DEFINING THE PREDATOR LANDSCAPE IN THE BESA-PROPHET

Part 3 of Project "An Ecosystem Approach to Habitat Capability Modelling and Cumulative Effects Management"

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EXECUTIVE SUMMARY

This project represents the predator component of a collaborative endeavor to examine the large-scale processes that structure a multi-predator multi-prey large mammal system in the mountains of northern British Columbia. The overall goal of this study on grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) was to understand the dynamics of the 'predator landscape' in the relatively non-impacted Besa-Prophet region of the Muskwa-Kechika Management Area. We used radio-telemetry data obtained from global positioning satellite (GPS) collars on grizzly bears and wolves, remote-sensing imagery of vegetation communities, and assessments of prey benefit from caribou (*Rangifer tarandus caribou*), Stone's sheep (*Ovis dalli stonei*), moose *(Alces alces)* and elk *(Cervus elaphus)* in the same area. We determined proportional use of different habitat classes, and use of the biophysical zones and habitat suitability classes incorporated in pre-tenure planning and terrestrial ecosystem mapping of the study area. We developed resource selection models to quantify the combinations of variables that predators were selecting or avoiding from what was available to them. These models showed that strategies differed among individuals and packs, but there were some consistencies. Grizzly bears often selected for burned and disturbed habitats, and areas with high vegetative diversity throughout the non-denning seasons. They also tended to select for higher elevations during the spring and the lowest elevations during the fall. Wolves selected consistently for shrub communities and high vegetative diversity, over a range of elevations.

We used stable isotopes of carbon and nitrogen to identify the proportions of plants and prey in the diets of grizzly bears and the dynamics of prey-switching in wolves. There was high seasonal variability in prey selection among individual grizzly bears, but generally both male and female grizzly bears increased their meat intake in the fall; and males consumed more meat than females throughout the year. The increase in meat intake identified for bears in the fall appeared to be primarily from elk. The diets of wolves were dominated by moose and elk, but caribou and Stone's sheep were also seasonally important to some packs. Diet determinations from fecal analyses in summer showed similar trends to stable isotope analyses, and that there were high numbers of juvenile ungulates in the summer diets of wolves.

This research provides a comprehensive analysis of habitat selection and use by grizzly bears and wolves, the two predator species that largely influence the distribution and abundance of ungulates in northern British Columbia. The findings help characterize the predator landscape of the Besa-Prophet area to better understand interactions within the large mammal predator-prey system. This research comprises the majority of Brian Milakovic's PhD research at the University of Northern British Columbia.

INTRODUCTION

Few studies have attempted to examine broad-scale ecosystem level dynamics of multi-predator multi-prey systems (Kunkel and Pletscher 1999). Large mammal predator-prey research has tended to focus on a single predator regulating a single prey population (e.g., Bergerud et. al. 1983, Hayes and Harestad 2000, Post et al. 2002, Vucetich et al. 2002), or the capacity of a single predator to regulate a multi-prey community (e.g., Bergerud and Elliott 1998, Dale et al. 1994) and possibly an entire ecosystem (e.g., Yellowstone: Smith et al. 2003, Ripple and Beschta 2004). The majority of research in North America has emphasized the dominant role of wolves (*Canis lupus*) in predator-prey dynamics (Carbyn et. al. 1995). Although the importance of ungulates in grizzly bear (*Ursus arctos*) diets has been recognized (Mattson 1997, Young and McCabe 1997), the relative and cumulative impacts of wolves and grizzly bears on ungulate population dynamics is still unclear. The relationships among major sources of mortality, such as predation, food limitation, competition, and density-dependent changes in key demographic parameters of ungulate populations, have been difficult to document (Messier 1989). In complex systems, however, an understanding of the interactions between numerous predators with potentially overlapping resources is vital to developing sound conservation and management strategies. In northern North America, wolves and bears are the primary predators considered to be in sufficient numbers to potentially limit and regulate ungulate populations.

Wolves are typically opportunistic predators with diverse diets, although cervids are often preferred prey (e.g., Spaulding et al. 1998). Several factors can affect selectivity by wolves for large prey items, such as availability and profitability of prey types, the degree of habitat overlap between predator and prey, risk of injury, probability of successful capture, and encounter rate (Huggard 1993). Wolves readily switch between ungulate prey species in response to shifts in ungulate abundance or ungulate migration (Ballard et al. 1997), but seasonal variation in prey selection may decrease with increasing availability of large wild herbivores (Meriggi et al. 1996). During periods of ungulate decline, alternative prey items can be locally or seasonally important (Spaulding et al. 1998). Additionally, wolves may exhibit prey selection at different scales, choosing home ranges that provide predictable prey encounters over the long term, and then selecting prey with the highest profitability within these ranges (Kunkel et al. 2004).

Grizzly bears can be effective terrestrial scavengers and predators (Mattson 1997, Green et al. 1997). Predation on ungulate calves potentially can regulate ungulate populations at low densities (Reynolds and Garner 1987, Boertje et al. 1988, Ballard et al. 1991,Gasaway et al. 1992). The use of ungulates by grizzly bears varies by month, season, and area of study, and depends on ungulate density (Mattson 1997). Although seasonal variation in bear diets has been well documented (e.g., Servheen 1983), how the use of ungulates and rates of predation vary with shifts in the composition of ungulate species, spatial and temporal variation in ungulate distributions and densities, and the availability of alternate food resources (e.g., vegetation) remains unclear (Mattson 1997).

The Besa-Prophet multi-predator multi-prey system in northern British Columbia (BC) presents a unique opportunity to contribute to conservation and to management planning of future access in the area. This study was designed to determine if grizzly bears display seasonal variability in habitat and prey selection, with movements related to the availability of

both vegetation communities and ungulates (as observed in southern British Columbia; McClellan and Hovey 1995, Hobson et al. 2000, McClellan and Hovey 2001). It was also conducted to assess to what degree wolves key in on particular prey species, including those that are restricted to specific geographical areas (e.g., Stone's sheep, *Ovis dalli stonei;* Walker 2005) and those that are known to move to geographically distinct calving sites (e.g., caribou, *Rangifer tarandus caribou*; Gustine 2005).

Information from this study contributes to the conservation of grizzly bears and wolves, as well as to effective land-use planning. These focal predators are highly visible species, and undoubtedly play major roles in the structure and processes that regulate a large mammal predator-prey system. Knowledge of landscape use, habitat selection, and prey consumption provide a foundation to maintain a functioning ecosystem and to effectively document impacts that future disturbance may have on these focal predators and the multi-species ungulate system around them.

PROJECT OBJECTIVES

The overall goal of this study was to quantify the dynamics of range use and food habits among grizzly bears and wolves in the Besa-Prophet area. To do this we used global positioning satellite (GPS) radio-locations, remote-sensing imagery of vegetation communities, stable isotope techniques for food habits, and habitat selection modelling. These analyses of food habits and habitat selection by the largest predators are helpful in characterizing the predator landscape of the Besa-Prophet watershed. They contribute to a better understanding of the interactions in the large mammal predator-prey system.

Specific objectives were to:

1) monitor seasonal movements and landscape use by grizzly bears and wolves;

2) define the relative concentrations of prey species in their seasonal diets and when prey switching occurs;

3) determine which habitat attributes are most important in habitat selection by grizzly bears and wolves; and

4) assess habitat use by collared individuals relative to Habitat Suitability Index (HSI) models and Terrestrial Ecosystem Mapping (TEM) classes, and relative to pre-tenure zones in the Besa-Prophet Pre-tenure Planning Area.

STUDY AREA

The Muskwa-Kechika Management Area (MKMA) in northern BC covers 6.4 million ha. The Besa-Prophet study area included the 204,245-ha Besa-Prophet Pre-tenure Planning Area and the 80,771-ha Redfern-Keily Provincial Park within the MKMA, as well as portions of surrounding areas for a total of 740,887 ha (Fig. 1). Three biogeoclimatic zones typify the region. The boreal white and black spruce (BWBS) zone (*Picea glauca* and *P. mariana*) at low elevations covers approximately 3% of the Besa-Prophet area. Valleys at ~800-1300 m are lined with white spruce, some lodgepole pine (*Pinus contorta*) and trembling aspen

(*Populus tremuloides*) on dry sites, and black spruce, willow-birch (*Salix* spp., *Betula glandulosa*) communities on poorly drained sites. South aspects often have burned grassland vegetation and deciduous trees. The spruce-willow-birch (SWB) zone is the subalpine area (~1300-1600 m) above the BWBS that covers ~81% of the land area in the Besa-Prophet. It 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.). The alpine tundra (AT) zone at elevations >1600 m, covers 16% of the Besa-Prophet. It is dominated by a dwarf scrub of prostrate woody plants and some herbs, bryophytes, and lichens, or rock and permanent snowfields (Demarchi 1996).

The topography of the Besa-Prophet is an interlaced network of ridges and east-west valleys with a prominence of south-facing slopes. The Besa-Prophet area is important for both ecological and geological diversity. Significant oil and gas reserves are potentially embedded in the sedimentary rock formations. Currently, there are no roads in the area. There are two guide-outfitting operations and recreation is limited to hunting, fishing, hiking, and a single ATV-snow machine trail. The combination of high biogeoclimatic diversity and limited access helps support one of the largest intact predator-prey systems in North America. Ungulates include moose (*Alces alces*), elk (*Cervus elaphus*), caribou, Stone's sheep, and a few mountain goats (*Oreamnos americanus*) and deer (*Odocoileus* spp.). Predators capable of preying on these ungulates include wolves, grizzly bears, black bears (*U. americanus*), cougars (*Felis concolor*), coyotes (*Canis latrans*), and wolverines (*Gulo gulo*), although it is believed that only wolves and grizzly bears are of sufficient numbers to be capable of potentially limiting or regulating ungulate communities.
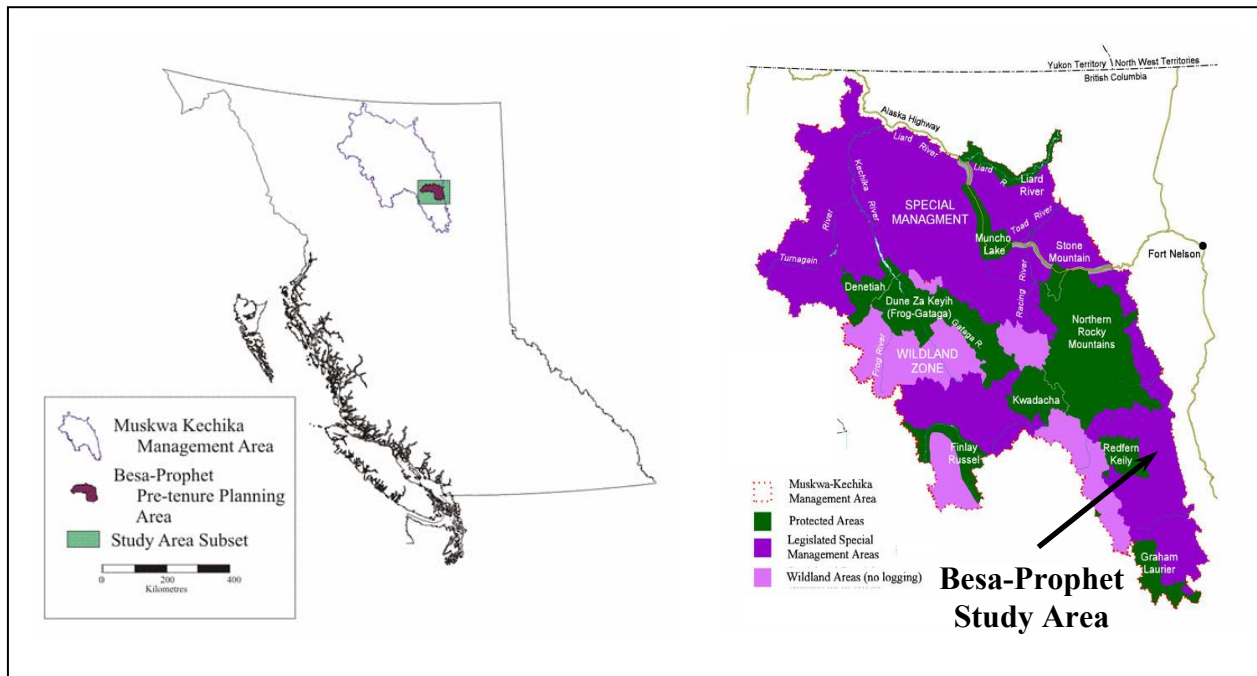

Figure 1. Besa-Prophet study area in relation to the Muskwa-Kechika Management Area in northern British Columbia, the Besa-Prophet Pre-tenure Planning Area, and land-use designations.

ACTIVITIES/TECHNIQUES/FINDINGS:

<u>Ranges and Movements</u>

Twenty-eight grizzly bears (21 females and 7 males) were captured and fitted with radio-collars (Simplex^{TM} Televilt, Lindesberg, Sweden) in May-June 2001-2003. We also monitored 5 wolf packs (Pocketknife, Lower Besa, Richards Prophet, Dopp Keily, Nevis) by capturing wolves between December and March 2001-2003 and maintaining 2 collared animals per pack. We programmed radio-collars on both grizzly bears and wolves to record locations 4 times daily. Data were retrieved during remote downloads 3 times per year (Fig. 2) as well as when collars were recovered from dead animals or at the end of a 2- or 3-year sampling period.

Annual and seasonal home ranges for grizzly bears and wolves were determined by 95% minimum convex polygons (Jennrich and Turner 1969) around GPS locations for each individual bear and each wolf pack. We used minimum convex polygons with 95% of the locations because 2-3 outlier points often increased the estimated size of the use areas significantly. For our analyses, we defined 3 bear seasons between den emergence in spring and the onset of denning in fall. These were identified primarily by changes in plant phenology (Table 1). We divided the year into 5 seasons for wolves based on life history demands, including breeding, denning, and travel by pups (Table 2).

Table 1. Seasons, dates and biological rationale for grouping data from radio-collared grizzly bears in the Besa-Prophet area, 2001-2004.

Bear Season	Date	Biology
Spring	Mid-April – 14 June	Den emergence to the beginning of plant green-up
Summer	15 June – 14 August	Start of plant green-up to start of senescence
Fall	15 August – end of October	Beginning of plant senescence to onset of denning

Table 2. Seasons, dates and biological rationale for grouping data from radio-collared wolves in the Besa-Prophet area, 2001-2004.

Wolf Season	Date	Biology
Winter	January and February	Breeding, peak snow depth
Late winter	March and April	Pre-denning
Denning	May through July	Beginning of denning until den is vacated
Late summer	August and September	Rendez-vous period when pups are beginning to travel, but not yet fully grown
Fall	October through December	Pups travelling with the pack and almost fully grown

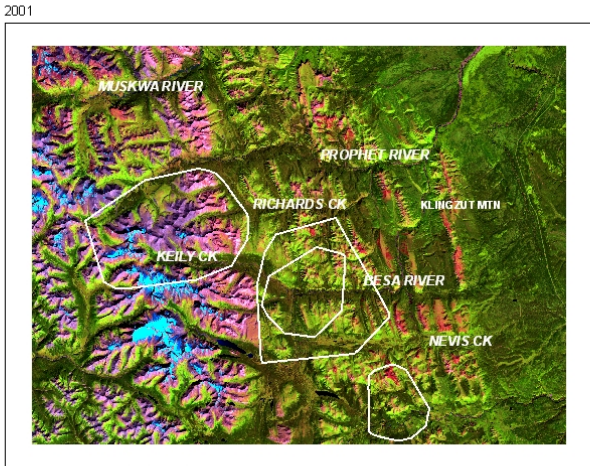**Figure 2. Downloading GPS locations from wolf collars in the Besa-Prophet area.**

Grizzly Bears: Most male grizzly bears shed their collars soon after capture or had collars that failed, and therefore we focused our analyses of range use on female bears for which we had spring, summer, and fall data. Annual home ranges determined over the non-denning period for female grizzly bears varied from approximately 80 to 700 km^2 (Table 3), with considerable spatial overlap among individuals (Fig. 3). Seasonal use areas within those ranges were highly variable in size, covering from as low as only 19 km^2 for one animal (G01) to 436 km^2 for another animal (G08) in spring 2004. Range size tended to be (but was not always) related to reproductive status. In spring 2004, bear G01 had 2 cubs of the year whereas G08 was with 3 yearlings. The trend for increasing size of seasonal and annual use areas with larger cub size was also observed across years for individual G01. With increasing age of the cubs, the sizes of the use areas increased (Table 3).

From the GPS locations that were obtained from consecutive 6-hr fixes ($n = 10,078$), we calculated monthly and seasonal movement rates for the individual bears, and then averaged across individuals to obtain 'bear movement rates'. Typically, grizzly bears moved at lowest rates in April after emerging from dens, and then increased movements to highest rates in late summer and early fall (~260 m/hr) (Fig. 4).

Table 3. Annual and seasonal range sizes by year and reproductive status of 13 radio-collared female <u>grizzly bears</u> in the Besa-Prophet study area. *n* is the number of GPS locations used to determine range sizes with 95% minimum convex polygons. COY indicates cubs of the year. Seasons are defined in Table 1.

Bear	Year	Cubs	Annual		Spring		Summer		Fall	
			km^2	*n*	km^2	*n*	km^2	*n*	km^2	*n*
G01	2001	2 yearlings	188	389			146	161	95	219
	2002	status unknown	279	418	150	129	222	151	142	138
	2003	with boar	511	465	309	72	410	161	250	231
	2004	2 COY	82	443	19	179	72	164	45	100
G05	2001	2 COY	126	602	48	170	92	213	83	218
	2002	2 yearlings	194	493	112	162	144	153	86	178
	2003	2 2-year olds	236	272	131	131	132	63	161	78
	2004	2 COY	no data							
G08	2001	alone	492	338	264	54	246	161	362	123
	2002	with boar	454	364			117	156	452	208
	2003	3 COY	529	508	327	192	331	146	411	170
	2004	3 yearlings	662	330	436	162	413	102	436	66
G15	2001	alone	no data							
	2002	status unknown	no data							
	2003	2 COY	130	371	51	49	96	165	107	157
	2004	2 yearlings	289	288	188	112	198	83	237	93
G18	2001	1 yearling	478	496	357	47	287	204	379	245
	2002	status unknown	no data							
	2003	2 COY	493	489	41	68	318	190	362	231
	2004	2 yearlings	474	378	389	218	372	160		
G20	2002	subadult	370	422	125	32	309	163	313	227
	2003	with boar	267	371	156	155	212	125	225	91
	2004	1 COY	no data							
G21	2002	2 COY	423	375	25	26	111	182	412	167
	2003	2 yearlings	582	378	221	128	357	142	403	108
G22	2002	3 2-year olds	360	438	108	44	345	164	276	230
	2003	2 COY	285	398	181	159	208	174	197	65
G23	2002	subadult	191	230			114	140	181	73
	2003	with boar	378	125	319	73	190	52		
	2004	alone	no data							
G24	2002	subadult	264	394			222	186	219	190
	2003	alone	394	303	346	97	233	45	191	160
G25	2002	2 COY	119	458			89	219	79	220
	2003	2 yearlings	219	537	168	194	109	178	128	164
G26	2003	3 COY	336	461	119	66	220	204	253	189
	2004	3 yearlings	284	388	74	128	252	207	224	53
G27	2003	with boar	429	359			356	150	361	209
	2004	status unknown			74	102				

Grizzly Bear Home Ranges, 2001-2002
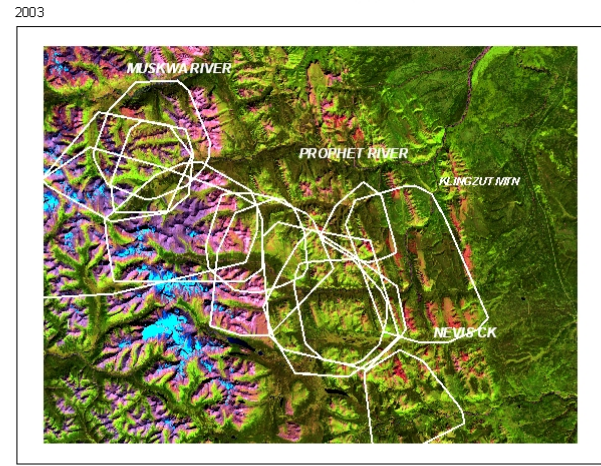
Grizzy Bear Home Ranges, 2003-2004

Figure 3. 2001-2004 annual ranges of individual female grizzly bears radio-collared in the Besa-Prophet study area based on 95% minimum convex polygons around GPS locations.
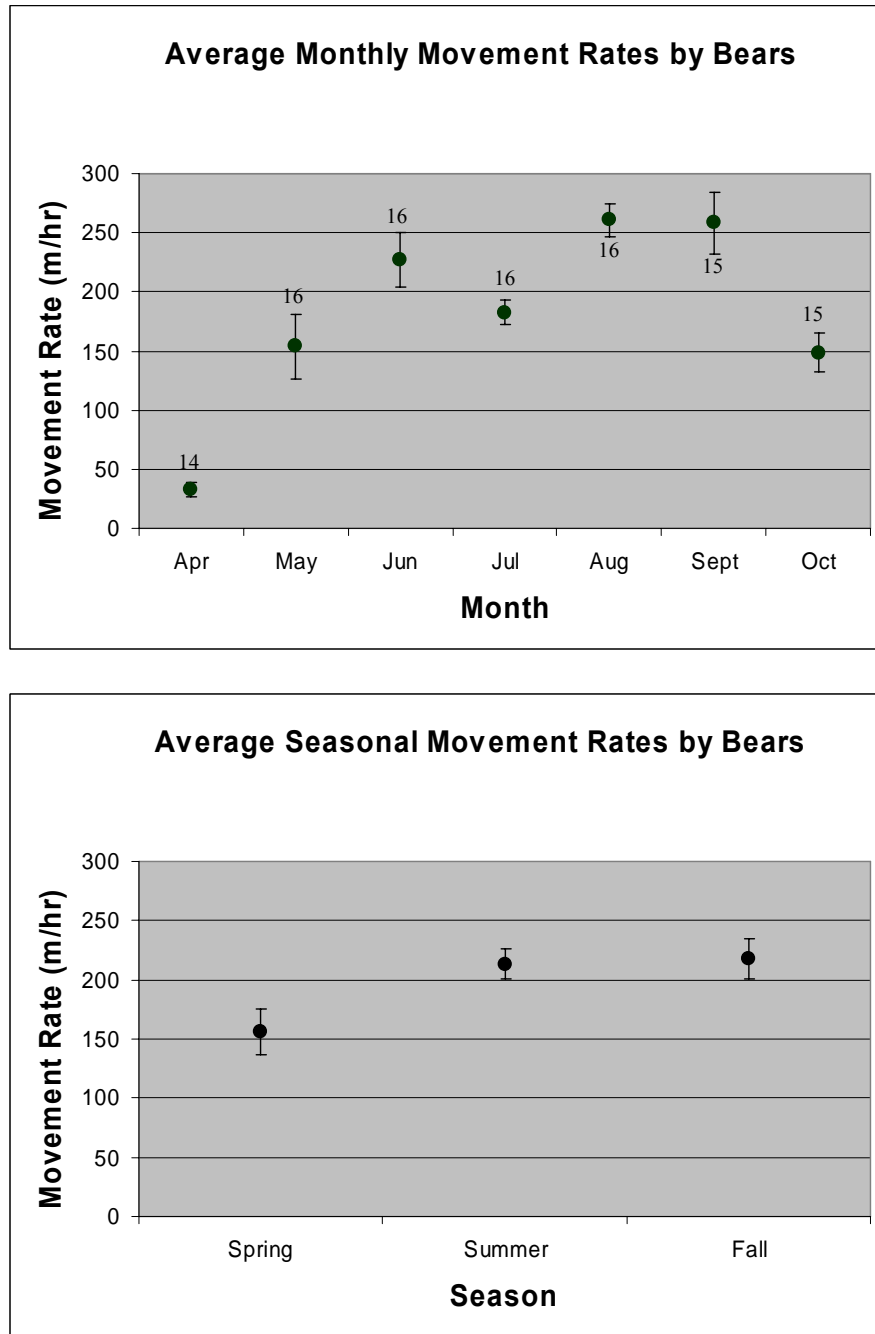
Average Monthly Movement Rates by Bears

Average Seasonal Movement Rates by Bears

Figure 4. Movement rates (m/hr, mean ± SE) of adult female <u>grizzly bears</u> averaged by individual and then averaged across individuals (as noted by sample sizes), by month and season (as defined in Table 1) in the Besa-Prophet area, 2001-2004.

Wolves: The core areas encompassed by wolf packs were often larger than those used by grizzly bears both annually and within comparable seasons (see Tables 1 and 2 to note differences in defined seasons between wolves and grizzly bears). Although there appeared to be some overlap in annual use areas of packs as drawn by MCPs (Fig. 5), there was almost no overlap of territories during any one month in contrast to individual grizzly bears. Among wolf packs, the size of the ranges varied between years and between seasons (Table 4). For example, in the Nevis pack, the summer range in 2002 was 272 km^2 - only half as large as in 2003 and 2004. Their annual use area was also much smaller in 2002 than the other years (549 versus ~900 km^2). The trend for the Richards Prophet pack was exactly opposite: range size was more than twice as large in 2004 (1200 km^2) as the previous years. Wolf use areas, therefore, are dynamic and can shift to some extent on the landscape (Fig. 5). Across the packs, annual ranges varied from approximately 375 to 1350 km^2 (Table 4). Range size was not directly related to pack size, but was probably more linked to food distribution and availability. Our data suggest that movements of wolves in the Besa-Prophet may occur in response to shifts in pack size (resulting from dispersal or mortality of pack members), and the presence of wolves in adjacent ranges. Individuals from both the original Dopp and Richards packs merged and reshuffled pack membership. The new packs were smaller in size, and occupied new territories north (Dopp Keily) and west (Richards Prophet) of their former ranges (Fig. 5). The range of the Pocketknife pack was significantly larger in 2003 than 2002, in part because one collared individual made 2 excursions of over 200 km twice, once during February (breeding season) and again near the end of April (prior to denning).

We determined movement rates from consecutive 6-hr GPS locations (n = 5,230) by calculating monthly and seasonal movement rates for each pack, and then averaging across packs to obtain general 'wolf movement rates'. Consistently, movement rates were lowest (291 ± 21 m/hr, mean ± SE) in March for all packs (Fig. 6). These lowest late-winter movements for wolves were generally greater than the highest rates of movement by grizzly bears in late summer and fall (Fig. 4). The movement rates by wolves were also extremely variable between packs, making the use of a general 'wolf movement rate' questionable (Fig. 6). For example, the Pocketknife pack, which had the largest use areas during winter, late winter, and denning in 2003 (Table 4), also travelled at rates that were 2-3 times higher than the other packs (Fig. 6). For all packs, however, movement rates increased during denning and/or summer. The timing of that increase was pack-specific. The Richards Prophet pack increased movements during denning, the Lower Besa pack increased movements later in summer, and both the Nevis and Dopp Keily packs showed relatively small increases in movement rates across the denning period (Fig. 6).

Wolf Home Ranges, 2002-2003

Figure 5. 2002-2003 annual ranges of 5 wolf packs in the Besa-Prophet study area based on 95% minimum convex polygons around GPS locations.

Table 4. Annual and seasonal range sizes by year of 5 <u>wolf</u> packs in the Besa-Prophet study area. *n* is the number of GPS locations from radio-collared individuals used to determine range sizes with 95% minimum convex polygons. Seasons are defined in Table 2.

Pack	Year	Pack Size	Annual		Winter		Late Winter		Denning		Late Summer		Fall	
			km²	*n*	km²	*n*	km²	*n*	km²	*n*	km²	*n*	km²	*n*
Pocketknife	2002	12 to 16	755	855	657	170	400	172	399	206	411	139	706	168
	2003	14+	1333	389	1205	164	1388	224	917	219	309	106	406	62
Lower Besa	2002	12+	1069	700	596	62	730	177	734	149	829	136	310	174
	2003	15+	1173	499	289	72	685	114	458	155	564	85	837	69
Nevis	2002	12+	549	653			355	176	315	130	272	128	410	219
	2003	12+	920	855	417	147	595	177	548	228	596	118	758	185
	2004	17	879	423	584	141	597	116	598	113	559	53		
Richards*	2002	5 to 8	1224	772			527	146	1132	260	442	126	398	240
Prophet	2003	6	476	731	238	127	231	170	284	216	163	48	429	170
	2004	6	603	304	398	94	508	109	333	101				
Dopp*	2002	8+	780	741			289	207	449	234	425	146	559	153
Keily	2003	2 to 5	375	525	285	95	195	174	257	221	171	33		

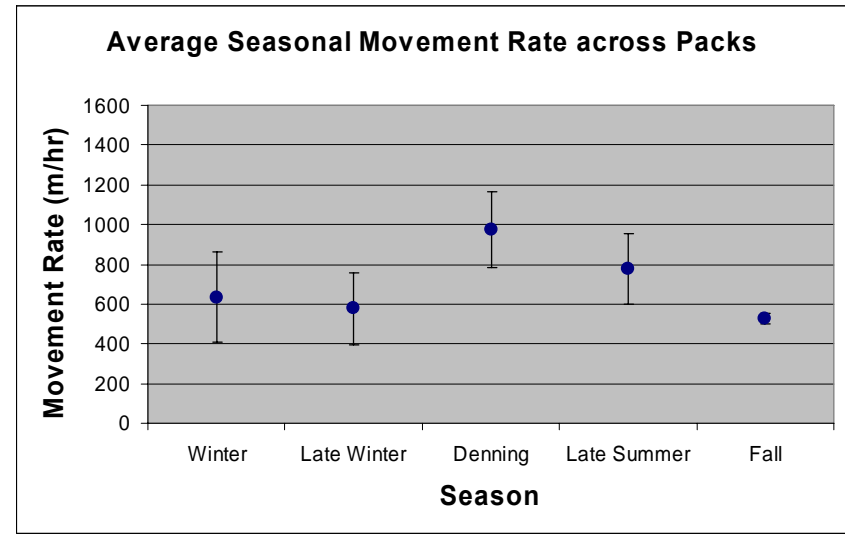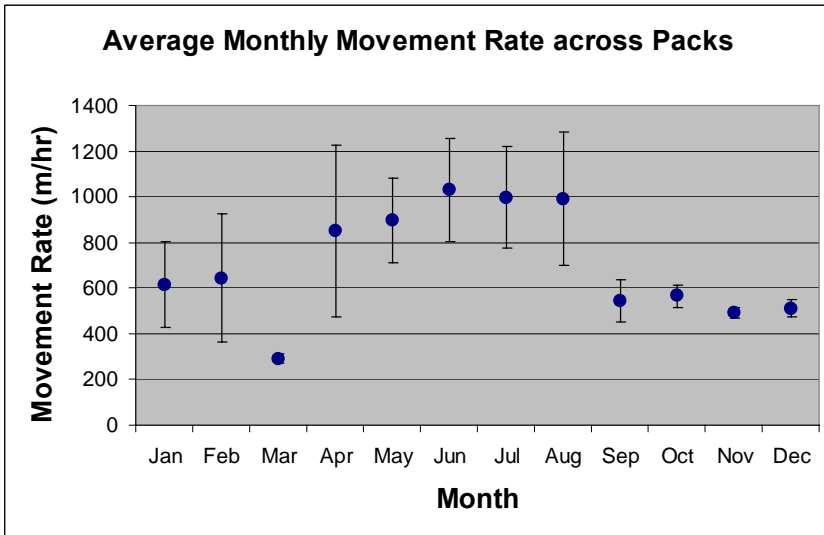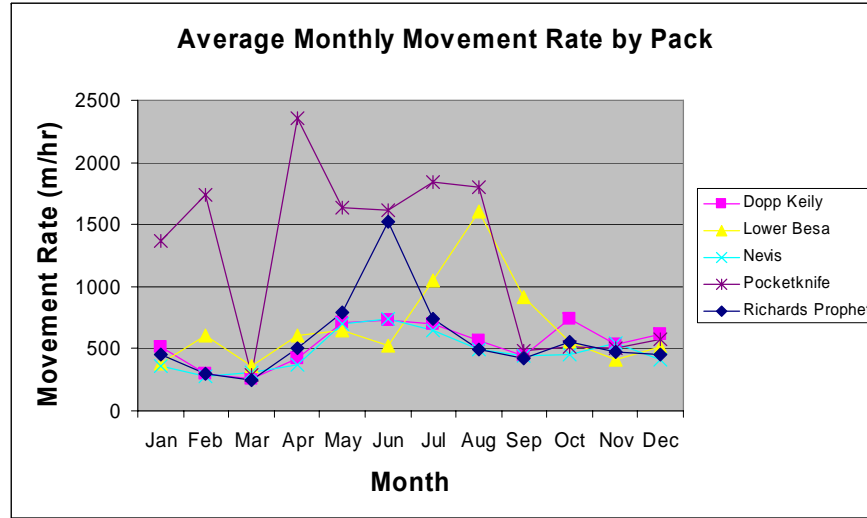* The Richards pack moved west to become the Prophet; the Dopp pack moved north to become Keily.

Figure 6. Movement rates (m/hr, mean ± SE) of <u>wolves</u> averaged by pack and then averaged across 5 packs by month and season (as defined in Table 2) in the Besa-Prophet area, 2001-2004.

Food Habits: Fecal Analyses for Wolves

The most widely used method to determine diets of carnivores is scat analysis (Spaulding et al. 2000). Scats are easy to collect, scat collection is noninvasive, and prey species can be identified from teeth, bones, feathers, and hair cuticular scale and medullary characteristics (Kennedy and Carbyn 1981). Scat analyses, however, even when corrected for differential disappearance, almost always estimate the diet at the level of the population rather than at that of the individual or subpopulation (e.g., males versus females) and cannot be used for foods that are completely digested and produce no quantifiable residues such as meat (Hilderbrand et al. 1996).

For wolves, efforts were placed on locating the den sites of the telemetered wolf packs. Den sites and rendez-vous areas were identified after plotting downloaded GPS locations on a contour map, and keying in on clusters of points representing numerous days at a site. High-use areas were visited in August after the dens had been vacated, and scat and bone materials were collected from the Dopp Keily, Lower Besa, Nevis, and Richards Prophet packs.

All wolf fecal samples ($n = 350$) collected during summers 2002 and 2003 were analyzed by consultant Cathy Conroy, Kimberly, BC. Prior to identification of prey remains, all samples were processed. Scats were autoclaved at 15 psi and 120 ºC for 20 min to prevent parasite transmission during processing. The scats were then washed using warm water and detergent to remove dirt, oils and unidentifiable materials, and air dried. Each sample was examined for identifiable hair, tooth, bone and feather remains. Mammal remains were identified using guard hairs. Four to 10 representative guard hairs with tip and base intact were selected. For some hair specimens, acetone was used as a solvent to clean adhering oils or dirt from the hairs.

Hair scale impressions were made by placing a thermoplastic strip on a glass slide and arranging selected hairs on the plastic strip. A second glass slide was then laid on top of the plastic and hairs, forming a layered sandwich. The slides, plastic and hairs were firmly clamped together using large clips. The sandwiches were heated to approximately 160 ºC for 15-20 min. After cooling, the top slide was removed. Each hair was then carefully displaced from its impression in the plastic. The hairs and the plastic scale impressions were examined under a compound microscope (100 - 400x). Microscopic scale pattern characteristics, medulla characteristics, and macroscopic color banding patterns were all used to determine the prey species. Reference slides using primary dorsal guard hairs obtained from live and deceased animals, and from museum skins also were prepared using the same methods, and were used to aid identification of prey species and age. Along with the reference slides, 2 research reports were used as identification keys and references: Adorjan and Kolenosky (1980), and Kennedy and Carbyn (1981).

Moose, elk, and caribou were observed much more frequently than Stone's sheep in the wolf scat samples (Table 5). Where possible, these were identified as adults or young. More moose, caribou, and sheep juveniles were consumed than adults. There also were very small amounts of mountain goats (1 case), beavers, small mammals (squirrels, voles, lagomorphs), and passeriform birds. Relatively few samples were classified as "unknown" species. For those cases, identification was not at least 90% certain based on macro- and microscopic hair characteristics.

Table 5. Prey species found in scat samples from <u>wolves</u>, expressed as the number of scat samples and as the percentage of the total number of scats analyzed, Besa-Prophet study area, summers 2002-2003.

Species	Number	% of Total
CARIBOU adult	30	8.6
CARIBOU juvenile	48	13.7
CARIBOU age unknown	1	0.3
ELK adult	40	11.4
ELK juvenile	39	11.1
ELK age unknown	3	0.9
MOOSE adult	62	17.7
MOOSE juvenile	100	28.3
MOOSE age unknown	3	0.9
SHEEP adult	5	1.4
SHEEP juvenile	16	4.6
SHEEP age unknown	1	0.3
Unknown ungulate species	6	1.7
Unknown species	2	0.6
Other	16	4.6
TOTAL NUMBER OF SCATS	350	

<u>Food Habits: Stable Isotope Analyses for Grizzly Bears and Wolves.</u>

Stable-isotope analyses of carnivore tissues can complement fecal analyses by overcoming the weaknesses associated with scat analysis mentioned above (Hilderbrand et al. 1996). In nature, carbon and nitrogen occur in 2 stable isotopes: ^{12}C and ^{13}C, and ^{14}N and ^{15}N. Ratios of carbon isotopes can distinguish between terrestrial, freshwater, and marine food sources, as well as between different plant communities. Nitrogen isotopes reflect both diet and trophic level. In general, the higher the nitrogen signature, the more protein (e.g., meat) is assumed to be in the diet. The specific combination of values of δ^{13}C and δ^{15}N results from the dietary interaction of species or individuals (DeNiro and Epstein 1981, Tieszen and Button 1988, Ambrose and DeNiro 1986, Hobson 1991 in Rosing et al. 1998, Ben-David et al. 1997, Jacoby et al. 1999).

Stable isotope analysis on red blood cells or muscle tissue provides an integrated index of diet over the previous 3 months, whereas isotope levels in blood plasma are indicative of diets over the previous 7-10 days. Hair samples reflect the time period over which the hair was grown. For species such as bears in which hair grows consistently from spring until fall (C.T. Robbins, personal communication), hairs can be sectioned into thirds and used to represent seasonal changes in diet. For example, the tip of the hair grows first in spring, the middle of the hair section grows in summer, and the hair nearest the root typically grows in late summer and fall. This technique was used to document seasonal shifts in gray wolf diets (Darimont and Reimchen 2002). Therefore, stable isotope analyses on blood, tissue, and hair can determine, by season, the proportions of plant and animal protein in the diets of bears and potentially the type of prey in the diets of bears and wolves, assuming isotopic signatures of prey species are distinct.

Hair and blood samples from grizzly bears, wolves, sheep, caribou, and moose were obtained during capture operations (Fig. 7), and samples of hair, meat, and bone were collected from ungulates killed in the study area during the hunting season. All samples were processed following Hilderbrand et al. (1996) and analyzed for carbon and nitrogen signatures (Stable Isotope Facility, University of California, Davis, CA). We also obtained additional bear hairs for analysis from the DNA mark-recapture study conducted by Mowat et al. (2001) in our study area. Some guard hairs from bears were sectioned into thirds, and from wolves into quarters, to determine if there were dietary shifts from spring through fall (during hair growth).

Figure 7. Blood and hair sampling for stable isotope analyses to determine food habits of grizzly bears in the Besa-Prophet area.

For bears that have the option of consuming meat or plants, differences in the nitrogen signature of hairs between populations can be used to determine the proportion of plant and animal protein in the diet. Plants assumed to be important in the diets of bears based on Ciarniello et al. (2002a, 2002b) were collected opportunistically between 1000 m and 2000 m elevation, and included above-ground foliage from *Festuca* sp., *Carex* sp., *Elymus* sp., *Equisetum* sp., *Epilobium angustifolium, Heracleum maximum*, and roots and bulbs of *H. maximum, Hedysarum* sp., *Astragalus* sp., and *Oxytropis* sp. Data from sectioned hairs indicated that the diets of bears were variable in protein signature, and that bears consumed higher amounts of prey in the fall (as indexed by higher ^{15}N signatures; Fig. 8). Males consumed significantly more protein than did females. ^{15}N signatures were considerably higher for wolves (ranging from δ^{15}N values of approximately 5.2 to 6.15) than bears (e.g.,

$\delta^{15}N$ values as low as 1.5) because they are obligate carnivores. Unlike bears, no obvious patterns across season were apparent for wolves.
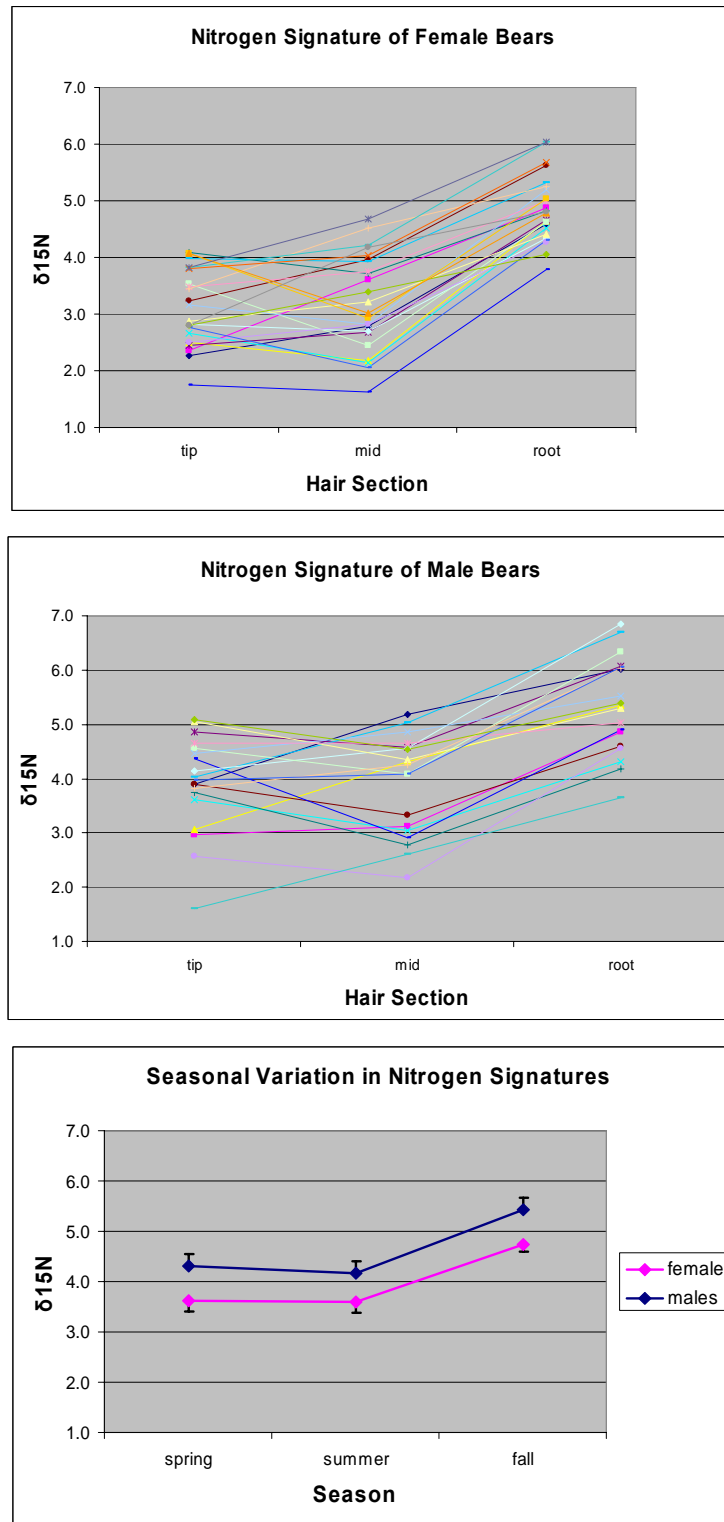

Figure 8. Nitrogen isotope signatures ($\delta^{15}N$) of sectioned <u>grizzly bear</u> hairs showing variability between individuals and between sexes by season, Besa-Prophet study area.

If the isotopic signatures of the primary prey species – Stone's sheep, caribou, elk, and moose - are relatively different between species, isotopic mixing models can be used to estimate how much of each prey species is consumed by carnivores (e.g., grizzly bears and wolves). Our results show that isotopic signatures of nitrogen and carbon do indeed differ significantly among prey species, and therefore, can be used to define dietary differences in predators during all seasons (Fig. 9). The mixing models assume that all of the prey species are consumed and that there are no other prey items consumed in significant amounts by the predators.

To estimate the proportion of ungulate species in the diets of grizzly bears and wolves, we used the hair, tissue, or blood samples that were most applicable to the season in question. For example, red blood cells (which typically last 120 days in the body) of prey species that were captured and radio-collared in the spring best represented the whole animal (and its diet) from the winter. We used 3 seasons for grizzly bears (spring, summer, fall as in Table 1), and 4 seasons for wolves (winter, spring (equivalent to late winter), summer (combining denning and late summer from May through August because of the types of tissues available and their respective turnover rates), and fall as in Table 2).

Grizzly Bears: Based on more than 900 model runs for bears using the recent IsoSource Model (Phillips and Gregg 2003), our analyses suggested that bears in the Besa-Prophet consumed relatively equal amounts of moose, elk, sheep, and caribou in spring and summer, and increased the amount of elk in fall (Fig. 10). We advise some caution relative to these results because we had the fewest number of elk samples (from guide outfitting operations) from which to determine a mean signature for elk as a prey species. We also were unable to determine if the increase in elk occurred through predation events or from scavenging on hunter kills.

Wolves: We used the IsoSource Model (>500 model runs) to determine seasonal diets for wolf packs in the Besa-Prophet area after averaging isotopic values for members of the same pack. During our study, wolf pack locations and individuals within packs changed. Consequently, the number of years for which we could assess dietary composition by pack depended on the samples available for isotope analysis; we averaged across years when data for multiple years were available. Seasonal changes in prey use were highly variable, although some trends emerged (Fig. 11). All packs, regardless of location within the study area, consumed large amounts of elk (38-80%) in winter. This prevalence of elk in wolf diets may be related to a general tripling in elk numbers than has occurred in the Peace-Liard region since the 1970's (Shackleton 1999). Consumption of moose by wolves was higher in summer and fall than in the other seasons. During winter, diets of western (Dopp Keily, Richards Prophet) and central (Nevis) wolf packs also contained large contributions from Stone's sheep, which continued to be an important prey item in the spring. In winter 2003, members of the Richards pack occupied a new range to the northwest (renamed Richards Prophet) and members of the Dopp pack moved to a new territory north of their former range (renamed Dopp Keily) (Fig. 5). With these changes, a large portion of the spring diet came from caribou, which were also predated by the Nevis pack (Fig. 11). Moose, in combination with elk, dominated the diets of the western and central packs in summer and fall. The Pocketknife pack in the southeast and the Lower Besa pack in the northeast showed a much more consistent reliance on elk throughout the year. Differences in prey selection by packs and between seasons undoubtedly reflect shifts in local prey composition and relative densities within the use areas of each pack.
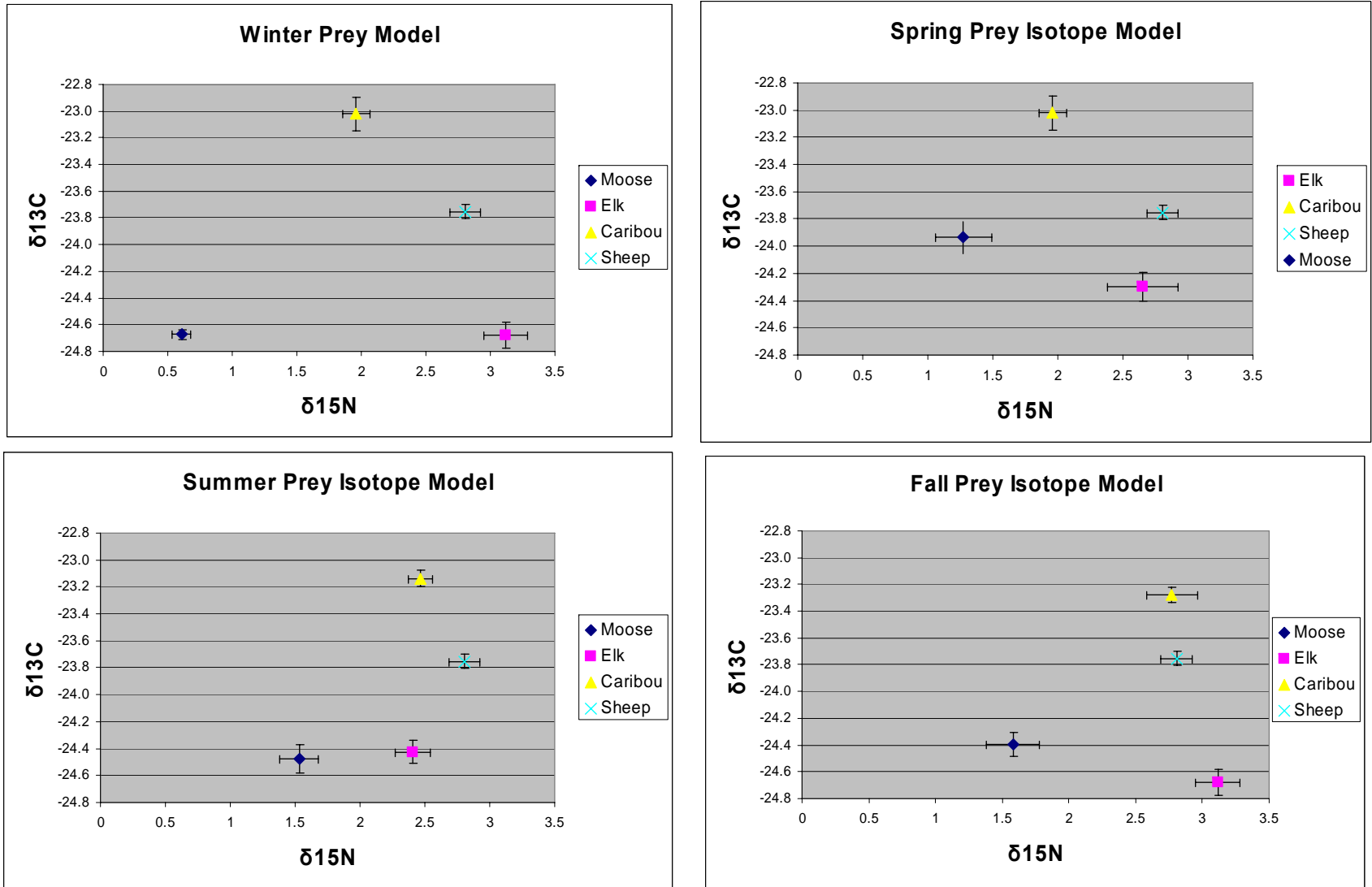
Figure 9. **Mean (± SE) prey isotope signatures (¹⁵N, ¹³C) determined from hair, blood, and tissue samples for moose, elk, caribou, and Stone's sheep by season in the Besa-Prophet study area.**
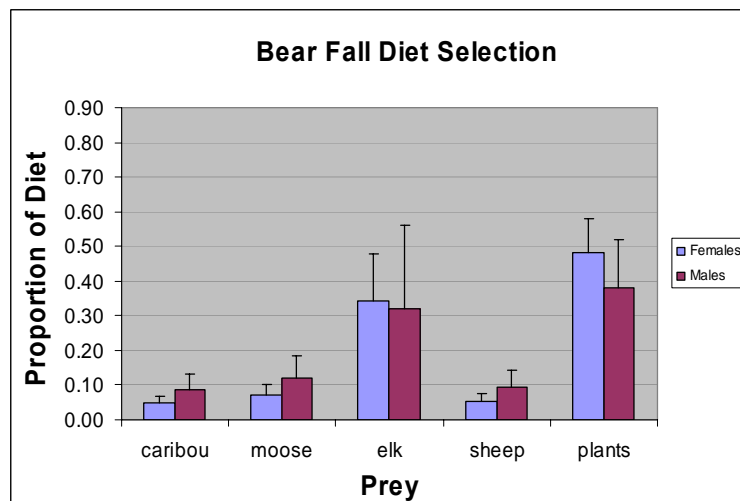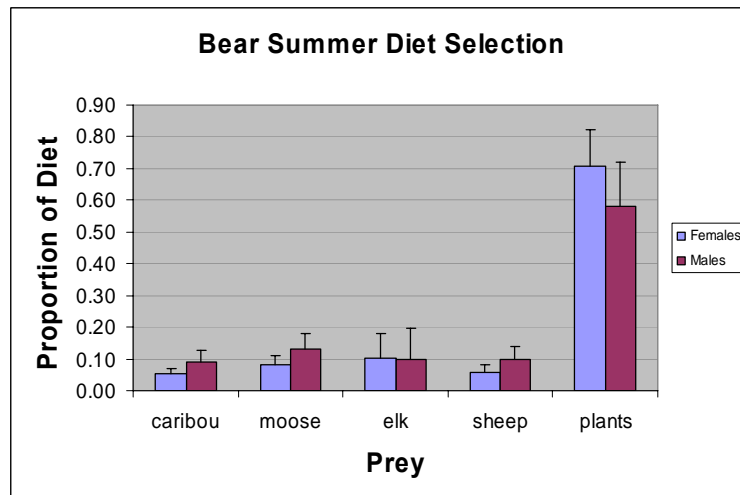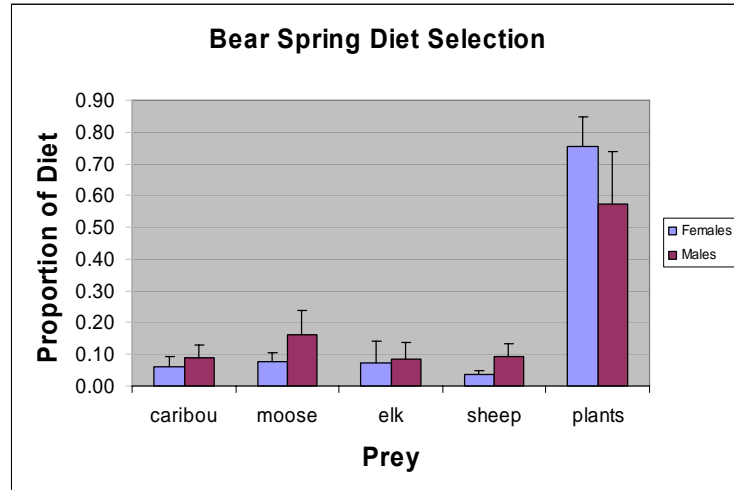
Figure 10. Seasonal diet composition (mean + SD) for male (*n* = 11) and female (*n* = 15) <u>grizzly bears</u> determined by stable isotope analysis of hair, blood, and tissue samples in the Besa-Prophet study area. Seasons are defined in Table 1.
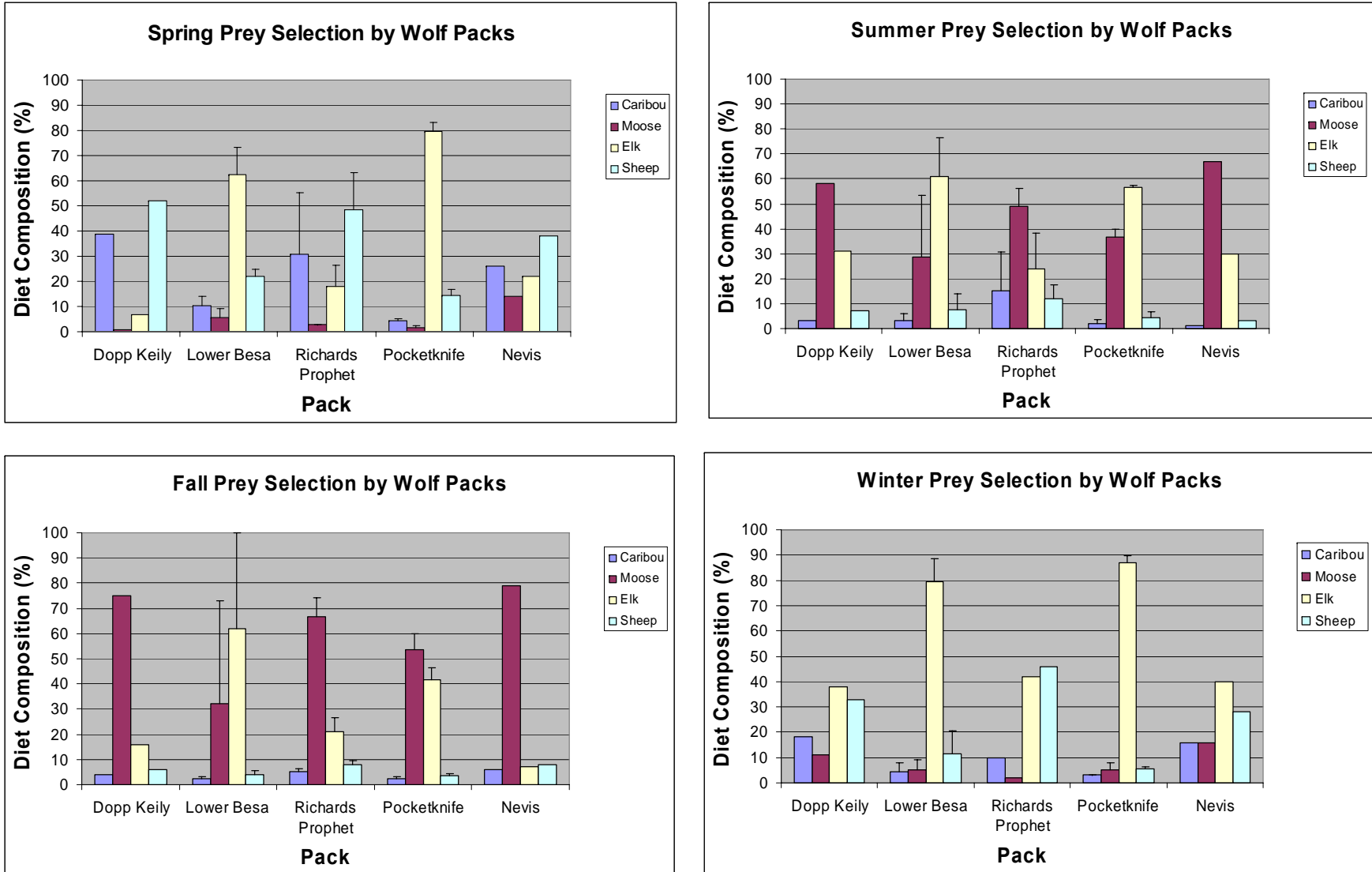
Figure 11. Seasonal diet composition (mean, + SD for packs with >1 year of data) for <u>wolf</u> packs in the Besa-Prophet study area, determined by stable isotope analysis of hair, blood, and tissue samples, 2001-2003.

Stable isotopes theoretically are a more powerful tool in estimating proportions of dietary components than scat analyses. Sample sizes of scats are often limited, and analyses of the fecal samples may not always work well for foods that are completely digested and produce no quantifiable residues (e.g., meat). However, given that wolves often bring prey (including digestible and non-digestible portions) to den sites, we were able to compare the composition of summer diets for wolves using both stable isotopes and scat analysis.

For the wolf packs in which we had corresponding fecal and isotope values, we compared the scat content and stable isotope determinations of dietary composition (Fig. 12). This comparison was done only for the 4 major ungulate species (moose, elk, caribou, and Stone's sheep). The two indices were highly correlated (r = 0.82). Consistently, however, isotopic determinations were higher for elk proportions and lower for caribou proportions in wolf diets compared to fecal samples. These differences may indeed be realistic given that scat samples are single estimates of intake rather than a more integrated dietary assessment over the summer season. Our scat samples were pooled from 2 years of collections, and assumed to represent average summer diets of wolves. Additional variation may have occurred because smaller non-ungulate prey species were not included in the already complex multi-source isotope model. Nonetheless, general estimates of dietary composition were similar between the 2 techniques during summer.
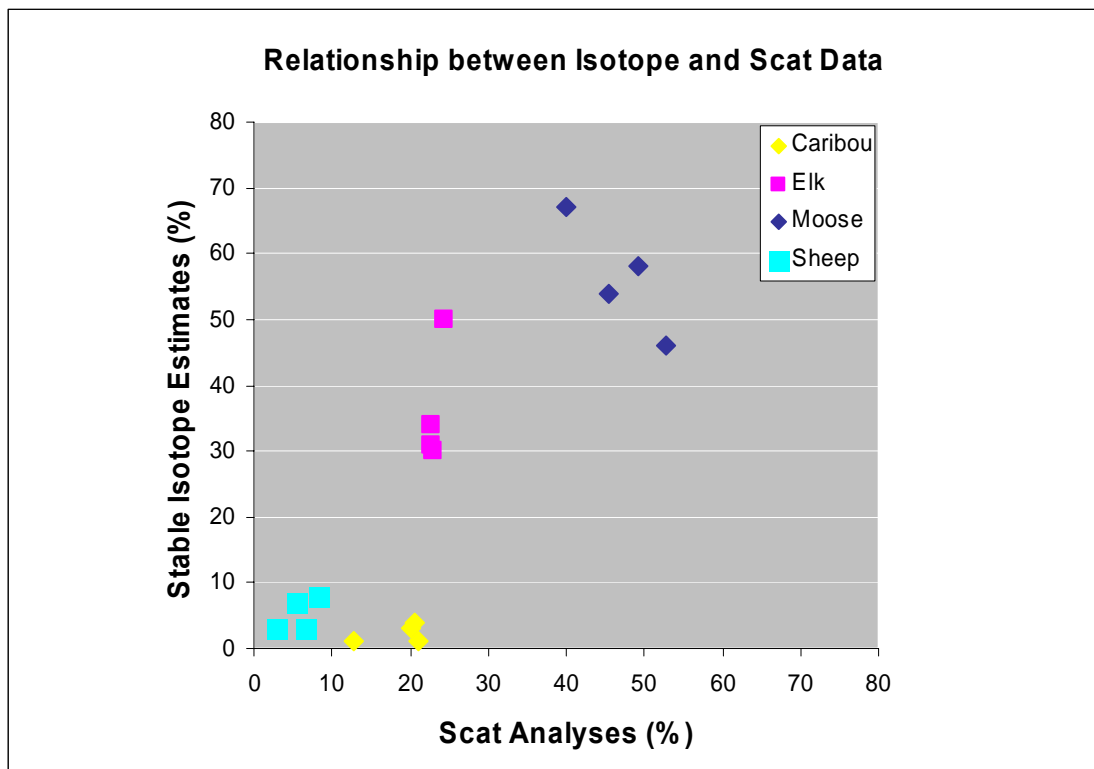

Figure 12. Comparison of summer diet composition of <u>wolves</u> determined by stable isotope analysis (of hair, blood, and tissue samples) and by scat analysis of fecal samples collected at den sites, Besa-Prophet study area, 2001-2003.

Habitat Use and Selection

We used the GPS data from radio-collared individuals to describe the habitat associations of grizzly bears and wolves on a seasonal basis in the Besa-Prophet area. We compared use to availability of different habitat classes, and then determined selection for combinations of variables. The habitat classification system for the Besa-Prophet area was developed using remote-sensing imagery (Fig. 13) by Roberta Lay as part of her thesis at the University of Northern British Columbia (Lay 2005). Fifteen general vegetation types were classified with a 2001 Landsat Enhanced Thematic Mapper image with 25-m resolution. For analyses on grizzly bears and wolves, we amalgamated several of these vegetation types, resulting in 10 habitat classes, to ensure that we had sufficient samples sizes for our analyses. Classes were lumped according to similarity of vegetation and elevation, and possible prey associations (e.g., moose and riparian; elk and deciduous burns; caribou and open alpine; Stone's sheep and *Elymus* grass burns). The 10 classes were: conifer, stunted spruce, shrub, alpine shrub, non-vegetated, riparian, open alpine, deciduous burns, *Elymus* burns, and subalpine spruce (Table 6). These 2 burn classes may also include other disturbed areas such as avalanche chutes, which could not be distinguished separately with remote-sensing imagery.

To determine use, we pooled GPS locations by season in each year, and the data were then mapped on the remote-sensing data layers. To index available resources, we placed 5 random locations for every use location within each individual bear's or pack's annual range for a particular year and season (as defined by 95% MCPs).

Table 6. Habitat classes (and their respective vegetation associations) used to analyze habitat selection by grizzly bears and wolves in the Besa-Prophet study.

| Habitat Class	Vegetation Associations
Conifer	Dense mid-elevation pine (*Pinus contorta*) and spruce (*Picea glauca*) forest stands; potentially some fir (*Abies lasiocarpa*).
Stunted spruce	Open spruce areas typical of north-facing slopes.
Shrub	Willow (*Salix* spp.) and birch (*Betula glandulosa*) shrub communities below 1600 m.
Alpine shrub	Willow and birch shrub communities above 1600 m.
Non-vegetated	Rock (boulder, talus), rock-lichen associations, water, snow.
Riparian	Low elevation (<1600 m) wetland spruce (*P. glauca* or *P. mariana* in poorly drained sites) along streams; includes gravel bars and sedge (*Carex* spp.) meadows.
Open alpine	Dry alpine tundra habitat >1600 m characterized by *Dryas* spp.; Wet alpine tundra habitat >1600 m dominated by *Cassiope* spp. and sedge (*Carex* spp.) meadows.
Deciduous burn	Older burns; characterized by deciduous shrubs and regenerating young aspen/poplar (*Populus tremuloides* and *P. balsamifera*) stands.
Elymus burn	Younger burns; meadows dominated by *Elymus innovatus*
Subalpine spruce	Open spruce; transition zone between dense mid-elevation spruce stands and open alpine areas.
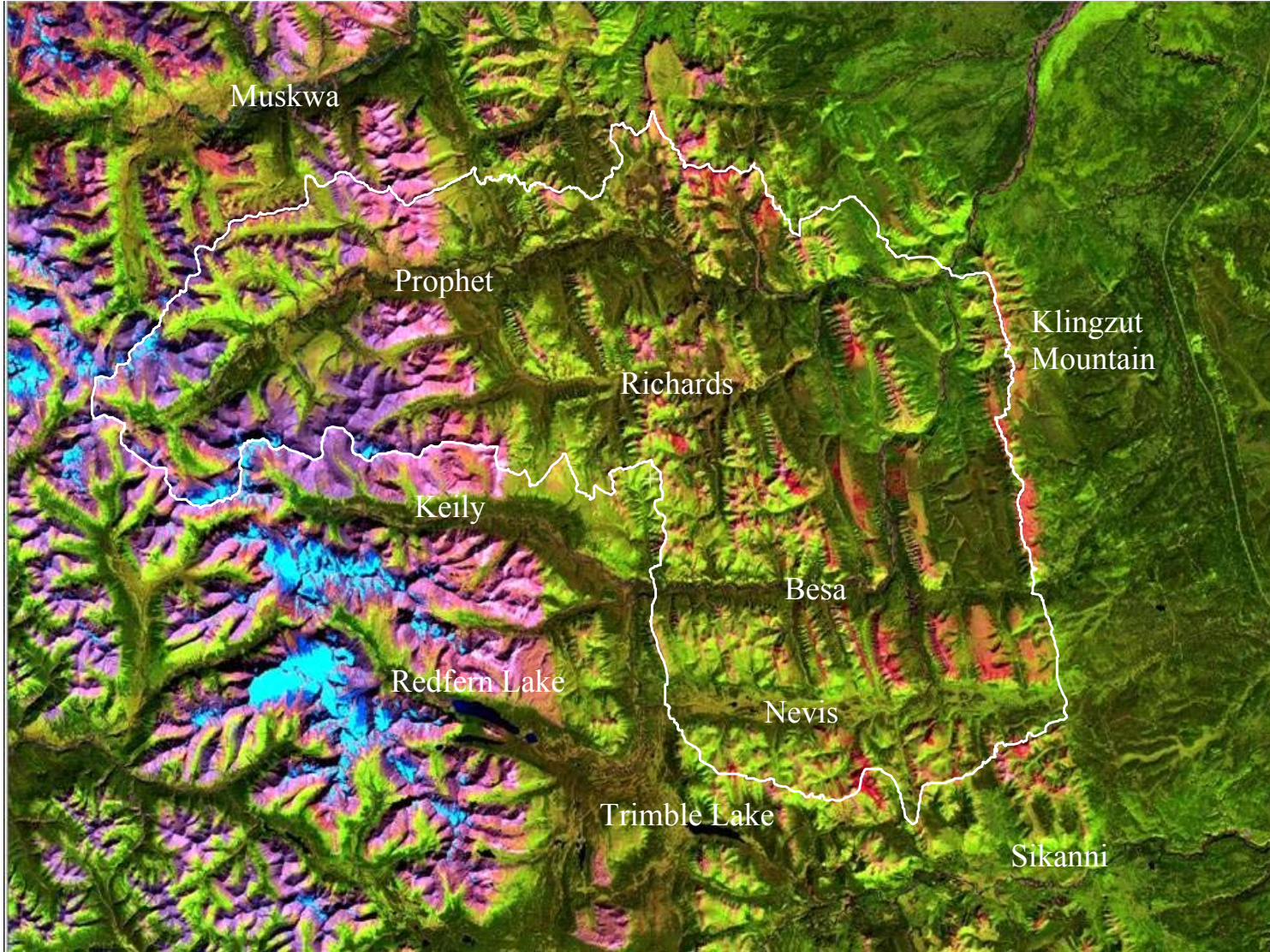
Figure 13. Remote-sensing image of the Besa-Prophet study area including outline of the Besa-Prophet Pre-tenure Planning Area and notable drainages and landscape features.

From 12,397 GPS locations of grizzly bears, we observed that bears used all habitat classes in the Besa-Prophet (Fig. 14). In spring, almost half of the locations were in non-vegetated, alpine shrub, and open alpine areas. In summer, bears tended to avoid non-vegetated areas and used alpine shrubs twice as much as in spring. In fall they continued to avoid non-vegetated areas and made more use of shrubs, but still used all habitat classes. In all 3 seasons, use of burned habitat classes (deciduous and *Elymus*, with potential inclusion of other disturbed areas) by bears was between 18 and 20% of locations. Den sites of grizzly bears were typically on hillsides with south or east orientation, and ranged from approximately 1170 to 1700 m in elevation on 16-46° slopes (Table 7).

Table 7. Characteristics of den sites used by individual <u>grizzly bears</u> in the Besa-Prophet area.

| Bear	Year	Habitat Class	Slope (°)	Elevation (m)	Aspect
G01	2001	*Elymus* burn	33	1365	E
	2002	Riparian	33	1302	S
	2003	Deciduous burn	36	1436	E
	2004	*Elymus* burn	41	1326	E
G05	2001	*Elymus* burn	32	1543	S
	2002	Non-vegetated	32	1374	W
	2003	Open alpine	41	1754	S
G08	2001	Alpine shrub	24	1721	S
	2002	Alpine shrub	30	1715	E
	2003	Riparian	22	1343	NE
	2004	Conifer	26	1545	NW
G15	2003	Conifer	26	1527	E
	2004	Alpine shrub	20	1742	E
G18	2001	Stunted spruce	46	1643	W
	2003	*Elymus* burn	27	1666	S
G20	2002	Stunted spruce	19	1172	S
	2003	Non-vegetated	28	1696	E
G21	2002	Non-vegetated	24	1784	E
	2003	Non-vegetated	35	1766	S
G22	2002	Open alpine	26	1882	E
G23	2002	Open alpine	29	1896	S
G24	2002	Open alpine	16	1793	S
	2003	Non-vegetated	31	1660	S
G25	2002	Non-vegetated	40	1870	S
	2003	Non-vegetated	38	1816	S
G26	2003	Non-vegetated	41	1965	W
G27	2003	Deciduous burn	31	1315	S
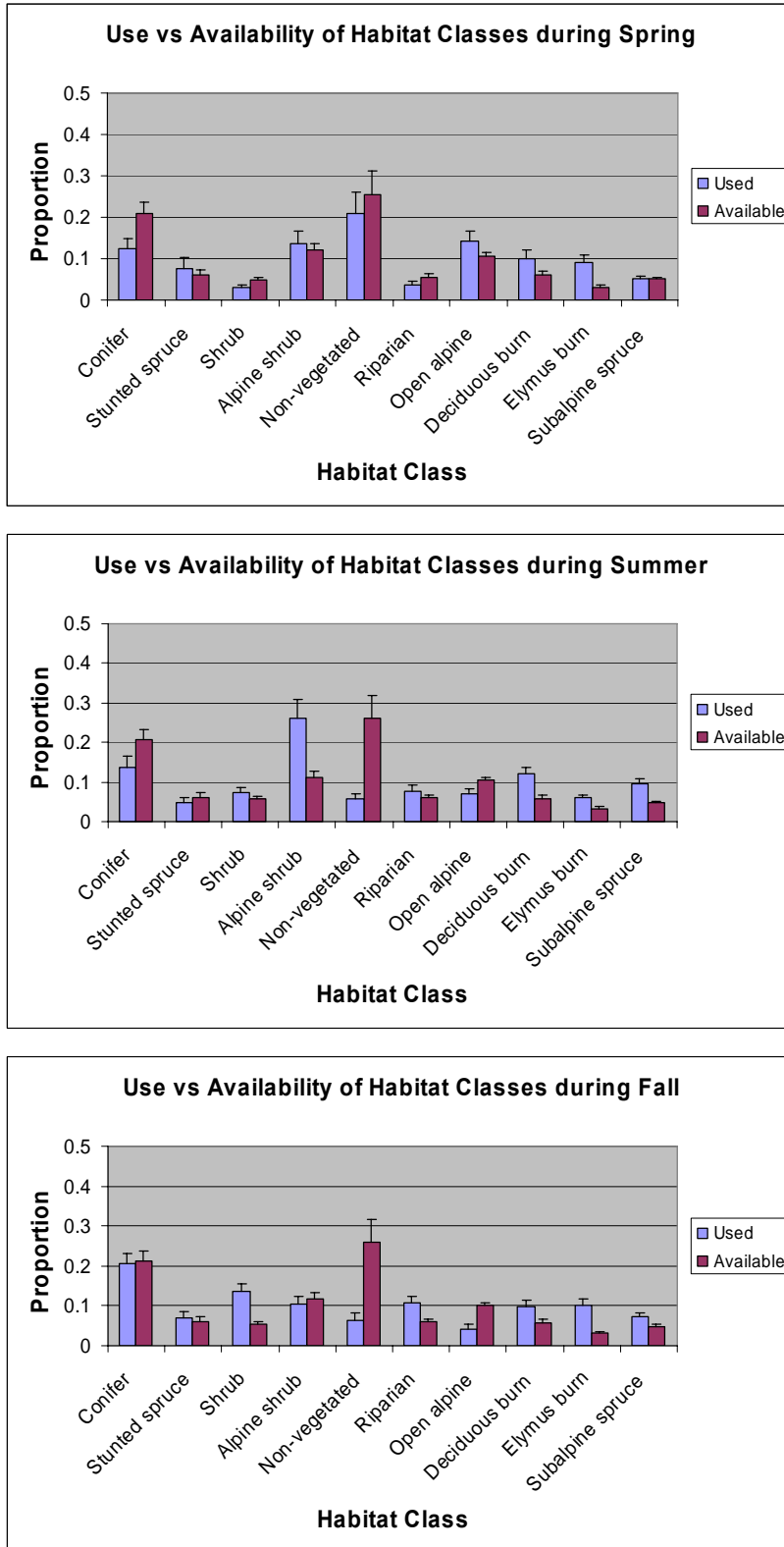
Figure 14. Proportional use versus availability (+ SE) of habitat classes for <u>grizzly bears</u> in the Besa-Prophet area of northern British Columbia. Standard errors were determined from averages of 13 GPS-collared bears by season as defined in Table 1.

From 7,414 GPS locations for wolves, we observed that wolves tended to avoid the non-vegetated areas during all seasons (Fig. 15). They used riparian and shrub classes most, ranging from 34 to 52% of locations in all seasons, with highest use of these classes during denning (May – July) and late summer (August – September). Use of the burned habitat classes by wolves was less than by bears; most locations in these classes were in late winter and fewest were in late summer. Most wolf den sites were on moderately sloped, well-drained, predominantly south-facing slopes in areas with significant forest cover and close proximity to water. It is apparent from Figures 14 and 15 which show these focal predators using all habitat (vegetation) classes without very strong affinities for or against specific classes, that other factors probably influence use of the landscape. We then developed resource selection models using the GPS data to describe the *combinations* of variables that may be important in the spatial and temporal habitat associations of grizzly bears and wolves in the Besa-Prophet area.

For both bears and wolves, resource selection functions (RSFs) help determine which particular attributes of habitat are selected for on a seasonal basis. The RSF models provide a broad-scale perspective of general selection patterns on the landscape (Boyce and McDonald 1999; Manly et al. 2002). They also accommodate any type of habitat variables (categorical and continuous) and easily incorporate spatial data acquired from Geographical Information Systems (GIS) or remote sensing (Boyce and McDonald 1999). We developed a suite of ecologically plausible models, chose the best model (Akaike's Information Criterion; Burnham and Anderson 2002), and then evaluated the relative importance of each of the variables in the models (using selection coefficients).

Our selection models typically included habitat class (Table 6), elevation, slope, aspect, fragmentation, and indices of forage biomass and quality. Aspect was categorized into north (316° - 45°), east (46° - 135°), south (136° - 225°), west (226° - 315°), and no aspect (NAS). Pixels with slopes of <1° were assigned to the NAS category. Fragmentation was an index assigned to each pixel based on the number of different habitat class polygons in broad open and closed cover types (Gustine 2005) in a 7 x 7-pixel window; values were grouped into high, medium and low fragmentation classes, and used as an index of habitat diversity. During the spring/summer months, we extracted NDVI (Normalized Difference Vegetation Index) values, which are related to leaf area and plant biomass (Tucker and Sellers 1986, Ruimy et al. 1994). For all vegetation types defined by Lay (2005) from remote-sensing imagery, plant biomass increased from June to July and August, and then declined in September (Fig. 16). Shrubs, burned and disturbed areas, and subalpine vegetation were highest in plant biomass; gravel bars were lowest. We mapped this index of relative biomass across the entire study area (e.g., the darkest green areas along south-facing slopes had the greatest biomass in July, whereas the lowest biomass (reddest areas) was on rocky areas and glaciers in Fig. 16). We also determined the rate of change in green-ness for each vegetation type from the change in NDVI between months (Fig. 17). Highest rates of change were between June and July for shrubs, burned and disturbed areas, and subalpine areas, and much less change occurred on gravel bars and riparian areas. Change was relatively stable from July to August, and was negative from August to September as plants declined in green-ness. We used this information as an index of forage quality (highest rates of green-up are likely the most digestible, best quality forage; Griffith et al. 2002, Oindo 2002), and mapped quality across the study area (e.g., the darkest green areas had the highest relative quality between June and July in Fig. 17).
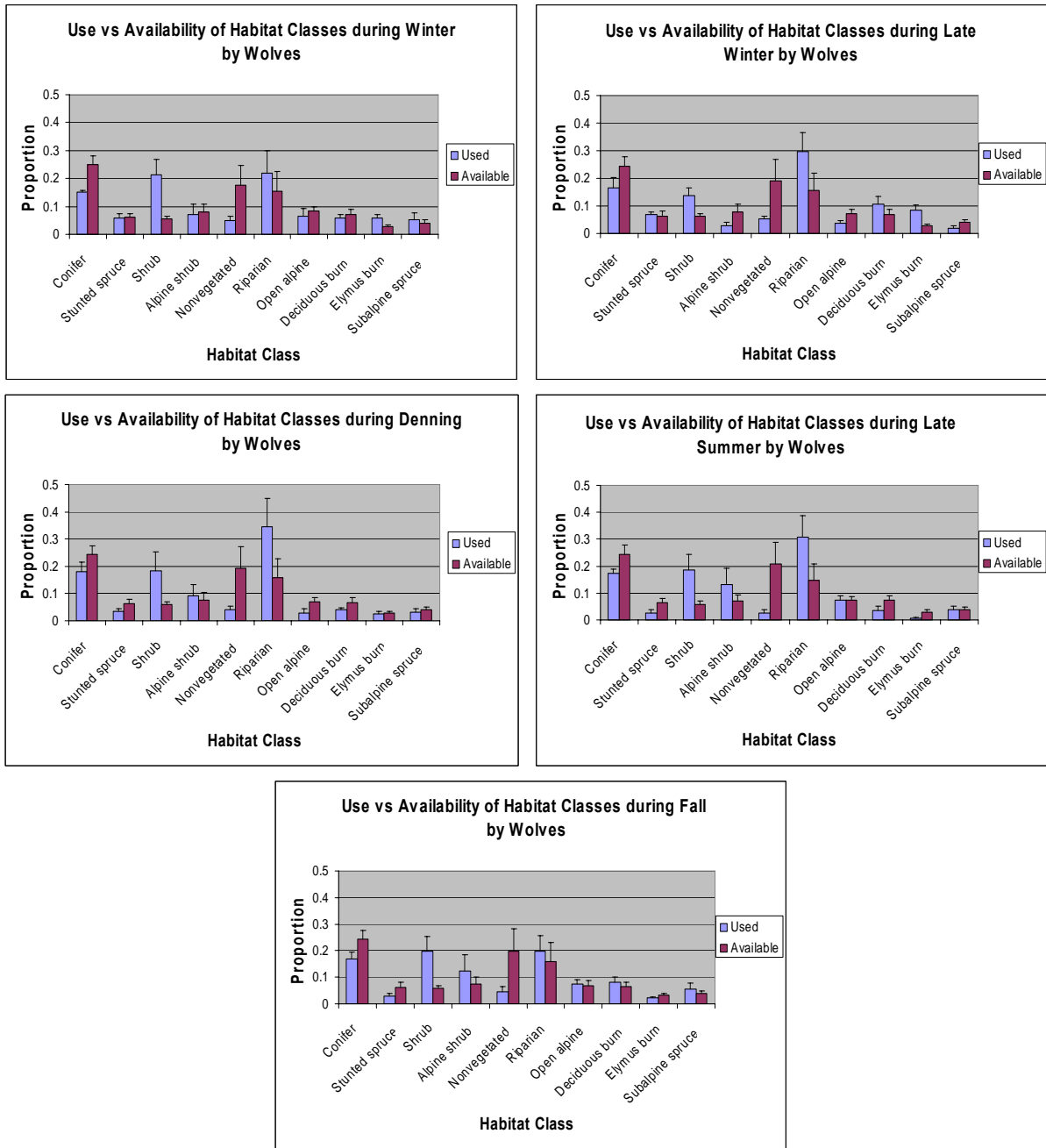
Figure 15. **Proportional use versus availability (+ SE) of habitat classes for <u>wolves</u> in the Besa-Prophet area of northern British Columbia. Standard errors were determined from averages for 5 wolf packs by season as defined in Table 2.**
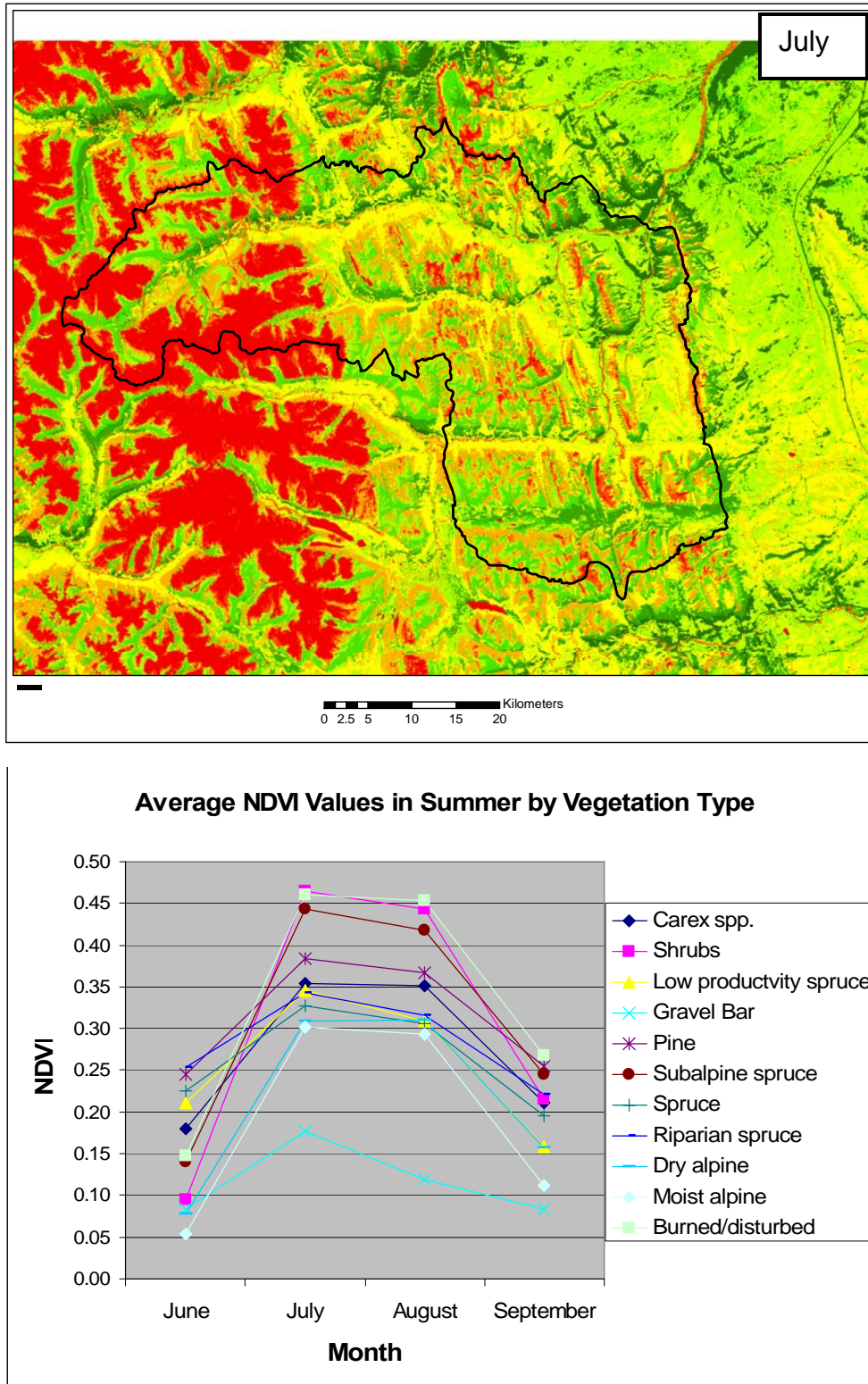
Figure 16. Relative forage biomass, as indexed by NDVI, across the Besa-Prophet study area in July, and for comparison among vegetation classes from June through September.
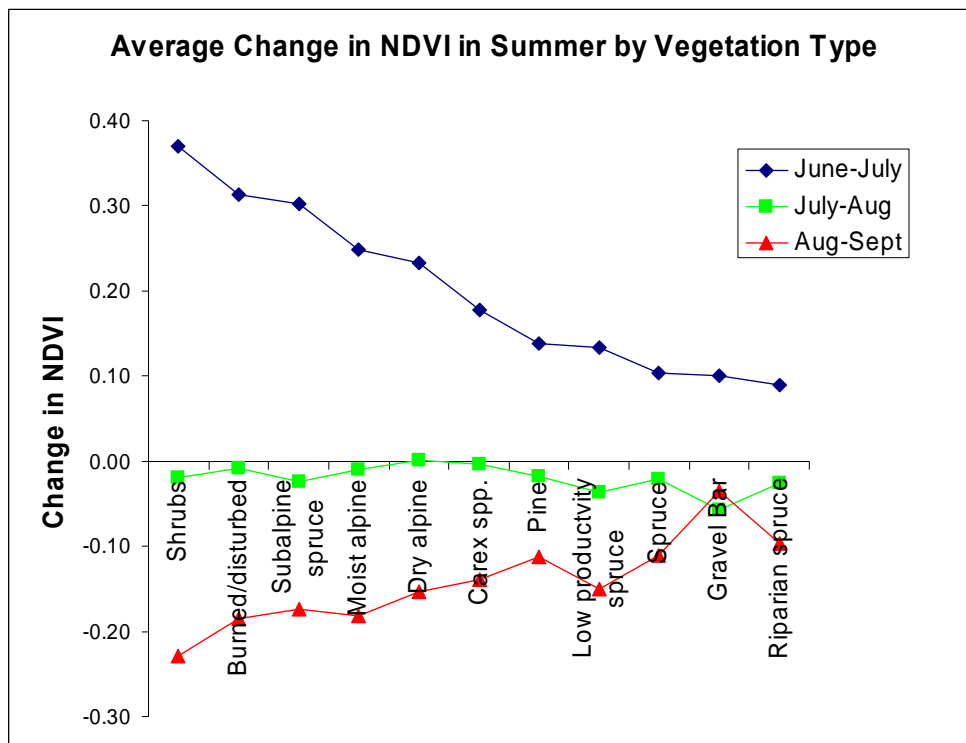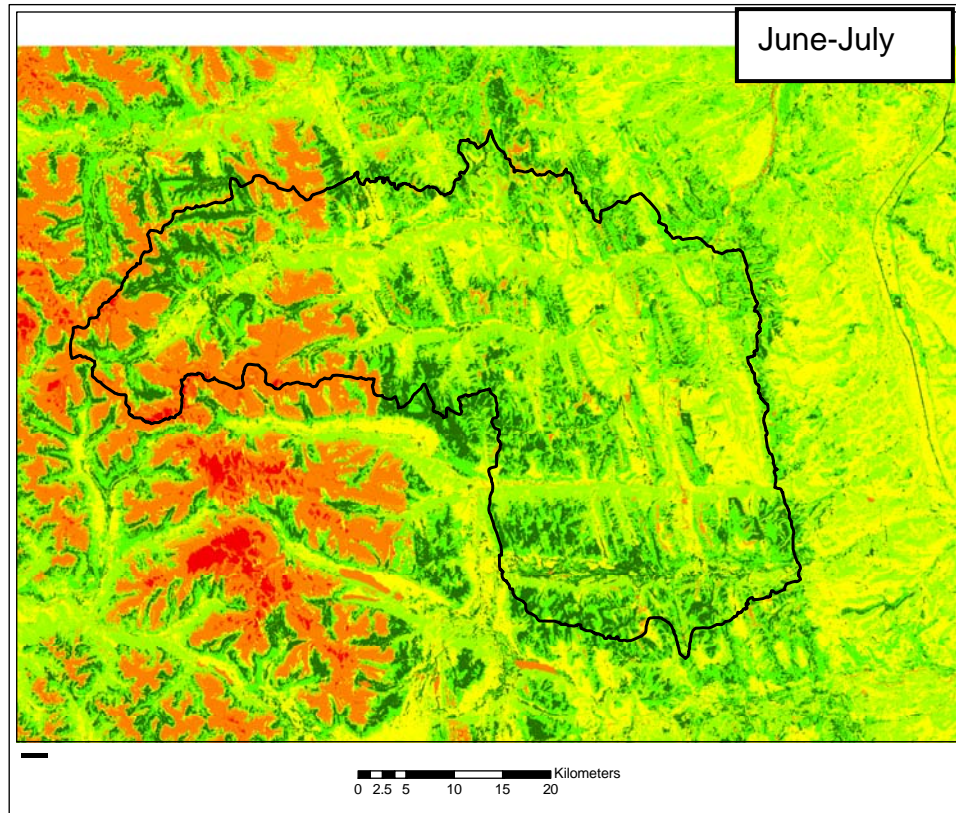
Figure 17. Relative forage quality, as indexed by change in NDVI, across the Besa-Prophet study area in June-July, and for comparison among vegetation classes from June to September.

For grizzly bears, the best model in each season, pooled across all individuals, always included habitat class, elevation, vegetation fragmentation, and aspect (Table 8). Habitat selection by wolves was also best characterized by the same variables in winter and late winter. During denning, late summer and fall, however, elevation was not as important in predicting selection by wolves. Rather, slope became an important contribution to the models (Table 8), although it did not have a significant selection coefficient except during spring when wolves selected against steep slopes. None of the pooled models for grizzly bears or wolves included vegetation biomass or quality.

Table 8. Resource selection models that best described seasonal habitat selection by grizzly bears and wolves in the Besa-Prophet study area. Statistics include the number of parameters in the model (K), sample size of use locations (n), Akaike's Information Criteria corrected for small sample size (AIC_c), Akaike weights (w_i), and average r_s values. The lowest AIC_c in a model set indicates the 'best' model, w_i provides a measure of the weight of evidence in favour of one model over the others, and r_s is an averaged Spearman's rank correlation from k-fold cross validation procedures that assess predictability of the model (Boyce et al. 2002). * indicates averaged models.

Season	Model	K	n	AICc	w_i	r_s
BEARS						
Spring	HABITAT x ELEVATION x FRAGMENTATION x ASPECT	18	18018	14989.27	1.00	0.99
Summer	HABITAT x ELEVATION x FRAGMENTATION x ASPECT	18	28669	23528.22	1.00	0.99
Fall	HABITAT x ELEVATION x FRAGMENTATION x ASPECT	18	27620	22461.62	1.00	0.99
WOLVES						
Winter	HABITAT x ELEVATION x FRAGMENTATION x ASPECT	18	5885	4778.21	0.99	0.87
Late Winter	HABITAT x ELEVATION x FRAGMENTATION x ASPECT	18	11082	8702.70	0.99	0.91
Denning	HABITAT x SLOPE x FRAGMENTATION x ASPECT	18	12852	9995.80	0.99	0.98
Late Summer*	HABITAT x SLOPE x FRAGMENTATION x ASPECT	18	5967	4644.32	0.77	0.97
	HABITAT x SLOPE x ASPECT	16	5967	4647.75	0.23	0.98
Fall*	HABITAT x SLOPE x FRAGMENTATION x ASPECT	18	8311	6741.84	0.82	0.99
	HABITAT x SLOPE x ASPECT	16	8311	6744.81	0.18	0.98

Resource Selection by Bears: During all seasons of the year, bears (all data pooled together) selected for the burned habitat classes (which also may include disturbed areas such as avalanche zones) and high fragmentation areas, and avoided conifer stands (Fig. 18) in comparison to what was available to them. The burned habitat classes combined (*Elymus* and deciduous) were consistently selected for the most of all the vegetation types. In spring, bears also selected for open alpine areas consisting of wet and dry alpine and *Carex* sites >1600 m, as well as non-vegetated and stunted spruce areas and east aspects. In contrast, they avoided all of these features during the summer and fall. In summer, bears selected for alpine shrubs >1600 m and subalpine spruce classes, with north or no aspect. In summer, they avoided the south-facing slopes, in contrast to selecting for them in spring and fall. In the fall, they selected for shrub and alpine shrub areas. Grizzly bears tended to select for higher elevations (~1400 to 1750 m) during the spring and the lowest elevations during the fall (~1100 to 1500 m) (at a RSF of 0.8). They selected for a broader range of elevations during the summer (~1100 to 1750 m).

The models for each individual bear showed that there also was seasonal variation in individual selection patterns for habitat classes and topographical features, but annual variation was minimal. Bears tended to be consistent in their selection of features in the same seasons of different years. However, there was variation in the characteristics selected by different bears. Selection patterns were most consistent among bears during summer, and most variable in spring. Although not found to be important in the pooled models for all bears, vegetation biomass was an important variable for predicting the habitat selection of 50% of the individuals during spring.

In general, habitat class, combined with topography and physiographic features, undoubtedly influences the availability of plant foods, as well as the likelihood of encountering ungulate prey. Prescribed burning, which has been used in the Besa-Prophet area to expand habitats and population sizes of elk and Stone's sheep (R. Woods, personal communication, BC Ministry of Environment), results in young regenerating stands that contain higher abundances of most critical bear foods including green herbaceous vegetation, roots, fruits, ants, and ungulates (e.g., Zager et al. 1983, Knight 1999). Similarly the selection of shrub habitats by bears in the summer and fall may be related to some berry production and ungulate encounters.

Resource Selection by Wolves: Wolves selected consistently for shrub communities, typically with high fragmentation, and against conifer classes during all seasons in the models pooled across the 5 packs (Fig. 19). In winter and late winter, animals selected for the burned *Elymus* grass class and open alpine areas, and relatively flat areas with no aspect. Late winter was the only season in which wolves selected against subalpine spruce and for riparian areas (which include wet spruce, gravel bars, *Carex* <1600 m). Selection for south aspects in late winter extended into the denning period, when wolves also used north aspects, avoided open alpine areas, and selected most for *Elymus* burns and shrub and alpine shrub communities. During late summer and fall, wolves continued to select for shrub and alpine shrub areas, but on north aspects. The predominant use of shrub classes year-round in addition to burned (and

disturbed) areas may be because these habitats are generally favoured by moose and elk. This finding is consistent with our stable isotope analyses of food habits (see previous section).
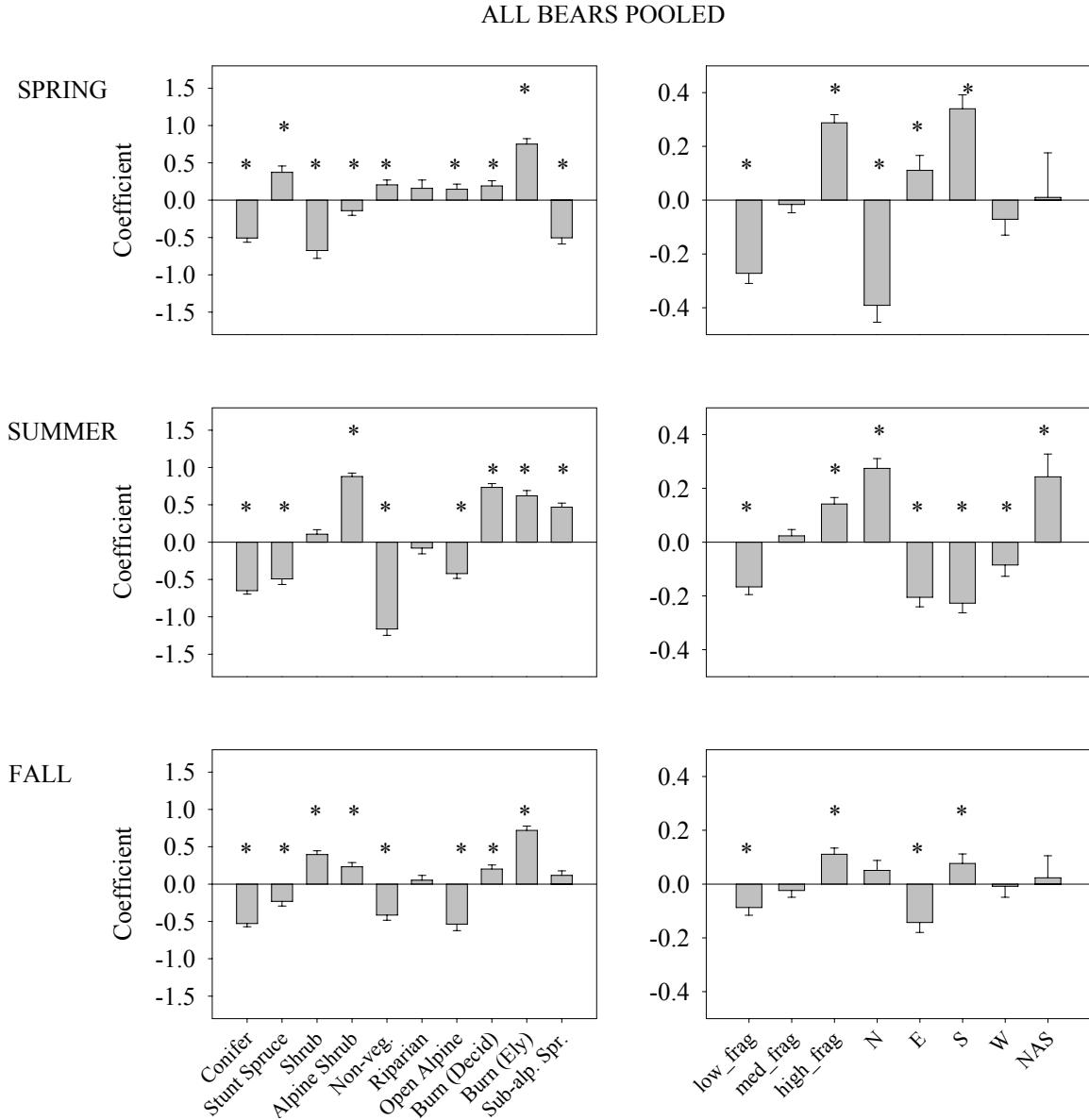
ALL BEARS POOLED

Figure 18. Seasonal selection patterns for habitat features (habitat class, fragmentation, aspect) by grizzly bears, pooled across years (2001-2004), in the Besa-Prophet study area of northern British Columbia. Coefficients >0.0 show selection and <0.0 show avoidance. * indicates significant seasonal coefficients as determined by 95% confidence intervals that do not encompass 0. Habitat classes are defined in Table 6. Low_frag = low fragmentation areas, med_frag = moderate fragmentation areas, high_frag = high fragmentation areas, N = north aspects, E = east aspects), S = south aspects, W = west aspects, NAS = no aspect, <1° slope.
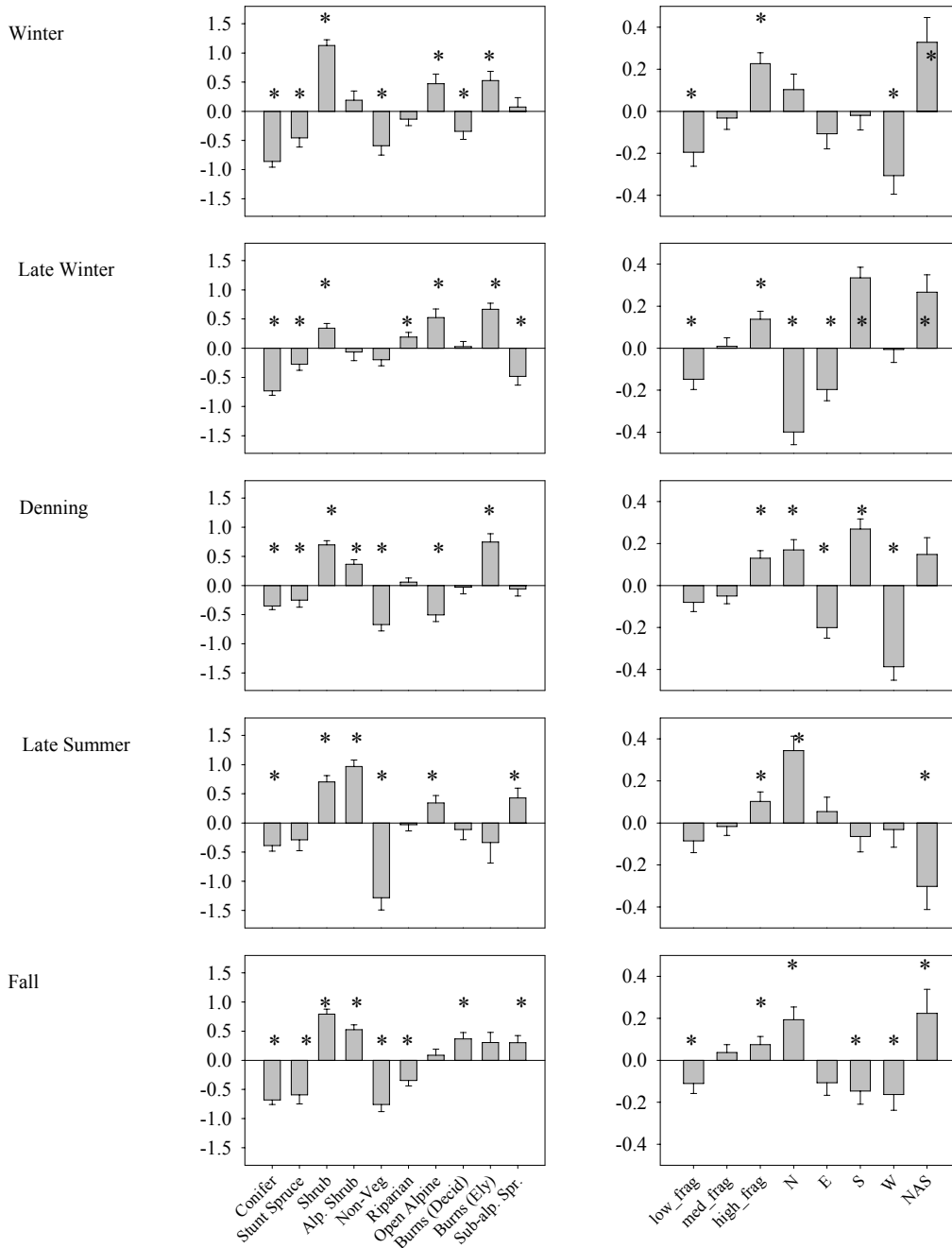
ALL WOLVES POOLED

Figure 19. Seasonal selection patterns for habitat features (habitat class, fragmentation, aspect) by <u>wolves</u>, pooled across years (2002-2003), in the Besa-Prophet study area of northern British Columbia. Coefficients >0.0 show selection and <0.0 show avoidance. * indicates significant seasonal coefficients as determined by 95% confidence intervals that do not encompass 0. Habitat classes are defined in Table 6. Low_frag = low fragmentation areas, med_frag = moderate fragmentation areas, high_frag = high fragmentation areas, N = north aspects, E = east aspects), S = south aspects, W = west aspects, NAS = no aspect, <1° slope.

Wolf packs used different elevation classes, probably in response to the distribution of classes within each home range and the seasonal movements of prey occupying each range. There was a preference for the use of low and moderate slopes, emphasizing the importance of ease of movement. The overall selection by wolves for high fragmentation areas (high habitat diversity) likely reflects both the expanded opportunity to encounter profitable ungulate prey, and the potential to randomly encounter alternative and supplemental prey items. We note that selection is relative to what is available on the landscape, and while some habitats may appear to be avoided, their use may still have some biological significance. For example, the general avoidance of conifer stands results from the wide distribution of this habitat class. These conifer stands, however, appear to provide important denning habitat for wolves in the Besa-Prophet area.

Mapping Selection Value: To generate mapped surfaces showing areas of relatively high selection value for predators, the coefficients for the variables within each seasonal model were multiplied by their appropriate input layers and summed. Because the values are relative to each data set (e.g., season) and species, they were then scaled between 0 and 1 and normalized for comparison between seasons. Each pixel within the mapped surface was given a relative value related to the relative selection value. All maps were plotted by quantiles of equal interval (0-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8, 0.8-1.0). These seasonal maps showing relative rankings of areas based on resource selection models indicate that areas that have the highest selection value for grizzly bears were on tops of ridges in spring, interspersed throughout the Besa-Prophet study area during summer, and on slopes bordering prominent valleys in fall (Fig. 20). Areas with characteristics that have highest selection value for wolves tended to be associated with major drainages during all seasons, as well as with eastern boreal flats during denning (Fig. 21).

In addition to the predator RSF models and digital surfaces for selection value, we developed prey RSF models in collaboration with other researchers (D. Gustine, A. Walker, M. Gillingham) in the Besa-Prophet area using data from GPS-collared caribou, Stone's sheep, and moose. GPS data were not available for elk, but we were able to use the habitat ratings for elk provided by Round River Conservation Studies in their Conservation Area Design of the Muskwa-Kechika Management Area (Round River Conservation Studies, unpublished data). 'Suitability landscapes' had been developed for both the growing and non-growing seasons for elk, with each polygon rated from 0-100 (worst to best habitat). These rankings were converted to a scale of 0-1 to match those of other prey layers. We then used the surfaces defining relative selection value for each of the 4 ungulate prey species as variables in seasonal RSF models to determine if 'prey benefit' was better at predicting habitat selection by grizzly bears and wolves than vegetative and topographic variables. The RSF models developed for bears and wolves using these prey variables, however, did not seem to perform as well as those based on the combination of habitat and topographic variables (Table 8). For the bears, none of the prey surfaces was even a significant coefficient in the models in summer and fall, presumably because the bears are not selective carnivores. For wolves, the significance of different prey coefficients varied with season, probably indicating that wolves can be opportunistic predators, not keying in on a specific ungulate per se. Further confounding this analysis, however, is the lack of data to quantify relative densities of ungulate species in the Besa-Prophet and to confirm that areas that we ranked 'best' (highest value) on the prey-benefit surfaces actually had those prey species there.
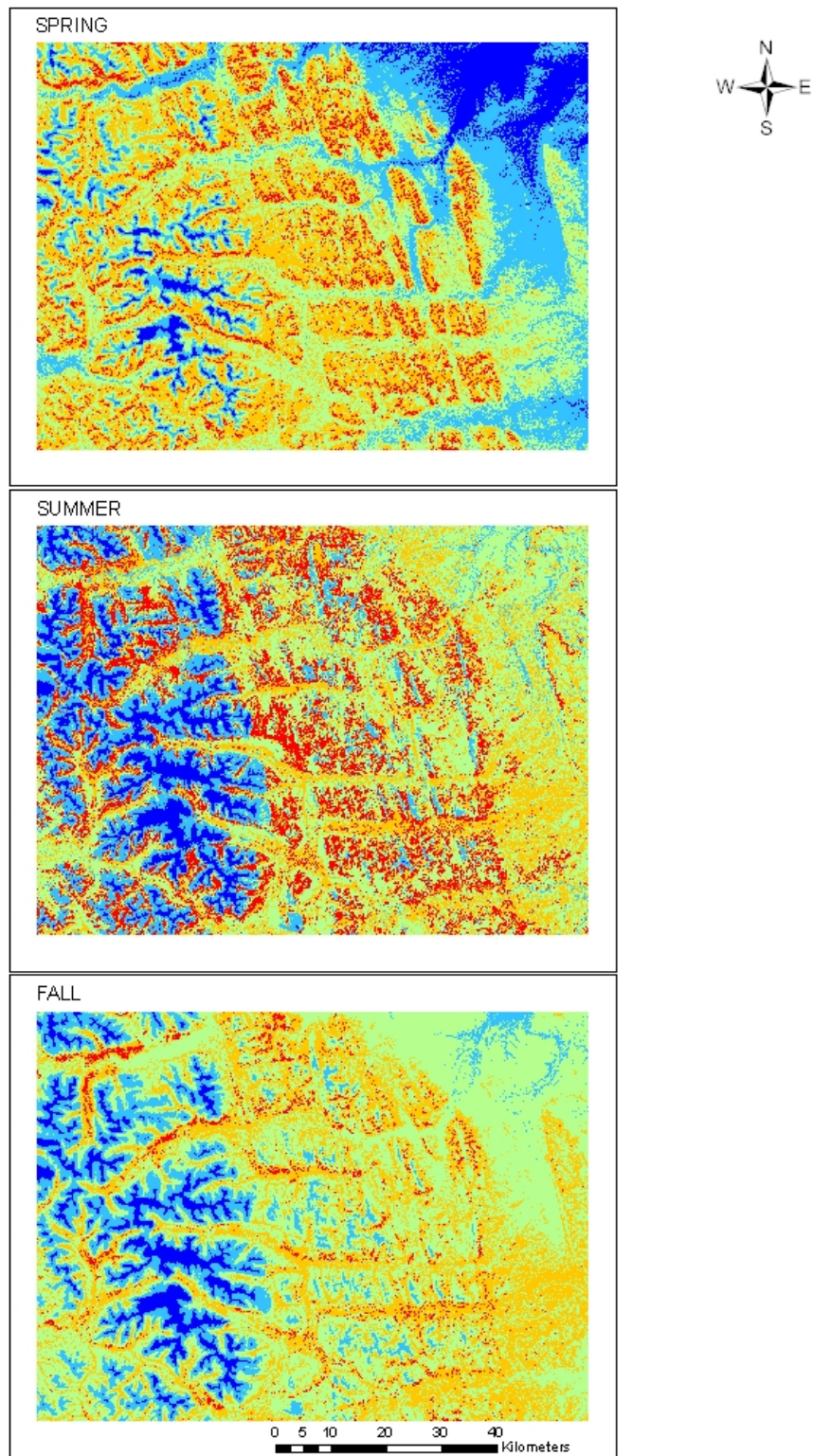
Figure 20. **Relative habitat selection values for <u>grizzly bears</u> by season in the Besa-Prophet study area based on attributes in resource selection models.**
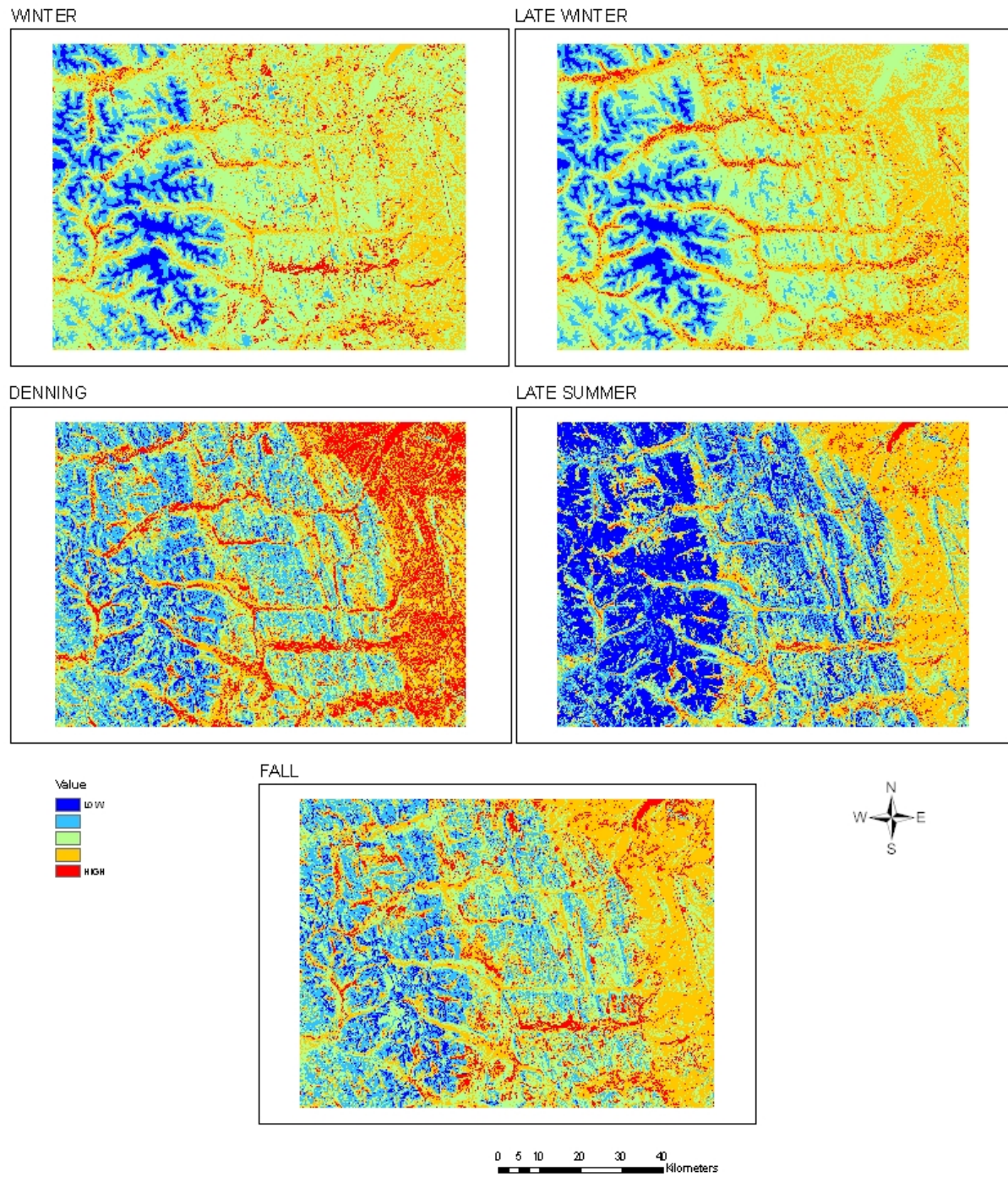
Figure 21. Relative habitat selection value for <u>wolves</u> by season in the Besa-Prophet study area based on attributes in resource selection models.

Habitat Use in Relation to Pre-tenure Plans

We compared the GPS use locations of the radio-collared grizzly bears in this study with the habitat suitability index (HSI) model developed by Ministry of Environment staff (Rod Backmeyer, Fort St John) for grizzly bears in spring. HSI models were not developed for wolves. The HSI grizzly bear model and HSI models developed for ungulates were based primarily on literature review and local accounts of high-use areas, and were developed to help rank the Besa-Prophet landscape using classes from 1 (high value) to 6 (low value) during pre-tenure planning processes. The Besa-Prophet Pre-tenure Plan incorporates a roll-up map from the HSI modelling efforts to be used across species. It categorizes habitats into zones, as defined by physical and topographical features (Table 9). We present our findings relative to both the Plan and suitability (HSI) models.

Table 9. Biophysical zones with wildlife value and management requirements in the pre-tenure planning areas of the Muskwa-Kechika Management Area (British Columbia Ministry of Sustainable Resource Management 2004). Not all biophysical zones are found in each plan area.

Code	Pre-tenure Biophysical Zone	Description
LEW	Wetlands – Low Elevation	Concentrated in valley bottoms and lowland areas. Consists of seasonal and year-round moisture saturated soils; watercourses and coniferous/deciduous forest patches can be dispersed throughout the wetland. Contains summer and critical winter habitat for moose, critical caribou habitat and high fisheries values. Various other wildlife species such as raptors, birds, rodents, furbearers, amphibians and reptiles inhabit this zone. High fisheries values are also found within this zone. The wetland zone is important for maintaining water quality and quantity.
HEW	Wetlands – High Elevation	Located in mid to high elevation valley bottoms. Consists of seasonal and year-round moisture saturated soils. Minimal if any coniferous forest within or adjacent to this zone. Contains summer moose habitat, critical caribou winter habitat and year-round furbearer habitat.
MOS	Mosaic	Contains a mixture of forested and open habitats interspersed with wetlands, meadows, and forested lowlands and hills. The zone provides a mixture of foraging and security cover for ungulates. It contains critical winter habitat for moose and caribou; as well the older forested stands provide habitat for furbearer species.
IS	Incised Stream	Consists of steep-sloped stream-banks with flat upland areas. Important values include riparian habitat, fish, wildlife movement corridor and water quality and quantity. A mixture of ungulate security and foraging cover primarily on the uplands with a minor component on the steep slopes. Critical moose and elk winter habitat on the upland region.
MWA	Warm Aspect Forest (moderate <45% slope)	Consists of both extensive tracks of coniferous tree species and open forested habitat on south-west aspect slopes of gentle to moderate sloped terrain and contains areas of old growth. Depending on the pre-tenure plan area, this zone can provide critical winter elk habitat depending on snow depths. Older forest stands are important year round habitat for a variety of furbearers, while younger willow stands provide critical winter moose habitat. Spring grizzly bear habitat is found on steeper slopes that experience early snowmelt.
CAF	Cool Aspect Forest (<45% slope)	Consists of wet and cool forests that occur on gentle to moderately sloped terrain. Some forest stands may be interspersed with smaller

		interconnected wetland complexes. Older forested stands contain critical winter caribou habitat and important year round habitat for a variety of furbearer species, while shrub areas provide critical moose habitat. Pockets of permafrost are found on north slopes in this habitat type. This zone is a wildlife movement corridor.
SWA	Steep Slope Warm Aspect (>45% slope)	Consists of open and forested habitat on steep, southwest facing slopes. A variety of terrain features and habitat types are found in this zone including: alpine meadows, old growth forested stands, parkland, young forests, cliffs, rock outcrops and talus slopes. Furbearers are found in this zone. Steeper slopes are primarily open and provide critical winter Stone's sheep habitat and important year round goat habitat. This zone also provides elk and moose winter habitat and birthing and rearing areas for Stone's sheep, mountain goat and caribou. Higher zone elevations have lower biological productivity.
SCA	Steep Slope Cool Aspect (>45% slope)	Consists of open and forested habitat on steep, northeast facing slopes, with pockets of permafrost found on north slopes. A variety of terrain features and habitat types are found in this zone including: alpine meadows, old growth forested stands, parkland, young forests, cliffs, rock outcrops and talus slopes. This zone is primarily mountainous terrain, highly visible throughout the plan area. Critical winter Stone's sheep habitat borders a large portion of this zone. Steep slopes offer security habitat for caribou, elk and moose. This zone is important as a wildlife movement corridor, for Grizzly bear denning and furbearer habitat. Higher zone elevations have lower biological productivity.
HEP	High Elevation Plateau	Consists of high elevation plateaus, often surrounded by steep open and treed terrain. The plateaus are primarily open and consist of vegetation types that are particularly sensitive to disturbance due to low biological productivity, shallow soils and low moisture and nutrient conditions. Isolated pockets of coniferous forest are found on some plateaus. These areas are prone to strong winter winds and provide critical winter caribou habitat especially during winters of high snowfall.
FFP	Forested Floodplain	Low elevation zone and adjacent to the River Zone. Forested Floodplain zone width is variable, dependent on valley bottom topography. Forest cover is dominated by conifers. May contain stable side/back water channels. Provides foraging, security and thermal cover for a diverse range of wildlife, including: elk, moose, bear, and a variety of furbearers, raptors and songbirds.
RFP	Major River Floodplain	A low elevation zone characterized by braided streams bordered by a multi-layered forest canopy and understory. Waterflow varies throughout the year with peak flows generally occurring late spring and early summer. Year to year, the active water channel can change location within the floodplain. The zone provides foraging, security and thermal cover for a diverse range of wildlife, including: elk, moose, bear, furbearers, raptors, and songbirds. High fisheries values exist in this zone.
G	Glacier	Consists of areas that have year-round accumulations of ice and snow that exclude the establishment of any vegetation. During summer months, various ungulate species may use accessible portions of glaciers to mitigate high ambient temperatures and/or to seek a reprieve from blood sucking insects.
R	River	Stream flow varies throughout the year with peak flows generally occurring late spring and early summer. Year to year, the active channel can change location within this zone. High fisheries values exist in this zone. May contain forested islands.
RB	River Breaks	Consists of actively eroding unstable steep-sloped banks of various heights and lengths bordering watercourses.

Bears*:*

      Grizzly bears collared in our study tended to have home ranges in the western portion of the Besa-Prophet Pre-tenure Planning Area (Fig. 22). Most of the GPS locations (~39%) recorded for grizzly bears were in habitat suitability class 3, although bears used classes 2 and 4 almost equally (~25% each, Table 10). Habitat class 4 occurred most frequently on the landscape (~40% of the area), but bears selected for classes 2 and 3 (~65% of locations) above what was available (46%, Table 10, Fig. 23). The British Columbia Ministry of Environment HSI model assumed that bears respond to areas of spring green-up, and evaluated those areas most highly. In early spring after denning, more than 80% of the GPS locations from collared bears were on steep slopes with warm or cool aspects (SWA, SCA) (Table 10, Fig. 23). There was strong selection for the warm aspects.

Table 10. Pre-tenure zones and final habitat suitability (FS) classes as a percentage of the Besa-Prophet Pre-tenure Planning Area compared to locations used by GPS-collared grizzly bears in the Plan Area in spring.

Pre-tenure Zone	% of Area	# GPS Locations	% Use
CAF	15.49	106	5.75
HEP	4.37	53	2.87
HEW	2.33	39	2.11
IS	1.39	10	0.54
LEW	2.96	20	1.08
MOS	1.31	37	2.01
MWA	10.01	62	3.36
RFP	1.35	5	0.27
SCA	33.98	628	34.04
SWA	26.32	885	47.97
		n = 1845	
FS Class	**% of Area**	**# GPS Locations**	**% Use**
1	1.37	1	0.05
2	15.64	482	25.93
3	30.42	721	38.78
4	39.96	457	24.58
5	6.33	64	3.44
6	6.28	134	7.21
		n = 1859	

Grizzly Bear Spring Locations

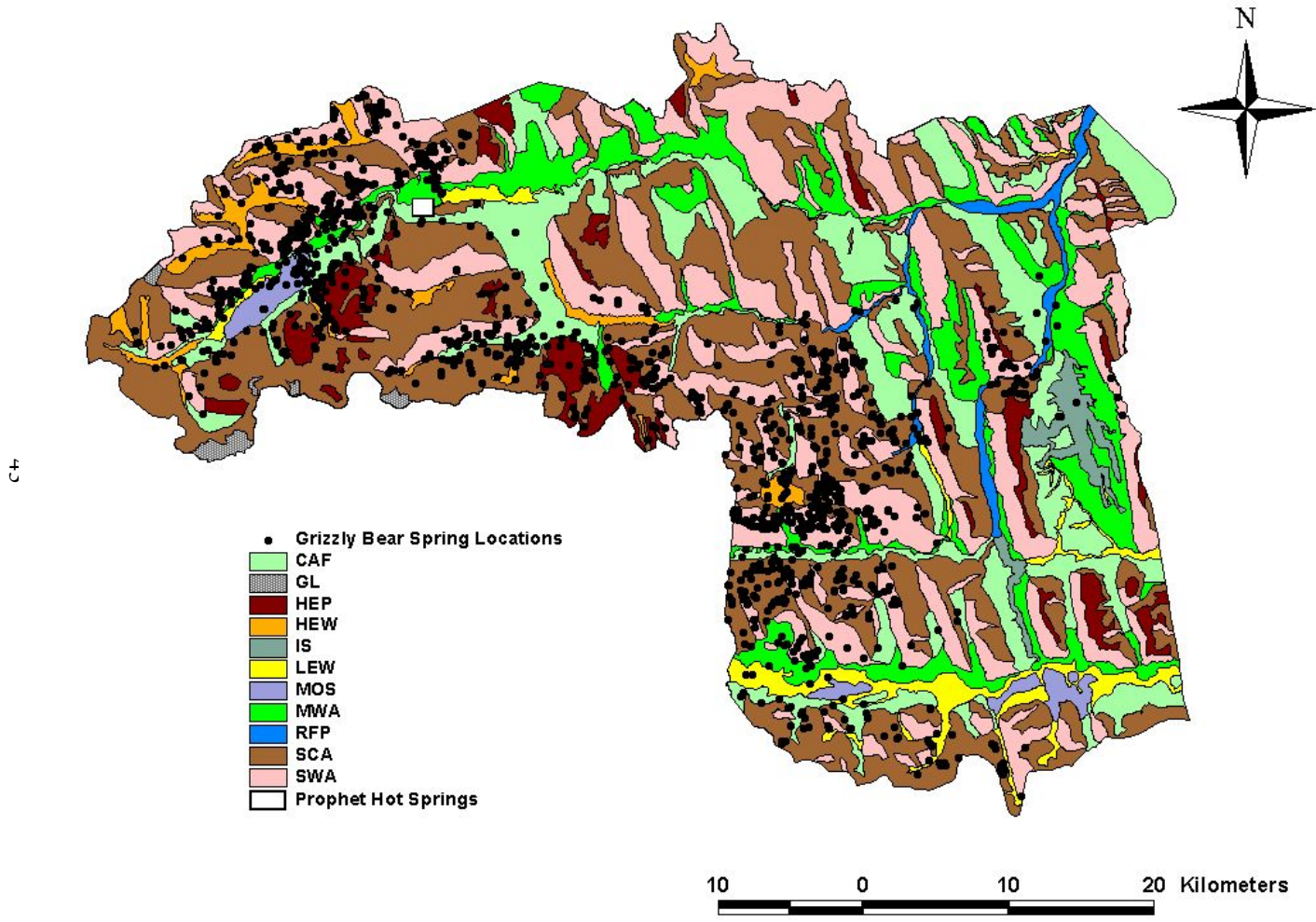|	
	CAF
	GL
	HEP
	HEW
	IS
	LEW
	MOS
	MWA
	RFP
	SCA
	SWA
	Prophet Hot Springs

Figure 22. Spring GPS locations of radio-collared <u>grizzly bears</u> in the Besa-Prophet Pre-tenure Planning Area, in relation to zones designated in the Besa-Prophet Pre-tenure Plan.
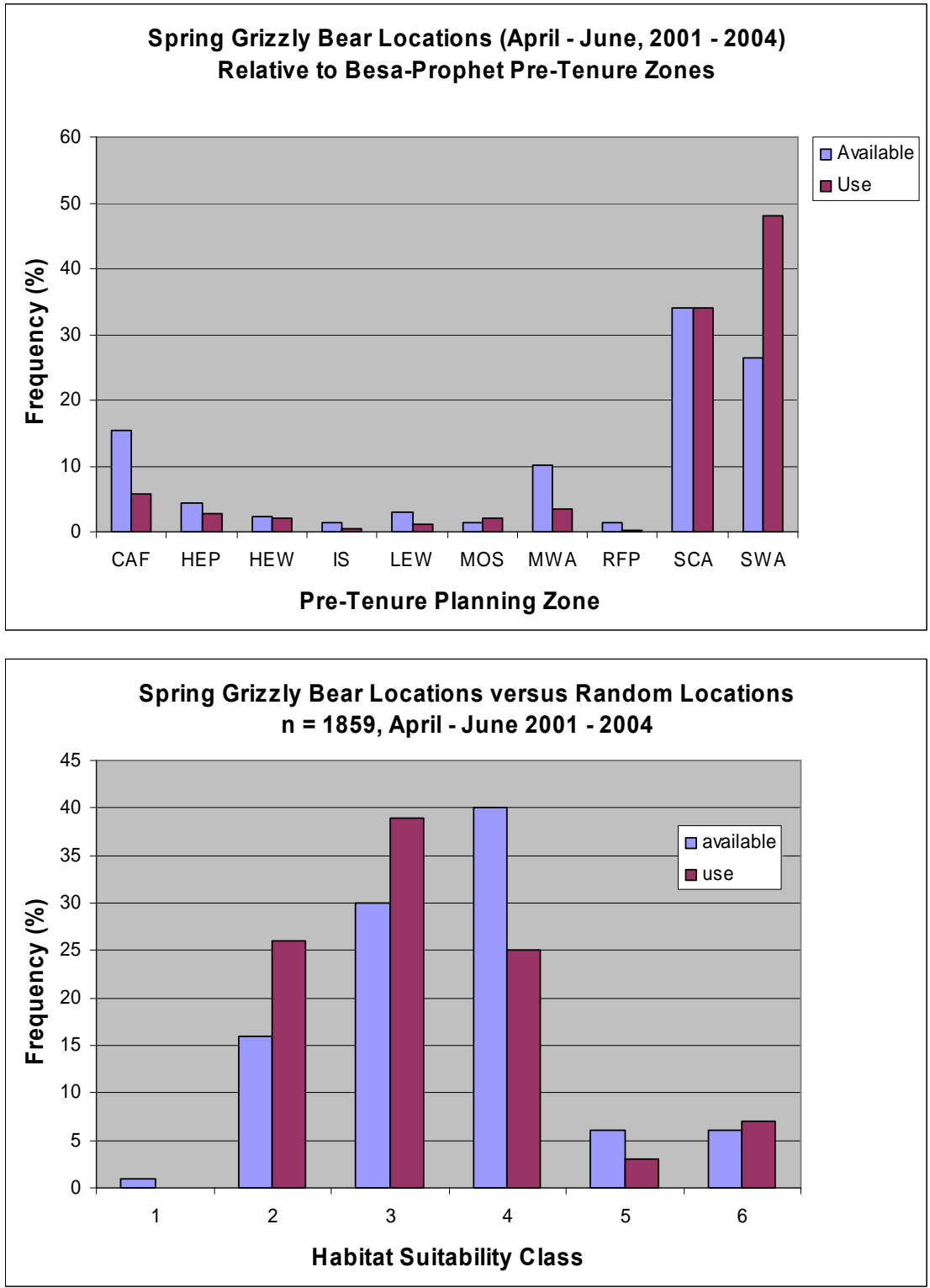
Figure 23. Spring GPS locations of radio-collared <u>grizzly bears</u> in relation to zones designated in the Besa-Prophet Pre-tenure Plan and availability of spring habitat suitability classes (developed by BC Ministry of Environment, Fort St John, BC).

Wolves*:*

Wolves collared in our study generally concentrated their use along and adjacent to rivers and valley bottoms, with movements from there into neighbouring valleys and onto finger ridges (Fig. 24). Wolves tended to use the low and high elevation wetland zones (LEW, HEW) and the moderate slopes with warm aspect (MWA) relatively more (~37% use) than was available on the landscape (~15% of the area) (Table 11, Fig. 25). The steep slope warm and cool aspects (SWA, SCA) and the cool aspect forests (CAF) were also important habitats for wolves in winter (~56% of use locations).

Table 11. Pre-tenure zones as a percentage of the Besa-Prophet Pre-tenure Planning Area compared to locations used by GPS-collared <u>wolves</u> in the Plan Area in winter.

Pre-tenure Zone	% of Area	# GPS Locations	% Use
CAF	15.49	257	15.11
HEP	4.37	34	2.00
HEW	2.33	125	7.35
IS	1.39	13	0.76
LEW	2.96	265	15.58
MOS	1.31	31	1.82
MWA	10.01	251	14.76
RFP	1.35	19	1.12
SCA	33.98	320	18.81
SWA	26.32	380	22.34
NA (Prophet Hot Springs)	0.09	6	0.35
		$n = 1701$	

No habitat suitability models have been developed for wolves in the Besa-Prophet area; so comparisons with actual use data were not made. Figure 26, however, shows the proportion of wolf GPS locations relative to the availability of habitat suitability classes developed for the major ungulate prey species in winter. The number of GPS locations recorded as a percentage of the number of attempted GPS locations for the wolf GPS collars was relatively low (~44%, range = 19-85%, $n = 25$); in contrast to mean fix success rate of 67% (SE = 12%, range = 26-87%, $n = 13$) in bears, presumably because wolves move closer to the ground and obstacles, including den sites, prohibit satellite signal connection. Consequently, our portrayal of time spent in different classes could be biased (as could the data from the ungulates). Nonetheless, our findings indicate that wolves tended to use the high suitability areas for elk and moose more than would be randomly encountered on the landscape (Fig. 26). Selective use of high-value Stone's sheep and caribou habitats across the winter was not apparent.
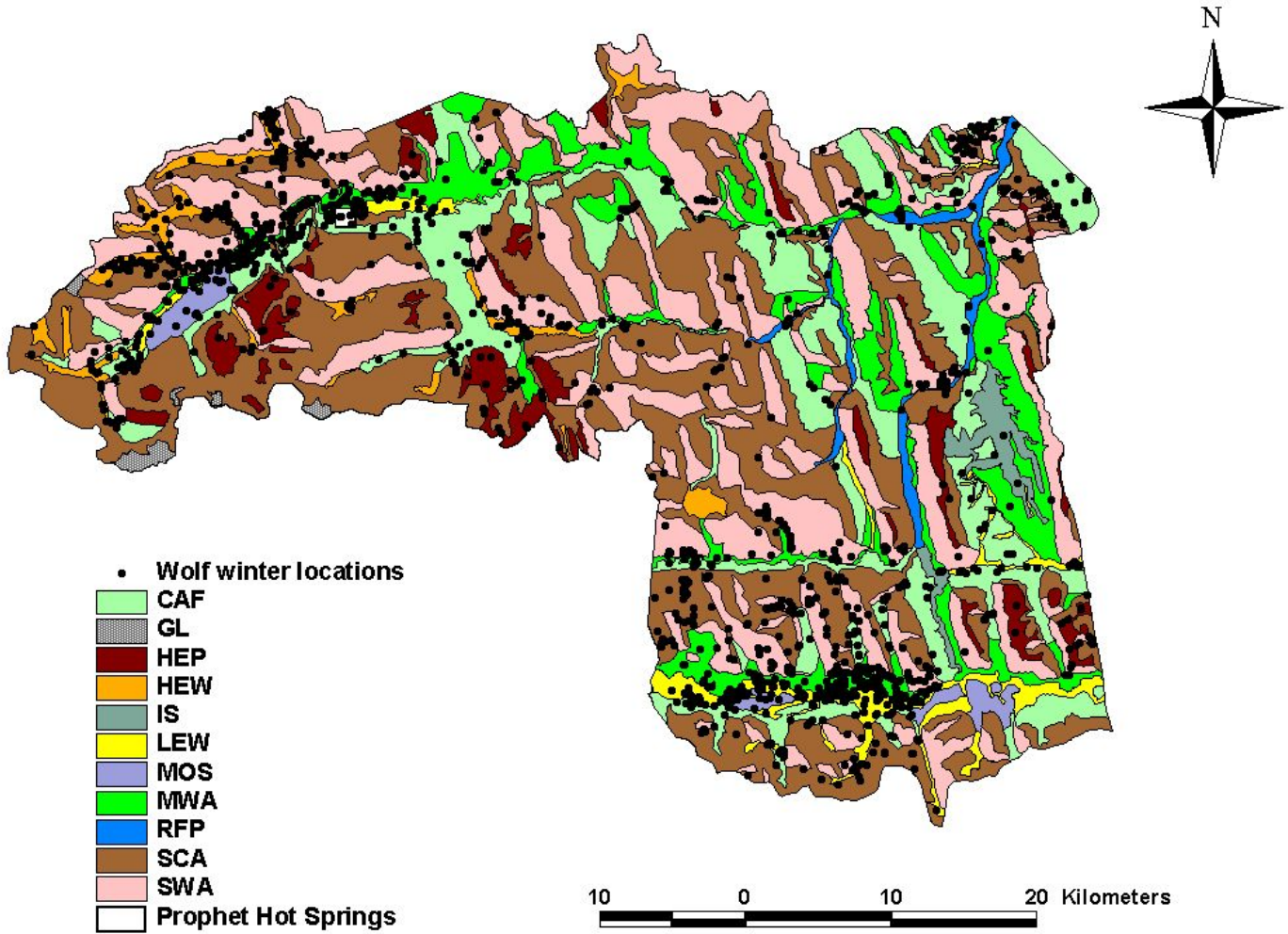
Figure 24. Winter GPS locations of radio-collared <u>wolves</u> in the Besa-Prophet Pre-tenure Planning Area, in relation to zones designated in the Besa-Prophet Pre-tenure Plan.
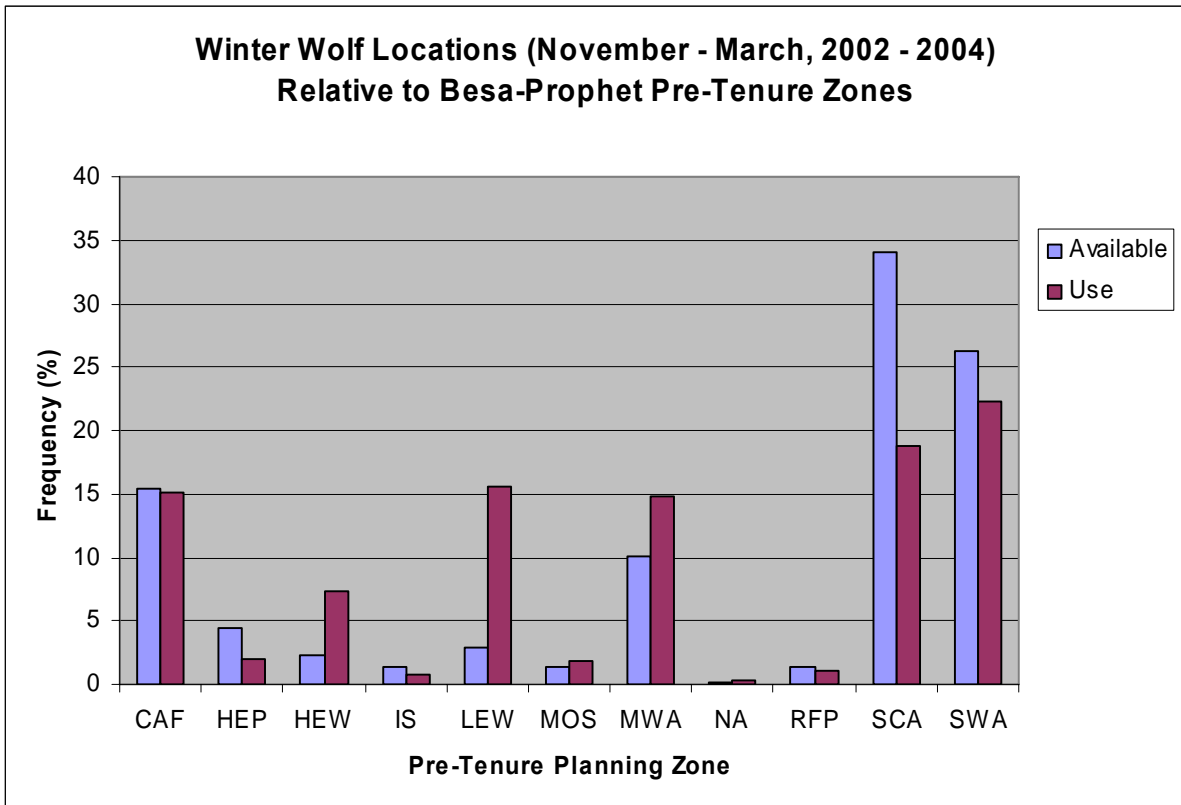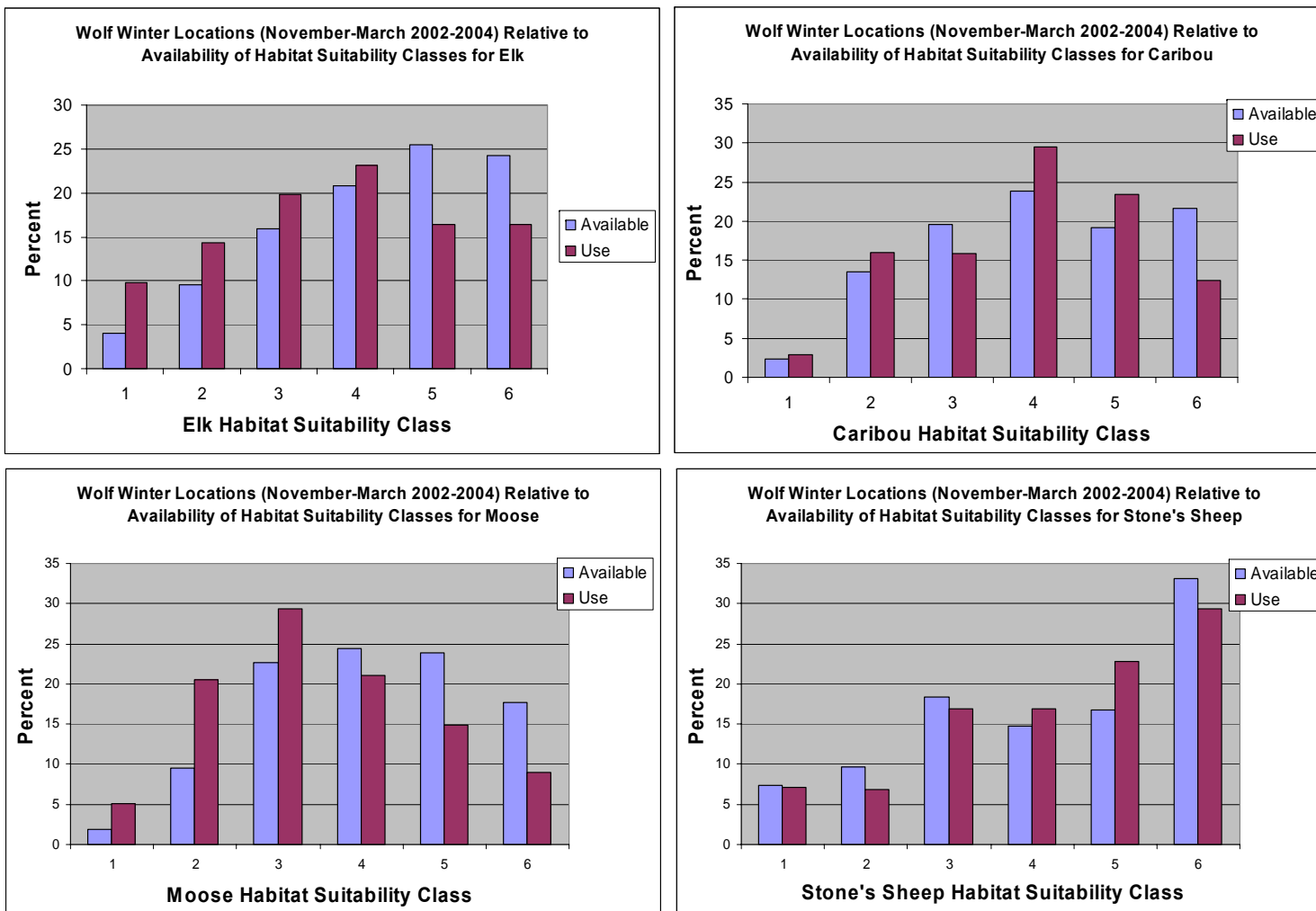
Figure 25. Winter GPS locations of radio-collared <u>wolves</u> in the Besa-Prophet Pre-tenure Planning Area, in relation to zones designated in the Besa-Prophet Pre-tenure Plan.

Figure 26. Winter GPS locations (*n* = 1604) of radio-collared <u>wolves</u> in the Besa-Prophet Pre-Tenure Planning Area, in relation to availability of winter habitat suitability classes for elk, caribou, moose and Stone's sheep (developed by BC Ministry of Environment, Fort St John, BC).

Habitat Use in Relation to Terrestrial Ecosystem Mapping

Seasonal habitat use by grizzly bears and wolves also was examined in relation to biogeoclimatic ecosystem classification (BEC) zones and site series, as used in Terrestrial Ecosystem Mapping (TEM), which is commonly referred to in provincial habitat studies (ftp://ftp.env.gov.bc.ca/dist/wis/tem/mapcodes_jan2003.xls). Site series were grouped by variants, but we did not include site modifiers in the overall groupings for this analysis. TEM classes for the Besa-Prophet area are presented in Table 12.

Table 12. Vegetative communities identified by site series during Terrestrial Ecosystem Mapping (TEM) in the Besa-Prophet area.

Site Series	Additional site description
Mountain arnica-Subalpine daisy meadow	Lower to upper meso slopes and level, deep, medium-textured soils
Talus	Angular rock fragments of any size accumulated at the foot of steep rock slopes as a result of successive rock falls. It is a type of colluvium
Mountain avens-Arctic lupine	Significant slope, warm aspect; shallow soils over bedrock, coarse-textured soils; herb-dominated community
Arctic lupine-Step moss	Gentle slope, deep medium-textured soils
Grey-leaved willow-Scrub birch	Gentle slope; deep, medium-textured soils
Willow-Crowberry	Significant slope, cool aspect; deep medium-textured soils
Talus	Angular rock fragments of any size accumulated at the foot of steep rock slopes as a result of successive rock falls. It is a type of colluvium
Grey-leaved willow-Scrub birch	Gentle slope; deep, medium-textured soils
Willow-Sitka valerian	Gentle slopes; deep, medium-textured soils, moist shrub units
Mountain arnica-Subalpine daisy meadow	Lower to upper meso slopes & level, deep, medium-textured soils
Mountain avens-Arctic lupine	Significant slope, warm aspect; shallow soils over bedrock, coarse-textured soils; herb-dominated community
Mountain avens-Arctic lupine	Significant slope, warm aspect; shallow soils over bedrock, coarse-textured soils; herb-dominated community
Juniper-Wildrye	Significant slope, warm aspect, deep, medium-textured soils
Willow-Bog birch-Sedge	Organic wetland
Willow-Step moss	Gentle slope; deep medium-textured soils
Scrub birch-Bluejoint	Significant slope, cool aspect; deep medium-textured soils
Willow-Crowberry	Significant slope, cool aspect; deep medium-textured soils
Arctic lupine-Step moss	Gentle slope, deep medium-textured soils
Shrubby cinquefoil-Horsetail	Gentle slope, deep, coarse-textured soils
Grey-leaved willow-Scrub birch	Gentle slope; deep, medium-textured soils
Juniper-Wildrye	Significant slope, warm aspect, deep, medium-textured soils
Willow-Crowberry	Significant slope, cool aspect; deep medium-textured soils

Willow-Mountain sagewort	Significant slope; cool aspect; deep, meduim-textured soils; shrub-dominated community
Scrub birch-Bluejoint	Significant slope, cool aspect; deep medium-textured soils
Grey-leaved willow-Scrub birch	Gentle slope; deep, medium-textured soils
Fescue-Arctic lupine	Upper, crest position; shallow, rapidly-drained, medium-textured soils
Mountain avens-Arctic lupine	Significant slope, warm aspect; shallow soils over bedrock, coarse-textured soils; herb-dominated community
Willow-Sitka valerian	Gentle slopes; deep, medium-textured soils, moist shrub units

GPS locations of grizzly bears and wolves between 2001 and 2004 were pooled by season, and only those TEM classes with ≥1% of the total overall locations were included in the frequency distributions. In Figures 27-31, E refers to EMR (Eastern Muskwa Ranges), and M refers to MUF (Muskwa Foothills) ecosections. All classes are within the spruce-willow-birch (SWB) sub-zone, unless prefixed with AT (alpine tundra) or BWBS (boreal white and black spruce), and separated between the mk (moist cool) and mks (moist cool scrub) variants.

Grizzly Bears: Grizzly bears frequented particular biogeoclimatic zones, and this use varied by season. Across seasons and years, most use locations occurred in Grey-leaved willow-Scrub birch communities within the ecosystem. Additional high use occurred in Willow-Sitka valerian (Muskwa Foothills) and Mountain avens-Arctic lupine communities of the Eastern Muskwa Ranges (Fig. 27). Within seasons, these classes were also most used in spring (Fig. 27) and summer (Fig. 28). In fall, bears concentrated on the Grey-leaved willow-Scrub birch areas (Fig. 28).

Wolves: Across all seasons, wolves were also found most frequently in Grey-leaved willow-Scrub birch communities of the Muskwa Foothills, as indexed by the highest percentage of GPS locations from collared individuals (Fig. 29). In winter, Grey-leaved willow-Scrub birch areas were important in both the Muskwa Foothills and Eastern Muskwa Ranges, in addition to Willow-Crowberry (Eastern Muskwa Ranges) and Willow-Bog birch-Sedge (Muskwa Foothills). By late winter, the highest percentage of locations was in Grey-leaved willow-Scrub birch (Fig. 30). Currant-Horsetail was the most frequented class during denning, whereas Willow-Bog birch-Sedge was highest in late summer. During fall, wolves were distributed across numerous communities, with most locations in Willow-Bog birch-Sedge, Willow-Sedge wetland, and Grey-leaved willow-Scrub birch of the Muskwa Foothills, and Mountain arnica-Subalpine daisy and Mountain avens-Arctic lupine in the Eastern Muskwa Ranges (Fig. 31).

Because of the relatively large extrapolation of data between TEM plots across the Besa-Prophet landscape, Figures 27-31 should be viewed with caution. In addition, highest use in particular communities was not a very high percentage of all observations if animals were found in numerous TEM classes. Further, the communities used should really be considered in relation to what is available. We believe that a habitat map generated from and validated for remote-sensing imagery is a more applicable tool to define habitats in our study area than the large mapped interpolation of habitat information between actual TEM plots.
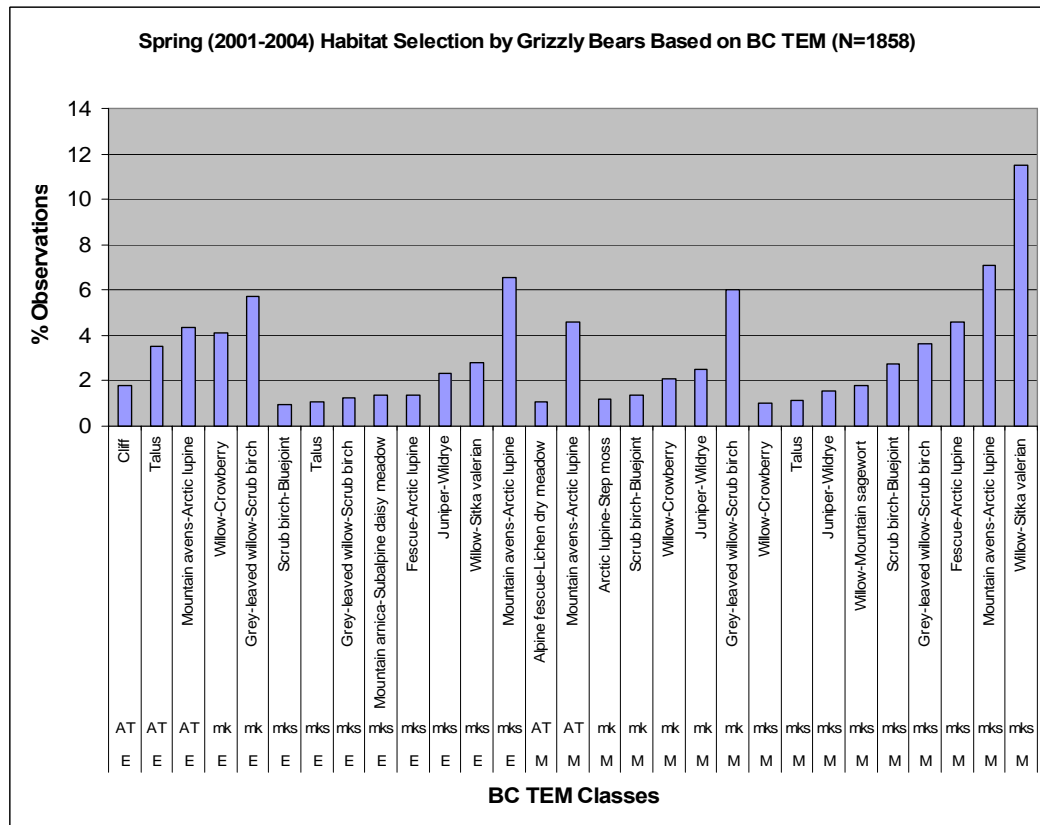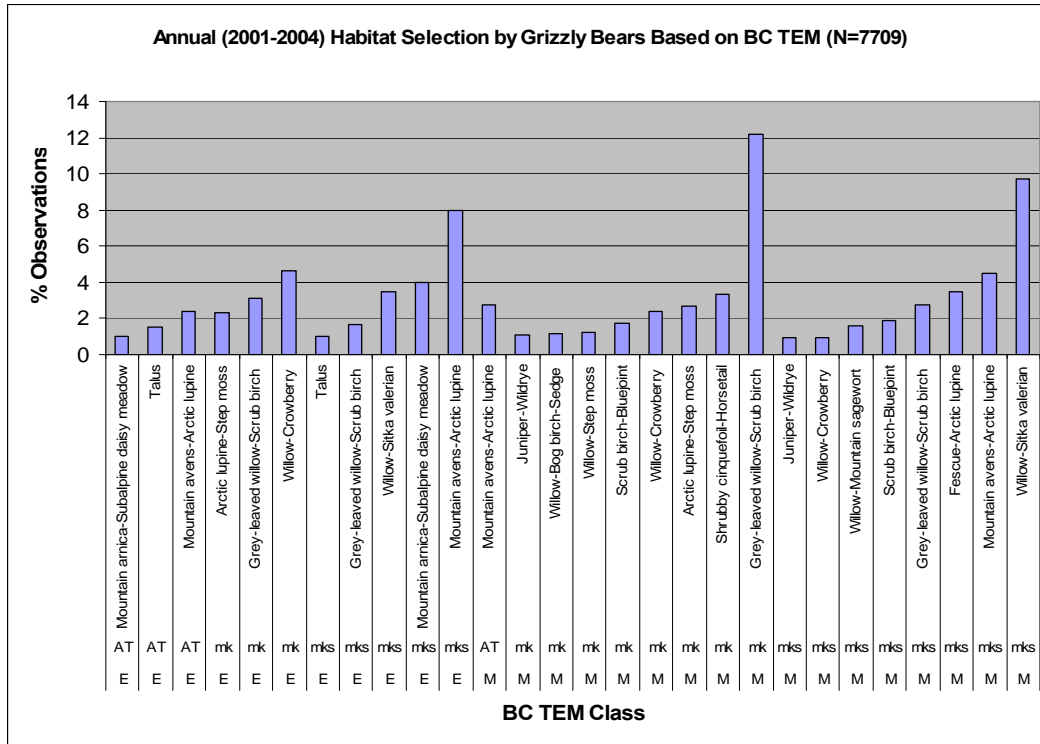
Figure 27. Grizzly bear annual and spring habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2001-2004.
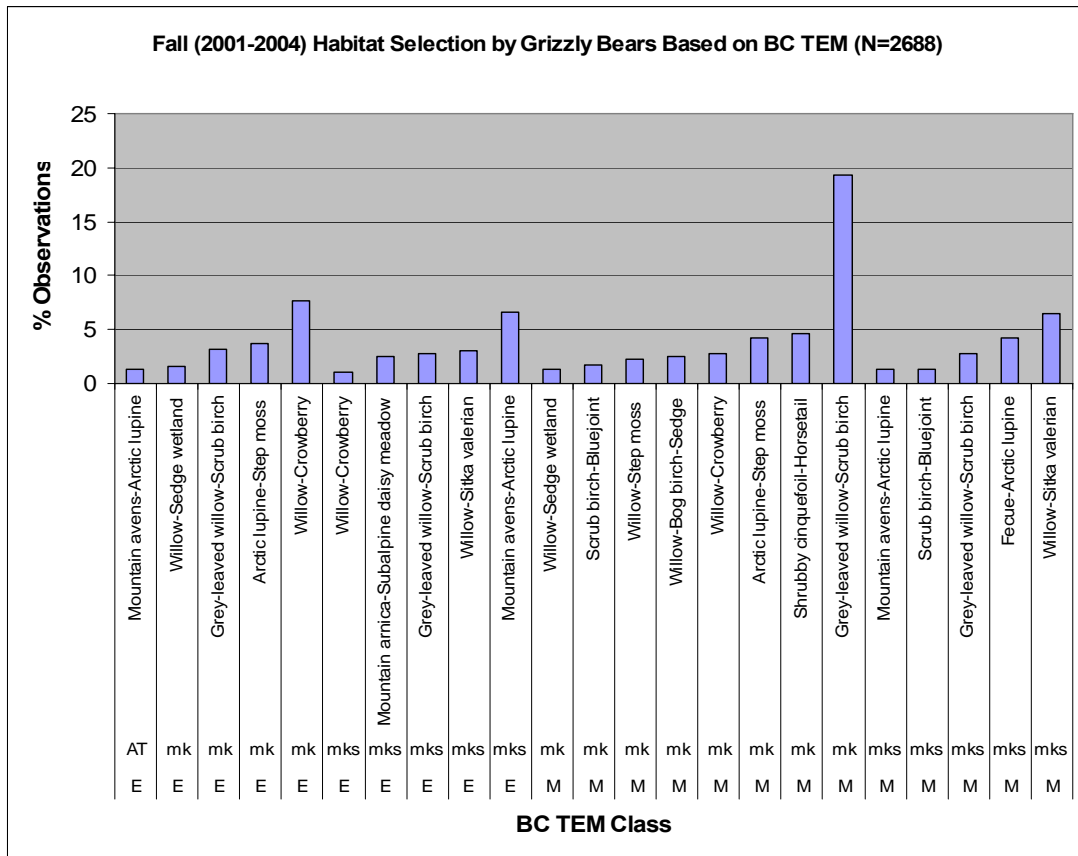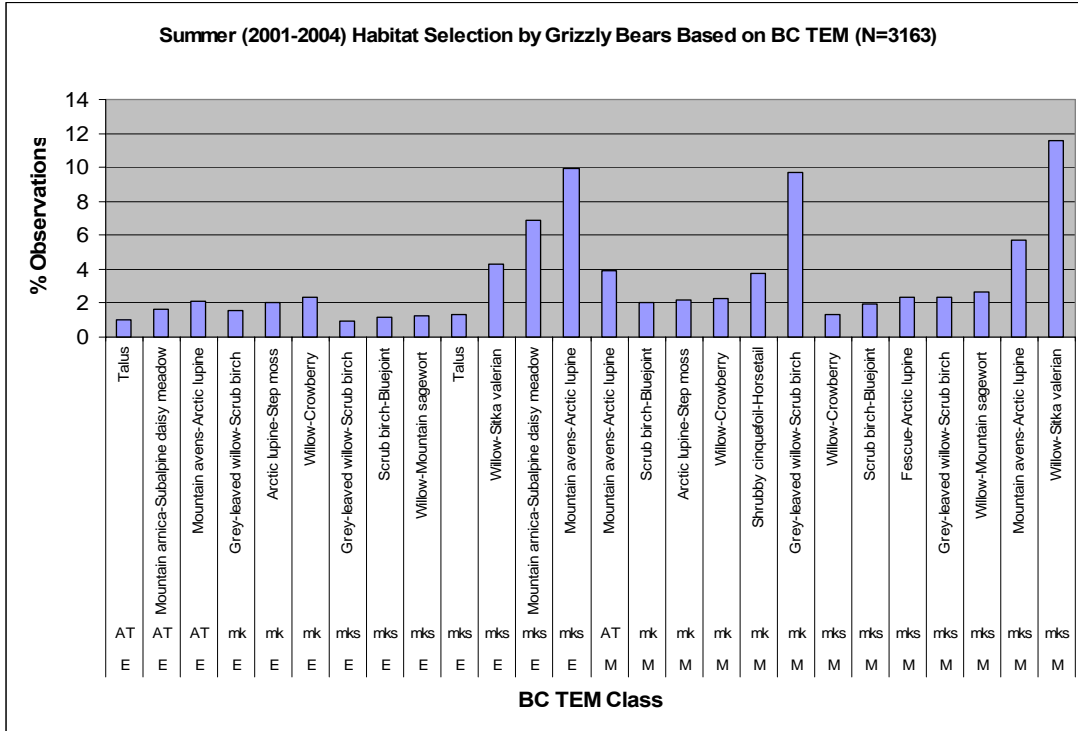
Summer (2001-2004) Habitat Selection by Grizzly Bears Based on BC TEM (N=3163)

Fall (2001-2004) Habitat Selection by Grizzly Bears Based on BC TEM (N=2688)

Figure 28. Grizzy bear summer and fall habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2001-2004.
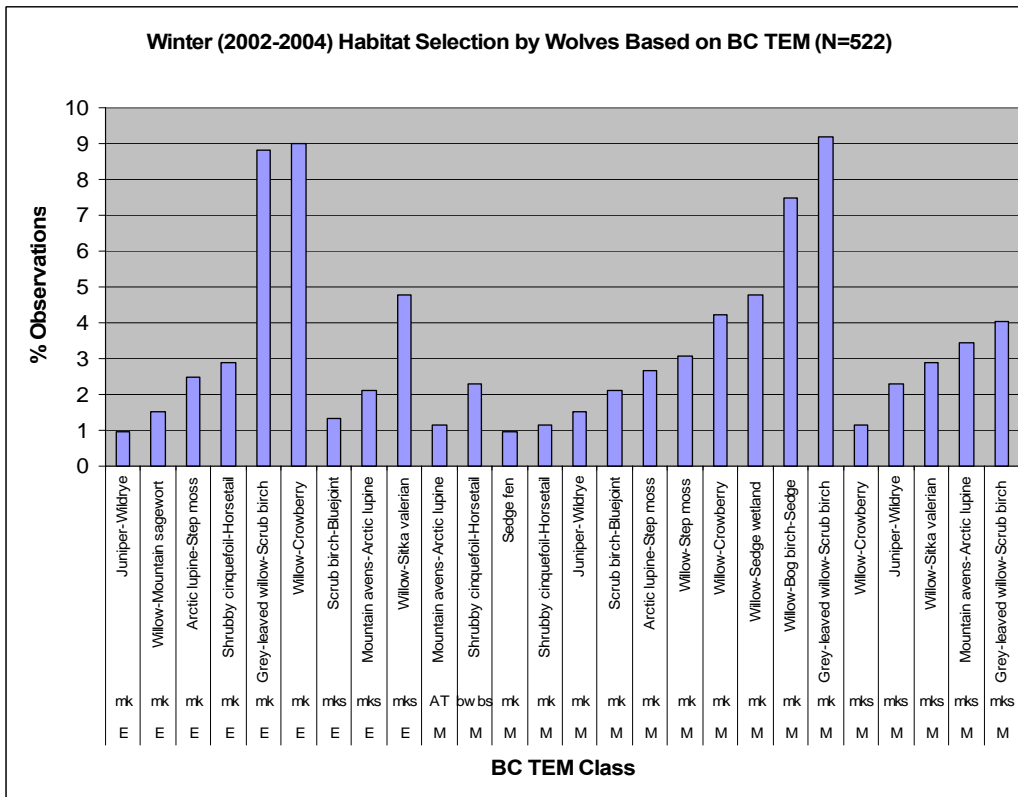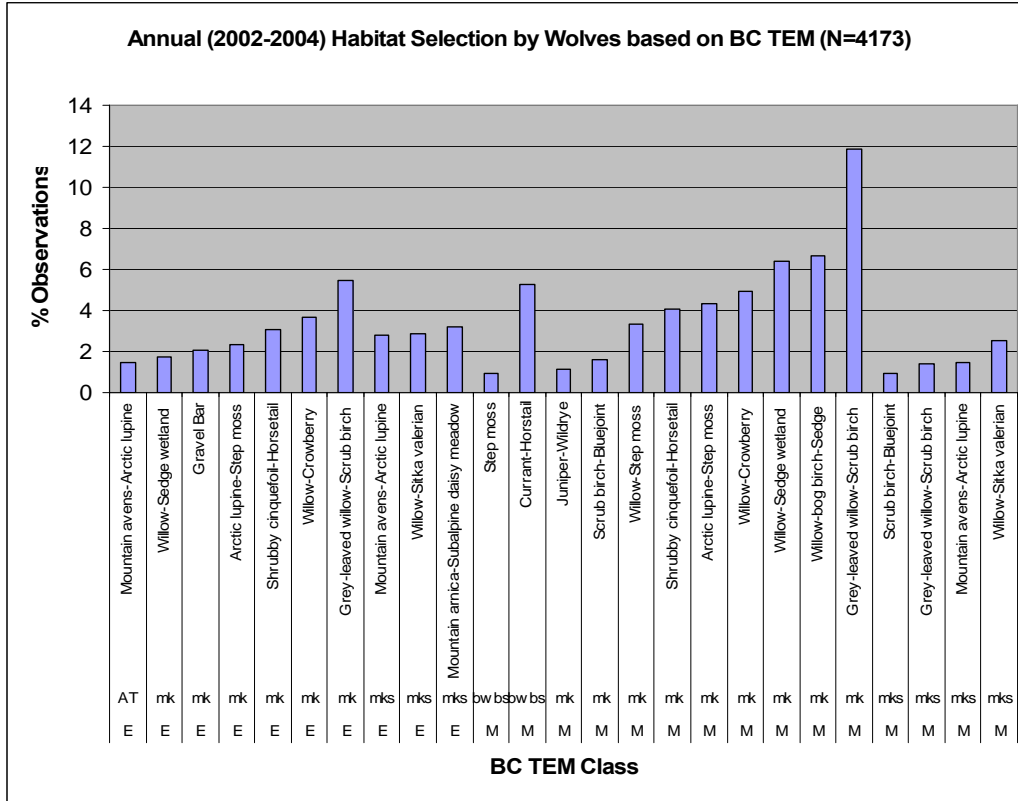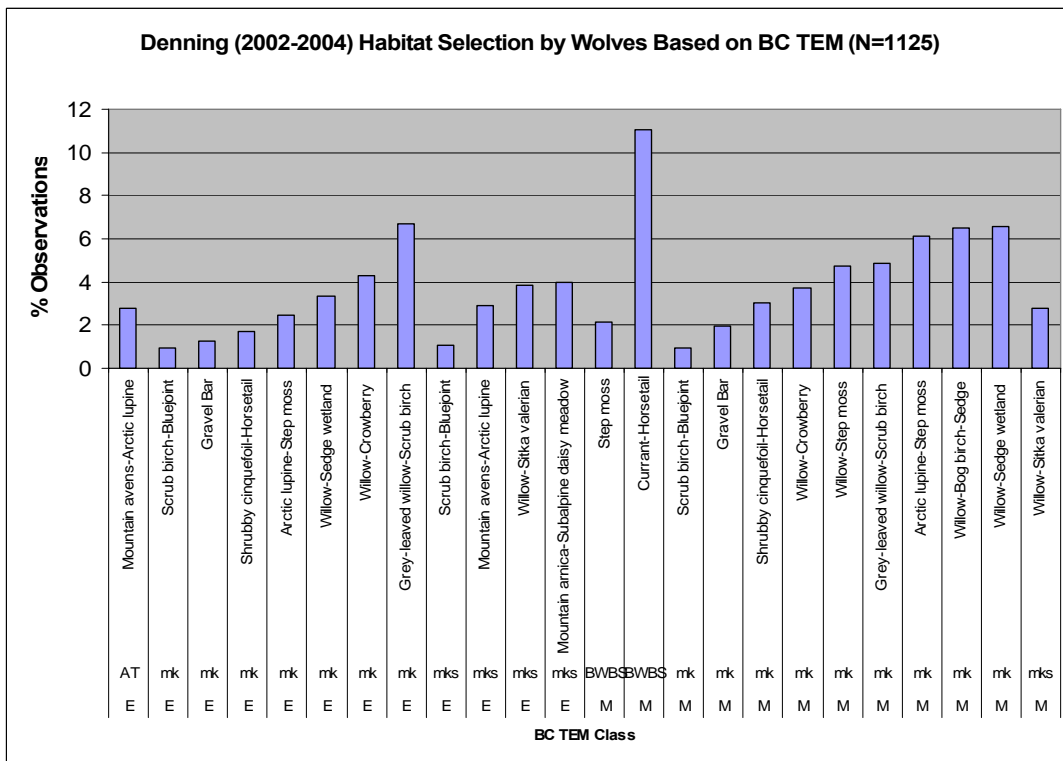
Figure 29. Wolf annual and winter habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2002-2004.
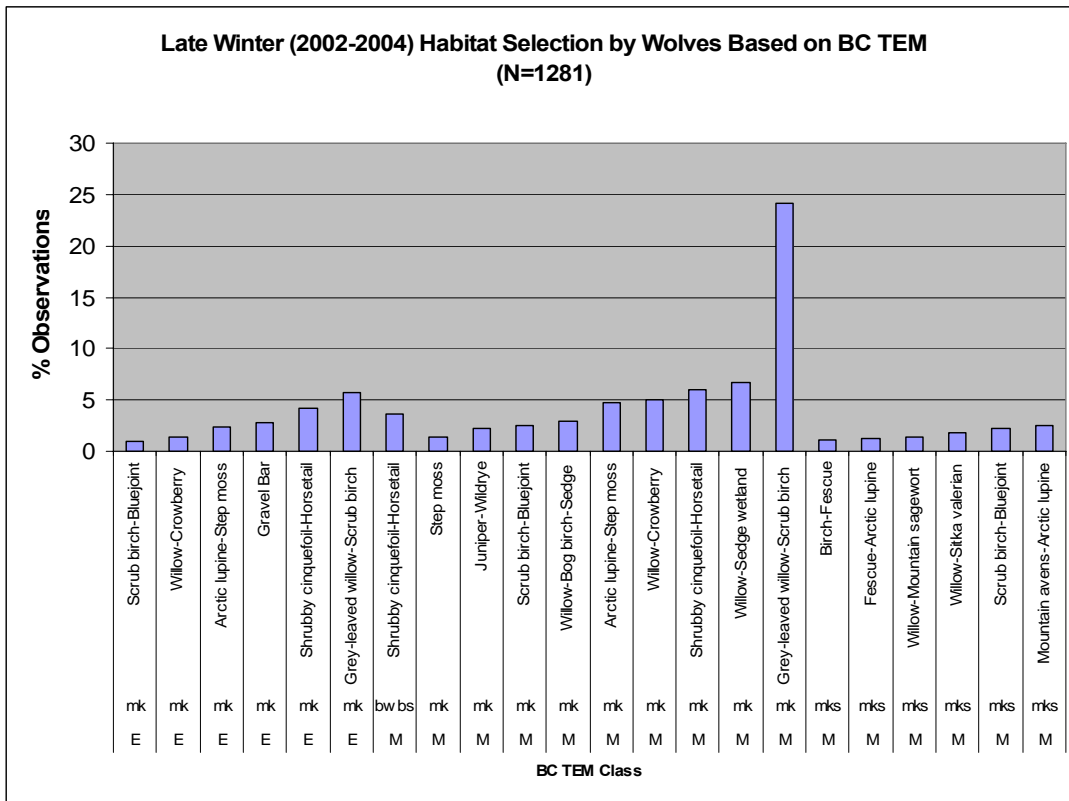
Figure 30. Wolf late winter and denning habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2002-2004.
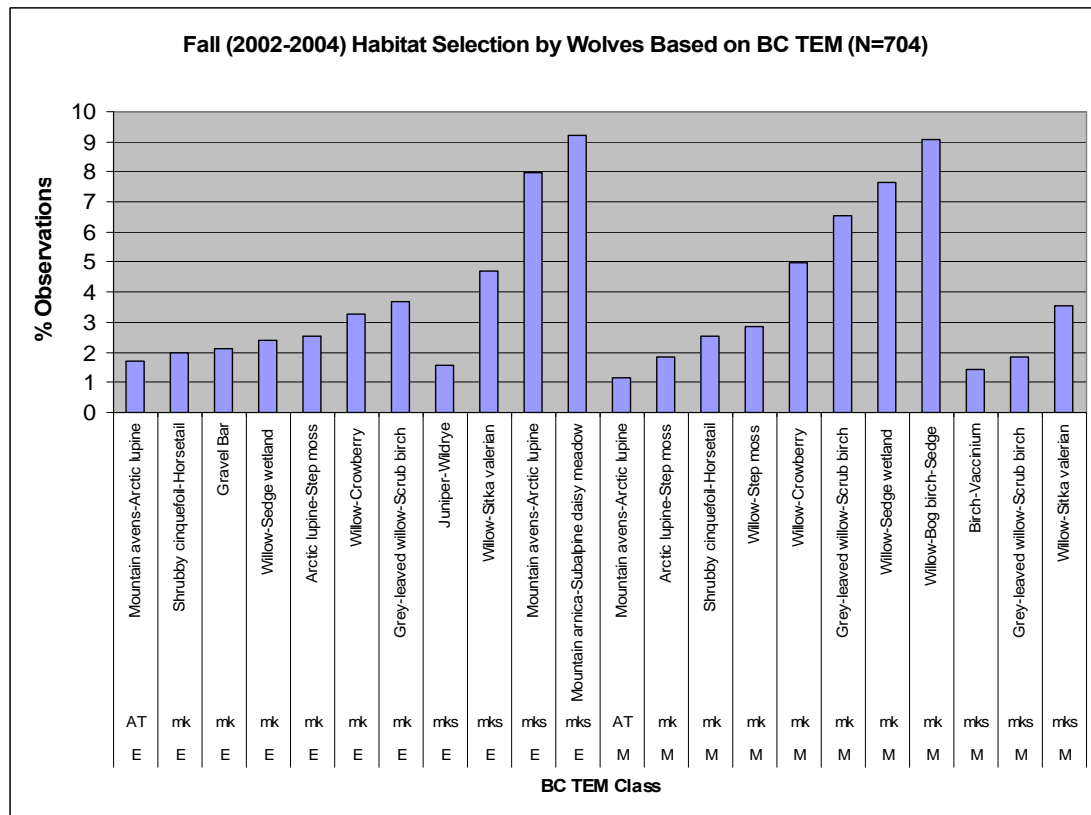
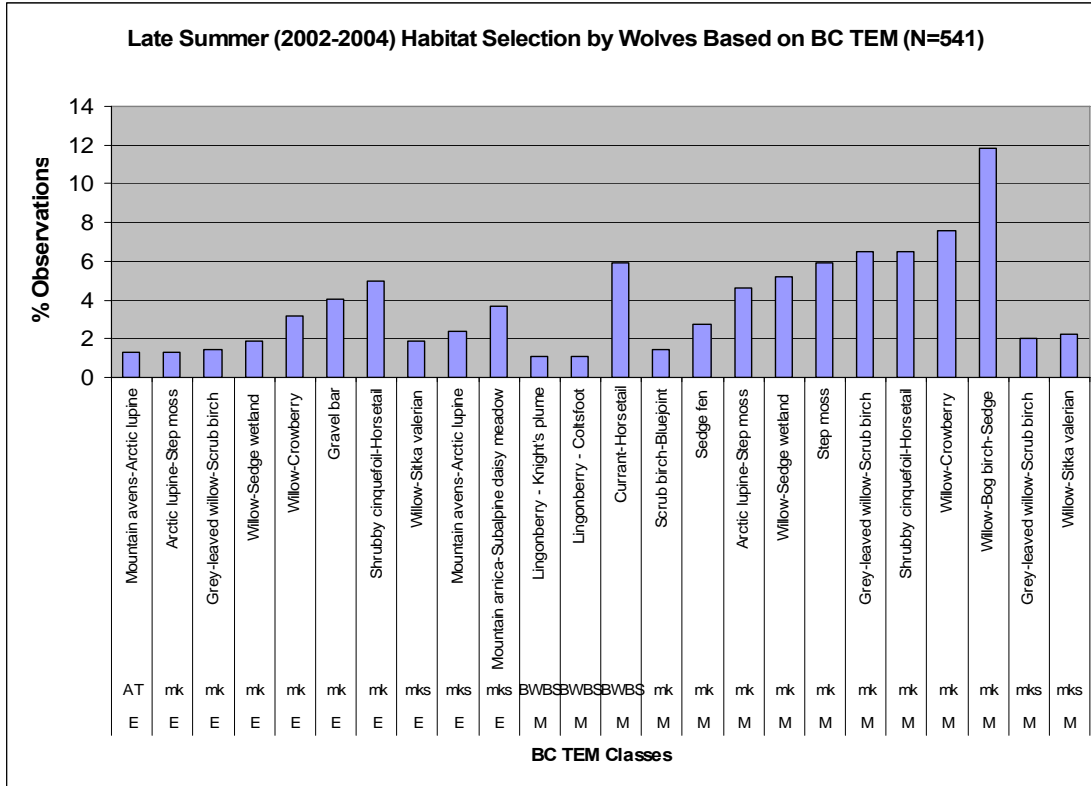**Figure 31. Wolf late summer and fall habitat use of Terrestrial Ecosystem Mapping (TEM) classes in the Besa-Prophet study area, 2002-2004.**

MANAGEMENT RECOMMENDATIONS

Rarely is there the opportunity to quantify the ecological relationships within relatively undisturbed ecosystems and to obtain baseline control data that can be used subsequently to monitor impacts. The general trend in many ecological studies has been to examine a system that has already been impacted to some extent by human activity and then attempt to make inferences about how the system has changed. In our study, the potential to make important contributions towards maintaining predator-prey ecosystems is significant, especially because there has been relatively little human interference in the Besa-Prophet region to date. Our data from the Besa-Prophet provide inputs to a management and conservation framework that is based on observed, natural ecosystem function. We believe that planning processes should include knowledge of ecosystem-level processes, and that the challenge will be to compile and use data obtained at different scales (e.g., in-depth biological knowledge obtained from relatively small scales in studies such as ours, conservation area designs at larger scales, and cumulative impact frameworks). Sustainable management strategies for natural resources and effective planning processes in the Besa-Prophet region must include details from studies such as this research on the focal predators (grizzly bears and wolves) to best operationalize activity on the ground while still maintaining ecological integrity.

The conservation of grizzly bears is a high-profile wildlife management issue in North America. The issue encompasses both concerns about land-use practices, as well as the impacts of hunting and other human-caused mortality (Mowat et al. 2005). Industrial resource-extraction activities threaten the persistence of grizzly bears (Banci et al. 1994, Clark et al. 1996, McLellan 1998) by fragmenting habitats and increasing access by humans to previously remote landscapes (Nielsen et al. 2004a). In the Central Rockies of Canada, unprecedented growth of human population and resource extraction has co-occurred (Schneider et al. 2003), amplifying human-caused mortality, the primary source of death for grizzly bears (Benn and Herrero 2002, Nielsen et al. 2004b). In the northern Rockies of British Columbia, there still remain expanses of wilderness relatively free of human disturbance and with minimal opportunities for access. The impending expansion of resource-extraction industries into this region, however, poses significant challenges for the future management and conservation of grizzly bears. Identifying habitats for grizzly bears in both a spatial and temporal context is an important first step in developing a management and conservation strategy that can incorporate increased human access and wildlife needs.

Optimal habitats for grizzly bears generally are considered roadless areas with a mosaic of early seral-staged forests and natural openings in proximity to secure forest stands that provide day beds and hiding cover (Herrero 1972, Blanchard 1983, Hamer and Herrero 1987). Loss of these types of habitats has the potential to cause population declines in bears (McLellan and Hovey 2001). Grizzly bears in the Besa-Prophet are opportunistic omnivores, with females obtaining as much as 50% of their protein intake from meat. In the Besa-Prophet, the availability of the plants that are typically consumed by bears in other mountainous habitats is limited to approximately half of the number of species as in the central Rockies (e.g., Jasper National Park, Nielsen et al. 2003). Prescribed burning for the management of elk and Stone's sheep may be providing additional opportunities for grizzly bears. Bears in the Besa-Prophet show strong patterns of elevational movement, using high elevations during the spring, a broad

range of elevations in summer, and lower elevations in the fall. These movement patterns are counter to populations of bears in other mountainous areas that often show strong seasonal elevational movements related to plant phenology, using low elevations in spring to exploit foods not available at higher elevations and returning to higher elevations when plants green up (Martinka 1972, Mundy and Flook 1973, Mealey 1980, Servheen 1983, Darling 1987, Stelmock and Dean 1988, Hamer and Herrero 1990, Waller and Mace 1997, Nielsen et al. 2002, Boyce and Waller 2003, Ciarniello et al. 2003). Bears in the Besa-Prophet are not unique, however, as resident mountain bears in southeastern BC (McClellan and Hovey 2001) also remain at high elevations during spring to graze in productive avalanche chutes. This highlights the importance of tracking specific bear populations for management purposes.

Unlike grizzly bears, wolves are obligate carnivores and habitat generalists. Most previous research on examining the spatial dynamics of wolves has typically focused on dispersal and colonization at the landscape scale and has often related habitat occupancy to human disturbance (e.g., Mladenoff et al. 1995, Mladenoff et al. 1999). In human-dominated landscapes in North America, favourable wolf habitat has been most often correlated with forest cover with some conifer component, avoidance of agricultural land, and low road and human density (e.g., Mech et al. 1988, Fuller 1989, Mladenoff et al. 1995). Wolves do not require wilderness to survive, but do require adequate prey and reduced killing by humans (Mech 1995). In areas with minimal human contact and a relatively natural system, wolves in the Besa-Prophet show that spatial dynamics can be complex. Home range boundaries may be in constant flux and related to numerous factors such as prey distribution, litter success, and the presence or absence of neighbouring packs. The selection of a home range is significant because all life history activities occur within its boundaries. In order to maximize survival and reproduction, however, selection and avoidance processes that occur within a home range may not necessarily focus on limiting factors, but rather on maximizing the likelihood of encountering a prey item with minimal effort. Consequently, habitat selection varies seasonally, likely in response to seasonal shifts in prey distributions; and varies between packs, likely because of differences in the proportions of different habitat types, and the seasonal composition and abundance of prey within the respective home ranges. For wolves, adaptability to change is therefore inherent. As such, management or industrial activities that alter the distribution of prey directly, or indirectly by enabling the movements of wolves to new areas, should be avoided until they can be evaluated for possible long-term effects on population productivities. In particular, linear developments and seismic activity during the winter months in Alberta have been linked to increased predation from wolves that use the corridors to increase encounter rates with prey (James 1999, James and Stuart-Smith 2000). Wolves selectively use linear corridors in winter (Gehring 1995) and can move 3 times faster on linear features than through adjacent habitats (James 1999).

In this study we demonstrated seasonal variation in habitat and prey selection by wolf packs in the Besa-Prophet area. Without accurate estimates of seasonal relative prey abundances in our area, we assume that the observed differences in prey selection by packs were in response to seasonal shifts in local prey composition and relative densities within the home ranges of each individual pack. Moose had been speculated to be the most important prey item for wolves throughout the year in northern British Columbia (Bergerud and Elliott 1986), but our results suggest that the dietary dynamics of wolves are more complex than previously considered. Moose was a major prey item during the summer and fall seasons, particularly in the diets of the western packs, but elk (and in some cases Stone's sheep) were

important prey items in the winter and spring seasons (and even year round in the eastern packs). Elk have been observed to be consistently important in wolf diets in numerous other systems, including Yellowstone (Smith et al. 2004), Banff National Park (Hebblewhite et al. 2002), Glacier National Park (Kunkel et al. 2004), Jasper National Park (Dekker et al. 1996), and Riding Mountain National Park (Carbyn 1983).

We recommend the following to incorporate this research into management decision-making and to follow up with projects that expand on our research findings in the Besa-Prophet:

1) Update the current Besa-Prophet Pre-tenure Plan. The Plan (British Columbia Ministry of Sustainable Resource Management 2004) allows for adaptive management and inclusion of new information. Grizzly bears and wolves, as large-ranging species for which there was little quantified information, were not included in the Plan and now that data are available, the Plan should call attention to important seasonal areas and the roles that these species play in prey dynamics. Inclusion of an appendix that provides recommended or suggested ways to minimize impacts on the predators per se and their prey base would be helpful to commercial and recreational users of the area. This could be accommodated by adding an appendix of information as was provided for each of the Planning Units in the original Besa-Prophet Pre-tenure Plan Phase I (British Columbia Ministry of Sustainable Resource Management 2002).

2) Estimate densities of the focal predators and of their ungulate prey base; and define ungulate-specific predation rates to quantify probable linkages with predator spatial and temporal dynamics (most importantly for wolves). This will provide a baseline from which consequences of increased access into the area can be gauged.

3) Define the role of ungulates in the fall diets of grizzly bears. Specifically, is the increase in meat consumption related to predation events or to scavenging hunter kills? Dietary assessments with stable isotopes identified that elk consumption by bears increased in the fall, but these analyses cannot distinguish between scavenged meat and prey that was depredated.

4) Define consequences of range burning. If prescribed burns are enabling increases in elk populations in the Besa-Prophet, it is likely that with this expanding prey base, wolf numbers will also increase. If so, wolves may expand into broader areas, potentially preying on caribou and Stone's sheep more frequently. Similarly, food habits of grizzly bears may change in response to additional prey opportunities.

Additional details of all methodologies, analyses, and results are being finalized in Brian Milakovic's PhD thesis at the University of Northern British Columbia.

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R. Botting

Figure 32. Authors Brian Milakovic and Kathy Parker, University of Northern British Columbia.

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