

Habitat selection by female Stone's sheep in relation to vegetation, topography, and risk of predation¹

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Abstract: Stone's sheep (*Ovis dalli stonei*) are susceptible to anthropogenic disturbances, but few data have been available to help minimize impacts. We used the movements of individuals to define use and availability, and resource-selection functions (RSF) and 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 patterns, with highest rates occurring in summer and fall. Models that contained vegetation, topography, and risk of predation best explained resource selection. 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. Selection strategies were variable among groups of Stone's sheep and between years within groups even though consistencies in selection for steep slopes, ridge-like topography, south 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 behavioural plasticity in selection of attributes within those ranges.

Keywords: information-theoretic approach, movement, *Ovis dalli stonei*, risk of predation, selection, Stone's sheep.

Résumé : Les mouflons de Stone (*Ovis dalli stonei*) sont susceptibles aux perturbations anthropiques mais peu de données existent pour aider à minimiser les impacts. Nous avons utilisé les mouvements des individus pour définir l'utilisation et la disponibilité ainsi que des fonctions de sélection des ressources (FSR) et une approche basée sur la théorie de l'information pour étudier la sélection des habitats saisonniers et la variabilité interannuelle dans la sélection d'attributs par des groupes de mouflons de Stone. Les taux de déplacement des mouflons suivaient des patrons similaires d'une année à l'autre avec les plus hauts taux se produisant en été et en automne. Les modèles qui incorporent la végétation, la topographie et le risque de prédation étaient ceux qui expliquaient le mieux la sélection des ressources. Les éléments topographiques expliquaient mieux la sélection d'habitat que les attributs de la végétation ou le risque de prédation par le grizzly (*Ursus arctos*) ou le loup (*Canis lupus*). Les stratégies de sélection variaient entre les groupes de mouflons et entre les années à l'intérieur des groupes mais des éléments demeuraient constants tels que la sélection pour des pentes fortes, une topographie en crêtes, les orientations sud et les élévations élevées. Cette étude est la première analyse complète de la sélection de l'habitat chez les mouflons de Stone. Elle révèle que ceux-ci sont très fidèles à leurs habitats saisonniers mais qu'ils démontrent aussi une plasticité comportementale quant au choix des attributs à l'intérieur de ces mêmes habitats.

Mots-clés : approche basée sur la théorie de l'information, mouflon de Stone, mouvement, *Ovis dalli stonei*, risque de prédation, sélection.

Nomenclature: Hultén, 1974; Nowak & Paradiso, 1983.

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 & Hartwig, 2004). Some habitats used by sheep (e.g., in provincial parks) are relatively secure, 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 & Demarchi, 1999), with unknown con-

sequences to sheep populations. Wild sheep are extremely susceptible to disturbance (MacArthur, Geist & Johnston, 1982; Miller, Hobbs & Sousa, 1991; Papouchis, Singer & Sloan, 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, Bateman & Berger, 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 & 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 lamb-

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ing, indicating that it may be especially important to Stone's sheep when the energetic constraints of gestation and lactation are high (Gittleman & 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 & 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 in order 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 type 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 & Bunnell, 1985b), 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 (Elliott, 1978; Seip & Bunnell, 1985a) and wolf control (Bergerud & Elliott, 1998) are the most widely employed management actions used to enhance Stone's sheep populations in British Columbia. Seip and Bunnell (1985b) 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 (Elliott, 1978; Seip & Bunnell, 1985a) and reduced lungworm counts (Seip & Bunnell, 1985a). Bergerud and Elliott (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) in 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 & Anderson, 2002; Johnson & Omland, 2004).

Our third objective was to quantify variation in habitat selection between years as a measure of behavioural 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; 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 & Schemnitz, 1985), and ability of a population to adapt to disturbances and changing habitats.

Methods

STUDY AREA

The study area was located within the Besa–Prophet (B–P) watersheds in the southeast portion of the 6.4-million-ha

Muskwa–Kechika Management Area (MKMA) in northern British Columbia. The study area encompassed ~140 000 ha between 57° 20' and 57° 40' N and 123° 10' and 123° 45' W.

The B–P study area includes 3 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 & Pojar, 1991). Valleys at ~800–1 300 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 (*Shepherdia 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 (~1 300–1 600 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 (~1 600–2 200 m) and is characterized in the study area by rocks with sparse vegetation, rounded peaks, and plateaus with plant communities consisting of fine grasslands (fescues and grasses), herbs, bryophytes, and lichens (Meidinger & 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 has little access and is relatively free of anthropogenic influences. 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 satellite (GPS) collars (Simplex™ Televilt, Lindesberg, Sweden) on 36 adult female Stone's sheep and programmed the collars to record locations 4 times daily for 2 y. During the same time period, 22 individual wolves from 5 packs and 15 female grizzly bears were captured by aerial darting and also fitted with Simplex™ GPS collars programmed to acquire locations 4 times daily. Locations from all animals were obtained by remote downloads 3 times per year and following collar retrieval at the end of the 2-y sampling period.

DATA ANALYSIS

We determined selection of habitats by Stone's sheep at Johnson's (1980) third-order selection (within the seasonal range) using logistic regression in resource selection functions (RSF) (Boyce & McDonald, 1999; Manly *et al.*, 2002). The seasonal-range scale was chosen because (1) it is the scale typically used in decision-making by management agencies, (2) attributes of selection can easily be incorporated in habitat maps, and (3) the range of variation

in attributes across the B–P was encompassed at this scale. Seasonal and annual selection models were developed for 5 groups of sheep that each contained radio-collared individuals in the B–P: Neves ($n = 12$), Tenmile ($n = 3$), Firstfork ($n = 4$), Townsley ($n = 9$), and Richards ($n = 5$). Individual animals were grouped together based on the major lick used within their yearly distribution. No radio-collared individual traveled outside its group's yearly distribution to use another lick. We assumed that these groups belonged to the same population of Stone's sheep, but we have no information on the degree of mixing among particular groups, especially by rams.

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 describe temporal trends in movement. Standard errors of mean rates of movement were calculated from 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 6 seasons for which RSF were developed. These were early winter (1 January–28 February), late winter (1 March–14 May), lambing (15 May–14 June), summer (15 June–14 August), fall (15 August–31 October), and rut (1 November–31 December).

For selection models, we determined use from an individual's GPS locations. We defined availability for each individual seasonally in 2002 and 2003 using the 95th percentile of the distances moved 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, but it frequently (based on 95% of observations) moved less. 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 attempts to accommodate changes in the availability of seasonal habitats. Availability buffers and random points were developed using Arcview 3.2TM (Environmental Systems Research Institute, Redlands, California, USA) and a random point generator extension (Jenness Enterprises, Flagstaff, Arizona, USA).

We used the information-theoretic approach to evaluate several models and hypotheses (Burnham & Anderson, 2002; Johnson & Omland, 2004) that defined habitat selection for the 5 groups of Stone's sheep by season and year (2002, 2003). We constructed global models across years and groups of sheep by pooling GPS locations. We used logistic regression (Hosmer & Lemeshow, 1989) to determine coefficients of selection (β_i) and to define differences between use and available points (Boyce *et al.*, 2002; Manly *et al.*, 2002). Deviation contrasts were used to code categorical variables (Menard, 2002); this allowed us to specify reference categories for the creation of dummy variables. To account for spatial and temporal autocorrelation between observations, we used the Huber–White sandwich estimator to obtain robust and inflated estimates of variance for each β_i (Boyce *et al.*, 2002). We used tolerance scores < 0.2

to identify correlated habitat variables (Menard, 2002). 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 & Anderson, 2002) was removed from the seasonal model set. Vegetation types and aspects that did not occur in use or available data were excluded from models (Menard, 2002).

We used AIC and corrected AIC (AIC_c) for small sample sizes to rank the suite of logistic regression models (Burnham & Anderson, 2002). The lowest AIC or AIC_c value and the highest AIC weight (w_i) in a model set indicated the best model. Competition for best model occurred when the top model had $w_i < 0.95$. We defined competing models as the top models for which the summed $w_i \geq 0.95$ and averaged these models (Burnham & Anderson, 2002). We evaluated the predictive ability of best models using the k -fold cross validation and Spearman's rank correlation (r_s) (Boyce *et al.*, 2002; Nielsen *et al.*, 2002), and determined P -values for r_s as per Siegel (1956).

We calculated Δ AIC as the difference between the best fitted model (lowest AIC or AIC_c) and each of the other models and then used the average change in AIC values (Δ AIC) to illustrate the relative rankings of models across years (Burnham & Anderson, 2002). We used 95% confidence intervals (CI) to determine whether selection coefficients (β_i) for the variables were different from zero. We inferred selection by Stone's sheep when the CI around β_i were positive and avoidance 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. 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, we inferred no consistency in annual selection for that season. StataTM 8.2 (Stata Corporation, College Station, Texas, USA), 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

We used a suite of geographical information system (GIS) layers to extract attributes for defining habitat selection by Stone's sheep: slope, aspect, curvature, elevation, vegetation type, vegetation quality, and risk of predation. We grouped 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) to test which general habitat factor explained most of the variation in Stone's sheep data. We evaluated relative rankings of these habitat factors as well as different combinations of the 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 ($^\circ$), aspect, elevation, and

curvature attributes. Aspect was categorized as north (316°–45°), east (46°–135°), south (136°–225°), west (226°–315°), or no aspect (NASP). Pixels with slopes of $\leq 1^\circ$ were assigned to the NASP category. Elevation was the only variable where exploratory analysis was conducted prior to model development. Elevation was included as a squared term (*i.e.*, elevation + elevation²) when it was detected to be nonlinear. 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 (RSF₀₋₁) to illustrate seasonal differences in selection of elevation. Curvature, which provided an indication of the overall concavity or convexity of a pixel in relation to its 3- × 3-pixel neighbourhood, was derived in ARCGrid (Environmental Systems Research Institute, Redlands, California, USA). Positive values were indicative of convex sites (ridges, mountain tops), whereas negative values indicated concave sites (gullies, valley bottoms).

VEGETATION TYPE AND QUALITY

We used a maximum-likelihood classifier to identify 10 vegetation types from Landsat 5 Thematic Mapper (TM) imagery using PCI Geomatics software (Richmond Hill, Ontario, Canada) (Table I). We assessed changes in the normalized difference vegetation index (NDVI) for the lambing and summer seasons using 3 monthly images (4 June, 22 July, and 15 August 2001) from Landsat 5 Thematic Mapper (TM) and Landsat 7 ETM (Lay, 2005). NDVI is correlated with aboveground net primary productivity and leaf area index (Tucker & Sellers, 1986; Ruimy, Dedieu & Saugier, 1994). A positive change in NDVI values over a multi-temporal image sequence during the growing season corresponds with changes in vegetative phenology such as growth of new tissue or increased above-ground biomass (Groten & Ocatre, 2002), and is positively correlated with forage of higher digestibility (Griffith *et al.*, 2002; Oindo, 2002). We assumed that relative monthly changes in NDVI were consistent across years (2002, 2003) and that they reflected changes in the forage of Stone's sheep.

RISK OF PREDATION

Grizzly bears and wolves are assumed to be the most significant large-mammal predators in the MKMA (Bergerud & Elliott, 1998). To quantify potential risk of predation to Stone's sheep, we used GPS locations from collared individuals to build RSF for bears during the lambing, summer, and fall seasons and for each of the 5 wolf packs across all 6 seasons during 2002 and 2003 (see Walker, 2005 for details). 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. GPS data were not available for wolves during November and December 2003, but we assumed risk of wolf predation during the rut season was similar to 2002 for the development of global Stone's sheep RSF.

Variables used in the grizzly bear and wolf RSF included slope, aspect, elevation, vegetation type (Table I), fragmentation, and distance to linear features. We developed fragmentation (an index of vegetation diversity) using

Idrisi32™ (Clark Labs, Worcester, Massachusetts, USA) 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 values were grouped into high-, medium-, and low-fragmentation classes rather than a continuous variable because of the skewed distribution of data. We developed a distance-to-linear-features layer using existing British Columbia Oil and Gas Commission data (1997–2000), orthophotos with 15-m resolution, and a Landsat 7 ETM image. Linear features consisted of roads, seismic lines and pipelines. We buffered these features by 10 m and developed the distance (km) surface using ArcGIS 8.3™ (Environmental Systems Research Institute, Redlands, California, USA). We set a more conservative tolerance score (< 0.4) to determine collinearity and multicollinearity of variables in predator models to increase our confidence in an extrapolated risk layer used in the Stone's sheep models (Gustine, 2005).

To ensure temporal and spatial consistency with the scale of Stone's sheep RSF, we defined availability for grizzly bears and each of the 5 wolf packs within 100% minimum

TABLE I. Description of vegetation types in the Besa–Prophet ecosystem, northern British Columbia, 2002–2003.

Vegetation type ^a	Description
Riparian	Permanent water bodies or water courses. Gravel bars of stream courses, including dry stream beds. Wet microsites, including wetlands dominated by <i>Carex aquatilis</i> and some moss species or <i>Salix</i> spp. May include <i>Picea glauca</i> or <i>Picea mariana</i> found in poorly drained sites.
Shrub	Shrubs < 2 m. Variable cover of <i>Salix</i> spp., <i>Betula glandulosa</i> , <i>Potentilla fruticosa</i> . Includes subalpine shrubs.
Conifer	<i>Picea glauca</i> , <i>Abies lasiocarpa</i> , or <i>Pinus contorta</i> stands, including mature and growing stands. Variable understories of grasses, mosses, and shrubs.
Subalpine spruce	Transition zone from mature <i>Picea glauca</i> or <i>Abies lasiocarpa</i> 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 lichens such as <i>Melanelia hepaticum</i> .
Dry alpine	<i>Dryas integrifolia</i> – and <i>Festuca altaica</i> –dominated alpine. Well drained sites on moderate to steep slopes.
Wet alpine	Poorly drained alpine sites. Primarily moss spp. with <i>Salix reticulata</i> . Also includes sites dominated by <i>Cassiope tetragona</i> .
Burn-deciduous	Older burned and disturbed areas. Contain <i>Populus tremuloides</i> and <i>Populus balsamifera</i> shrubs (< 2 m) and trees (> 2 m). Can be associated with small stands of <i>Pinus contorta</i> .
Burn-grass	Recently burned and open disturbed sites dominated by <i>Elymus</i> spp.

^aDefined by satellite imagery and validated by Lay (2005).

convex polygons (MCP) by “sheep season” and year using Arcview 3.2™ (Environmental Systems Research Institute, Redlands, California, USA). Data that extended beyond the B–P study area were excluded from the analyses. 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, we used a global model incorporating data from all bears or wolves to rank risk in those few parts of the landscape. Where MCP of wolf packs overlapped, we assigned the lowest risk values because the peripheries of wolf pack territories have been shown to act as refuges for ungulates (Rogers *et al.*, 1980). Individual wolf pack models were excluded from seasonal risk layers when the best model performed extremely poorly using k -fold validations and $r_s < 0.55$ (5 random subsets, $P > 0.10$; Siegel, 1956). These areas were assigned global (pooled across packs) risk values. Permanent lakes were masked and given RSF values of zero relative to risk of predation during the lambing, summer, and fall months (periods of open water).

We developed predation-risk layers by applying the coefficients (β_i) in the predator models to each pixel in the B–P area and scaling values between zero and one to standardize bear and wolf seasonal RSF. The predation-risk layers were subsequently normalized using the SCALE function in PCI XSpace™ (Richmond Hill, Ontario, Canada) to give relative selection values, and the layers were smoothed using a 3×3 -pixel median filter to make a continuous risk surface. We assumed that the risk of predation to Stone’s sheep from grizzly bears and wolves was directly related to selection values from the RSF of those species.

Results

COLLAR PERFORMANCE AND MOVEMENT

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 $73.4 \pm 2.80\%$ (mean \pm SE) fix success rate. Distances moved between 6-h fixes and corresponding movement rates were similar between 2002 and 2003. Distances ranged from no movement between fixes to a maximum straight-line distance of 8 496 m. Average movement rates decreased from a high in fall of $98.8 \text{ m}\cdot\text{h}^{-1} \pm 3.71$ (SE) through the rut ($63.6 \pm 3.20 \text{ m}\cdot\text{h}^{-1}$) and early winter ($42.0 \pm 1.83 \text{ m}\cdot\text{h}^{-1}$) to a low in late winter of $23.8 \pm 1.36 \text{ m}\cdot\text{h}^{-1}$ and then increased again through lambing ($48.6 \pm 3.54 \text{ m}\cdot\text{h}^{-1}$) and summer ($93.2 \pm 3.73 \text{ m}\cdot\text{h}^{-1}$).

EVALUATION OF PREDATOR MODELS

Models predicted resource selection by grizzly bears extremely well across all 3 seasons in 2002 and 2003 ($r_s = 0.946$, $n = 7$, $P < 0.001$; see Walker, 2005 for details). Grizzly bears selected consistently across both years for low to moderate elevations regardless of the season (1 100–1 500 m, $P < 0.001$) and avoided areas with low fragmentation (all $\beta_i < -0.178$, all $P < 0.001$). During the lambing season, they selected for areas with high fragmentation (high vegetation diversity) more than any other season, but they did not select or avoid any vegetation type consistently

between years. In summer, grizzly bears selected for shrubs, subalpine, and burn-deciduous habitats (all $\beta_i > 0.317$, all $P < 0.05$) and avoided conifer and alpine classes, especially rocks and rockcrust (all $\beta_i < -0.186$, all $P < 0.05$). In fall, grizzly bears also selected for subalpine and burn-deciduous habitats with high vegetation diversity (all $\beta_i > 0.163$, all $P < 0.001$) and avoided conifer-dominated vegetation types ($\beta_i > 0.341$, $P < 0.001$).

Resource selection models for wolves performed reasonably well in the k -fold cross validations (global wolf models, all $r_s > 0.801$, $n = 11$, $P < 0.001$; wolf pack models $r_s = 0.696$, $n = 73$, $P = 0.025$). Although there was variation in selection strategies within packs, there were also similarities across packs (*e.g.*, global models) between years and among seasons (see Walker, 2005 for details). In particular, wolves never avoided highly fragmented habitats and always selected for less steep slopes (all $\beta_i < -0.083$, $P < 0.05$) when slope was included in the top model. During the winter seasons, wolves consistently avoided conifer vegetation types and east aspects (all $\beta_i < -0.185$, all $P < 0.05$), while selecting shrub-dominated communities in early winter (both $\beta_i > 0.612$, both $P < 0.001$) and both south and flat aspects (no aspect) in late winter (all $\beta_i > 0.273$, all $P < 0.05$). With the onset of green-up during lambing, wolves again selected shrub vegetation types and continued to avoid east aspects. In the summer, rut, and fall seasons, there were no annual consistencies in the selection of resources between 2002 and 2003.

SEASONAL SELECTION ACROSS GROUPS OF STONE’S SHEEP

Vegetation type, aspect, curvature, elevation, and risk of wolf predation were consistent seasonal components of resource selection across the 5 groups of Stone’s sheep (Appendix I). All but the fall model also incorporated slope. Because wolf risk and slope were highly collinear during the fall, we removed slope from the fall models. When seasonally present, risk of bear predation and areas of high vegetative change also were important parameters. The probability that each of the global models was best (w_i) approached 1.0 during every season except late winter ($w_i = 0.991$), and the predictive ability was excellent, ranging from a maximum r_s of 0.992 ($n = 5$, $P < 0.0001$) in early winter to a minimum r_s of 0.884 ($n = 5$, $P < 0.001$) in summer. Although large sample sizes can lend themselves to overfitting models with more parameters and the potential inclusion of parameters with no explanatory value (Burnham & Anderson, 2002), we do not believe that overfitting greatly affected our model selection because $> 82\%$ of the attributes in the top global models were significant.

Across seasons, Stone’s sheep selected for steeper slopes, convex curvatures, and south aspects (as indexed by β_i different from zero) (Figure 1). They selected for rock and dry alpine vegetation types all year and for burn-grass in early and late winter, lambing, and fall (Figure 2). Stone’s sheep consistently avoided subalpine spruce vegetation types and east aspects across seasons and conifer habitats during late winter, summer, and fall. North aspects were avoided except during summer (Figure 1). Stone’s sheep during the summer and rut avoided burn-deciduous the most of all vegetation classes (Figure 2).

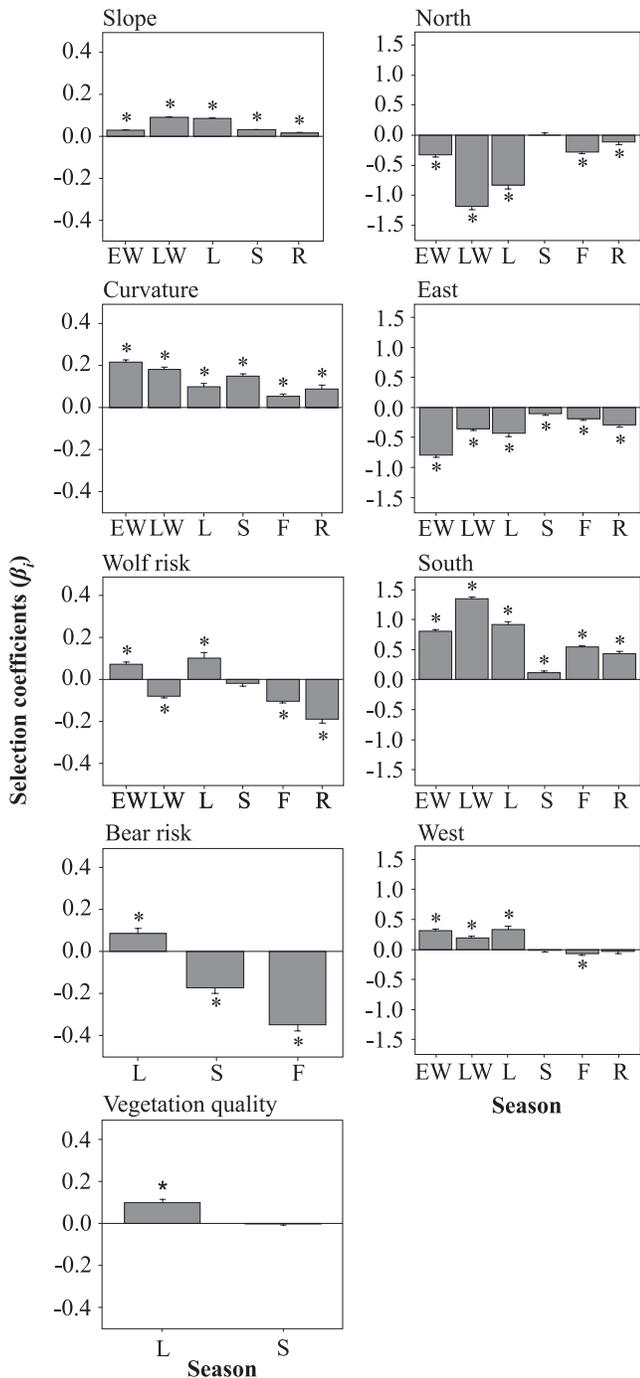


FIGURE 1. Habitat attributes from the best global resource selection models by season for Stone's sheep in the Besa-Prophet, 2002–2003. Selection coefficients ($\beta_i \pm SE$) for slope, curvature, wolf risk, bear risk, vegetation quality, and four aspects are presented. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut, as defined in text. Seasons for which an attribute could not be incorporated into a model are not shown. * indicates each seasonal selection coefficient is different from zero based on 95% confidence intervals.

Stone's sheep tended to select upper elevations in the study area (Figure 3) 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 ~1 200 m which was 150 m higher than

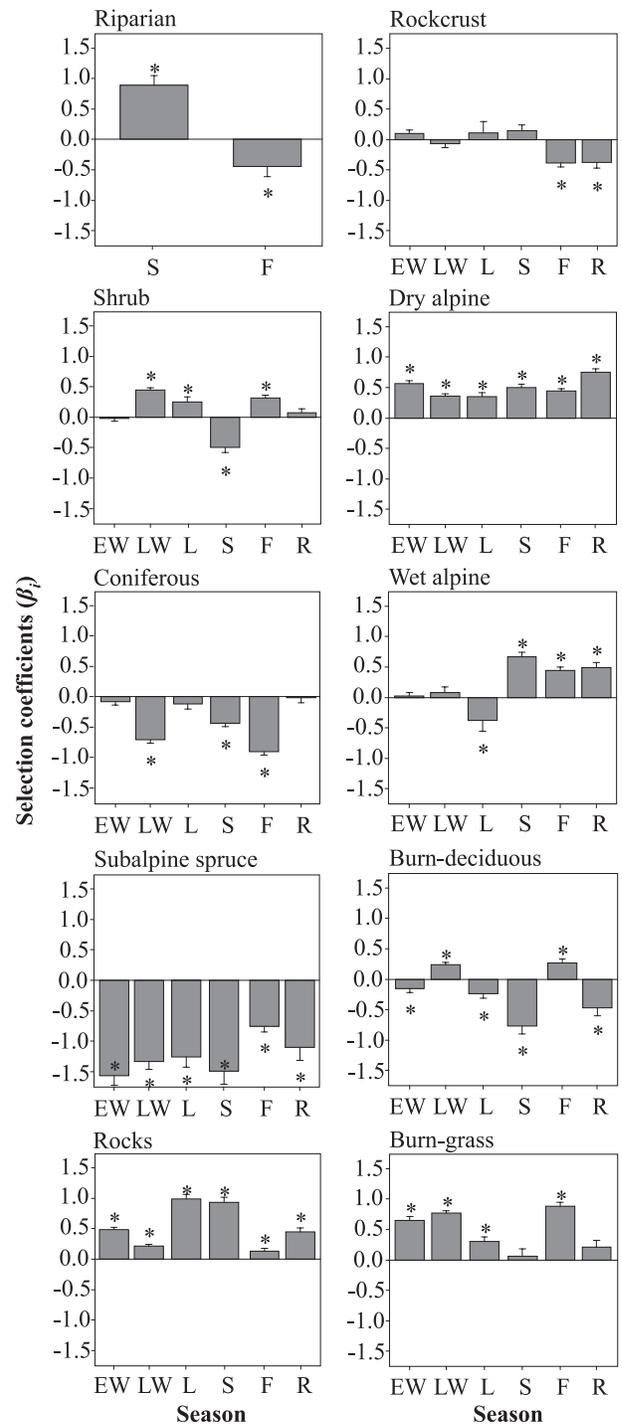


FIGURE 2. Vegetation types and their selection coefficients ($\beta_i \pm SE$) from the best global resource selection models by season for Stone's sheep in the Besa-Prophet, 2002–2003. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut, as defined in text. Seasons for which an attribute could not be incorporated into a model are not shown. * indicates each seasonal selection coefficient is different from zero based on 95% confidence intervals.

the lowest elevation used during any other season. Lambing was the only season in which Stone's sheep did not select for highest elevations, selecting instead elevations around 1 700 m (Figure 3).

Sheep selected for vegetation quality and were exposed to the highest risk of bear and wolf predation relative to other seasons during lambing (Figure 1). 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 that had relatively low risk of predation from both predator species.

SEASONAL SELECTION WITHIN GROUPS OF STONE'S SHEEP

Vegetation type, aspect, curvature, and elevation were important in characterizing seasonal resource selection within each group of Stone's sheep each year. Only 2 of the 59 seasonal models were not the most saturated (containing the most parameters) or were not averaged with a saturated model (Appendix I). Stone's sheep selected for different variables, however, between 2002 and 2003 in 32% (8/25) of the cases.

The ability of seasonal models to predict the habitat attributes selected by groups of Stone's sheep was generally excellent. Across the 5 groups the seasonal variation in predictive ability ranged from a high in late winter, with an average r_s of 0.898 ± 0.010 (mean \pm SD, $n = 5$) to an average low in summer of 0.846 ± 0.008 ($n = 5$). There were only 2 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 $r_s = 0.499$, $n = 5$, $P = 0.142$) (Appendix I). This may have occurred because of the small number of radio-collared individuals in the Tenmile group; this early winter model had the fewest GPS locations of all models in our study.

Predicting resource selection by Stone's sheep was better when more than one general habitat factor was incorporated in a model (Table II). Of the 3 factors (vegetation, risk of predation, topography), topography typically ranked higher in explaining the variation in selected attributes (*i.e.*, the lowest ΔAIC) 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, followed by risk of predation from grizzly bears, consistently ranked the lowest (Table II).

Within groups of Stone's sheep, there were few consistencies among seasons and between years in the selection of habitat attributes (Table III and Table IV) even though model selection (Appendix I) and relative rank of habitat factors were similar (Table II). The most notable consistency exhibited across all groups of Stone sheep was avoidance of or indifference towards subalpine spruce vegetation. Groups of sheep rarely selected concave curvatures or avoided south 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 south slopes and avoided north aspects. More groups selected for dry alpine vegetation than any other vegetation type at this time. In summer, groups of sheep often selected for rock and dry alpine vegetation types. Stone's sheep either selected for or were indifferent in their use of burns during the fall.

Groups of Stone's sheep selected resources differently from the predictions of global models in several instances.

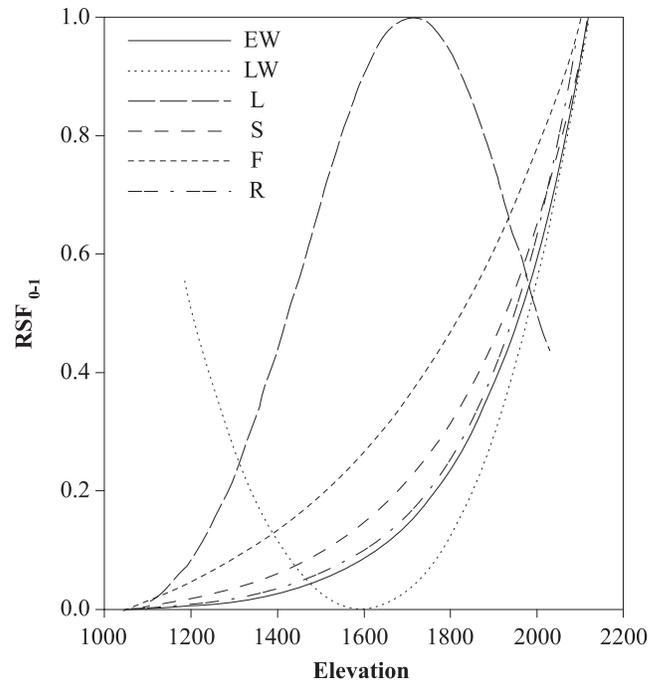


FIGURE 3. Relative selection by female Stone's sheep for elevation assuming other habitat variables are constant in the best global resource selection models, by season in the Besa-Prophet, 2002–2003. Resource selection functions were scaled 0–1 (RSF_{0-1}). EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut, as defined in text.

TABLE II. The relative rank of habitat factors developed by season for 5 groups of Stone's sheep in the Besa-Prophet from 2002 and 2003 as denoted by the average change in AIC (ΔAIC). Smaller values indicate models that, on average, have more substantial support. EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut, as defined in text.

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

^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 III. The number of groups of Stone's sheep 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 text.

	Year	β_i sign or shape	Season					R
			EW	LW	L	S	F	
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)
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 \cap indicates selection for mid elevations where β_i is positive for elevation and negative for elevation².

^b U indicates positive selection for low and high elevations where β_i is negative for elevation and positive for elevation².

^c β_i for linear elevation was always a positive coefficient ($/$).

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 (Figure 3), 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

TABLE IV. The number of groups of Stone's sheep 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 text.

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

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 (Figure 1), but within groups they were indifferent in 2003, and in 2002, 2 groups selected areas where wolf risk was higher than what was available and 2 groups avoided areas with increased wolf risk (Table III).

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 (Figure 2), but only one group of sheep selected for burn-deciduous each year (Table IV). The global model also suggested that sheep strongly selected rocks all year, including fall (Figure 2), which is in contrast

to the selection strategies within groups that mostly avoided rocks (Table IV).

Discussion

SEASONAL HABITAT SELECTION

This is the first comprehensive analysis of habitat selection by Stone's sheep; it thus provides a foundation from which to gauge and mitigate issues relating to future access and disturbance in the B–P area. Habitat selection was best explained by incorporating vegetation, topography, and risk of predation. 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, south aspects, and upper elevations.

By employing logistic regression, RSF provide a broad-scale perspective of general selection patterns on the landscape (Boyce & McDonald, 1999; Manly *et al.*, 2002). They do not indicate the absolute probability of use by an animal or species (Keating & Cherry, 2004), but can provide relative measures of selection. Defining the selection of habitats, however, is constrained by technological, biological, and statistical factors. Habitat bias and missing data in the GPS collars can be of concern. We believe that selection bias from habitat attributes within the seasonal ranges of Stone's sheep was probably low given the open environments with relatively few timbered habitats and low crown closure. Frair *et al.* (2004) noted that closed (> 60% canopy cover) conifer forests significantly reduced GPS fix rates and could bias selection coefficients, whereas open conifer / mixed deciduous–conifer forest did not affect location acquisition. Steep slopes also may interfere with fix acquisition rates, yet Stone's sheep in the B–P selected for steep slopes consistently, and fixes were acquired despite potential increased blockage of satellites by terrain. D'Eon *et al.* (2002) and Frair *et al.* (2004) reported that terrain variables on their own did not significantly affect fix rates unless combined with the influence of canopy cover. We did not produce a model specific to collars in our study to correct for bias in fix rates related to habitat attributes. Although we cannot rule out some influence of vegetation type and topography on acquisition success, the overall fix rate reported in our study was also conservative; it included collars for which we were unable to extract all data because of transmission errors during downloading and collars that were not retrieved.

The inability of logistic regression to accommodate explanatory variables that have missing data in either the used or available response variable limits the inferences that can be made regarding selection of habitat attributes that are excluded from modeling (Menard, 2002). 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 seasonal 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. The spatial and temporal influence of licks on Stone's sheep is well recognized (Geist, 1971; Luckhurst, 1973; Seip, 1983). 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.

The seasonal movements exhibited by Stone's sheep affect the resources available to them and the heterogeneity of those resources. A variable buffer size like we used in our models could 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 and the ability to detect selection is reduced (McClellan *et al.*, 1998; Boyce *et al.*, 2003). This could potentially be of concern with respect to late winter, when Stone's sheep moved the least. However, Stone's sheep selected or avoided many habitat attributes to the strongest extent during this season (Figures 1 and 2), and they showed a relatively high annual consistency for particular attributes at this time. Selection by Stone's sheep varied the most during fall, when their movements and the availability of resources were greatest.

EARLY WINTER

During the early winter (1 January–28 February), Stone's sheep ewes generally selected for upper elevations and steep slopes along ridges and mountain tops with south and west-facing aspects (Figures 1, 2, and 3). 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 east 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, and there was 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. This habitat is generally densely timbered with short spruce and subalpine fir in krummholz form. It has limited graminoid understory and extremely poor visibility, both of which likely contribute to the strong avoidance. Decreased habitat visibility has been well documented to negatively affect selection (Tilton & Willard, 1982; Bentz & Woodard, 1988; Smith, Harden & Flinders, 1999) and foraging efficiency of bighorn sheep (Risenhoover & Bailey, 1985).

LATE WINTER

During the late winter season (1 March–14 May), Stone's sheep showed the strongest selection for sites with

steep slopes and south aspects compared to other seasons. All groups except one in 2002 selected for convex curvatures. The interaction between slope and aspect contributes to the amount of solar radiation and subsequent air temperature of a site (Kumar, Skidmore & Knowles, 1997), whereas the convexity or shape of a site influences the deposition of snow and exposure to wind (Pomeroy *et al.*, 1998). Increased air temperatures and wind exposure reduce the amount of snow a site receives (Pomeroy *et al.*, 1998). Deep snow and lack of wind have contributed to large die-offs of Dall's sheep (*Ovis dalli dalli*) in the Yukon (Burles & Hoefs, 1984).

Snow is important in the selection of late-winter habitats by Stone's sheep (Geist, 1971; Seip & Bunnell, 1985b) and other North American sheep (Hoefs & Cowan, 1979; Tilton & Willard, 1982; Goodson, Stevens & Bailey, 1991). Stone's sheep in the B-P appeared to exhibit 2 strategies during late winter, highlighted by their selection for low and high elevations (Figure 3). Lower elevations tend to have warmer temperatures on south and west aspects, whereas higher elevations may have increased exposure to wind (Geist 1971; Hoefs & Cowan, 1979). Most groups appeared to use only one of the strategies. All groups selected for mid-elevations within their late winter distribution, but the range of elevations available to each group differed considerably during this time. Stone's sheep moved the least during late winter, making the sizes of these seasonal ranges the smallest. We believe that the selection for both low and high elevations in the global models occurred because the elevations available to the Tenmile group to select from, for example, were lower than the elevations available to the Richards group. Even though seasonal ranges and availability were the most restricted during late winter, both the predictive ability of Stone's sheep RSF (both global and group) and the β_i for resources were often strongest.

Vegetation type was also important in the late winter season. More groups of Stone's sheep selected for burned areas in late winter than in any other season. Stone's sheep most strongly selected burn-grass, followed by shrub, dry alpine, and burn-deciduous types. The shrub and burn vegetation types have higher vegetation biomass than dry alpine, but this advantage comes potentially at the expense of increased snow depths. Brushier habitats have more evenly distributed snow in comparison to low-vegetation habitats, which have 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 & Bunnell, 1985a).

LAMBING

Newborn lambs were first observed in the B-P during the first week of June during 2002 and 2003. Stone's sheep generally selected for mid-elevations during the lambing season (15 May–14 June) and across a less variable range of elevations than was observed among groups during late winter.

Across groups, Stone's sheep selected for dry alpine, burn-grass, shrub, and especially rock areas during lamb-

ing (Figure 2). 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 & Spowart, 1984; Seip & Bunnell, 1985b). The selection for these areas with higher quality forage, however, was at an apparent increased risk of predation from both wolves and grizzly bears. 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. Both wolves and grizzly bears in the B-P 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). Bears may have responded primarily to new plant growth, but they also have been observed to prey on thimhorn sheep (Hoefs & Cowan, 1979). The increased risk of predation to sheep during the lambing season may have resulted from the relatively late springs, especially in 2002, which delayed plant green-up. Hoefs, Hoefs, and Burles (1986) observed especially high wolf-caused mortality during the lambing season after a severe winter, which they partially attributed to a delay in plant green-up.

The variability and lack of consistency in annual selection of more habitat attributes during lambing by Stone's sheep may be influenced by the timing of new plant growth and maternal status of ewes. Within groups, Stone's sheep showed the strongest selection for rocks, no group ever avoided areas of high vegetative quality (Table IV), and all groups both years selected for steep slopes. The trade-off between forage and risk of predation in female mountain sheep during lambing is well documented and has been used to explain intrasexual segregation (Festa-Bianchet, 1988; Bleich, Bowyer & Wehausen, 1997; Walker, Parker & Gillingham, 2006). 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). Corti and Shackleton (2002) demonstrated that Dall's sheep groups with lambs placed themselves closer to escape cover than nonmaternal groups because of their risk to predation. We were unable to conclusively determine whether collared individuals did or did not have lambs in 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 its 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 north aspects, several groups actually selected

for north aspects during 2002. In summer, the warm south aspects were least selected for compared to other seasons. 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, corresponding with the use of low elevations. Selection for increasingly high elevations from lambing to summer (Seip & Bunnell, 1985b; Walker, Parker & Gillingham, 2006) may be a form of environmental tracking by sheep to areas of more nutritious forage (Hebert, 1973). 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 & Bunnell, 1985b). As with other temperate ungulates that migrate over altitudinal gradients (Boyce, 1991; Albon & Langvatn, 1992; Demarchi, 2003), Stone's sheep may prolong their access to nutritious forage by choosing a specific phenological stage as they move up in elevation (Seip, 1983), which may allow them access to forage with higher levels of crude protein (Albon & Langvatn, 1992) and fewer chemical defences (Bryant *et al.*, 1991).

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 for or avoidance of either type of risk in their selection of resources during this time. Sheep did not select for areas of highest vegetative quality and showed the lowest seasonal selection for burns and shrub vegetation types. Selection for wet alpine was most prevalent (Figure 2) during summer (Table IV). This vegetation type, which is typically covered by snow for much of the year, is one of the last habitats to green up in summer and may provide 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 III). 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 selected vegetation types, with most groups avoiding coniferous, subalpine spruce and rockcrust habitats (Figure 2). 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 (1985b) documented early fall as 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 may partially explain the attraction for lower-elevation burns.

RUT

Wild sheep have strong fidelity to breeding ranges and make large movements in order to access them (Geist,

1971; Festa-Bianchet, 1986). Generally, the sites selected by Stone's sheep in the B-P during the rut (1 November–31 December) were similar to those selected in other seasons in terms of steep slopes, convex curvatures, south aspects, and dry and wet alpine vegetation. Groups selected for upper elevations, and their selection for burns was not as strong as during the fall (Figure 2). Risk of wolf predation continued to decline from summer to fall to rut (Figure 1). The variation in selection strategies among groups persisted during the rut. Selection by the Richards group for flatter slopes, as in early winter, emphasizes the importance of habitat juxtaposition in quantifying selection (Mysterud & Ims, 1998; Garshelis, 2000).

RELATIVE HABITAT RANK

Topography ranked consistently better than both vegetation and risk of predation for 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 & Anderson, 2002), models with more parameters incorporating vegetation, risk of predation, and quality were further from the "true model" (had larger AIC scores) than topography (Table II). Vegetation and vegetation quality consistently ranked second to topography, whereas risk of wolf and bear predation were the poorest in explaining the distribution of Stone's sheep.

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 & Bailey, 1985; Rachlow & Bowyer, 1998). Sheep evade predation by fleeing to and in precipitous terrain (Geist, 1971). In northern British Columbia, predation, particularly by wolves, is reported to be the leading cause of mortality of Stone's sheep (Luckhurst, 1973; Bergerud & Elliott, 1998). Aspect, curvature, and elevation also have been shown to provide biologically meaningful surrogates that influence the distribution of mountain sheep in North America (Bleich, Bowyer & Wehausen, 1997; Rachlow & Bowyer, 1998; Nichols & Bunnell, 1999), including Stone's sheep (Elliott, 1978; Seip & Bunnell, 1985a,b). Aspect and slope, which affect the amount of solar radiation a site receives, combine with curvature (a site's exposure to wind) to restrict accumulation of snow on exposed sites and thereby improve availability of forage. Convex curvatures and higher elevations where plant development is limited enable mountain sheep, which perceive risk through visual cues (Bleich, 1999; Frid & Dill, 2002), to detect predators by improving sight lines.

The lack of response to risk of predation by 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 selected against risk at scales larger than their seasonal distribution (*i.e.*, seasonal range was lower in risk of predation than the surrounding landscape), they may not have responded to perceived risk within seasonal ranges. Alternatively, Stone's sheep may select for certain topographical attributes (*e.g.*, steep slopes) as a response to risk at smaller scales within the seasonal range.

CONSISTENCIES IN ANNUAL SELECTION

Wild sheep show strong fidelity to seasonal ranges (Geist, 1971; Festa-Bianchet, 1986). In the B–P, range selection was consistent between years for most individuals, particularly in the Neves, Firstfork, and Richards groups, because of year-round occupancy of local mountains. The selection of habitat attributes within seasonal ranges, 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 behavioural plasticity of Stone's sheep and their susceptibility to disturbance.

Stone's sheep showed the highest consistencies in annual selection of habitat attributes during the winter and summer seasons. The most consistently selected vegetation type was dry alpine. The influence of snow depth on movement rates and availability probably contributed to the consistencies that sheep exhibited for the topographic attributes of steep slopes, south aspects, and convex sites. Selection models that validated best occurred during winter, when sheep were most predictable. Of all the habitat attributes, the weakest consistency in seasonal selection by groups of Stone's sheep between years was for elevation. This was probably influenced by its inclusion as a quadratic in selection models. Risk of predation was extremely variable between 2002 and 2003. Few groups placed themselves at a consistent risk of predation from bears and wolves, possibly as a result of different strategies exhibited by the predators between study years.

Our assessment of the consistency in selection of attributes between years may have been affected by availability changing from year to year (Arthur *et al.*, 1996). Changing availability has been shown to elicit different behavioural responses in animals when resources become more or less abundant (Mysterud & Ims, 1998), which may contribute to variability in annual consistencies, particularly if the juxtaposition or patterns of attributes change considerably (Porter & Church, 1987; Garshelis, 2000). Nonetheless, our study documents that Stone's sheep show behavioural plasticity in selection of attributes within seasonal ranges even though their fidelity to particular ranges may be high (Geist, 1971; Worley *et al.*, 2004). Our research provides a baseline measure of the habitats selected by Stone's sheep within their seasonal ranges and highlights the importance of topographic features on their distribution.

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APPENDIX I. 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 , used and available), log likelihood (LL), Akaike's Information Criterion (AIC), Akaike weights (w_i), and average Spearman's rank correlation (\bar{r}_s) from k -fold cross-validation procedure. ** and * indicate $P < 0.01$ and $P < 0.05$ respectively for the model's 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	43 058	-15 237.390	30 508.779	1.000	0.992**
Global		LW	V+S+A+C+E+E ² +W	17	61 912	-22 116.221	44 266.441	0.991	0.982**
Global		L	V+S+A+C+E+E ² +W+B+Q	19	21 482	-7 265.025	14 568.050	1.000	0.939**
Global		S	V+S+A+C+E+W+B+Q	19	42 045	-13 438.790	26 915.580	1.000	0.884**
Global		F	V+A+C+E+W+B	17	51 493	-18 841.375	37 716.750	1.000	0.970**
Global		R	V+S+A+C+E+W	16	20 870	-7 478.605	14 989.210	1.000	0.987**
Neves	2002	EW	V+S+A+C+E+E ² +W	17	7 904	-2 537.361	5 108.721	0.997	0.933**
Neves	2003	EW	V+S+A+C+E+E ² +W	17	7 327	-2 527.427	5 088.854	1.000	0.938**
Neves	2002	LW	V+S+A+C+E+E ² +W	17	11 388	-3 836.929	7 707.859	0.999	0.958**
Neves	2003	LW	V+S+A+C+E+E ² +W	16	9 524	-3 268.646	6 569.293	1.000	0.977**
Neves	2002	L	V+S+A+C+E+E ² +W+B+Q	18	4 563	-1 349.464	2 734.929	0.993	0.849**
Neves	2003	L	V+S+A+C+E+E ² +W+B+Q	19	3 540	-1 065.411	2 168.821	1.000	0.880**
Neves	2002	S	V+S+A+C+E+E ² +W+B+Q	19	7 920	-2 426.739	4 891.478	1.000	0.841**
Neves	2003	S	V+S+A+C+E+E ² +W+B+Q	19	6 904	-2 152.864	4 343.727	1.000	0.849**
Neves	2002	F	S+A+C+E+E ²	8	11 019	-3 948.963	7 913.927	0.975	0.908**
Neves	2003	F	V+A+C+E+E ² +W+B	17	7 932	-2 874.645	5 783.290	1.000	0.966**
Neves	2002	R	V+S+A+C+E+W	16	8 180	-2 791.740	5 615.481	1.000	0.942**
Neves	2003	R	V+S+A+C+E+E ²	16	4 222	-1 579.387	3 190.774	1.000	0.935**
Tenmile	2002	EW	V+S+A+C+E+E ² +W	17	2 316	-714.198	1 462.397	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	1 601	-460.879	953.758	0.999	0.658*
Tenmile	2003	LW	V+S+A+C+E+E ² +W	15	1 921	-526.396	1 082.791	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*
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	1 094	-268.878	571.757	1.000	0.665*
Tenmile	2003	S	V+S+A+C+E+E ² +W+B+Q	16	1 893	-467.648	967.295	1.000	0.810**
Tenmile ^d	2002	F	V+A+C+W+B	14	1 499	-322.010	672.021	0.643	0.641*
	2002	F	V+A+C+E+W+B	15	1 499	-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	1 216	-457.616	941.232	1.000	0.818**
Firstfork ^d	2002	EW	V+S+A+C+W	12	1 625	-552.253	1 128.505	0.836	0.857**
	2002	EW	V+S+A+C+E+E ² +W	14	1 625	-551.852	1 131.703	0.164	0.882**
Firstfork	2003	EW	V+S+A+C+E+E ² +W	17	3 123	-1 030.808	2 095.616	1.000	0.918**
Firstfork ^d	2002	LW	V+S+A+C+E+E ² +W	17	3 539	-1 091.556	2 217.111	0.746	0.870**
	2002	LW	V+S+A+C+W	15	3 539	-1 094.649	2 219.297	0.254	0.894**
Firstfork	2003	LW	V+S+A+C+E+E ² +W	17	3 518	-1 172.141	2 378.281	1.000	0.919**
Firstfork	2002	L	V+S+A+C+E+E ² +W+B+Q	17	1 128	-406.095	846.191	1.000	0.902**
Firstfork	2003	L	V+S+A+C+E+W+B+Q	17	1 561	-510.419	1 054.838	0.999	0.858**
Firstfork	2002	S	V+S+A+C+E+E ² +W+B+Q	19	2 398	-593.254	1 224.508	1.000	0.790**
Firstfork	2003	S	V+S+A+C+E+E ² +W+B+Q	19	2 952	-807.169	1 652.339	1.000	0.867**
Firstfork	2002	F	V+A+C+E+E ² +W+B	17	3 079	-1 119.744	2 273.488	0.998	0.942**
Firstfork	2003	F	V+A+C+E+E ² +W+B	17	3 228	-1 059.394	2 152.787	1.000	0.955**
Firstfork	2002	R	V+S+A+C+E+E ² +W	17	2 507	-863.814	1 761.628	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	6 881	-2 325.728	4 685.456	1.000	0.970**
Townsley	2003	EW	V+S+A+C+E+E ² +W	17	5 990	-1 805.791	3 645.581	1.000	0.939**
Townsley	2002	LW	V+S+A+C+E+E ² +W	17	11 108	-3 950.812	7 935.623	1.000	0.945**
Townsley	2003	LW	V+S+A+C+E+E ² +W	17	7 871	-2 621.550	5 277.099	1.000	0.958**
Townsley	2002	L	V+S+A+C+E+E ² +W+B+Q	19	3 844	-1 299.447	2 636.893	0.990	0.928**
Townsley	2003	L	V+S+A+C+E+W+B+Q	18	2 034	-692.986	1 421.972	1.000	0.913**
Townsley	2002	S	V+S+A+C+E+E ² +W+B+Q	19	7 017	-2 263.962	4 565.924	1.000	0.926**
Townsley	2003	S	V+S+A+C+E+E ² +W+B+Q	19	4 365	-1 334.458	2 706.916	1.000	0.891**
Townsley ^d	2002	F	V+A+C+E+E ² +W+B	17	8 395	-2 934.228	5 902.456	0.744	0.878**
	2002	F	V+A+C+W+B	15	8 395	-2 937.302	5 904.604	0.256	0.865**
Townsley	2003	F	V+A+C+E+E ² +W+B	17	6 966	-2 374.425	4 782.849	1.000	0.928**
Townsley	2002	R	V+S+A+C+E+W	16	6 400	-2 152.011	4 336.023	1.000	0.948**
Townsley	2003	R	V+S+A+C+E+E ²	16	3 619	-1 291.011	2 614.023	1.000	0.905**
Richards	2002	EW	V+S+A+C+E+E ² +W	14	2 880	-1 042.239	2 112.477	1.000	0.894**
Richards	2003	EW	V+S+A+C+E+E ² +W	15	3 886	-1 248.856	2 527.713	1.000	0.937**
Richards	2002	LW	V+S+A+C+E+E ² +W	15	4 985	-1 522.168	3 074.337	1.000	0.937**
Richards	2003	LW	V+S+A+C+E+E ² +W	16	5 936	-1 724.365	3 480.731	1.000	0.938**
Richards	2002	L	V+S+A+C+E+E ² +W+B+Q	18	1 737	-504.648	1 045.296	1.000	0.836**
Richards	2003	L	V+S+A+C+E+E ² +W+B+Q	19	1 436	-451.955	941.910	0.999	0.822**
Richards	2002	S	V+S+A+C+E+E ² +W+B+Q	19	2 980	-944.706	1 927.413	1.000	0.873**

APPENDIX I. Concluded.

Group	Year	Season ^a	Model ^b	<i>K</i>	<i>n</i>	LL	AIC	<i>w_i</i>	\bar{r}_s
Richards	2003	S	V+S+A+C+E+E ² +W+B+Q	18	2 843	-924.427	1 884.853	1.000	0.949**
Richards ^d	2002	F	V+A+C+W+B ²	14	3 152	-1 080.804	2 189.609	0.535	0.930**
	2002	F	V+A+C+E+E ² +W+B	16	3 152	-1 078.926	2 189.851	0.465	0.936**
Richards	2003	F	V+A+C+E+E ² +W+B	15	3 336	-1 233.704	2 497.409	1.000	0.959**
Richards ^d	2002	R	V+S+A+C+E+E ² +W	16	2 363	-874.575	1 781.150	0.623	0.830**
	2002	R	V+S+A+C+W	14	2 363	-877.435	1 782.269	0.365	0.795**
Richards	2003	R	V+S+A+C+E	12	1 330	-526.114	1 076.228	0.982	0.796**

^a EW = early winter, LW = late winter, L = lambing, S = summer, F = fall, R = rut, as defined in text.

^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.