DIFFERENTIAL HABITAT SELECTION BY MOOSE AND ELK IN THE BESA-PROPHET AREA OF NORTHERN BRITISH COLUMBIA

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ABSTRACT: Elk (*Cervus elaphus*) populations are increasing in the Besa-Prophet area of northern British Columbia, coinciding with the use of prescribed burns to increase quality of habitat for ungulates. Moose (*Alces alces*) and elk are now the 2 large-biomass species in this multi-ungulate, multi-predator system. Using global positioning satellite (GPS) collars on 14 female moose and 13 female elk, remote-sensing imagery of vegetation, and assessments of predation risk for wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*), we examined habitat use and selection. Seasonal ranges were typically smallest for moose during calving and for elk during winter and late winter. Both species used largest ranges in summer. Moose and elk moved to lower elevations from winter to late winter, but subsequent calving strategies differed. During calving, moose moved to lowest elevations of the year, whereas elk moved back to higher elevations. Moose generally selected for mid-elevations and against steep slopes; for Stunted spruce habitat in late winter; for Pine-spruce in summer; and for Subalpine during fall and winter. Most recorded moose locations were in Pine-spruce during late winter, calving, and summer, and in Subalpine during fall and winter. Elk selected for mid-elevations except in summer and for steep slopes in late winter. Use and selection of 3 habitat classes were prominent for elk: Deciduous and *Elymus* burns, and Subalpine. Highest overlap between moose and elk occurred during fall and winter when both species used and strongly selected for Subalpine habitat. Neither elk nor moose selected areas to minimize the risk of wolf predation, but elk selected areas with lower risk of predation by grizzly bears and higher vegetation quality during calving and summer.

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Key words: *Alces alces*, *Cervus elaphus*, elevation, habitat selection, habitat use, home range, individual variation, movement rates, resource selection

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Moose (*Alces alces*) and elk (*Cervus elaphus*) often provide the majority of prey biomass for large predators in complex predator-prey systems of North America. As examples, elk support wolf (*Canis lupus*) populations in Yellowstone and Yukon (Hayes and Harestad 2000, Smith et al. 2003), moose are common prey for wolves in northern coniferous forests (e.g., Post et al. 2002, Vucetich et al. 2002), and both moose and elk provide a prey base for wolves and grizzly bears (*Ursus arctos*) in northern British Columbia (Bergerud et. al. 1983, Bergerud and Elliott 1998, Parker and Milakovic 2007). Moose and elk are relatively profitable prey types in comparison to smaller ungulates or alternative prey, and given sufficient densities, can sustain large predator populations. Hence, moose and elk are keystone species in the functioning of large-scale large-mammal systems. In multi-ungulate, multi-predator systems, however, they are not studied as commonly as other species because they are less susceptible to disturbance than some species (e.g., Stone's sheep, *Ovis dalli stonei*), use smaller areas and, therefore, are not as subjected to landscape disturbance as other species (e.g., woodland caribou, *Rangifer tarandus caribou*), or have large populations that are less vulnerable to, and can better accommodate change. In addition, the requirements of moose and elk are assumed to be relatively well known (e.g., Franzman and Schwartz 1998, Toweill and Thomas 2002). Because moose and elk are highly visible species with strong social and ecological values, and have the benefit of being high-profile game species, they are often managed to maintain or increase numbers. Yet there are relatively few published studies that have examined the concurrent resource use by these 2 species (e.g., Jenkins and Wright 1988).

Moose have long occurred in northern British Columbia (Kelsall 1987), but elk herds are expanding into new areas in response to habitat fragmentation and management, and in some cases translocations (Spalding 1992). Prescribed burning has traditionally been used to create and maintain elk habitat in portions of northeastern British Columbia (Peck and Peek 1991). Fires temporarily result in shrub- and herb-dominated communities and increases in forage biomass, often with higher nutritional value. Burning and its impacts on vegetative communities have been linked to the increase and expansion of elk herds (e.g., Luckhurst 1973, Silver 1976, Parminter 1983). Following fire, elk winter primarily on younger post-burn vegetation dominated by grasses or shrubs, except during severe winter conditions when there is higher use of conifer stands (Peck and Peek 1991). Moose also frequent fire-associated habitats (Peek 1998), but their use of burned habitats can depend on their past exposure to burned areas (Gasaway et al. 1989).

Throughout most of their range, moose are primarily browsers and are associated with habitats containing a high proportion of preferred shrubs (Boer 1998). Elk on the other hand, are classified as grazers (Cook 2002, Stewart et al. 2002), but their food selection can shift in response to food availability and they are successful using browsing strategies (Houston 1982). Because of their flexible foraging habits, ability to use a wide variety of terrain types and high fecundity, elk could compete with moose for food (Flook 1964) although competition between the 2 species is thought to be low (Miller 2002).

In complex predator-prey systems, high numbers of high-biomass ungulates may alter predator populations, and in turn other species in the same system. The overall goal of this study was to provide an initial description of habitat use and selection by moose and an expanding elk population in the Besa-Prophet area of northern British Columbia. Specifically, we asked whether there was overlap in use and selection by moose and elk that may have implications to the system, and if there might be potential impacts through predation on other species. To do this we used global positioning satellite (GPS) radio-locations, remote-sensing imagery of vegetative communities, assessments of predation risk from concurrent studies on grizzly bears and wolves in the same area, and habitat selection modeling. These data and analyses help characterize the ungulate-predator landscape of the Besa-Prophet watershed and contribute to better land-use planning.

STUDY AREA

The Muskwa-Kechika Management Area (MKMA) in northern British Columbia is known for its abundance of large ungulates (moose, elk, caribou, Stone's sheep, a few mountain goats (*Oreamnos americanus*) and deer (*Odocoileus* spp.)) and large predators (wolves, grizzly bears, black bears (*U. americanus*), coyotes (*Canis latrans*), wolverines (*Gulo gulo*), and a few cougars (*Puma concolor*)). The Besa-Prophet study area is within the Besa-Prophet Pre-tenure Planning area (Fig. 1), one of several pre-tenure areas within the MKMA requiring specific wildlife planning prior to resource extraction or development. It is a highly diverse area including the Besa River south of the Prophet River, and covering ~740,887 ha. Located within the Muskwa Ranges and Rocky Mountain Foothills between 57°11' and 57°15' N, and 121°51' and 124°31' W, the Besa-Prophet is characterized

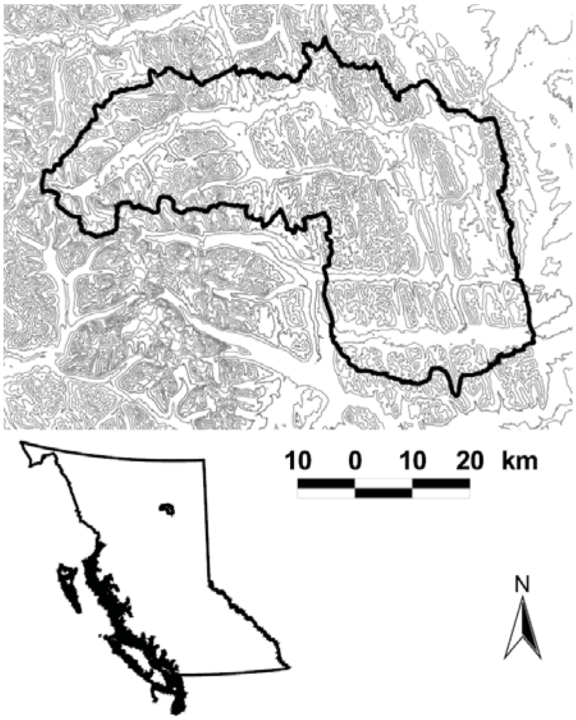

Fig. 1. Location of the study area within the Besa-Prophet Pre-tenure Planning area (inset) in northeastern British Columbia. Contour lines (200-m intervals) illustrate the predominance of east-west valleys within the study area.

by numerous east-west drainages and south-facing slopes (Fig. 1) that provide benefits to wintering species because they are often blown free of deep snows. Other than several permanent outfitter camps and 1 government-designated all-terrain vehicle trail, there is relatively little access into the Besa-Prophet. This activity occurs mostly during late summer and fall during hunting seasons, with some snowmobile use in winter.

Valleys at ~800-1300 m are commonly lined with white spruce (*Picea glauca)*, some lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*) on dry sites, and black spruce (*P. mariana)*, willow-birch (*Salix* spp., *Betula glandulosa*) communities on poorly drained sites (Meidinger and Pojar 1991). There also are slopes that have been burned by the British Columbia Ministry of Environment and local guide outfitters to enhance ungulate populations, especially Stone's sheep. The subalpine area is characterized by an abundance of willow and scrub birch, as well as some balsam fir (*Abies lasiocarpa*) and white spruce often in krummholz form, and various grasses, sedges and fescues (*Festuca* spp.). Treeline occurs between ~1,450-1,600 m. Alpine tundra above ~1600 m consists of permanent snowfields, rock, mat vegetation, and grasslands (Demarchi 1996).

Anecdotal evidence in the Besa-Prophet suggests that elk populations are expanding, enabled by prescribed burns that are conducted primarily for the enhancement of Stone's sheep populations. In this area, prescribed fire has been officially managed since the early 1980s, although there also have been natural burns and locally initiated fires before and since that time. Concerns regarding the implications of a rapidly increasing elk population on ecosystem dynamics were the impetus for the comparisons in our study. Densities of moose and elk populations in the Besa-Prophet are not well documented; very rough estimates are approximately 2000 moose and 500 elk (J.P. Elliott, BC Ministry of Environment, Fort St John, personal communication). It is important to note, however, that habitat use and selection will vary as a consequence of population density (Boyce et al. 2003).

METHODS

Fifteen adult female moose and 14 adult female elk were fitted with GPS (global positioning satellite) collars (GTX, Advanced Telemetry Systems, Isanti, MN) between March 2003 and January 2005. Collars were programmed to record locations 4 times daily at 6-h intervals with a range of start times between midnight and 0500 hr. Data were retrieved when collars were recovered at the end of a 1-year sampling period.

We defined 5 seasons distinguished by biological and ecological characteristics for our analyses of range use and movements, and habitat use and selection: winter (1 November–28 February) corresponding with the formation of sex-specific groups following rut; late winter (1 March – 15 May) when movement rates were lowest; calving (16 May – 15 June) during which parturient females became solitary and the onset of plant greening occurred; summer (16 June – 15 August) from plant green-up through peak vegetation biomass to the start of plant senescence; and fall (16 August – 31 October) when senescence of vegetation occurred, males and females formed mixed sex groups, and females came into estrus.

Seasonal Movements and Home Ranges

To identify seasonal movement rates of moose and elk, we averaged movement rates (m/h) per individual using GPS locations obtained from consecutive 6-h fixes by season, and then averaged across individuals for each season by species (*n* = number of individuals). We compared movement rates between moose and elk within seasons using a repeated measures analysis of variance (ANOVA), with differences identified following Bonferroni adjustment of confidence intervals. We used the same approach to compare seasonal elevations used by both species.

We determined sizes of annual and seasonal home ranges using 100% minimum convex polygons (MCP, Jennrich and Turner 1969) around GPS locations, as well as by fixed-kernel analysis (Worton 1989) for each individual. The MCPs, calculated by connecting the outer locations of all animal-use points, tend to overestimate range sizes for animals that have infrequent movements away from a centralized area, but they provide a relative comparison of the extents of the landscape used by moose and elk. In fixed-kernel analyses, kernels are calculated from the 95% probability density of all locations and delineate areas of higher use (core areas) within the home range. Depending on the arrangement of animal locations, the fixed-kernel analysis may identify multiple core areas. Hereafter, we use the term ‘kernel area’ to refer to the total area identified by the fixed-kernel analysis. Because kernels are mathematical interpolations, however, they may exclude some areas where movements take place between core areas, and may include substantial ‘buffer’ areas with no animal locations around high-density locations, particularly with small numbers of locations (Seaman et al. 1999). For comparison with other studies on moose and elk, however, we used the Animal Movement Extension (Hooge and Eichenlaub 2000) in ArcView (ESRI 2002) to calculate both MCP and fixed-kernel range sizes. We used ANOVA to compare annual and seasonal range sizes between species within season. We used SpatialViewer (M. Gillingham, unpublished Visual Basic program) to examine movement patterns of individual animals.

Habitat Use and Availability

To compare seasonal use of habitat classes between moose and elk, we determined the proportion of GPS locations within each class by individual within season. To index resources available to each collared individual, we defined availability at the scale of seasonal movement, within Johnson’s (1980) third order of selection. Seasonal movement is an animal’s movement potential within a season (e.g., Gustine et al. 2006b), or a circle around each use point with a radius equivalent to the distance traveled at each individual’s 95th percentile movement rate from 6-h GPS fixes. Within that area of movement potential, we selected 5 random points for availability locations. We used a raster geographic information system (GIS; Imageworks XPACE; PCI Geomatics Corp. 2001) to query habitat classes for used and available points. We ensured that no 2 points were used twice and that there was no overlap between used and available points (Manly et al. 2002). For both moose and elk within season, we then averaged the proportions of habitat classes that were used by, and available to, each individual to eliminate effects of uneven sample sizes among individuals (SE was based on number of collared individuals). We visually compared use to availability of different habitat classes, but then determined resource selection for combinations of additional variables because habitat use occurs in response to multiple variables and not to vegetation class alone.

We defined 10 habitat classes for the Besa-Prophet based on a vegetation classification system with 25-m resolution for the area, developed using Landsat TM and Enhanced Thematic Mapper (ETM) remote-sensing imagery (Lay 2005) (Table 1). Two burn classes (*Elymus* burn and Deciduous burn) may have included small, but unknown amounts of other disturbed areas such as avalanche chutes, which could not be distinguished separately with remote-sensing imagery. Avalanche chutes were relatively rare in the areas used by moose and elk.

Resource Selection

We used a suite of GIS layers to extract the attributes for defining resource selection by moose and elk by season, using all GPS use locations and available locations as defined above. These layers included habitat class, vegetation biomass, vegetation quality, slope, aspect, elevation, and risk of predation by grizzly bears and wolves.

Habitat class and vegetation indices – In addition to defining habitat class as we did in analyses for habitat use and availability, we used the same TM (4 June and 22 July 2001) and ETM (15 August 2001) imagery to index vegetation biomass during June, July, and August using a normalized difference vegetation index (NDVI) that is related to leaf area and plant biomass (Tucker and Sellers 1986, Ruimy et al. 1994). We also developed an index to vegetation quality during the calving and summer seasons by calculating the change in NDVI (subtraction of individual pixel values) between June and July, and July and August images. A positive change in NDVI during the growing season corresponds with growth of new tissue (Groten and Ocatre 2002) and highest rates of green-up are likely the most digestible forage (Griffith et al. 2002, Oindo 2002).

Table 1. Description of the 10 habitat classes, derived from Landsat TM and Enhanced Thematic Mapper remote-sensing imagery, used to describe habitat use and selection by moose and elk in the Besa-Prophet area of northern British Columbia.

Habitat Class	Description
Non-vegetated	Rock and rock habitats; permanent snowfields or glaciers and water bodies.
Elymus burn	Recently burned and open disturbed sites dominated by *Elymus innovatus.*
Deciduous burn	Older burned and disturbed areas containing *Populus tremuloides* and *Populus balsamifera* shrubs (<2 m) and trees (≥2 m).
Subalpine	Deciduous shrubs ≥1600 m in elevation; and spruce-shrub transition zone at middle to upper elevations with white and hybrid spruce (*Picea glauca* and *P. glauca* x *engelmanni*), and dominated by birch and willow.
Stunted spruce	Low productivity sites often on north-facing slopes with *Picea glauca* of limited tree height and percent cover.
Pine-spruce	White and hybrid spruce-dominated communities; and lodgepole pine dominated communities.
Riparian	Low-elevation, wet areas with black (*Picea mariana*) and hybrid spruce; often with standing water in spring and summer; exposed gravel bars adjacent to rivers and creeks.
Alpine	Dry alpine tundra habitat ≥1600 m characterized by *Dryas* spp.; and wet alpine tundra habitat ≥1600 m dominated by *Cassiope* spp. and sedge (*Carex* spp.) meadows.
Low shrub	Deciduous shrubs <1600 m dominated by birch and willow.
Carex	Wetland meadows dominated by sedges (*Carex* spp.) at elevations <1600 m, with intermittent *Salix* shrubs.

Slope, aspect and elevation – We obtained elevation, slope, and aspect from a digital elevation model (DEM) in the 1:20,000 British Columbia Terrain and Resource Inventory Management program (British Columbia Ministry of Crown Lands 1990). We modeled aspect as 2 continuous variables (i.e., northness and eastness; Roberts 1986) to avoid introducing additional categorical variables. Northness (the cosine of aspect) values of 1.00 and -1.00 suggest selection for north and south aspects, respectively, whereas values near 0.00 suggest selection for east and west aspects. Eastness (the sine of aspect) values show selection for east (i.e., 1.00) and west (i.e., -1.00) aspects; values of 0.00 show selection for northern/southern exposures (Palmer 1993). We did not assign an aspect to pixels with a slope ≤1°.

Predation risk – We defined potential risk of predation using logistic regression models by season from GPS-collared wolves and grizzly bears, which are assumed to be the most significant large mammal predators in the Besa-Prophet area (Bergerud and Elliott 1998). Details of these predator models are in Gustine et al. (2006a, b) and Walker et al. (2007). The predation-risk models included slope, aspect, elevation, habitat class, fragmentation (an index of vegetation diversity), and distance to linear features (e.g., seismic lines). From these models, we generated a risk surface as a GIS layer that defined selection value to grizzly bears or wolves in each season by applying the coefficients from models to each 25 x 25-m pixel, based on its topographic and vegetation features. We scaled values from 0 to 1 to standardize selection surfaces, and then assumed that the risk of predation to moose and elk by grizzly bears and wolves was directly related to selection values of the predators.

Table 2. Candidate models developed a priori to describe resource selection by moose and elk by season in the Besa-Prophet area of northern British Columbia. Vegetation biomass during calving, summer, and fall was based on NDVI measures for June, July, and August, respectively. Vegetation quality, assessed by the change in NDVI between summer months, was only used in calving and summer models. No risk of predation by grizzly bears was included during hibernation (winter and late winter seasons).

Model	Calving	Summer	Fall	Winter	Late Winter
Elevation[1]+Aspect+Habitat[2]	✓	✓	✓	✓	✓
Elevation+Slope+Aspect+Habitat	✓	✓	✓	✓	✓
Wolf[3]+Habitat	✓	✓	✓	✓	✓
Elevation+Slope+Aspect+Wolf+Bear[3]+Biomass+Habitat	✓	✓	✓		
Elevation+Slope+Aspect+Wolf+Bear+Quality+Habitat	✓	✓			
Aspect+Wolf+Bear+Biomass+Habitat	✓	✓	✓		
Aspect+Wolf+Bear+Quality+Habitat	✓	✓			
Elevation+Slope+Aspect+Wolf+Biomass+Habitat	✓	✓	✓		
Elevation+Slope+Aspect+Wolf+Quality+Habitat	✓	✓			
Aspect+Wolf+Biomass+Habitat	✓	✓	✓		
Aspect+Wolf+Quality+Habitat	✓	✓			

[1] Elevation was modeled as a quadratic with both a linear and squared term.

[2] Habitat as defined by classes in Table 1.

[3] Wolf and Bear represent risk of predation by wolves and grizzly bears, respectively; see text for details.

Selection models – We developed 11 *a priori*, ecologically plausible models (Table 2) from the previously described attributes to define resource selection by moose and elk by season. We used logistic regression with these parameters (*K*) to characterize differences between use and availability for each individual, and ranked the suite of models using Akaike's Information Criterion (AIC) values corrected for small sample size (AIC_c) when $n/K < 40$ (Burnham and Anderson 2002). Deviation coding was used for categorical variables (Hendrickx 1999). To avoid inflated coefficients and inflated error terms in the models, we used tolerance scores to assess model inputs for collinearity and multicollinearity. If tolerance scores were <0.20, covariates were not included in the same model (Menard 2002). Because logistic regression models do not provide reliable estimates if there is complete or near-complete separation in levels of categorical variables (Menard 2002), we dropped both used and available points for those habitats in which either use or available points in a habitat were ≤4 (Gillingham and Parker 2008).

We validated the top models using k-fold, cross-validation (Boyce et al. 2002), and an averaged Spearman's rank correlation coefficient. Within each model set (i.e., by individual and season), we calculated Akaike weights (w_i). If there was not a single model for which this relative weight of evidence, w_i, was ≥0.95, we considered competing models to be those for which the sum of w_i was ≥0.95 (Burnham and Anderson 2002). For each model set for each individual animal, we averaged the selection coefficients (β) in competing models based on their relative w_i. We evaluated the importance of specific resources to moose and elk in general after developing pooled models from these averaged individual models by averaging coefficients from the individual models within species during each of the 5 seasons. We assumed significance of all tests at $\alpha = 0.05$. We used STATA for all statistical and modeling procedures (version 9.2; StataCorp 2007). All means are presented as $\bar{X} \pm 1$ SE unless noted otherwise.

RESULTS

We retrieved 14,534 GPS locations from 14 of the collared moose and 14,870 locations from 13 collared elk. The number of GPS locations recorded as a percentage of the number of attempted GPS locations was 76.7 ± 0.03% ($\bar{X}$ ± SE) for moose and 82 ± 1.6% for elk.

Seasonal Movements and Home Ranges

Distances moved between consecutive 6-h GPS fixes ranged from <1 m to 14.5 km (straight-line distance) by moose and from <1 m to 10.3 km by elk. Both species moved at lowest rates during winter and late winter (35-41 m/h), and then increased movements to highest rates in summer (>100 m/h) (Fig. 2). Moose usually tended to move at rates slightly lower than elk (repeated-measures ANOVA, $P = 0.049$), but these rates were significantly lower only during the calving season (moose = 59 ± 21 m/h, elk = 93 ± 27 m/h).

The range sizes estimated by fixed-kernel analyses were always smaller, as expected, than those determined by MCP for both

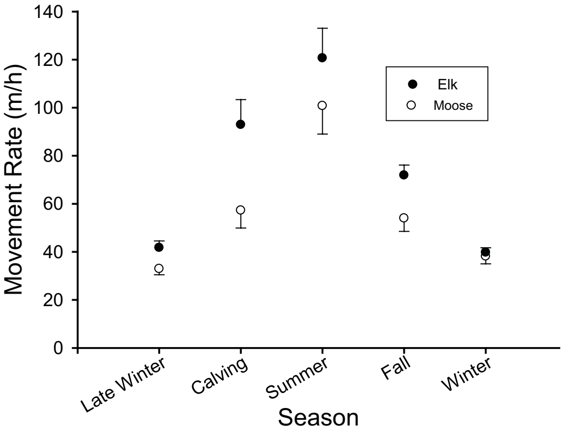

Fig. 2. Comparative differences in the movement rates (m/hr, X ± SE) of adult female moose ($n = 14$) and elk ($n = 13$), averaged by individual and then averaged across individuals, by season in the Besa-Prophet area of northern British Columbia.

species (Table 3). Kernel areas were most comparable to MCPs (~85-90 % of MCP size) during the calving season for moose, and during calving and fall for elk. They were less than half the size of MCPs during fall for moose, and during winter and late winter for elk. Annual home ranges by MCP for moose averaged 195 km^2, but were highly variable among individuals, ranging from a minimum of 39 to a maximum of 899 km^2 (kernel area = 14-124 km^2). Seasonal ranges for moose were typically smallest during the calving season (18 km^2), and more than 7 times larger during summer. Annual ranges of MCP for elk averaged 191 km^2 and were not different than those of moose (Table 3), and also were highly variable among individuals (MCP range = 50-1000 km^2; kernel area = 10-107 km^2). Excluding 1 animal that made a large circular excursion in July away from its other seasonal use areas, annual ranges for elk averaged 123 ± 19 km^2 (range = 50-250 km^2; kernel area = 10-107 km^2). In contrast to moose, seasonal ranges for elk were smallest during the winter and late winter seasons (16-20 km^2). Similar to moose, seasonal ranges for elk were largest during summer (Table 3). Compared to elk, the seasonal ranges of moose (by MCP) were more than twice as large during winter and late winter, but less than half as large during calving.

Habitat Use and Availability

Moose and elk used elevations on the landscape differently among seasons (repeated-measures ANOVA, $P < 0.001$) (Fig. 3). During calving and summer (May–August) and winter (November–February), moose used lower elevations than elk (moose = 1333 ± 81 m in calving, 1397 ± 53 in summer, 1519 ± 88 in winter; elk = 1551 ± 49 m in calving, 1671 ± 40 m in summer, 1624 ± 51 m in winter) (all $P < 0.016$). Both species moved to lower elevations from winter to late winter, however, calving strategies appeared to differ between the 2 species. In June, moose were at lowest elevations of the year, and after the calving season moved gradually upslope dur-

Table 3. Comparison of annual and seasonal home-range sizes (km^2) for 14 female moose and 13 female elk based on 100% minimum convex polygons (MCP) and 95% fixed-kernel (Kernel) estimates. *P*-values are from one-way ANOVAs comparing home-range sizes between species for a given technique and season.

Season	Estimate	Moose[1]		Elk		*P*
		Mean	SE	Mean	SE	
Annual	MCP	195.28	59.71	190.81	69.61	0.961
	Kernel	57.04	8.81	45.64	8.19	0.355
Calving	MCP	17.59	4.09	38.00	4.05	0.002
	Kernel	15.05	4.28	34.09	5.82	0.013
Summer	MCP	132.80	60.25	118.38	63.66	0.871
	Kernel	99.42	52.81	57.76	28.70	0.504
Fall	MCP	46.85	10.96	60.22	12.86	0.434
	Kernel	26.86	6.69	51.02	13.16	0.107
Winter	MCP	45.91	9.83	20.40	2.24	0.015
	Kernel	32.16	8.88	8.82	1.14	0.012
Late Winter	MCP	30.49	4.60	15.52	4.60	0.030
	Kernel	25.49	6.39	6.04	1.60	0.009

[1] Only 12 animals were used in the winter models because of collar failure.

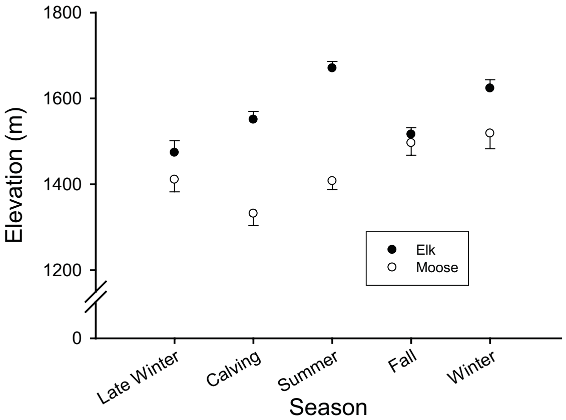

Fig. 3. Comparative differences in elevations ($\overline{X}$ ± SE) used by GPS-collared female moose (*n* = 14) and elk (*n* = 13), averaged by individual and then averaged across individuals, by season in the Besa-Prophet area, northern British Columbia.

ing summer and fall. Elk, in contrast, moved from their late wintering areas to higher elevations to calve in June, continuing upslope in July, and descending to the same elevations used by moose in the fall (Fig. 3).

Predominant use of specific habitat classes differed between moose and elk, coinciding with some of the elevational differences between the species. During late winter, calving, and summer, most locations for moose (28-36% across animals) were in the Pine-spruce habitat class (Fig. 4). This contrasts to the fall and winter periods, when most locations were in Subalpine vegetation (33-39%). There was relatively little use by moose during any season of Riparian (<6 % of locations; distinct from Low shrub and *Carex*), Alpine (<4%), or Non-vegetated (<1%) habitat classes. Low shrub vegetation was used least (10 %) by moose during the calving season, and most during winter (22%). Use of the Deciduous burn class by moose was relatively consistent at 13-16% throughout the year.

For elk, the use of 3 habitat classes was prominent: *Elymus* burn, Deciduous burn, and Subalpine (Fig. 5). Seasonally, the 3 classes always totaled between 59 and 83% of use locations. Highest use by elk occurred in the Subalpine in all seasons (33.0% of locations during calving; 29.5% during fall, and 40.5% in winter) except late winter (13.1% of locations), when they increased use of both burned habitat classes (~70% of locations). During summer when elk used the Subalpine more than any other season (64% of locations), they spent less time in *Elymus* and Deciduous burn habitats. Compared to moose, elk used the Pine-spruce habitat class very little (≤5% of locations) in any season except fall (17 ± 2%).

Resource Selection

There were relatively few variables that were selected for or against by moose because of variation in individual selection strategies (Table 4). In general, moose selected for mid-elevations in all seasons but late winter. During calving, summer, and fall they avoided Non-vegetated areas and steep slopes. In the calving season, most moose rarely used (<4 locations) Subalpine (10/14 animals), Alpine (13/14), or *Carex* (12/14) habitat classes even though avoidance of these classes was not indicated by the pooled calving model. Moose selected strongly for Pine-spruce habitat in summer, Subalpine and Low shrub in fall, Subalpine in winter, and Stunted spruce in late winter. In no seasons were vegetation biomass and quality important to overall resource selection (although some individual moose selected for or against these variables). Risk of predation was an important factor for some moose, but was only important in the pooled selection models during fall, when moose locations were in areas of relatively higher predation risk than that present in the area around them.

Elk exhibited selection by season for and against more variables than did moose (Table 5). Mid-elevations were selected in all seasons but summer, when higher elevations were more important. Elk selected against steep slopes from summer through winter, but for them in late winter. They consistently selected against northness and Alpine habitat in all seasons,

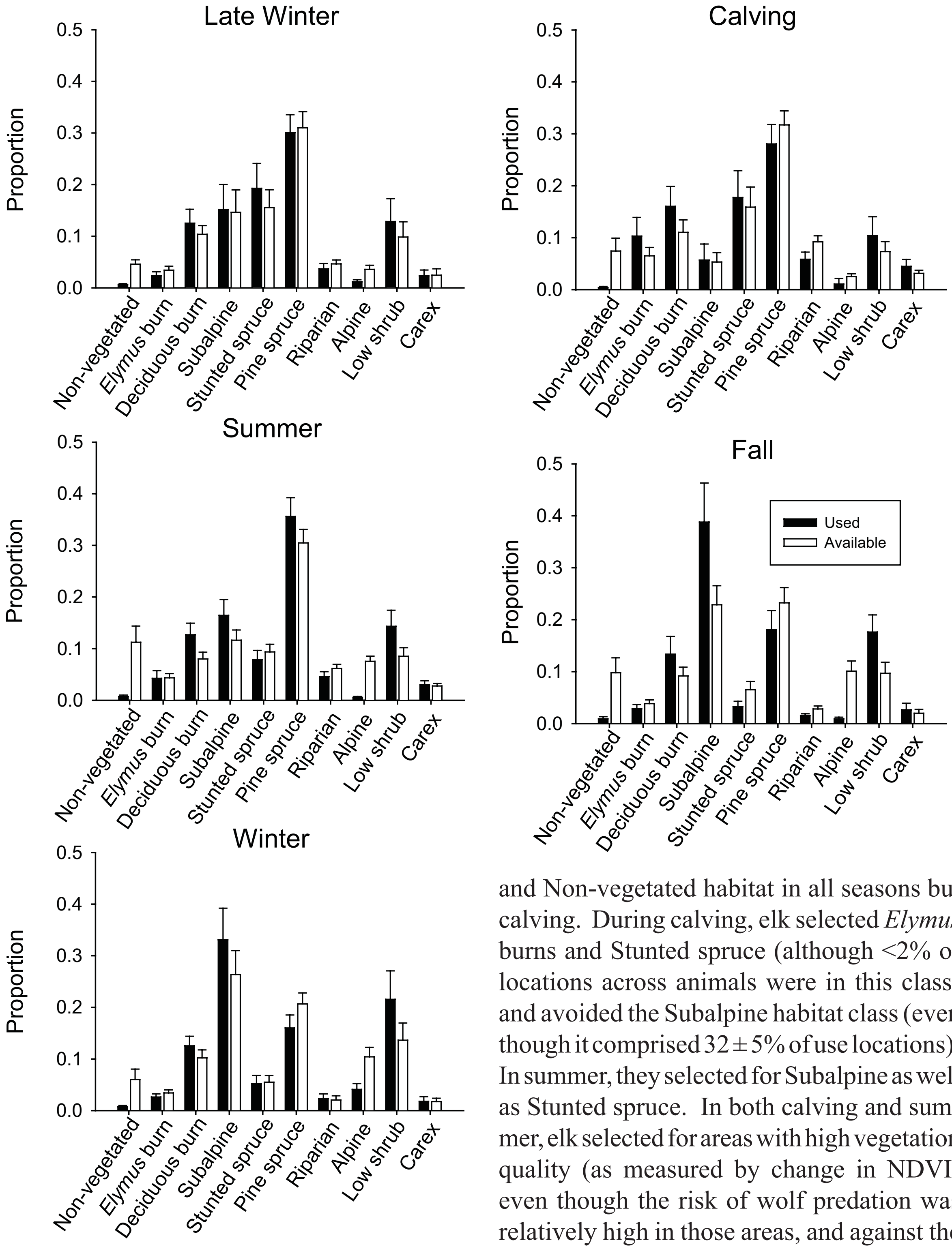

Fig. 4. Comparison of proportional use versus availability (+ SE) of habitat classes for female moose in the Besa-Prophet area of northern British Columbia. Standard errors were determined from averages for each individual by season.

and Non-vegetated habitat in all seasons but calving. During calving, elk selected *Elymus* burns and Stunted spruce (although <2% of locations across animals were in this class) and avoided the Subalpine habitat class (even though it comprised 32 ± 5% of use locations). In summer, they selected for Subalpine as well as Stunted spruce. In both calving and summer, elk selected for areas with high vegetation quality (as measured by change in NDVI) even though the risk of wolf predation was relatively high in those areas, and against the risk of bear predation (although coefficients were very small; Table 5) and Low shrub habitat. From calving through fall, elk selected against areas with high vegetation biomass (as indexed by NDVI). From fall through late winter, there was strong selection for *Elymus*

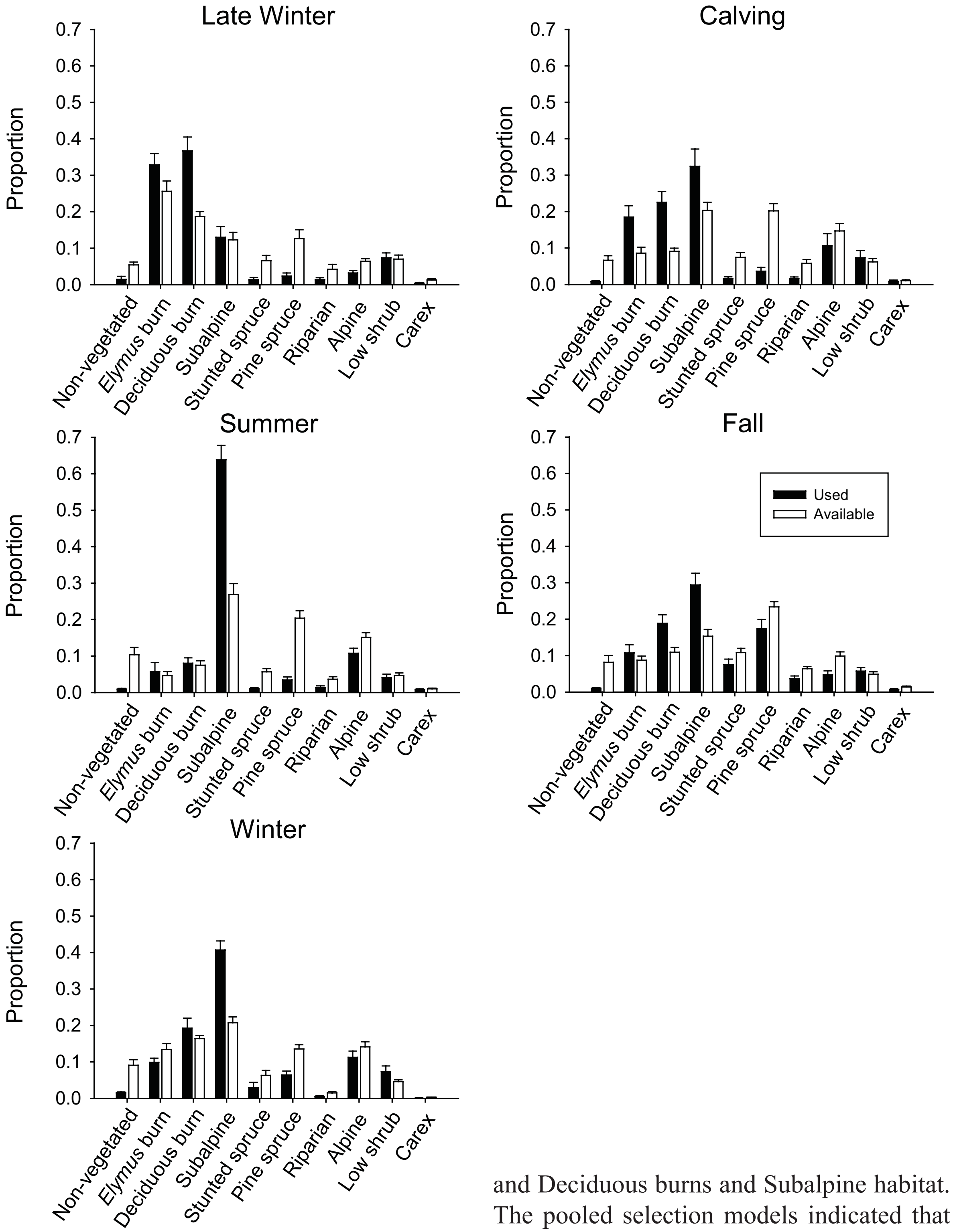

Fig. 5. Comparison of proportional use versus availability (+ SE) of habitat classes for female elk in the Besa-Prophet area of northern British Columbia. Standard errors were determined from averages for each individual by season.

and Deciduous burns and Subalpine habitat. The pooled selection models indicated that the *Carex* habitat class was selected by elk in all seasons, but <1% of used locations were in this class and the majority of individuals (n = 7-11, depending on season) rarely or never used the class.

Table 4: Comparison of significant selection coefficients by season from averaged resource selection models for 14 female moose in the Besa-Prophet area of northern British Columbia. For each season, the number under the + indicates the number of individual final models that showed selection for that parameter; the number under the – indicates the number of individuals that avoided that attribute. Coefficients, SE, and *P*-values refer to the pooled models.

Parameter	Calving					Summer				
	Coef	SE	*P*	+	-	Coef	SE	*P*	+	-
Elevation	78.94	40.01	0.048	7	1	40.74	15.75	0.010	10	0
Elevation^2	-30.0	15.19	0.048	1	7	-14.4	5.59	0.010	0	10
Slope	-0.05	0.02	0.029	1	6	-0.04	0.01	0.007	1	8
Northness	<0.01	0.18	0.994	0	1	-0.06	0.14	0.672	0	1
Eastness	0.01	0.19	0.962	1	0	-0.01	0.13	0.968	0	0
Wolf Risk	-1.91	2.11	0.365	1	2	0.46	0.97	0.639	2	0
Bear Risk	0.06	1.30	0.962	1	1	0.48	0.99	0.624	0	0
Biomass	-0.49	0.88	0.574	0	1	-1.27	1.00	0.206	1	3
Quality	1.28	1.61	0.428	2	1	0.78	0.77	0.308	3	0
Nonveg	-1.22	0.15	<0.001	0	1	-2.47	0.50	<0.001	0	4
Elymus burn	0.25	0.37	0.487	1	1	0.23	0.51	0.648	2	1
Deciduous burn	0.24	0.45	0.594	3	1	0.62	0.35	0.077	5	0
Subalpine	-0.17	0.28	0.554	0	0	0.59	0.50	0.234	5	1
Stunt	0.07	0.39	0.854	1	0	0.57	0.41	0.167	5	0
Pine/Spruce	-0.19	0.51	0.711	2	2	0.80	0.33	0.016	5	0
Riparian	-0.45	0.53	0.398	1	1	0.50	0.51	0.328	3	1
Alpine	0.18	0.09	0.055	0	0	-0.13	0.59	0.831	0	0
Low Shrub	0.51	0.51	0.321	1	0	0.08	0.40	0.834	3	4
Carex	0.11	0.14	0.434	0	0	-0.80	0.37	0.032	1	1

Parameter	Fall					Winter[1]					Late Winter				
	Coef	SE	*P*	+	-	Coef	SE	*P*	+	-	Coef	SE	*P*	+	-
Elevation	54.99	23.93	0.022	7	0	37.65	13.67	0.006	6	2	58.26	33.70	0.084	7	0
Elevation^2	-18.6	8.15	0.023	0	7	-12.3	4.41	0.005	1	7	-21.7	12.84	0.092	0	7
Slope	-0.03	0.01	0.005	0	8	-0.01	0.01	0.235	2	4	-0.01	0.01	0.305	2	4
Northness	0.01	0.12	0.946	1	0	<0.01	0.08	0.987	0	1	0.03	0.10	0.748	0	0
Eastness	-0.02	0.13	0.879	0	1	-0.02	0.08	0.838	0	0	-0.02	0.11	0.836	0	1
Wolf Risk	0.94	0.44	0.033	4	0	0.47	0.62	0.443	2	0	-0.21	0.76	0.787	1	2
Bear Risk	-0.06	1.35	0.966	2	2										
Biomass	-1.16	1.25	0.351	1	5										
Quality	<0.01			0	0										
Nonveg	-1.39	0.51	0.006	1	3	-0.74	0.46	0.107	0	4	-0.46	0.47	0.330	0	2
Elymus burn	0.30	0.37	0.413	4	0	-0.10	0.34	0.779	1	1	0.00	0.36	0.989	2	0
Deciduous burn	0.65	0.36	0.068	8	0	0.35	0.18	0.055	6	1	0.29	0.24	0.220	2	0
Subalpine	1.12	0.30	<0.001	11	0	0.53	0.23	0.021	9	0	0.09	0.27	0.738	2	0
Stunt	-0.36	0.44	0.404	0	1	0.06	0.23	0.782	1	0	0.42	0.22	0.050	6	1
Pine/Spruce	0.01	0.32	0.966	1	3	-0.22	0.20	0.275	2	6	0.08	0.22	0.733	2	1
Riparian	-0.30	0.38	0.430	0	2	0.08	0.26	0.774	1	0	-0.09	0.41	0.822	1	0
Alpine	-0.94	0.67	0.157	0	5	-0.40	0.40	0.310	0	4	-0.27	0.33	0.414	0	1
Low Shrub	0.87	0.35	0.012	9	0	0.44	0.23	0.054	6	0	-0.06	0.37	0.882	2	0
Carex	0.03	0.21	0.888	0	0	-0.01	0.25	0.970	1	0	-0.01	0.20	0.979	0	0

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[1] Only 12 animals were used in the winter models because of collar failure.

Table 5: Comparison of significant selection coefficients by season from averaged resource selection models for 13 female elk in the Besa-Prophet area of northern British Columbia. For each season, the number under the + indicates the number of individual final models that showed selection for that parameter; the number under the – indicates the number of individuals that avoided that attribute. Coefficients, SE, and *P*-values refer to the pooled models.

Parameter	Calving					Summer				
	Coef	SE	*P*	+	-	Coef	SE	*P*	+	-
Elevation	37.31	4.82	<0.001	8		7.81	3.65	0.032	7	3
Elevation^2	-11.9	1.55	<0.001	1	9	-2.02	1.09	0.065	3	7
Slope	0.00	0.01	0.350	4	5	-0.02	0.00	<0.001	2	9
Northness	-0.31	0.07	<0.001	4	8	0.20	0.05	<0.001	8	3
Eastness	-1.74	0.12	<0.001		13	-0.71	0.06	<0.001		12
Wolf Risk	0.98	0.48	0.042	6	2	1.22	0.35	<0.001	6	4
BearRisk	-0.00	0.00	<0.001	10	2	-0.00	0.00	<0.001	4	5
Biomass	-2.68	0.30	<0.001	1	7	-1.51	0.13	<0.001		9
Quality	5.46	0.88	<0.001	10	1	5.62	0.67	<0.001	12	
Nonveg	0.06	0.28	0.824	1	6	-0.91	0.29	0.002	2	6
Elymus burn	0.34	0.16	0.036	6	4	-0.09	0.20	0.660	3	4
Deciduous burn	0.14	0.17	0.415	8	3	0.25	0.19	0.200	6	3
Subalpine	-0.63	0.21	0.003	4	7	0.39	0.20	0.045	6	2
Stunt	0.48	0.18	0.006	4	2	0.59	0.18	0.001	5	1
Pine/Spruce	0.05	0.23	0.814	3	6	0.11	0.24	0.655	6	4
Riparian	0.35	0.21	0.097	4	3	0.56	0.18	0.002	5	1
Alpine	-0.84	0.19	<0.001	1	7	-1.25	0.18	<0.001		11
Low Shrub	-1.02	0.24	<0.001	3	6	-0.89	0.23	<0.001	2	10
Carex	1.07	0.14	<0.001	4		1.23	0.17	<0.001	5	

Parameter	Fall					Winter					Late Winter				
	Coef	SE	*P*	+	-	Coef	SE	*P*	+	-	Coef	SE	*P*	+	-
Elevation	8.58	2.46	<0.001	7	4	11.50	2.63	<0.001	5	6	54.31	6.19	<0.001	12	1
Elevation^2	-2.55	0.85	0.003	5	7	-2.49	0.83	0.003	6	5	-18.1	2.13	<0.001	1	12
Slope	-0.02	0.00	<0.001	2	9	-0.04	0.00	<0.001		12	0.02	0.01	<0.001	8	3
Northness	0.02	0.04	0.649	6	5	0.06	0.03	0.059	6	4	-0.09	0.07	0.197	3	6
Eastness	-0.45	0.06	<0.001	1	11	-0.81	0.05	<0.001		13	-1.90	0.16	<0.001		13
Wolf Risk	-0.03	0.14	0.841	3	3	0.58	0.29	0.047	5	5	-0.22	0.40	0.587	3	6
BearRisk	-0.28	0.44	0.526	4	6										
Biomass	-2.92	0.47	<0.001	2	11										
Quality															
Nonveg	-2.63	0.33	<0.001		12	-1.52	0.18	<0.001		12	-0.84	0.23	<0.001	1	7
Elymus burn	0.91	0.15	<0.001	12	1	0.24	0.08	0.005	8	2	0.45	0.12	<0.001	8	
Deciduous burn	1.39	0.13	<0.001	13		0.37	0.07	<0.001	10	2	0.59	0.11	<0.001	11	2
Subalpine	1.01	0.10	<0.001	11	1	0.51	0.07	<0.001	8	1	0.34	0.16	0.034	6	2
Stunt	-0.40	0.19	0.032	4	6	0.10	0.11	0.386	5	3	-0.69	0.29	0.018		7
Pine/Spruce	0.00	0.09	0.985	5	4	0.01	0.10	0.940	5	5	-0.66	0.11	<0.001		7
Riparian	-0.52	0.17	0.002	4	6	0.23	0.18	0.183	6	2	0.26	0.16	0.111	4	1
Alpine	-0.71	0.14	<0.001	1	9	-0.30	0.09	0.001	2	7	-0.32	0.15	0.040	2	6
Low Shrub	0.51	0.14	<0.001	7	1	0.20	0.11	0.077	6	4	0.37	0.17	0.029	5	1
Carex	0.44	0.16	0.007	3		0.18	0.03	<0.001	2		0.50	0.11	<0.001	3	

DISCUSSION

Resource partitioning by ungulates typically occurs relative to habitat, dietary, and special niche requirements (Bowyer and Kie 2004). Both moose (Miquelle et al. 1992, Bowyer 2004) and elk (Peek and Lovaas 1968, Weckerly 1998) sexually segregate to a greater or lesser extent throughout their range. Consequently, we make inferences only to female moose and elk in the Besa-Prophet, with the recognition that our findings provide preliminary comparative insights based on only 1 year of data for each species. Further, although locations of animals were based on 4 fixes per day distributed throughout noctural and diurnal periods, these fixes that were 6 h apart do not allow us to examine habitat selection at finer feeding-patch scales.

Seasonal Movements and Home Ranges

Home-range estimates are difficult to compare among studies because of differences in methodologies (e.g., definitions of seasons), analyses (Lawson et al. 1997), and available resources. In this study, most fixed-kernel home ranges had multiple core areas and, particularly for moose, often did not include large portions of the valley bottoms that were used regularly for moving back and forth between core areas within a season. Consequently, defining availability of resources within just the core areas would have greatly underestimated available habitat during a given season.

We observed large seasonal variation in moose and elk home ranges whether we compared the extent of use (MCP) or kernel areas. Sizes of annual home ranges for moose in the Besa-Prophet probably reflect the relatively open, mountainous terrain of the study area and were more similar in size to MCP home ranges of female moose reported for the Kenai Peninsula of Alaska (Hundertmark 1998: 128 km^2), south-central Alaska (Ballard et al. 1991: 290 km^2), and the Mackenzie Valley of Northwest Territories (Stenhouse et al. 1994: 174 km^2) than to the smaller ranges from more southern latitudes (Hundertmark 1998). In summer, when moose exhibited the longest average movements between 6-h fixes, the extent of their ranges (MCP) was also comparable to the large home ranges reported for south-central Alaska (Hundertmark 1998). In winter, the seasonal ranges of moose were comparable in size to MCP home ranges at more similar latitudes (e.g., 42-47 km^2 in north-central Alberta; Lynch and Morgantini 1984). Cederlund and Sand (1994) observed that female moose with calves had larger home ranges than those without calves. Although we do not know the reproductive status of the animals in our study, home ranges for moose during calving were the smallest of all seasons, an observation that would be consistent with an ungulate with a hiding reproductive strategy. Elk also hide their young, and their home ranges during calving were small, although they were not the smallest by season.

Home-range size can be related to the abundance of important resources because a seasonal home range must meet an animal's energy and nutritional requirements (Anderson et al. 2005). For example, the home-range sizes of elk in summer and winter in Alberta and Wisconsin were inversely related to mean forage biomass; elk increased home-range sizes in winter when quality of forage was reduced and snow cover reduced forage biomass (Anderson et al. 2005). In our study, elk did not have larger range sizes in winter or late winter than summer. Rather, home ranges were smallest during winter and late winter. This may indicate that snow was more limiting in our system, but perhaps more likely that food was not limiting, particularly on the wind-blown south-facing slopes in the Besa-Prophet.

Elk home ranges during summer are reported to be highly variable even within the same study area (Strohmeyer and Peek 1996: MCP = 79-593 km^2) because of the juxtaposition of habitat components within the area. Summer was also the season with the most variability in home ranges for elk in the Besa-Prophet. In our study, elk exhibited the highest 6-h movement rates during summer (as much as 10 km in 6 h) and summer home ranges based on fixed-kernel estimates were comparable to those reported for large-herd, migratory elk in Yellowstone National Park (Boyce 1991). We recorded a very long movement of a minimum of 138 km (MCP area around those locations was ~800 km^2) over 20 days in July by 1 animal that returned to its original starting point. Edge et al. (1986) found that only 2-3% of marked female elk dispersed and most other studies have reported strong philopatry by female elk for seasonal and annual home ranges (e.g., Craighead et al. 1972).

Resource Selection Models

Calculations of use, based on proportions of GPS locations, give some indication of areas that are most frequented, and therefore, important to managers. Selection of locations by animals on the landscape, however, is usually a response to multiple variables and not simply to elevation or habitat alone. Selection models allow the quantification of tradeoffs that animals make, for example, in relation to predation risk or nutritional value. At the same time, selection models require that numerous assumptions be met (e.g., Thomas and Taylor 2006), sometimes resulting in the exclusion of habitats that are rarely used or completely avoided (Gillingham and Parker 2008).

In our analyses, we presented seasonal selection models for moose and elk after pooling individual models instead of developing a seasonal global model across individuals. Rather than unequally weight individual animals with more GPS locations, delete known observations from some animals to equalize sample sizes (Thomas and Taylor 2006), or use a random-effects approach to account for unequal sample sizes (Gillies et al. 2006), we chose to develop models for each individual in each season, dropping those habitats that had complete or near-complete separation (<4 used points). Further, our approach for considering which competing models were averaged was conservative (sum $w_i \geq 0.95$) (Burnham and Anderson 2002). We then determined a pooled model for each season by averaging the final individual models within each season. There are 2 different approaches that can be used when averaging competing models for which estimates of all coefficients are not found in each model (e.g., predation risk was not in all competing models; Burnham and Anderson 2002). We chose the more conservative approach of assuming that missing coefficients had the value of 0 in a given model. Our approach ensures that the final models are not unduly weighted by individual animals (Burnham and Anderson 2002), but it has the effect of reducing the magnitude of coefficients that occur in only some models and likely results in models with fewer significant coefficients when compared to the alternative approach of simply combining all individual data to develop seasonal, global models.

It is important to understand (but not over-emphasize) the influence of individual variation. In our study, other than elk selecting against eastness (i.e., for western exposures) during calving and for Deciduous burns in fall, all animals did not show the same selection for any attribute on the landscape. Our approach incorporates into each seasonal pooled model any zero selection value by an animal for an attribute with a weighting equal to significant selection coefficients by other animals. As such, the final pooled models do not overemphasize the importance of attributes selected by one or a few individuals. We also recommend presenting selection analyses with observations of use to identify habitat classes (or other categorical variables) that are avoided or rarely used, and to assess the relative magnitude of use for highly selected classes.

Findings in our study may be limited by biases attributed to relatively low fix rates (Moen et al. 1996, Frair et al. 2004), particularly for moose. Most locations within each season (55-65%), however, were obtained from habitat classes with forest cover (Pine-spruce, Stunted spruce, Subalpine) that probably had the poorest signal attenuation. Therefore, although our interpretation may underestimate the magnitude of use and selection of those classes, the classes were nonetheless noted as important in our analyses despite potential fix bias.

Habitat Use and Selection

Moose were often at lower elevations than elk on the Besa-Prophet landscape. Both species, however, moved down in elevation between winter and late winter. In other areas of British Columbia with high topographical diversity, the greatest single determinant of late winter habitat use by moose was decreasing elevation, which may be a surrogate for snow depth (Poole and Stuart-Smith 2005, 2006). Snow depth is a primary factor affecting late winter distribution of moose populations (Peek 1998), and moose in interior mountainous areas typically move to lower elevations throughout the winter (e.g., Pierce and Peek 1984, van Dyke et al. 1995). Elk also move to lower elevations during the winter (e.g., Unsworth et al. 1998, Boyce et al. 2003), possibly to take advantage of increased food availability. Because of the abundance of south-facing, wind-swept slopes in the Besa-Prophet, moose and elk may not be as affected by snow depth as they are in other areas.

Moose frequently inhabit shrub communities throughout their range whenever snow depths do not exceed 100 cm (Peek 1974), and select coniferous forests in regions of deeper snow, provided that browse is available (Bunnell and Eastman 1976, Peek et al. 1982, Pierce and Peek 1984). In the mountainous interior regions of Alaska, shrub-dominated communities above timberline are important moose habitat (Peek 1998) and those dominated by willow species appear to be the most important to moose (Risenhoover 1989). Moose in our study used Subalpine habitats most in fall and winter, and the Pine-spruce habitat class most during late winter, calving, and summer.

Elk often occupy south-facing, seral brushfields (Irwin and Peek 1983) or wind-swept, grass-dominated slopes (Knight 1970; Houston 1982) during winter, except when deep or crusted snow causes them to seek timber (Houston 1982). Peck and Peek (1991) reported that elk in northeastern British Columbia wintered primarily in post-fire grass and shrub communities, except during severe weather when conifer stands were used. Timbered habitats also have been reported to be important in other seasons. For example, elk in Idaho shifted from using a high proportion of shrub and open timber habitats in spring to using more timbered habitats in fall (Unsworth et al. 1998). The availability of forest cover may help reduce thermal stress and predation risk (Anderson et al. 2005). Habitats most used by elk in the Besa-Prophet were Deciduous and *Elymus* burns during late winter, and Subalpine during all other seasons.

According to pooled selection models, when elk selected areas with relatively high wolf risk, they did not select significantly for forest cover to help minimize risk. In Yellowstone National Park, when wolf activity was centered around dens and rendezvous sites in summer, elk apparently avoided wolves by selecting higher elevations, less open habitat, burned forest, and, in areas of high wolf density, steeper slopes (Mao et al. 2005). Elk did not spatially separate themselves from wolves in winter, but relied on behavioral anti-predatory strategies such as grouping (Mao et al. 2005). Although we have no data on group sizes, anecdotally elk in the Besa-Prophet tended to group together more frequently than moose during summer through winter.

Elk typically select habitats characterized by early seral stage (Thomas et al. 1979, Irwin and Peek 1983, Grover and Thompson 1986), which may be facilitated by burns. In the Besa-Prophet, the relative selection by elk for Deciduous and *Elymus* burns varied by season. Elk showed greater selection for the more open *Elymus* burns during calving, and for Deciduous burns during fall, winter, and late winter. Moose response to burns also is generally positive throughout their range, although Gasaway et al. (1989) observed that traditional movement patterns by moose apparently prevented animals without pre-fire use from finding burns. In the Besa-Prophet, moose did not specifically select for burned areas, but frequented the older Deciduous burns as a small, but consistent part of their habitat use.

Potentially related to predation risk and forage quality, the calving strategies of moose and elk appeared to differ in our study. Moose used the lowest elevations of the year (1333 ± 81 m) during calving and had the smallest seasonal use areas. These locations were not typically on valley bottoms (~800-1300 m) per se, but rather on the coniferous side slopes. Use and selection of Pine-spruce by moose was greatest during the subsequent summer season. Poole et al. (2007) reported that moose in southern British Columbia showed 2 elevational strategies during calving related to predation risk. They described 'climber' moose, which moved to higher elevations to calve in areas with lower forage quality and quantity and, therefore, farther from grizzly bears found at lower elevations. In contrast, 'non-climber' moose calved at low elevations with much higher forage values, but potentially at increased risk of predation. Given that grizzly bears in the Besa-Prophet tend to remain in higher areas during spring (Parker and Milakovic 2007), moose at lower elevations would avoid bears and have access to early green-up of shrub vegetation. This calving strategy, however, would come with the potential risk of wolf predation, given than wolves select for shrub vegetation in spring (Parker and Milakovic 2007). Although the pooled selection models did not indicate that moose selected locations to specifically avoid predation risk during calving or summer, they did, however, avoid risk of wolf predation during the fall.

In contrast to moose, elk moved upslope from their late winter locations to calve ~220 m higher than moose. During calving and summer, the higher elevations corresponded with the high use of the Subalpine habitat class. Their selection for vegetation quality was probably facilitated by access to *Elymus* and Deciduous burns, which typically green up earlier in spring, and then by the spruce-shrub transition zone of the Subalpine in summer. Unlike moose, elk appeared to select calving and summer areas on the landscape that minimized some predation risk by bears given that they used similar elevations during these seasons (Parker and Milakovic 2007).

Management Implications and Recommendations

Combining both use and selection information from this study, it appears that the highest potential for overlap between moose and elk may be during fall and winter, when both species used the Subalpine habitat class more than other classes and selected strongly for it. In winter, there may be some elevational separation between the 2 species, given that elk locations were on average 100 m higher than those of moose. In fall, however, the elevations used by moose and elk were not different. Both species also selected for Low shrub habitat during fall, where elk undoubtedly consume higher amounts of forbs and grass that are not yet senescent (Stevens 1970) compared to the more browse-dominated diets of moose. Elk are generalist feeders that maximize their food intake through mechanisms of habitat selection rather than selection of specific foods (Irwin and Peek 1983). Consequently, they can successfully shift from herbaceous species to browse (Houston 1982), and may be efficient competitors with moose when resources are limited (Flook 1964). During periods when resources are limited, overlap in resource use between the 2 species could result in temporary interspecific competition (Jenkins and Wright 1988).

If prescribed burns that are conducted primarily to enhance Stone's sheep populations are enabling increases in non-target elk populations in the Besa-Prophet, there also may be potential for competition between elk and Stone's sheep during some times of the year (Walker et al. 2007). Further, it is likely that with an expanding elk population, predator numbers will increase in response to the increased prey base. Higher wolf numbers would be expected to affect predator-prey dynamics by expanding into adjacent areas, particularly via burned slopes to upper elevations, and by increasingly preying on Stone's sheep and caribou. Prescribed burning also may provide additional opportunities for grizzly bears that select for burned vegetation classes (i.e., *Elymus* burn and Deciduous burn) throughout the non-denning period (Parker and Milakovic 2007), thereby augmenting predation risks to moose and elk. The management action of prescribed fire may help to sustain some of the diversity and abundance of large mammals for which the Besa-Prophet area is known, but it could also shift the prey base for predators and change the dynamics of the system. Additional studies involving population estimates and animal distributions should be specifically designed to determine how intensity, frequency, and locations of prescribed burns affect habitat use by ungulates (principally elk, moose, and Stone's sheep) and subsequently predators (e.g., wolves and grizzly bears) and their movements relative to ungulate prey. Our findings suggest that there is currently some seasonal overlap between elk and moose in the Besa-Prophet, and that expanding elk numbers will affect other species in the system.

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