HABITAT SELECTION AND BEHAVIOURAL STRATEGIES OF STONE'S SHEEP IN NORTHERN BRITISH COLUMBIA

by

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Abstract

Baseline information on Stone's sheep (*Ovis dalli stonei*) and their habitat is needed because of increased industrial development and recreational activity in the mountains of northern British Columbia. To provide a foundation from which to gauge and mitigate issues relating to access and disturbance, I used global positioning system (GPS) radiotelemetry data acquired from 33 female Stone's sheep in the Besa and Prophet river drainages to develop resource selection functions (RSF) and to define areas important to Stone's sheep. Attributes of topography (slope, aspect, elevation, curvature), vegetation (vegetation type, vegetation quality) and risk of predation from grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) were used to examine seasonal broad-scale habitat selection and interannual variation in selection of attributes by groups of Stone's sheep. Habitat selection was best explained by incorporating vegetation, topography and risk of predation using logistic regression and the information-theoretic approach. Topographic features alone, however, ranked better than components of vegetation or risk of predation in explaining habitat selection and were often excellent predictors of habitat use. Considerable variation existed within selection strategies among groups of Stone's sheep and between years within groups, even though there were general consistencies in selection for steep slopes, ridge-like topography, southerly aspects and upper elevations. Behavioural observations and fine-scale habitat and vegetation measurements were used to characterize intrasexual habitat use of female Stone's sheep relative to maternal status during spring and early summer. Nursery groups spent shorter durations of time active, more time active in solid-rock-escape features, and less time in shrub habitat. The best predictive model using logistic regression to describe differences in habitat use relative to maternal status incorporated distance to nearest-escape feature and size of nearest-escape feature. These intrasexual differences in maternal status were well described by predictions of the predation-risk hypothesis (originally proposed to explain sexual segregation between males and females). Regardless of maternal status, Stone's sheep ewes followed an elevational gradient using low-elevation plant communities in spring and moving up in elevation while tracking plant phenology as the growing season progressed. Fecal samples collected seasonally from two areas that differed in anthropogenic use provided natural variation in stress levels. Fecal glucocorticoid concentrations fluctuated seasonally with higher levels in summer than late winter. Corticosterone was a less variable measure of glucocorticoid concentration than cortisol. This research provides a comprehensive analysis of habitat selection and habitat use by Stone's sheep for which life-history characteristics make them susceptible to environmental and anthropogenic disturbance.

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Chapter 1: Introduction

Background

Stone's sheep (*Ovis dalli stonei*) are one of two subspecies of thinhorn sheep (*Ovis dalli*) (Bowyer and Leslie 1992). The Dall's sheep (*Ovis dalli dalli*) of Alaska, the Yukon, the western mountains of the Northwest Territories, and the Tatshenshini region of British Columbia are the most abundant North American wild sheep. After bighorns (*Ovis canadensis*), Stone's sheep are the third most abundant native sheep in North America and the most abundant native sheep in British Columbia. They occur in the northern part of the province (north of the 56th parallel) and in the southern Yukon (Bowyer and Leslie 1992), with the largest numbers residing in the Muskwa-Kechika Management Area (Blower 1998). Hybridization is common where the ranges of the two subspecies overlap.

Stone's sheep were a blue-listed species in British Columbia prior to 1998, indicating that certain life-history characteristics made them vulnerable to human activities and/or natural events (Shackleton 1999). In 1998 the Conservation Data Centre reclassified them to the yellow list (species not at risk) with the justification that populations appeared to be stable and their habitats were secure (Paquet and Demarchi 1999). Recently, however, concerns over declining numbers of Stone's sheep throughout the Peace-Liard and Omineca regions have resulted in a reduction in outfitter quotas and resident hunter bag limits (Demarchi and Hartwig 2004). Increasing fossil-fuel exploration, development and recreational use in northern British Columbia may place stressors on thinhorn sheep (Paquet and Demarchi 1999) with unknown implications. Wild sheep are a disturbance-sensitive species (MacArthur et al. 1982;

Stockwell et al. 1991; Bleich et al. 1994; Frid 2003) and are assumed to be limited by or at risk from predation, severe winters, anthropogenic access, fire suppression and disease, but there is little quantification of those factors (Demarchi and Hartwig 2004).

The overall goal of this thesis was to contribute both to the conservation of Stone's sheep and to effective land-use planning in northern British Columbia. Stone's sheep are a highly visible species of special concern in the mountains of northern British Columbia and southern Yukon and unlike other ungulates found there, Stone's sheep are found nowhere else in the world. The plant communities associated with higher elevations are fragile with slow recovery rates. Alteration or destruction of highly selected plant communities during certain times of year could seriously affect the sheep populations dependent upon them (Luckhurst 1973). Knowledge of habitat selection (including behavioural use of habitats and fine-scale habitat associates), current stress levels and mortality rates helps provide a foundation to maintain Stone's sheep populations and effectively document any impacts that anthropogenic or environmental disturbance may have on this species in the future.

Objectives

This research had four specific objectives across different ecological scales. The first two objectives follow a hierarchical reduction in scale, from broad-scale selection by Stone's sheep to their behaviour and fine-scale habitat use. A noninvasive measure for quantifying disturbance to Stone's sheep is described in the third objective. The final objective references the findings of this research to summarize current management actions associated with Stone's sheep.

1) To characterize broad-scale habitat selection of Stone's sheep in relation to topography, risk of predation and vegetation.

Relatively few data are available to define habitat requirements for Stone's sheep and current habitat capability models have been supplemented with data from Rocky Mountain bighorns (*O. c. canadensis*). Because of this lack of information, it is important to understand and quantify limiting factors so that effective management guidelines for this species can be incorporated in land-use plans for the Muskwa-Kechika Management Area. Data from 33 GPS-collared Stone's sheep ewes were used to determine seasonal movement rates. Along with the lambing and breeding biology of the species, these movement rates helped delineate six biological seasons. 'Strategies' of selection in relation to topography, risk of predation, and vegetation were assessed seasonally and annually among five groups of Stone's sheep to determine variation in habitat selection. Fidelity of Stone's sheep to particular 'strategies' and sites may have significant implications to the distribution (Seip 1983), risk of predation (Watts and Schemnitz 1985) and ability of populations to adapt to disturbances or changing habitats.

2) To describe behaviour and habitat use of female Stone's sheep relative to maternal status during the growing season and to assess the appropriateness of intersexual segregation hypotheses to explain segregation of female sheep.

Stone's sheep segregate intersexually and intrasexually (Geist 1971; Luckhurst 1973; Seip 1983) as do Dall's sheep (Hoefs and Cowan 1979; Rachlow and Bowyer 1994; Rachlow and Bowyer 1998; Corti and Shackleton 2002). Intrasexual segregation is most pronounced when energy demands associated with lactation are greatest and vulnerability of offspring is highest (Ruckstuhl and Neuhaus 2000). I reviewed three prominent hypotheses of intersexual segregation (predation-risk, forage-selection and activity-budget hypotheses) to determine which if any of these also explained the intrasexual segregation of female Stone's sheep using behaviour, habitat measures and plant community associations to differentiate among them.

3) To determine baseline levels of stress in Stone's sheep using cortisol metabolites extracted from fecal samples.

Environmental stressors, such as immune deficiencies, hypertension and alterations in feeding behaviour, have been identified as having detrimental consequences to the health of mammals (Breazile 1987). Quantifying the natural levels of variation in environmental stress exhibited by Stone's sheep is useful to assess potential impacts associated with future anthropogenic disturbance. Fecal glucocorticoids were measured from Stone's sheep occupying two areas that differed in anthropogenic access and development over three seasons (early winter, late winter and summer). Two glucocorticoid metabolites (corticosterone and cortisol) were quantified for Stone's sheep.

4) To assess the implications of current management practices in the context of seasonal mortalities and selection strategies of Stone's sheep.

Potentially declining numbers of Stone's sheep have resulted in restrictions to hunting. Knowledge of the timing of mortality coupled with seasonal selection strategies can help provide insights into cause-specific mortality and limiting seasons. The most prevalent management practices other than hunting regulations associated with thinhorn sheep in British Columbia include range-burning and predator control. I reviewed current literature to highlight the beneficial aspects and recent concerns associated with management practices pertaining to Stone's sheep. Potential impacts associated with increased oil and gas exploration and development are also discussed.

I offer considerations addressing research needs identified in Demarchi and Hartwig (2004) with special emphasis on the development of habitat maps. The development of spatially explicit maps highlighting the distribution of highly selected habitats is often an important step to making informed management decisions (Corsi et al. 2000). The feasibility of accurately predicting a species' distribution is often difficult (Corsi et al. 2000) and may require unique approaches (Gustine 2005). I used resource selection functions and logistic regression to develop spatially explicit maps and to assess the ability of topographic measures, which are easily acquired, to explain the distribution of Stone's sheep.

Organization of thesis

This thesis is arranged as three 'stand alone' chapters to be submitted for peer-reviewed publication. These are preceded by this introduction and followed by a chapter on management implications for Stone's sheep. The first thesis objective addressing broad-scale habitat selection by Stone's sheep is incorporated in Chapter 2 (*Habitat selection and movements of Stone's sheep in relation to vegetation, topography and risk of predation*). The second objective describing behaviour and habitat use of Stone's sheep relative to maternal status corresponds to Chapter 3 (*Behaviour, habitat associations and intrasexual* *differences of Stone's sheep ewes*). The third objective characterizing stress levels of Stone's sheep is included in Chapter 4 (*Fecal glucocorticoid concentrations of free-ranging Stone's sheep*). The final objective, reviewing current wildlife management practices pertinent to Stone's sheep and providing considerations for developing spatially explicit habitat models, is detailed in Chapter 5 (*Management of Stone's sheep: implications and considerations*), a chapter that also synthesizes the findings of this research.

Chapter 2: Habitat selection and movements of Stone's sheep in relation to vegetation, topography and risk of predation[1]

Abstract: Stone's sheep (*Ovis dalli stonei*) are susceptible to anthropogenic disturbances, but data on seasonal habitat selection and movements are few. We used the movements of individuals to define availability, and resource-selection functions (RSF) along with the information theoretic approach to examine seasonal habitat selection and interannual variation in selection of attributes by groups of Stone's sheep. Movement rates of Stone's sheep followed consistent yearly trends with the greatest movements occurring in summer and fall. Models that contained vegetation, topography and risk of predation were typically the best at explaining resource selection by Stone's sheep. Topographic features ranked better, however, than components of vegetation or risk of predation from grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) at explaining habitat selection. Considerable variation existed within selection strategies among groups of Stone's sheep and between years within groups even though consistencies in selection for steep slopes, ridge-like topology, southerly aspects and upper elevations were common. This research provides the first comprehensive analysis of habitat selection by Stone's sheep, which show strong fidelity to seasonal ranges, but also exhibit plasticity in selection of attributes within those ranges.

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[1] A version of this chapter will be submitted for publication with the following authorship: Andrew B. D. WALKER, Katherine L. PARKER, Michael P. GILLINGHAM, David D. GUSTINE and Roberta J. LAY

Introduction

Stone's sheep (*Ovis dalli stonei*) are one of two subspecies of thinhorn sheep (*Ovis dalli*) found in North America and the most abundant native sheep in British Columbia (Blower 1999). Habitat factors that are assumed to be the most limiting to thinhorn sheep populations include predation, severe winters, access and development, reduced range quality and disease (Demarchi and Hartwig 2004). Some habitats used by sheep are relatively secure in provincial parks whereas others may be exploited for industrial purposes. Competing land-use practices such as oil and gas activities and commercialized recreation on sheep ranges are increasing (Paquet and Demarchi 1999) with unknown consequences to sheep populations. Wild sheep are extremely susceptible to disturbance (MacArthur et al. 1982; Miller et al. 1991; Papouchis et al. 2001). Overflights by helicopters and fixed-wing aircraft can impose energetic costs to sheep by altering use of habitat, increasing susceptibility to predation and/or increasing nutritional stress (Stockwell et al. 1991; Bleich et al. 1994; Frid 2003). Bleich et al. (1994) and Frid (2003) noted that mountain sheep failed to habituate to repeated aircraft overflights.

Relatively few data are available to develop models that define and spatially describe habitat selection by Stone's sheep and no data are available on selection of habitats in relation to risk of predation, despite the need for such models (Demarchi and Hartwig 2004). Luckhurst (1973) used exclosures to document plant community associations of Stone's sheep relative to soil morphology and climate in the Neves valley of northern British Columbia. The *Elymus-Agropyron* community was highly selected during late winter and lambing, indicating it may be especially important to Stone's sheep when the energetic constraints of gestation and lactation are high (Gittleman and Thompson 1988). The lack of information at larger scales, however, has made it important to understand and quantify broad-scale selection so that effective management guidelines for this species can be incorporated into land-use plans (Demarchi and Hartwig 2004). The primary goal of our research was to improve habitat suitability models for Stone's sheep by specifically defining habitat requirements in relation to vegetation, topography and risk of predation to direct management actions and mitigate potential consequences of increasing development.

Our initial objective was to assess the seasonal importance of habitat factors to Stone's sheep by determining the selection of vegetation types and quality, topography and risk of predation from grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*). Stone's sheep have been observed using habitats differently among seasons (Geist 1971; Luckhurst 1973; Seip and Bunnell 1985*b*), but a quantification of selection is lacking. This is especially relevant with respect to habitats that are managed for the benefit of Stone's sheep. Range burning (Elliot 1978; Seip and Bunnell 1985*a*) and wolf control (Bergerud and Elliot 1998) are the most widely employed management actions used to enhance Stone's sheep populations in British Columbia. Seip and Bunnell (1985*b*) observed that Stone's sheep used burned areas seasonally unless they became unavailable with increasing snow depths. Stone's sheep that used burned areas had higher lamb/ewe ratios (Elliot 1978; Seip and Bunnell 1985*a*) and reduced lungworm counts (Seip and Bunnell 1985*a*). Bergerud and Elliot (1998) documented a numerical response in lamb recruitment following wolf reductions in northern British Columbia, but could not quantify Stone's sheep selection of habitats in relation to wolves. We incorporated data from wolves and range burning to assess the influence of vegetation, topography and predators on the seasonal selection strategies of Stone's sheep.

A second objective was to determine the relative ranking of habitat factors (topography, vegetation, risk of predation) towards explaining the spatial and temporal distribution of Stone's sheep. These factors are subject to different anthropogenic influences. Incorporating the information-theoretic approach makes it feasible to assess multiple explanatory models and a relative ranking of habitat factors (Burnham and Anderson 2002; Johnson and Omland 2004). We assumed that a relative ranking would provide insights into whether vegetation, topography or risk of predation was most important in explaining the distribution of Stone's sheep.

Our third objective was to quantify variation in habitat selection between years as a measure of plasticity by Stone's sheep. Stone's sheep and other North American wild sheep show a strong affinity to specific seasonal ranges and sites (Geist 1971; Heimer 1973; Luckhurst 1973; Seip 1983; Festa-Bianchet 1986; Worley et al. 2004). This seasonal affiliation may affect distribution (Geist 1971; Seip 1983; Worley et al. 2004), risk of predation (Watts and Schemnitz 1985) and ability of a population to adapt to disturbances and changing habitats. Research regarding range fidelity by Stone's sheep has been addressed (Geist 1971), but there is a lack of data regarding the attributes selected at those sites. We assessed the annual consistency in selection among habitat attributes by Stone's sheep within their seasonal ranges.

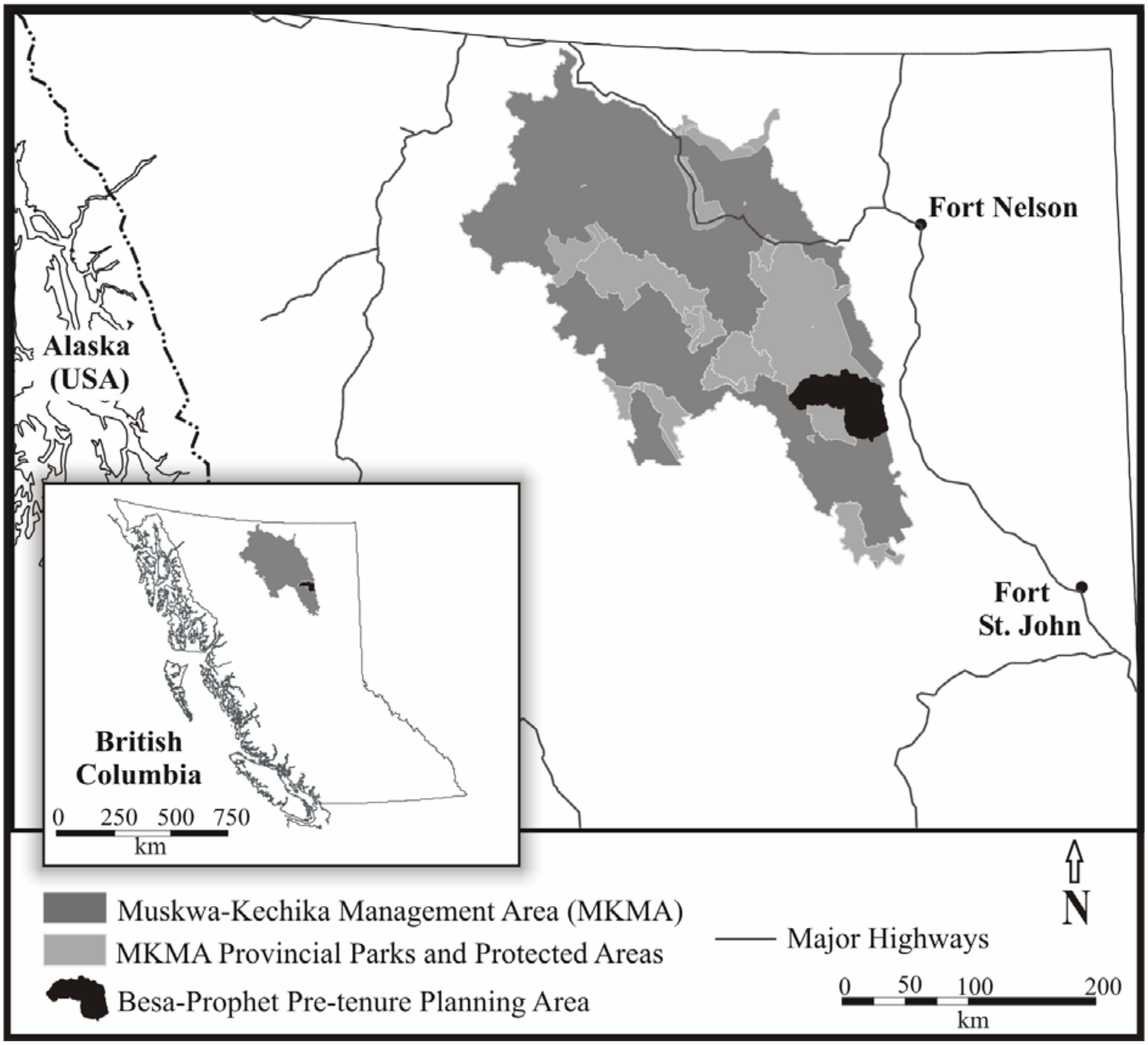
Methods

Study area

The study area was located within the Besa-Prophet (B-P) Pre-tenure Planning Area in the southeast portion of the 6.3 million-ha Muskwa-Kechika Management Area (MKMA) in northern British Columbia (Fig. 2.1). The study area encompassed ~140,000 ha of the ~200,000-ha B-P Pre-tenure Planning Area between 57° 20' and 57° 40'N and 123° 10' and 123° 45'W, and was based on the distribution of study animals.

The B-P study area includes three biogeoclimatic zones: the boreal white and black spruce (BWBS) zone of the lower valleys, the spruce-willow-birch (SWB) zone of the subalpine, and the alpine tundra (AT) zone at highest elevations (Meidinger and Pojar 1991). Valleys at ~800-1300 m elevation are often lined with white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*) on dry sites, and black spruce (*Picea mariana*), willow-birch (*Salix* spp., *Betula glandulosa*) communities on poorly drained sites. Plants that dominate the understory include soapberry (*Sheperdia canadensis*), Labrador tea (*Ledum groenlandicum*), grasses (*Poa* spp.), sedges (*Carex* spp.), alder (*Alnus* spp.) and various mosses. Subalpine habitats of the SWB zone occur at higher elevations (~1300-1600 m) immediately above the BWBS zone. These subalpine habitats are characterized by an abundance of willow and scrub birch, as well as balsam fir (*Abies lasiocarpa*), white spruce and various grasses, sedges and fescues (*Festuca* spp.). The AT zone occurs at the highest elevations (~1600-2200 m) and is characterized in the study area by rock with sparse vegetation, rounded peaks and plateaus with plant communities consisting of fine grasslands (fescues and grasses), herbs, bryophytes and lichens in which

Fig 2.1. Study area (within the Besa-Prophet Pre-tenure Planning Area) in the Muskwa-Kechika Management Area of northern British Columbia.



trees are non-existent (Meidinger and Pojar 1991).

Low snow accumulations, exposed subalpine and alpine ridges, and numerous southern exposures contribute to the MKMA supporting almost half of the world’s population of Stone’s sheep (Blower 1999). The area is further distinguished by east-west drainages and longitudinal mountains; it is rich in wildlife and habitat diversity. Stone's sheep share the area with several other ungulates including Rocky Mountain elk (*Cervus elaphus nelsoni*), moose (*Alces alces*), caribou (*Rangifer tarandus*), mountain goats (*Oreamnos americanus*), mule deer (*Odocoilus hemionus*) and white-tailed deer (*O. virginianus*). This diversity in large herbivores helps support numerous large predators including grizzly bears, black bears (*U. americanus*), wolves, coyotes (*C. latrans*), and wolverines (*Gulo gulo*).

Forest fires are the most influential disturbance in the B-P. In the BWBS biogeoclimatic zone, the most frequent natural disturbance type includes stand-initiating events on a 100 to 150-year rotation (British Columbia Ministry of Forests 1995). Fire also has been implemented by both wildlife managers and outfitters to improve elk and Stone’s sheep habitat (Elliot 1978; Seip 1983; Peck and Peek 1991). The area has little access and is relatively free of other anthropogenic influences. There is one all-terrain vehicle (ATV) trail, that experiences limited snowmobile activity in winter. Two permanent outfitter camps are accessible by bush plane; hunting for Stone’s sheep by both residents (non-guided) and nonresidents (guided) takes place from 1 August to 15 October (Blower 1999; Demarchi and Hartwig 2004). Although seismic exploration within the study area has been uncommon, a northward progression of oil and gas development into the area is likely.

Field procedures

Stone's sheep were captured in the southern portion of the B-P study area by helicopter net gunning during the winters of 2002 and 2003. We fitted global positioning collars (GPS) (Simplex^{TM} Televilt, Lindesberg, Sweden) on 36 adult female Stone's sheep and programmed the collars to record locations four times daily for 2 years. During the same time period, 22 individual wolves from five packs and 15 female grizzly bears were captured by aerial darting and also fitted with Simplex^{TM} GPS collars (Televilt, Lindesberg, Sweden) programmed to acquire locations four times daily. Locations from all animals were obtained from remote downloads three times per year at scheduled download times and additional data were gathered following collar retrieval at the end of the 2-year sampling period. Locational data from the day and subsequent day of capture were excluded in analyses for all species. Locations that exceeded realistic animal movements or had erroneous fix times were identified and excluded using a spatial analysis program (M. P. Gillingham, unpublished data). All GPS locations were assumed to represent spatial use by the study animals.

Data analysis

Broad-scale seasonal selection of habitats by Stone's sheep was determined with resource selection functions (RSF). By employing logistic regression, RSF provide a broad-scale perspective of general selection patterns on the landscape (Boyce and McDonald 1999; Manly et al. 2002). Although they do not indicate the absolute probability of use by an animal or species (Keating and Cherry 2004), the exponential model of Manly et al. (2002) does provide relative measures of selection. RSF accommodate any type of habitat variables (categorical and continuous) and incorporate spatial data acquired from Geographical

Information Systems (GIS) or remote sensing (Boyce and McDonald 1999). We developed seasonal and annual selection models for five groups of sheep in the B-P area: Neves, Tenmile, Firstfork, Townsley and Richards (Appendix A, Table A.1). We assumed that considerable variation in selection strategies occurs among seasons (Boyce et al. 2002) and years (Schooley 1994). Individual animals were grouped together based on the major lick used within their yearly distribution. No individual traveled outside of its group's yearly distribution to use another lick. Our interpretation of selection by Stone's sheep is consistent with Johnson's (1980) third-order selection where seasonal ranges are identified and the use of resources within them is quantified.

We followed the terminology suggested by Hall et al. (1997) and defined habitat as the collection of resources required by a species. We used availability instead of abundance because the accessibility of resources was defined by the individual. We defined use as the procurement of resources and selection as the disproportionate use of a resource in relation to its availability (Johnson 1980; Hall et al. 1997). We inferred avoidance when a resource was used disproportionately less than its availability.

Movement rates of Stone's sheep were determined from the straight-line distance between consecutive 6-h GPS fixes. We averaged mean monthly and seasonal movement rates of individual Stone's sheep to capture temporal trends in movement. Standard errors of mean rates of movement were calculated using the number of collared individuals. Movement rates, behaviour, patterns of range use and the lambing and breeding biology of thinhorn sheep were used to delineate six seasons for which RSF were developed (Table 2.1). In the selection models, use was determined from an individual's GPS locations. Availability was defined for each individual seasonally, in 2002 and 2003, using the 95th percentile of the distances moved

Table 2.1. Seasons, dates and biological reasons for the six defined seasons used to develop seasonal resource selection models for Stone's sheep in the Besa-Prophet area, 2002-2003.

Season	Date	Biology
Early winter (EW)	1 January – 28 February	Formation of sex-specific groups following rut[a].
Late winter (LW)	1 March – 14 May	Smallest range use size[a,c]; movement to subalpine slopes in preparation for green-up[a,c].
Lambing (L)	15 May – 14 June	Two days before the mean onset and two days after the mean end dates of lambing[d]. Parturient females become solitary[a,b,c,d]; onset of plant green-up[a,b,c,d,e].
Summer (S)	15 June – 14 August	Movement to higher elevations[a,b,c]; high use of mineral licks[a,b,c]; formation of nursery groups[a,b,d].
Fall (F)	15 August – 31 October	Senescence of vegetation[e]; movement to lower elevations in relation to burn vegetation[c].
Rut (R)	1 November – 31 December	Males and females form mixed sex groups on or near winter range; ewes come into estrous[a,d].

[a] Geist (1971)
[b] Luckhurst (1973)
[c] Seip (1983)
[d] Nichols and Bunnell (1999)
[e] Lay (2005)

by that individual between 6-h fixes. We refer to this distance as an individual's seasonal movement potential because the individual was capable of moving that distance during that time period. To obtain potential availability points, each use location was buffered by the individual's movement potential and a contiguous outline was then used to define the individual's seasonal distribution. Five random locations for every use location were placed within each individual's seasonal distribution to quantify availability. This variable buffer used to define selection strategies of Stone's sheep attempts to accommodate changes in the availability of seasonal habitats. Availability buffers and random points were developed using Arcview 3.2® (Environmental Systems Research Institute 1999) and a random point generator extension (Jenness Enterprises, Flagstaff, Arizona, USA).

We used the information-theoretic approach of model selection to evaluate several models and hypotheses (Burnham and Anderson 2002; Johnson and Omland 2004). A suite of biologically relevant models (Table 2.2) was developed *a priori* for each season and year of study (2002, 2003) to define habitat selection within and across the five groups of Stone's sheep in the study area. We constructed global models across years and groups of sheep by pooling GPS locations. Logistic regression (Hosmer and Lemeshow 1989) was used to quantify coefficients of selection (β_i) to define differences between use and available points (Manly et al. 2002; Boyce et al. 2002). Deviation contrasts were used to code categorical variables (Menard 2002). To account for spatial and temporal autocorrelation, we used the Huber-White sandwich estimator to obtain robust and inflated estimates of variance for each β_i (Boyce et al. 2002).

Collinearity and multicollinearity among habitat variables were assessed seasonally because they can inflate selection coefficients and cause large standard errors (Menard 2002). Tolerance scores <0.2 were used to identify correlated variables (Menard 2002).

Table 2.2. Suite of ecologically plausible models, developed *a priori* to define logistic regression models for Stone's sheep in the Besa-Prophet area, 2002-2003.

Model
vegetation type + slope + aspect + curvature + elevation + elevation^{2a} + bear risk^{b} + wolf risk^{c} + vegetation quality^{d}
vegetation type + slope + aspect + curvature + bear risk^{b}+ wolf risk^{c} + vegetation quality^{d}
vegetation type + slope + aspect + curvature + bear risk^{b}+ wolf risk^{c}
slope + aspect + curvature + elevation + elevation^{2a}
vegetation type + bear risk^{b}+ wolf risk^{c} + vegetation quality^{d}
vegetation type + bear risk^{b}+ wolf risk^{c}
vegetation type + slope
vegetation type + vegetation quality^{d}
vegetation type
bear risk^{b}
wolf risk^{c}

[a] available only in models with nonlinear elevation.
[b] bear risk available only during lambing, summer and fall models.
[c] wolf risk not available during the 2003 rut season.
[d] vegetation quality available only during lambing and summer models.

Correlated variables were included separately in identical, but mutually exclusive, models. The correlate found in the model with the higher Akaike's Information Criterion (AIC; Burnham and Anderson 2002) was removed from the seasonal model set. Zero-cell counts (when there were no data available for a used or available response variable) resulted in the seasonal exclusion of some categorical variables (vegetation types and aspects).

AIC and corrected AIC (AIC_c) for small sample sizes ($n/K < 40$) were used to rank the suite of logistic regression models by providing an estimate of the relative distance each candidate model was from the "true model" (Burnham and Anderson 2002). The lowest AIC or AIC_c value in a model set indicates the model that achieves the best parsimony or trade-off between bias in the number of parameters (K) and amount of variance captured in the model. Within AIC, log likelihood (LL) provides an indication of model fit with smallest values, relative to competing models, indicating better prediction of the dependent (use and availability) variables (Menard 2002). AIC weights (w_i) were used to choose the most parsimonious (best) model by providing an estimate of the relative probability that the top model was the best from the suite of proposed models. The w_i in a model set sum to one and provide a measure of the weight of evidence in favour of one model over the others (Burnham and Anderson 2002; Johnson and Omland 2004). Competition for best model was recognized when the top model had $w_i < 0.95$. Competing models were defined as the top models for which the summed $w_i \geq 0.95$; these models were averaged (Burnham and Anderson 2002). Inferences were only made using averaged models or best models with $w_i > 0.95$ (Burnham et al. 2000; Burnham and Anderson 2002). The predictive ability of best models was evaluated using the k-fold cross validation procedure averaged across five random subsets and a Spearman's rank correlation ($\bar{r}_s$) (Boyce et al. 2002; Nielsen et al.

2002). *P* values were determined for $\bar{r}_s$ to document each model's level of significance (Siegel 1956).

We calculated $\bar{\Delta}_i$ as the difference between the minimum AIC and the AIC for the *i*th model in the set, and then used the average change in AIC values ($\bar{\Delta}_i$) to illustrate the relative rankings of models across years (Burnham and Anderson 2002). We used 95% confidence intervals (CI) to determine whether selection coefficients (β_i) for the variables were different from zero. Selection by Stone's sheep was inferred when the CI around β_i were positive; avoidance was inferred when the CI around β_i were negative. Consistency in annual selection of habitat attributes by groups of Stone's sheep was determined by qualitatively assessing the similarities in coefficients from 2002 to 2003 using the criteria of selection and avoidance. If a group of Stone's sheep selected a habitat attribute for which the CI were not similar in sign, relative to zero between years, no consistency in annual selection for that season was inferred. We defined consistency across groups to occur when resource selection by ≥75% of the groups was similar between years. Only habitat attributes found in the top models for both years were used and habitat attributes with zero-cell counts were excluded from analysis for that season. Stata^{TM} 9.0 (StataCorp 2005), including a design matrix (desmat) add-on for deviation coding (Hendrickx 1999), was used for all statistical analyses and model evaluation and validation.

Model inputs

A suite of geographical information system (GIS) layers was used to extract attributes for defining habitat selection by Stone's sheep. The variables were slope, aspect, curvature, elevation, vegetation type, vegetation quality and risk of predation, which influence (e.g., risk of predation) or provide surrogates of attributes (e.g., aspect and solar radiation) that have all been shown to influence the distribution of mountain sheep in North America (Festa-Bianchet 1988; Berger 1991; Bleich et al. 1997; Rachlow and Bowyer 1998; Nichols and Bunnell 1999), including Stone's sheep (Elliot 1978; Seip and Bunnell 1985*a*; Seip and Bunnell 1985*b*). We evaluated specific *a priori* combinations of biologically relevant habitat attributes to determine their potential effects on habitat selection by Stone's sheep (Table 2.2). Attributes associated with topography (i.e., slope, aspect, elevation, curvature), risk of predation (i.e., wolf risk, bear risk) and vegetation (i.e., vegetation type and vegetation quality) were grouped individually to test which explained most of the variation in the Stone's sheep data. We evaluated the relative ranking of these habitat factors as well as combinations of those attributes. All data used as attributes in the models were collected across the same spatial and temporal scales as the data for Stone's sheep.

Topography

We used a Terrain Resource Information Management (TRIM) digital elevation model (DEM) with a spatial resolution of 25 m to develop slope, aspect, elevation and curvature attributes. Slope and aspect were measured in degrees. Aspect was categorized into north (316° - 45°), east (46° - 135°), south (136° - 225°), west (226° - 315°) and no aspect (NASP). Pixels with slopes of ≤1° were assigned to the NASP category. Elevation was included as a squared term (i.e., elevation + elevation^2) when it was detected to be nonlinear. Elevation was the only variable where exploratory analysis was conducted prior to model development. The graphical representation of selection functions for elevation was determined by holding habitat variables in a model constant while multiplying β_i of elevation by elevations of actual locations used by Stone's sheep within that season (as in Boyce et al.

2003). The selection functions were scaled between zero and one to illustrate seasonal differences in selection of elevation by Stone's sheep. Curvature was derived using ArcInfo^{TM} 8.3 and the ArcGrid^{TM} extension (Environmental Systems Research Institute 2003*b*) and provided an indication of the overall concavity or convexity of a pixel in relation to its 3 × 3 pixel neighbourhood. Positive values were indicative of convex sites (ridges, mountain tops) whereas negative values indicated concave sites (gullies, valley bottoms).

Vegetation type and quality

We identified 10 vegetation types from remotely sensed Landsat 5 Thematic Mapper (TM) and Landsat 7 Enhanced Thematic Mapper (ETM) images, analyzed with PCI Geomatics software (PCI Geomatics 2004) (Table 2.3). More than 200 sites within the study area were visited to describe plant community associations, and to develop and assess the accuracy of a supervised classification of the study area (Appendix C, Table C.1; Lay 2005). We used three 2001 monthly (4 June, 22 July, and 15 August) images from Landsat 5 TM and Landsat 7 ETM to assess changes in the normalized difference vegetation index (NDVI) for the lambing and summer seasons (Lay 2005). We refer to the change in NDVI between monthly images as vegetation quality because it is positively correlated with forage of higher digestibility (Griffith et al. 2002) and new plant growth, which sheep select during the spring (Geist 1971; Seip and Bunnell 1985*b*). We assumed that relative change in NDVI was consistent across years (2002-2003).

Risk of predation

We developed predation risk layers for bears and wolves because they are assumed to be

Table 2.3. Description of vegetation types identified in the Besa-Prophet ecosystem, 2002-2003.

Vegetation Type	Description
Riparian	Permanent water bodies or water courses. Gravel bars of stream courses including dry stream beds. Wet microsites including wetlands dominated by *Carex aquatilis* and some moss species or *Salix* spp. May include *Picea glauca* or *Picea mariana* found in poorly drained sites.
Shrub	Shrubs <2 m. Variable cover of *Salix* spp., *Betula glandulosa*, *Potentilla fruiticosa*. Includes subalpine shrubs.
Conifer	*Picea glauca*, *Abies lasiocarpa* or *Pinus contorta* stands including mature and growing stands. Variable understories of grass, moss and shrub.
Subalpine spruce	Transition zone from mature *Picea glauca* or *Abies lasiocarpa* to subalpine shrubs at treeline. Includes krummholz.
Rocks	Rocky sites dominated by steep outcrops, talus slopes and scree slides and non-vegetated bedrock.
Rockcrust	Large frost-broken boulders with significant cover of crustose lichen such as *Melanelia hepatizon.*
Dry alpine	*Dryas integrifolia*- and *Festuca altaica*-dominated alpine. Well drained sites on moderate to steep slopes.
Wet alpine	Poorly drained alpine sites. Primarily moss spp. with *Salix reticulata.* Also includes sites dominated by *Cassiope tetragona.*
Burn-deciduous	Older burned and disturbed areas. Contain *Populus tremuloides* and *Populus balsamifera* shrubs (<2 m) and trees (>2 m). Can be associated with small stands of *Pinus contorta.*
Burn-grass	Recently burned and open disturbed sites dominated by *Elymus innovatus*.

the most significant predators in the MKMA (Bergerud and Elliot 1998). We incorporated GPS locations from wolves and grizzly bears residing in the B-P Pre-tenure Planning Area in RSF using logistic regression to define relative risk of predation to sheep. RSF were built for bears during the lambing, summer and fall seasons and for five wolf packs across all seasons during 2002 and 2003 using PCI Imageworks^{TM} (PCI Geomatics 2004). Because GPS data were not available for wolves during November and December 2003, a risk of predation layer was not developed during this time. We assumed risk of wolf predation was consistent, however, across years during the rut season (November-December) in the development of global Stone's sheep RSF. Due to the social nature and territoriality of wolf packs, all but one duplicate wolf location occurring at the same date and time within a pack were randomly excluded to minimize issues of data dependency.

We set a more conservative tolerance score (<0.4) to determine collinearity and multicollinearity of variables in risk models to increase our confidence in an extrapolated predation risk layer used for the Stone's sheep models (Gustine 2005). Variables used in the bear (Appendix D, Table D.1) and wolf (Appendix E, Table E.1) RSF models included slope, aspect, elevation, vegetation type, fragmentation and distance to linear features. Fragmentation was used as an index of vegetation type diversity. We developed fragmentation using Idrisi32^{TM} (Clark Labs 2001) and a moving 7 × 7 pixel window to assign each pixel a fragmentation value based on the number of different vegetation type polygons within each window. Fragmentation was grouped into high-, medium- and low-fragmentation classes based on the distribution of data. A distance-to-linear-features layer was developed using existing British Columbia Oil and Gas commission data (1997 - 2000), orthophotos with 15-m resolution and a Landsat 7 ETM image. The linear features consisted of roads, seismic lines and pipelines. These features were buffered by 10 m and a distance (km) surface was developed using ArcGIS 8.3^{TM} (Environmental Systems Research Institute 2003*a*). The risk of predation layers otherwise followed the same criteria used to select and develop the Stone's sheep models.

Availability was defined for bears and individual wolf packs within 100% minimum convex polygons (MCP) by 'sheep season' and year using Arcview 3.2^{TM} (Environmental Systems Research Institute 1999). MCP that extended beyond the B-P area were clipped to the border of the satellite image and five random locations for each use location were placed within an individual bear's or wolf pack's MCP. Where data for wolf packs or bears were not available, a global model incorporating data from all bears (Appendix D, Table D.2) or wolves (Appendix E, Table E.2) was developed and used to rank risk in those parts of the landscape. Where MCP overlapped, the minimum risk values between wolf packs were used because the peripheries of wolf pack territories have been shown to act as refuges for ungulates (Rogers et al. 1980). Individual pack models were excluded from seasonal risk layers when the best model performed extremely poorly using *k*-folds and $\bar{r}_s < 0.55$ (5 random subsets, $P > 0.10$; Siegel 1956). These areas were assigned global (pooled across packs) risk values.

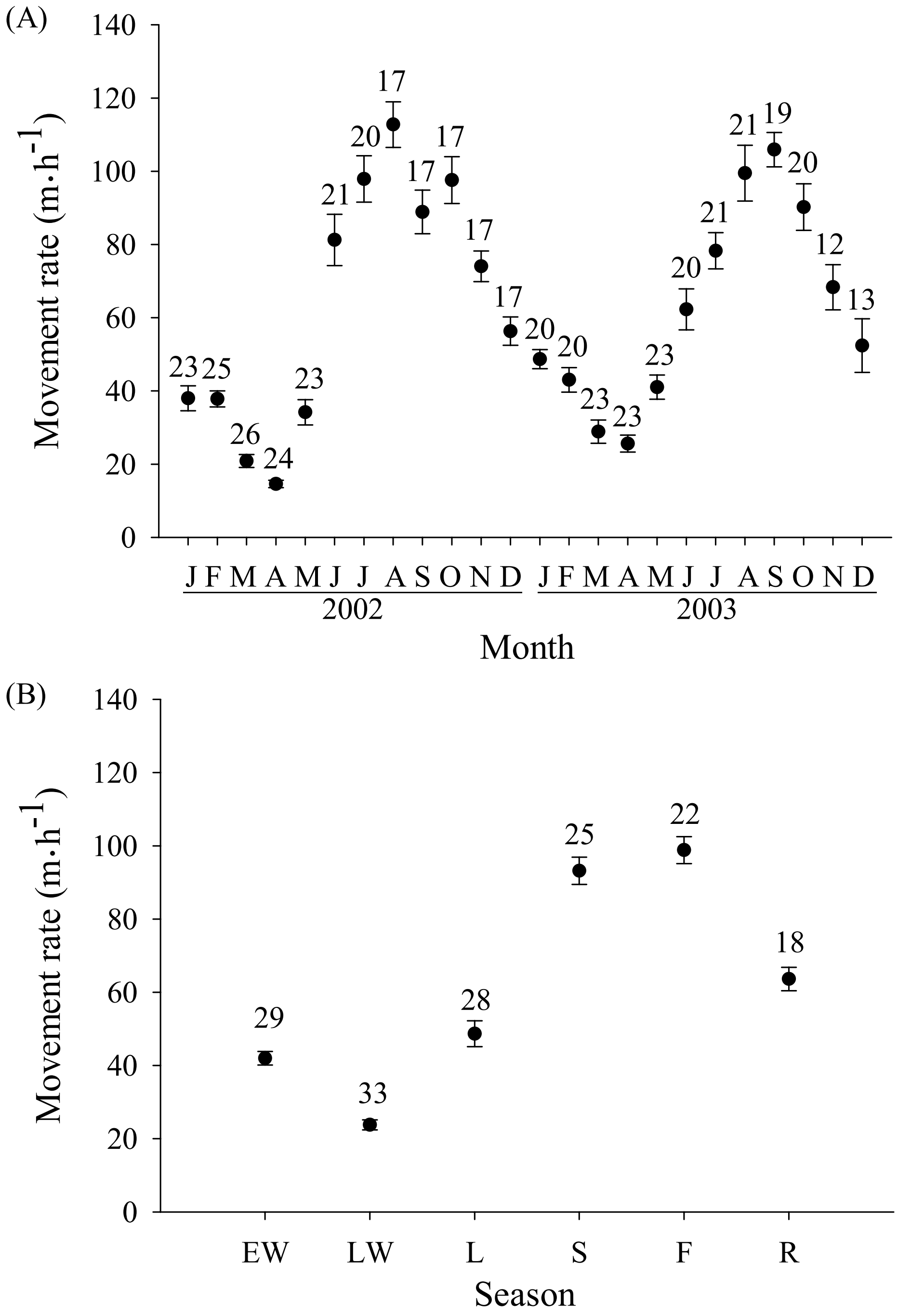
Coefficients (β_i) within the predator-risk models (Appendix D, Table D.3; Appendix E, Table E.3) were multiplied by their appropriate input layer and summed. These values were then scaled between zero and one to standardize values for comparison among wolf and bear seasonal RSF. The predation risk layers were subsequently normalized using the SCALE function in PCI XPace^{TM} (PCI Geomatics 2004) to give relative selection. The SCALE function removed the effect of outliers and images were smoothed using a 3 × 3 pixel median filter to make a continuous risk surface. Each pixel was thus given a value relative to the chance of a sheep encountering a wolf or bear. Permanent lakes were masked and given RSF values of zero during the lambing, summer and fall months (periods of open water).

Results

Movement rates

We retrieved 42,420 GPS locations from 33 of the 36 collared Stone's sheep between January 2002 and December 2003. Of those locations 35,482 had consecutive 6-h fixes. We observed a 73.4 ± 2.80% ($\bar{x}$ ± SE) fix success rate from 33 individual collars with a minimum of 10% and maximum of 91%. The remaining three collars, and data they may contain, were unable to be recovered. The distances moved between 6-h fixes were similar between 2002 and 2003 (Fig. 2.2A). Movements decreased through the rut and winter seasons to a low in late winter of 23.8 ± 1.36 $m \cdot h^{-1}$ ($\bar{x}$ ± SE) and increased through lambing and summer to a high in fall of 98.8 ± 3.71 $m \cdot h^{-1}$ (Fig. 2.2B). The largest documented movement by an individual Stone's sheep in 6 h occurred during the fall of 2002 and covered a straight-line distance of 8496 m. The movement crossed a major valley and was repeated several times, to a lesser extent, during late August and September. These movements were related to the use of a mineral lick. There also were several instances when the distance moved between 6-h fixes was zero, indicating that an individual either did not move or returned to the same location during consecutive fixes. The changes in monthly movements (Fig. 2.2A) support our seasonal designations (Table 2.1).

Fig. 2.2. (A) Monthly and (B) seasonal movement rates ($m \cdot h^{-1}$, $\bar{x}$ ± SE) of Stone's sheep in the Besa-Prophet study area between January 2002 and December 2003. Values above error bars indicate the number of individuals that were averaged to calculate means and standard errors. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1.



Model development

During the fall, wolf risk and slope were highly collinear with tolerance scores of 0.13 and 0.14 respectively. The AIC values had a positive Δ_i of 33.158 in the most parameterized global model for fall when slope was substituted for wolf risk. This suggested that less was explained when using slope to approximate the "true model" during this season. Slope was subsequently removed from all fall models.

Zero-cell counts were problematic with the categorical attributes of no aspect (NASP) and riparian vegetation because of limited availability and often no use by sheep. Riparian and NASP were missing in the use locations for groups of Stone's sheep in ~73% (43/59) and 58% (34/59) of the models developed across seasons and years, respectively. NASP was subsequently excluded from all models and because of small sample sizes, riparian vegetation was excluded from all models except the global summer and fall models when the use of mineral licks was most prevalent. Zero-cell counts persisted in several other vegetation types seasonally (Table 2.4). Rockcrust contained the most cases (n = 14) for which there were no use or available locations in six seasons across the five sheep groups in 2002 and 2003. This was followed by subalpine spruce (n = 12), burn-deciduous (n = 11), burn-grass (n = 8), wet alpine (n = 3) and northerly aspects (n = 1). In most instances zero-cell counts occurred when there was a lack of Stone's sheep (use) locations in a habitat. Excluding no aspect and riparian vegetation, zero-cell counts were most abundant during lambing in the rockcrust vegetation type, which was also the only vegetation type that lacked locations in the available response variable (Table 2.4). Burned vegetation types (burn-deciduous, burn-grass) always had some use by Stone's sheep during late winter in both years of the study. This is in contrast to all other seasons, especially rut and early winter, which contained the most cases of no use.

Table 2.4. Number of groups of Stone's sheep for which seasonal habitat attributes were missing (zero-cell counts) in either the used or available response variable in seasonal resource selection models. Numbers are relative to a maximum of five groups of Stone's sheep in the Besa-Prophet study area, 2002-2003. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1.

		Year	Response	Season					
			Variable	EW	LW	L	S	F	R
Vegetation type	Riparian	2002	Used	4	5	2	2	1	3
			Available	1					
		2003	Used	4	3	4	2	2	2
			Available						
	Subalpine spruce	2002	Used	2	1	1		1	1
			Available						
		2003	Used		1		2	1	2
			Available						
	Rockcrust	2002	Used		2	3			1
			Available			1		1	
		2003	Used	1	1	1			
			Available		1	2			
	Wet alpine	2002	Used			1			
			Available						
		2003	Used		2				
			Available						
	Burn-deciduous	2002	Used	2		1	1		2
			Available						
		2003	Used	1			1	2	1
			Available						
	Burn-grass	2002	Used	2		1	1		1
			Available						
		2003	Used	1			1		1
			Available						
Aspect	No Aspect	2002	Used	4	5	4	3	2	2
			Available	2	2	1			1
		2003	Used	4	5	5	3	3	3
			Available	2	2	1			1
	North	2002	Used			1			
			Available						
		2003	Used						
			Available						

Seasonal selection across groups

The best global models of selection across the five groups of Stone's sheep consistently contained the most parameters (Table 2.5; Appendix B, Table B.1). Vegetation type, aspect, curvature, elevation and risk of wolf predation were attributes in each of the seasonal models. All but the fall model incorporated slope. When seasonally present, risk of bear predation and areas of high vegetative change were included. The probability that each of these global models was best (w_i) approached 1.0 during every season except late winter ($w_i = 0.991$), and the predictive ability ranged from a maximum $\bar{r}_s$ of 0.992 ($n = 5$, $P < 0.0001$) in early winter to a minimum $\bar{r}_s$ of 0.884 ($n = 5$, $P < 0.001$) in summer.

Specific topographic and vegetation factors were consistently selected by Stone's sheep in the B-P. Across seasons, animals selected for steeper slopes, convex curvatures and southerly aspects (as indexed by β_i different from zero) (Fig. 2.3). They selected for rock and dry alpine vegetation types all year and for burn-grass in early and late winter, lambing and fall (Fig. 2.4). Stone's sheep consistently avoided subalpine spruce vegetation types and easterly aspects across seasons, and conifer habitats during late winter, summer and fall. Northerly aspects were avoided except during summer (Fig. 2.3). Stone's sheep during the summer and rut did not select for burn vegetation types. During these seasons sheep avoided burn-deciduous the most of all vegetation classes (Fig. 2.4).

Stone's sheep tended to select upper elevations in the study area (Fig. 2.5) in summer, fall, rut and early winter. During late winter they selected for both upper and lower elevations, although the lowest elevation used by an individual occurred at ~1200 m, which was 150 m higher than the lowest elevation used during any other season. Lambing was the only season in

Table 2.5. The best resource selection models for Stone's sheep in the Besa-Prophet across and within groups, by season and year (2002-2003). Statistics include number of parameters (*K*), sample size (*n*), log likelihood (LL), Akaike's information Criteria (AIC), Akaike weights (w_i) and average Spearman's rank correlation ($\bar{r}_s$) from *k*-fold cross-validation procedure. ** and * indicate a $P <$ 0.01 and $P <$ 0.05 respectively, for the models ability to predict habitat attributes selected by Stone's sheep.

Group	Year	Season[a]	Model[b]	*K*	*n*	LL	AIC	w_i	$\bar{r}_s$
Global		EW	V+S+A+C+E+E^2+W	17	43058	-15237.390	30508.779	1.000	0.992**
Global		LW	V+S+A+C+E+E^2+W	17	61912	-22116.221	44266.441	0.991	0.982**
Global		L	V+S+A+C+E+E^2+W+B+Q	19	21482	-7265.025	14568.050	1.000	0.939**
Global		S	V+S+A+C+E+W+B+Q	19	42045	-13438.790	26915.580	1.000	0.884**
Global		F	V+A+C+E+W+B	17	51493	-18841.375	37716.750	1.000	0.970**
Global		R	V+S+A+C+E+W	16	20870	-7478.605	14989.210	1.000	0.987**
Neves	2002	EW	V+S+A+C+E+E^2+W	17	7904	-2537.361	5108.721	0.997	0.933**
Neves	2003	EW	V+S+A+C+E+E^2+W	17	7327	-2527.427	5088.854	1.000	0.938**
Neves	2002	LW	V+S+A+C+E+E^2+W	17	11388	-3836.929	7707.859	0.999	0.958**
Neves	2003	LW	V+S+A+C+E+E^2+W	16	9524	-3268.646	6569.293	1.000	0.977**
Neves	2002	L	V+S+A+C+E+E^2+W+B+Q	18	4563	-1349.464	2734.929	0.993	0.849**
Neves	2003	L	V+S+A+C+E+E^2+W+B+Q	19	3540	-1065.411	2168.821	1.000	0.880**
Neves	2002	S	V+S+A+C+E+E^2+W+B+Q	19	7920	-2426.739	4891.478	1.000	0.841**
Neves	2003	S	V+S+A+C+E+E^2+W+B+Q	19	6904	-2152.864	4343.727	1.000	0.849**
Neves	2002	F	S+A+C+E+E^2	8	11019	-3948.963	7913.927	0.975	0.908**
Neves	2003	F	V+A+C+E+E^2+W+B	17	7932	-2874.645	5783.290	1.000	0.966**
Neves	2002	R	V+S+A+C+E+W	16	8180	-2791.740	5615.481	1.000	0.942**
Neves	2003	R	V+S+A+C+E+E^2	16	4222	-1579.387	3190.774	1.000	0.935**
Tenmile	2002	EW	V+S+A+C+E+E^2+W	17	2316	-714.198	1462.397	1.000	0.847**
Tenmile	2003	EW	S+A+C+E+E^2	8	267	-105.974	228.383[c]	0.996	0.499
Tenmile	2002	LW	V+S+A+C+E+E^2+W	16	1601	-460.879	953.758	0.999	0.658*
Tenmile	2003	LW	V+S+A+C+E+E^2+W	15	1921	-526.396	1082.791	1.000	0.817**
Tenmile	2002	L	V+S+A+C+E+E^2+W+B+Q	15	451	-142.186	315.337[c]	1.000	0.738*

Table 2.5: Continued

Group	Year	Season[a]	Model[b]	*K*	*n*	LL	AIC	w_i	$\bar{r}_s$
Tenmile[d]	2003	L	V+S+A+C+W+B+Q	16	907	-272.105	576.211	0.690	0.822**
	2003	L	V+S+A+C+E+E^2+W+B+Q	18	907	-270.834	577.668	0.309	0.790**
Tenmile	2002	S	V+S+A+C+E+E^2+W+B+Q	17	1094	-268.878	571.757	1.000	0.665*
Tenmile	2003	S	V+S+A+C+E+E^2+W+B+Q	16	1893	-467.648	967.295	1.000	0.810**
Tenmile[d]	2002	F	V+A+C+W+B	14	1499	-322.010	672.021	0.643	0.641*
	2002	F	V+A+C+E+W+B	15	1499	-321.578	673.157	0.357	0.593
Tenmile	2003	F	V+A+C+E+E^2+W+B	16	785	-185.869	403.738	0.958	0.663*
Tenmile	2002	R	V+S+A+C+E+E^2+W	13	1216	-457.616	941.232	1.000	0.818**
Firstfork[d]	2002	EW	V+S+A+C+W	12	1625	-552.253	1128.505	0.836	0.857**
	2002	EW	V+S+A+C+E+E^2+W	14	1625	-551.852	1131.703	0.164	0.882**
Firstfork	2003	EW	V+S+A+C+E+E^2+W	17	3123	-1030.808	2095.616	1.000	0.918**
Firstfork[d]	2002	LW	V+S+A+C+E+E^2+W	17	3539	-1091.556	2217.111	0.746	0.870**
	2002	LW	V+S+A+C+W	15	3539	-1094.649	2219.297	0.254	0.894**
Firstfork	2003	LW	V+S+A+C+E+E^2+W	17	3518	-1172.141	2378.281	1.000	0.919**
Firstfork	2002	L	V+S+A+C+E+E^2+W+B+Q	17	1128	-406.095	846.191	1.000	0.902**
Firstfork	2003	L	V+S+A+C+E+W+B+Q	17	1561	-510.419	1054.838	0.999	0.858**
Firstfork	2002	S	V+S+A+C+E+E^2+W+B+Q	19	2398	-593.254	1224.508	1.000	0.790**
Firstfork	2003	S	V+S+A+C+E+E^2+W+B+Q	19	2952	-807.169	1652.339	1.000	0.867**
Firstfork	2002	F	V+A+C+E+E^2+W+B	17	3079	-1119.744	2273.488	0.998	0.942**
Firstfork	2003	F	V+A+C+E+E^2+W+B	17	3228	-1059.394	2152.787	1.000	0.955**
Firstfork	2002	R	V+S+A+C+E+E^2+W	17	2507	-863.814	1761.628	1.000	0.921**
Firstfork[d]	2003	R	V+S+A+C+E+E^2	15	806	-288.585	607.170	0.650	0.805**
	2003	R	S+A+C+E+E^2	8	806	-296.401	608.801	0.350	0.737*
Townsley	2002	EW	V+S+A+C+E+E^2+W	17	6881	-2325.728	4685.456	1.000	0.970**
Townsley	2003	EW	V+S+A+C+E+E^2+W	17	5990	-1805.791	3645.581	1.000	0.939**
Townsley	2002	LW	V+S+A+C+E+E^2+W	17	11108	-3950.812	7935.623	1.000	0.945**
Townsley	2003	LW	V+S+A+C+E+E^2+W	17	7871	-2621.550	5277.099	1.000	0.958**

Table 2.5: Continued

Group	Year	Season[a]	Model[b]	*K*	*n*	LL	AIC	w_i	$\bar{r}_s$
Townsley	2002	L	V+S+A+C+E+E^2+W+B+Q	19	3844	-1299.447	2636.893	0.990	0.928**
Townsley	2003	L	V+S+A+C+E+W+B+Q	18	2034	-692.986	1421.972	1.000	0.913**
Townsley	2002	S	V+S+A+C+E+E^2+W+B+Q	19	7017	-2263.962	4565.924	1.000	0.926**
Townsley	2003	S	V+S+A+C+E+E^2+W+B+Q	19	4365	-1334.458	2706.916	1.000	0.891**
Townsley[d]	2002	F	V+A+C+E+E^2+W+B	17	8395	-2934.228	5902.456	0.744	0.878**
	2002	F	V+A+C+W+B	15	8395	-2937.302	5904.604	0.256	0.865**
Townsley	2003	F	V+A+C+E+E^2+W+B	17	6966	-2374.425	4782.849	1.000	0.928**
Townsley	2002	R	V+S+A+C+E+ W	16	6400	-2152.011	4336.023	1.000	0.948**
Townsley	2003	R	V+S+A+C+E+E^2	16	3619	-1291.011	2614.023	1.000	0.905**
Richards	2002	EW	V+S+A+C+E+E^2+W	14	2880	-1042.239	2112.477	1.000	0.894**
Richards	2003	EW	V+S+A+C+E+E^2+W	15	3886	-1248.856	2527.713	1.000	0.937**
Richards	2002	LW	V+S+A+C+E+E^2+W	15	4985	-1522.168	3074.337	1.000	0.937**
Richards	2003	LW	V+S+A+C+E+E^2+W	16	5936	-1724.365	3480.731	1.000	0.938**
Richards	2002	L	V+S+A+C+E+E^2+W+B+Q	18	1737	-504.648	1045.296	1.000	0.836**
Richards	2003	L	V+S+A+C+E+E^2+W+B+Q	19	1436	-451.955	941.910	0.999	0.822**
Richards	2002	S	V+S+A+C+E+E^2+W+B+Q	19	2980	-944.706	1927.413	1.000	0.873**
Richards	2003	S	V+S+A+C+E+E^2+W+B+Q	18	2843	-924.427	1884.853	1.000	0.949**
Richards[d]	2002	F	V+A+C+W+B^2	14	3152	-1080.804	2189.609	0.535	0.930**
	2002	F	V+A+C+E+E^2+W+B	16	3152	-1078.926	2189.851	0.465	0.936**
Richards	2003	F	V+A+C+E+E^2+W+B	15	3336	-1233.704	2497.409	1.000	0.959**
Richards[d]	2002	R	V+S+A+C+E+E^2+W	16	2363	-874.575	1781.150	0.623	0.830**
	2002	R	V+S+A+C+W	14	2363	-877.435	1782.269	0.365	0.795**
Richards	2003	R	V+S+A+C+E	12	1330	-526.114	1076.228	0.982	0.796**

[a] EW=Early winter, LW=Late winter, L=Lambing, S=Summer, F=Fall, R=Rut; as defined in Table 2.1.

[b] V=Vegetation type, S=Slope, A=Aspect, C=Curvature, E=Elevation, W=Wolf risk, B=Bear risk, Q=Vegetation quality.

[c] corrected AIC (AIC_c).

[d] models were averaged to determine selection coefficients for habitat attributes.

Fig. 2.3. Habitat attributes from the best global resource selection models by season for Stone's sheep in the Besa-Prophet, 2002-2003. Selection coefficients ($\beta_i \pm$ SE) for slope, curvature, wolf risk, bear risk, vegetation quality and four aspects are presented. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1. Seasons for which an attribute could not be incorporated into a model are not shown. * indicates each seasonal β_i is different from zero based on 95% confidence intervals.

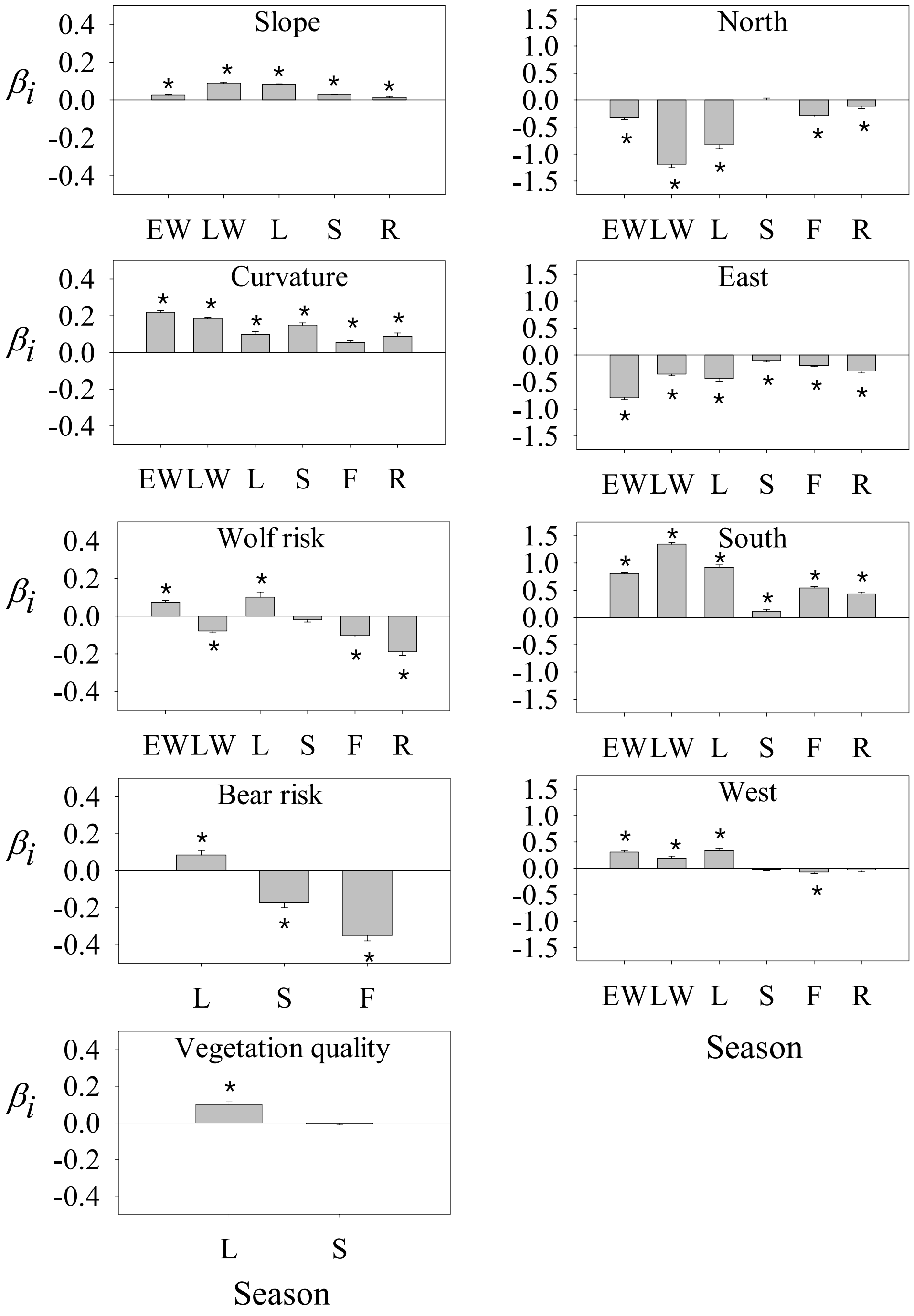


Fig. 2.4. Vegetation types and their selection coefficients (β_i ± SE) from the best global resource selection models by season for Stone's sheep in the Besa-Prophet, 2002-2003. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1. Seasons for which an attribute could not be incorporated into a model are not shown. * indicates each seasonal β_i is different from zero based on 95% confidence intervals.

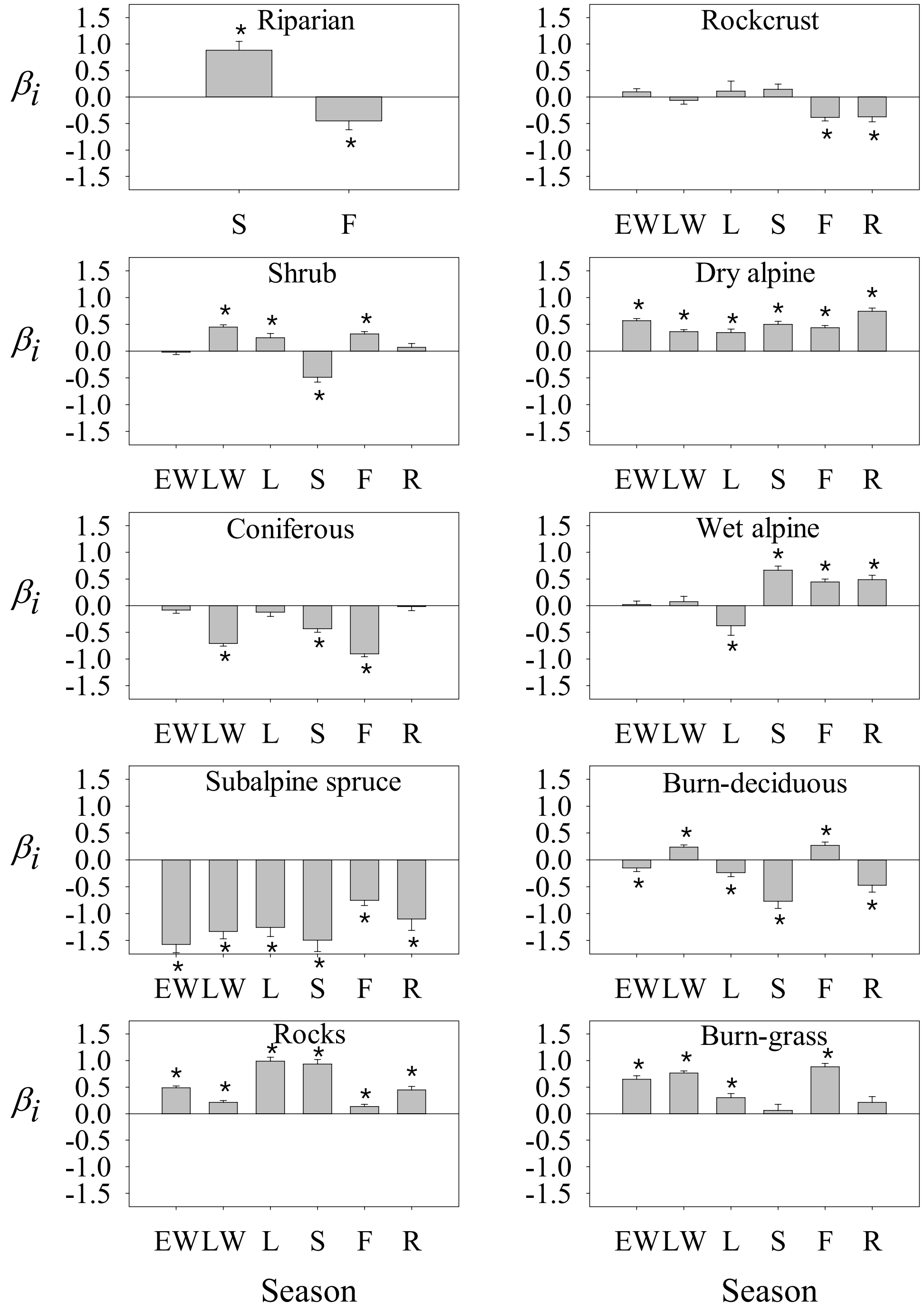
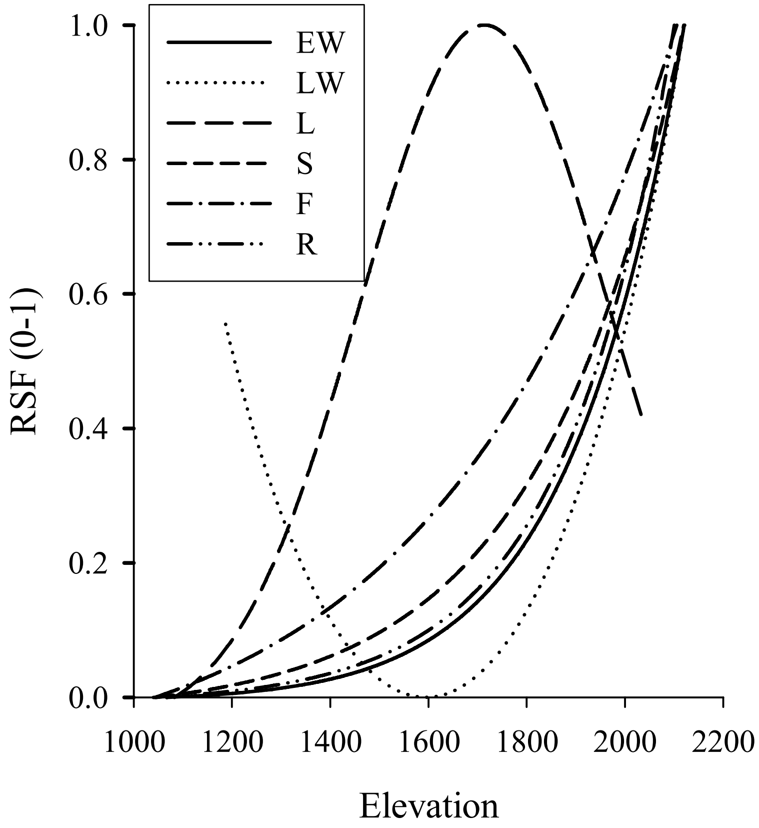


Fig. 2.5. Relative selection for elevation by Stone's sheep in the Besa-Prophet, 2002-2003, in the best global resource selection models. The selection functions were determined by holding habitat variables in the model constant while multiplying β_i of elevation by actual elevations from locations used by Stone's sheep within that season and subsequently scaled between 0-1. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1.



which Stone's sheep did not select for highest elevations, but rather elevations around 1700 m (Fig. 2.5).

Sheep selected for vegetation quality and were exposed to the highest risk of bear and wolf predation, relative to other seasons, during lambing (Fig. 2.3). In summer they avoided areas frequented by bears and appeared indifferent in their use of vegetation quality and risk of predation from wolves. In fall, they selected areas with low risk of predation from either predator species.

Seasonal selection within groups

Within each group of Stone's sheep the best seasonal selection models each year tended to contain the most parameters and all incorporated vegetation type, aspect, curvature and elevation (Appendix B, Table B.1). Only two of the 59 seasonal models were not the most saturated (i.e., contained the model with the most parameters) or were not averaged with a saturated model (Table 2.5). Stone's sheep selected for different variables, however, between 2002 and 2003 in 32% (8/25) of the cases. These differences included instances when models were averaged and even if the top ranking models with the lowest AIC were similar between years. This excludes the rut season when estimates of wolf risk were not available in November and December 2003.

The ability of seasonal models to predict the habitat attributes selected by groups of Stone's sheep was generally excellent. Across the five groups the seasonal variation in the predictive ability of models ranged from a low in summer with an average $\bar{r}_s$ of 0.846 ± 0.008 ($\bar{x}$ ± SD, $n = 5$) to an average high in late winter of 0.898 ± 0.010 ($n = 5$). There were only two instances, both in the Tenmile group during early winter 2003 and fall 2002, when the predictive ability of top-ranking models was not significant (lowest $\bar{r}_s = 0.499$, $n = 5$, $P = 0.142$) (Table 2.5).

Predicting resource selection by Stone's sheep was better when more than one habitat factor was incorporated in a model (Table 2.6). Of the three factors (vegetation, risk of predation, topography) used in developing predictive models, topography typically ranked higher in explaining the variation in attributes selected, by consistently having the lowest $\bar{\Delta}_i$ between years. Topography often contained fewer parameters than the vegetation factor, yet it always ranked better than mixed models incorporating both vegetation and risk of predation. Risk of predation from wolves consistently ranked the lowest followed by bear risk (Table 2.6).

Within groups of Stone's sheep, there were few consistencies among seasons and between years in the selection of habitat attributes (Table 2.7 and Table 2.8) even though model selection (Table 2.5) and relative rank of habitat factors were similar (Table 2.6). The most notable consistency exhibited across all groups of Stone sheep was the avoidance and indifference towards subalpine spruce vegetation. Groups of sheep rarely selected concave curvatures or avoided southerly aspects (except in a few cases during summer and rut). In both winter seasons Stone's sheep preferred ridges, mountain tops and sloped hillsides, not selecting concave or gully-like topography. During late winter all groups of Stone's sheep selected for steep southerly slopes and avoided northerly aspects. More groups selected for dry alpine vegetation than any other vegetation type at this time. Stone's sheep never avoided rock and rockcrust vegetation or areas of high vegetative quality during lambing. In summer groups of sheep often selected rock and dry alpine vegetation types. Stone's sheep either selected or were indifferent in their use of burns during the fall and burn-grass vegetation was never avoided

Table 2.6. The relative rank of habitat factors developed by season for five groups of Stone's sheep in the Besa-Prophet from 2002 and 2003 using the average change in AIC ($\bar{\Delta}_i$). Smaller values indicate models that, on average, rank better at achieving parsimony. Values in parentheses indicate the number of groups for which a model was developed. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1. Sample sizes are given in parentheses under each entry.

	Season					
Model[a]	EW	LW	L	S	F	R
	$\bar{\Delta}_i$	$\bar{\Delta}_i$	$\bar{\Delta}_i$	$\bar{\Delta}_i$	$\bar{\Delta}_i$	$\bar{\Delta}_i$
V+S+A+C+E+(E^2)+W+B^b+Q^b	1.431 (10)	0.000 (10)	0.146 (10)	0.000 (10)	0.867 (10)	0.000 (5)
V+S+A+C+W+B+Q			29.023 (10)	128.393 (10)		
V+S+A+C+W+B^b	115.997 (10)	81.615 (10)	32.082 (10)	133.574 (10)	24.020 (10)	75.063 (9)
S+A+C+E+(E^2)	72.878 (10)	191.730 (10)	61.623 (10)	160.228 (10)	69.920 (10)	48.892 (9)
V+W+B+Q			221.467 (10)	251.609 (10)		
V+W+B^b	481.908 (10)	747.153 (10)	233.448 (10)	257.378 (10)	137.205 (10)	171.044 (5)
V+S	483.500 (10)	503.381 (10)	173.904 (10)	309.483 (10)	361.901 (10)	253.894 (9)
V+Q			294.964 (10)	336.585 (10)		
V	565.711 (10)	823.819 (10)	319.444 (10)	342.623 (10)	439.782 (10)	301.449 (9)
B			499.717 (10)	540.398 (10)	551.622 (10)	
W	902.733 (10)	1335.255 (10)	528.803 (10)	790.693 (10)	995.484 (10)	481.496 (5)

[a] V=Vegetation type, S=Slope, A=Aspect, C=Curvature, E=Elevation, W=Wolf risk, B=Bear risk, Q=Vegetation quality.

[b] seasonally available habitat attributes.

Table 2.7. The number of Stone's sheep groups that selected (+) or avoided (-) slope, aspect, curvature, elevation, wolf risk and bear risk based on 95% confidence intervals around selection coefficients (β_i) in the best resource selection models by year (2002, 2003). Numbers in parentheses are the number of groups for which an attribute was found in the best model. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1.

		Year	β_i Sign or Shape	Season					
				EW	LW	L	S	F	R
Slope		2002	-	1(5)	0(5)	0(5)	1(5)		1(5)
			+	4(5)	5(5)	5(5)	3(5)		2(5)
		2003	-	1(5)	0(5)	0(5)	0(5)		1(4)
			+	2(5)	5(5)	5(5)	5(5)		3(4)
Aspect	North	2002	-	3(5)	5(5)	3(4)	1(5)	3(5)	0(5)
			+	0(5)	0(5)	0(4)	3(5)	0(5)	1(5)
		2003	-	3(5)	5(5)	3(5)	0(5)	3(5)	0(4)
			+	0(5)	0(5)	0(5)	1(5)	0(5)	2(4)
	East	2002	-	5(5)	3(5)	1(5)	2(5)	2(5)	3(5)
			+	0(5)	0(5)	2(5)	1(5)	1(5)	0(5)
		2003	-	5(5)	2(5)	1(5)	2(5)	1(5)	3(4)
			+	0(5)	1(5)	0(5)	2(5)	0(5)	0(4)
	South	2002	-	0(5)	0(5)	0(5)	1(5)	0(5)	1(5)
			+	4(5)	5(5)	3(5)	3(5)	4(5)	2(5)
		2003	-	0(5)	0(5)	0(5)	1(5)	0(5)	1(4)
			+	4(5)	5(5)	2(5)	2(5)	3(5)	3(4)
	West	2002	-	0(5)	1(5)	0(5)	2(5)	3(5)	1(5)
			+	4(5)	2(5)	2(5)	0(5)	1(5)	2(5)
		2003	-	0(5)	0(5)	0(5)	2(5)	1(5)	0(4)
			+	5(5)	2(5)	4(5)	2(5)	1(5)	1(4)
Curvature		2002	-	0(5)	0(5)	0(5)	0(5)	0(5)	0(5)
			+	5(5)	4(5)	3(5)	4(5)	1(5)	2(5)
		2003	-	0(5)	0(5)	0(5)	1(5)	0(5)	1(4)
			+	4(5)	5(5)	3(5)	3(5)	0(5)	2(4)
Elevation		2002	$\cap^a$	3(5)	3(5)	4(5)	1(5)	0(5)	0(5)
			U^b	0(5)	0(5)	0(5)	3(5)	2(5)	2(5)
			$/^c$	0(5)	0(5)	0(5)	0(5)	1(5)	2(5)
		2003	$\cap^a$	2(5)	5(5)	1(5)	0(5)	0(5)	1(4)
			U^b	2(5)	0(5)	0(5)	3(5)	2(5)	1(4)
			$/^c$	0(5)	0(5)	2(5)	0(5)	0(5)	1(4)
Wolf risk		2002	-	2(5)	4(5)	0(5)	2(5)	1(4)	2(5)
			+	2(5)	1(5)	3(5)	0(5)	2(4)	2(5)
		2003	-	0(4)	0(5)	1(5)	1(5)	3(5)	0(0)
			+	2(4)	5(5)	1(5)	2(5)	0(5)	0(0)

Table 2.7. Continued

	Year	β_i Sign or Shape	Season					
			EW	LW	L	S	F	R
Bear risk	2002	-			0(5)	1(5)	3(4)	
		+			2(5)	1(5)	0(4)	
	2003	-			0(5)	2(5)	2(5)	
		+			5(5)	0(5)	0(5)	

[a] ∩ indicates selection for mid elevations where β_i is positive for elevation and negative for elevation^2.

[b] ∪ indicates positive selection for low and high elevations where β_i is negative for elevation and positive for elevation^2.

[c] β_i for linear elevation was always a positive coefficient (/).

Table 2.8. The number of Stone's sheep groups that selected (+) or avoided (-) vegetation types and quality based on 95% confidence intervals around selection coefficients (β_i) in the best resource selection models by year (2002, 2003). Numbers in parentheses are the number of groups for which an attribute was found in the best model. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1.

		Year	β_i Sign	Season					
				EW	LW	L	S	F	R
Vegetation type	Shrub	2002	-	3(5)	2(5)	1(5)	2(5)	0(4)	2(5)
			+	0(5)	2(5)	1(5)	1(5)	2(4)	1(5)
		2003	-	1(4)	1(5)	0(5)	2(5)	1(5)	1(4)
			+	2(4)	3(5)	3(5)	1(5)	3(5)	1(4)
	Conifer	2002	-	2(5)	4(5)	0(5)	1(5)	2(4)	1(5)
			+	2(5)	0(5)	0(5)	0(5)	1(4)	2(5)
		2003	-	0(4)	3(5)	0(5)	3(5)	2(5)	0(4)
			+	2(4)	1(5)	2(5)	0(5)	0(5)	1(4)
	Subalpine spruce	2002	-	2(3)	3(4)	3(4)	2(5)	2(3)	1(4)
			+	0(3)	0(4)	0(4)	0(5)	0(3)	0(4)
		2003	-	2(4)	3(4)	2(5)	2(3)	1(4)	1(2)
			+	0(4)	0(4)	0(5)	0(3)	0(4)	0(2)
	Rocks	2002	-	0(5)	0(5)	0(5)	0(5)	2(4)	0(5)
			+	5(5)	2(5)	5(5)	3(5)	1(4)	3(5)
		2003	-	1(4)	1(5)	0(5)	0(5)	3(5)	1(4)
			+	2(4)	4(5)	2(5)	4(5)	1(5)	0(4)
	Rockcrust	2002	-	0(5)	0(3)	0(2)	1(5)	2(3)	1(4)
			+	2(5)	1(3)	0(2)	1(5)	0(3)	0(4)
		2003	-	1(4)	1(4)	0(3)	1(5)	3(5)	2(4)
			+	0(4)	2(4)	0(3)	1(5)	0(5)	1(4)
	Dry alpine	2002	-	1(5)	0(5)	0(5)	0(5)	1(4)	1(5)
			+	3(5)	4(5)	0(5)	4(5)	1(4)	2(5)
		2003	-	0(4)	0(5)	0(5)	0(5)	0(5)	0(4)
			+	3(4)	3(5)	3(5)	2(5)	2(5)	3(4)
	Wet alpine	2002	-	0(5)	0(5)	0(4)	0(5)	1(4)	1(5)
			+	0(5)	1(5)	0(4)	2(5)	1(4)	2(5)
		2003	-	1(4)	0(3)	1(5)	0(5)	0(5)	0(4)
			+	0(4)	0(3)	0(5)	2(5)	4(5)	1(4)
	Burn-deciduous	2002	-	1(3)	2(5)	0(4)	2(4)	0(4)	1(3)
			+	0(3)	1(5)	1(4)	0(4)	1(4)	1(3)
		2003	-	0(3)	2(5)	3(5)	0(4)	0(3)	0(3)
			+	2(3)	2(5)	0(5)	0(4)	1(3)	1(3)
	Burn-grass	2002	-	0(3)	1(5)	0(4)	0(4)	0(4)	0(4)
			+	2(3)	3(5)	1(4)	0(4)	3(4)	1(4)
		2003	-	0(3)	1(5)	1(5)	0(4)	0(5)	0(3)
			+	2(3)	2(5)	0(5)	1(4)	1(5)	1(3)

Table 2.8. Continued

	Year	β_i Sign	EW	LW	L	S	F	R
					Season			
Vegetation quality	2002	-			0(5)	0(5)		
		+			2(5)	2(5)		
	2003	-			0(5)	1(5)		
		+			1(5)	0(5)		

during the rut and early winter.

Groups of Stone's sheep in the B-P exhibited substantial interannual variation in their selection of habitat. Stone's sheep had the most consistent selection of habitat attributes between years during the winter seasons (Table 2.9). Approximately 47% (8/17) and 41% (7/17) of habitat attributes were consistently selected in 2002 and 2003 by at least 75% of the Stone's sheep groups during early and late winter, respectively. This is in contrast to the consistency in interannual selection of habitat attributes during summer (37%, 7/19), rut (25%, 4/16), lambing (21%, 4/19) and fall (6%, 1/17) by ≥75% of the groups. Three quarters of Stone's sheep groups also selected for curvature and against subalpine spruce consistently in four of the six seasons and for slope 60% of the year. Fall was the only season when no attribute was ever selected consistently by three-quarters of sheep groups between years.

Groups of Stone's sheep selected resources differently from the predictions of global models in several instances (Fig. 2.3 and Fig. 2.4). This was most prevalent for attributes that Stone's sheep were least consistent in selecting between years. Across groups during late winter, Stone's sheep selected for high and low elevations (Fig. 2.5), but within each group all selected for mid-elevations in their seasonal ranges. Elevation was also selected differently during the summer, fall and rut seasons when most groups of sheep selected for nonlinear elevations, predominantly the high and low areas found within their seasonal distribution. This is in contrast to the linear function for elevation in the global models. Stone's sheep across groups avoided areas of high wolf risk most predominantly during the rut (Fig. 2.3), but within groups they were indifferent in 2003, and in 2002, two groups selected areas where wolf risk was higher than what was available and two groups avoided areas with increased wolf risk (Table 2.7).

Table 2.9. The number of Stone's sheep groups that were consistent in their selection, avoidance or indifference to habitat attributes between 2002 and 2003, in the Besa-Prophet. Values in parentheses indicate the number of groups for which an attribute was found in both of the best models for 2002 and 2003. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut; as defined in Table 2.1.

	EW	LW	L	S	F	R
Elevation	0(5)	2(5)	0(5)	3(5)	2(5)	1(4)
Quality			2(5)	2(5)		
Slope	3(5)	5(5)	5(5)	3(5)		3(4)
Curvature	4(5)	4(5)	3(5)	4(5)	4(5)	2(4)
Bear risk			2(5)	4(5)	0(4)	
Wolf risk	1(4)	1(5)	3(5)	2(5)	2(4)	
North	5(5)	5(5)	2(4)	2(5)	2(5)	2(4)
East	5(5)	3(5)	3(5)	2(5)	2(5)	4(4)
South	3(5)	5(5)	2(5)	4(5)	2(5)	2(4)
West	4(5)	2(5)	3(5)	1(5)	2(5)	2(4)
Shrub	0(4)	3(5)	2(5)	3(5)	2(4)	2(4)
Coniferous	2(4)	4(5)	3(5)	1(5)	2(4)	2(4)
Subalpine spruce	2(2)	3(4)	3(4)	2(3)	0(3)	2(2)
Rocks	2(4)	2(5)	2(5)	4(5)	2(4)	2(4)
Rockcrust	2(4)	0(3)	2(2)	5(5)	1(3)	2(4)
Dry alpine	4(4)	2(5)	2(5)	3(5)	2(4)	3(4)
Wet alpine	3(4)	2(3)	3(4)	5(5)	1(4)	1(4)
Burn-deciduous	0(2)	4(5)	1(4)	2(4)	1(2)	1(3)
Burn-grass	2(2)	2(5)	2(4)	3(4)	1(4)	1(3)

There were also vegetation types that differed between global models and individual group models. The selection for burn-deciduous vegetation was strongest in fall according to global models (Fig. 2.4), but only one group of sheep selected burn-deciduous each year (Table 2.8). The global model also suggested that sheep strongly selected rock all year including fall (Fig. 2.4), which is in contrast to the selection strategies within groups that mostly avoided rocks (Table 2.8).

Discussion

Seasonal habitat selection

This is the first comprehensive analysis of habitat selection by Stone's sheep. As with other species, defining the selection of habitats is constrained by technological, biological and statistical factors. Habitat bias and missing data in the GPS collars can be of concern (D'Eon et al. 2002; Frair et al. 2004). Selection bias from habitat attributes within the seasonal ranges of Stone's sheep, however, was minimal given very few timbered habitats and low crown closure and tree heights when present. The inability of logistic regression to accommodate explanatory variables that have missing data (zero-cell count) in either the used or available response variable (Menard 2002) limits the inferences that can be made regarding selection of a habitat attribute because that attribute is excluded from modeling. This was especially notable with the lack of use locations for some attributes, which may indeed be avoidance of particular attributes by Stone's sheep. Arguably Stone's sheep in the B-P avoided riparian habitats unless using licks or accessing new ranges. Stone's sheep used licks, which were within or contained riparian habitat, most frequently during the summer season and, therefore, showed a strong selection for riparian habitats at this time. Locations of Stone's sheep at licks occurred in all seasons except late winter, when all but one group lacked use locations in riparian habitats (Table 2.4). The spatial and temporal influence of licks on Stone's sheep is well recognized (Geist 1971; Luckhurst 1973; Seip 1983; Ayotte 2004). Incorporating distance to lick(s), as an explanatory covariate, may improve selection models pending prior knowledge of lick locations and an appropriate GPS fix rate of sampling. Observations of Stone's sheep from the Tuchodi drainage of north-central British Columbia indicated considerable variation in the duration and frequency of lick use (Ayotte 2004). Fix rates exceeding the duration of an individual's visit would lead to inappropriate conclusions regarding the influence of licks on habitat use.

The seasonal movements exhibited by Stone's sheep may affect the resources available to them and the heterogeneity of those resources. Boyce et al. (2003) noted that a variable buffer size used in models may result in reduced habitat selection for areas that are most highly preferred because small buffers may include less habitat heterogeneity from which to measure selection. This was first highlighted by McLean et al. (1998) who used radiolocations as measures of use and found that as availability decreased from the study area to smaller buffer sizes, the ability to detect selection became more difficult. This could potentially be of special concern during late winter when Stone's sheep moved the least. Stone's sheep selected or avoided many habitat attributes to the strongest extent, however, during this season (Fig. 2.3 and Fig. 2.4) and showed a relatively high annual consistency for particular attributes at this time (Table 2.9). The fall was the most variable season in terms of selection by Stone's sheep (Table 2.9), and their movements and the availability of resources were greatest (Fig. 2.2). Nevertheless, inferences regarding selection strategies of Stone's sheep may have been influenced by changes in availability.

Early winter

During the early winter (January - February), Stone's sheep ewes generally selected for upper elevations and steep slopes along ridges and mountain tops with south and west-facing aspects (Fig. 2.3, Fig. 2.4, and Fig. 2.5). The early winters of 2002 and 2003 were relatively warm with little snow cover. Across all groups of Stone's sheep the dry alpine, rock and open burn-grass were the most highly selected vegetation types, whereas subalpine spruce and north and easterly aspects were the most strongly avoided. Across groups of Stone's sheep the risk of wolf predation was higher than what was available to them during this period of time.

Individual groups differed in their selection strategies from the models developed across all groups for this season with considerable interannual variation. In particular, the Richards group deviated substantially from global models. They selected flatter slopes across both years, corresponding with their use of several mid-elevation timbered knobs and large rocky outcrops.

During the early winter, avoidance of the subalpine spruce habitat was strongest. The habitat is generally densely timbered with short spruce and subalpine fir stands, often referred to as krummholz. It has limited graminoid understory with extremely poor visibility, both of which likely contribute to the strong avoidance. Decreased habitat visibility has been well documented to negatively affect selection (Shannon et al. 1975;

Tilton and Willard 1982; Risenhoover and Bailey 1985; Bentz and Woodward 1988; Smith et al. 1999) and foraging efficiency of bighorn sheep (Risenhoover and Bailey 1985).

Late winter

During the late winter season (March – 14 May), Stone's sheep showed the strongest selection for sites with steep slopes and southerly aspects compared to other seasons. All groups, except for one in 2002, also selected for convex curvatures during this time. The interaction between slope and aspect contributes to the amount of solar radiation and subsequent air temperature of a site (Kumar et al. 1997), whereas the convexity or shape of a site influences the deposition of snow and exposure to wind (Pomeroy et al. 1998). Both increased air temperatures and wind exposure contribute to a reduction in the amount of snow a site receives (Pomeroy et al. 1998). Deep snow and lack of wind contributed to a large die-off of Dall's sheep in the Yukon (Burles and Hoefs 1984). The selection for steep slopes by Stone's sheep may also be in response to predator evasion opportunities (Geist 1971; Daily and Hobbs 1989).

Snow is important in the selection of late-winter habitats by Stone's sheep (Geist 1971; Seip and Bunnell 1985*b*) and other North American sheep (Hoefs and Cowan 1979; Tilton and Willard 1982; Goodson et al. 1991). It affects both foraging efficiency (Geist 1971; Goodson et al. 1991) and energetic expenditures (Dailey and Hobbs 1989). Seip and Bunnell (1985*b*) noted that Stone's sheep avoided areas once snow depths reached 30 cm, which is approximately front knee height of mountain sheep (Geist 1971). Stone's sheep in the B-P appeared to exhibit two strategies during late winter, highlighted by their selection for low and high elevations (Fig. 2.5). These two strategies may relate to accessing forage of the highest quality depending on its availability (Seip and Bunnell 1985*b*). Lower elevations tend to have warmer temperatures on south and westerly aspects whereas higher elevations may have increased exposure to wind (Geist 1971; Hoefs and Cowan 1979). Within groups, most appeared to use only one of the strategies in late winter. All groups selected for mid-elevations within their late winter distribution, although the range of elevations available to each group differed considerably during this time.

Although the constraints of snow can limit the distribution and influence the selection of habitat by sheep, vegetation type was also important. Stone's sheep in late winter most strongly selected burn-grass followed by shrub, dry alpine and burn-deciduous types. All groups of Stone's sheep selected for dry alpine vegetation throughout the year, but other vegetation types, especially shrub, were selected strongly during late winter. The shrub and burn vegetation types have higher vegetation biomass than dry alpine, but potentially at the expense of increased snow depths. Pomeroy et al. (1998) reported that increasing vegetation height and density lessen the variation in snow water equivalents whereas reduced vegetation cover creates highly variable snow conditions. Brushier habitats have more evenly distributed snow in comparison to low vegetation habitats with high variation in snow depths as a result of increased differences in wind patterns (Pomeroy et al. 1998). This relationship between vegetation and wind appears to be especially important in determining habitat selection by Stone's sheep during years of high snowfall (Seip and Bunnell 1985*a*).

Two of the most strongly selected vegetation types by Stone's sheep during late winter were burn-grass and burn-deciduous. All ungulates in the B-P, except caribou, have been documented to use burns during the winter (Hobbs and Spowart 1984; Peck and Peek

1991; Pearson et al. 1995; Weixelman et al. 1998). More groups of Stone’s sheep selected for burned areas in the late winter season than any other season.

Lambing

Newborn lambs were first observed during the initial week of June in the B-P during 2002 and 2003. Stone’s sheep generally selected for mid-elevations during the lambing season (15 May – 14 June) and across a more consistent range of elevations than was observed between groups during late winter. In the Neves Valley of the B-P, Luckhurst (1973) observed Stone's sheep ewes seeking rocky terrain to have their lambs in late May and early June. This is consistent with observations from the Cassiar Mountains of British Columbia where lambing by Stone's sheep also began during the first week of June (Geist 1971).

Across groups, Stone’s sheep selected for dry alpine, burn-grass, shrub and especially rock areas during lambing (Fig. 2.4). They also selected for areas with increased vegetation quality from the emergence of new plant growth. Burned areas have been identified as promoting plant growth earlier in the spring (Hobbs and Spowart 1984; Seip and Bunnell 1985*b*). The selection for these areas, however, was at an apparent increased risk of predation from both wolves and grizzly bears. Although bears may be responding primarily to new plant growth, their predation on thinhorn sheep has been observed (reviewed in Hoefs and Cowan 1979). The increased risk of predation observed by sheep during the lambing season may have been in response to relatively late springs, especially in 2002, which delayed plant green-up. Sheep may place themselves at a higher risk of predation in order to access higher quality forage. Hoefs et al. (1986) observed especially high wolf mortality during the lambing season after a severe winter, which they partially attributed to a delay in plant green-up. Most mortalities occurred in May with over 70% attributed to predation (Burles and Hoefs 1984).

The variability and relative lack of consistency in annual selection of more habitat attributes during lambing by Stone's sheep may be attributed to the timing of new plant growth and maternal status of ewes. Within groups, Stone's sheep had the strongest selection for rock, no group ever avoided areas of high vegetative quality (Table 2.8) and all groups, both years, selected for steep slopes (Table 2.9) during lambing. The trade-off between forage and predation risk in female mountain sheep during lambing is well documented (Festa-Bianchet 1988, Berger 1991; Bleich et al. 1997; Rachlow and Bowyer 1998). Both Geist (1971) and Luckhurst (1973) observed intrasexual segregation of Stone's sheep ewes during parturition. Festa-Bianchet (1988), Berger (1991) and Bleich et al. (1997) helped explain the intrasexual segregation of bighorn ewes based on the trade-off between predation risk, forage quantity and forage quality. Predation risk during parturition by wild sheep seems to dictate selection of lambing sites whereas timing and synchrony of parturition may be influenced more by climatic variables, especially in northern latitudes (Rachlow and Bowyer 1998). We were unable to determine whether collared individuals were parturient or non-parturient during our study. Incorporating maternal status and an annual vegetative quality layer would likely improve our understanding of selection during this season.

Summer

The progression from lambing to summer resulted in several differences in habitat selection by Stone's sheep. Movements were more variable during the summer season (15

June – 14 August), and the strength of selection for most habitat attributes was at their lowest across all groups. All habitats became readily available to sheep with the lack of snow at this time. In contrast to other seasons when sheep avoided northerly aspects, several groups actually selected for northerly aspects during 2002, and across groups there was no selection or avoidance. The warm southerly aspects were selected for least during the summer. Most groups also selected for both high and low elevations. The use of mineral licks by Stone's sheep was highest during late summer and early fall, which was probably responsible for the selection of low elevations by some groups during this time. Seip and Bunnell (1985*b*) and Hebert (1973) documented similar selection for increasingly higher vegetation types from lambing to summer which was explained as a form of environmental tracking by sheep to areas of more nutritious forage (Hebert 1973).

Stone's sheep were exposed to a lower risk of predation from both bears and wolves during summer, as compared to lambing. Most groups exhibited no selection or avoidance to either type of risk in their selection of resources during this time. Sheep no longer selected for areas of highest vegetative quality and had the lowest seasonal selection for burns and shrub vegetation types. Selection for wet alpine was most prevalent (Fig. 2.4) during summer with no groups avoiding it (Table 2.8). Wet alpine, which was typically covered by snow for much of the year, was one of the last habitats to green-up in summer and may have provided small-scale nutritious microsites.

Fall

Habitat selection and consistency in annual selection of habitats by Stone's sheep were variable during fall (15 August – 31 October). Groups showed a very weak association with elevation and selected all but mid-elevations in their seasonal ranges. They were generally non-selective in their use of curvature with only one group selecting convex or ridge-like sites (Table 2.7). The risk of predation during fall was generally low, and there were no consistencies in selection between years.

There was also a wide array of vegetation types selected during fall with most groups avoiding coniferous, subalpine spruce and rockcrust habitats (Fig. 2.4). There were noticeable differences in selection for riparian, shrub, rockcrust, burn-deciduous and burn-grass habitats between the summer and fall seasons. Selection of dry and wet alpine and rocks was highly variable between years, as exemplified by differences between groups, calling into question broad inferences that are made from global models.

Seip and Bunnell (1985*b*) documented that early fall was the time when Stone's sheep with different wintering strategies, related to access to burn areas, diverged in their selection of elevation. In the B-P, selection for burned and shrub vegetation was strongest when available during this season. Senescence of vegetation at high elevations in fall (Lay 2005) may partially explain the attraction for lower elevation burns.

Rut

Sheep have strong fidelity to breeding ranges and make large movements in order to access them (Geist 1971; Festa-Bianchet 1986). Most information regarding the breeding season of wild sheep pertains to reproductive strategies, but not to habitat selection. Changes in activity may be influenced more by reproductive decisions than nutritional ones (Geist 1971). Generally, the sites selected by Stone's sheep in the B-P during the rut (1 November – 31 December) were similar to other seasons in terms of steep slopes, convex curvatures, southerly aspects and dry and wet alpine vegetation. Their selection for burns was not as strong as during the fall (Fig. 2.4). Risk of wolf predation continued to decline from summer to fall to rut (Fig. 2.3). Groups selected for upper elevations and no group ever selected against northerly aspects.

The variation in selection strategies among groups persisted during the rut. Selection by the Richards group for flatter slopes during the rut as well as in early winter emphasizes the importance of habitat juxtaposition in quantifying selection (Mysterud and Ims 1998; Garshelis 2000). At scales less than Johnson's (1980) fourth-order selection, North American wild sheep have rarely (if ever) been shown to select for flat slopes.

Relative habitat rank

The habitat variables used to model selection of resources by Stone's sheep consisted of three components: topography, vegetation and risk of predation. Topography ranked consistently better than both vegetation and risk at describing habitat selection by Stone's sheep regardless of season and year. Although AIC may be biased toward models with more parameters when sample sizes are large (Burnham and Anderson 2002), models with more parameters incorporating vegetation, risk of predation and quality consistently had larger AIC scores (models were further from the "true model") than topography (Table 2.6). Vegetation and vegetation quality consistently ranked second to topography, whereas risk of wolf and bear predation consistently were the poorest in explaining the distribution of Stone's sheep at the measured scale.

The slope component of topography, particularly its role in defining escape terrain, has been well recognized as an integral component in the ecology of mountain sheep (Geist

1971; Risenhoover and Bailey 1985; Berger 1991; Bleich et al. 1997; Rachlow and Bowyer 1998; Bleich 1999). Sheep evade predation by fleeing to and in precipitous terrain (Geist 1971) and rapid flights up and down steep inclines, may have lead sheep to develop shorter, thicker legs to counter the increased stress associated with their antipredator strategies (Daily and Hobbs 1989). The association with steeper slopes has been used to classify suitable habitat and animal locations of other mountain Caprinae. Gross et al. (2002) subjectively defined escape terrain for mountain goats in Colorado as ≥33° and correctly classified 87% of their observations using distance to escape terrain. The Colorado study area lacked the diversity and concentration of predators generally found in the Northern Rockies where the association between escape terrain and habitat selection of Stone's sheep is likely influenced by more variables.

The influence of predation risk on habitat use and sexual segregation of sheep is well documented (Geist 1971; Festa-Bianchet 1988; Berger 1991; Bleich et al. 1997; Bleich 1999; Corti and Shackleton; 2002). Predation, particularly by wolves, is reported to be the leading cause of mortality of Stone's sheep in northern British Columbia (Bergerud and Elliot 1998, Luckhurst 1973). The lack of response to predation risk from wolves in the B-P at the scale we measured may be a result of several factors. Kie et al. (2002) demonstrated that ungulates may select for resource variables beyond their seasonal home ranges. If Stone's sheep select against risk at scales larger than their seasonal distribution, they may not have responded to perceived risk within seasonal ranges. However, selection for certain topographical attributes (e.g. steep slopes) may be a response to risk at smaller scales.

Stone's sheep probably respond to both actual and perceived risk in order to improve and maintain their fitness (Lima and Dill 1990). The perception of risk by sheep at the landscape level may be responsible for the lack of use locations in certain habitats and general selection for steep mountainous terrain where predator evasion opportunities and ability to detect predators is high (Geist 1971). Sheep are known to perceive actual risk through visual (Frid and Dill 2002; Bleich 1999) and chemosensory cues (reviewed in Kats and Dill 1998) and it is well documented that thinhorn sheep are influenced by group size and composition in their selection of habitats (Frid 1997; Rachlow and Bowyer 1998). This provides further indication that Stone's sheep as with other animals probably assess risk on a continuum of both scale and perception (Lima and Dill 1990).

Our models generally performed well at explaining resource selection by Stone's sheep in the B-P both across and within groups. The two cases when models performed poorly ($P > 0.05$) in our study both occurred in the Tenmile group (Table 2.5). The lack of predictive ability in the early winter model of 2003 may be attributed to a limited number of use locations (45) acquired from just one individual. The fall model of 2002 was a competing model during this time period and was subsequently averaged. Although an independent dataset from Stone's sheep outside the study area would be ideal for model validation and extrapolation, we have relatively high confidence in our inferences regarding habitat selection because of model performance.

Consistencies in annual selection

Wild sheep show strong fidelity to seasonal ranges particularly during winter. Geist (1971) documented an 88% fidelity to seasonal home ranges for Stone's sheep rams and 90% fidelity for a combined sample of bighorn and Stone's sheep ewes. This was similar to the observations of Festa-Bianchet (1986), which ranged from 98.5% in mid-October during the pre-rut, 77% during the rut and 63% in the summer. The philopatric nature of wild sheep is partially responsible for the substantial genetic variation and population substructure exhibited by thinhorn sheep across North America (Worley et al. 2004). Range selection in the B-P was consistent between years for most individuals, particularly in the Neves, Firstfork and Richards groups, because of consistent year-round occupancy of localized mountains. The selection of habitat attributes within seasonal ranges by Stone's sheep in the B-P, however, was variable between years. This variability in resource selection within a seasonal range is less understood yet may be important in terms of the plasticity of Stone's sheep and their susceptibility to disturbance.

Stone's sheep had the highest consistencies in annual selection of habitat attributes during the winter and summer seasons. The restrictiveness of winter and its effect on movement rates and availability may contribute to the consistencies sheep exhibit for the topographic attributes of slope, aspect and curvature (Table 2.9) considering their role in affecting snow depth. The models that validated best also occurred during winter providing further indication of the predictable nature of Stone's sheep during winter. Of all habitat attributes, groups of Stone's sheep had the weakest consistencies in seasonal selection of elevation between years. This was probably influenced by its inclusion as a quadratic in selection models. Risk was extremely variable between 2002 and 2003 with few groups ever placing themselves at a consistent risk of predation from bears and wolves. This may have been confounded by differences in strategies exhibited by the predators between study years. Steep slopes, dry alpine habitats, southerly aspects and convex sites were the most consistently selected attributes.

Consistency in the selection of attributes by Stone's sheep between years may be affected by changing availability from year to year. Garshelis (2000) summarized several limitations of use-availability studies including the affect of changing availability and its nonlinear relationship with selection. Changing availability has been shown to illicit different behavioural responses in animals when resources become more or less abundant (Mysterud and Ims 1998), which may contribute to variability in annual consistencies particularly if the juxtaposition or patterns of attributes change considerably (Porter and Church 1987; Garshelis 2000). The disproportionate contribution of individual Stone's sheep to the selection strategies of a group, including effects of mortality, collar failure and differential fix rates of GPS collars, may further affect variation in selection (Arthur et al. 1996).

Nonetheless our study documents that Stone's sheep show plasticity in selection of attributes within seasonal ranges even though their fidelity and philopatric nature to particular ranges may be high (Geist 1971; Worley et al. 2004). Considerable variation exists in selection strategies among groups of sheep, yet general consistencies in selection for steep slopes, ridge-like topology, southerly aspects and upper elevations persist among most groups most seasons. Our research provides a baseline measure of the habitats selected by Stone's sheep within their seasonal ranges and highlights the influence of topographic features on their distribution.

Chapter 3: Behaviour, habitat associations and intrasexual differences of Stone's sheep ewes[2]

Abstract: Stone's sheep (*Ovis dalli stonei*) in northern British Columbia segregate sexually most of the year, and intrasexually between maternal and nonmaternal ewes during spring and early summer. Our objective was to quantify intrasexual habitat use of female Stone's sheep relative to maternal status during this time period. Along with behaviour and habitat measures, we employed nonmetric multidimensional scaling (NMS) to characterize plant community associations of Stone's sheep ewes. We reviewed three hypotheses of intersexual segregation (predation-risk, forage-selection and activity-budget hypotheses) to determine if they also explained intrasexual segregation of female Stone's sheep. Stone's sheep spent the majority of active time foraging with few behavioural differences between maternal and nonmaternal ewes. Nursery groups, however, spent shorter durations of time active, more time active in solid-rock-escape features, and less time in shrub habitat. The best predictive model using logistic regression to describe differences in habitat use relative to maternal status incorporated distance to nearest-escape feature and size of nearest-escape feature. Regardless of maternal status, Stone's sheep ewes followed an elevational gradient over the summer according to our NMS analysis. Early in the growing season females used low-elevation plant communities that were characterized by an increase in shrub species and cover. As the growing season progressed ewes tracked a phenological stage, moving up in elevation and associating with communities that contained increasing amounts of moss and

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lichen cover. The patterns in behaviour, habitat use and vegetation associations between intrasexual groups of Stone's sheep were best characterized by the predation-risk hypothesis.

Introduction

Stone's sheep (*Ovis dalli stonei*) evolved in periglacial environments (Geist 1971), and are generally found in subalpine and alpine habitats foraging on alpine vegetation near or in steep, rocky terrain (Luckhurst 1973; Seip 1983). Stone's sheep segregate sexually (Geist 1971; Luckhurst 1973; Seip 1983) as do other North American wild sheep (Hoefs and Cowan 1979; Morgantini and Hudson 1981; Gionfriddo and Krausman 1986; Corti and Shackleton 2002), and most other ungulates (reviewed in Main and Coblentz 1990; Main et al. 1996; Ruckstuhl and Neuhaus 2002). Although spatial and temporal overlap may exist between ewes and rams, they generally occupy distinct ranges or portions of a range most of the year (Geist 1971). Intersexual segregation in North American wild sheep is largely credited to differences in antipredator strategies (Festa-Bianchet 1988; Berger 1991; Bleich et al. 1997; Corti and Shackleton 2002) and to factors related to activity budgets imposed by physiological differences in nutritional demands (Shank 1982; Ruckstuhl 1998). These theories were initially described by Main et al. (1996) as the reproductive-strategy and sexual-dimorphism-body-size hypotheses and have subsequently been referred to as the predation-risk hypothesis and forage-selection hypothesis (Ruckstuhl and Neuhaus 2000). The foundation of the predation-risk hypothesis lies in the satisficing concept, described for herbivores as an aspect of foraging theory (Bunnell and Gillingham 1985). The hypothesis suggests that males exploit nutritionally superior areas to increase growth and development at a greater risk of predation, whereas females trade-off security of offspring at the expense of better foraging conditions (Main and Coblentz 1990; Main et al. 1996; Ruckstuhl and Neuhaus 2000). The forage-selection hypothesis predicts that energetic constraints resulting from differences in body size result in males feeding on abundant low quality forages, and females exploiting areas with less abundant but higher quality forage to meet energetic requirements (Main et al. 1996; Ruckstuhl and Neuhaus 2000). These hypotheses are not necessarily mutually exclusive and findings on bighorn sheep (*Ovis canadensis canadensis*) and Dall's sheep (*Ovis dalli dalli*) document aspects of both (Ruckstuhl 1998; Corti and Shackleton 2002). More recently, Ruckstuhl and Neuhaus (2000) proposed the activity-budget hypothesis (initially referred to as the body-size predation hypothesis by Ruckstuhl [1998]), that intersexual segregation of bighorns is a function of differences in foraging behaviour (energy requirements) and movement patterns. Smaller females are less efficient at digesting forage, due to a small stomach size and quicker passage rate of food, which forces them to spend more time foraging and active (Bunnell and Gillingham 1985; Main and Coblentz 1990; Main et al. 1996; Ruckstuhl and Neuhaus 2000; Ruckstuhl and Neuhaus 2002). Although using similar ranges, the segregation but similar range use by Stone's sheep rams and ewes in the Toad River region of northern British Columbia was explained by differences in foraging time per day (Seip and Bunnell 1985*b*).

Segregation is not exclusive to the sexes and females should segregate relative to maternal status when energy demands and predator avoidance strategies differ (Ruckstuhl 2000). Intrasexual segregation has been observed within female Dall's (Hoefs and Cowan 1979; Rachlow and Bowyer 1994; Rachlow and Bowyer 1998; Corti and Shackleton 2002) and Stone's sheep (Geist 1971; Luckhurst 1973). Comparisons of habitat use relative to maternal status may contribute to a better understanding of why animals segregate (Hoefs and Cowan 1979; Main et al. 1996) by eliminating issues associated with physical dimorphism (e.g., defense, energy conversion). Even among maternal females, the activity of offspring may influence habitat selection and foraging (White and Berger 2001; Kohlmann et al. 1996). Maternal Nubian ibex (*Capra ibex nubiana*) with young confined to a "nursery" because of topographical constraints, increased their duration of foraging bouts and ventured further from escape terrain in smaller groups to use higher quality habitats than mothers with young at heel (Kohlmann et al. 1996). Once the offspring were physically able to leave the "nursery", differences between females with young previously confined to the "nursery" and females with unrestricted young were indistinguishable. The conflicting needs of temperate ungulates to acquire enough energy reserves for the upcoming winter and to support the growth and development of young while avoiding predation highlight the trade-off that females confront (Rachlow and Bowyer 1998). Differences in maternal status of North American sheep have been described as a trade-off between predation risk, forage quantity and forage quality (Festa-Bianchet 1988; Berger 1991). Female thinhorns with young generally remain separate from nonmaternal ewes through late spring and early summer (Nichols and Bunnell 1999). The mechanisms influencing intrasexual segregation during the spring and early summer, however, have not been described for Stone's sheep.

Numerous studies have addressed the influence of social and environmental factors on foraging efficiency and vigilance in wildlife (reviewed in Elgar 1989; Lima and Dill 1990), including several studies involving sheep (Risenhoover and Bailey 1985; Warrick and Krausman 1987; Frid 1997; Rachlow and Bowyer 1998). Female sheep with lambs generally forage less efficiently, spending proportionally less time foraging and more time vigilant than nonmaternal ewes (Risenhoover and Bailey 1985; Frid 1997). Female Dall's sheep foraged more efficiently prior to lambing than after (Rachlow and Bowyer 1998). Increased energy requirements of lactation (Gittleman and Thompson 1988; Parker et al. 1999) and vulnerability of young to predation (Berger 1991; Bleich et al. 1997; Bleich 1999) may lead to differences in foraging and walking behaviour because increased movement may make ewes with lambs less spatially predictable by predators, potentially reducing their risk of predation (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000). Foraging behaviour is further affected by environmental, physiological and social constraints (reviewed in Bunnell and Gillingham 1985; Kie 1999).

Although not mutually exclusive, an inverse relationship exists between feeding and vigilance (Lima and Dill 1990; Illius and Fitzgibbon 1994; Frid 1997). Vigilance is energetically expensive as an animal standing with its head upright cannot rest (lowest energy expenditure) or feed (energy intake) (Illius and Fitzgibbon 1994; Toïgo 1999). This relationship between feeding and vigilance for sheep has largely been explained by habitat visibility (Risenhoover and Bailey 1985), group size and distance to escape terrain (Risenhoover and Bailey 1985; Warrick and Krausman 1987; Frid 1997; Rachlow and Bowyer 1998). The interaction of group size and distance to escape terrain is probably the most influential factor explaining foraging efficiency and vigilance of Stone's sheep (Frid 1997). Escape terrain is well recognized as an integral component in the ecology of wild sheep (Geist 1971; Berger 1991; Bleich et al. 1997; Frid 1997; Rachlow and Bowyer 1998; Bleich 1999), but does not encompass all attributes important to sheep. Forage quality has been shown to influence reproductive performance (Geist 1971) and body growth in bighorns

(Hebert 1973) and may have influential effects on the growth and reproduction of ungulates at northern latitudes (White 1983).

Research on Stone’s sheep has provided brief descriptions of intrasexual differences in habitat use relative to maternal status, but with few quantifiable measures (Geist 1971; Luckhurst 1973). The observations were made during the growing season when lambs are most vulnerable to predation, and suggested females without young associated away from nursery groups to increase their foraging opportunities. Our primary objective was to describe behaviour and habitat use of female Stone’s sheep relative to maternal status during the growing season while addressing the appropriateness of three intersexual segregation hypotheses to explain segregation of female sheep. Tests of these hypotheses may provide insights into why female thinhorns are commonly observed in distinct nursery and nonnursery groups. We used measures of escape features to provide an indication of antipredator strategies (Frid 1997; Bleich 1999; Corti and Shackleton 2002; Frid 2003) and measures of group size, behaviour (i.e., foraging, standing, walking, alert, nursing) and vegetation characteristics to highlight differences in activity and habitat use (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000) between maternal and nonmaternal Stone’s sheep. Predictions of the predation-risk hypothesis are that maternal females should associate with safer habitats where offspring are less vulnerable to predation and food quality or quantity is often inferior, whereas nonmaternal females should choose areas where nutritious resources are more abundant at a potentially higher risk to predation (Ruckstuhl and Neuhaus 2000; Ruckstuhl and Neuhaus 2002). For the forage-selection hypothesis to explain intrasexual segregation, maternal females should use high quality forage in order to meet the high energy demands associated with lactation. The forage-selection hypothesis is appropriate only during periods of high lactation (i.e., post lambing and early summer; Nichols and Bunnell 1999) in non-dimorphic species or between maternal and nonmaternal ewes. If ewes with young spend a greater proportion of time walking (Ruckstuhl 1998) and foraging than ewes without and/or are more active, then support for the activity-budget hypothesis would exist (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000; Ruckstuhl and Neuhaus 2002). We rejected hypotheses when data contradicted their predictions. We broadly described group size and habitat in order to account for social and environmental influences on the behaviour of Stone's sheep ewes and incorporated components of vegetation (phenology, forage availability) and escape features (type, distance, and size) to predict sites used by groups of Stone's sheep with and without lambs.

A secondary objective was to describe how female Stone's sheep associate with plant communities relative to maternal status. Few studies have addressed whether intrasexual differences extend directly to plant community associations, and a quantification of how Stone's sheep simultaneously relate temporally to vegetation cover, type, quality and quantity is lacking. We used nonmetric multidimensional scaling (NMS) to ordinate plant species communities relative to temporal, environmental and vegetative attributes at sites used by nursery and nonnursery groups of Stone's sheep ewes. These ordinations aim to organize data by emphasizing underlying patterns on how and why Stone's sheep associate with plant communities. If intrasexual differences exist in plant community associations used by maternal and nonmaternal ewes, distinct ordination groupings should be discernable and readily describable by overlays of the most correlated environmental attributes. These ordinations and correlations provide an indication of how Stone's sheep associate with particular plant communities.

Methods

Study area

This study was conducted on a portion of the Besa-Prophet (B-P) Pre-tenure Planning Area in the Muskwa-Kechika Management Area of northern British Columbia. The study area was based on the distribution of free-ranging Stone’s sheep, observed between 57° 20' and 57° 40'N and 123° 10' and 123° 45'W. The area lies in the foothills of the northern Rockies at an elevation of 800-2200 m and is dominated by coniferous trees, riparian vegetation and shrub-covered meadows at lower elevations. Southerly aspects often have burned grassland vegetation and deciduous trees, whereas upper elevations are dominated by finer grassland, rock, lichen and bryophyte communities. The area has little access and is relatively free of industrial influences. There is one all-terrain vehicle (ATV) trail which experiences some snowmobile activity in winter. Two permanent outfitting camps exist in the study area which is open to hunting for Stone’s sheep rams from 1 August to 15 October (Blower 1999).

Behavioural observations

Observations of Stone’s sheep ewes were conducted during daylight hours between 18 May and 26 July in 2002 and 2003 prior to the hunting season. Sheep were located using telemetry, binoculars and/or spotting scopes and were approached on foot or horseback to distances (ranging from 50 m to 500 m) from which observations could be accurately made. The first group(s) located in a day was observed. Care was taken not to disturb sheep and observations were discontinued if animals exhibited alert behaviour towards the observer or towards any anthropogenic stimulus. Observations were conducted on 10 different mountains spread throughout the study area, and separated by a major creek or river drainage. Identifiable markings were noted to discern individuals in groups and only one individual was observed at a time to minimize dependence within and among samples. Observations were continuously recorded using focal animal sampling (Altmann 1974), employing a small handheld clock-equipped computer (HP 200LX; Hewlett Packard, Corvallis, Oregon, USA). Behaviours (foraging, walking, standing, alert, nursing and out of sight) were entered by first letter code for randomly selected females ≥ two years old (Rachlow and Bowyer 1998). In addition, habitat (i.e., herbaceous, shrub, tree, broken rock and solid rock) for each observed animal was recorded with a habitat-specific code to allow for simultaneous assessment of both behaviour and habitat use. We assumed that an observed individual's use of a habitat was representative of the group with which it associated. Group size was recorded and later examined in relation to foraging efficiency (the proportion of active time an observed individual spent foraging, Bunnell and Gillingham 1985; Rachlow and Bowyer 1998). Lambs were treated as a pair with their respective mothers and were not included in the measure of group size because of the close dependence they have with their mothers (Shackleton and Haywood 1985; Corti and Shackleton 2002). Rams > one year old were included in the measure of group size, but were not included in the measure of lamb to ewe ratio described for nursery groups.

Sheep were considered alert when standing with their heads and ears upright, fixed in a particular direction, mutually exclusive of chewing, ingesting food or participating in other behaviours. Foraging was recorded when an individual was standing with its head oriented towards forage or while ingesting forage (Risenhoover and Bailey 1985). Nursing was defined by ewes with lambs that were actively suckling. Walking was defined by an individual that was moving towards other individuals or another area without foraging. Individuals that were standing, scratching, defecating or urinating without exhibiting alert behaviour were recorded as standing. Observations were terminated if the subject animal left the field of view for >10 min. When individuals were out of sight for <10 min in duration, the time was subtracted from both the total time observed and the time active.

Stone's sheep were considered inactive whenever bedded and active whenever not bedded. Complete active bouts consisted of the time from when an animal stood after bedding, until it lay down again; a complete inactive bout was the entire time spent lying between active periods. Complete bouts were averaged for each trial. A trial consisted of a continuous period of observation on one individual in a group and may have spanned several complete bouts. Only data from complete bouts were used in the analysis of active and inactive bout durations.

The proportion of time sheep spent in each behaviour was calculated for each trial. To remove the influence of young on the behaviour of individuals, we analyzed data for individuals without lambs only when the group they were associated with did not have any lambs. Analysis of behaviour data and the proportion of behaviours that Stone's sheep exhibited while active were from observations of animals that were active >5.5 min in duration. The 5.5-min threshold was the longest complete active bout in which an individual Stone's sheep did not forage. Bouts <5.5 min were typically times when Stone's sheep switched beds after stretching or rising to urinate and/or defecate.

Habitat measurements

Fine-scale habitat measurements were conducted during the growing season on sites where Stone's sheep ewes were observed active for >25 min (25 min ≈ 75% of the average complete active bout duration for all ewes). Animals that spent a greater portion of active time walking than foraging often left the field of view before 25 min was attained. Our habitat assessments, therefore, were conducted on sites where Stone's sheep spent a high portion of time foraging.

Sites used by sheep were identified by recording the location of observed individuals at 5-min intervals. Similar to Rachlow and Bowyer (1998), locations were plotted on a hand-drawn map for habitat sampling of use sites which took place approximately one to two days after behavioural observations. Polygons were drawn around plotted locations as with the minimum convex polygon method (Jennrich and Turner 1969). The center of each use site was determined on a line drawn down the center of the longest axis of the activity polygon. This provided the middle point for a 50-m transect that ran the bearing of the longest axis. Elevation (m) and slope (°) were measured from the middle of the transect, with a GPS to determine elevation and a clinometer to average 50-m up-slope and down-slope steepness.

We used the line-intercept method along each 50-m transect to determine vegetation cover by forage class (herbaceous [graminoids and forbs], shrubs, trees and mosses/lichens) (Rachlow and Bowyer 1998). In addition to canopy interception (allowing for overlapping canopies), exposed soil/rock was also measured by line intercept. At five stations (12.5-m intervals) along each transect, distance to the nearest-escape feature (broken rock or solid rock) was measured as the straight-line distance and measurements were averaged across the stations for each use site. We defined broken-rock-escape features as slopes of steep shale, scree, talus or boulder fields. Solid-rock-escape features were defined as cliffs and steep rocky outcrops. Distance to nearest-escape feature was the closest distance to one of these features. Area (ha) of an escape feature was determined by measuring the height and width of the escape feature. All distance and area measurements were made using a tape and/or laser range finder (Yardage pro compact 800; Bushnell, Lenexa, Kansas, USA).

Fine-scale measurements of vegetation type and phenology at the five stations were determined within 1- × 1-m^2 quadrats. Percent cover by species, bare ground/rock and litter was estimated using Daubenmire coverage classes (Daubenmire 1959). For each plant species, the midpoint of the Daubenmire coverage class was summed and averaged for five quadrats to estimate percent cover of that species across the area used by individual Stone's sheep. Phenology was used as an index of forage quality because digestibility and protein levels of plants are highest in early phenological stages (Johnston et al. 1968; Bryant et al. 1991). Phenology was described for each species on an ordinal scale from 1 to 7, representing emergent, new shoot, leaves unfurled, budding, flowering, fruiting or seeded; respectively. The most frequently occurring phenological stage by species among the five quadrats was assigned to the site. An availability index of forage quantity was developed after measuring the average above-ground new growth height (m) of each species. Ten representative plants of each species (unless too few specimens were present) were measured to determine average plant growth. The availability index (m^3) was calculated by multiplying the quadrat area (1 m^2) by the cover of each plant species (%) and the average growth (m) of that species. The individual species-availability index was averaged across the five quadrats and all species were subsequently summed to provide an index of total vegetation quantity or availability for each use site.

Data analyses

We contrasted mean group size, active and inactive durations and proportion of time spent active for maternal and nonmaternal Stone's sheep ewes, using the Student's t-test of independent samples (Zar 1999). "Typical" group size was also determined as a more animal-centered measure of average group size (Jarman 1974; reviewed in Heard 1992) and differences between maternal status were compared relative to both measures. Data were log-transformed where appropriate to meet assumptions of normality and homogeneity of variance (Levene's test, Zar 1999). The Mann-Whitney *U*-test adjusted for ties (Siegel 1956) was employed to further examine differences in behaviour, phenology, forage availability, slope, escape features and vegetation cover between intrasexual groups of Stone's sheep ewes. We presented the median as well as the mean ($\bar{x}$) to describe the central tendency of samples in nonparametric tests with skewed samples (Zar 1999). Values were generally presented as the untransformed $\bar{x}$ along with standard errors (SE), unless otherwise noted. Simple linear regression (Zar 1999) was used to assess the relationship between group size and foraging efficiency of Stone's sheep ewes. Statistical significance was assumed at $\alpha \leq 0.05$ for all tests and all statistical procedures were conducted using Stata^{TM} (Release 9.0, StataCorp 2005).

Habitat use by intrasexual groups of Stone's sheep ewes during the growing season was evaluated using logistic regression (Hosmer and Lemeshow 1989; Menard 2002) and the information-theoretic approach (Burnham and Anderson 2002). Logistic regression was used to predict the presence of groups with and without lambs on the basis of environmental variables (Hosmer and Lemeshow 1989; Menard 2002). Eleven ecologically plausible models were derived from site-specific measurements of availability index, phenology, slope, nearest solid rock, solid-rock area, nearest broken rock, broken-rock area, nearest-escape feature and escape area to predict differences in habitat use between ewes with and without lambs. These explanatory inputs were assessed for collinearity and multicollinearity using tolerance scores. If tolerance scores were <0.2, variables were not included in the same model (Menard 2002). Corrected Akaike's Information Criteria (AIC_c) for small sample sizes ($n/K < 40$), where K is the number of parameters in a model, were used to rank the suite of models by indicating the model that achieved the best parsimony or trade-off between bias in K and amount of variance captured in the model (Burnham and Anderson 2002). Within AIC_c, log likelihood (LL) provides an indication of model fit with smallest values, relative to competing models, indicating better prediction of the dependent variables (Menard 2002). AIC weights (w_i) were used to choose the most parsimonious model by providing an estimate of the relative probability that the top model was the best from the suite of proposed models. The w_i in a model set sum to one and provide a measure of the weight of evidence in favour of one model over the others (Burnham and Anderson 2002; Johnson and Omland 2004). Competition for best model was recognized when the top model had $w_i < 0.95$. Competing models were defined as the top models for which the summed $w_i \geq 0.95$. P values for coefficients of selection (β_i) and odds ratios, and their standard errors were calculated to quantify importance of the variables within the models. Odds ratios indicate the likelihood of an attribute associating with one group relative to another (Zar 1999). Models were validated using the areas under the receiver operating characteristic curves (ROC) (Fielding and Bell 1997). The area, which provides a single measure of overall accuracy that is not dependent on a particular threshold, varies between 0.5 (no discrimination) and 1 (perfect discrimination) (Fielding and Bell 1997). Values between 0.7

and 0.9 have acceptably good model discrimination (Manel et al. 2001; Boyce et al. 2002) whereas values >0.9 have high model prediction accuracy (Manel et al. 2001). Models exceeding a ROC score of 0.7 were deemed acceptable at distinguishing between nursery and nonnursery groups.

Plant community composition as a function of measured environmental variables was ordinated with NMS (Kruskal 1964*a*, 1964*b*; McCune and Mefford 1999) to describe the patterns of species associated with sites used by Stone's sheep ewes. Ordinations were developed for both plant species and sites in order to describe vegetative associations and intrasexual differences in habitat use by Stone's sheep ewes. Pearson correlation coefficients (*r*) and their associated *P* values, determined from a two-tailed sample distribution (Zar 1999), were determined to characterize the relationship between the ordination axis and environmental variable or plant species. All analyses associated with NMS were completed using PC-ORD 4.35 (McCune and Mefford 1999). NMS allows for a robust and effective method of multivariate analyses when data are non-normal and discontinuous (McCune and Grace 2002), and is flexible relative to the choice of standardizations and transformations, allowing for a biologically meaningful presentation of the data (Clarke 1993). The method is an iterative search based on ranked distances, which tends to linearize the relation between distance on an environmental gradient and degree of difference between community samples (Neitlich and McCune 1997). Rare species occurring in <5% of the sites were removed from the ordination analysis (for a full species list see Appendix F, Table F.1) in order to enhance detection of relationships between broad community composition and environmental factors (McCune and Grace 2002). Three outlier plots with a community dissimilarity >two standard deviations from the average also were deleted in the final ordination. All three outlier plots were associated with low-elevation sites where Stone's sheep were observed using licks. There were 65 species in the primary matrix and 10 environmental variables in the secondary matrix for the 75 use sites. The environmental variables consisted of date, phenology, availability index, slope (°), elevation (m), % herbaceous, % shrubs, % trees, % bare and % litter. Vectors of the most highly correlated environmental variables were overlaid on the ordination to indicate the direction and strength of correlations between axis scores and attributes. Frequency of species occurrence was also tabulated, and although not incorporated in the ordination, was used to provide additional descriptive measures of the sites used by Stone's sheep ewes. Beal's smoothing was used for all species data because of the large number of zeros (missing species per transect) (McCune and Grace 2002). All environmental variables that consisted of proportion data were arcsine squareroot-transformed whereas other variables were log-transformed if they did not meet assumptions of normality (Zar 1999). We used the Sorenson distance measure (Faith et al. 1987) to calculate a matrix of distances among plant species and sites in a multidimensional or ordination space (McCune and Grace 2002). A random starting configuration and two axes were used as subsequent axes explained no additional information. Stress, expressed as a percentage, measures the poorness of fit or departure from monotonicity between the ordination and measured ecological distances, with lower stress being attained when points fall closer to a monotonic line (McCune and Grace 2002). We set stress <15 as an acceptable level of fit, given that most data from ecological communities have a stress between 10 and 20 with values in the lower portion of the range being satisfactory (McCune and Grace 2002). Following the NMS ordination, date and elevation data were examined using simple correlation coefficients to determine whether Stone's sheep followed a temporal pattern in elevation use (Zar 1999).

Results

Individual behaviours

Observations were obtained over 126 h from 93 individuals, 78 of which were used in analysis of complete bouts. Stone's sheep in the B-P appeared to differentiate into nursery and nonnursery groups. Nursery groups contained an average of 0.82 lambs/ewe (± 0.038, *n* = 35) during the spring and summer, indicating that most females in nursery groups had lambs. Only two nursery groups contained fewer than 0.50 lambs/ewe. Mean adult group size of female Stone's sheep in the B-P was 4.3 ± 0.32 (*n* = 78, range 1-12) and did not differ between groups with lambs (3.9 ± 0.38, *n* = 35) and groups without lambs (4.7 ± 0.50, *n* = 43, *P* = 0.448). "Typical" group size was 6.2 (*n* = 78) for all female groups in the B-P. Groups with lambs were slightly smaller (5.2, *n* = 35) than groups without lambs (6.9, *n* = 43).

Female Stone's sheep in the B-P spent more time active (33 ± 3.1 min, *n* = 51) than inactive (24.4 ± 1.68 min, *n* = 74) during complete bouts (*P* = 0.008). Groups differed, however, relative to maternal status. Ewes with lambs showed no statistical differences in durations of active (25 ± 3.1 min, *n* = 20,) and inactive (22.0 ± 2.19 min, *n* = 30) bouts (*P* = 0.502). Nonmaternal ewes were active for significantly longer bouts (39 ± 4.4 min, *n* = 31) than inactive bouts (10.9 ± 2.38 min, *n* = 44, *P* = 0.006); their active bouts were longer than those of maternal ewes (*P* = 0.011), but inactive bouts between groups did not differ (*P* = 0.374).

Stone's sheep ewes spent a large proportion of their active time in herbaceous habitats with no differences between ewes with and without lambs (0.37 ± 0.057 for 41 maternal ewes; 0.50 ± 0.051 for 52 nonmaternal ewes; *P* = 0.804, Fig. 3.1A). Proportions of active time in herbaceous (*P* = 0.108), tree (*P* = 0.184) and broken rock (*P* = 0.704) habitats were similar between groups. Ewes with lambs spent more of their active time in solid-rock-escape features (0.35 ± 0.058) than ewes without lambs (0.17 ± 0.030; *P* = 0.019). In contrast, the nonmaternal ewes spent significantly more active time (0.23 ± 0.043) in shrub habitat than ewes with lambs (0.11 ± 0.039, *P* = 0.003).

Nonmaternal ewes showed similar patterns in the habitats they used while inactive (bedded, Fig. 3.1B), with the majority of that time spent in herbaceous habitat (0.05 ± 0.065, *n* = 56) followed by shrubs (0.24 ± 0.056). Maternal ewes also spent the greatest proportion of inactive time in herbaceous habitats (0.48 ± 0.082, *n* = 34). Unlike active bouts they spent very little time in cliffs and outcrops (solid-rock-escape features, 0.018 ± 0.0145) and increased the proportion of time bedded in broken-rock escape features such as scree and talus (0.33 ± 0.077). Use of the tree (*P* = 0.009) and broken-rock-escape features (*P* = 0.012) was significantly greater than by nonmaternal ewes, which were never observed bedded in tree habitat (Fig. 3.1B).

No intrasexual differences in behaviours occurred within active bouts (Fig. 3.2). Both maternal (0.67 ± 0.032, *n* = 41) and nonmaternal (0.689 ± 0.0251, *n* = 52) ewes spent more than two-thirds of their time foraging. Animals averaged 0.156 ± 0.0130 (*n* = 93) of the time standing, 0.123 ± 0.0099 walking and 0.031 ± 0.0040 alert. Maternal ewes were first observed

Fig. 3.1. The proportion ($\bar{x}$ ± SE) of (A) active and (B) inactive times that maternal and nonmaternal Stone's sheep ewes spent in different habitats in the Besa-Prophet area of northern British Columbia. * indicates $P < 0.05$ as determined by the Mann-Whitney *U*-test.

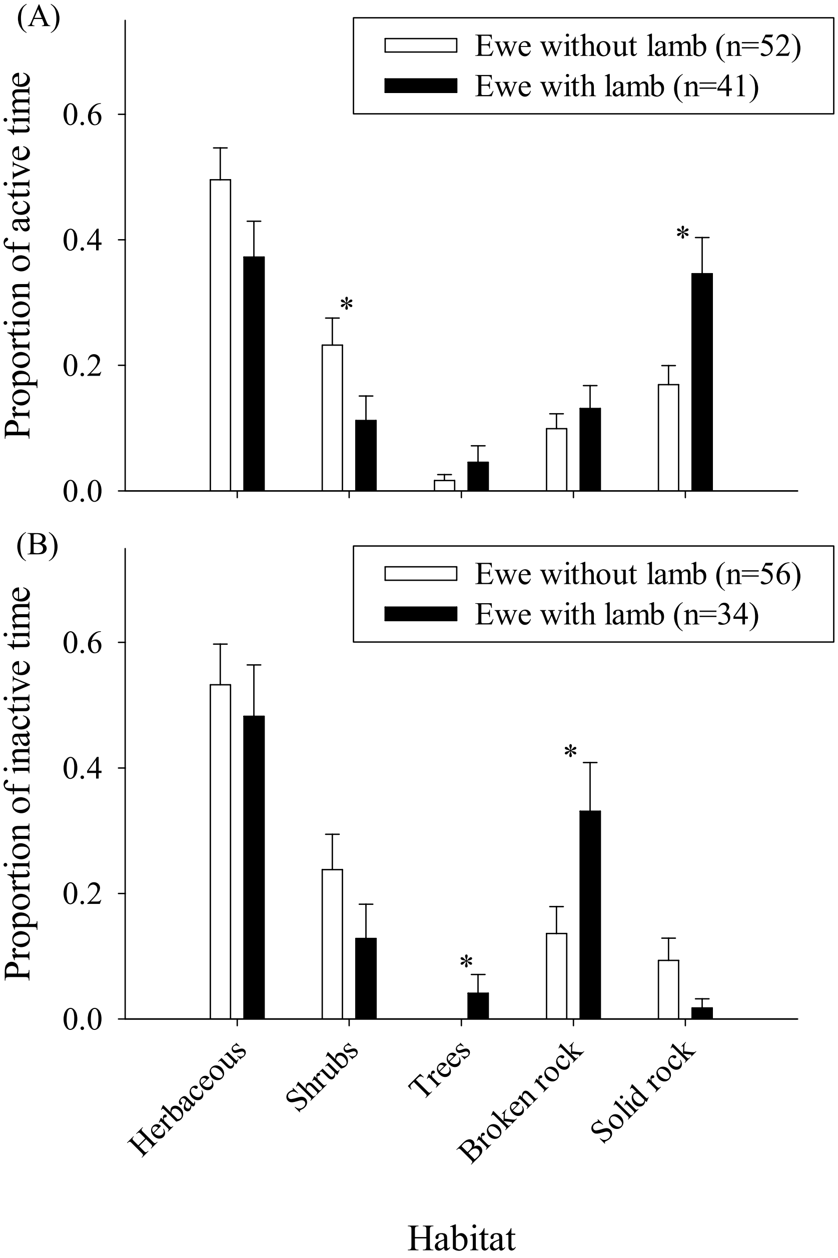
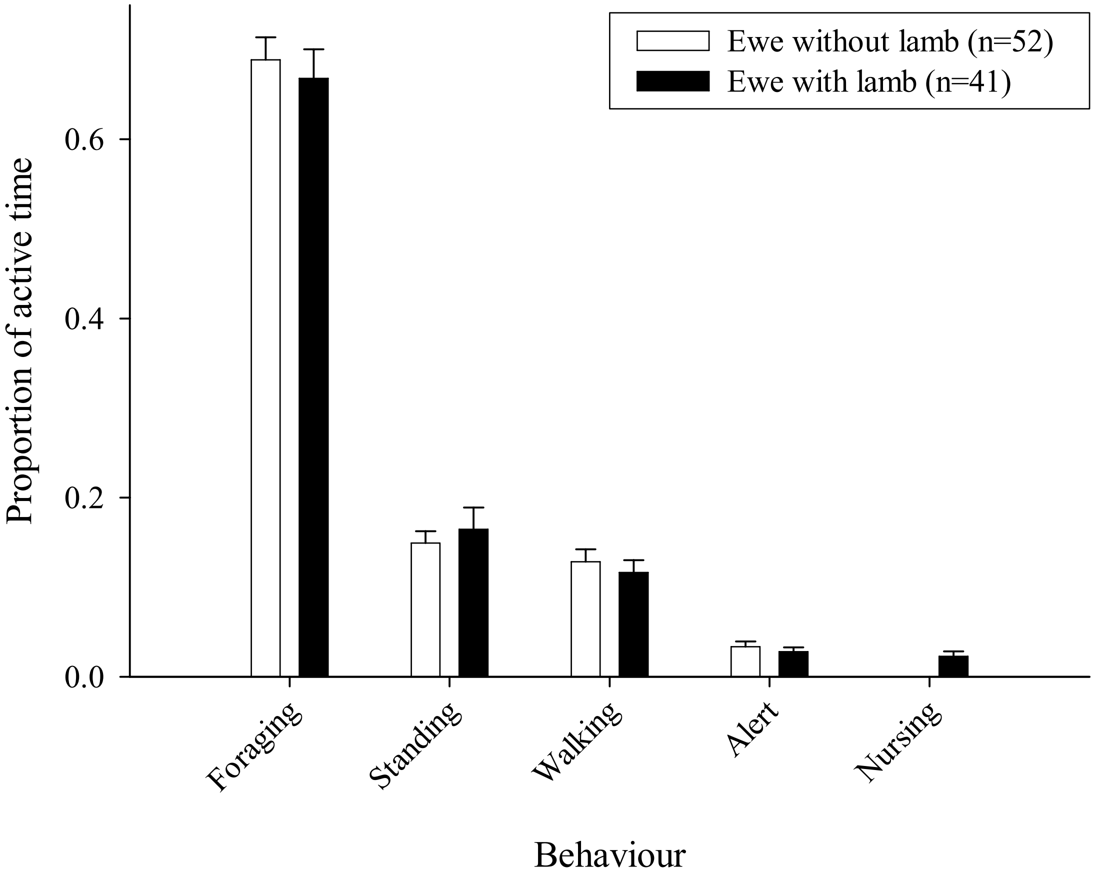


Fig. 3.2. The proportion ($\bar{x}$ ± SE) of active time that maternal and nonmaternal Stone's sheep ewes spent foraging, standing, walking, alert and nursing in the Besa-Prophet area of northern British Columbia. Differences between groups were not significant as determined by the Mann-Whitney *U*-test.



on the 8th of June and only nursed a small proportion of active time (0.023 ± 0.0054), which decreased as the summer progressed (Appendix G, Fig. G.1). Group size was not a significant predictor of foraging efficiency ($P = 0.704$, $r^2 = 0.002$, $n = 93$).

Habitat use

Intrasexual differences in habitat use between groups of Stone's sheep ewes included phenology, broken-rock area, distance to nearest-escape feature, escape area, % shrub cover and % of exposed soil/rock cover (Table 3.1). Over the growing season groups with lambs were found associated with older phenological stages (2.94 ± 0.091) than ewes without lambs (2.70 ± 0.113). In comparison with nonnursery groups, groups of ewes with lambs tended to be closer to the nearest-escape feature (8.6 versus 14 m), and associated with larger nearest-escape features (1.7 ± versus 0.41 ha) and larger broken-rock-escape features (1.6 versus 0.47 ha) (Table 3.1). These escape features were typically three to four times larger in size. When lambs were present, groups were never observed >69 m from an escape feature. This contrasts with the 150 m observed for a group without lambs. Ewes without lambs used habitats that averaged more than twice as much shrub cover and 18.6% less exposed soil/rock then sites used by groups with lambs. Sites used by nursery groups always had some exposed soil/rock (Table 3.1).

The ability to predict intrasexual differences in habitat use between groups with and without lambs using AIC_c was best explained by a model based on distance to nearest-escape feature and area of nearest-escape feature (Table 3.2). Indeed five of the top six competing models contained distance to nearest-escape feature and area of nearest-escape feature (Table 3.3).

Table 3.1. Intrasexual differences in habitat attributes used by groups of Stone's sheep ewes in the Besa-Prophet area of northern British Columbia. Mean ($\bar{x}$ ± SE), median (*M*), minimum and maximum values (min, max), and the probability (*P*) determined using the two-sample Mann-Whitney *U* test are shown for vegetative and topographic features.

Feature	Ewes with lambs n = 35			Ewes without lambs n = 43			*P*
	$\bar{x}$ ± SE	median	(min, max)	$\bar{x}$ ± SE	median	(min, max)	
Vegetation features							
Availability index (m^3)	0.043 ± 0.0076	0.0255	(0.001, 0.179)	0.061 ± 0.0092	0.039	(0.005, 0.253)	0.076
Phenology (stage)	2.94 ± 0.091	3	(2, 5)	2.70 ± 0.113	3	(1, 5)	0.036
Topographic features							
Slope (°)	37.4 ± 1.50	35	(23.5, 60)	34.8 ± 1.36	34	(18.5, 55)	0.204
Distance to nearest broken rock (m)	21 ± 5.8	8.8	(0, 169.2)	21 ± 4.1	15	(0, 149.8)	0.163
Broken-rock area (ha)	1.6 ± 0.48	0.56	(0.01, 12.00)	0.47 ± 0.135	0.07	(0.002, 4.50)	0.003
Distance to nearest solid rock (m)	25 ± 5.1	13.2	(0.1, 113.6)	30 ± 5.0	20.4	(1.8, 161.4)	0.220
Solid-rock area (ha)	0.68 ± 0.204	0.18	(0.01, 6.00)	0.343 ± 0.0815	0.10	(0.002, 2.40)	0.127
Distance to nearest-escape feature (m)	8.6 ± 2.12	4.8	(0, 69.0)	14 ± 3.5	9.8	(0, 149.8)	0.029
Escape area (ha)	1.7 ± 0.48	0.56	(0.01, 12.00)	0.41 ± 0.121	0.09	(0.002, 4.50)	0.001
Ground Cover							
Herbaceous cover (%)	63 ± 5.1	66.6	(2.0, 100)	73 ± 4.0	78.4	(0.4, 100)	0.112
Shrub cover (%)	9.2 ± 2.90	2.5	(0, 77.7)	22 ± 3.9	8.2	(0, 83.4)	0.020
Tree cover (%)	1.5 ± 0.75	0	(0, 20.1)	1.5 ± 0.62	0	(0, 22.6)	0.765
Moss/lichen cover (%)	22 ± 5.2	7.4	(0, 100)	20 ± 4.5	4.4	(0, 100)	0.523
Soil/rock cover (%)	44 ± 5.2	40.8	(3.4, 100)	26 ± 4.0	14.3	(0, 100)	0.004

Table 3.2. Logistic regression models developed to assess intrasexual differences in habitat use by nursery and nonnursery groups of Stone's sheep ewes in the Besa-Prophet area of northern British Columbia, ranked from lowest to highest AIC_c. Statistics include number of parameters (K), sample size (n), log likelihood (LL), corrected Akaike's Information Criteria (AIC_c), Akaike weights (w_i) and area under the Receiver Operating Characteristic curve (ROC).

Model	K	n	LL	AIC_c	Δ_i	w_i	ROC
Nearest-escape feature + Escape area	3	78	-47.345	100.852	0.000	0.297	0.707
Phenology + Nearest-escape feature + Escape area	4	78	-46.455	101.239	0.387	0.245	0.746
Phenology + Slope + Nearest-escape feature + Escape area	5	78	-45.848	102.252	1.399	0.147	0.744
Availability index + Phenology + Nearest-escape feature + Escape area	5	78	-45.851	102.258	1.406	0.147	0.741
Availability index + Phenology + Slope + Nearest-escape feature + Escape area	6	78	-45.218	103.282	2.430	0.088	0.747
Availability index + Phenology + Slope	4	78	-48.239	104.806	3.954	0.041	0.710
Phenology	2	78	-51.412	106.878	6.026	0.015	0.630
Availability index + Phenology + Nearest solid rock + Solid-rock area + Nearest broken rock + Broken-rock area	7	78	-46.307	107.813	6.961	0.009	0.736
Nearest solid rock + Solid-rock area + Nearest broken rock + Broken-rock area	5	78	-49.224	109.004	8.152	0.005	0.683
Availability index + Phenology + Slope + Nearest solid rock + Solid-rock area + Nearest broken rock + Broken-rock area	8	78	-45.785	109.194	8.342	0.005	0.745
Slope	2	78	-53.509	111.071	10.219	0.002	0.575

Table 3.3. The best logistic models, as determined by AIC$_c$ and their associated variables for characterizing intrasexual segregation of nursery and nonnursery groups of Stone's sheep in the Besa-Prophet area of northern British Columbia. Models are arranged in order of parsimony based on AIC$_c$ in descending rank. Statistics include coefficients (β_i ± SE), odds ratios (Odds ± SE) and probabilities (*P*).

Model	Variable	β_i ± SE	Odds ± SE	*P*
Nearest-escape feature + Escape area	Nearest-escape feature	-0.047 ± 0.031	0.954 ± 0.029	0.126
	Escape area	0.614 ± 0.274	1.848 ± 0.506	0.025
Phenology + Nearest-escape feature + Escape area	Phenology	0.611 ± 0.481	1.843 ± 0.886	0.203
	Nearest-escape feature	-0.040 ± 0.031	0.961 ± 0.030	0.193
	Escape area	0.572 ± 0.292	1.772 ± 0.517	0.050
Phenology + Slope + Nearest-escape feature + Escape area	Phenology	0.732 ± 0.494	2.080 ± 1.028	0.138
	Slope	0.034 ± 0.031	1.035 ± 0.032	0.278
	Nearest-escape feature	-0.030 ± 0.03	0.970 ± 0.029	0.318
	Escape area	0.566 ± 0.294	1.760 ± 0.518	0.055
Availability index + Phenology + Nearest-escape feature + Escape area	Availability index	-1.443 ± 1.369	0.236 ± 0.323	0.292
	Phenology	0.663 ± 0.488	1.940 ± 0.947	0.175
	Nearest-escape feature	-0.032 ± 0.032	0.969 ± 0.031	0.318
	Escape area	0.526 ± 0.286	1.692 ± 0.484	0.066
Availability index + Phenology + Slope + Nearest escape feature + Escape area	Availability index	-1.528 ± 1.433	0.217 ± 0.311	0.286
	Phenology	0.790 ± 0.503	2.203 ± 1.109	0.117
	Slope	0.035 ± 0.032	1.036 ± 0.033	0.268
	Nearest-escape feature	-0.021 ± 0.030	0.979 ± 0.029	0.477
	Escape area	0.517 ± 0.287	1.677 ± 0.482	0.072
Availability index + Phenology + Slope	Availability index	-2.325 ± 1.337	0.098 ± 0.131	0.082
	Phenology	1.053 ± 0.456	2.867 ± 1.307	0.021
	Slope	0.043 ± 0.029	1.044 ± 0.030	0.135

Within the top model predicting intrasexual differences, area of the nearest-escape feature was the most influential variable (Table 3.3). Groups containing lambs were ~1.8 times more likely to be associated with a larger nearest-escape feature. Across models, there were only three instances in which individual variables were significant, two attributed to the area of the nearest-escape feature and one to phenology (Table 3.3). Phenology was the most important variable in the one competing model that did not include any escape features. In this model, Stone's sheep groups with lambs were ~2.9 times more likely to be associated with older stages of vegetation. Variation around the odds ratios and coefficients of phenology was high, which may have contributed to the lack of significance of the variable in models containing area of nearest-escape feature.

Vegetation associations

Stone's sheep associated with plant communities on a temporal and elevational gradient in the B-P (Fig. 3.3, Table 3.4). Most (96.7%) of the variation in plant species found at sites used by Stone's sheep ewes was captured by the NMS ordination (Fig. 3.3), with 34.4% of the variation loaded on axis 1, 62.3% on axis 2, and a final stress of 8.41 following 80 iterations. The first axis was most correlated with date (r = 0.510), moss/lichen cover (r = 0.499) and elevation (r = 0.406) (Table 3.4). More important were the environmental attributes of axis 2, which explained the majority of variation in sites used by Stone's sheep. Of all environmental attributes, date was the highest positive correlate (r = 0.761), followed by elevation (r = 0.717) and moss/lichen cover (r = 0.538) (Table 3.4). Shrub cover was the most negatively correlated environmental variable (r = -0.632) and along with availability

Fig. 3.3. Nonmetric multidimensional scaling ordination (NMS) of plant communities used by Stone's sheep ewes in the Besa-Prophet area of northern British Columbia showing the position of species and most correlated environmental vectors in relationship to the ordination axes. Plots are labeled with the first three letters of both the genus and species for each plant (as noted in Table 3.5).

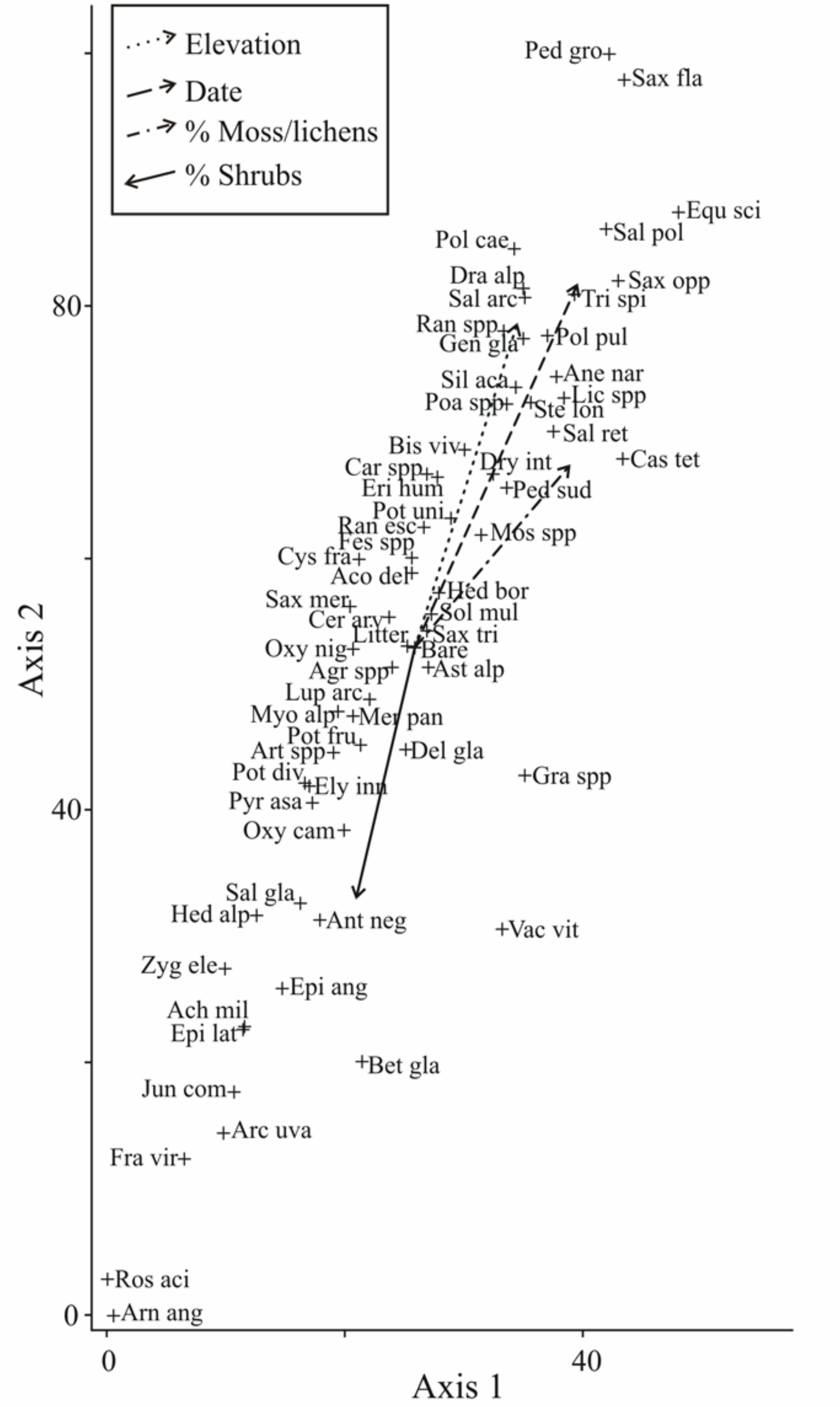


Table 3.4. Pearson correlation coefficients (*r*) of environmental variables measured from 75 sites used by Stone's sheep ewes in the Besa-Prophet area of northern British Columbia along two axes of the nonmetric multidimensional scaling ordination (NMS). * indicates $P \leq 0.05$ for the relationship between an ordination axis and environmental variable.

Environmental Variable	Axis 1 *r*	Axis 2 *r*
Date	0.510*	0.761*
Phenology	0.255*	0.384*
Availability index	-0.311*	-0.314*
Slope (°)	-0.245*	-0.293*
Elevation (m)	0.406*	0.717*
Herbaceous cover (%)	-0.374*	-0.042
Shrub cover (%)	-0.306*	-0.632*
Tree cover (%)	-0.070	-0.370*
Moss/lichen cover (%)	0.499*	0.538*
Exposed soil/rock cover (%)	0.219	0.094

index, slope, herbaceous cover and tree cover had negative associations with both ordination axes (Table 3.4). Only herbaceous cover and exposed soil/rock were not significantly related to axis 2. The positive correlations between the ordination axes and date indicate that Stone's sheep associated with the plant species at the top of Fig. 3.3 later in the summer. The elevational gradient of plant species is highlighted by the distribution of species in Fig. 3.3. Shrub species, such as *Rosa acicularis* and *Juniperus communis*, and other plants associated with lower elevations (*Arnica angustifolia*), are located near the bottom of Fig. 3.3 whereas species associated with higher elevations such as *Pedicularis groenlandica* and *Saxifraga flagellaris* are found near the top (Fig. 3.3).

Intrasexual groups of Stone's sheep ewes did not separate into distinct clusters in the ordination of use sites (Fig. 3.4). Sites used by ewes without lambs were more widely distributed across the ordination than sites used by groups with lambs, suggesting that ewes without lambs used a broader array of plant communities. Both groups were associated with lower elevation communities and increased amounts of shrub cover early in spring. Later in summer communities used by Stone's sheep were found at higher elevations and contained more moss/lichen cover. Although clusters indicative of intrasexual status were not apparent in the ordination overlays, sites associated with large amounts of moss and lichen cover were dominated by ewes with lambs whereas sites with an abundance of shrub cover were almost always associated with ewes without lambs (Fig. 3.4).

Numerous graminoid, forb and shrub species were associated with sites used by Stone's sheep in the B-P study area (Table 3.5). Subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmanii*) and *Populus* were removed from the ordination due to the rarity of occurrence at use sites, although Stone's sheep were observed on rare occasions

Fig. 3.4. Nonmetric multidimensional scaling (NMS) ordination showing the position of 75 sites used by Stone's sheep ewes in the Besa-Prophet area of northern British Columbia relative to the plant species composition and associated environmental attributes. Symbols indicate whether lambs were present (●) or not (Δ) at sites used by Stone's sheep ewes. Vectors on the ordination indicate direction and strength of correlations between axis scores and the most important environmental attributes.

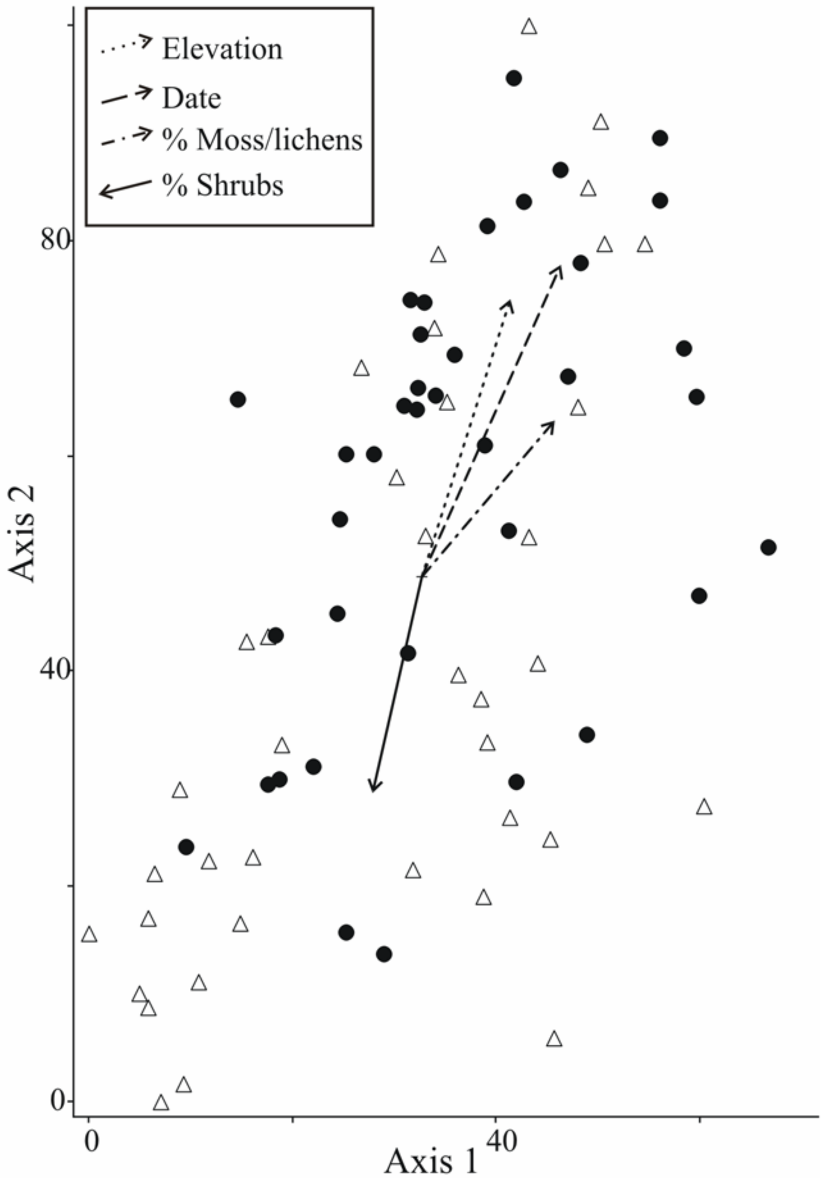


Table 3.5. Pearson correlation coefficients (*r*) and frequency of species occurence at 75 sites used by Stone's sheep ewes in the Besa-Prophet area of northern British Columbia along two axes of the nonmetric multidimensional scaling ordination (NMS). * indicates $P \leq 0.05$ for the relationship between an ordination axis and plant species.

Abreviation	Species	Axis 1 *r*	Axis 2 *r*	Frequency (%)
Graminoids				
Agr spp	*Agropyron* spp.	-0.105	-0.054	10.7
Car spp	*Carex* spp.	0.081	0.721*	30.7
Ely inn	*Elymus innovatus*	-0.907*	-0.697*	61.3
Fes spp	*Festuca* spp.	-0.037	0.666*	62.7
Gra spp	Unknown graminoid spp.	0.433*	-0.294*	21.3
Poa spp	*Poa* spp.	0.575*	0.881*	40.0
Tri spi	*Trisetum spicatum*	0.535*	0.686*	8.0
Forbs				
Ach mil	*Achillea millefolium*	-0.727*	-0.938*	42.7
Aco del	*Aconitum delphiniifolium*	0.546*	0.725*	74.7
Ane nar	*Anemone narcissiflora*	0.667*	0.743*	22.7
Ant neg	*Antennaria neglecta*	-0.350*	-0.585*	13.3
Arn ang	*Arnica angustifolia*	-0.641*	-0.828*	6.7
Art spp	*Artemisia* spp.	-0.368*	-0.274*	18.7
Ast alp	*Astragalus alpinus*	0.056	-0.047	10.7
Bis viv	*Bistorta vivipara*	0.399*	0.930*	54.7
Cer arv	*Cerastium arvense*	-0.368*	0.263*	54.7
Cys fra	*Cystopteris fragilis*	-0.406*	0.375*	28.0
Del gla	*Delphinium glaucum*	-0.047	-0.300*	18.7
Dra alp	*Draba alpina*	0.326*	0.626*	10.7
Epi ang	*Epilobium angustifolium*	-0.634*	-0.944*	40.0
Epi lat	*Epilobium latifolium*	-0.491*	-0.634*	6.7
Equ sci	*Equisetum scirpoides*	0.702*	0.676*	10.7
Eri hum	*Erigeron humilis*	0.153	0.670*	21.3
Fra vir	*Fragaria virginiana*	-0.728*	-0.937*	26.7
Gen gla	*Gentiana glauca*	0.398*	0.662*	9.3
Hed alp	*Hedysarum alpinum*	-0.728*	-0.718*	22.7
Hed bor	*Hedysarum boreale*	-0.022	0.345*	21.3
Lup arc	*Lupinus arcticus*	-0.508*	-0.338*	44.0
Mer pan	*Mertensia paniculata*	-0.719*	-0.461*	45.3
Myo alp	*Myosotis alpestris*	-0.829*	-0.404*	49.3
Oxy cam	*Oxytropis campestrus*	-0.300*	-0.453*	10.7
Oxy nig	*Oxytropis nigrescens*	-0.632*	-0.011	44.0

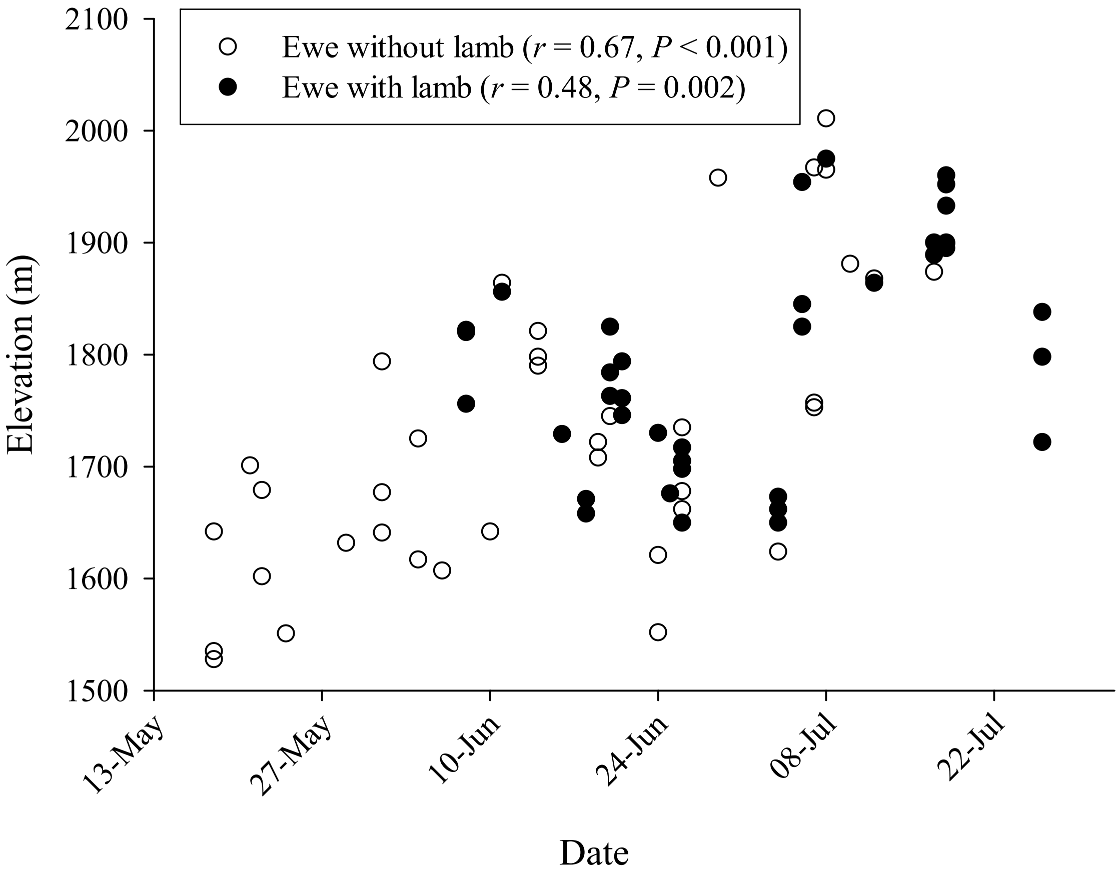
Table 3.5. Continued

Abreviation	Species	Axis 1 *r*	Axis 2 *r*	Frequency (%)
Ped gro	*Pedicularis groenlandica*	0.534*	0.951*	16.0
Ped sud	*Pedicularis sudetica*	0.579*	0.589*	26.7
Pol cae	*Polemonium caeruleum*	0.396*	0.929*	26.7
Pol pul	*Polemonium pulcherrimum*	0.555*	0.763*	22.7
Pot div	*Potentilla diversifolia*	-0.459*	-0.326*	8.0
Pot uni	*Potentilla uniflora*	0.404*	0.843*	61.3
Pyr asa	*Pyrola asarifolia*	-0.680*	-0.600*	28.0
Ran esc	*Ranunculus escholtzii*	0.054	0.406*	12.0
Ran spp	*Ranunculus* spp.	0.382*	0.789*	14.7
Sax fla	*Saxifraga flagellaris*	0.551*	0.867*	6.7
Sax mer	*Saxifraga mertensiana*	-0.256*	0.093	8.0
Sax opp	*Saxifraga oppositifolia*	0.495*	0.520*	6.7
Sax tri	*Saxifraga tricuspidata*	0.455*	0.350*	85.3
Sil aca	*Silene acaulis*	0.612*	0.924*	42.7
Sol mul	*Solidago multiradiata*	0.490*	0.548*	77.3
Ste lon	*Stellaria longipes*	0.570*	0.698*	24.0
Zyg ele	*Zygadenus elegans*	-0.829*	-0.817*	29.3
Dwarf Shrubs				
Arc uva	*Arctostaphylos uva-ursi*	-0.650*	-0.964*	26.7
Cas tet	*Cassiope tetragona*	0.653*	0.342*	8.0
Dry int	*Dryas integrifolia*	0.709*	0.912*	58.7
Sal arc	*Salix arctica*	0.407*	0.755*	16.0
Sal pol	*Salix polaris*	0.700*	0.892*	22.7
Sal ret	*Salix reticulata*	0.745*	0.671*	28.0
Vac vit	*Vaccinium vitis-idaea*	0.225*	-0.420*	9.3
Shrubs				
Bet gla	*Betula glandulosa*	-0.180	-0.810*	21.3
Jun com	*Juniperus communis*	-0.492*	-0.705*	6.7
Pot fru	*Potentilla fruiticosa*	-0.671*	-0.699*	53.3
Ros aci	*Rosa acicularis*	-0.767*	-0.915*	18.7
Sal gla	*Salix glauca*	-0.646*	-0.840*	29.3
Miscellaneous				
Bare	Exposed soil/rock	0.000	0.000	100.0
Lic spp	Lichen spp.	0.834*	0.808*	45.3
Litter	Litter	-0.370*	0.054	92.0
Mos spp	Moss spp.	0.717*	0.716*	62.7

browsing new subalpine fir tips and *Populus* buds (this study; Seip and Bunnell 1985*b*). *Elymus innovatus*, *Festuca* and *Poa* were the most frequently described graminoids at sites used by Stone's sheep ewes (Table 3.5). *Poa*, *Carex* spp. and *Trisetum spicatum* were the graminoids most positively correlated with axis 2, indicating that Stone's sheep ewes associated with these species at higher elevations later in summer. Sheep generally associated with *Elymus innovatus* and *Agropyron* at lower elevation sites earlier in the growing season. Both of these were negatively correlated with the ordination axes (Table 3.5). *Achillea*, *Artemisia*, *Astragalus*, *Lupinus*, *Oxytropis* and *Zygadenus*, which are the most common forb species in the spring and summer diets of thinhorn sheep (Luckhurst 1973; Hoefs and Cowan 1979; Seip and Bunnell 1985*b*), were negatively correlated with axis 2 and found in >10% of the sites used by Stone's sheep in the B-P (Table 3.5). Only *Astragalus* a*lpinus* and *Oxytropis nigrescens* were not significantly related to axis 2. All shrubs and the dwarf shrub *Arctostaphylos* were negatively correlated with both ordination axes and all were significantly related to axis 2. This is opposite to the positive correlation for moss and lichen species in the ordination (Table 3.5), and supports the direction of the shrub and moss/lichen vectors (Table 3.4) used for describing the plant community associations of Stone's sheep ewes.

The similar direction (Fig. 3.3 and Fig. 3.4), sign and correlation (Table 3.4) associated with date and elevation vectors suggested a possible relationship between correlates. Indeed, the elevational movement exhibited by Stone's sheep ewes in their use of plant communities followed a temporal trend (Fig. 3.5). The elevation of sites used by ewes without lambs was positively correlated ($r = 0.67$, $n = 75$, $P < 0.001$) with date, indicating that sheep used lower elevation sites in May than in July (Fig. 3.5). The relationship was weaker for ewes with lambs

Fig. 3.5. Elevation of sites used by maternal and nonmaternal Stone's sheep ewes from mid-May to August (2002-2003) in the Besa-Prophet area of northern British Columbia.



but still significant ($r = 0.48$, $n = 75$, $P = 0.002$) (Fig. 3.5). The temporal trend in altitudinal movement may be in response to the environmental tracking of plant quality because >93% (70/75) of sites occurred in phenological stage three or less and approximately 68% (51/75) of sites were characterized by plants with unfurled leaves and no visual reproductive structures. Selection for this stage lasted from the first week of June (week 23) until the end of data collection during the last week of July (week 30). This was reflected in the ordination for which phenology was only weakly correlated with both axes (Table 3.4), and indicating that sheep did not associate with the phenology of plant communities on a continuum as they did with elevation.

Discussion

Rarely, if ever, do ecologists explicitly describe intrasexual segregation of female ungulates in the context of hypotheses predicting intersexual segregation. We had the opportunity to use activity budgets, bout behaviours, and measures of habitat use to distinguish between groups of Stone's sheep ewes in northern British Columbia. These data reflected the combined influence of nutrition and predation, which has been noted in other mountain sheep (Risenhoover and Bailey 1985; Festa-Bianchet 1988; Bleich et al. 1997; Rachlow and Bowyer 1998; Corti and Shackleton 2002), and mountain bovid studies (Geist 1971; Shank 1984; Kohlmann et al. 1996; Toïgo 1999).

Stone's sheep ewes spent the greatest proportion of their active time foraging as has been documented for most wild herbivores (Bunnell and Gillingham 1985). Although not statistically different, maternal Stone's sheep tended to spend proportionally less active time foraging then nonmaternal ewes, which is probably related to nursing or other behaviours associated with raising young (Bunnell and Gillingham 1985; Rachlow and Bowyer 1998). Proportion of time spent foraging by Stone's sheep in the B-P was similar to Stone's sheep in other British Columbia populations (63-66% of time, Seip and Bunnell 1985*b*; Geist 1971) Surprisingly, Stone's sheep in the B-P spent considerably less active time foraging (~67% for maternal and ~69% for nonmaternal ewes) than has been documented for Dall's sheep in Alaska and Yukon (~91% and ~96%, respectively, Bunnell and Gillingham 1985). Foraging efficiency in our study was even low compared to Alaskan Dall's sheep that foraged least efficiently (>75%) after lambing during a year with an extremely late spring and short growing season (Rachlow and Bowyer 1998). Rachlow and Bowyer (1998) attributed differences in foraging efficiency between years to changes in group size, yet the average group size of ~4.3 individuals in the B-P was similar to that found in Alaska. Group sizes of Dall's sheep in the Yukon were greater with average nursery groups exceeding 7.5 individuals and nonnursery groups of ~5.6 individuals (Corti and Shackleton 2002). Even though group size was not a predictor of foraging efficiency by Stone's sheep in the B-P, it has been reported to significantly influence foraging efficiency and habitat use of both Dall's and bighorn sheep (Risenhoover and Bailey 1985; Frid 1997; Rachlow and Bowyer 1998). In groups, individuals increased the amount of time foraging in an active bout and ventured farther from escape terrain when in larger groups (Risenhoover and Bailey 1985; Rachlow and Bowyer 1998). This has been hypothesized as an adaptation enabling sheep to utilize less secure habitats (Risenhoover and Bailey 1985).

Assuming the age and weight of our study animals were similar to other Dall's sheep (Seip and Bunnell 1984) and Stone's sheep (Bunnell and Gillingham 1985; Rachlow and

Bowyer 1998), the reduced foraging efficiency may be related to available forage, intake rate or risk of predation. The quantity of forage available to Stone's sheep in the B-P could be greater because of its more southerly latitude. Ranges contain enough fuels to be routinely burned as a method of promoting and enhancing Stone's sheep habitat in British Columbia (Elliot 1978; Seip and Bunnell 1985*a*), which is rarely if ever done for Dall's sheep (Nichols and Bunnell 1999). If the B-P is higher in forage biomass, Stone's sheep may spend less time foraging (Seip and Bunnell 1985*b*). Festa-Bianchet (1988) documented that female bighorns using areas with lower forage biomass spent more time foraging and less time biting vegetation than ewes in areas with more available forage. Both bite size and rate are related to forage structure, and bite size is largely influenced by range condition (Bunnell and Gillingham 1985). The sward height of grasses has been shown to affect intake rates of domestic sheep (Penning et al. 1991) and may influence the selection or avoidance of a grass species (O'Reagain 1993). Animals experiencing greater energy demands (i.e., lactation) should feed more intensively as observed in maternal bighorns that had higher bite rates than nonmaternal ewes (Ruckstuhl et al. 2003). This assertion is especially true if individuals are not forced into poor quality areas to reduce their risk of predation.

Risk of predation can be extremely influential on foraging and may overshadow forage structure as animals in riskier habitats spend more time conducting nonforaging related activities and are often forced into more restrictive habitats (Lima and Dill 1990; Kie 1999). There are no data on how risk differs between Dall's sheep ranges in Alaska and the Yukon versus the ranges of Stone's sheep in the B-P. Sheep mountain in the Yukon where data were collected for review in Bunnell and Gillingham (1985), however, generally lacks other ungulates and golden eagles (*Aquila chrysaetos*) and coyotes (*Canis latrans*) were the only common predators (Hoefs and Cowan 1979). The B-P area contains an abundance of grizzly bears (*Ursus arctos*), coyotes, golden eagles, wolverines (*Gulo gulo*) and wolves (*Canis lupus*) (Bergerud and Elliot 1998), which were observed in sheep habitat throughout the course of the study. The diversity and abundance of predators suggest it is potentially a riskier place to live. The decrease in proportion of active time spent foraging by Stone's sheep ewes in the B-P most likely results from an interaction of increased foraging efficiency in habitats containing greater biomass at a potentially increased risk of predation.

Even though behaviours were not different between Stone's sheep ewes with lambs and those without (Fig. 3.2), duration of active bouts did differ. In contrast to previous findings (reviewed in Bunnell and Gillingham 1985), maternal Stone's sheep spent shorter times active than nonmaternal ewes albeit with considerable variation. How activity changes relative to environmental constraints or predation risk, interacting with maternal status, is not clear.

The high use of herbaceous habitat (Fig. 3.1) is within the context of Stone's sheep spending the majority of active time foraging, largely on graminoids and alpine forbs (Seip 1983). Trends in the habitats used while active were similar between maternal and nonmaternal ewes except for shrub and solid-rock-escape features. Differences in use of shrub habitat may be related to timing of use and habitat visibility. Stone's sheep ewes with lambs were first observed in early June, but the majority of observations of sheep observed using shrub-dominated habitat occurred in May, prior to observations of maternal ewes. It is possible that parturient sheep also used shrub habitats. Low habitat visibility has been recognized to reduce foraging efficiency by bighorn sheep, and may be an important predictor of high predation risk (Risenhoover and Bailey 1985). If intrasexual differences do exist between Stone's sheep ewes related to predation risk, ewes with lambs may be less likely to use brushier habitats. The significantly greater amount of active time spent in solid-rock-escape features by maternal ewes lends support for this contention. In addition, the lack of difference in alert behaviour between maternal and nonmaternal ewes may be further indication that maternal ewes are associating with more secure habitats. Reasons for the increased use of broken-rock-escape features and tree habitat by maternal ewes while bedded are less clear.

Habitat use of ungulates while inactive is rarely described, but has been related to antipredator behaviour of Dall's sheep in Alaska (Corti and Shackleton 2002). Low-elevation habitats contain greater forage biomass and lower visibility, both of which are contrary to the predation-risk trade-off described for Stone's sheep when active. The few timbered sites where maternal ewes bedded, however, were extremely steep and may have been in response to avian predators such as golden eagles that were observed throughout the study area and are known to predate thinhorn lambs (Nette et al. 1984). Stone's sheep also are extremely cryptic in rocky habitats, and the use of broken-rock habitat while bedded may be an antipredator response capitalizing on this. Broken rock can also be extremely noisy and approaching terrestrial predators may be more easily detected. Distance to secure cover has been shown to differ among males, nonmaternal females and maternal females, with groups containing lambs placing themselves closest to escape cover (Corti and Shackleton 2002).

Predictive modeling (Table 3.3) and pairwise comparisons (Table 3.1) of differences between groups of ewes with and without lambs contribute to the increasing evidence supporting the trade-off used by Stone's sheep ewes during spring and summer. The simplest model best describing the differences between nursery and nonnursery groups consisted of distance to nearest-escape feature and size of nearest-escape feature. Although size is generally not included as a measure of escape features, it was the single most important explanatory variable. Incorporating patch size into maintaining and establishing desert bighorn populations has increasingly become imperative (McKinney et al. 2003). Extirpation rates and variability in lamb density decrease with increasing size of escape terrain. Patch size of escape terrain has been positively correlated with total population size and female and lamb population size of desert bighorns in Arizona (McKinney et al. 2003). Only two variables, size of nearest-escape area and phenology, were significant in any of the top models for Stone's sheep. The majority of pairwise differences between nursery and nonnursery groups also involved features associated with avoiding predators. The amount of exposed soil and rock, the size of broken escape features and size of nearest-escape features were significantly greater in sites used by nursery groups. Nursery groups were also significantly closer to an escape feature than nonnursery groups. Regardless of maternal status, Stone's sheep in the B-P tended to be closer to escape features than the 20.50 m documented for Dall's sheep in Alaska (Rachlow and Bowyer 1998) and further than the 2.37 m for maternal Dall's sheep in the Yukon (Corti and Shackleton 2002), indicating that risk of predation or perceived risk may differ markedly between thinhorn populations.

Behavioural differences in the use of escape features suggest that Stone's sheep use broken rock and solid-rock-escape features differently. Although not differentiated in other studies, broken- and solid-rock-escape features may mean different things to sheep. Generally the broken-rock-escape features lacked much if any vegetation whereas shelves and small outcrops associated with solid-rock-escape features supported significant amounts of forage; this provides some clarification as to why Stone's sheep spent relatively little amounts of active time in broken-rock habitat. Why differences between intrasexual groups occurred in habitat use recorded during behavioural observations of active sheep (Fig. 3.1), but were not reflected in the measures of habitat attributes (Table 3.1), may largely be due to differences in scale. Behavioural observations provided a coarser scale of resolution than habitat assessments of smaller microsites. Inferences on ecological mechanisms can vary with the scale of analysis (Rachlow and Bowyer 1998; Johnson et al. 2001) as animals respond to environmental attributes in a hierarchical fashion (Johnson 1980; Schaefer and Messier 1995; Johnson et al. 2001).

The constraints imposed on maternal ungulates relative to the energetic demands of lactation (White 1983; Gittleman and Thompson 1988; Parker et al. 1999) are confounded by the vulnerability of young to predation (Berger 1991; Bleich et al. 1997). The trade-off between forage and predation risk in female mountain sheep during lambing is well documented (Rachlow and Bowyer 1998; Festa-Bianchet 1988; Berger 1991; Bleich et al. 1997). Pregnant bighorn ewes in southwestern Alberta moved from winter range to higher elevation lambing areas prior to green-up (Festa-Bianchet 1988). The climate was harsher and the forage of lower quality at lambing sites than on the winter range where forage selected by nonparturient ewes was at its highest quality. The lambing areas, however, were rugged and apparently free of terrestrial predators (Festa-Bianchet 1988). Somewhat in contrast, the parturient Stone's sheep ewes observed by Geist (1971) occupied high cliffs close to or above the wintering areas and never deserted the winter range entirely. Berger (1991) documented the significance of steep and variable terrain to mountain sheep in predator-rich environments as bighorn lambs and ewes were more than three times as susceptible to predation when away from slopes >15°. Berger (1991) also confirmed the trade-off between nutrition and predation in bighorn ewes, as ewes not accompanied by young utilized areas with elevated risks to predation more often than ewes with young.

Phenology and shrub cover were the only habitat attributes that differed between nursery and nonnursery groups in pairwise comparisons (Table 3.1). Both reflect a temporal difference in observations and a temporal and elevational change in plant community associations. The nursery groups were not observed before the beginning of June, subsequent to when sheep were most frequently observed in low-elevation shrub habitat. At that time, vegetation growth had already commenced although the progression of green-up was in the early stages. This temporal and elevational gradient exhibited by Stone's sheep in the B-P was best described in the NMS ordination of plant species.

The low stress and strong relationships between ordination axes, environmental vectors and plant species indicate that NMS was a useful tool for describing plant community associations of herbivores. Stress <10 indicates a good measure of community structure with no real risk of drawing inappropriate conclusions (Clarke 1993). NMS simultaneously describes complex community datasets in reference to several explanatory attributes while avoiding the limiting assumptions associated with many other ordination techniques (Clarke 1993; McCune and Grace 2002). It is bias free and accommodates extremely complex datasets that are often plagued by zeros as is often the case with plant community data (McCune and Grace 2002).

In our study, NMS did not discern intrasexual differences of Stone's sheep, but described the plant communities that Stone's sheep associate with along a gradient of time, elevation, and cover of shrubs and moss/lichens. The ordination of plant species and subsequent scatterplot of elevation and date described the altitudinal gradient over which sheep moved from spring to summer. Plant communities change along elevational gradients (Meidinger and Pojar 1991; Albon and Langvatn 1992) with the onset of vegetation growth occurring later at higher elevations (Johnston et al. 1968; Albon and Langvatn 1992). Stone's sheep associated with lower elevation shrub communities in spring and moved up in elevation as time progressed into communities with increased cover of moss and lichens. The altitudinal movement exhibited by Stone's sheep in the B-P is similar to observations of Stone's sheep in the Toad River region of British Columbia (Seip and Bunnell 1985*b*). As with other temperate ungulates that migrate over altitudinal gradients (Boyce 1991; Albon and Langvatn 1992; Nichols and Bunnell 1999; Demarchi 2003), Stone's sheep prolong their access to nutritious forage by choosing a specific phenological stage as they move up in elevation (Seip 1983). Such phenological tracking has been shown to allow animals access to forage with higher levels of crude protein (Albon and Langvatn 1992) and fewer chemical defenses (Bryant et al. 1991). The most frequently described phenological stage at sites used by Stone's sheep in the B-P was characterized by plants with fully formed leaves that had yet to develop reproductive structures. This stage has been shown to yield the highest percentage of crude protein and phosphorous in graminoids from alpine ranges used extensively by bighorn sheep (Johnston et al. 1968).

Thinhorn sheep are recognized primarily as grazers with graminoids constituting the largest portion of their diet in spring and summer (Luckhurst 1973; Hoefs and Cowan 1979; Seip and Bunnell 1985*b*) and unlike bighorns, they often ingest terrestrial lichen and moss (Luckhurst 1973; Hoefs and Cowan 1979; Simmons et al. 1984; Seip and Bunnell 1985*b*). The most commonly described forage species of thinhorn sheep were identified in the B-P and almost all were included in the final ordination. The foraging strategies of Stone's sheep in relation to species selectivity observed by both Luckhurst (1973) and Seip and Bunnell (1985*b*) were consistent with the location and correlations of species found on the NMS ordination. During the spring and early stages of plant green-up, Stone's sheep have been observed to forage on and frequent communities dominated by *Elymus innovatus* and *Agropyron* graminoids; *Achillea, Myosotis*, *Oxytropis* and *Zygadenus* forbs; and *Arctostaphylos* and *Rosa* shrubs (Luckhurst 1973, Seip and Bunnell 1985*b*). Although forage intake and species selection were not quantified, in our study these forages were frequently recorded and negative coefficients for these species in the ordination indicated that ewes in the B-P associated with these species earlier in the growing season at lower elevations. The similarity between the plant community associations of Stone's sheep in the B-P and forage selection by Stone's sheep observed by Luckhurst (1973) and Seip and Bunnell (1985*b*) was also apparent as the growing season progressed. Prominent forages observed in the diet of Stone's sheep during summer include *Carex*, *Poa*, *Festuca*, *Astragalus* and *Lupinus*, which are all associated with higher elevation sites used later in summer by Stone's sheep ewes in the B-P. The ability to simultaneously characterize species communities and describe them in relation to environmental variables highlights the utility of the NMS ordination.

The evidence from behavioural observations, vegetation attributes and habitat use support the predation-risk hypothesis towards explaining the intrasexual segregation of Stone's sheep ewes during the spring and early summer (Table 3.6). Although our data do not definitively reject Ruckstuhl and Neuhaus' (2000) activity-budget hypothesis, there was less support for it. In order for the less energetically constrained nonmaternal ewes to conform to the activity-budget hypothesis they would need to spend proportionally less time

Table 3.6. Summary of results (from Table 3.1 and Fig. 3.2) and their fit to the predictions of the predation-risk, forage-selection and activity-budget hypotheses used to explain differences between nursery and nonnursery groups of Stone's sheep ewes in the Besa-Prophet area of northern British Columbia (2002, 2003). Fit indicates whether the predictions of the hypotheses were met.

Hypothesis	Predictions	Fit
Predation-risk	Maternal females should associate with safer habitats where offspring are less vulnerable to predation at the expense of foraging opportunities by associating with:	
	1) steeper slopes	no
	2) closer escape features	yes
	3) larger escape features	yes
	4) sites of older phenological stages	yes
Forage-selection	Maternal females should use high quality habitat where foraging opportunities are greater in order to meet the high energy demands associated with lactation by choosing sites with:	
	1) younger phenological stages	no
	2) greater forage availability	no
Activity-budget	Maternal females should increase their forage intake to compensate for higher energy demands by spending proportionally:	
	1) more time foraging	no
	2) more time walking[a]	no
	3) more time active[a]	no[b]

[a] prediction is not associated with forage intake but may lead to segregation under the activity-budget hypothesis (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000)

[b] result contradicts prediction, but differences in the duration of time spent active may cause segregation (Seip 1985*b*; Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000; Ruckstuhl and Neuhaus 2002)

foraging and walking or walk less during an active bout and be associated with habitats similar to those of maternal ewes (Main et al. 1996; Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000). We did not measure differences in distances moved, but assumed that the proportion of time foraging and walking provided reasonable surrogates. There were no statistical differences, but both proportions of time foraging and walking were on average slightly greater for nonmaternal ewes. In contrast to previous findings, the duration of active bouts was longer for nonmaternal ewes even though energy demands are considerably less (reviewed in Bunnell and Gillingham 1985; Ruckstuhl and Neuhaus 2002). It is this counterintuitive result that gives some support for the activity-budget hypothesis. If activity budgets are sufficiently different, segregation may occur (Ruckstuhl and Neuhaus 2002; Ruckstuhl and Neuhaus 2002).

Predictions for the forage-selection hypothesis suggest that physiologically less constrained individuals should choose forage of potentially lower quality (Main et al. 1996) (Table 3.6). Even if spatial overlap cannot be clearly distinguished, lactating females should exploit areas with higher quality or quantity of forage (Ruckstuhl and Neuhaus 2000). Because sites used by maternal females were of poorer quality (i.e., older phenological stage) or were not different using our availability index of forage, the forage-selection hypothesis does not appear to explain intrasexual segregation of Stone's sheep ewes in the B-P. Instead, data from our study conform to the predation-risk hypothesis as female Stone's sheep segregated relative to reproductive status as a result of apparent predation constraints more so than differences in behaviours or forage quality and quantity. Maternal ewes spent more time in solid-rock-escape features and less time in shrub habitat while associating with sites closer to escape features, having larger escape features and containing more exposed soil and rock. No differences in maternal status were exhibited in walking or foraging behaviour. Plant communities were similar between nursery and nonnursery groups, both associating with those plant communities on a temporal and elevational gradient. This predation-risk trade-off has characterized intersexual segregation in wild sheep (Bleich et al. 1997; Corti and Shackleton 2002) and has close parallels to the maternal trade-offs described for bighorns (Festa-Bianchet 1988; Berger 1991).

Chapter 4: Fecal glucocorticoid concentrations of free-ranging Stone's sheep[3]

Introduction

Wild sheep are particularly susceptible to disturbance and elicit physiological and behavioural responses to humans and aircraft in close proximity (MacArthur et al. 1982; Stockwell et al. 1991; Bleich et al. 1994; Papouchis et al. 2001; Frid 2003). These disturbances have been recognized as imposing energetic costs on sheep and may alter habitat use, increase susceptibility to predation and/or increase nutritional stress (Stockwell et al. 1991; Bleich et al. 1994). Chronic environmental stress is believed to contribute to the pneumonia epizootics in bighorn sheep (*Ovis canadensis*) (Kraabel and Miller 1997). Although such large-scale epizootics have not been observed in wild thinhorns (*Ovis dalli*) and disease has not been identified as a factor limiting thinhorn populations (Nichols and Bunnell 1999), Dall's sheep (*O. d. dalli*) under experimental conditions are as susceptible to pneumonia from *Pasteurella haemolytica* as bighorn sheep (Foreyt et al. 1996). Lungworm (*Protostrongylus* spp.), an associate of certain pneumonia pathogens (Bunch et al. 1999), has been identified in Stone's sheep (*O. d. stonei*) (Luckhurst 1973; Seip 1983). The susceptibility to disease, philopatric nature, and inability to readily disperse or expand ranges (Geist 1971; Worley et al. 2004) make Stone's sheep particularly sensitive to disturbance. With increasing resource development of sheep habitat and access to sheep ranges, stressors imposed on Stone's sheep are likely to escalate with potentially serious consequences (Paquet and Demarchi 1999).

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[3] A version of this chapter will be submitted for publication with the following authorship: Andrew B. D. WALKER and Katherine L. PARKER

Stress elicits physiological and behavioural responses that can be invoked by physical or psychological stressors (Reeder and Kramer 2005). Response to stressors culminates in the release of adrenaline and glucocorticoids from the sympathetic nervous system (SNS) and hypothalamic-pituitary-adrenal axis (HPA). Both systems play a role in the fitness of an individual by enabling it to deal with challenges over short (SNS) and long terms (HPA) (Reeder and Kramer 2005). Prolonged production of glucocorticoids, however, can be detrimental to the health of an animal (Breazile 1987; Reeder and Kramer 2005). Chronic stress can impede reproduction, alter feeding behaviour and efficiency, cause hypertension and ulceration, and suppress the immune system (Breazile 1987).

Monitoring environmental and anthropogenic stress in animals is difficult because of the stress placed on the animal by the act of sampling (Moberg 1987). Traditionally, measures of stress have been obtained from glucocorticoids (i.e., corticosterone and cortisol) in blood serum or plasma (Moberg 1987; Harlow et al. 1987), but measures were often inflated because of the rapid response to stress during handling (Moberg 1987). Plasma glucocorticoids can increase within 2-3 min of an animal being induced with a stressor (Sapolsky et al. 2000). In contrast, fecal excretion of glucocorticoids is largely determined by the time needed for cortisol metabolites to travel through the digestive system (Millspaugh and Washburn 2004). Sheep and other large ruminants have relatively long digestive systems with slow passage rates (Millspaugh and Washburn 2004). Millspaugh et al. (2002) documented a temporal delay in glucocorticoid response in fecal samples of at least 10 to 12 h, following adrenocorticotropic hormone (ACTH) challenges on white-tailed deer (*Odocoileus virginianus*). Within 30 h of the induced stressor, fecal glucocorticoid measures returned to pretreatment levels. Bighorn sheep responded similarly under comparable ACTH treatments (Miller et al. 1991). The temporal lag between glucorticoid secretion in blood and fecal excretion limits the ability of fecal glucocorticoids to detect circadian periodicity (observed in desert bighorn sheep (*O. c. nelsonii*), Turner 1984). This indicates that fecal measures better reflect average daily concentrations of circulating glucocorticoids and, therefore, are ideal for measuring long-term stress in wild animals (Millspaugh and Washburn 2004). In addition, collection of samples can be accomplished without disturbing or handling study subjects (Wasser et al. 2000; Millspaugh et al. 2002; Reeder and Kramer 2005).

Fecal glucorticoid assays have been used with numerous vertebrate taxa (reviewed in Millspaugh and Washburn 2004). Miller et al. (1991) validated the assays in bighorn sheep and monitored responses of chronic stress in fecal and urine samples using cortisol concentrations. Even though sampling is noninvasive, sampling protocols and biological factors can influence measures of fecal glucocorticoids (reviewed in Millspaugh and Washburn 2004). Sampling issues include sample age and condition, storage and transportation, sample selection, weight and assay type. Known biological issues influencing fecal glucocorticoid concentrations of free-living mammals are sex, age, diet, body condition and reproductive status of sampled individuals (reviewed in Millspaugh and Washburn 2004). Seasonal trends in glucocorticoid concentrations are also common in most mammals (reviewed in Romero 2002). None of these issues have been quantified for wild sheep.

Our goal was to define baseline levels and seasonal variation in concentrations of glucocorticoids for Stone's sheep. We compared samples from two areas that differed in anthropogenic access and development, predicting that glucocorticoid concentrations would be higher with greater human disturbance. A secondary objective was to examine the relationship between cortisol and corticosterone, the two most readily used glucocorticoids for describing stress in vertebrates (Moberg 1987). This study was part of a larger project investigating habitat selection and behavioural strategies of Stone's sheep (see Chapters 2 and 3).

Study Area

The study area was situated in the Besa and Prophet (B-P) River watersheds of the Muskwa-Kechika Management Area (MKMA) in northern British Columbia, between 57° 20' and 57° 40'N and 123° 10' and 123° 45'W (an additional description is found in Chapter 2). The 6.3 million-ha MKMA is distinguished by protected areas (i.e., provincial parks) and zones accommodating industrial development as long as wildlife and other socio-environmental values are recognized (i.e., special management zones). The B-P watersheds are largely unprotected with Stone's sheep found throughout their mountainous regions. Although no significant industrial development has taken place, the southern portion of the study area is likely to see an influx of oil and gas exploration in the near future. Recreational activity is almost entirely confined to the southern portion of the study area where there is a permanent outfitter camp and a government designated all-terrain vehicle (ATV) trail. The trail is used from spring through fall and extends the length of the Neves valley in close proximity to several easily accessible mountains inhabited by Stone's sheep. Several seismic lines have also been established in the Neves valley (Appendix A, Fig. A.1). The majority of activity occurs during the summer and fall with the start of hunting season. Snowmobile activity is also present during winter. The northern portion of the study area, encompassing Duffield Creek, is extremely remote and lacks any permanent anthropogenic development.

The Neves and Duffield drainages are separated by the Besa River and data from GPS-collared individuals indicated that there were no movements between these areas (Appendix A, Fig. A.1).

Methods

Fecal samples were collected during early winter (December and January), late winter (March/April) and summer (July) of 2002 and 2003. Samples in early winter were taken from captured adult Stone's sheep ewes throughout the study area. Samples from late winter and summer were collected opportunistically after observing maternal females. To minimize samples coming from the same individual, we selected at least three different sites occupied by sheep within the Neves and Duffield ranges each year. Although time since excretion, age of individuals, sex, diet, body condition and reproductive status (Millspaugh and Washburn 2004) were not determined, we tried to alleviate several of these issues by selecting only fresh samples from sites recently or still occupied by female sheep. We did not select samples from lambs, which were easily distinguished by small pellet size, and went to ranges unoccupied by rams. Stone's sheep are known to segregate sexually (Geist 1971; Luckhurst 1973; Seip 1983) with rams occupying distinct ranges or portions of a range away from ewes most of the year except during the breeding season (Geist 1971). We collected samples more than two days after any aircraft activity took place near collection sites to remove the influence of aerial disturbance and to allow for quantification of stress levels uninfluenced by the act of sampling itself.

All 85 fecal specimens were frozen within 2 hours of collection until subsequent analyses for glucocorticoid content (Prairie Diagnostic Services, Saskatoon, Saskatchewan). Fecal samples (10-12 pellets) were moved to 20-ml vials for lyophilization. Dried feces were then ground. Approximately 0.25 g of each dry fecal sample were combined with 5 ml of 90% AnalaR grade methanol and mixed frequently by inversion over a 24-hour period. Following refrigeration overnight, samples were centrifuged for 20 min at 1500 g. One-ml aliquots of each methanol supernatant were then dried under air. Each aliquot was reconstituted with 100:1 absolute ethanol (to redissolve green pigments) and 1 ml of steroid diluent (from the corticosterone assay kit), capped, vortexed and left overnight.

Corticosterone content of 50-µl aliquots was determined using the ICN corticosterone RIA antibody (MP Biomedicals, Costa Mesa, California), which is effective in detecting endogenous adrenal activity in a wide array of species (reviewed in Wasser et al. 2000). Samples (50 µl) were also quantified for cortisol using the DPC Cortisol Coat-A-Count radioimmunoassay (Diagnostic Products Corporation, Los Angeles, California). Results were calculated to give $ng \cdot g^{-1}$ feces. Sample concentrations were multiplied by two for the 50-µl sample size, multiplied by five for the 1 ml of methanol originally dried down, and then divided by the weight of the original fecal sample to give final units of ng $glucocorticoid \cdot g\ feces^{-1}$.

We compared glucocorticoid measures between Neves and Duffield populations using a two-way ANOVA of fixed effects with population nested within three seasons. Values were log-transformed after examining assumptions of normality and homogeneity of variance (Levene's test). Tukey's honestly significant difference (HSD) test was used as a post-hoc comparison of main effects within significant models (Zar 1999). The relationship between corticosterone and cortisol was described using Pearson's correlation coefficient (Zar 1999). Statistical significance was assumed at $\alpha \leq 0.05$ and all statistical procedures were conducted using Statistica 6.0 (Statsoft 2001).

Results

Average fecal glucocorticoids of Stone's sheep followed similar seasonal change in the Neves and Duffield Creek drainages (Fig. 4.1A, B). Populations were not significantly different for either corticosterone ($F_{3,79} = 0.96$, $P = 0.418$) or cortisol ($F_{3,79} = 0.11$, $P = 0.954$). Seasonal differences were prevalent, however, for both corticosterone ($F_{2,79} = 24.28$, $P < 0.001$) and cortisol ($F_{2,79} = 3.62$, $P = 0.031$). Corticosterone levels across all sheep successively increased from early winter (33.5 ± 1.94 ng·g^{-1} feces, $\bar{x} \pm$ SE) through late winter to summer (56.0 ± 2.94 ng·g^{-1} feces) and all seasonal comparisons were significant after post-hoc analysis (Fig. 4.1A). Average cortisol levels were similar from early winter to late winter and between early winter and summer (Fig. 4.1B), but late winter was significantly lower than summer (Fig. 4.1B).

As an assay, cortisol was much more variable than corticosterone. Across seasons cortisol ranged from a minimum of 3.6 to a maximum of 111.8 ng·g^{-1} of feces, with variation averaging 63% of the mean. The variability in cortisol was higher than the range (21.5 – 94.2 ng·g^{-1}) and coefficient of variation (36%) observed for corticosterone. In spite of differences in variation and temporal patterns, corticosterone and cortisol measures were positively correlated ($r = 0.68$, $n = 85$, $P < 0.001$) (Fig. 4.2).

Fig. 4.1. (A) Corticosterone and (B) cortisol concentrations ($\bar{x}$ ± SE) in fecal samples collected from Stone's sheep in the Besa-Prophet study area of northern British Columbia during early winter, late winter and summer of 2002 and 2003. For both glucocorticoids, values above error bars are sample sizes from the Neves Valley population; values below error bars are sample sizes for the Duffield population. For each glucocorticoid, seasons sharing the same letters next to the mean values were not significantly different from each other.

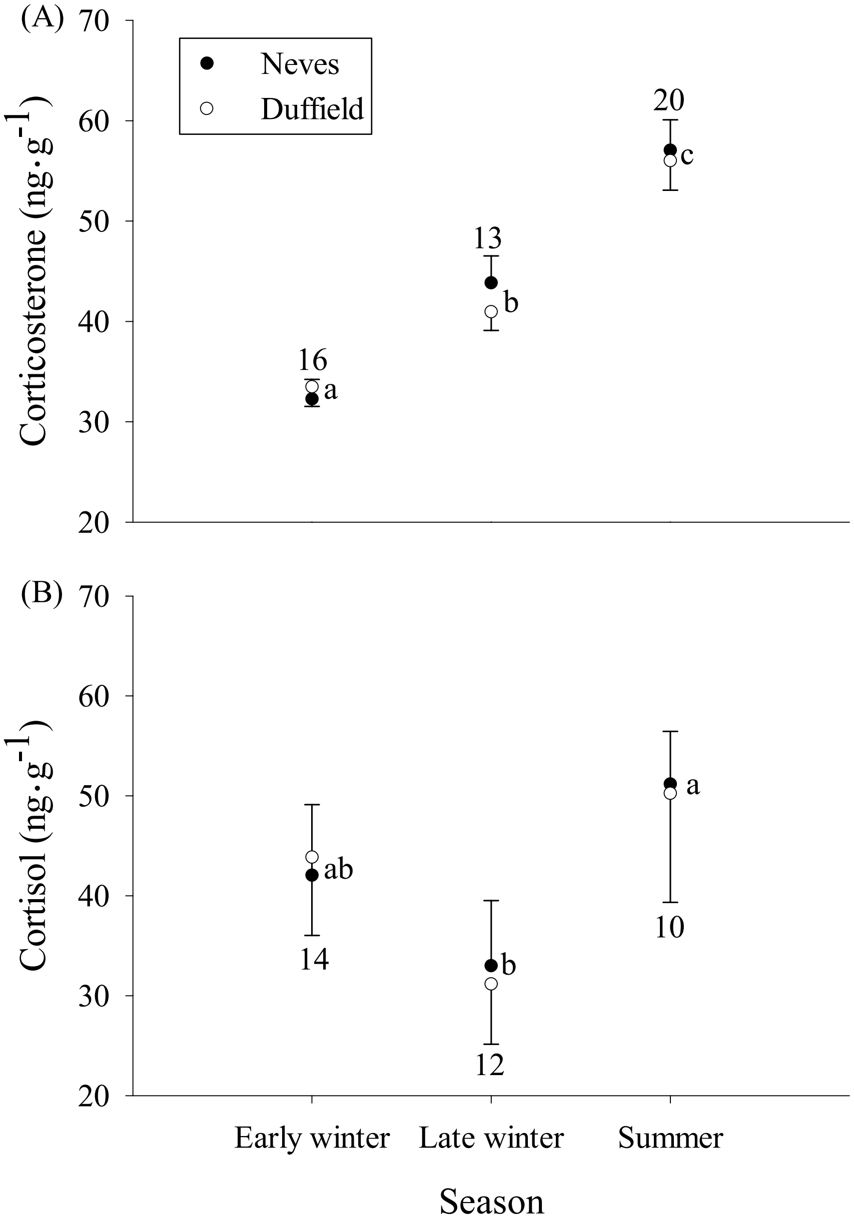
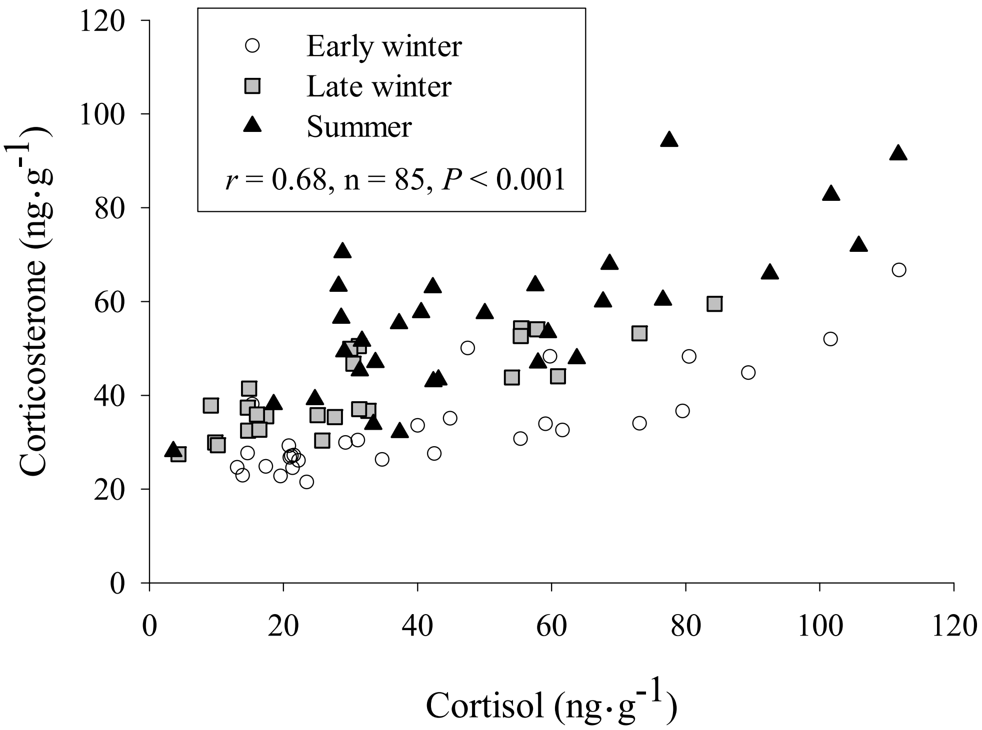


Fig. 4.2. Relationship between corticosterone and cortisol concentrations by season in fecal samples collected from Stone's sheep in the Besa-Prophet study area of northern British Columbia during 2002 and 2003.



Discussion

Glucocorticoid concentrations are recognized as a physiological index for monitoring stress responses in sheep (Harlow et al. 1987). Both corticosterone and cortisol were readily detectable in the feces of Stone's sheep. Typically one hormone tends to be more prevalent than the other in a given species, but both may persist in measurable quantities (Millspaugh and Washburn 2004). Their relationship to each other has been poorly described and trends between cortisol and corticosterone have been shown to differ between captive and free-ranging desert bighorns (Turner 1984). Cortisol is generally the most prevalent glucocorticoid of large mammals (Millspaugh and Washburn 2004). In Stone's sheep, however, corticosterone provided a less variable measure of glucocorticoid concentrations than cortisol in every season. This may be due, in large part, to the ability of the assay to cross-react or recover corticosterone more consistently than cortisol in fecal samples of Stone's sheep (Wasser et al. 2000). The variation exhibited in fecal corticosterone was still considerably greater than the 10% coefficient of variation described for fecal assays used on bighorn sheep under experimental conditions (Miller et al. 1991).

Contrary to our predictions, the glucocorticoid concentrations in the Neves and Duffield populations of sheep were similar even though anthropogenic development and access in the Neves Valley are greater. We did not measure whether direct interactions between human activities and sheep occurred, but assumed that increased access to Stone's sheep via the Neves Valley would elevate glucocorticoids of those individuals. Due to the lack of difference, however, the glucocorticoid concentrations probably represent relatively undisturbed levels of stress.

Fecal glucocorticoid concentrations in Stone’s sheep fluctuated seasonally with higher levels in summer than late winter. This trend is similar to that of elk (*Cervus elaphus*) from Custer State Park in South Dakota, which experienced highest fecal glucocorticoid concentrations during summer when air temperatures and anthropogenic disturbance were highest (Millspaugh et al. 2001). These factors, as well as seasonal metabolic rhythms, could potentially contribute to the elevated glucocorticoid concentrations experienced by Stone’s sheep during summer. Compared to the 1.5 million visitors to Custer State Park annually (Millspaugh et al. 2001), sheep in our study area experience minimal anthropogenic influences (as reflected in the lack of difference between the Neves and Duffield populations). Temperatures are highest during the summer months in northern BC, but snow is not uncommon during any month of the year (Meidinger and Pojar 1991) and sheep are unlikely to be thermally stressed. Seasonal variability in glucocorticoids has largely been described for the breeding season and to a lesser extent during parturition in mammals (Romero 2002; Millspaugh and Washburn 2004). Both of these temporal periods are generally associated with increases in adrenal activity of most vertebrates. No seasons, however, are consistently associated with elevated glucocorticoid concentrations across mammalian taxa (Romero 2002).

Romero (2002) described three hypotheses for explaining seasonal patterns in glucocorticoid concentrations. The energy-mobilization hypothesis predicts that glucocorticoid concentrations will be elevated during energetically expensive seasons such as breeding or parturition. The behaviour hypothesis infers that glucocorticoids exert control over the behaviours of an animal and that the stressor is irrelevant. The preparative hypothesis posits that glucocorticoids prepare the individual for seasonal life history changes and that changes in seasonal concentrations are evolutionary reflections preparing an individual for upcoming challenges. These hypotheses are not mutually exclusive and all likely contribute to the seasonal glucocorticoid rhythm of a species (Romero 2002). Selecting the hypothesis that best explains the seasonal trends in Stone's sheep is difficult considering fecal samples were not collected throughout the year. Increased movement rates by telemetered sheep (see Chapter 2) and the high energy costs of lactation (Gittleman and Thompson 1988) during summer lend support to the energy-mobilization hypothesis. Stone's sheep ewes also were at an increased risk of predation during lambing (see Chapter 2) and experienced the greatest mortality during lambing and early summer (see Chapter 5). If female Stone's sheep perceive themselves to be at an increased risk of mortality during this time, the preparative hypothesis may also apply.

Fundamental to understanding the impacts of disturbance using fecal glucocorticoids is determining the range of acceptable concentrations and duration of chronic stress an individual can withstand without experiencing the deleterious effects associated with it (Millspaugh et al. 2004). Glucocorticoids are important to an animal's well-being (Romero 2002; Reeder and Kramer 2005) and elevated levels do not automatically equate to reduced fitness. Without understanding normal variation and effects, inferences regarding the consequences of elevated glucocorticoids are inappropriate (Millspaugh et al. 2004). Continued research on baseline glucocorticoid measures throughout the life history of a species is required to enhance our understanding of the physiological status of disturbance-sensitive species in the wild. Our study documents the first baseline information on glucocorticoid levels and the range of naturally occurring variation during three seasons for

Stone's sheep in an area where future disturbance associated with resource extraction and increased access is likely to occur.

Management Implications

Wild sheep do not readily expand their ranges or colonize new areas (Geist 1971; Worley et al. 2004), which makes them especially susceptible to local anthropogenic and environmental stressors. Increases of glucocorticoids under captive conditions have shown to increase the susceptibility of bighorn sheep to pneumonic pasteurollosis (Kraabel and Miller 1997), the most serious infectious disease of wild bighorn sheep (Bunch et al. 1999). By describing baseline levels of glucocorticoids in Stone's sheep, we provide a reference to gauge the physiological cost of potential disturbance from environmental or anthropogenic sources. Anthropogenic disturbances have been shown to elevate glucocorticoid concentrations in other large mammals (Wasser et al. 2000; Millspaugh et al. 2001; Creel et al. 2002). We recommend measuring corticosterone concentrations for describing fecal glucocorticoid levels in Stone's sheep because of lower within-season variation than cortisol and easy recovery (Wasser et al 2000). Fecal glucocorticoids currently serve as the best measure for monitoring the physiological response of stressors with a non-invasive and easily attainable source of data (Wasser et al. 2000; Millspaugh and Washburn 2004). Improved understanding of when glucocorticoids become deleterious to an individual, along with measures of population health, will continue to promote the utility of fecal glucocorticoids (Millspaugh and Washburn 2004).

Chapter 5: Management of Stone's sheep: implications and considerations

Introduction

Stone's sheep (*Ovis dalli stonei*) are found nowhere in the world but British Columbia and the Yukon (Bowyer and Leslie 1992) with British Columbia containing the vast majority of individuals (Valdez and Krausman 1999). Stone's sheep are intrinsically, socially and economically valuable to British Columbians (Paquet and Demarchi 1999; Demarchi and Hartwig 2004). They provide the backbone of the guide-outfitting industry in northern British Columbia and are partially the impetus for the development of local (i.e., Wild Sheep Society of British Columbia) and international (i.e., Foundation for North American Wild Sheep, Grand Slam Club) wildlife and hunting organizations (Demarchi and Hartwig 2004).

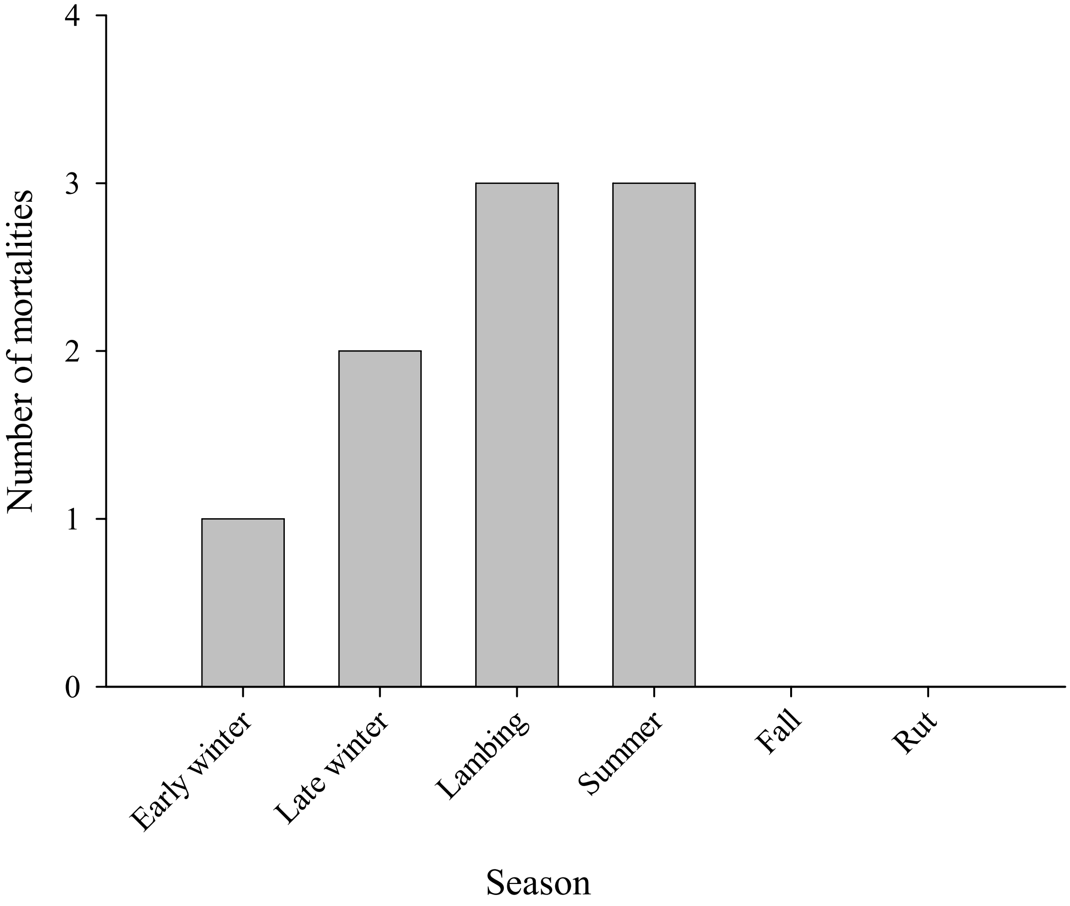
Predation, severe winters, anthropogenic access, fire suppression and disease have been identified as factors potentially limiting the distribution and abundance of thinhorn sheep (*Ovis dalli*) in British Columbia (Demarchi and Hartwig 2004). Demarchi and Hartwig (2004) prioritized research needs regarding factors that limit or pose risks of decline to thinhorn populations. Recently, concerns over declining Stone's sheep numbers have caused a reduction in outfitter quotas and to slightly reduced bag limits in the Peace-Liard and Omineca regions (Demarchi and Hartwig 2004). Fossil fuel development and recreational use in Stone's sheep habitat are increasing and may impose additional stressors on Stone's sheep (Paquet and Demarchi 1999). Management actions used to enhance Stone's sheep populations have focused on range burning (Elliot 1978; Seip and Bunnell 1985*a*) and wolf control (Bergerud and Elliot 1998), but public opposition has often been extreme (except locally)

(Mech et al. 1996; Jacobsen et al. 2001; Hayes et al. 2003) and may or may not increase thinhorn sheep numbers (Gasaway et al. 1983; Seip and Bunnell 1985*a*; Bergerud and Elliot 1998; Hayes et al. 2003). I discuss the implications of current management practices on Stone's sheep in light of the research presented in this thesis. Considerations are also offered to address some of the research needs proposed by Demarchi and Hartwig (2004) particularly relative to the development of habitat maps.

Mortality

Mortalities of adult Stone's sheep ewes collared between December 2001 and January 2004 in the Besa-Prophet (B-P) area were determined after remotely downloading collars and reviewing individual movements (see Chapter 2). Collars were retrieved as soon as logistically possible, but often months after an individual had died. I was unable to verify cause-specific mortality and determined the time of death as the first of four consecutive GPS locations in which the cumulative distance moved did not exceed 25 m (i.e., the individual did not move the length or width of one pixel on a satellite image in 24 h). Mortalities were highest between late winter and summer as eight of the nine mortalities occurred between 13 April and 5 Aug (Fig. 5.1). Annual mortality rates were 22.7% (5 of 22 collared individuals) and 14.3% (3 of 21 collared individuals) in 2002 and 2003, averaging 18.5% over the two-year period. One additional mortality occurred in 2004, but was excluded in a calculation of yearly mortality rate because most collars had been retrieved. Luckhurst (1973) also observed late-winter and early-spring mortalities of adult Stone's sheep in the same study area a quarter of a century earlier. Mortality rates in the B-P were

Fig. 5.1. Seasonal mortalities of Stone's sheep ewes collared between December 2001 and January 2004 (*n* = 33) in the Besa-Prophet. Early winter = 1 January to 28 February, Late winter = 1 March to 14 May, Lambing = 15 May to 14 June, Summer = 15 June to 14 August, Fall = 15 August to 31 October, Rut = 1 November to 31 December (as defined in Chapter 2, Table 2.1).



similar to the range of 20.0% and 14.8% documented for adult Dall's sheep (*Ovis dalli dalli*) ewes from the Yukon and Northwest territories (Hoefs and Cowan 1979, Simmons et al. 1984). Dall's sheep in the Yukon experienced greatest mortalities during late winter and lambing following a severe and prolonged winter (Burles and Hoefs 1984).

Causes of mortality in my study could have been attributed to either or both nutrition and predation. The early winter mortality, in close proximity to the upper Neves lick, and one summer mortality occurred in coniferous vegetation types. Two late-winter mortalities, one lambing and one summer mortality occurred in burn-deciduous vegetation, which was often selected by bears (Appendix D, Table D.3) and wolves (Appendix E, Table E.3) during these times of year, and which was avoided by more groups of Stone's sheep than selected during these seasons (see Chapter 2; Fig. 2.4). The other two mortalities during lambing occurred in shrub and dry alpine vegetation types, both of which were selected by most groups of Stone's sheep in the B-P at this time (see Chapter 2, Table 2.8). The remaining summer mortality occurred in wet alpine vegetation, which was never avoided by any group of Stone's sheep during summer (Table 2.8). The location of mortalities had some consistencies with how intrasexual groups of Stone's sheep used habitats through the growing season (lambing and summer; see Chapter 3). As the growing season progressed Stone's sheep tracked a phenological stage as they moved up in elevation (Fig. 3.3 and Fig. 3.4). This was especially apparent for nonmaternal ewes, which associated with low-elevation shrub communities earlier in the growing season and higher elevation communities with increased moss and lichen cover later (Fig. 3.3 and Fig. 3.5).

No study has explicitly addressed cause-specific mortality of Stone's sheep in northern British Columbia. Generally the quantity and quality of available forage, which are largely affected by weather and topography, have been considered the ultimate factors limiting thinhorn populations (reviewed in Nichols and Bunnell 1999; Demarchi and Hartwig 2004). This was contradicted by Bergerud and Elliot (1998), who documented that Stone's sheep between 9-21 months of age were influenced more by wolf (*Canis lupus*) densities than winter severity. Their study also found a greater than two-fold increase in the recruitment of Stone's sheep populations following wolf reductions in several areas of northern British Columbia (Bergerud and Elliot 1998). Wolves have been cited as the most significant predators of Stone's sheep in British Columbia (Luckhurst 1973, Bergerud and Elliot 1998), yet in both the Yukon and Alaska wolf reductions did not improve the recruitment and survival rates of Dall's sheep (Gasaway et. al. 1983; Hayes et al. 2003). Predation by wolverines (*Gulo gulo*) has recently been identified as a significant cause of woodland caribou (*Rangifer tarandus caribou*) calf mortality in the B-P watersheds, equaling that of wolves (Gustine 2005). Grizzly (*Ursus arctos*) and black (*U. americanus*) bears were also observed throughout the study area, but have not been identified as primary predators of thinhorn sheep in North America (Nichols and Bunnell 1999; Demarchi and Hartwig 2004). In order to better implement predator control measures that might reduce predation of Stone's sheep, a detailed study of cause-specific mortality should be undertaken because of the diversity of predators in the area and the mixed response of thinhorn sheep following wolf reductions in British Columbia, Alaska and Yukon.

Mortalities of Stone's sheep in the B-P often occurred at upper elevations, except for the last mortality in January of 2004, which occurred along Neves creek adjacent to the upper Neves lick. Individuals often spent more than one day at the Neves lick, which also provides adequate escape terrain along its steep banks (Luckhurst 1973), but requires travel through closed conifer forests over several hundred meters in order to access. Closed vegetation types such as conifer and subalpine spruce were the most consistently avoided vegetation types by female Stone’s sheep in the B-P (see Chapter 2; Fig. 2.4, Table 2.8). GPS locations of collared Stone’s sheep ewes indicated female sheep used mineral licks the most during late summer and early fall, although GPS locations were recorded at licks in every season except late winter. Movements to mineral licks likely contributed to the higher movement rates during summer and fall (see Chapter 2, Fig. 2.2). The largest documented movement (>8 km) by any sheep in this study was in relation to a lick. Thinhorn sheep appear to have specific demands for mineral licks, which alter seasonal distributions and patterns of range use (Luckhurst 1973; Heimer 1973; Seip 1983; Watts and Schemnitz 1985). Duffield, Neves and Tenmile licks were particularly high in predation risk during summer and fall when maximum risk values exceeded 0.9 for wolves and 0.7 for bears (on a normalized scale of zero to one). Watts and Schemnitz (1985) also noted a significant predation risk associated with using licks. Stone's sheep in the Neves Valley were observed by Luckhurst (1973) to frequent one particular lick during summer and early fall. Visitations by both sexes were common with some sheep ranging 16 km to use this lick. In Alaska, Heimer (1973) identified preferential use of mineral licks by lactating ewes and 100% probability that all ewes would return to the same lick. The risk of predation, predictable nature of use and distance sheep travel emphasize the ecological importance of mineral licks to Stone’s sheep. The apparent need for this mineral supplementation, however, may occasionally result in mortality.

Range-burning

Burning for wild sheep has been employed to enhance, maintain and create sheep habitat (Elliot 1978; Riggs and Peek 1980; Bentz and Woodard 1988) by reducing shrub and conifer encroachment (to aid in predator detection by creating more open habitat) (Risenhoover and Bailey 1985; Smith et al. 1999) and increasing availability of forage (Seip and Bunnell 1985*a*; Hobbs and Spowart 1984). Burning specifically for Stone's sheep has been recognized to reduce counts of *Protostrongylus* spp., an internal parasite associated with verminous pneumonia (Bunch et al. 1999; Seip and Bunnell 1985*a*), and potentially increase availability of forage through increased exposure to wind (Elliot 1978). Stone's sheep populations with access to burned ranges have been documented to have higher lamb/ewe ratios (Elliot 1978; Seip and Bunnell 1985*a*) and for this reason I believe burns can be important to Stone's sheep. The assertion that fire suppression is a limiting factor restricting Stone's sheep (by reducing forage availability because of increasing shrub and conifer encroachment, Demarchi and Hartwig 2004), however, seems unlikely given that wildfires are rarely suppressed throughout and adjacent to thinhorn range in northern British Columbia and have only recently (from an ecological perspective) been prescribed and employed (i.e., beginning in 1948 in the Prophet River; Demarchi and Hartwig 2004).

Range burning that maintains and creates open habitats and improves forage could be advantageous to Stone's sheep, unless mortality and interspecific competition override the benefits of associating with burn vegetation types. Habitat selection (see Chapter 2), behavioural use (see Chapter 3) and mortalities of adult Stone's sheep ewes in my study suggest open burns, dominated by *Elymus innovatus*, are important to groups of Stone's sheep during late winter and lambing seasons (see Chapter 2; Table 2.3), which have been recognized as energetically expensive times of the year for ungulates (Gittleman and Thompson 1988; Dailey and Hobbs 1989). Burn-grass vegetation was selected by at least one group in every season and no mortalities were recorded in burn grass vegetation (see Chapter 2; Fig. 2.4, Table 2.8). Older burn deciduous habitat, however, was not important to Stone's sheep considering the avoidance of this vegetation type most seasons (see Chapter 2; Fig. 2.4, Table 2.8) and its association with four of the nine mortalities. Stone's sheep ewes spent most of their active and inactive time in open herbaceous habitats regardless of maternal status (see Chapter 3, Fig. 3.1). Both habitat selection (see Chapter 2) and behavioural observations (see Chapter 3) of Stone's sheep ewes suggest that open habitats are selected for by Stone's sheep.

The benefits of prescribed burns for wild sheep may be less in areas where larger sympatric foragers (i.e., bison [*Bison bison*], elk [*Cervus elaphus*], mountain goats [*Oreamnos americanus*] and deer [*Odocoileus* spp.]) are present. Interspecific competition between Stone's sheep and other ungulates has never been quantified, but concerns over competition between wild sheep, elk and mountain goats have increased. Elk densities are high and increasing in the Peace region (Shackleton 1999) and they already occupy a quarter of Stone's sheep range (Nichols and Bunnell 1999). Elk numbers are increasing throughout the northern Rockies as a result of extensive prescribed burning (Nichols and Bunnell 1999). Stone's sheep that wintered at low elevations alongside elk have had significant infestations of winter ticks (*Dermacenter albipictus*) and were in worse body condition than sheep that wintered away from elk at higher elevations (M. Wood, Peace/Williston Fish and Wildlife Compensation Program, unpublished data). Simulation models of an expanding mountain goat population have shown a combined population-level effect of increased competition and susceptibility to disease on bighorn sheep (*Ovis canadensis*) (Gross 2001). Competitive displacement of mule deer (*Odocoileus hemionus*) by elk has been documented (Kie et al. 1991; Johnson et al. 2000; Stewart et al. 2002) and the forages of bison, elk, deer, mountain goats and wild sheep are similar (Demarchi and Hartwig 2004). The benefits of range burning may be reduced, therefore, if summer-long grazing by bison, elk, goats and deer reduce availability of fall and winter forages of Stone's sheep (reviewed in Demarchi and Hartwig 2004). Bison, elk, mule deer and moose (*Alces alces*) have all been shown to select for burned areas (Spowart and Hobbs 1985; Peck and Peek 1991; Pearson et al. 1995; Weixelman et al. 1998).

Both wolves and grizzly bears in the B-P selected for burns seasonally (Appendix D, Table D.3; Appendix E, Table E.3) and may benefit from range burning due to increased diversity and number of ungulates (Gasaway et al. 1983; Ballard et al. 2000) and promotion of seral vegetation (Nielsen et al. 2002). Stone's sheep were not a large component in the diet of wolves and grizzly bears in the B-P (B. Milakovic, University of Northern British Columbia, unpublished data), which may partially reflect their availability across the landscape or that they were only opportunistically preyed on when grizzly bears and wolves were seeking other prey or forages. The influence of predation, however, was particularly evident in differentiating habitat use by maternal and nonmaternal Stone's sheep ewes as maternal ewes associated with areas closer to larger escape features (see Chapter 3, Table 3.2 and Table 3.3). With increased ungulate biomass and diversity, interactions between ungulates and wolves may become unstable with sheep being regulated at lower densities than in simpler predator-prey systems, where wolves have fewer alternate prey sources (Bergerud and Elliot 1998).

Access and disturbance

Access specifically resulting from oil and gas development could potentially limit thinhorn populations in British Columbia (Demarchi and Hartwig 2004). The most common features associated with oil and gas development in northern British Columbia include roads, seismic lines, pipelines and well sites. Development of these linear features alters vegetation composition and increases vehicle access (all-terrain vehicles and snowmobiles) (Appendix A, Figure A.1). These features may be maintained and used long after industrial development has ceased. Linear developments have been associated with increased predation on caribou by wolves (James and Stuart-Smith 2000) and may place Stone's sheep at an increased risk of predation (Dyer et al. 2001; Dyer et al. 2002). Increased aircraft activity, especially helicopters, is generally associated with fossil fuel developments (reviewed in Paquet and Demarchi 1999). Overflights from helicopters and fixed-wing aircraft are recognized as imposing energetic costs on sheep and may cause sheep to leave preferred sites where they may be at an increased risk of predation and/or in habitats of poorer nutritional quality (Stockwell et al. 1991; Bleich et al. 1994; Frid 2003). Wild sheep have shown the ability to adapt to disturbances associated with industrial development in some areas (Weisenburger et al. 1996; Krausman et al. 1998, reviewed in Nichols and Bunnell 1999). The collection of fecal samples to describe glucocorticoid concentrations may provide insights into the potential implications associated with disturbance or the ability of sheep to habituate to disturbance (see Chapter 4). My data suggested that variations in stress levels were higher in summer relative to early and late winter and may reflect the energetic costs of movement, lactation or factors associated predation risk and/or anthropogenic use in the B-P (see Chapter 4; Fig. 4.1). My research provides a baseline measure of naturally occurring glucocorticoid concentrations and may provide insights into potential disturbances associated with resource extraction and increased access. Establishment of explicit guidelines and policy that limit access to and development of Stone's sheep habitat will help minimize the influence associated with disturbance and promote the resiliency of Stone's sheep.

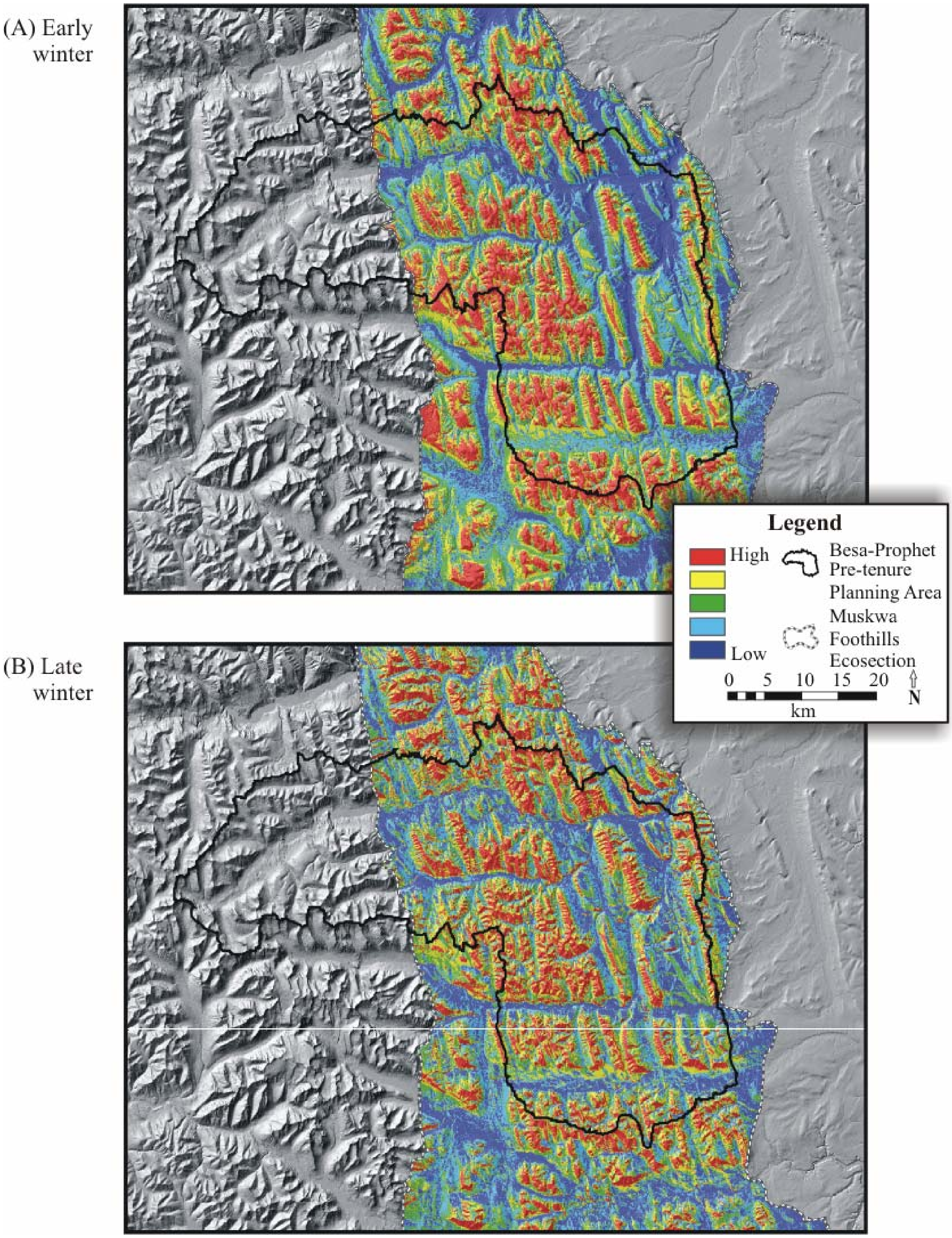
Seasonal selection models

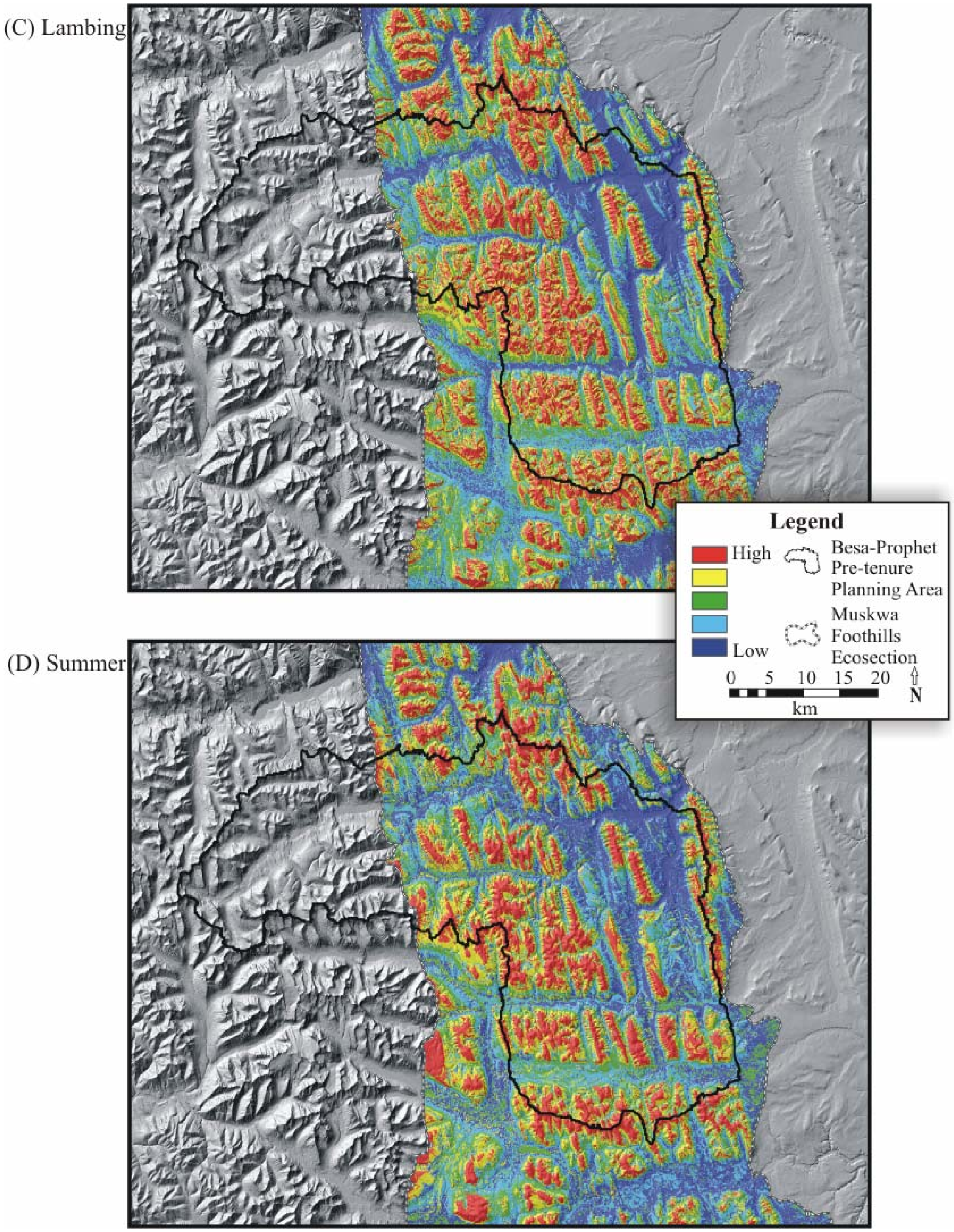
Managers are forced to interpret events, assess their effects and make decisions once costs and benefits are weighed (Riley et al. 2002). Knowledge of an area in which an event occurs is fundamental to the implementation of adequate management strategies and often involves modeling of species distributions (Corsi et al. 2000). Modeling the distribution of a species highlights where and when animals occupy an area and may provide insights into why an area is used. Habitat capability/suitability maps across thinhorn range in British Columbia may help to identify sensitive sites (e.g., mineral licks, winter ranges) and facilitate management decisions regarding enhancement activities (Demarchi and Hartwig 2004). In order to do so, several factors including variation among individuals (Nielsen et al. 2002; Gustine 2005), seasons (Apps et al. 2001) and years (Schooley 1994) should be considered prior to modeling the distribution of a species. Pooling of data across seasons, years and individuals may be appropriate if similarities within groups of animals exist and to address different scales of selection (Nielsen et al. 2002; Gustine 2005).

In my study I described broad-scale selection of Stone's sheep for six seasons (i.e., early winter, late winter, lambing, summer, fall, rut) using the selection models presented in Chapter 2 (Table 2.5). These models were based on the movements and biology of Stone's sheep. The saturated models (i.e., the full model or models containing the most parameters) having attributes of topography (slope, aspect, elevation, curvature), risk of predation (wolf risk and/or bear risk) and vegetation (vegetation type and/or vegetation quality) ranked best relative to a suite of competing models (see Chapter 2). From the global models I created spatially explicit maps, scaled between zero and one, in a raster geographic information system (PCI Geomatics 2004). These maps were developed for part of the Muskwa-Foothills ecosection from subsetted satellite images captured using Landsat 5 TM and Landsat 7 ETM (Fig. 5.2A-F). Because seasonal selection maps were correlated between years (ranging from $r = 0.81$ during fall to $r = 0.97$ during early winter), seasonal RSF values were averaged across years and then divided into five quantiles (i.e., 20th, 40th, 60th, 80th, and 100th percentile values) to create one seasonal map (Fig. 5.2A-F). Stone's sheep in the B-P exhibited different selection strategies across relatively short temporal seasons. Considerable variability in selection existed among groups and between years, but some consistencies were present. This was especially true during the winter and summer seasons as groups of Stone's sheep selected attributes more consistently and predictably than other times of the year. The avoidance of subalpine spruce and selection for steep slopes, convex curvatures and southerly aspects, especially during winter months, was relatively synonymous among groups.

Aspect, elevation and size of areas best distinguished differences among the seasonal maps generated from resource selection models for Stone's sheep (Fig. 5.2A-F). Notable

Fig. 5.2. Relative habitat selection value for Stone's sheep ewes in the Muskwa-Foothills Ecosection.

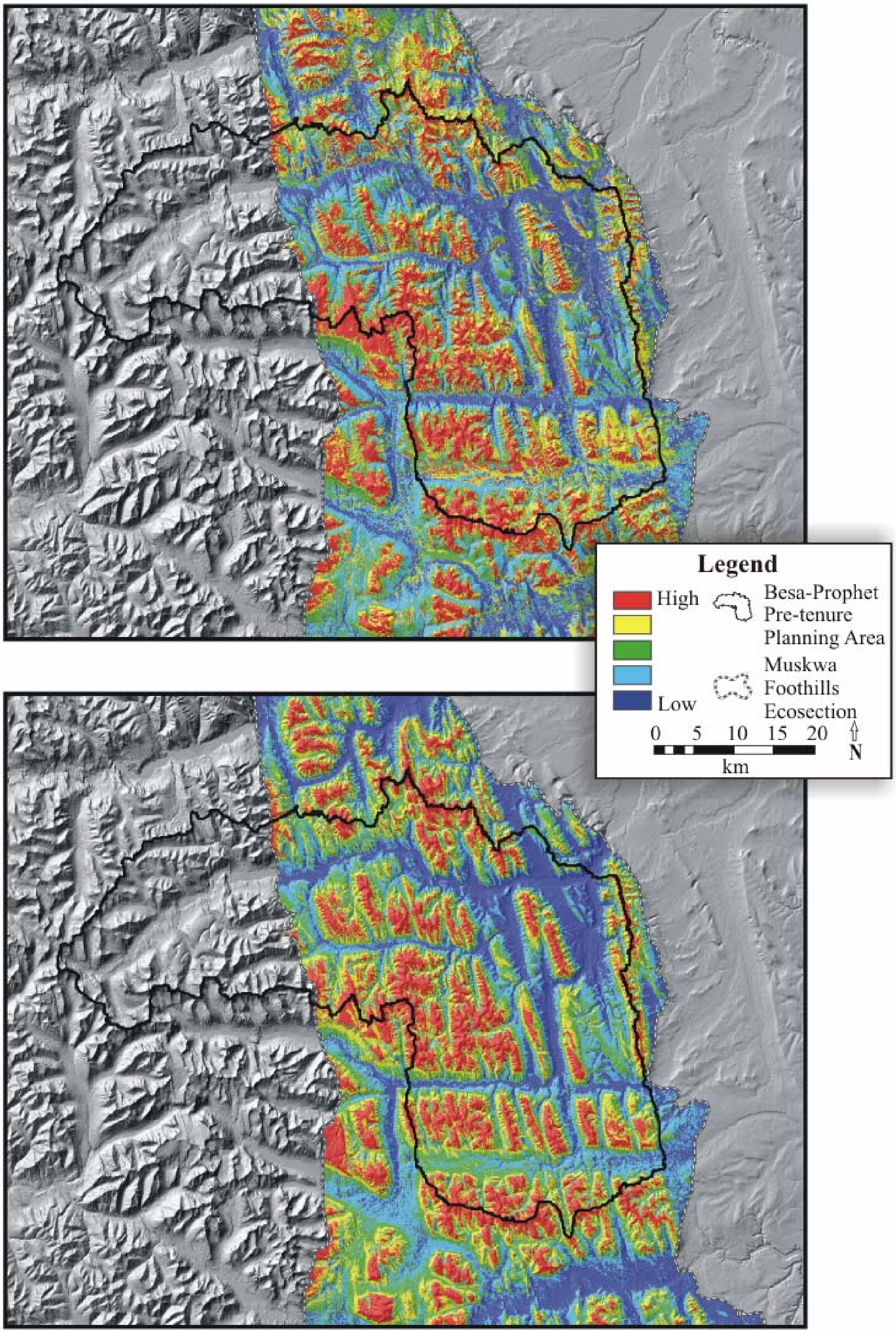



(C) Lambing

(D) Summer

(E) Fall

(F) Rut


Legend
High
Low
Besa-Prophet Pre-tenure Planning Area
Muskwa Foothills Ecosection
0 5 10 15 20
km
N

changes between early (Fig. 5.2A) and late winter (Fig. 5.2B) are illustrated by the increasing importance of southerly aspects, preference for lower elevations and smaller size of highly selected sites during late winter. These are consistent with changes in selection strategies (i.e., relative selection models; see Chapter 2) of Stone's sheep between the two seasons. With the beginning of the growing season and onset of lambing (Fig. 5.2C), Stone's sheep associated with steep rocky areas in close proximity to areas where 'green-up' was greatest. The summer map (Fig. 5.2D) shows a marked increase in the size and contiguity of highly selected sites. Ridgelines and mountain tops, regardless of aspect, were used extensively during summer. The substantial use of burned areas by Stone's sheep in the fall likely contributed to the relative increase in selection of southerly slopes (Fig. 5.2E). Fall was also the only season when Stone's sheep significantly avoided westerly aspects and areas identified as highly selected for were often associated with other aspects. During the breeding season (Fig. 5.2F) selection for steep slopes was least, even with an increase in selection for upper elevations. Early winter and rut are probably the hardest to differentiate except on the basis of slope; flatter sites along ridges and mountain tops were often rated as high selection value during rut.

In order to minimize effects of development on Stone's sheep, disturbances that allow access to specific sites (i.e., mineral licks) or alter important areas (e.g., winter range) should be minimized (Paquet and Demarchi 1999). Aircraft activity should be minimized around mid- and upper- elevations of south-facing aspects especially during winter and lambing. Strong selection for convex curvatures at upper elevations during summer (see Chapter 2, Fig. 2.3) indicates aircraft activity near ridges and mountain tops (Fig. 5.2D) is likely to disturb sheep at this time. Upper elevations on south- and west-facing aspects are consistently rated as highly selected by Stone's sheep in the Muskwa-Foothills ecosection

(Fig. 5.2A-F). Aircraft should travel well above the mountains or at low elevations along major drainages, away from mineral licks during summer and fall, to limit disturbances whenever possible. If roads and linear developments are necessary in the B-P, access restricting the movements of Stone's sheep to mineral licks and different seasonal ranges should be minimized. Movement data from collared ewes indicated that the westerly portion of the Neves valley west of Tenmile Lake, the lower Neves valley along the eastern edge of Mt. Luckhurst, the valley separating Mt. Luckhurst from the mountain immediately east (locally known as Little Ram) and Richards Creek valley west of the confluence with Duffield Creek were regularly crossed by Stone's sheep in order to access mineral licks (Appendix A, Fig. A.1). Disturbances in and around mineral licks should also be minimized during summer and fall because of high lick use during these seasons. If at all possible roads should not be developed within the Duffield Creek and Townsley Creek watersheds (Appendix A, Fig. A.1). These watersheds provide considerable amounts of contiguous habitat that are highly selected by Stone's sheep (Fig. 5.2A-F). The drainages are often traveled through and across by Stone's sheep accessing different ranges and/or mineral licks. Individuals were never documented crossing the Besa River over the duration of this study (Appendix A, Fig. A.1). The development of linear features (i.e., roads, seismic lines) should be restricted to low-elevation river valleys away from mineral licks and areas used to access them.

It is possible that RSF may provide unreliable estimates of selection if extrapolated beyond the definition of availability because availability of resources may differ between areas (Garshelis 2000). This limitation is most obvious in the designation of highly selected sites that do not contain sheep or are rarely used by sheep. Klingzut mountain, on the eastern edge of the Muskwa-Foothills boundary (Appendix A, Fig. A.1), is rarely if ever used by Stone's sheep yet consistently contains areas ranked as high selection value. Therefore, expert knowledge regarding the distributions of animals outside the study area should be used to enhance the utility of RSF.

Topographic modeling

The fundamental roles of predation, vegetation and topography in the ecology of wild sheep are well documented (Valdez and Krausman 1999) and none should be excluded in descriptions of the ecology of Stone's sheep. This was apparent in the relative rankings of RSF models in Chapter 2 that incorporated different combinations of attributes. The global or most saturated model containing aspects of all attributes consistently ranked better than individual models (see Chapter 2, Table 2.5 and Table 2.6). Explanatory ecological attributes such as predation risk and vegetation types, however, can be difficult to acquire and may be temporally dynamic over relatively short periods (e.g., range burning). In contrast, topographic attributes associated with geological features (i.e., slope, elevation, aspect, curvature) can be easily attained and developed entirely from digital elevation models (DEM). Furthermore topographic features generally change slowly. The habitat selection by Stone's sheep was described better by topographical attributes than by aspects of vegetation or risk of predation, regardless of season (see Chapter 2, Table 2.6).

With the topographical attributes only, I developed selection models and assessed their predictive ability (as in Chapter 2). All attributes were developed from a DEM for the topographical model (i.e., slope, elevation, aspect and curvature). Model performance was generally excellent both across and within groups of sheep (Table 5.1). The two cases when models performed poorly (*P* > 0.05) both occurred in the Tenmile group. The Tenmile group of sheep had the least number of collared individuals. The lack of predictive ability in the early winter model of 2003 may be partially attributed to a small sample of use locations ($n = 45$) acquired from just one individual. Stone's sheep in the Tenmile group also had the largest range size and traveled farther than any other group to access a mineral lick. Not surprisingly, individuals from the Tenmile population had the largest movements of any sheep in the study. The association with steeper slopes has been used to classify suitable habitat and animal locations of mountain Caprinae. Both Gross et al. (2002) and McKinney et al. (2003) subjectively defined escape terrain using attributes of topography to predict the distribution of mountain goats and viability of desert bighorn populations, respectively. In the case of mountain goats, 87% of their observations were correctly classified using distance to escape terrain (Gross et al. 2002). Although it is not as ecologically comprehensive as models that also incorporate predation risk and vegetation types, the application of topographic measures using RSF and logistic regression provides an effective way to map the distribution of areas selected by Stone's sheep (e.g., Fig. 5.2A-F).

Overall conclusions

In summary, data on rates, timing and causes of mortality in Stone's sheep are few and should be further researched to help identify limiting factors to population growth. Habitat selection studies and maps developed from RSF using logistic regression (Chapter 2) can help define and visualize the seasonal 'selection strategies' across or within specific groups of sheep

Table 5.1. The best resource selection models based on topographical attributes for Stone's sheep in the Besa-Prophet across and within groups, by season and year (2002-2003). Statistics include number of parameters (K_i), sample size (n), log likelihood (LL), Akaike's information Criteria (AIC), Akaike weights (w_i) and average Spearman's rank correlation ($\bar{r}_s$) from k-fold cross-validation procedure with associated P values.

Group	Year	Season^a	Model^b	n	$\bar{r}_s$	P
Global		EW	$S+A+C+E+E^2$	43058	0.994	<0.001
Global		LW	$S+A+C+E+E^2$	61912	0.981	<0.001
Global		L	$S+A+C+E+E^2$	21482	0.947	<0.001
Global		S	S+A+C+E	42045	0.894	<0.001
Global		F	S+A+C+E	51493	0.945	<0.001
Global		R	S+A+C+E	20870	0.952	<0.001
Neves	2002	EW	$S+A+C+E+E^2$	7904	0.920	<0.001
Neves	2003	EW	$S+A+C+E+E^2$	7327	0.962	<0.001
Neves	2002	LW	$S+A+C+E+E^2$	11388	0.973	<0.001
Neves	2003	LW	$S+A+C+E+E^2$	9524	0.973	<0.001
Neves	2002	L	$S+A+C+E+E^2$	4563	0.747	0.013
Neves	2003	L	$S+A+C+E+E^2$	3540	0.868	0.001
Neves	2002	S	$S+A+C+E+E^2$	7920	0.850	0.002
Neves	2003	S	$S+A+C+E+E^2$	6904	0.814	0.004
Neves	2002	F	$S+A+C+E+E^2$	11019	0.931	<0.001
Neves	2003	F	$S+A+C+E+E^2$	7932	0.905	<0.001
Neves	2002	R	S+A+C+E	8180	0.907	<0.001
Neves	2003	R	$S+A+C+E+E^2$	4222	0.957	<0.001
Tenmile	2002	EW	$S+A+C+E+E^2$	2316	0.914	<0.001
Tenmile	2003	EW	$S+A+C+E+E^2$	267	0.514	0.129
Tenmile	2002	LW	$S+A+C+E+E^2$	1601	0.505	0.137
Tenmile	2003	LW	$S+A+C+E+E^2$	1921	0.804	0.005
Tenmile	2002	L	$S+A+C+E+E^2$	451	0.744	0.014
Tenmile	2003	L	$S+A+C+E+E^2$	907	0.756	0.011
Tenmile	2002	S	$S+A+C+E+E^2$	1094	0.824	0.003
Tenmile	2003	S	$S+A+C+E+E^2$	1893	0.861	0.001
Tenmile	2002	F	S+A+C+E	1499	0.717	0.020
Tenmile	2003	F	$S+A+C+E+E^2$	785	0.773	0.009
Tenmile	2002	R	$S+A+C+E+E^2$	1216	0.839	0.002
Firstfork	2002	EW	$S+A+C+E+E^2$	1625	0.914	<0.001
Firstfork	2003	EW	$S+A+C+E+E^2$	3123	0.932	<0.001
Firstfork	2002	LW	$S+A+C+E+E^2$	3539	0.965	<0.001
Firstfork	2003	LW	$S+A+C+E+E^2$	3518	0.928	<0.001
Firstfork	2002	L	$S+A+C+E+E^2$	1128	0.916	<0.001
Firstfork	2003	L	S+A+C+E	1561	0.867	0.001
Firstfork	2002	S	$S+A+C+E+E^2$	2398	0.920	<0.001
Firstfork	2003	S	$S+A+C+E+E^2$	2952	0.949	<0.001

Table 5.1. Continued

Group	Year	Season[a]	Model[b]	*n*	$\bar{r}_s$	*P*
Firstfork	2002	F	S+A+C+E+E^2	3079	0.963	<0.001
Firstfork	2003	F	S+A+C+E+E^2	3228	0.961	<0.001
Firstfork	2002	R	S+A+C+E+E^2	2507	0.953	<0.001
Firstfork	2003	R	S+A+C+E+E^2	806	0.809	0.005
Townsley	2002	EW	S+A+C+E+E^2	6881	0.961	<0.001
Townsley	2003	EW	S+A+C+E+E^2	5990	0.950	<0.001
Townsley	2002	LW	S+A+C+E+E^2	11108	0.865	0.001
Townsley	2003	LW	S+A+C+E+E^2	7871	0.932	<0.001
Townsley	2002	L	S+A+C+E+E^2	3844	0.914	<0.001
Townsley	2003	L	S+A+C+E	2034	0.867	0.001
Townsley	2002	S	S+A+C+E+E^2	7017	0.922	<0.001
Townsley	2003	S	S+A+C+E+E^2	4365	0.821	0.004
Townsley	2002	F	S+A+C+E+E^2	8395	0.882	<0.001
Townsley	2003	F	S+A+C+E+E^2	6966	0.900	<0.001
Townsley	2002	R	S+A+C+E	6400	0.916	<0.001
Townsley	2003	R	S+A+C+E+E^2	3619	0.901	<0.001
Richards	2002	EW	S+A+C+E+E^2	2880	0.901	<0.001
Richards	2003	EW	S+A+C+E+E^2	3886	0.912	<0.001
Richards	2002	LW	S+A+C+E+E^2	4985	0.891	<0.001
Richards	2003	LW	S+A+C+E+E^2	5936	0.850	0.002
Richards	2002	L	S+A+C+E+E^2	1737	0.857	0.002
Richards	2003	L	S+A+C+E+E^2	1436	0.869	0.001
Richards	2002	S	S+A+C+E+E^2	2980	0.969	<0.001
Richards	2003	S	S+A+C+E+E^2	2843	0.921	<0.001
Richards	2002	F	S+A+C+E+E^2	3152	0.906	<0.001
Richards	2003	F	S+A+C+E+E^2	3336	0.924	<0.001
Richards	2002	R	S+A+C+E+E^2	2363	0.861	0.001
Richards	2003	R	S+A+C+E	1330	0.816	0.004

[a] EW=Early winter, LW=Late winter, L=Lambing, S=Summer, F=Fall, R=Rut; as defined in Chapter 2, Table 2.1.

[b] S=Slope, A=Aspect, C=Curvature, E=Elevation.

(Fig. 5.2A-F). Topographic attributes in particular can be useful in indexing habitat selection values across Stone's sheep range because of their easy acquisition. Behavioural observations and fine-scale measures of habitat use by Stone's sheep highlight the importance of escape features and phenology in distinguishing differences between maternal and nonmaternal ewes (Chapter 3). The elevational tracking of a specific phenological stage over the growing season highlights the importance of forage quality to Stone's sheep (Chapter 3). Range burning to promote forage and create open habitats may be beneficial to sheep in systems where other ungulates and their predators are not enhanced by the management activity. Fecal glucocorticoid concentrations (Chapter 4) and attributes selected by Stone's sheep (Chapter 2) provide measures from which to gauge and mitigate the impacts associated with anthropogenic and environmental disturbances. Guidelines limiting access to and disturbance on sheep range may serve as a conservative approach to ensuring the persistence of a species that tends towards geographic isolation because of range and herd fidelity.

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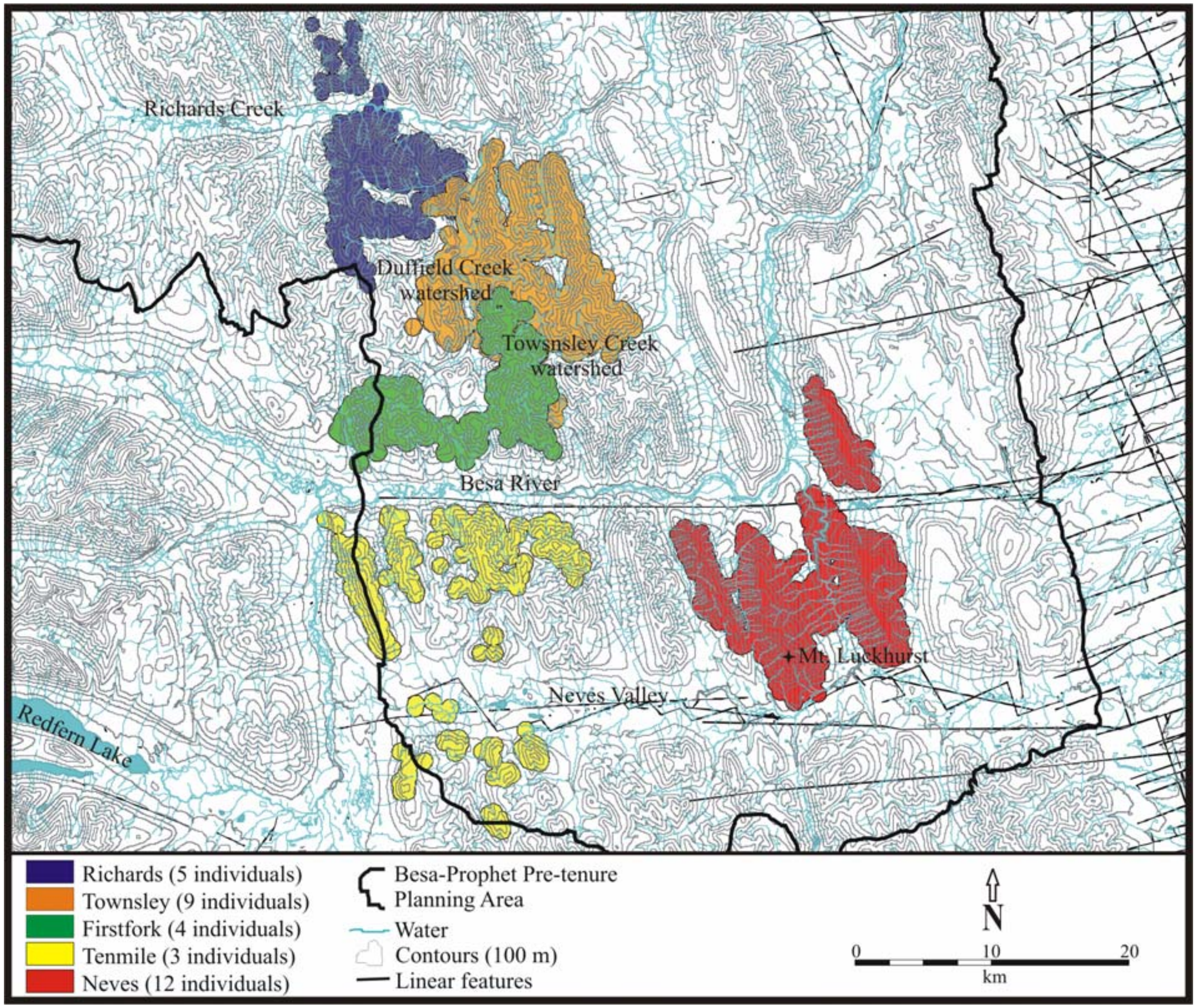
Appendix A: The distribution of groups of female Stone's sheep in the Besa-Prophet area of northern British Columbia delineated by their use of a particular mineral lick.

Fig. A.1. Areas used by 5 groups of female Stone's sheep in the Besa-Prophet area of northern British Columbia. Global Positioning System (GPS) locations of individual Stone's sheep were buffered by their group's average annual movement rate to delineate areas of use. Individuals were assigned to groups based on their use of a particular mineral lick.



Appendix B: Selection coefficients (β_i) and standard errors (SE) of attributes from final models in Table 2.5, used to model selection of resources by groups of Stone's sheep in the Besa-Prophet area of northern British Columbia. Models were developed across six seasons and two years (2002-2003).

Table B.1. Selection coefficients (β_i) and standard errors (SE) of resource selection models from global and group models of Stone' sheep presented in Table 2.5. Covariates include vegetation types, topographical attributes and risk of predation risk from grizzly bears and wolves in the Besa-Prophet area of northern British Columbia (2002-2003). Seasons are defined in Table 2.1. * indicates 95% confidence intervals (CI) of the β_i were different from zero.

Covariates	Global Models by Season					
	EW	LW	L	S	F	R
Elevation	7.379 ± 1.757*	-4.434 ± 1.259*	27.125 ± 2.995*	3.432 ± 0.136*	2.106 ± 0.186*	4.449 ± 0.198*
Elevation^2	-0.738 ± 0.512	1.390 ± 0.391*	-7.915 ± 0.938*			
Quality			0.099 ± 0.016*	-0.003 ± 0.006		
Slope	0.028 ± 0.002*	0.090 ± 0.002*	0.083 ± 0.003*	0.030 ± 0.002*		0.014 ± 0.003*
Curvature	0.217 ± 0.011*	0.182 ± 0.010*	0.098 ± 0.016*	0.149 ± 0.012*	0.054 ± 0.011*	0.088 ± 0.018*
Bear risk			0.084 ± 0.025*	-0.174 ± 0.026*	-0.350 ± 0.030*	
Wolf risk	0.074 ± 0.010*	-0.078 ± 0.010*	0.101 ± 0.028*	-0.017 ± 0.014	-0.103 ± 0.007*	-0.189 ± 0.019*
North	-0.326 ± 0.036*	-1.184 ± 0.058*	-0.827 ± 0.073*	0.001 ± 0.035	-0.279 ± 0.032*	-0.113 ± 0.048*
East	-0.793 ± 0.033*	-0.351 ± 0.035*	-0.429 ± 0.053*	-0.102 ± 0.030*	-0.191 ± 0.025*	-0.292 ± 0.040*
South	0.808 ± 0.024*	1.345 ± 0.027*	0.919 ± 0.044*	0.116 ± 0.028*	0.542 ± 0.024*	0.435 ± 0.036*
West	0.310 ± 0.027*	0.191 ± 0.031*	0.336 ± 0.045*	-0.016 ± 0.028	-0.073 ± 0.026*	-0.030 ± 0.038
Riparian				0.885 ± 0.165*	-0.449 ± 0.169*	
Shrub	-0.019 ± 0.047	0.448 ± 0.042*	0.248 ± 0.083*	-0.491 ± 0.089*	0.321 ± 0.041*	0.072 ± 0.067
Coniferous	-0.081 ± 0.061	-0.710 ± 0.049*	-0.123 ± 0.079	-0.433 ± 0.065*	-0.901 ± 0.057*	-0.018 ± 0.078
Subalpine spruce	-1.571 ± 0.158*	-1.333 ± 0.136*	-1.258 ± 0.168*	-1.494 ± 0.211*	-0.752 ± 0.098*	-1.101 ± 0.211*
Rocks	0.485 ± 0.039*	0.212 ± 0.032*	0.988 ± 0.075*	0.933 ± 0.088*	0.133 ± 0.043*	0.445 ± 0.066*
Rockcrust	0.100 ± 0.058	-0.063 ± 0.073	0.113 ± 0.188	0.144 ± 0.102	-0.384 ± 0.065*	-0.374 ± 0.094*
Dry alpine	0.568 ± 0.040*	0.364 ± 0.036*	0.348 ± 0.064*	0.499 ± 0.056*	0.437 ± 0.040*	0.746 ± 0.057*
Wet alpine	0.020 ± 0.065	0.076 ± 0.099	-0.377 ± 0.178*	0.667 ± 0.075*	0.446 ± 0.054*	0.490 ± 0.082*
Burn-deciduous	-0.150 ± 0.068*	0.238 ± 0.040*	-0.238 ± 0.076*	-0.769 ± 0.133*	0.270 ± 0.063*	-0.472 ± 0.127*
Burn-grass	0.647 ± 0.065*	0.767 ± 0.040*	0.300 ± 0.077*	0.060 ± 0.117	0.880 ± 0.064*	0.212 ± 0.110

Table B.1. Continued

Covariates	Neves Group by Season					
	EW 2002	EW 2003	LW 2002	LW 2003	L 2002	L 2003
Elevation	7.688 ± 5.307	38.077 ± 6.923*	19.968 ± 4.975*	72.619 ± 5.739*	8.696 ± 8.006	35.948 ± 10.272*
Elevation^2	-1.893 ± 1.619	-9.743 ± 2.077*	-6.254 ± 1.567*	-22.697 ± 1.857*	-2.237 ± 2.526	-9.306 ± 3.211*
Quality					0.143 ± 0.039*	0.071 ± 0.041
Slope	0.063 ± 0.006*	0.018 ± 0.005*	0.138 ± 0.006*	0.102 ± 0.006*	0.114 ± 0.009*	0.063 ± 0.008*
Curvature	0.068 ± 0.028*	0.066 ± 0.033*	0.036 ± 0.025	0.076 ± 0.023*	0.058 ± 0.039	-0.017 ± 0.041
Bear risk					0.178 ± 0.082*	0.397 ± 0.115*
Wolf risk	-0.159 ± 0.048*	0.270 ± 0.081*	0.156 ± 0.032*	0.185 ± 0.078*	0.114 ± 0.069	0.099 ± 0.167
North	-0.514 ± 0.137*	-0.382 ± 0.110*	-0.518 ± 0.202*	-1.201 ± 0.322*	-0.553 ± 0.212*	-1.035 ± 0.285*
East	-1.718 ± 0.156*	-1.092 ± 0.098*	-0.839 ± 0.138*	-0.423 ± 0.213*	-0.980 ± 0.178*	-0.735 ± 0.185*
South	1.504 ± 0.075*	0.848 ± 0.065*	1.284 ± 0.086*	1.431 ± 0.146*	1.214 ± 0.106*	1.286 ± 0.156*
West	0.728 ± 0.086*	0.626 ± 0.081*	0.074 ± 0.099	0.192 ± 0.137	0.319 ± 0.119*	0.484 ± 0.135*
Shrub	-0.060 ± 0.191	-0.880 ± 0.272*	-0.697 ± 0.269*	-1.514 ± 0.352*	-0.099 ± 0.272	-0.153 ± 0.427
Coniferous	-0.915 ± 0.217*	0.520 ± 0.207*	-0.328 ± 0.166*	0.409 ± 0.191*	-0.083 ± 0.261	1.732 ± 0.260*
Subalpine spruce	-1.019 ± 0.299*	-2.761 ± 0.635*	-0.898 ± 0.356*	-0.787 ± 0.388*	-1.577 ± 0.545*	-1.178 ± 0.570*
Rocks	0.461 ± 0.097*	0.720 ± 0.175*	0.114 ± 0.089	0.417 ± 0.102*	1.123 ± 0.187*	0.551 ± 0.232*
Rockcrust	0.202 ± 0.175	0.467 ± 0.191*	0.126 ± 0.234	0.623 ± 0.309*	-0.553 ± 0.476	-0.274 ± 0.432
Dry alpine	0.919 ± 0.106*	0.597 ± 0.135*	0.283 ± 0.101*	0.028 ± 0.120	0.245 ± 0.163	0.540 ± 0.260*
Wet alpine	0.055 ± 0.286	-0.429 ± 0.247	0.370 ± 0.342			-1.073 ± 0.941
Burn-deciduous	-0.225 ± 0.169	0.957 ± 0.185*	0.523 ± 0.111*	0.528 ± 0.140*	0.516 ± 0.174*	-0.114 ± 0.243
Burn-grass	0.583 ± 0.127*	0.810 ± 0.151*	0.507 ± 0.108*	0.296 ± 0.131*	0.428 ± 0.166*	-0.032 ± 0.231

Table B.1. Continued

Covariates	Neves Group by Season					
	S 2002	S 2003	F 2002	F 2003	R 2002	R 2003
Elevation	-38.961 ± 2.797*	-19.105 ± 3.259*	-1.017 ± 2.661	2.214 ± 3.393	4.166 ± 0.726*	27.564 ± 6.195*
Elevation^2	13.906 ± 0.922*	7.631 ± 1.087*	1.661 ± 0.835*	-0.115 ± 1.164		-7.550 ± 1.919*
Quality	0.054 ± 0.017*	0.010 ± 0.018				
Slope	0.055 ± 0.006*	0.041 ± 0.005*	0.065 ± 0.004*		0.036 ± 0.005*	0.063 ± 0.007*
Curvature	0.099 ± 0.032*	-0.137 ± 0.035*	0.013 ± 0.027	-0.013 ± 0.030	0.066 ± 0.031*	-0.081 ± 0.040*
Bear risk	-0.069 ± 0.068	-0.207 ± 0.115		-0.327 ± 0.084*		
Wolf risk	0.035 ± 0.031	0.142 ± 0.037*		-0.259 ± 0.023*	-0.119 ± 0.058*	
North	0.030 ± 0.092	0.227 ± 0.119	-0.434 ± 0.070*	-0.228 ± 0.091*	-0.037 ± 0.083	0.311 ± 0.106*
East	-0.156 ± 0.074*	-0.675 ± 0.094*	-0.238 ± 0.050*	-0.596 ± 0.073*	-0.250 ± 0.067*	-1.115 ± 0.117*
South	0.369 ± 0.064*	0.258 ± 0.075*	0.881 ± 0.046*	0.689 ± 0.058*	0.464 ± 0.056*	0.687 ± 0.080*
West	-0.243 ± 0.070*	0.190 ± 0.070*	-0.209 ± 0.056*	0.134 ± 0.064*	-0.177 ± 0.066*	0.117 ± 0.090
Shrub	-0.275 ± 0.238	-0.850 ± 0.354*		0.171 ± 0.181	-0.236 ± 0.197	-0.292 ± 0.230
Coniferous	-0.645 ± 0.162*	0.249 ± 0.198		-1.132 ± 0.129*	-0.426 ± 0.204*	0.588 ± 0.144*
Subalpine spruce	-0.713 ± 0.495	-1.513 ± 0.675*		0.088 ± 0.199	-0.510 ± 0.291	-0.410 ± 0.296
Rocks	0.746 ± 0.242*	1.087 ± 0.270*		-0.399 ± 0.128*	0.528 ± 0.125*	-0.262 ± 0.121*
Rockcrust	-0.460 ± 0.261	-0.088 ± 0.291		-0.775 ± 0.191*	-0.156 ± 0.143	-1.015 ± 0.259*
Dry alpine	0.641 ± 0.138*	0.808 ± 0.162*		0.633 ± 0.124*	0.730 ± 0.150*	0.491 ± 0.125*
Wet alpine	0.578 ± 0.211*	0.515 ± 0.249*		0.482 ± 0.192*	0.567 ± 0.213*	-0.150 ± 0.292
Burn-deciduous	-0.095 ± 0.252	-0.111 ± 0.352		0.557 ± 0.137*	-0.441 ± 0.209*	0.436 ± 0.162*
Burn-grass	0.223 ± 0.242	-0.097 ± 0.358		0.375 ± 0.148*	-0.057 ± 0.168	0.614 ± 0.150*

Table B.1. Continued

Covariates	Tenmile Group by Season					
	EW 2002	EW 2003	LW 2002	LW 2003	L 2002	L 2003[a]
Elevation	86.196 ± 15.312*	33.355 ± 21.799	46.330 ± 17.649*	84.615 ± 14.074*	121.295 ± 29.374*	-6.722 ± 6.172
Elevation^2	-23.217 ± 4.844*	-9.111 ± 6.906	-15.011 ± 5.191*	-28.501 ± 4.864*	-38.816 ± 9.668*	2.216 ± 1.970
Quality					0.108 ± 0.122	0.403 ± 0.125*
Slope	0.073 ± 0.013*	0.027 ± 0.021	0.053 ± 0.014*	0.024 ± 0.010*	0.059 ± 0.019*	0.060 ± 0.019*
Curvature	0.168 ± 0.040*	0.083 ± 0.119	0.189 ± 0.050*	0.263 ± 0.049*	0.302 ± 0.115*	0.041 ± 0.076
Bear risk					-0.325 ± 0.293	0.789 ± 0.209*
Wolf risk	0.063 ± 0.451		-0.461 ± 0.235	0.838 ± 0.225*	0.824 ± 0.364*	-0.989 ± 0.329*
North	-0.063 ± 0.144	0.425 ± 0.272	-1.347 ± 0.313*	-1.827 ± 0.253*	-0.173 ± 0.279	-0.865 ± 0.331*
East	-0.545 ± 0.196*	-0.882 ± 0.407*	-0.211 ± 0.209	0.870 ± 0.372*	1.201 ± 0.372*	-0.279 ± 0.275
South	0.816 ± 0.172*	-0.270 ± 0.350	1.658 ± 0.211*	0.649 ± 0.252*	-0.923 ± 0.722	0.644 ± 0.254*
West	-0.208 ± 0.171	0.727 ± 0.354*	-0.099 ± 0.217	0.308 ± 0.132*	-0.105 ± 0.440	0.500 ± 0.208*
Shrub	-0.847 ± 0.375*		-0.778 ± 0.428	1.333 ± 0.543*	-2.539 ± 1.034*	0.236 ± 0.564
Coniferous	1.337 ± 0.414*		0.506 ± 0.467	0.911 ± 0.524	0.089 ± 0.638	1.465 ± 0.513*
Subalpine spruce	-1.143 ± 0.600		-1.601 ± 0.902	0.797 ± 0.474		-0.368 ± 0.625
Rocks	1.214 ± 0.321*		1.868 ± 0.297*	1.525 ± 0.258*	1.693 ± 0.691*	2.297 ± 0.512*
Rockcrust	2.858 ± 1.603					
Dry alpine	-0.649 ± 0.316*		1.703 ± 0.306*	-0.433 ± 0.636	-0.166 ± 0.709	-0.207 ± 0.438
Wet alpine	-0.210 ± 0.389		0.386 ± 0.978		0.924 ± 0.627	-1.890 ± 0.847*
Burn-deciduous	-2.322 ± 0.676*		-1.599 ± 0.692*	-1.818 ± 0.656*		-1.366 ± 0.621*
Burn-grass	-0.238 ± 0.477		-0.485 ± 0.490	-2.315 ± 0.983*		-0.168 ± 0.534

[a] averaged coefficients of selection (β_i) from competing models.

Table B.1. Continued

Covariates	Tenmile Group by Season					
	S 2002	S 2003	F 2002^a	F 2003	R 2002	R 2003
Elevation	-8.113 ± 10.128	-7.743 ± 16.847	1.420 ± 2.011	19.012 ± 29.536	-11.300 ± 9.743	
Elevation^2	3.864 ± 3.201	4.725 ± 4.890		-2.105 ± 7.847	7.979 ± 3.149*	
Quality	-0.019 ± 0.060	0.061 ± 0.039				
Slope	0.076 ± 0.018*	0.086 ± 0.012*			0.019 ± 0.012	
Curvature	0.113 ± 0.091	0.114 ± 0.063	0.088 ± 0.095	0.064 ± 0.141	0.062 ± 0.082	
Bear risk	-0.404 ± 0.295	-0.413 ± 0.378	-2.211 ± 0.463*	0.601 ± 0.460		
Wolf risk	0.106 ± 0.090	0.260 ± 0.216	0.359 ± 0.062*	-0.014 ± 0.098	1.699 ± 0.330*	
North	0.830 ± 0.276*	0.763 ± 0.355*	-0.529 ± 0.244*	0.442 ± 0.311	0.527 ± 0.202*	
East	-0.583 ± 0.237*	-0.37 ± 0.274	0.406 ± 0.205*	-0.022 ± 0.295	0.099 ± 0.181	
South	-0.137 ± 0.241	0.158 ± 0.238	0.915 ± 0.257*	0.168 ± 0.304	-0.983 ± 0.269*	
West	-0.110 ± 0.221	-0.55 ± 0.181*	-0.793 ± 0.222*	-0.588 ± 0.246*	0.358 ± 0.223	
Shrub	0.411 ± 0.999	-0.668 ± 1.083	-0.616 ± 0.330	-1.538 ± 0.649*	-1.364 ± 0.248*	
Coniferous	-0.470 ± 0.452	-0.884 ± 0.445*	-0.986 ± 0.563	-1.431 ± 1.030	1.418 ± 0.352*	
Subalpine spruce	0.062 ± 1.376		-0.975 ± 0.976	-2.329 ± 1.020*		
Rocks	1.384 ± 0.866	0.994 ± 0.493*	0.532 ± 0.422	1.613 ± 0.556*	1.393 ± 0.299*	
Rockcrust	-2.653 ± 1.365	0.544 ± 0.655		0.861 ± 1.377		
Dry alpine	0.875 ± 0.354*	0.396 ± 0.242	-0.781 ± 0.407	1.138 ± 0.468*	-1.078 ± 0.250*	
Wet alpine	0.391 ± 0.506	-0.382 ± 0.305	-0.391 ± 0.415	1.140 ± 0.505*	-0.369 ± 0.266	
Burn-deciduous			1.295 ± 0.877			
Burn-grass			1.922 ± 1.141	0.547 ± 1.491		

[a] averaged coefficients of selection (β_i) from competing models.

Table B.1. Continued

Covariates	Firstfork Group by Season					
	EW 2002[a]	EW 2003	LW 2002[a]	LW 2003	L 2002	L 2003
Elevation	-1.092 ± 2.522	-24.597 ± 7.753*	-13.028 ± 7.196	66.156 ± 8.003*	135.924 ± 22.826*	6.736 ± 1.581*
Elevation^2	0.336 ± 0.715	8.528 ± 2.280*	3.501 ± 2.034	-18.529 ± 2.338*	-41.674 ± 6.991*	
Quality					0.005 ± 0.060	0.025 ± 0.061
Slope	0.026 ± 0.011*	0.065 ± 0.008*	0.048 ± 0.009*	0.062 ± 0.010*	0.038 ± 0.015*	0.120 ± 0.015*
Curvature	0.312 ± 0.055*	0.227 ± 0.043*	0.171 ± 0.032*	0.267 ± 0.038*	0.056 ± 0.059	0.146 ± 0.071*
Bear risk					-0.201 ± 0.190	1.154 ± 0.179*
Wolf risk	-0.501 ± 0.058*	0.107 ± 0.162	-0.260 ± 0.123*	0.662 ± 0.127*	0.009 ± 0.260	-0.355 ± 0.307
North	-1.482 ± 0.331*	-0.515 ± 0.167*	-1.188 ± 0.212*	-0.868 ± 0.238*		0.173 ± 0.350
East	-0.543 ± 0.226*	-0.715 ± 0.141*	-0.192 ± 0.135	-0.137 ± 0.191	-0.742 ± 0.422	-0.284 ± 0.220
South	1.290 ± 0.155*	0.600 ± 0.117*	1.687 ± 0.118*	0.785 ± 0.125*	0.421 ± 0.291	-0.325 ± 0.236
West	0.735 ± 0.163*	0.629 ± 0.122*	-0.307 ± 0.137*	0.220 ± 0.122	0.321 ± 0.289	0.436 ± 0.172*
Shrub	-0.848 ± 0.297*	0.674 ± 0.223*	-1.038 ± 0.287*	-0.232 ± 0.217	-0.526 ± 0.362	2.049 ± 0.353*
Coniferous	-1.302 ± 0.456*	-0.310 ± 0.385	-1.258 ± 0.397*	-0.528 ± 0.244*	-0.621 ± 0.419	0.557 ± 0.344
Subalpine spruce		-0.634 ± 0.449	-0.944 ± 0.501	-1.082 ± 0.359*	-0.464 ± 0.530	-0.188 ± 0.682
Rocks	0.828 ± 0.173*	1.038 ± 0.238*	1.402 ± 0.171*	0.714 ± 0.145*	0.862 ± 0.360*	-0.123 ± 0.369
Rockcrust	0.699 ± 0.368	-0.033 ± 0.353	2.662 ± 0.276*	1.023 ± 0.756		
Dry alpine	0.895 ± 0.193*	0.798 ± 0.210*	1.373 ± 0.204*	0.476 ± 0.171*	0.502 ± 0.309	0.505 ± 0.363
Wet alpine	-0.272 ± 0.385	-0.057 ± 0.302	1.731 ± 0.361*	0.552 ± 0.316	-0.049 ± 0.980	-0.748 ± 0.518
Burn-deciduous		-0.822 ± 0.470	-2.023 ± 0.499	-0.546 ± 0.205*	0.089 ± 0.325	-0.989 ± 0.327*
Burn-grass		-0.654 ± 0.615	-1.898 ± 0.574	-0.378 ± 0.244	0.206 ± 0.413	-1.062 ± 0.414*

[a] averaged coefficients of selection (β_i) from competing models.

Table B.1. Continued

Covariates	Firstfork Group by Season					
	S 2002	S 2003	F 2002	F 2003	R 2002	R 2003[a]
Elevation	-21.557 ± 7.029*	-38.847 ± 7.166*	-13.367 ± 4.734*	-27.68 ± 5.453*	-34.284 ± 5.379*	-56.704 ± 12.217*
Elevation^2	7.299 ± 2.084*	11.559 ± 2.132*	6.318 ± 1.475*	9.474 ± 1.799*	11.495 ± 1.702*	17.899 ± 3.638*
Quality	-0.036 ± 0.032	-0.078 ± 0.025*				
Slope	-0.049 ± 0.018*	0.065 ± 0.009*			0.053 ± 0.008*	0.098 ± 0.021*
Curvature	0.205 ± 0.048*	0.157 ± 0.048*	0.053 ± 0.046	0.004 ± 0.040	0.086 ± 0.046	0.203 ± 0.115
Bear risk	-0.562 ± 0.12*	-0.615 ± 0.137*	0.212 ± 0.286	-0.337 ± 0.169*		
Wolf risk	-0.878 ± 0.139*	-0.458 ± 0.160*	0.390 ± 0.055*	-0.388 ± 0.049*	0.096 ± 0.266	
North	0.401 ± 0.203*	0.195 ± 0.162	-0.172 ± 0.136	-0.417 ± 0.159*	-0.059 ± 0.184	-0.164 ± 0.297
East	-0.146 ± 0.171	-0.773 ± 0.143*	-0.255 ± 0.106*	-0.245 ± 0.127	-0.571 ± 0.134*	-0.697 ± 0.267*
South	0.419 ± 0.143*	-0.119 ± 0.117	0.189 ± 0.114	0.610 ± 0.106*	0.368 ± 0.158*	0.630 ± 0.228*
West	-0.675 ± 0.228*	0.697 ± 0.117*	0.239 ± 0.116*	0.051 ± 0.114	0.261 ± 0.142	0.232 ± 0.247
Shrub	1.278 ± 0.401*	2.390 ± 0.510*	-0.266 ± 0.171	0.731 ± 0.188*	0.406 ± 0.179*	-0.220 ± 0.297
Coniferous	-0.039 ± 0.346	-1.439 ± 0.335*	0.729 ± 0.287*	-0.298 ± 0.321	0.199 ± 0.318	-0.093 ± 0.381
Subalpine spruce	1.042 ± 0.56	0.502 ± 0.731	-2.672 ± 0.651*	-0.050 ± 0.438	-1.223 ± 0.716	
Rocks	0.322 ± 0.424	-0.366 ± 0.426	1.296 ± 0.227*	0.266 ± 0.199	0.959 ± 0.200*	0.090 ± 0.284
Rockcrust	-1.686 ± 0.581*	-1.423 ± 0.483*	0.139 ± 0.399	-2.092 ± 0.537*	-0.340 ± 0.351	-0.011 ± 0.469
Dry alpine	0.325 ± 0.278	0.011 ± 0.237	-0.263 ± 0.206	0.228 ± 0.198	0.297 ± 0.199	0.497 ± 0.293
Wet alpine	-0.195 ± 0.386	0.504 ± 0.310	-0.619 ± 0.257*	0.480 ± 0.249	-0.351 ± 0.290	-0.295 ± 0.406
Burn-deciduous	-0.958 ± 0.926	-0.509 ± 0.707	0.184 ± 0.397	0.143 ± 0.314	-0.077 ± 0.373	0.320 ± 0.385
Burn-grass	-0.09 ± 0.955	0.329 ± 0.699	1.471 ± 0.352*	0.592 ± 0.324	0.130 ± 0.412	-0.287 ± 0.595

[a] averaged coefficients of selection (β_i) from competing models.

Table B.1. Continued

Covariates	Townsley Group by Season					
	EW 2002	EW 2003	LW 2002	LW 2003	L 2002	L 2003
Elevation	16.795 ± 4.193*	16.632 ± 7.319*	-6.738 ± 2.677*	15.103 ± 3.889*	15.018 ± 6.753*	7.016 ± 1.326*
Elevation^2	-3.387 ± 1.143*	-2.19 ± 2.082	1.498 ± 0.877	-4.000 ± 1.199*	-4.154 ± 2.194	
Quality					0.049 ± 0.045	-0.100 ± 0.076
Slope	0.067 ± 0.006*	0.004 ± 0.006	0.089 ± 0.005*	0.083 ± 0.006*	0.083 ± 0.008*	0.086 ± 0.012*
Curvature	0.379 ± 0.030*	0.249 ± 0.033*	0.116 ± 0.023*	0.247 ± 0.028*	0.124 ± 0.039*	0.187 ± 0.047*
Bear risk					0.231 ± 0.095*	0.681 ± 0.127*
Wolf risk	0.250 ± 0.090*	0.063 ± 0.064	-0.151 ± 0.028*	0.101 ± 0.043*	0.366 ± 0.125*	0.666 ± 0.209*
North	-0.561 ± 0.104*	-0.416 ± 0.117*	-1.196 ± 0.137*	-1.216 ± 0.163*	-1.124 ± 0.170*	-0.641 ± 0.270*
East	-0.741 ± 0.082*	-0.666 ± 0.092*	-0.424 ± 0.081*	-0.440 ± 0.089*	-0.171 ± 0.124	-0.249 ± 0.168
South	1.046 ± 0.067*	0.635 ± 0.079*	1.449 ± 0.081*	1.311 ± 0.078*	0.929 ± 0.126*	-0.022 ± 0.192
West	0.255 ± 0.080*	0.447 ± 0.088*	0.171 ± 0.073*	0.344 ± 0.088*	0.366 ± 0.123*	0.913 ± 0.165*
Shrub	0.179 ± 0.144	0.403 ± 0.136*	0.568 ± 0.124*	0.372 ± 0.110*	0.287 ± 0.190	1.182 ± 0.334*
Coniferous	-0.331 ± 0.191	-0.377 ± 0.231	-0.786 ± 0.123*	-0.620 ± 0.127*	-0.135 ± 0.219	-0.015 ± 0.326
Subalpine spruce	-2.250 ± 0.561*	-1.010 ± 0.352*	-2.301 ± 0.519*	-1.686 ± 0.277*	-0.660 ± 0.283*	-2.023 ± 0.939*
Rocks	0.341 ± 0.113*	-0.388 ± 0.155*	0.081 ± 0.102	-0.293 ± 0.113*	0.762 ± 0.201*	-0.069 ± 0.337
Rockcrust	0.815 ± 0.147*	-0.478 ± 0.188*	0.258 ± 0.187	0.887 ± 0.171*	0.236 ± 0.404	0.067 ± 0.620
Dry alpine	0.734 ± 0.106*	0.236 ± 0.115*	0.660 ± 0.105*	0.254 ± 0.089*	-0.277 ± 0.161	0.963 ± 0.290*
Wet alpine	-0.070 ± 0.226	0.263 ± 0.183	0.230 ± 0.283	-0.180 ± 0.272	-0.142 ± 0.353	0.276 ± 0.611
Burn-deciduous	-0.113 ± 0.167	0.468 ± 0.162*	0.164 ± 0.103	0.113 ± 0.102	-0.319 ± 0.170	-0.693 ± 0.259*
Burn-grass	0.694 ± 0.183*	0.884 ± 0.200*	1.125 ± 0.107*	1.154 ± 0.104*	0.249 ± 0.186	0.311 ± 0.264

Table B.1. Continued

Covariates	Townsley Group by Season					
	S 2002	S 2003	F 2002[a]	F 2003	R 2002	R 2003
Elevation	-9.419 ± 5.400	15.361 ± 9.369	-4.366 ± 3.921	28.814 ± 17.003	13.709 ± 1.058*	6.636 ± 6.304
Elevation^2	4.255 ± 1.559*	-2.651 ± 2.700	1.955 ± 1.321	-5.760 ± 4.498		-0.446 ± 1.816
Quality	-0.003 ± 0.017	0.027 ± 0.022				
Slope	0.055 ± 0.009*	0.020 ± 0.006*			-0.001 ± 0.005	0.029 ± 0.006*
Curvature	0.362 ± 0.030*	0.227 ± 0.034*	0.159 ± 0.027*	0.025 ± 0.028	0.107 ± 0.032*	0.332 ± 0.037*
Bear risk	0.187 ± 0.069*	-0.505 ± 0.152*	-0.805 ± 0.217*	-0.182 ± 0.180		
Wolf risk	0.069 ± 0.054	0.446 ± 0.114*	-0.027 ± 0.017	-0.021 ± 0.024	0.962 ± 0.163*	
North	-0.188 ± 0.082*	-0.056 ± 0.132	-0.163 ± 0.086	-0.201 ± 0.093*	0.117 ± 0.100	-0.114 ± 0.119
East	-0.013 ± 0.074	0.286 ± 0.099*	-0.061 ± 0.068	0.045 ± 0.079	-0.575 ± 0.077*	-0.570 ± 0.107*
South	0.180 ± 0.079*	0.222 ± 0.102*	0.708 ± 0.085*	0.204 ± 0.073*	0.170 ± 0.091	0.379 ± 0.091*
West	0.021 ± 0.095	-0.453 ± 0.097*	-0.484 ± 0.089*	-0.048 ± 0.076	0.288 ± 0.084*	0.304 ± 0.088*
Shrub	-0.775 ± 0.221*	-0.466 ± 0.380	0.698 ± 0.088*	0.784 ± 0.182*	-0.104 ± 0.147	0.475 ± 0.150*
Coniferous	0.083 ± 0.167	-0.872 ± 0.291*	-0.396 ± 0.194*	0.324 ± 0.198	1.386 ± 0.183*	0.009 ± 0.185
Subalpine spruce	-1.641 ± 0.430*	-2.206 ± 0.930*	-0.808 ± 0.298*	-0.429 ± 0.352	-2.517 ± 0.530*	-1.666 ± 0.539*
Rocks	1.914 ± 0.258*	0.992 ± 0.387*	-0.470 ± 0.124*	-0.486 ± 0.169*	0.232 ± 0.139	-0.161 ± 0.151
Rockcrust	0.372 ± 0.304	-0.112 ± 0.423	-0.891 ± 0.172*	-0.696 ± 0.213*	-0.853 ± 0.221*	-0.613 ± 0.261*
Dry alpine	0.976 ± 0.146*	0.229 ± 0.220	-0.006 ± 0.119	0.052 ± 0.151	0.152 ± 0.137	0.603 ± 0.132*
Wet alpine	1.550 ± 0.186*	0.911 ± 0.251*	0.114 ± 0.152	0.492 ± 0.175*	-0.341 ± 0.169*	0.657 ± 0.177*
Burn-deciduous	-2.010 ± 0.414*	0.383 ± 0.440	0.485 ± 0.229*	0.021 ± 0.283	0.674 ± 0.229*	0.298 ± 0.227
Burn-grass	-0.470 ± 0.303	1.140 ± 0.437*	1.275 ± 0.216*	-0.064 ± 0.342	1.372 ± 0.206*	0.400 ± 0.280

[a] averaged coefficients of selection (β_i) from competing models.

Table B.1. Continued

Covariates	Richards Group by Season					
	EW 2002	EW 2003	LW 2002	LW 2003	L 2002	L 2003
Elevation	35.957 ± 15.196*	-12.984 ± 10.504	129.878 ± 22.865*	12.367 ± 5.289*	48.912 ± 11.523*	19.144 ± 14.567
Elevation^2	-6.914 ± 4.156	7.597 ± 2.938*	-36.548 ± 6.333*	-0.642 ± 1.541	-12.848 ± 3.523*	-4.047 ± 4.369
Quality					0.132 ± 0.067*	-0.049 ± 0.065
Slope	-0.026 ± 0.008*	-0.018 ± 0.006*	0.067 ± 0.009*	0.039 ± 0.006*	0.080 ± 0.014*	0.074 ± 0.015*
Curvature	0.258 ± 0.036*	0.201 ± 0.036*	0.307 ± 0.039*	0.256 ± 0.032*	0.147 ± 0.048*	0.114 ± 0.049*
Bear risk					-0.057 ± 0.158	0.549 ± 0.187*
Wolf risk	0.901 ± 0.347*	0.544 ± 0.114*	-0.361 ± 0.129*	0.994 ± 0.090*	0.773 ± 0.220*	0.068 ± 0.283
North	-0.204 ± 0.123	-0.184 ± 0.136	-1.655 ± 0.187*	-1.470 ± 0.156*	-1.171 ± 0.232*	-0.448 ± 0.230
East	-0.498 ± 0.125*	-0.555 ± 0.122*	-0.274 ± 0.127*	0.127 ± 0.097	0.426 ± 0.165*	-0.146 ± 0.176
South	0.043 ± 0.097	0.243 ± 0.100*	1.646 ± 0.118*	1.435 ± 0.086*	0.515 ± 0.188*	0.237 ± 0.211
West	0.660 ± 0.099*	0.497 ± 0.126*	0.283 ± 0.128*	-0.092 ± 0.105	0.230 ± 0.209	0.357 ± 0.184
Shrub	-0.395 ± 0.166*	0.324 ± 0.207	0.691 ± 0.125*	0.232 ± 0.101*	0.769 ± 0.283*	1.918 ± 0.388*
Coniferous	0.645 ± 0.262*	1.649 ± 0.292*	-2.277 ± 0.460*	-1.141 ± 0.169*	0.680 ± 0.404	-0.116 ± 0.376
Subalpine spruce		-1.493 ± 0.895			-1.905 ± 0.876*	-0.916 ± 0.934
Rocks	0.612 ± 0.113*	0.148 ± 0.246	-0.061 ± 0.146	1.184 ± 0.107*	1.461 ± 0.331*	0.157 ± 0.333
Rockcrust	-0.347 ± 0.216	0.071 ± 0.250		-0.907 ± 0.269*		-1.901 ± 1.072
Dry alpine	-0.272 ± 0.196	-0.166 ± 0.211	-0.112 ± 0.143	0.230 ± 0.113*	0.337 ± 0.335	0.929 ± 0.364*
Wet alpine	-0.243 ± 0.203	-0.533 ± 0.224*	-0.240 ± 0.244	-0.298 ± 0.225	-1.456 ± 0.950	-0.557 ± 0.627
Burn-deciduous			0.257 ± 0.233	0.456 ± 0.166*	-0.419 ± 0.392	-0.222 ± 0.447
Burn-grass			1.742 ± 0.138*	0.243 ± 0.186	0.533 ± 0.350	0.709 ± 0.374

Table B.1. Continued

Covariates	Richards Group by Season					
	S 2002	S 2003	F 2002^a	F 2003	R 2002^a	R 2003
Elevation	14.530 ± 6.558*	-13.528 ± 5.809*	-4.525 ± 3.024	-19.705 ± 7.016*	2.507 ± 4.045	4.077 ± 0.625*
Elevation^2	-3.180 ± 1.951	5.396 ± 1.777*	1.594 ± 1.047	7.713 ± 2.150*	-0.140 ± 1.259	
Quality	0.050 ± 0.023*	0.032 ± 0.024				
Slope	-0.015 ± 0.012	0.066 ± 0.010*			-0.020 ± 0.008*	-0.024 ± 0.008*
Curvature	0.190 ± 0.043*	0.181 ± 0.059*	-0.037 ± 0.048	0.038 ± 0.043	0.030 ± 0.044	0.165 ± 0.056*
Bear risk	0.153 ± 0.120	-0.181 ± 0.181	-0.997 ± 0.206*	-0.064 ± 0.203		
Wolf risk	-0.687 ± 0.093*	0.178 ± 0.162	-0.249 ± 0.041*	-0.228 ± 0.039*	-0.602 ± 0.236*	
North	0.529 ± 0.119*	0.222 ± 0.144	-0.267 ± 0.138	0.091 ± 0.119	-0.095 ± 0.148	0.540 ± 0.156*
East	0.295 ± 0.118*	0.286 ± 0.128*	-0.362 ± 0.126*	0.061 ± 0.115	-0.237 ± 0.144	-0.058 ± 0.153
South	-0.656 ± 0.131*	-0.517 ± 0.127*	0.581 ± 0.124*	0.059 ± 0.099	-0.015 ± 0.159	-0.583 ± 0.157*
West	-0.167 ± 0.115	0.010 ± 0.110	0.047 ± 0.115	-0.212 ± 0.111	0.348 ± 0.140*	0.102 ± 0.151
Shrub	-0.879 ± 0.419*	-0.962 ± 0.425*	0.917 ± 0.182*	0.524 ± 0.211*	-0.545 ± 0.235*	-0.616 ± 0.224*
Coniferous	0.119 ± 0.223	-0.707 ± 0.368	-0.929 ± 0.259*	-0.633 ± 0.237*	-0.407 ± 0.283	-0.460 ± 0.246
Subalpine spruce	-2.009 ± 0.978*				-0.035 ± 0.612	
Rocks	1.503 ± 0.454*	1.017 ± 0.339*	-0.520 ± 0.199*	-0.381 ± 0.178*	-0.184 ± 0.220	0.104 ± 0.181
Rockcrust	1.448 ± 0.549*	1.096 ± 0.393*	-1.006 ± 0.287*	-0.146 ± 0.223	-0.141 ± 0.275	0.489 ± 0.225*
Dry alpine	1.634 ± 0.257*	0.484 ± 0.225*	0.477 ± 0.183*	0.066 ± 0.149	0.895 ± 0.205*	0.492 ± 0.171*
Wet alpine	0.577 ± 0.310	0.402 ± 0.259	0.641 ± 0.204*	0.450 ± 0.184*	0.680 ± 0.215*	-0.009 ± 0.190
Burn-deciduous	-2.161 ± 0.737*	-0.823 ± 0.623	-0.564 ± 0.568			
Burn-grass	-0.231 ± 0.453	-0.506 ± 0.667	0.986 ± 0.417*	0.121 ± 0.374	-0.263 ± 0.559	

[a] averaged coefficients of selection (β_i) from competing models.

Appendix C: Accuracy assessment of vegetation types defined by remote-sensing satellite imagery in the Besa-Prophet area of northern British Columbia.

Table C.1. Accuracy assessment of vegetation types used for analyses of habitat selection by Stone's sheep in the Besa-Prophet area of northern British Columbia, 2002-2003.

Vegetation Type	Producer's Accuracy[a] (%)[c]	User's Accuracy[b] (%)[c]
Riparian	87.18	85.00
Shrub	80.00	53.33
Conifer	86.67	92.86
Subalpine spruce	80.00	100.00
Rocks	100.00	62.50
Rockcrust	70.00	87.50
Dry alpine	60.00	75.00
Wet alpine	60.00	75.00
Burn-deciduous	40.00	50.00
Burn-grass	70.00	77.78
Overall accuracy	79.17	

[a] producer's accuracy was calculated by dividing the total number of correctly classified pixels in an individual class by the total number of sample pixels classified as that class (Lay 2005).

[b] user's accuracy was calculated by dividing the total number of correct sample units in an individual class by the total number of reference units (Lay 2005).

[c] modified from Lay (2005).

Appendix D: Defining the risk of predation from grizzly bears (*Ursus arctos*) for female Stone’s sheep across three seasons and two years (2002-2003) in the Besa-Prophet area of northern British Columbia.

Table D.1. An ecologically plausible set of models used to define the risk of predation from grizzly bears during lambing, summer and fall seasons in the Besa-Prophet area of northern British Columbia (2002-2003).

Models
vegetation type + aspect + fragmentation + elevation + elevation^{2a}
vegetation type+ aspect + elevation + elevation^{2a}
vegetation type+ fragmentation + elevation + elevation^{2a}
vegetation type+ fragmentation
vegetation type
aspect + fragmentation + elevation + elevation^{2a}
aspect + elevation + elevation^{2a}
elevation + elevation^{2a} + fragmentation
fragmentation + slope

[a] available only in models with nonlinear elevation.

Table D.2. Final global models of bear risk (based on locations from 15 female grizzly bears) by season and year in the Besa-Prophet area of northern British Columbia, 2002-2003. Statistics include number of parameters (*K*), sample size (*n*), log-likelihood (LL), Akaike's Information Criterion (AIC), Akaike weights (w_i), and average (n = 5) Spearman's correlation coefficient ($\bar{r}_s$) from *k*-fold cross-validation with associated *P* values. ** and * indicate a $P < 0.01$ and $P < 0.05$ respectively.

Group	Year	Season[a]	Model[b]	*K*	*n*	LL	AIC	w_i	$\bar{r}_s$
Global	2002	L	$V+F+E+E^2$	13	1986	-824.886	1675.773	0.954	0.900**
Global	2003	L	$V+A+F+E+E^2$	17	4931	-2102.896	4239.791	0.994	0.910**
Global[c]	2002	S	$V+F+E+E^2$	13	6645	-2720.525	5467.050	0.508	0.950**
	2002	S	$V+A+F+E+E^2$	17	6645	-2716.638	5467.275	0.454	0.970**
Global	2003	S	$V+A+F+E+E^2$	17	10307	-4220.158	8474.316	0.999	0.970**
Global	2002	F	$V+A+E+E^2$	15	7434	-3002.652	6035.305	0.951	0.948**
Global	2003	F	$V+A+F+E+E^2$	17	10332	-4170.925	8375.850	0.982	0.978**

[a] L=Lambing, S=Summer, F=Fall; as defined in Table 2.1.

[b] V=Vegetation type, A=Aspect, F=Fragmentation, E=Elevation

[c] models were averaged to determine selection coefficients for habitat attributes.

Table D.3. Coefficients of selection (β_i) and standard errors (SE) of the covariates for the final pooled models of bear risk by season and year in the Besa-Prophet area of northern British Columbia, 2002-2003. Seasons are defined in Table 2.1. * indicates 95% confidence intervals (CI) of the β_i were different from zero.

Covariates	Global Models by Season					
	L 2002	L 2003	S 2002^a	S 2003	F 2002	F 2003
Elevation	21.512 ± 5.193*	14.270 ± 2.439*	5.128 ± 1.537*	6.196 ± 1.130*	11.176 ± 1.849*	17.297 ± 1.508*
Elevation^2	-7.088 ± 1.688*	-4.836 ± 0.757*	-1.608 ± 0.478*	-2.238 ± 0.370*	-4.581 ± 0.593*	-6.210 ± 0.524*
Low fragmentation	-0.336 ± 0.106*	-0.240 ± 0.066*	-0.232 ± 0.047*	-0.178 ± 0.045*		-0.178 ± 0.049*
Medium fragmentation	-0.101 ± 0.091	0.014 ± 0.056	0.037 ± 0.040	0.126 ± 0.038*		0.015 ± 0.041
High fragmentation	0.437 ± 0.088*	0.226 ± 0.057*	0.196 ± 0.041*	0.053 ± 0.041		0.163 ± 0.039*
Slope						
North		-0.194 ± 0.101	0.044 ± 0.036	0.182 ± 0.061*	-0.121 ± 0.075	0.078 ± 0.061
East		-0.190 ± 0.095*	-0.038 ± 0.034	-0.255 ± 0.059*	-0.011 ± 0.072	-0.191 ± 0.059*
South		0.180 ± 0.087*	-0.067 ± 0.039	-0.271 ± 0.059*	0.162 ± 0.067*	0.039 ± 0.059
West		-0.118 ± 0.104	-0.059 ± 0.043	-0.083 ± 0.069	-0.256 ± 0.085*	0.073 ± 0.064
No aspect (flat)		0.323 ± 0.256	0.120 ± 0.090	0.427 ± 0.137*	0.226 ± 0.168	0.001 ± 0.136
Spruce	-0.037 ± 0.153	-0.094 ± 0.114	-0.186 ± 0.075*	-0.453 ± 0.076*	-0.341 ± 0.075*	-0.428 ± 0.066*
Shrubs	-0.557 ± 0.289	-0.375 ± 0.188*	0.322 ± 0.106*	0.317 ± 0.098*	-0.133 ± 0.113	0.653 ± 0.075*
Subalpine	-0.209 ± 0.175	-0.031 ± 0.119	0.618 ± 0.072*	0.901 ± 0.070*	0.254 ± 0.094*	0.366 ± 0.081*
Carex spp.	1.082 ± 0.439*	-0.384 ± 0.368	0.412 ± 0.186*	-0.026 ± 0.189	0.545 ± 0.205*	0.414 ± 0.151*
Non-vegetated	-0.315 ± 0.209	0.511 ± 0.122*	-1.323 ± 0.140*	-0.879 ± 0.132*	0.012 ± 0.119	-0.777 ± 0.116*
Pine	-1.111 ± 0.478*	-0.472 ± 0.243	-0.165 ± 0.154	-0.314 ± 0.154*	-0.184 ± 0.141	0.022 ± 0.105
Riparian spruce	1.146 ± 0.299*	0.169 ± 0.239	0.319 ± 0.137*	-0.115 ± 0.134	-0.451 ± 0.137*	0.125 ± 0.109
Alpine	-0.226 ± 0.237	0.207 ± 0.147	-0.527 ± 0.122*	-0.258 ± 0.120*	-0.098 ± 0.163	-0.789 ± 0.154*
Burned/disturbed	0.227 ± 0.182	0.468 ± 0.120*	0.530 ± 0.083*	0.825 ± 0.078*	0.395 ± 0.086*	0.416 ± 0.076*

[a] averaged coefficients of selection (β_i) from competing models.

Appendix E: Defining the risk of predation from wolves (*Canis lupus*) for female Stone's sheep in the Besa-Prophet area of northern British Columbia (2002-2003).

Table E.1. An ecologically plausible set of models used to define the risk of predation from wolves in the Besa-Prophet area of northern British Columbia (2002-2003). Models were developed for 6 wolf packs: Dopp-Keily, Lower Besa, Neves, Pocketknife, Richards-Prophet and Withrow.

Models
vegetation type + aspect + fragmentation + elevation + elevation^{2a}
vegetation type + aspect + elevation + elevation^{2a}
vegetation type + fragmentation + elevation + elevation^{2a}
vegetation type + fragmentation
vegetation type
aspect + elevation + elevation^{2a}
aspect + fragmentation
slope + aspect
elevation + elevation^{2a} + fragmentation
[b]vegetation type+ fragmentation + distance to linear features + distance to linear features^{2a}
[b]distance to linear features + distance to linear features^{2a}
[b]vegetation type+ distance to linear features + distance to linear features^{2a}
[b]fragmentation + distance to linear features + distance to linear features^{2a}

[a] available only in models with nonlinear elevation and distance to linear features.

[b] models evaluated only for the Pocketknife pack which occurs on the eastern edge of the study area where linear features are present.

Table E.2. Final global and pack models of wolf risk (based on locations from 22 individuals in 5 wolf packs) by season and year in the Besa-Prophet area of northern British Columbia, 2002-2003. Statistics include number of parameters (*K*), sample size (*n*), log-likelihood (LL), Akaike's Information Criterion (AIC), Akaike weights (w_i), and average ($n = 5$) Spearman's correlation coefficient ($\bar{r}_s$) from *k*-fold cross-validation with associated *P* values. ** and * indicate a $P < 0.01$ and $P < 0.05$ respectively.

Pack	Year	Season^a	Model^b	*K*	*n*	LL	AIC	w_i	$\bar{r}_s$
Global	2002	EW	V+F+E+E^2	13	2379	-971.305	1968.611	0.981	0.801**
Global	2003	EW	V+A+F+E+E^2	17	3843	-1490.509	3015.018	0.955	0.901**
Global	2002	LW	V+A+F+E+E^2	17	7854	-3251.704	6537.407	1.000	0.960**
Global	2003	LW	V+A+F+E+E^2	17	5217	-1849.381	3732.762	0.954	0.972**
Global	2002	L	V+A+F+E+E^2	17	1891	-751.959	1537.917	0.973	0.881*
Global	2003	L	V+A+F+E+E^2	17	1791	-866.135	1766.269	0.995	0.929**
Global	2002	S	S+A	6	4321	-1707.875	3427.749	1.000	0.970**
Global	2003	S	V+A+F+E+E^2	17	3052	-1213.817	2461.633	0.961	0.947**
Global	2002	F	S+A	6	5688	-2283.441	4578.881	1.000	0.958**
Global	2003	F	S+A	6	2007	-735.444	1482.888	1.000	0.878**
Global	2002	R	V+A+E+E^2	15	4794	-1935.164	3900.328	0.982	0.939**
Dopp-Keily	2003	EW	V+A+E+E^2	15	672	-252.988	536.616^c	0.974	0.895**
Dopp-Keily	2002	LW	V+A+F+E+E^2	17	1542	-578.667	1191.334	1.000	0.902**
Dopp-Keily^d	2003	LW	V+A+F+E+E^2	17	1308	-429.609	893.218	0.413	0.872**
	2003	LW	V+A+E+E^2	15	1308	-431.727	893.455	0.367	0.851**
	2003	LW	A+E+E^2	7	1308	-440.236	894.471	0.221	0.884**
Dopp-Keily^d	2002	L	V+A+E	14	390	-129.068	287.107^c	0.757	0.491
	2002	L	V+A+F+E	16	390	-128.381	290.049^c	0.195	0.550
Dopp-Keily	2003	L	V+A+F+E	16	522	-226.110	485.171^c	0.889	0.790**
Dopp-Keily	2002	S	S+A	6	999	-380.482	772.963	1.000	0.855**
Dopp-Keily^d	2003	S	V	9	809	-293.722	605.444	0.593	0.642*
	2003	S	V+F+E+E^2	13	809	-290.788	607.576	0.197	0.860**
	2003	S	V+A+E+E^2	15	809	-289.257	608.513	0.164	0.880**
Dopp-Keily	2002	F	V+F+E+E^2	13	1206	-429.865	885.731	0.999	0.891**

Table E.2: Continued

Pack	Year	Season[a]	Model[b]	K	n	LL	AIC	w_i	$\bar{r}_s$
Dopp-Keily	2002	R	V+A+F+E+E^2	17	734	-256.821	547.641	0.958	0.882**
Lower Besa	2002	EW	V+A+E+E^2	14	468	-173.821	376.446[c]	0.994	0.689*
Lower Besa	2003	EW	A+E+E^2	7	447	-196.048	406.287[c]	0.345	0.364
Lower Besa	2002	LW	V+A+E+E^2	15	1308	-482.152	994.303	0.601	0.830**
Lower Besa[d]	2003	LW	E+F	4	869	-299.961	607.922	0.520	0.750*
	2003	LW	V+F+E	11	869	-293.520	609.039	0.298	0.730*
	2003	LW	V+A+F+E	15	869	-290.014	610.028	0.182	0.800**
Lower Besa	2002	L	E+E^2+F	5	169	-66.041	142.327[c]	0.921	0.620
Lower Besa[d]	2003	L	V+A+E+E^2	12	346	-106.841	238.475[c]	0.567	0.610
	2003	L	V+F+E+E^2	11	346	-108.324	239.307[c]	0.350	0.640*
	2003	L	V+A+F+E+E^2	15	346	-105.782	242.837[c]	0.082	0.561
Lower Besa	2002	S	S+A	6	720	-248.151	508.302	1.000	0.830**
Lower Besa	2003	S	V+F+E	10	406	-128.960	278.375[c]	0.957	0.747*
Lower Besa	2002	F	S+A	6	996	-395.774	803.549	1.000	0.861**
Lower Besa	2003	F	S+A	6	990	-335.227	682.455	1.000	0.877**
Lower Besa	2002	R	S+A	6	774	-343.232	698.463	0.450	0.324
Neves	2003	EW	V+F+E+E^2	13	900	-340.858	707.716	0.988	0.688*
Neves	2002	LW	V+A+F+E+E^2	17	1182	-473.747	981.494	0.510	0.720*
Neves[d]	2003	LW	V+A+E	14	1070	-400.393	828.786	0.505	0.750*
	2003	LW	V+A+F+E	16	1070	-398.433	828.865	0.485	0.722*
Neves	2002	L	E+E^2+F	5	105	-38.078	86.561[c]	0.472	0.714*
Neves	2003	L	V+F+E+E^2	13	238	-79.500	186.393[c]	0.812	0.670*
Neves	2002	S	V+A+F+E+E^2	17	678	-228.694	491.388[c]	0.930	0.750*
Neves	2003	S	V+A+E+E^2	14	564	-212.066	452.794[c]	0.684	0.673*
Neves	2002	F	S+A	6	1110	-427.003	866.007	0.994	0.851**
Neves	2003	F	S+A	6	276	-118.354	248.931[c]	0.508	0.360
Neves	2002	R	V+A+E+E^2	15	972	-356.677	743.353	0.958	0.801**
Pocketknife	2002	EW	V+A+E+E^2	14	892	-380.680	789.360	0.989	0.799**

Table E.2: Continued

Pack	Year	Season[a]	Model[b]	K	n	LL	AIC	w_i	$\bar{r}_s$
Pocketknife	2003	EW	$V+L+L^2$	10	987	-304.445	628.889	0.979	0.688*
Pocketknife	2002	LW	$V+A+F+E+E^2$	17	1266	-507.279	1048.557	0.759	0.702*
Pocketknife[d]	2003	LW	$V+A+E+E^2$	14	749	-264.305	556.610	0.635	0.694*
	2003	LW	$V+A+F+E+E^2$	16	749	-262.747	557.495	0.323	0.692*
Pocketknife[d]	2002	L	$V+A+F+E+E^2$	15	349	-122.426	276.113[c]	0.773	0.630
	2002	L	$V+F+L+L^2$	11	349	-128.956	280.565[c]	0.179	0.601
Pocketknife[d]	2003	L	$V+A+E+E^2$	13	302	-143.091	313.265[c]	0.674	0.581
	2003	L	$V+A+F+E+E^2$	15	302	-141.947	315.363[c]	0.284	0.520
Pocketknife	2002	S	$V+F+E+E^2$	13	840	-326.815	679.629	0.621	0.804**
Pocketknife	2003	S	$F+L+L^2$	4	420	-176.011	360.080[c]	0.684	0.690*
Pocketknife	2002	F	$V+F+E+E^2$	13	1308	-532.828	1091.657	0.982	0.675*
Pocketknife	2003	F	$V+F+E+E^2$	13	496	-160.112	346.871[c]	0.990	0.685*
Pocketknife	2002	R	$V+F+E+E^2$	13	1163	-455.077	936.154	0.950	0.802**
Richards-Prophet	2003	EW	$V+A+F+E+E^2$	17	820	-294.473	622.946	0.985	0.820**
Richards-Prophet	2002	LW	V+A+F+E	16	1308	-428.973	889.946	0.961	0.864**
Richards-Prophet	2003	LW	V+A+F+E	17	1173	-282.258	598.515	1.000	0.780**
Richards-Prophet	2002	L	V+A+E	14	510	-175.829	380.394[c]	0.965	0.710*
Richards-Prophet	2003	L	$E+E^2+F$	5	357	-169.374	348.861[c]	0.962	0.707*
Richards-Prophet[d]	2002	S	V+A+E	14	964	-343.989	715.978	0.805	0.809**
	2002	S	V+A+F+E	16	964	-343.870	719.739	0.149	0.886**
Richards-Prophet	2003	S	$V+F+E+E^2$	13	779	-283.188	592.375	0.728	0.850**
Richards-Prophet	2002	F	S+A	6	1068	-406.245	824.489	0.998	0.855**
Richards-Prophet	2002	R	$V+A+E+E^2$	15	972	-380.463	790.926	0.976	0.905**
Withrow	2002	EW	$V+F+E+E^2$	13	994	-370.275	766.551	0.984	0.548
Withrow[d]	2002	LW	$V+A+E+E^2$	15	1248	-485.417	1000.835	0.753	0.693*
	2002	LW	$V+A+F+E+E^2$	17	1248	-484.533	1003.066	0.247	0.691*
Withrow[d]	2002	L	$E+E^2+F$	5	250	-108.547	227.259[c]	0.490	0.368
	2002	L	A+F	6	250	-107.652	227.552[c]	0.466	0.313

Table E.2: Continued

Pack	Year	Season[a]	Model[b]	K	n	LL	AIC	w_i	$\bar{r}_s$
Withrow[d]	2002	S	V+F	5	58	-29.742	70.252[c]	0.329	0.351
	2002	S	A+F	6	58	-28.868	70.912[c]	0.242	0.311
	2002	S	V	3	58	-32.408	71.038[c]	0.209	0.253
	2002	S	E+E^2+F	5	58	-30.610	71.989[c]	0.171	0.321

[a] EW=Early winter, LW=Late winter, L=Lambing, S=Summer, F=Fall, R=Rut; as defined in Table 2.1.

[b] V=Vegetation type, S=Slope, A=Aspect, F=Fragmentation, E=Elevation, L=Distance to linear feature

[c] corrected AIC (AIC_c).

[d] models were averaged to determine selection coefficients for habitat attributes.

Table E.3. Coefficients of selection (β_i) and standard errors (SE) of the covariates for the final global and pack models of wolf risk by season and year in the Besa-Prophet area of northern British Columbia, 2002-2003. Seasons are defined in Table 2.1. * indicates 95% confidence intervals (CI) of the β_i were different from zero.

Covariates	Global Models by Season					
	EW 2002	EW 2003	LW 2002	LW 2003	L 2002	L 2003
Elevation	10.120 ± 3.224*	7.746 ± 1.394*	11.851 ± 1.442*	11.924 ± 1.741*	7.234 ± 2.839*	6.812 ± 1.827*
Elevation^2	-4.448 ± 1.327*	-2.884 ± 0.523*	-4.819 ± 0.551*	-5.203 ± 0.701*	-3.090 ± 1.056*	-2.982 ± 0.740*
Low fragmentation	0.016 ± 0.102	-0.228 ± 0.089*	0.306 ± 0.054*	-0.091 ± 0.067	-0.374 ± 0.117*	-0.368 ± 0.105*
Medium fragmentation	-0.087 ± 0.087	0.018 ± 0.069	0.614 ± 0.044*	-0.068 ± 0.059	0.192 ± 0.092*	0.244 ± 0.082*
High fragmentation	0.071 ± 0.080	0.209 ± 0.068*	0.092 ± 0.045*	0.158 ± 0.058*	0.182 ± 0.096	0.124 ± 0.087
Slope						
North		0.159 ± 0.092	-0.472 ± 0.075*	-0.385 ± 0.093*	-0.130 ± 0.128	-0.373 ± 0.120*
East		-0.201 ± 0.092*	-0.185 ± 0.063*	-0.288 ± 0.084*	-0.386 ± 0.131*	-0.346 ± 0.122*
South		0.112 ± 0.088	0.402 ± 0.057*	0.374 ± 0.074*	0.219 ± 0.123	0.269 ± 0.109*
West		-0.322 ± 0.117*	-0.019 ± 0.074	-0.011 ± 0.100	-0.546 ± 0.181*	-0.270 ± 0.135*
No aspect (flat)		0.253 ± 0.147	0.273 ± 0.102*	0.310 ± 0.130*	0.843 ± 0.168*	0.720 ± 0.177*
Spruce	-0.412 ± 0.148*	-0.652 ± 0.127*	-0.374 ± 0.077*	-0.686 ± 0.108*	-0.604 ± 0.184*	-0.152 ± 0.150
Shrubs	0.612 ± 0.166*	0.983 ± 0.119*	0.187 ± 0.099	0.402 ± 0.119*	0.659 ± 0.188*	0.864 ± 0.166*
Subalpine	-0.173 ± 0.374	0.331 ± 0.141*	-0.133 ± 0.132	0.023 ± 0.168	-0.158 ± 0.262	0.130 ± 0.221
Carex spp.	0.044 ± 0.226	0.488 ± 0.181*	0.287 ± 0.132*	0.103 ± 0.169	0.395 ± 0.234	0.329 ± 0.218
Non-vegetated	-0.114 ± 0.307	-0.790 ± 0.202*	-0.005 ± 0.127	-0.054 ± 0.158	0.171 ± 0.272	-0.115 ± 0.273
Pine	-0.568 ± 0.264*	-0.571 ± 0.212*	-0.837 ± 0.159*	-0.476 ± 0.192*	-0.811 ± 0.304*	-0.235 ± 0.265
Riparian spruce	-0.125 ± 0.177	0.139 ± 0.145	0.057 ± 0.095	0.247 ± 0.122*	0.215 ± 0.186	0.497 ± 0.182*
Alpine	0.404 ± 0.360	0.220 ± 0.205	0.482 ± 0.155*	0.302 ± 0.242	0.211 ± 0.361	-1.063 ± 0.496*
Burned/disturbed	0.333 ± 0.150*	-0.147 ± 0.140	0.335 ± 0.076*	0.140 ± 0.108	-0.078 ± 0.193	-0.254 ± 0.195

Table E.3. Continued

Covariates	Global Models by Season					
	S 2002	S 2003	F 2002[a]	F 2003	R 2002	R 2003
Elevation		4.647 ± 1.459**			12.276 ± 1.399*	n/a
Elevation^2		-1.695 ± 0.566*			-4.739 ± 0.552*	
Low fragmentation		0.001 ± 0.080				
Medium fragmentation		-0.156 ± 0.073*				
High fragmentation		0.155 ± 0.073*				
Slope	-0.089 ± -0.005*		-0.083 ± 0.005*	-0.086 ± 0.008*		
North	0.371 ± 0.081*	0.024 ± 0.098	0.238 ± 0.070*	0.036 ± 0.124	0.041 ± 0.081	
East	0.021 ± 0.082	-0.229 ± 0.104*	0.018 ± 0.069	-0.107 ± 0.121	-0.157 ± 0.077*	
South	0.234 ± 0.085*	-0.158 ± 0.102	0.140 ± 0.074	0.084 ± 0.138	-0.079 ± 0.080	
West	-0.410 ± 0.117*	-0.018 ± 0.115	-0.173 ± 0.091	-0.129 ± 0.154	-0.095 ± 0.095	
No aspect (flat)	-0.216 ± 0.143	0.381 ± 0.164*	-0.223 ± 0.117	0.116 ± 0.175	0.290 ± 0.132*	
Spruce		-0.140 ± 0.135			-0.723 ± 0.110*	
Shrubs		1.087 ± 0.147**			0.709 ± 0.105*	
Subalpine		0.561 ± 0.137**			0.584 ± 0.126*	
Carex spp.		0.524 ± 0.202*			0.547 ± 0.149*	
Non-vegetated		-1.558 ± 0.310**			-0.652 ± 0.175*	
Pine		-0.237 ± 0.224			-0.505 ± 0.173*	
Riparian spruce		0.541 ± 0.173*			-0.092 ± 0.136	
Alpine		-0.414 ± 0.259			0.311 ± 0.217	
Burned/disturbed		-0.364 ± 0.209			-0.179 ± 0.121	

[a] averaged coefficients of selection (β_i) from competing models.

Table E.3. Continued

Covariates	Dopp-Keily Pack by Season					
	EW 2002	EW 2003	LW 2002	LW 2003[a]	L 2002[a]	L 2003
Elevation		15.876 ± 7.134*	38.316 ± 10.557*	17.980 ± 9.917	-4.013 ± 1.091*	-2.113 ± 1.154
Elevation^2		-6.062 ± 2.328*	-13.358 ± 3.675*	-7.622 ± 3.422*		
Low fragmentation			-0.599 ± 0.139*	-0.070 ± 0.129	-0.056 ± 0.063	-0.206 ± 0.189
Medium fragmentation			0.472 ± 0.104*	-0.178 ± 0.123	0.012 ± 0.046	0.462 ± 0.164*
High fragmentation			0.127 ± 0.112	0.246 ± 0.124*	0.045 ± 0.054	-0.255 ± 0.224
Slope						
North		0.413 ± 0.248	-0.503 ± 0.174*	-0.773 ± 0.238*	-0.275 ± 0.342	-1.011 ± 0.294*
East		-0.076 ± 0.246	-0.587 ± 0.168*	0.209 ± 0.188	-0.216 ± 0.382	-0.265 ± 0.273
South		0.601 ± 0.226*	0.129 ± 0.132	0.525 ± 0.154*	0.930 ± 0.307*	0.552 ± 0.209*
West		-0.370 ± 0.336	0.600 ± 0.170*	-0.315 ± 0.246	-1.442 ± 0.612*	-0.534 ± 0.336
No aspect (flat)		-0.569 ± 0.549	0.361 ± 0.248	0.354 ± 0.376	1.003 ± 0.367*	1.257 ± 0.502*
Spruce		-0.862 ± 0.291*	-0.055 ± 0.183	-0.552 ± 0.214*	-0.831 ± 0.389*	1.083 ± 0.292*
Shrubs		-0.212 ± 0.378	-0.665 ± 0.424	0.166 ± 0.301	-0.393 ± 0.635	-0.729 ± 0.579
Subalpine		1.084 ± 0.314*	-0.109 ± 0.236	0.149 ± 0.285	0.118 ± 0.495	0.606 ± 0.370
Carex spp.		0.820 ± 0.686	0.400 ± 0.443	-0.265 ± 0.541	-0.288 ± 0.461	-0.581 ± 0.996
Non-vegetated		-0.666 ± 0.427	0.084 ± 0.247	-0.577 ± 0.402	0.471 ± 0.507	-0.821 ± 0.717
Pine		-0.983 ± 0.581	-0.758 ± 0.374*	0.282 ± 0.335	-1.624 ± 0.678*	0.521 ± 0.545
Riparian spruce		-0.468 ± 0.451	0.726 ± 0.243*	-0.124 ± 0.307	1.009 ± 0.416*	0.322 ± 0.507
Alpine		1.504 ± 0.474*	-0.228 ± 0.410	0.836 ± 0.521	1.108 ± 0.594	-0.708 ± 0.811
Burned/disturbed		-0.217 ± 0.375	0.605 ± 0.211*	0.083 ± 0.224	0.429 ± 0.443	0.306 ± 0.489

[a] averaged coefficients of selection (β_i) from competing models.

Table E.3. Continued

Covariates	Dopp-Keily Pack by Season					
	S 2002	S 2003^a	F 2002	F 2003	R 2002	R 2003
Elevation		3.551 ± 2.740	13.795 ± 7.626	n/a	11.622 ± 8.353	n/a
Elevation^2		-1.327 ± 0.910	-4.593 ± 2.411		-5.566 ± 2.861	
Low fragmentation		-0.001 ± 0.029	0.160 ± 0.136		-0.383 ± 0.221	
Medium fragmentation		-0.006 ± 0.028	-0.072 ± 0.120		0.068 ± 0.175	
High fragmentation		0.007 ± 0.032	-0.087 ± 0.123		0.314 ± 0.158*	
Slope	-0.095 ± -0.010*					
North	0.613 ± 0.185*	-0.044 ± 0.044			-0.493 ± 0.252	
East	0.451 ± 0.193*	-0.016 ± 0.035			0.020 ± 0.225	
South	0.684 ± 0.182*	-0.001 ± 0.030			0.398 ± 0.208	
West	-0.950 ± 0.318*	0.041 ± 0.047			-0.616 ± 0.268*	
No aspect (flat)	-0.797 ± 0.364*	0.020 ± 0.098			0.692 ± 0.432	
Spruce		0.625 ± 0.193*	-0.809 ± 0.251*		-0.477 ± 0.251	
Shrubs		0.799 ± 0.340*	0.772 ± 0.349*		0.118 ± 0.294	
Subalpine		0.655 ± 0.180*	0.499 ± 0.227*		1.051 ± 0.321*	
Carex spp.		-0.289 ± 0.534	0.390 ± 0.562		-0.398 ± 0.649	
Non-vegetated		-2.575 ± 0.446*	-1.705 ± 0.377*		0.007 ± 0.392	
Pine		0.281 ± 0.413	0.808 ± 0.360*		-0.558 ± 0.395	
Riparian spruce		0.704 ± 0.315*	1.399 ± 0.359*		-0.460 ± 0.433	
Alpine		-0.230 ± 0.332	0.156 ± 0.340		1.012 ± 0.591	
Burned/disturbed		0.030 ± 0.357	-1.510 ± 0.477*		-0.295 ± 0.355	

[a] averaged coefficients of selection (β_i) from competing models.

Table E.3. Continued

Covariates	Lower Besa Pack by Season					
	EW 2002	EW 2003	LW 2002	LW 2003[a]	L 2002	L 2003[a]
Elevation	33.877 ± 8.528*	5.677 ± 4.513	15.181 ± 5.326*	-4.224 ± 0.392*	-27.960 ± 10.267*	-41.949 ± 7.320*
Elevation^2	-14.524 ± 3.528*	-2.031 ± 1.822	-7.566 ± 2.412*	-0.212 ± 0.140	9.267 ± 4.230	14.674 ± 3.044*
Low fragmentation				-0.422 ± 0.116*	-0.315 ± 0.444	-0.041 ± 0.160
Medium fragmentation				0.635 ± 0.099*	-0.537 ± 0.379	-0.006 ± 0.114
High fragmentation					0.852 ± 0.307*	0.046 ± 0.120
Slope				-0.048 ± 0.042		
North	-0.596 ± 0.271*	0.370 ± 0.241	-0.621 ± 0.224*	-0.054 ± 0.042		-0.391 ± 0.234
East	-0.428 ± 0.279	0.358 ± 0.228	-0.367 ± 0.271	0.028 ± 0.036		-0.077 ± 0.182
South	-0.251 ± 0.357	-0.172 ± 0.312	1.279 ± 0.161**	0.038 ± 0.039		-0.030 ± 0.236
West	0.318 ± 0.277	-1.088 ± 0.446*	-0.835 ± 0.281*	0.037 ± 0.050		0.293 ± 0.198
No aspect (flat)	0.958 ± 0.379*	0.532 ± 0.369	-0.115 ± 0.257	-0.013 ± 0.119		0.206 ± 0.232
Spruce	-1.103 ± 0.333*		-1.068 ± 0.357*	0.378 ± 0.206		-0.909 ± 0.357*
Shrubs	1.405 ± 0.414*		0.035 ± 0.283	0.283 ± 0.342		1.623 ± 0.566*
Subalpine	0.630 ± 1.082		1.178 ± 0.746	-0.049 ± 0.170		
Carex spp.	0.024 ± 0.522		-0.681 ± 0.337*	-0.323 ± 0.277		-0.478 ± 0.401
Non-vegetated	0.612 ± 0.547		0.701 ± 0.351*	-0.660 ± 0.498		-1.359 ± 1.156
Pine	-0.470 ± 0.592		-1.554 ± 0.578*	0.191 ± 0.152		1.359 ± 0.591*
Riparian spruce	-0.195 ± 0.364		0.057 ± 0.261	0.193 ± 0.156		0.523 ± 0.385
Alpine			1.335 ± 0.751	-4.224 ± 0.392*		
Burned/disturbed	-0.902 ± 0.416*		-0.066 ± 0.235	-0.212 ± 0.140		-0.759 ± 0.484

[a] averaged coefficients of selection (β_i) from competing models.

Table E.3. Continued

Covariates	Lower Besa Pack by Season					
	S 2002	S 2003[a]	F 2002	F 2003	R 2002	R 2003
Elevation		-8.854 ± 1.358**				n/a
Elevation^2						
Low fragmentation		-0.135 ± 0.304				
Medium fragmentation		-0.335 ± 0.263				
High fragmentation		0.470 ± 0.214*				
Slope	-0.158 ± 0.021*		-0.088 ± 0.011*	-0.126 ± 0.013*	-0.021 ± 0.009*	
North	-0.239 ± 0.222		0.181 ± 0.167	0.159 ± 0.174	0.026 ± 0.184	
East	0.305 ± 0.195		-0.027 ± 0.158	-0.362 ± 0.186	0.077 ± 0.166	
South	0.600 ± 0.232*		0.204 ± 0.192	-0.013 ± 0.195	-0.119 ± 0.229	
West	-0.561 ± 0.304		-0.300 ± 0.228	-0.189 ± 0.225	-0.267 ± 0.267	
No aspect (flat)			-0.058 ± 0.258	0.405 ± 0.267	0.282 ± 0.269	
Spruce		-0.030 ± 0.347				
Shrubs		1.153 ± 0.366*				
Subalpine						
Carex spp.		-0.587 ± 0.408				
Non-vegetated						
Pine		-0.303 ± 1.005				
Riparian spruce		0.455 ± 0.353				
Alpine						
Burned/disturbed		-0.688 ± 0.551				

[a] averaged coefficients of selection (β_i) from competing models.

Table E.3. Continued

Covariates	Neves Pack by Season					
	EW 2002	EW 2003	LW 2002	LW 2003[a]	L 2002	L 2003
Elevation	n/a	36.120 ± 11.709*	-22.085 ± 5.642*	-3.130 ± 0.664*	-183.927 ± 32.562	-31.149 ± 20.319
Elevation^2		-11.786 ± 3.880*	6.151 ± 1.921*		57.321 ± 10.660*	7.201 ± 6.560
Low fragmentation		-0.414 ± 0.177*	-0.410 ± 0.147*		0.242 ± 0.453	-0.105 ± 0.347
Medium fragmentation		0.277 ± 0.135*	0.188 ± 0.123		-0.133 ± 0.428	-0.389 ± 0.298
High fragmentation		0.137 ± 0.144	0.222 ± 0.118		-0.110 ± 0.446	0.493 ± 0.307
Slope						
North			-0.220 ± 0.226	0.201 ± 0.198		
East			0.393 ± 0.200*	-0.635 ± 0.233*		
South			0.315 ± 0.198	0.382 ± 0.174*		
West			0.221 ± 0.218	0.074 ± 0.215		
No aspect (flat)			-0.709 ± 0.568	-0.023 ± 0.412		
Spruce		-1.345 ± 0.306*	-0.221 ± 0.207	-0.517 ± 0.224*		-1.390 ± 0.599*
Shrubs		1.525 ± 0.224*	0.293 ± 0.245	0.332 ± 0.222		1.445 ± 0.481*
Subalpine		-0.421 ± 0.276	0.243 ± 0.295	0.028 ± 0.319		0.127 ± 1.111
Carex spp.		1.202 ± 0.416*	-1.167 ± 0.790	0.316 ± 0.574		-1.105 ± 0.691
Non-vegetated		-0.312 ± 0.400	0.087 ± 0.387	0.230 ± 0.332		0.264 ± 1.092
Pine		-0.494 ± 0.347	-0.528 ± 0.385	-0.546 ± 0.388		-2.356 ± 0.967*
Riparian spruce		0.134 ± 0.444	-0.599 ± 0.370	-1.008 ± 0.442*		-0.791 ± 0.702
Alpine		0.164 ± 0.408	0.865 ± 0.361*	0.524 ± 0.377		1.792 ± 1.317
Burned/disturbed		-0.453 ± 0.399	1.026 ± 0.237*	0.641 ± 0.245*		2.014 ± 0.817

[a] averaged coefficients of selection (β_i) from competing models.

Table E.3. Continued

Covariates	Neves Pack by Season					
	S 2002	S 2003	F 2002	F 2003	R 2002	R 2003
Elevation	77.485 ± 39.200*	17.879 ± 10.485		36.120 ± 11.709*	-9.435 ± 7.268	n/a
Elevation^2	-25.108 ± 13.496	-5.391 ± 3.381		-11.786 ± 3.880*	2.259 ± 2.339	
Low fragmentation	0.370 ± 0.183*			-0.414 ± 0.177*		
Medium fragmentation	0.196 ± 0.162			0.277 ± 0.135*		
High fragmentation	-0.566 ± 0.189*			0.137 ± 0.144		
Slope			-0.106 ± 0.013*			
North	1.046 ± 0.197*	0.647 ± 0.209*	0.390 ± 0.153*		0.288 ± 0.208	
East	-0.945 ± 0.315*	-0.558 ± 0.307	-0.243 ± 0.168		-0.449 ± 0.198*	
South	-0.864 ± 0.254*	-0.441 ± 0.25	-0.236 ± 0.179		-0.318 ± 0.187	
West	-0.250 ± 0.280	0.197 ± 0.277	-0.029 ± 0.189		-0.120 ± 0.240	
No aspect (flat)	1.014 ± 0.374*	0.155 ± 0.385	0.118 ± 0.274		0.600 ± 0.414	
Spruce	-0.867 ± 0.328*	-0.728 ± 0.312*		-1.345 ± 0.306*	-0.871 ± 0.295*	
Shrubs	1.225 ± 0.332**	1.683 ± 0.297**		1.525 ± 0.224*	1.455 ± 0.231*	
Subalpine	-0.988 ± 0.585	-0.234 ± 0.370		-0.421 ± 0.276	0.785 ± 0.285*	
Carex spp.	-0.604 ± 1.059	1.872 ± 0.496**		1.202 ± 0.416*	0.425 ± 0.488	
Non-vegetated	-0.225 ± 0.697	-1.457 ± 0.672*		-0.312 ± 0.400	-1.706 ± 0.648*	
Pine	0.755 ± 0.375*	0.306 ± 0.371		-0.494 ± 0.347	-1.283 ± 0.496*	
Riparian spruce	1.302 ± 0.474*	-0.192 ± 0.607		0.134 ± 0.444	-0.667 ± 0.472	
Alpine	-0.398 ± 1.072	-1.250 ± 0.649		0.164 ± 0.408	0.358 ± 0.409	
Burned/disturbed	-0.201 ± 0.640			-0.453 ± 0.399	1.504 ± 0.305*	

Table E.3. Continued

Covariates	Pocketknife Pack by Season					
	EW 2002	EW 2003	LW 2002	LW 2003^a	L 2002^a	L 2003^a
Elevation	17.292 ± 6.136*		17.576 ± 6.293*	25.774 ± 10.390*	45.017 ± 21.275*	13.712 ± 8.067
Elevation^2	-7.096 ± 2.575*		-6.562 ± 2.55*	-11.246 ± 4.940*	-20.024 ± 9.509*	-4.854 ± 3.712
Linear distance		-1.143 ± 0.330*			-0.090 ± 0.053	
Linear distance^2		0.146 ± 0.042*			0.048 ± 0.016*	
Low fragmentation			-0.341 ± 0.144*	-0.295 ± 0.212	-0.871 ± 0.338*	-0.086 ± 0.092
Medium fragmentation			0.206 ± 0.113	0.250 ± 0.159	0.297 ± 0.241	0.076 ± 0.068
High fragmentation			0.135 ± 0.120	0.045 ± 0.171	0.616 ± 0.218*	0.010 ± 0.063
Slope						
North	0.336 ± 0.180		-0.415 ± 0.166*		0.128 ± 0.265	0.307 ± 0.250
East	0.200 ± 0.167		-0.381 ± 0.146*		-0.045 ± 0.239	-0.586 ± 0.304
South	0.196 ± 0.193		0.031 ± 0.169		-0.516 ± 0.370	-0.556 ± 0.329
West	-0.439 ± 0.256		-0.206 ± 0.207		-1.059 ± 0.429*	-0.143 ± 0.349
No aspect (flat)	-0.293 ± 0.321		0.970 ± 0.184*		1.536 ± 0.323*	0.978 ± 0.300*
Spruce	-0.692 ± 0.288*	-0.939 ± 0.319*	-0.417 ± 0.263	-1.367 ± 0.436*	-0.261 ± 0.395	0.775 ± 0.469
Shrubs	0.742 ± 0.296*	0.831 ± 0.275*	0.990 ± 0.269*	1.247 ± 0.403*	1.527 ± 0.487*	0.873 ± 0.401*
Subalpine			-0.630 ± 0.978			
Carex spp.	0.137 ± 0.340	0.620 ± 0.235*	1.178 ± 0.295*	0.280 ± 0.428	0.033 ± 0.450	0.988 ± 0.383*
Non-vegetated	-0.679 ± 0.947	-0.883 ± 0.647	-0.564 ± 0.540	1.285 ± 0.940	1.086 ± 0.908	-0.204 ± 0.973
Pine	-0.506 ± 0.371	0.141 ± 0.413	-1.312 ± 0.438*	-0.898 ± 0.589	-1.619 ± 0.807*	0.146 ± 0.554
Riparian spruce	-0.170 ± 0.290	0.065 ± 0.227	0.297 ± 0.275	0.203 ± 0.390	-0.383 ± 0.345	0.625 ± 0.392
Alpine	0.824 ± 0.663	0.708 ± 0.458	0.357 ± 0.582	1.762 ± 1.534		
Burned/disturbed	0.343 ± 0.305	-0.543 ± 0.353	0.100 ± 0.284	-2.513 ± 0.927*	-0.529 ± 0.671	-1.654 ± 0.899

[a] averaged coefficients of selection (β_i) from competing models.

Table E.3. Continued

Covariates	Pocketknife Pack by Season					
	S 2002	S 2003	F 2002	F 2003	R 2002	R 2003
Elevation	-3.778 ± 8.080		8.698 ± 4.466	30.994 ± 7.578*	28.011 ± 4.449*	n/a
Elevation^2	0.802 ± 3.363		-2.664 ± 1.783	-11.441 ± 3.101*	-11.567 ± 2.008*	
Linear distance		-0.199 ± 0.042*				
Linear distance^2						
Low fragmentation	-1.011 ± 0.227*	-0.669 ± 0.270*	-0.066 ± 0.157	-0.152 ± 0.273	0.027 ± 0.147	
Medium fragmentation	0.228 ± 0.157	0.191 ± 0.200	-0.160 ± 0.117	0.011 ± 0.213	-0.261 ± 0.130*	
High fragmentation	0.782 ± 0.158*	0.478 ± 0.196*	0.226 ± 0.113*	0.141 ± 0.204	0.234 ± 0.116*	
Slope						
North						
East						
South						
West						
No aspect (flat)						
Spruce	-0.580 ± 0.327		-0.391 ± 0.243	-1.577 ± 0.491*	-1.425 ± 0.308*	
Shrubs	0.834 ± 0.368*		1.169 ± 0.272*	0.193 ± 0.442	0.855 ± 0.261*	
Subalpine	0.078 ± 1.162		-0.267 ± 0.525	1.487 ± 0.982	0.507 ± 0.801	
Carex spp.	0.679 ± 0.361		1.275 ± 0.250*	0.638 ± 0.474	0.899 ± 0.305*	
Non-vegetated	-0.979 ± 0.805		-2.716 ± 0.913*	-1.161 ± 0.957	-0.920 ± 0.653	
Pine	-0.241 ± 0.407		0.285 ± 0.287	-0.683 ± 0.448	-0.852 ± 0.341*	
Riparian spruce	0.311 ± 0.353		0.537 ± 0.254*	0.723 ± 0.453	-0.250 ± 0.299	
Alpine	0.204 ± 0.855		0.892 ± 0.362*	1.976 ± 0.825*	1.963 ± 0.697*	
Burned/disturbed	-0.307 ± 0.424		-0.783 ± 0.330*	-1.597 ± 0.540*	-0.777 ± 0.307*	

Table E.3. Continued

Covariates	Richards-Prophet Pack by Season					
	EW 2002	EW 2003	LW 2002	LW 2003	L 2002	L 2003
Elevation	n/a	15.898 ± 5.066*	-5.893 ± 0.672*	-1.838 ± 0.837*	-3.800 ± 0.989*	-5.182 ± 5.938
Elevation^2		-5.601 ± 1.785*				0.719 ± 1.987
Low fragmentation		-0.471 ± 0.222*	-0.100 ± 0.139	0.266 ± 0.164		-0.967 ± 0.307*
Medium fragmentation		-0.016 ± 0.166	0.272 ± 0.120*	-0.279 ± 0.158		0.415 ± 0.217
High fragmentation		0.487 ± 0.157*	-0.172 ± 0.128			0.552 ± 0.203*
Slope				0.013 ± 0.162		
North		0.098 ± 0.222	-0.226 ± 0.185	-0.161 ± 0.245	-0.313 ± 0.291	
East		-0.562 ± 0.251*	0.027 ± 0.179	-0.172 ± 0.228	-0.565 ± 0.316	
South		0.204 ± 0.201	0.220 ± 0.171	-0.024 ± 0.231	0.257 ± 0.266	
West		-0.464 ± 0.279	0.497 ± 0.204*	-0.036 ± 0.259	-0.577 ± 0.383	
No aspect (flat)		0.724 ± 0.462	-0.519 ± 0.328	0.394 ± 0.512	1.197 ± 0.615	
Spruce		-0.021 ± 0.282	-0.407 ± 0.184*	-0.640 ± 0.388	-0.720 ± 0.337*	
Shrubs		0.996 ± 0.312*	0.821 ± 0.254*	0.006 ± 0.400	1.235 ± 0.434*	
Subalpine		-0.090 ± 0.288	-0.644 ± 0.442	0.387 ± 0.260	-0.088 ± 0.420	
Carex spp.		-0.162 ± 0.626	0.431 ± 0.348	2.034 ± 0.490*	-0.254 ± 0.681	
Non-vegetated		-0.671 ± 0.322*	-0.368 ± 0.322	-1.432 ± 0.461*	-0.163 ± 0.463	
Pine		-0.376 ± 0.603	-0.030 ± 0.336	-0.632 ± 0.988	-0.861 ± 0.741	
Riparian spruce		0.789 ± 0.343*	-0.227 ± 0.263	0.168 ± 0.539	0.131 ± 0.429	
Alpine		-0.805 ± 0.501	0.490 ± 0.497	-0.159 ± 0.437	0.736 ± 0.590	
Burned/disturbed		0.340 ± 0.276	-0.067 ± 0.248	0.266 ± 0.386	-0.016 ± 0.478	

Table E.3. Continued

Covariates	Richards-Prophet Pack by Season					
	S 2002[a]	S 2003	F 2002	F 2003	R 2002	R 2003
Elevation	-2.025 ± 0.606*	4.444 ± 7.664		n/a	17.462 ± 6.480*	n/a
Elevation^2		-1.887 ± 2.342			-6.040 ± 2.014*	
Low fragmentation	0.001 ± 0.020	0.278 ± 0.164				
Medium fragmentation	0.007 ± 0.018	-0.298 ± 0.156				
High fragmentation	-0.008 ± 0.022	0.021 ± 0.161				
Slope			-0.095 ± 0.010*			
North	0.568 ± 0.180*		0.221 ± 0.169		0.375 ± 0.251	
East	0.107 ± 0.178		0.200 ± 0.170		-0.013 ± 0.259	
South	0.021 ± 0.170		0.135 ± 0.171		0.176 ± 0.249	
West	-0.298 ± 0.230		-0.282 ± 0.214		0.625 ± 0.260*	
No aspect (flat)	-0.398 ± 0.361		-0.273 ± 0.305		-1.162 ± 0.763	
Spruce	-1.061 ± 0.232*	-0.688 ± 0.369			-0.641 ± 0.316*	
Shrubs	1.034 ± 0.285*	0.037 ± 0.392			0.100 ± 0.331	
Subalpine	0.810 ± 0.211*	0.232 ± 0.284			0.615 ± 0.250*	
Carex spp.	0.612 ± 0.494	2.151 ± 0.454*			0.571 ± 0.782	
Non-vegetated	-1.404 ± 0.368*	-1.408 ± 0.441*			-0.664 ± 0.302*	
Pine	-0.957 ± 0.540	-0.716 ± 0.964			-0.668 ± 0.619	
Riparian spruce	0.984 ± 0.312*	0.469 ± 0.539			0.557 ± 0.395	
Alpine	-0.007 ± 0.342	-0.270 ± 0.425			0.016 ± 0.394	
Burned/disturbed	-0.011 ± 0.288	0.194 ± 0.362			0.114 ± 0.341	

[a] averaged coefficients of selection (β_i) from competing models.

Table E.3. Continued

Covariates	Withrow Pack by Season					
	EW 2002	LW 2002[a]	L 2002[a]	S 2002[a]	F 2002	R 2002
Elevation	-13.947 ± 5.723*	15.982 ± 6.307*	10.352 ± 6.240	3.684 ± 3.902	n/a	n/a
Elevation^2	4.395 ± 2.119*	-5.182 ± 2.34*	-3.540 ± 2.221	-1.401 ± 1.496		
Low fragmentation	0.173 ± 0.153		-0.327 ± 0.256	0.096 ± 0.231		
Medium fragmentation	0.029 ± 0.136		0.707 ± 0.186*	0.674 ± 0.249*		
High fragmentation	-0.202 ± 0.131		-0.380 ± 0.214	-0.770 ± 0.270*		
Slope						
North		-0.451 ± 0.252	-0.314 ± 0.252	0.387 ± 0.239		
East		-0.328 ± 0.200	-0.156 ± 0.163	-0.133 ± 0.125		
South		0.597 ± 0.167*	0.227 ± 0.151	0.068 ± 0.110		
West		-0.034 ± 0.204	0.243 ± 0.184	-0.322 ± 0.205		
No aspect (flat)		0.216 ± 0.422				
Spruce	0.278 ± 0.228	-0.470 ± 0.218*		0.050 ± 0.152		
Shrubs	0.326 ± 0.286	-0.600 ± 0.335		0.354 ± 0.260		
Subalpine	0.032 ± 0.426	0.164 ± 0.333				
Carex spp.	-0.194 ± 0.561	-0.040 ± 0.479				
Non-vegetated	-0.331 ± 0.478	0.439 ± 0.300				
Pine	-1.047 ± 0.660	-0.365 ± 0.497				
Riparian spruce	-0.194 ± 0.387	-0.378 ± 0.361				
Alpine	0.113 ± 0.467	0.606 ± 0.34				
Burned/disturbed	1.017 ± 0.226*	0.643 ± 0.188*		-0.405 ± 0.206*		

[a] averaged coefficients of selection (β_i) from competing models.

Appendix F: List of plant species found at sites used by Stone's sheep ewes in the Besa-Prophet area of northern British Columbia (2002, 2003).

Table F.1. List of plant species and their frequency (%) of occurrence at 75 sites used by Stone's sheep ewes in the Besa-Prophet area of northern British Columbia (2002, 2003).

Scientific Name	Common Name	Frequency (%)
Abies lasiocarpa	Subalpine fir	1.3
Achillea millefolium	Yarrow	42.7
Aconitum delphiniifolium	Mountain monkshood	72.0
Agropyron spp.	Wheatgrass spp.	10.7
Anemone narcissiflora	Narcissus anemone	22.7
Anemone richardsonii	Yellow anemone	2.7
Antennaria monocephala	One-headed pussytoe	4.0
Antennaria neglecta	Field pussytoe	12.0
Antennaria racemosa	Racemose pussytoe	1.3
Aquilegia brevistyla	Blue columbine	1.3
Arctostaphylos uva-ursi	Kinnikinnick	29.3
Arnica angustifolia	Alpine arnica	8.0
Artemisia norvegica	Mountain sagewort	2.7
Artemisia spp.	Artemisia spp.	18.7
Astragalus alpinus	Alpine milk-vetch	10.7
Betula glandulosa	Scrub birch	25.3
Bistorta vivipara	Alpine bistort	54.7
Campanula lasiocarpa	Mountain harebell	5.3
Carex spp.	Sedge spp.	29.3
Cassiope tetragona	Four-angled mountain-heather	8.0
Cerastium arvense	Field chickweed	52.0
Clintonia uniflora	Queen's cup lily	2.7
Cystopteris fragilis	Fragile fern	29.3
Danthonia spp.	Oatgrass spp.	2.7
Delphinium glaucum	Tall larkspur	18.7
Deschampsia spp.	Hairgrass spp.	2.7
Draba alpina	Alpine draba	10.7
Dryas integrifolia	Smooth-leaved mountain-aven	57.3
Elymus innovatus	Fuzzy-spiked wildrye	61.3
Empetrum nigrum	Crowberry	2.7
Epilobium angustifolium	Fireweed	41.3
Epilobium latifolium	Broad-leaved willowherb	5.3
Equisetum scirpoides	Dwarf scouring-rush	10.7
Erigeron acris	Bitter fleabane	1.3
Erigeron humilis	Arctic daisy	20.0
Erigeron spp.	Daisy spp.	4.0
Festuca spp.	Fescue spp.	60.0
Fragaria virginiana	Wild strawberry	24.0
Gentiana glauca	Gentiana glauca	9.3
Hedysarum alpinum	Alpine sweet-vetch	20.0
Hedysarum boreale	Northern sweet-vetch	21.3

Table F.1. Continued

Scientific Name	Common Name	Frequency (%)
Juniperus communis	Common juniper	8.0
Leptarrhena pyrolifolia	Leatherleaf saxifrage	1.3
Lupinus arcticus	Arctic lupine	46.7
Mertensia paniculata	Mertensia paniculata	48.0
Minuartia biflora	Mountain stitchwort	2.7
Minuartia spp.	Minuartia spp.	1.3
Myosotis alpestris	Mountain forget-me-not	49.3
Orthilia secunda	One-sided wintergreen	1.3
Oxytropis campestrus	Field locoweed	10.7
Oxytropis nigrescens	Blackish locoweed	40.0
Parnassia palustris	Northern grass-of-parnassus	1.3
Pedicularis groenlandica	Elephant’s head	14.7
Pedicularis sudetica	Sudeten lousewort	26.7
Picea engelmanni	Englemann spruce	6.7
Poa spp.	Bluegrass	38.7
Polemonium caeruleum	Tall Jacob’s ladder	26.7
Polemonium pulcherrimum	Showy Jacob’s ladder	21.3
Potentilla diversifolia	Diverse-leafed cinquefoil	8.0
Potentilla fruiticosa	Shrubby cinquefoil	56.0
Potentilla uniflora	One-flowered cinquefoil	60.0
Pyrola asarifolia	Pink wintergreen	25.3
Ranunculus escholtzii	Subalpine buttercup	12.0
Ranunculus spp.	Buttercup spp.	14.7
Rosa acicularis	Prickly rose	18.7
Rubus arcticus	Dwarf nagoonberry	4.0
Rumex acetosa	Common sorrel	5.3
Salix alexensis	Felt-leaved willow	1.3
Salix arctica	Arctic willow	14.7
Salix glauca	Grey-leaved willow	28.0
Salix polaris	Polar willow	21.3
Salix reticulata	Net-veined willow	28.0
Salix spp.	Willow spp.	6.7
Saxifraga flagellaris	Stoloniferous saxifrage	6.7
Saxifraga lyalii	Red-stemmed saxifrage	1.3
Saxifraga mertensiana	Wood saxifrage	8.0
Saxifraga nivalis	Alpine saxifrage	2.7
Saxifraga oppositifolia	Purple mountain saxifrage	5.3
Saxifraga spp.	Saxifrage spp.	1.3
Saxifraga tricuspidata	Three-toothed saxifrage	84.0
Senecio lugens	Black-tipped groundsel	1.3
Sheperdia canadensis	Soopolallie	1.3
Silene acaulis	Moss campion	40.0

Table F.1. Continued

Scientific Name	Common Name	Frequency (%)
Solidago multiradiata	Northern goldenrod	73.3
Stellaria longipes	Long-stalked starwort	22.7
Taraxacum ceratophorum	Horned dandelion	5.3
Trisetum spicatum	Spike trisetum	8.0
Vaccinium uliginosum	Bog blueberry	2.7
Vaccinium vitis-idaea	Lingonberry	10.7
Viola spp.	Violet spp.	1.3
Zygadenus elegans	Mountain death-camas	30.7

Appendix G: Proportion of active time spent nursing by Stone’s sheep ewes in the Besa-Prophet area of northern British Columbia (2002, 2003).

Fig. G.1. (A) Proportion of active time ($\bar{x}$ ± SE) spent nursing and (B) duration of nursing bouts by Stone's sheep ewes in the Besa-Prophet area of northern British Columbia, 2002 and 2003 (June 1 – July 31). (A) Values above error bars indicate the number of ewes for which data were averaged by week. (B) Duration of nursing bouts were averaged per lamb; values above error bars indicate the number of lambs for which mean data were then averaged by week.