Behaviour, habitat associations, and intrasexual differences of female Stone's sheep

Andrew B.D. Walker, Katherine L. Parker, and Michael P. Gillingham

Abstract: Stone's sheep (*Ovis dalli stonei* Allen, 1897) in northern British Columbia segregate sexually during most of the year, and intrasexually between maternal and nonmaternal females during spring and early summer. Our objective was to quantify intrasexual habitat use of female Stone's sheep relative to maternal status using measures of behaviour and habitat use. 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. Female Stone's sheep spent the majority of their active time foraging. Nursery groups spent shorter durations of time active, more time active in solid rock escape features, and less time active in shrub habitat than nonmaternal groups. The best predictive model describing intrasexual differences incorporated distance to nearest escape feature and size of nearest escape feature. Regardless of maternal status, female Stone's sheep used low-elevation plant communities early in the growing season that were characterized by more shrub species and increased cover. As the growing season progressed, they tracked a phenological stage, moving up in elevation and associating with communities that contained increasing amounts of moss and 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.

Résumé : Les mouflons de Stone (*Ovis dalli stonei* Allen, 1897) dans le nord de la Colombie-Britannique se séparent dans l'espace en fonction du sexe durant la plus grande partie de l'année; chez les femelles, il y a ségrégation intrasexuelle des mères et de celles qui ne le sont pas au printemps et au début de l'été. Notre objectif est de quantifier, à l'aide des comportements et de l'exploitation des milieux, l'utilisation de l'habitat chez les mouflons de Stone femelles en fonction de leur statut maternel. Nous examinons trois hypothèses reliées à la ségrégation intersexuelle (les hypothèses du risque de prédation, de la sélection alimentaire et du bilan d'activités) pour voir si elles s'appliquent aussi à la sélection intrasexuelle chez les mouflons de Stone. Les mouflons de Stone femelles passent la majorité de leur temps d'activité à s'alimenter. Les groupes de nursery sont actifs pendant des périodes plus courtes et passent une partie plus importante de leur période active dans les structures rocheuses d'échappée et moins de temps dans les habitats de buissons que les groupes non maternels. Le meilleur modèle prédictif pour décrire la ségrégation intrasexuelle incorpore la distance à la structure d'échappée la plus proche et la taille de cette structure. Quel que soit leur statut maternel, les mouflons de Stone femelles utilisent tôt dans la saison de croissance des communautés de plantes de basse altitude caractérisées par une quantité plus grande de buissons et une couverture végétale plus importante. À mesure que la saison de croissance progresse, ils recherchent des stades phénologiques particuliers, se déplaçant en altitude et s'associant à des communautés qui contiennent une couverture de plus en plus importante de mousses et de lichens. Les patrons de comportement, d'utilisation de l'habitat et d'associations végétales chez les différents groupes intrasexuels de mouflons de Stone s'expliquent le mieux par l'hypothèse du risque de prédation.

[Traduit par la Rédaction]

Introduction

Stone's sheep (*Ovis dalli stonei* Allen, 1897) 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; Walker 2005). 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 overlaps may exist between adult females (ewes) and males (rams), they generally occupy distinct ranges or portions of a range during 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 have been referred to as the predation-risk hypothesis and the forage-selection hypothesis (Ruckstuhl and Neuhaus 2000). The predation-risk 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 ex-

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pense of better foraging conditions (Main and Coblentz 1990; Main et al. 1996; Ruckstuhl and Neuhaus 2000). The forage-selection hypothesis predicts that the consequences of energetic constraints resulting from differences in body size are (*i*) males feeding on abundant low-quality forages and (*ii*) 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* Shaw, 1804) and Dall's sheep (*Ovis dalli dalli* Nelson, 1884) document aspects of both (Ruckstuhl 1998; Corti and Shackleton 2002). Ruckstuhl and Neuhaus (2000) proposed an activity-budget hypothesis whereby intersexual segregation of bighorn sheep is a function of differences in foraging behaviour (energy requirements) and movement patterns. Smaller females are less efficient at digesting forage because of their small stomach size and quicker passage rates of food, which force them to spend more time foraging and being active (Bunnell and Gillingham 1985; Main and Coblentz 1990; Main et al. 1996; Ruckstuhl and Neuhaus 2000, 2002).

Segregation is not exclusive to the sexes, and females should segregate relative to maternal status when energy demands and predator avoidance strategies differ (Ruckstuhl and Neuhaus 2000). Intrasexual segregation has been observed within female Dall's sheep (Hoefs and Cowan 1979; Rachlow and Bowyer 1994, 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). 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 related to 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 sheep with lambs generally forage less efficiently, spending proportionally less time foraging and more time being vigilant than nonmaternal females (Risenhoover and Bailey 1985; Frid 1997). 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 behaviours because increased movement may make females with lambs less spatially predictable by predators, potentially reducing their risk of predation (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000).

Although not mutually exclusive, an inverse relationship exists between feeding and vigilance (Lima and Dill 1990; Illius and Fitzgibbon 1994; Frid 1997). This relationship 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 it does not encompass all attributes important to sheep. Forage quality has been shown to influence reproductive performance (Geist 1971) and body growth in bighorn sheep (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). These observations suggested that 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 the three intersexual segregation hypotheses to explain intrasexual segregation of female sheep. We used measures of escape features (type, distance, size) to provide an indication of antipredator strategies and measures of group size, behaviour (i.e., foraging, standing, walking, alert, nursing), and vegetation (phenology, forage availability) to highlight differences in activity and habitat use. For the predation-risk hypothesis to explain intrasexual differences, maternal females should associate with safer habitats where offspring are less vulnerable to predation and food quality or quantity is often inferior; nonmaternal females should choose areas where nutritious resources are more abundant at a potentially higher risk of predation. For the forage-selection hypothesis to explain intrasexual segregation, maternal females should use higher quality forage to meet the higher energy demands associated with lactation. Support for the activity-budget hypothesis would exist if ewes with young spent a greater proportion of time walking (Ruckstuhl 1998) and foraging or were more active than ewes without young.

Our second objective was to describe how female Stone's sheep associate with plant communities relative to maternal status. We used nonmetric multidimensional scaling (NMS) to ordinate plant species communities relative to temporal, environmental, and vegetative attributes (cover, type, quality, and quantity) at sites used by nursery and non-nursery groups of Stone's sheep ewes. If intrasexual differences exist in plant community associations used by maternal and nonmaternal individuals, then distinct ordination groupings should be discernable and describable by the most correlated environmental attributes.

Materials and methods

Study area

This study was conducted in 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′N–57° 40′N and 123°10′W–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 human access and is relatively free of industrial influences. There is one all-terrain vehicle (ATV) trail that experiences some snowmobile activity in winter.

Behavioural observations

Observations of female Stone's sheep were conducted during daylight hours between 18 May and 26 July in 2002 and 2003 prior to the hunting season (1 August – 15 October). Sheep were located using telemetry, binoculars, and (or) spotting scopes and were approached on foot or horseback to distances (50–500 m) from which observations could be accurately made. Observations were conducted on 10 different mountains separated by major creeks or river drainages. Care was taken not to disturb sheep and observations were discontinued if animals exhibited alert behaviour towards the observer or towards any anthropogenic stimulus. 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). Behaviours (foraging, walking, standing, alert, nursing, and out of sight) were entered by first letter code for randomly selected females ≥2 years old (Rachlow and Bowyer 1998). 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. In addition, habitat type (i.e., herbaceous, shrub, tree, broken rock, and solid rock) was recorded for each observed animal to allow for simultaneous assessment of behaviour and habitat use. 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 out of sight was subtracted from both the total time observed and the time active.

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 (i.e., the proportion of active time that 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 that they have with their mothers (Shackleton and Haywood 1985; Corti and Shackleton 2002). Males older than 1 year of age were included in the measure of group size, but were not included in the measure of lamb to ewe ratio described for nursery groups.

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 that 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 that 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 for >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 female Stone's sheep were observed active for >25 min (25 min ≈ 75% of the average complete active bout duration for all observed ewes). Animals that spent a greater portion of active time walking than foraging often left the field of view before 25 min was attained.

Sites used by sheep were identified by recording the locations of observed individuals at 5 min intervals. Similar to Rachlow and Bowyer (1998), we plotted locations on a hand-drawn map for habitat sampling of use sites that took place approximately 1–2 days after behavioural observations. Polygons were drawn around plotted locations using 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.

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.

Fine-scale measurements of vegetation type and phenology at the five stations were determined within 1 m × 1 m quadrats. We estimated percent cover by species, bare ground/rock, and litter 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. We used phenology 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. We developed an availability index of forage quantity after measuring the average aboveground new growth height (m) of each species. Ten representative plants of each species were measured to determine average plant growth. The availability index (m^3) was calculated by multiplying the quadrat area (1 m × 1 m) 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 the values for all species were subsequently summed to provide an index of total vegetation quantity or availability for each use site.

Data analyses

Behavioural observations and microsite measurements

We compared mean group size, active and inactive durations, and proportion of time spent active for maternal and nonmaternal Stone's sheep ewes using Student's t test; data were log-transformed where appropriate to meet the assumptions of normality and homogeneity of variance (Levene's test; Zar 1999). We used the Mann–Whitney U test adjusted for ties (Siegel 1956) to further examine differences in behaviour, phenology, forage availability, slope, escape features, and vegetation cover between intrasexual groups of Stone's sheep ewes. We calculated the median, as well as the mean, to describe the central tendency of samples in nonparametric tests with skewed samples (Zar 1999). Values are presented as the untransformed mean and standard error (SE) unless otherwise noted. We used linear regression (Zar 1999) 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™ release 9.0 (StataCorp LP 2005).

Habitat use

We evaluated habitat use by intrasexual groups of Stone's sheep ewes during the growing season using logistic regression (Hosmer and Lemeshow 1989; Menard 2002) and the information–theoretic approach (Burnham and Anderson 2002). We developed 11 ecologically plausible models 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 variables 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). We used Akaike's information criterion corrected for small sample sizes ($\mathrm{AIC_c}$; $n/K < 40$, where K is the number of parameters in a model) to rank the suite of models (Burnham and Anderson 2002). Akaike 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 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 $w_i \geq 0.95$. We calculated P values for coefficients of selection (β_i) and odds ratios, and their SE, to quantify the importance of the variables in the models. Odds ratios indicate the likelihood of an attribute associating with one group relative to another (Zar 1999). We validated models using the areas under the receiver operating characteristic curves (ROC) (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). We defined models with ROC scores >0.7 as being acceptable at distinguishing between nursery and non-nursery groups.

Plant community associations

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. We developed ordinations for both plant species and sites to describe vegetative associations and intrasexual differences in habitat use. Pearson's correlation coefficients (r) and their associated P values, determined from a two-tailed sample distribution (Zar 1999), were used to characterize the relationship between an ordination axis and environmental variable or plant species. We completed all analyses associated with NMS using PC-ORD version 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). 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 and three outlier plots where Stone's sheep were observed using licks were removed from the ordination analysis to enhance detection of relationships between broad community composition and environmental factors (McCune and Grace 2002). There were 65 plant 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), percent herbaceous, percent shrubs, percent trees, percent bare, and percent 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 plant species data because of the large number of zeros (missing species per transect) (McCune and Grace 2002). Stress, expressed as a percentage, measures the poorness of fit between the ordination and the measured ecological distances, with lower stress being attained when points fall closer to a monotonic line (McCune and Grace 2002). We set a stress value <15 as an acceptable level of fit, given that most data from ecological communities have a stress value 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

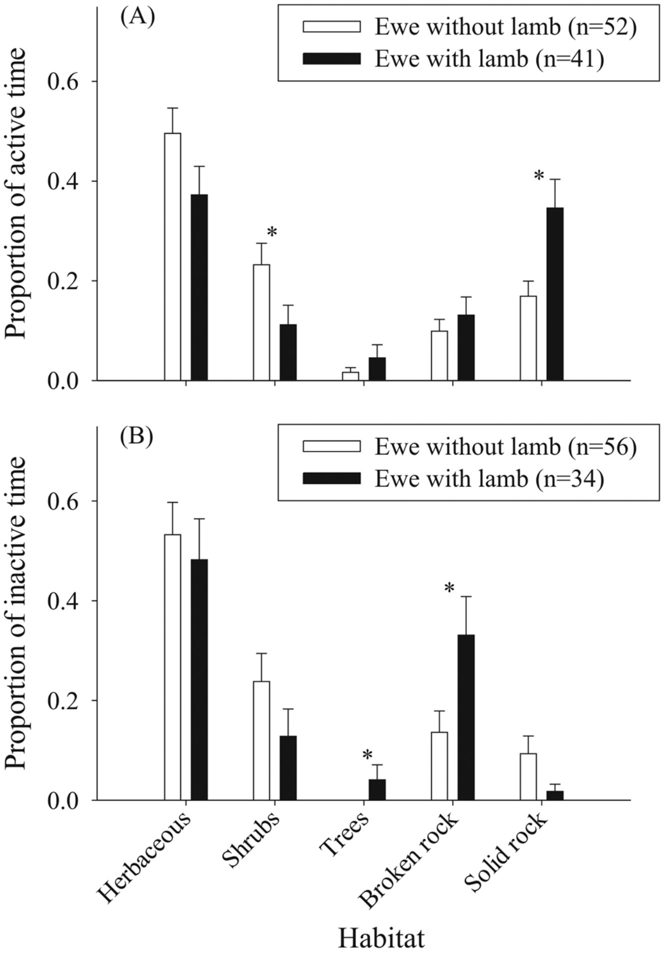
Behavioural observations were obtained over 126 h from 93 individuals, 78 of which were used in the analysis of complete bouts. Stone's sheep in the B–P appeared to differentiate into nursery and non-nursery groups. Nursery groups contained 0.82 ± 0.04 lambs/ewe (mean ± SE; n = 35) during the spring and summer, indicating that most females in nursery groups had lambs. Only two nursery groups contained fewer than 0.50 lambs/ewe. Mean (±SE) adult group size of female Stone's sheep in the B–P was 4.3 ± 0.3 (n = 78, range 1–12) and did not differ between groups with lambs (3.9 ± 0.4, n = 35) and groups without lambs (4.7 ± 0.5, n = 43, P = 0.448).

Female Stone's sheep in the B–P spent more time active (33.0 ± 3.1 min (mean ± SE), n = 51) than inactive (24.4 ± 1.7 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 (25.0 ± 3.1 min, n = 20) and inactive (22.0 ± 2.2 min, n = 30) bouts (P = 0.502). Nonmaternal ewes were active for significantly longer bouts (39.0 ± 4.4 min, n = 31) than inactive bouts (10.9 ± 2.4 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).

Female Stone's sheep spent a large proportion of their active time in herbaceous habitats with no differences between ewes with and without lambs (0.37 ± 0.06 for 41 maternal ewes, 0.50 ± 0.05 for 52 nonmaternal ewes, P = 0.108; Fig. 1A). Proportions of active time in tree (P = 0.184) and broken rock (P = 0.704) habitats were also similar between groups. Ewes with lambs, however, spent proportionally more of their active time in solid rock escape features (0.35 ± 0.06) than did ewes without lambs (0.17 ± 0.03; P = 0.019). In contrast, the nonmaternal ewes spent significantly more active time (0.23 ± 0.04) in shrub habitat than did ewes with lambs (0.11 ± 0.04; P = 0.003).

Nonmaternal ewes showed similar patterns in the habitats that they used while inactive (bedded; Fig. 1B), with the majority of that time spent in herbaceous habitat (0.05 ± 0.07, n = 56) followed by shrubs (0.24 ± 0.06). Maternal ewes also spent the greatest proportion of inactive time in herbaceous habitats (0.48 ± 0.08, n = 34). Unlike active bouts, they spent very little time in cliffs and outcrops (solid rock escape features, 0.018 ± 0.015) and increased the proportion of time bedded in broken rock escape features such as scree and talus (0.33 ± 0.08). Use of tree habitat (P = 0.009) and broken rock escape features (P = 0.012) by maternal females was significantly greater than those used by nonmaternal females, which were never observed bedded in tree habitat (Fig. 1B).

Fig. 1. The proportion (mean + SE) of active (A) and inactive (B) times that maternal and nonmaternal female Stone's sheep (*Ovis dalli stonei*) spent in different habitats in the Besa–Prophet area of northern British Columbia. *, $P < 0.05$ as determined by the Mann–Whitney U test.



No intrasexual differences in behaviours occurred within active bouts. Both maternal (0.67 ± 0.03, n = 41) and nonmaternal (0.69 ± 0.03, n = 52) ewes spent more than two-thirds of their time foraging. Ewes spent 0.16 ± 0.01 (n = 93) of the time standing, 0.12 ± 0.01 walking, and 0.03 ± 0.004 being alert. Maternal Stone's sheep were first observed on 8 June and they only nursed a small proportion of the active time (0.02 ± 0.005). Group size was not a significant predictor of foraging efficiency (r^2 = 0.002, n = 93, P = 0.704).

Habitat use

Intrasexual differences in habitat use between groups of female Stone's sheep included phenology, broken rock area, distance to nearest escape feature, escape area, percent shrub cover, and percent exposed soil/rock cover (Table 1). Throughout the growing season, groups with lambs were found associated with older phenological stages (2.94 ± 0.091) than those without lambs (2.70 ± 0.113). In comparison with non-nursery groups, groups of ewes with lambs tended to be closer to the nearest escape feature (8.6 vs.

Table 1. Intrasexual differences in habitat attributes used by groups of female Stone's sheep (*Ovis dalli stonei*) in the Besa–Prophet area of northern British Columbia, 2002–2003.

	Ewes with lambs (*n* = 35)			Ewes without lambs (*n* = 43)			
Feature	Mean ± SE	Median	Min., max.	Mean ± SE	Median	Min., max.	*P*
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

14 m) and were associated with larger nearest escape features (1.7 vs. 0.41 ha) and with larger broken rock escape features (1.6 vs. 0.47 ha) (Table 1). These escape features were typically 3–4 times larger in size for groups with lambs. 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 than sites used by ewes with lambs. Sites used by nursery groups always had some exposed soil/rock (Table 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 2). Indeed, five of the top six competing models contained distance to nearest escape feature and area of nearest escape feature (Table 2).

Within the top model predicting intrasexual differences, area of the nearest escape feature was the most influential variable (Table 2). Groups containing lambs were ~1.8 times more likely to be associated with a larger nearest escape feature (as determined by odds ratios). 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 2). 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 phenology variable in the other 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. 2). The majority (96.7%) of the variation in plant species found at sites used by female Stone's sheep was captured by the NMS ordination (Fig. 2), 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). More important were the environmental attributes of axis 2, which explained the majority of variation (62.3%) 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). Shrub cover was the most negatively correlated environmental variable (r = –0.632). Shrub cover, availability index, slope, herbaceous cover, and tree cover all had negative associations with both ordination axes. Only herbaceous cover and exposed soil/rock were not significantly related to axis 2. The positive correlations between ordination axes and date indicate that Stone's sheep associated with the plant species at the top of Fig. 2 later in the summer. The elevational gradient of plant species is highlighted by the distribution of species in Fig. 2. 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. 2, whereas species associated with higher elevations such as *Pedicularis groenlandica* and *Saxifraga flagellaris* are found near the top (Fig. 2).

Intrasexual groups of female Stone's sheep did not separate into distinct clusters in the ordination of use sites (Fig. 3). 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

Table 2. The best logistic models, as determined by corrected Akaike's information criteria (AIC_c), and their associated variables for characterizing intrasexual segregation of nursery and non-nursery groups of female Stone's sheep in the Besa–Prophet area of northern British Columbia.

Models and variables	*K*	*n*	LL	β_i ± SE	Odds ± SE	*P*
Nearest escape feature + escape area[*]	3	78	–47.345			
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[†]	4	78	–46.455			
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[‡]	5	78	–45.848			
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[§]	5	78	45.851			
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[‖]	6	78	–45.218			
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[¶]	4	78	–48.239			
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

Note: Models are arranged in order of parsimony based on AIC_c in descending rank, with number of parameters (*K*), sample size (*n*), log likelihood (LL), variable coefficients (β_i ± SE), odds ratios (odds ± SE), and probabilities (*P*) included. Statistics in footnotes include AIC_c, change in AIC_c ($\Delta\text{AIC}_\text{c}$) from the best model, Akaike weights (w_i), and area under the receiver operating characteristic curve (ROC).

[*] $\text{AIC}_\text{c} = 100.852$, $\Delta\text{AIC}_\text{c} = 0.000$, $w_i = 0.297$, ROC = 0.707.

[†] $\text{AIC}_\text{c} = 101.239$, $\Delta\text{AIC}_\text{c} = 0.387$, $w_i = 0.245$, ROC = 0.746.

[‡] $\text{AIC}_\text{c} = 102.252$, $\Delta\text{AIC}_\text{c} = 1.399$, $w_i = 0.147$, ROC = 0.744.

[§] $\text{AIC}_\text{c} = 102.258$, $\Delta\text{AIC}_\text{c} = 1.406$, $w_i = 0.147$, ROC = 0.741.

[‖] $\text{AIC}_\text{c} = 103.282$, $\Delta\text{AIC}_\text{c} = 2.430$, $w_i = 0.088$, ROC = 0.747.

[¶] $\text{AIC}_\text{c} = 104.806$, $\Delta\text{AIC}_\text{c} = 3.954$, $w_i = 0.041$, ROC = 0.710.

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 high abundance of shrub cover were almost always associated with ewes without lambs (Fig. 3).

Numerous graminoid, forb, and shrub species were associated with sites used by Stone's sheep in the B–P study area (Appendix Table A1). Subalpine fir (*Abies lasiocarpa* (Hook). Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and *Populus* L. were removed from the ordination because of their rarity of occurrence at the use sites, although Stone's sheep were observed on rare occasions browsing new subalpine fir tips and *Populus* buds. *Elymus*, *Festuca*, and *Poa* were the most frequently described graminoids at sites used by female Stone's sheep. *Poa*, *Carex*, and *Trisetum spicatum* were the graminoids most positively correlated with axis 2, indicating that female Stone's sheep associated with these species at higher elevations later in summer. Sheep generally associated with *Elymus* and *Agropyron* at lower elevation sites earlier in the growing season. Both of these were negatively correlated with the ordination axes. *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*a*), were negatively correlated with axis 2 and found in >10% of the sites used by Stone's sheep in the B–P (Appendix Table A1). Only *Astragalus alpinus* 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 (Appendix Table A1), and supports the direction of the shrub and moss/lichen vectors (Figs. 2, 3) used for describing the plant community associations of female Stone's sheep.

The similar direction (Figs. 2, 3), sign, and correlation as-

Fig. 2. Nonmetric multidimensional scaling (NMS) ordination of plant communities used by female Stone's sheep in the Besa–Prophet area of northern British Columbia showing the position of plant 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 the species for each plant (as noted in Appendix Table A1).

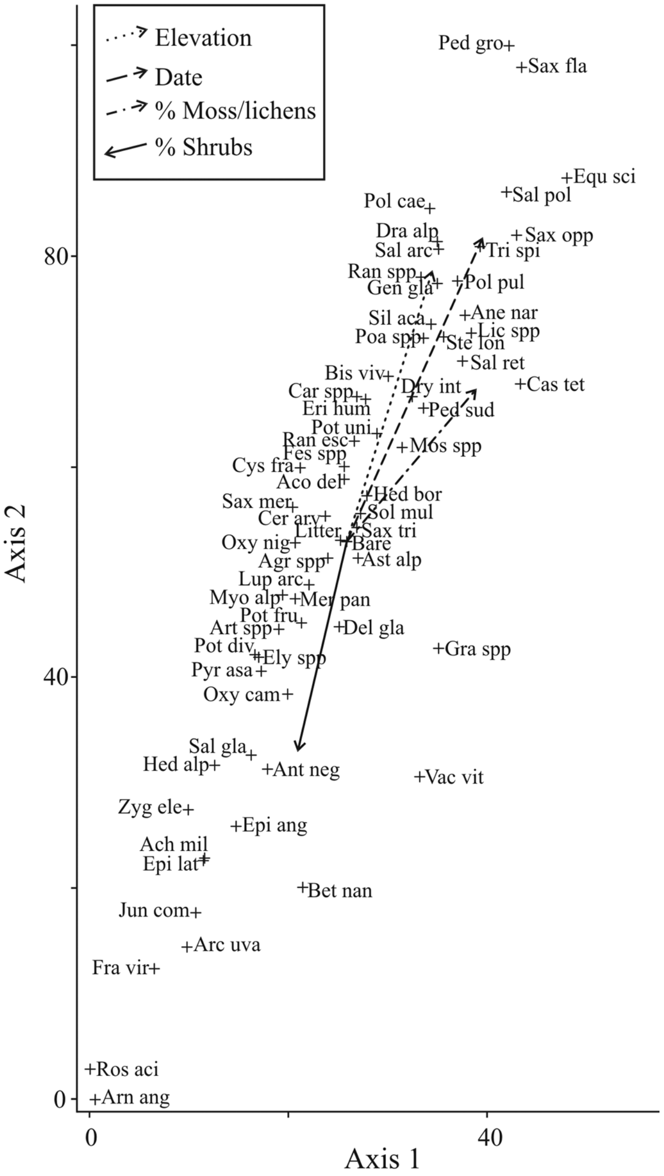
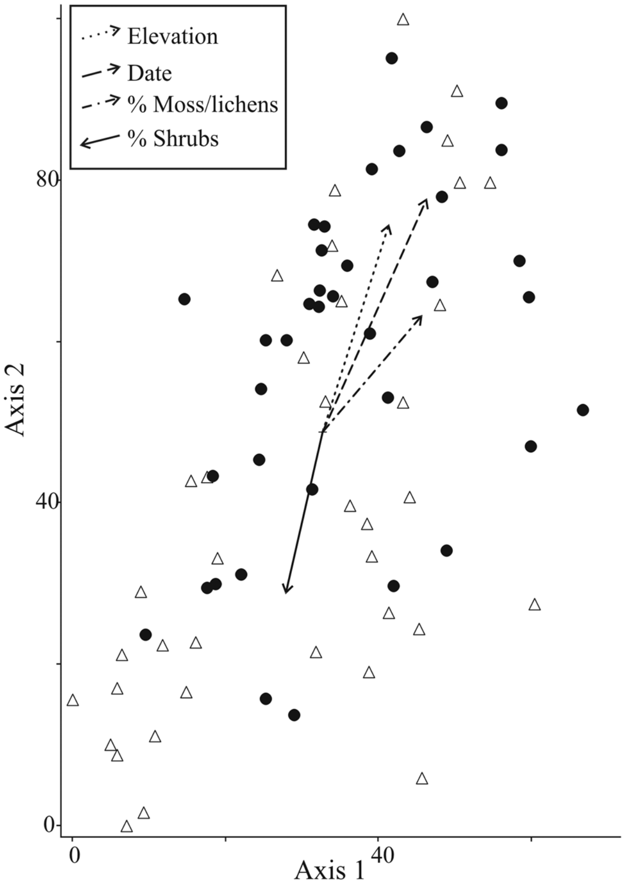


Fig. 3. NMS ordination showing the position of 75 sites used by female Stone's sheep in the Besa–Prophet area of northern British Columbia relative to the plant species composition and associated environmental attributes. Lambs present (●) and absent (△) from sites used by female Stone's sheep. Vectors on the ordination indicate direction and strength of correlations between the axis scores and the most important environmental attributes.



sociated with date and elevation vectors suggested a possible relationship between correlates. Indeed, the elevational movement exhibited by female Stone's sheep in their use of plant communities followed a temporal trend. 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. The relationship was weaker for ewes with lambs, but it was still significant ($r = 0.48$, $n = 75$, $P = 0.002$). 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 until the end of data collection during the last week of July. This was reflected in the ordination for which phenology was only weakly correlated with both axes, indicating that sheep did not associate with the phenology of plant communities on a continuum as they did with elevation.

Discussion

Intrasexual segregation of female ungulates has not typically been considered 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 female Stone's sheep in northern British Columbia. These data reflected the combined influence of nutrition and predation, which has been noted for other mountain sheep (Risenhoover and Bailey 1985; Festa-Bianchet 1988; Bleich et al. 1997; Rachlow and Bowyer 1998; Corti and Shackleton 2002) and mountain bovids (Geist 1971; Shank 1985; Kohlmann et al. 1996; Toïgo 1999).

Activity budgets and behaviour

Female Stone's sheep 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 than nonmaternal females, 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 that of Stone's sheep in other British Columbian populations (63%–66% of time; Seip and Bunnell 1985*a*; Geist 1971). Surprisingly, Stone's sheep in the B–P spent considerably less active time foraging (~67% for maternal ewes 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 with those of 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 non-nursery 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 by both Dall's and bighorn sheep (Risenhoover and Bailey 1985; Frid 1997; Rachlow and Bowyer 1998). 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).

Assuming the age and mass of our study animals were similar to other Stone's sheep (Seip and Bunnell 1984) and Dall'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 (Elliott 1978; Seip and Bunnell 1985*b*), 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*a*). Festa-Bianchet (1988) documented that female bighorn sheep using areas with lower forage biomass spent more time foraging and less time biting vegetation than females in areas with more available forage. Animals experiencing greater energy demands (i.e., lactation) should feed more intensively as observed in maternal bighorn sheep that had higher bite rates than nonmaternal females (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 influences 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 had golden eagles (*Aquila chrysaetos* (L., 1758)) and coyotes (*Canis latrans* Say, 1823) as the only common predators (Hoefs and Cowan 1979). The B–P area contains an abundance of grizzly bears (*Ursus arctos arctos*, L., 1758), coyotes, golden eagles, wolverines (*Gulo gulo* (L., 1758)), and wolves (*Canis lupus* L., 1758) (Bergerud and Elliott 1998), which were observed in sheep habitat throughout the course of the study. The diversity and abundance of predators in the B–P suggest that it is potentially a riskier place to live. Therefore, the decrease in proportion of active time spent foraging by female Stone's sheep 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, 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 females, albeit with high variation. How activity levels change relative to environmental constraints or predation risk, interacting with maternal status, is not clear.

Habitat use and plant community associations

The high use of herbaceous habitat (Fig. 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 on sheep 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 female Stone's sheep that are 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 by 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, which are both 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 are very cryptic in rocky habitats, and the use of broken rock habitat while bedded may be an antipredator response that capitalizes on this trait. Broken rock habitat can also be noisy, resulting in the possibility that 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 the escape cover (Corti and Shackleton 2002).

Predictive modeling (Table 2) and pairwise comparisons (Table 1) of differences between groups of ewes with and without lambs contribute to the increasing evidence supporting the trade-off used by female Stone's sheep during spring and summer. The simplest model that best described 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 become increasingly important (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 sizes of desert bighorn sheep (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 non-nursery groups also involved features associated with avoiding predators. The amount of exposed soil and rock, the size of broken escape features, and the 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 non-nursery 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 farther 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 among 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 rock 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. 1), but were not reflected in the measures of habitat attributes (Table 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), because animals respond to environmental attributes in a hierarchical fashion (Johnson 1980; Schaefer and Messier 1995; Johnson et al. 2001).

Phenology and shrub cover were the only habitat attributes that differed between nursery and non-nursery groups in pairwise comparisons (Table 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, spring vegetation growth had already commenced, although the progression of green-up was in the early stages. Stone's sheep maternal females were observed using sites with plants in slightly older phenological stage than sites used by nonmaternal females. New plant growth has been shown to contain the highest percentage of crude protein in graminoids from alpine ranges used extensively by bighorn sheep (Johnston et al. 1968).

The 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 can be a useful tool for describing plant community associations of herbivores. A stress value <10 indicates a good measure of community structure with no real risk of drawing inappropriate conclusions (Clarke 1993). 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 gradients of time, elevation, and cover of shrubs and moss/lichens. The ordination of plant species, and the subsequent correlation between elevation and date, described the altitudinal gradient over which sheep moved from spring to summer. 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. 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 selecting a specific phenological stage as they move up in elevation where the onset of vegetative growth occurs later (Seip 1983). Such phenological tracking allows animals access to forage with higher levels of crude protein (Albon and Langvatn 1992) and fewer chemical defenses (Bryant et al. 1991).

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*a*), but unlike bighorn sheep, they often ingest terrestrial lichen and moss (Luckhurst 1973; Hoefs and Cowan 1979; Simmons et al. 1984; Seip and Bunnell 1985*a*). 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

Table 3. Summary of whether the predictions of the predation-risk, forage-selection, and activity-budget hypotheses were met (fit) to explain the differences between nursery and non-nursery groups of female Stone's sheep in the Besa–Prophet area of northern British Columbia (2002, 2003).

Prediction	Fit
Predation-risk hypothesis	
Maternal females should use safer habitats, where offspring are less vulnerable to predation at the expense of foraging opportunities, by associating with	
(*i*) steeper slopes	No
(*ii*) closer escape features	Yes
(*iii*) larger escape features	Yes
(*iv*) sites of older phenological stages	Yes
Forage-selection hypothesis	
Maternal females should use high-quality habitat, where foraging opportunities are greater, to meet the high-energy demands associated with lactation by choosing sites with	
(*i*) younger phenological stages	No
(*ii*) greater forage availability	No
Activity-budget hypothesis	
Maternal females should increase their forage intake to compensate for higher energy demands by spending proportionally	
(*i*) more time foraging	No
(*ii*) more time walking*	No
(*iii*) more time active*	No[†]

*Prediction is not associated with forage intake but may lead to segregation under the activity-budget hypothesis (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000).

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

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* and *Agropyron* graminoids; *Achillea*, *Myosotis*, *Oxytropis*, and *Zygadenus* forbs; and *Arctostaphylos* and *Rosa* shrubs (Luckhurst 1973, Seip and Bunnell 1985*a*). 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. During summer, prominent forages observed in the diet of Stone's sheep include *Carex*, *Poa*, *Festuca*, *Astragalus*, and *Lupinus* (Luckhurst 1973; Seip and Bunnell 1985*b*), which are all associated with the 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.

Trade-offs and intrasexual selection strategies

Constraints imposed on maternal ungulates relative to the energetic demands of lactation are confounded by the vulnerability of young to predation. Evidence from behavioural observations, vegetation attributes, and habitat use support the predation-risk hypothesis in explaining the intrasexual segregation of female Stone's sheep during the spring and early summer (Table 3). Although our data do not definitively reject Ruckstuhl and Neuhaus' (2000) activity-budget hypothesis, there was much less support for it. In order for the less energetically constrained nonmaternal ewes to conform to the activity-budget hypothesis, they should spend proportionally less time 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. Although not statistically different, proportions of time foraging and walking were both 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 may indicate some support for the activity-budget hypothesis. If activity budgets are sufficiently different, segregation may occur (Ruckstuhl and Neuhaus 2000, 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). 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 female Stone's sheep in the B–P. Instead, data from our study conform to the predation-risk hypothesis because female Stone's sheep segregated relative to reproductive status, more as a result of apparent predation constraints than differences in behaviour or forage quality and quantity. Maternal Stone's sheep 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 behaviours. Plant communities were similar between nursery and non-nursery groups, both associating with 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 bighorn sheep (Festa-Bianchet 1988; Berger 1991).

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Appendix A (continued on subsequent pages)

Table A1. Pearson's correlation coefficients (*r*) and frequency of species occurrence at 75 sites used by female Stone's sheep (*Ovis dalli stonei*) in the Besa–Prophet area of northern British Columbia along two axes of the nonmetric multidimensional scaling (NMS) ordination.

		Pearson's *r*		
Abbreviation	Taxon	Axis 1	Axis 2	Frequency (%)
Graminoids				
Agr spp	*Agropyron* Gaertn. spp.	–0.105	–0.054	10.7
Car spp	*Carex* L. spp.	0.081	0.721*	30.7
Ely spp	*Elymus* L. spp.	–0.907*	–0.697*	61.3
Fes spp	*Festuca* L. spp.	–0.037	0.666*	62.7
Gra spp	Unknown graminoid spp.	0.433*	–0.294*	21.3
Poa spp	*Poa* L. spp.	0.575*	0.881*	40.0
Tri spi	*Trisetum spicatum* (L.) Richter	0.535*	0.686*	8.0
Forbs				
Ach mil	*Achillea millefolium* L.	–0.727*	–0.938*	42.7
Aco del	*Aconitum delphiniifolium* DC.	0.546*	0.725*	74.7
Ane nar	*Anemone narcissiflora* L.	0.667*	0.743*	22.7
Ant neg	*Antennaria neglecta* Greene	–0.350*	–0.585*	13.3
Arn ang	*Arnica angustifolia* Vahl	–0.641*	–0.828*	6.7
Art spp	*Artemisia* L. spp.	–0.368*	–0.274*	18.7
Ast alp	*Astragalus alpinus* L.	0.056	–0.047	10.7
Bis viv	*Bistorta vivipara* (L.) S.F. Gray	0.399*	0.930*	54.7
Cer arv	*Cerastium arvense* L.	–0.368*	0.263*	54.7
Cys fra	*Cystopteris fragilis* (L.) Bernh.	–0.406*	0.375*	28.0
Del gla	*Delphinium glaucum* S. Wats.	–0.047	–0.300*	18.7
Dra alp	*Draba alpina* L.	0.326*	0.626*	10.7
Epi ang	*Epilobium angustifolium* L.	–0.634*	–0.944*	40.0
Epi lat	*Epilobium latifolium* L.	–0.491*	–0.634*	6.7
Equ sci	*Equisetum scirpoides* Michx.	0.702*	0.676*	10.7
Eri hum	*Erigeron humilis* Graham	0.153	0.670*	21.3
Fra vir	*Fragaria virginiana* Duchesne	–0.728*	–0.937*	26.7
Gen gla	*Gentiana glauca* Pallas	0.398*	0.662*	9.3
Hed alp	*Hedysarum alpinum* L.	–0.728*	–0.718*	22.7
Hed bor	*Hedysarum boreale* Nutt.	–0.022	0.345*	21.3
Lup arc	*Lupinus arcticus* S. Wats.	–0.508*	–0.338*	44.0
Mer pan	*Mertensia paniculata* (Ait.) G. Don	–0.719*	–0.461*	45.3
Myo alp	*Myosotis alpestris* F.W. Schmidt	–0.829*	–0.404*	49.3
Oxy cam	*Oxytropis campestris* (L.) DC.	–0.300*	–0.453*	10.7
Oxy nig	*Oxytropis nigrescens* (Pallas) Fisch. ex DC.	–0.632*	–0.011	44.0
Ped gro	*Pedicularis groenlandica* Retz.	0.534*	0.951*	16.0
Ped sud	*Pedicularis sudetica* Willd.	0.579*	0.589*	26.7
Pol cae	*Polemonium caeruleum* L.	0.396*	0.929*	26.7
Pol pul	*Polemonium pulcherrimum* Hook.	0.555*	0.763*	22.7
Pot div	*Potentilla diversifolia* Lehm.	–0.459*	–0.326*	8.0
Pot uni	*Potentilla uniflora* Ledeb.	0.404*	0.843*	61.3
Pyr asa	*Pyrola asarifolia* Michx.	–0.680*	–0.600*	28.0
Ran esc	*Ranunculus eschscholtzii* Schlecht.	0.054	0.406*	12.0
Ran spp	*Ranunculus* L. spp.	0.382*	0.789*	14.7
Sax fla	*Saxifraga flagellaris* Willd. ex Sternb.	0.551*	0.867*	6.7
Sax mer	*Saxifraga mertensiana* Bong.	–0.256*	0.093	8.0
Sax opp	*Saxifraga oppositifolia* L.	0.495*	0.520*	6.7
Sax tri	*Saxifraga tricuspidata* Rottb.	0.455*	0.350*	85.3
Sil aca	*Silene acaulis* (L.) Jacq.	0.612*	0.924*	42.7
Sol mul	*Solidago multiradiata* Ait.	0.490*	0.548*	77.3
Ste lon	*Stellaria longipes* Goldie	0.570*	0.698*	24.0
Zyg ele	*Zygadenus elegans* Pursh	–0.829*	–0.817*	29.3
Dwarf Shrubs				
Arc uva	*Arctostaphylos uva-ursi* (L.) Spreng.	–0.650*	–0.964*	26.7

Table A1 (*concluded*).

		Pearson's *r*		
Abbreviation	Taxon	Axis 1	Axis 2	Frequency (%)
Cas tet	*Cassiope tetragona* (L.) D. Don	0.653*	0.342*	8.0
Dry int	*Dryas integrifolia* Vahl	0.709*	0.912*	58.7
Sal arc	*Salix arctica* Pallas	0.407*	0.755*	16.0
Sal pol	*Salix polaris* Wahlenb.	0.700*	0.892*	22.7
Sal ret	*Salix reticulata* L.	0.745*	0.671*	28.0
Vac vit	*Vaccinium vitis-idaea* L.	0.225*	–0.420*	9.3
Shrubs				
Bet nan	*Betula nana* L.	–0.180	–0.810*	21.3
Jun com	*Juniperus communis* L.	–0.492*	–0.705*	6.7
Pot fru	*Potentilla fruticosa* L.	–0.671*	–0.699*	53.3
Ros aci	*Rosa acicularis* Lindl.	–0.767*	–0.915*	18.7
Sal gla	*Salix glauca* L.	–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

*$P \leq 0.05$ for the relationship between an ordination axis and a plant species.