested some uncertainty in model selection. However, parameters among top models were similar. At this scale, individual variable weights indicated that density of trees ($\omega = 0.78$), moose shrub coverage (0.51), and distance to water (0.35) were 3.2–8.7 times stronger variables than green-up (0.11) and solar radiation (0.09).

Nonclimbing strategy.—Similar to the climbing strategy, at the broad scale a model with the single variable of elevation (negative) was most supported ($\chi^2 = 7.4$, *d.f.* = 1, $P = 0.007$; Table 6). However, this model provided a moderately low weight for the top model (0.268), suggesting model uncertainty. Other models 2–3 times less supported by the data all

included terms with elevation, as well as solar (negative) and crown closure (positive). The individual weight for elevation ($\omega = 0.88$) was 5–8 times greater than weights for logged cover type (0.17), solar (0.15), and crown closure (0.11).

At the fine scale, the model with the terms moose shrub coverage (positive), slope (negative), and distance to water (negative) was most supported ($\chi^2 = 19.9$, *d.f.* = 3, $P = 0.0002$), with an ROC value of 0.66 (Table 6). Model weight (0.241) suggested some uncertainty in model selection. Examination of the data suggests that 2 other models also could be considered: moose shrub coverage and slope alone; and slope, distance to water, and solar radiation (positive). Relative strength of moose shrub coverage ($\omega = 0.79$), slope (0.79), and distance to water (0.52) were 2.0–6.6 times stronger than solar (0.26) and density of trees (0.12).

DISCUSSION

Our analyses suggest that moose in southeastern British Columbia followed 1 of 2 broad strategies for calving. Climbers moved into areas where forage quantity and quality were reduced, but where risk of predation (mainly by grizzly bears) also was presumably reduced (see below). Nonclimbers calved in areas with high forage values and presumably higher predation risk, and appeared to select areas at the finer scale to reduce predation risk (e.g., associating with water and slightly reduced tree density for visibility). The differences in habitat selection between moose following the 2 strategies may partially explain why previous researchers have documented conflicting results regarding selection of topographic and habitat variables at various scales (Addison et al. 1990; Altmann 1963; Bailey and Bangs 1980; Bowyer et al. 1999; Chekchak et al. 1998; Jackson et al. 1991; Langley and Pletscher 1994; Leptich and Gilbert 1986; Stringham 1974; Welch 2000; Wilton and Garner 1991). Studies on other ungulates have shown differences in survival and habitat

TABLE 4.—Summary statistics for field-derived habitat characteristics of moose calving areas (CAs) and extended calving areas (CAEXTs; 100-ha area) between climber and nonclimber strategies in maternal moose in southeastern British Columbia, 2002–2003. Variable descriptions are provided in Table 2.

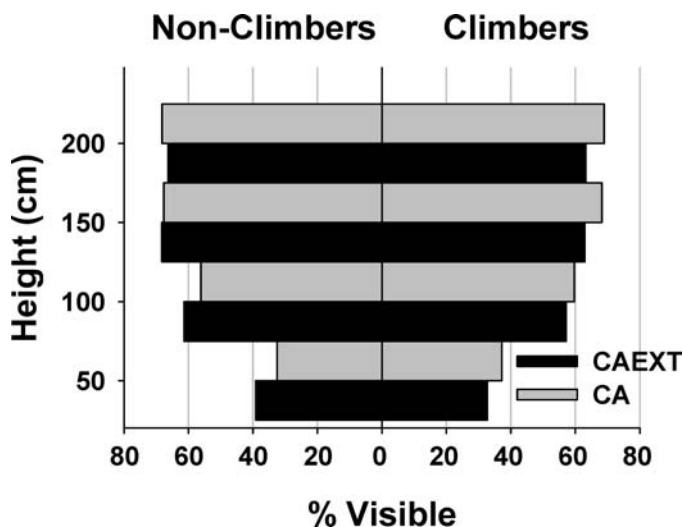| | Climbers ($n = 16$) | | | | Nonclimbers ($n = 15$) | | | |
| | CA | | CAEXT | | CA | | CAEXT | |
Variable	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Elev (m)	1,733	39.3	1,704	43.4	1,409	70.1	1,411	70.0
Slope (%)	34	4.3	35	4.1	5	2.5	11	4.0
Solar (hours)	574	31.6	571	30.3	578	33.8	574	34.1
DistWater (m)	548	53.4	456	60.3	168	48.2	228	38.0
DensTrees (no./ha)	1,054	190	1,406	202	858	255	1,116	222
DensSnags (no./ha)	91	30.1	132	46.2	128	78.9	69	23.4
Meandbh (cm)	16.6	0.91	15.0	0.61	17.4	1.93	17.5	2.85
Smalltrees (no./ha)	780	258	1,450	256	790	176	970	142
Sumshrub (%)	37.2	5.63	34.9	3.93	45.0	5.22	35.0	4.27
Mooseshrub (%)	8.9	2.43	10.2	2.31	21.4	4.53	12.7	2.74
Greenup (1−5)	3.6	0.38	3.5	0.35	4.2	0.32	4.2	0.32
Browsing (1−5)	2.3	0.23	1.7	0.15	2.4	0.17	2.2	0.16
CCfield (%)	61	5.2	57.4	4.7	70.2	5.6	60.1	4.3
Visibility (%)	59	4.3	54	3.3	56	4.7	59	3.1

Fig. 7.—Profile of horizontal visibility from the ground at moose calving areas (CA) and extended calving areas (CAEXT; 100-ha area) subdivided into 4 equal 50-cm classes, southeastern British Columbia, 2005.

Table 5.—Variables, number of parameters (K), Akaike's information criterion adjusted for small sample size (AIC_c), ΔAIC_c, and AIC weights (ω_i) for the top candidate models and the null model (for comparison) considered in analysis of habitat variables influencing calving area selection by moose following the climbing strategy, at the extended calving area (CAEXT; 100 ha) to home-range (HR) scale, and the calving area (CA) to extended calving area (CAEXT) scale, southeastern British Columbia, 2002–2003. Variable descriptions are provided in Tables 1 and 2.

Model (climbers)	K	AIC_c	ΔAIC_c	ω_i
CAEXT to HR comparison (broad scale)				
Elev (+)	1	5.86	0	0.418
Riparian (−)	1	7.97	2.11	0.145
Elev (+), Logged (−)	2	8.00	2.14	0.143
Null	0	22.18	16.32	0.000
CA to CAEXT comparison (fine scale)				
DensTrees (−), Mooseshrub (−), DistWater (+)	3	106.25	0	0.224
DensTrees (−)	1	107.66	1.41	0.111
DensTrees (−), Mooseshrub (−)	2	107.75	1.50	0.106
DistWater (+)	1	108.23	1.98	0.084
Null	0	110.63	4.34	0.025

quality among sympatric resident and migratory populations, which include use of different elevations (e.g., mule deer [*Odocoileus hemionus*]—McNay and Voller 1995; Nicholson et al. 1997).

The majority of the movement by climbers occurred immediately before calving, as shown by 2- to 3-fold increases in hourly movement rates. To get to their calving areas, climbers moved greater distances and at faster rates compared with nonclimbers, but movements by all maternal females were highly directional. As would be expected, movement rates for all maternal females were greatly reduced at parturition. This behavior pattern differentiated maternal females from barren females. The pattern of increased movement rate and distance to calving site before and after calving was even greater than that observed by Bowyer et al. (1999) and Testa et al. (2000) in Alaska, and Welch (2000) in northern Ontario. Testa et al. (2000) found a 2.4 times increase in daily movements immediately before birth, and a median distance from eventual birth site of 4 km up to 2 days before parturition. Forty-four percent of moose tracked by Welch (2000) had movements >2 km during the day before moving to the calving site. Testa et al. (2000) detected highly directional movements, but Welch (2000) did not, with some moose zigzagging or nearly doubling back before calving. Similar to our observations, Testa et al. (2000) observed a gradual increase in movement rates after parturition.

Habitat modeling suggested that, at the broad scale relative to the home range, elevation was the primary variable driving calving area selection. However, the direction of selection differed between strategies: positive for climbers and negative for nonclimbers. Calving moose employing either strategy also tended to avoid open cover types (logged or open). At the finer scale, moose appeared to select variables differently depending upon strategies. Climbers selected areas with reduced density of trees, reduced moose shrub coverage, and increased distance

from water, whereas nonclimbers selected areas with increased moose shrub coverage, decreased distance from water, and decreased slope.

Although a number of researchers have suggested that calving moose select higher elevation (Addison et al. 1990; Bowyer et al. 1999; Chekchak et al. 1998; Langley and Pletscher 1994; Wilton and Garner 1991), the average 310-m elevation gain compared with 9–12 days before calving shown by climbers is the largest difference documented. Bowyer et al. (1999) interpreted use of higher elevation to the need for increased visibility for predators, and not as a means to space away from predators occupying lower-elevation sites.

Table 6.—Variables, number of parameters (K), Akaike's information criterion adjusted for small sample size (AIC_c), ΔAIC_c, and AIC weights (ω_i) for the top candidate models and the null model (for comparison) considered in analysis of habitat variables influencing calving area selection by moose following the nonclimbing strategy, at the extended calving area (CAEXT; 100 ha) to home-range (HR) scale, and the calving area (CA) to extended calving area (CAEXT) scale, southeastern British Columbia, 2002–2003. Variable descriptions are provided in Tables 1 and 2.

Model (nonclimbers)	K	AIC_c	ΔAIC_c	ω_i
CAEXT to HR comparison (broad scale)				
Elev (−)	1	15.68	0	0.268
Elev (−), Solar (−)	2	17.21	1.53	0.125
Elev (−), CC (+)	2	17.70	2.02	0.098
Null	0	20.79	5.11	0.021
CA to CAEXT comparison (fine scale)				
Mooseshrub (+), Slope (−), DistWater (−)	3	106.96	0.00	0.241
Mooseshrub (+), Slope (−)	2	107.18	0.23	0.215
Slope (−), DistWater (−), Solar (+)	3	107.50	0.55	0.183
Null	0	118.70	11.75	0.001

However, the higher-elevation calving sites in our study had high densities of trees and were not open areas. Rather, increased elevation in our study area may afford some removal from grizzly bears, which are likely to be the most important predators on moose neonates (Ballard 1992), and can be a significant source of adult cow mortality at calving (Boertje et al. 1988). Seven of 8 deaths of collared cow moose recorded during our study occurred between mid-April and early June, with grizzly bear predation suspected in at least 2 of these deaths and wolves suspected in 1 death (Poole and Stuart-Smith 2004). Thus, the late-pregnancy to immediately postpartum period appears to be a time of higher adult female mortality in this moose population. McLellan and Hovey (2001) observed that the median average elevation of collared grizzly bears in the Flathead study area declined from den emergence because bears moved down to riparian habitats. Although a small proportion of grizzly bears remained at high elevation and selected avalanche chutes during spring, the upper 75th percentile of elevation for bear locations in the Flathead Valley during late May was approximately 1,500 m for males and 1,600 m for females (McLellan and Hovey 2001). Thus, climbing moose may have selected a calving strategy to remove themselves from the majority of grizzly bears at that period. Flathead moose also appear to be most vulnerable to wolf predation at the lowest elevations, although data specific to the spring are lacking (Kunkel and Pletscher 2000).

We were unable to determine calf survival between calving strategies, to compare the fate and ultimate reproductive success of these 2 strategies. The mean estimated weights of moose differed between strategies, with lighter moose climbing to areas of lower forage value and presumably lower risk of predation, and heavier moose staying low where forage values are higher but at a presumed cost of increased predation risk. The reasons for this pattern are unclear. One might expect that lighter moose may have greater nutritional demands because they have less body reserves to devote to lactation, and thus must place relatively more emphasis on food than predation risk (and use lower elevations, contrary to what we observed). Alternatively, lighter moose may have been younger, and thus may tend to climb to calve because their inexperience makes their calves more vulnerable to predation (Schwartz 1997). We have no age information to examine this theory.

Many researchers have suggested that quality of forage and hiding cover may be important aspects of selection of calving areas by moose (Altmann 1958, 1963; Bailey and Bangs 1980; Bowyer et al. 1999; Chekchak et al. 1998; Langley and Pletscher 1994; Leptich and Gilbert 1986; Stringham 1974). Use of higher-elevation sites did not translate into enhanced forage values for climbers in late May. Snow cover was still present, patchy, or very recently melted at sites occupied by most climbers, thus availability of succulent new growth in the form of protein-rich forbs or browse was likely reduced, as shown by reduced green-up index. Nonclimbers had nearly 3 times more moose shrub coverage in their calving areas compared with climbers. This implies that movements to higher elevation come at the cost of lower forage availability and quality. Maternal moose that remain at lower elevations may

face increased predation risk (McLellan and Hovey 2001), but greater quantities of higher-quality forage.

Examination of the field data does not support the contention that hiding cover or horizontal visibility played important roles in selection of calving areas. However, tree density was significantly reduced on average at calving areas for climbers, where it was the single most important variable in model selection at the fine scale. Tree density also was lower for nonclimbers, but figured far less prominently in model selection. Reduced tree density, particularly smaller understory trees, would presumably enhance horizontal visibility within the broader calving area that may not have been captured by the visibility measurements within the plots. Bowyer et al. (1999) suggested that visibility was important to maternal females to observe predators before they can approach closely, but their "concealment cover" (collected using techniques similar to our horizontal visibility) did not differ significantly between random and calving areas. Wilton and Garner (1991) concluded that bedding in more open, elevated areas without dense concealing vegetation provides a visual advantage over predators. Langley and Pletscher (1994) concluded that the majority of their calving areas had dense hiding cover, but this was assessed at 31 and 71 m from plot center, far larger distances than measured in our study.

Moose that did not climb before calving appeared to select low-slope, low-elevation, and generally moist areas for calving. Although characterized by high forage values, riparian habitats would be considered to be among the habitats where the risk of predation is greatest within the landscape in spring, with the highest habitat selection by grizzly bears (McLellan and Hovey 2001). Within these riparian habitats, calving moose may have tried to reduce predation risk in part by site selection. Of the 8 areas used by nonclimbers in riparian zones (swamps, river edges, and braided channels), 2 were immediately adjacent to rivers, and 3 were located on islands or raised areas within braided sections of rivers. It was obvious to us that spring flooding conditions along rivers caused great difficulty in access to calving sites used by some moose employing this strategy. Selection by calving moose for water, including islands, has been shown in many areas, all of which had significant water bodies available (Addison et al. 1993; Jackson et al. 1991; Leptich and Gilbert 1986; Stephens and Peterson 1984), and most did not have grizzly bears as potential predators (except for the study of Bailey and Bangs [1980]). Water was not deemed to be a significant factor in moose calving areas in numerous other studies (Chekchak et al. 1998; Langley and Pletscher 1994; Markgren 1969; Stringham 1974; Welch 2000). Other than associations with water, broad use of available cover types suggested no clear habitat preference by nonclimbers (as shown by Addison et al. [1990] and Welch [2000]), which may itself be a strategy to reduce the risk of predation (Bowyer et al. 1999).

Although almost half (48%) of the moose had some logged habitat within the extended calving area, only 1 of the 31 moose calved in a logged area (35 years old). Examination of the data suggested that logged stands were used less than available at both scales of analysis. Although recently logged

areas would generally provide enhanced visibility and forage, some aspects of these habitats, possibly a paucity of hiding cover, appear to discourage use. Grizzly bears consistently selected regenerating cutblocks less than most other habitats during spring in the Flathead Valley (McLellan and Hovey 2001), and logging did not appear to increase the vulnerability of moose to predation by wolves (Kunkel and Pletscher 2000), suggesting that predation risk in cutblocks would be low. Welch (2000) found that 20% of calving sites in Ontario were in cutblocks, with no evidence of avoidance of cut-overs, although risk of predation would vary among areas based on species, distribution, and abundance of predators.

Bowyer et al. (1999) suggested that the unpredictable behavior of maternal females (20% of the moose in their study made extensive movements before birth), no selection for vegetation types, and random spatial arrangement of birth sites were all strategies to reduce the risk of predation. This unpredictability in selection of a calving site purportedly could prevent a predator from learning to associate specific habitats with moose calving areas. However, in our study it was apparent that half the sample of maternal females moved higher in elevation relative to where they were both at the home-range scale and in the days immediately before calving, to areas with greatly reduced forage quality and quantity, using what could be interpreted as a predictable strategy to reduce risk of predation by spacing away from areas of suspected higher predator density. The other half of the sampled moose did not climb before calving and selected high moose shrub coverage areas at lower elevation at the home-range scale, and may have attempted to reduce predation risk at a finer scale by either selecting wet and inaccessible areas for calving, or choosing random, undistinguishable areas within the forest matrix. Both strategies may result in a compromise, and neither provides both high forage values and low predation risk. Moose living in montane areas have more options compared to moose in areas with less topographic relief, namely the ability to move on a vertical rather than just a horizontal plane. This decision may be a 1st step in the trade-off between maximizing forage while minimizing predation risk in selecting calving areas.

Management implications.—The main factor driving moose calving area selection at the home-range scale was elevation. With the possible exception of selection for riparian areas, it appeared that calving areas were distributed throughout the range of leading tree species and age classes in the forest matrix. Calving moose used the most prevalent cover types (pine and spruce–subalpine fir), and appeared to select areas with lower tree density of large and small trees. Given that calving moose avoided logged areas but were located in areas with lower tree densities, it is possible that low-removal partial cutting using individual tree selection would increase the likelihood of such stands being used by moose relative to clear-cuts. In addition, ensuring minimal disturbance to riparian areas and a logging rotation that ensures a range of forage (especially at low elevations), hiding cover, and visibility will likely maintain moose calving habitat in a matrix of forest management.

The distribution of predators would probably influence selected strategies of forage and predation risk considered by maternal moose. The Flathead Valley has been the site of extensive studies on grizzly bears over the past 25 years (e.g., McLellan and Hovey 2001), including collared bears during 2002 and 2003 (B. McLellan, in litt.). Additional analyses incorporating predator risk modeling for grizzly bears, black bears, and wolves could further elucidate moose calving strategies in montane ecosystems.

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