

Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance

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Summary. The migratory and foraging behavior of individually marked bighorn ewes (*Ovis canadensis*) was studied to test the hypothesis that forage quality determined seasonal range selection. Forage quality was monitored through analysis of fecal crude protein. Ewes in the study population utilized two distinct ranges differing in elevation and possibly predation risk. Pregnant ewes migrated in May from the low-elevation winter range to lambing areas at higher elevation, before plant growth had started there. In so doing, they moved from a range of high-quality forage to one of low-quality forage, apparently to avoid predation on newborn lambs. Non-pregnant adult ewes migrated later. Most yearling ewes (which are not pregnant) migrated with the adult ewes to the lambing areas, but returned to the winter range within a few days, then migrated again to high-elevation areas in June. Forage quality was higher at high elevation from mid-June at least through July, but forage availability appeared to be lower than in the winter range. Seasonal range selection is likely determined by a combination of nutritional and antipredator constraints. The antipredator strategy of bighorn ewes does not always allow them to utilize the range with the best forage.

Key words: Bighorn sheep – Foraging – Migration – Predator avoidance – Range selection

Optimal foraging models attempt to predict how animals may select the best foraging sites at the best times (Pyke 1984; Krebs and McCleery 1984). Applications of foraging theory to ungulates have emphasized selection of nutritious plants and plant parts (Westoby 1974; Owen-Smith and Novellie 1982). Several constraints other than forage quality may be important. For example, heat exposure (Belovsky 1981), predation risk (Berger 1978), mineral requirements (Hebert and Cowan 1971), forage availability (Vivas and Saether 1987) and avoidance of toxic compounds (Cooper and Owen-Smith 1985) may affect foraging behavior independently of forage quality. Predicting foraging behavior may be more difficult when constraints are conflicting, for example if nutritious forage and sources of minerals are

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not adjacent, or if predation pressure is greater in areas of preferred forage.

Most bighorn sheep (*Ovis canadensis*) migrate seasonally over an altitudinal gradient (Geist 1971). Onset of vegetation growth occurs later at higher elevations (Johnston et al. 1968; Hoefs 1979). By migrating to higher elevations in spring and summer, bighorns may have access to nutritious, growing forage for an extended time. Hebert (1973) demonstrated experimentally that migration resulted in greater body growth of yearling bighorns. Langvatn and Albon (1986) reported that migratory red deer (*Cervus elaphus*) hinds were heavier than sedentary hinds. Seasonal migrations to exploit temporal differences in vegetation phenology have been reported for other ungulates (Klein 1965; Sinclair 1977; Oosenbrug and Theberge 1980; Hamr 1984; Berger 1986). White (1983) pointed out that small differences in the quality of summer forage eaten by northern ungulates could have major effects on growth and reproductive success. Differences in reproductive performance among bighorn populations have been attributed to differences in forage quality (Geist 1971; Shackleton 1973).

Several aspects of bighorn sheep behavior appear to be antipredator adaptations. These include gregariousness, traditional dispersion patterns, traditional migration routes, and use of areas close to escape terrain such as cliffs and steep hillsides (Geist 1971). Bighorn ewes in groups of less than five may forage less efficiently and spend more time alert (Berger 1978; Risenhoover and Bailey 1985). As distance from escape terrain increases, ewes may increase the proportion of time spent scanning for predators (Risenhoover and Bailey 1985), and their heart rate may increase (MacArthur et al. 1982), possibly indicating greater anxiety. A trade-off between security from predators and access to high-quality forage may exist among bighorn ewes.

Here I describe the migratory and foraging behavior of individually marked bighorn ewes in a population utilizing distinct winter (low-elevation) and summer (alpine) ranges. The objective of this study was to test the hypothesis that ewes always select the seasonal range where forage has the highest protein content. Protein (nitrogen) content is generally acknowledged to determine the nutritive value of forage for ruminants (Klein 1965; Klein and Schonheyder 1970; Hebert 1973; Walker et al. 1975; Owen-Smith and Novellie 1982; Bryant et al. 1983; Robbins 1983). Nitrogen enrichment of forage can improve the reproductive performance of wild cervids (Anderson 1983; Iason et al. 1986).

Materials and methods

Study population. The study population was referred to as the Sheep River ewes in Festa-Bianchet (1986a). Bighorns were marked with plastic ear tags. Twenty of 49 ewes were recognizable by May 1981. The proportion of tagged ewes increased to 85% by May 1982, and afterwards was always >85%. Data reported here were collected from 105 ewes from May 1981 to August 1987.

Study area. Bighorn ewes in the study population utilized two distinct ranges in southwestern Alberta, Canada (50°N, 114°W). The winter range was in the foothills of the Rocky Mountains, where all areas utilized by ewes (approximately 10 km²) were within 1 km of a road, at elevations of 1420 to 1740 m. This range was also utilized by two other groups of ewes (Festa-Bianchet 1986a) and by rams (Festa-Bianchet 1986b). The winter range included south-facing grassy slopes kept clear of snow by chinook winds. A shale canyon provided escape terrain and included several salt licks.

The alpine range was in the Rocky Mountains, approximately 12 km west of the winter range. The area between the two ranges was almost entirely forested and was not used by the ewes other than during migration. The alpine range was at 1800 to 2550 m elevation, and extended over approximately 38 km². Most of this area was covered by bare rock and scree slopes. Sheep utilized small habitat patches that included alpine meadows, open coniferous forest, krumholtz, and other areas with sparse vegetation. No known mineral licks existed in the alpine range of the study population.

Observations. The winter range was searched regularly, and the identity and location of all marked ewes were noted. In May–October, the winter range was searched on average 5.8 times/month. Migration dates of marked ewes were estimated from observations during searches, casual observations in other days, and while observing behavior. In 1987, only approximate dates of migration were obtained, and because spring migration may have occurred significantly earlier than in other years (see Results), data for 1987 were not included in statistical analyses. In winter, when all ewes were in the winter range, an average of 97% of those marked were located during each search, therefore searching efficiency was very high.

Observations of behavior were conducted in May–September 1984 (427 hours, 61% in the winter range) and 1985 (358 hours, 63% in the winter range). Ten-minute focal-animal samples were collected from foraging ewes. The time spent biting vegetation was recorded using a stopwatch. The occurrence of browsing (five or more bites at browse) and number of alert postures were also noted.

Time budgets were constructed by observing 1–4 marked ewes and noting transition times between foraging (including biting vegetation, alert postures, and walking between forage patches) and other activities (resting, standing, extended walking, or licking at a mineral lick). In June–July 1984, ewes were observed for as long as possible. In August 1984 and in 1985, the day was divided into seven 2-hour periods from 6:00 to 20:00 hours, and observations included one or more of these periods.

Fecal analyses. Fresh fecal samples were collected in the two ranges. They were dried and analyzed for crude protein

(nitrogen × 6.25) in the Soil & Feed Testing Laboratory of Alberta Agriculture.

Hebert (1973) found that fecal crude protein of captive bighorns was correlated with forage protein and digestibility. Research on domestic sheep has confirmed the suitability of fecal crude protein as an indicator of forage quality (Fels et al. 1959; O'Donovan et al. 1963; Walker et al. 1975). Fecal crude protein has been used to assess forage quality in studies of wild ungulates (Klein 1965; Shank 1979; Seip 1983; Leslie and Starkey 1985, 1987; Renecker and Hudson 1985). Mould and Robbins (1981), Hobbs (1987), and Robbins et al. (1987) criticized this use of fecal crude protein because it is affected by secondary compounds, synthesized by plants as a defense against herbivores (Freeland and Janzen 1974; Sinclair and Smith 1984). These compounds bind with proteins, making them undigestible and thereby inflating the amount of fecal protein without a corresponding increase in diet quality. Mould and Robbins (1981) found a severe alteration of the forage protein/fecal protein correlation only when captive elk were fed diets with very high contents of secondary compounds. Otherwise, forage protein explained 97% of the variance in fecal protein.

Secondary compounds are found mostly in browse (Bryant et al. 1983; Sinclair and Smith 1984; Robbins et al. 1987), and bighorn sheep are mostly grazers (Hobbs et al. 1983). Free-ranging ruminants avoid plants with high concentrations of secondary compounds (Cooper and Owen-Smith 1985). Monitoring the frequency of browsing during focal-animal observations allowed a relative estimate of its prevalence in the two ranges.

Statistical analyses. Parametric statistics (ANOVA and *t*-tests) were used to analyze data on migratory and foraging behavior. ANOVAs were followed by Scheffe's multiple range test to detect significant pairwise differences. Frequency distributions were compared using *G*-tests, and Mann-Whitney *U* tests were used for data reported as percentages (Sokal and Rohlf 1981). To analyze data on migration from the winter to the alpine range, the estimated date of departure of each ewe was assigned a numerical value (April 30 = day 1). Migration from the alpine to the winter range could not be quantified in a similar way because most ewes moved more than once between the two ranges. Therefore, the number of days spent by each ewe in the winter range from 20 June to 30 November was used to quantify the return migration. These dates were chosen to avoid including days spent in the winter range before migrating to the summer range in the spring, and to include all days before final return to the winter range in autumn.

The average of all focal-animal observations for each ewe from each range was used for analyses. When time-budget data were collected from the same ewe in the same 2-h period in the same range, the average of all observations was utilized. The average departure date from the winter range in the spring did not vary between 1981 and 1986 (see Results), and some pooled analyses were performed on a subset of 141 data points. To balance sample sizes according to ewe age and reproductive status, data collected in two years from 40 ewes were included in the subset. These included ewes that were one or two years old, and ewes that failed to conceive in one year. The time spent in the winter range during 20 June–30 November varied between years, and many analyses were restricted to data collected

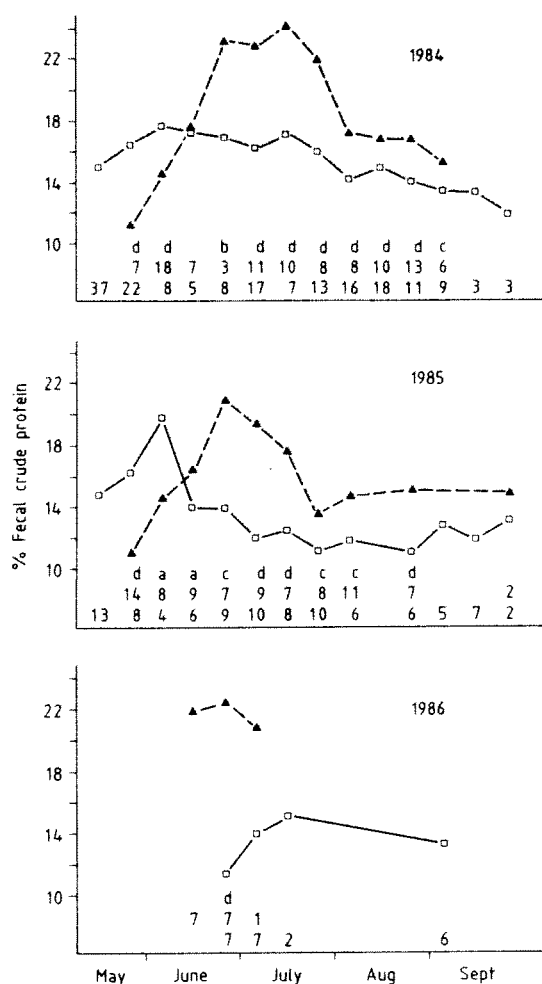


Fig. 1. Average crude protein content (percent of dry weight) of feces of bighorn ewes, averaged over 10-day periods from 10 May to 30 September in the winter (squares) and alpine (triangles) range, 1984–1986. Numbers above ordinate indicate sample size: alpine range on top, winter range below. Letters above sample sizes indicate results of Mann-Whitney *U*-tests: *a* $P < 0.1$; *b* $P < 0.025$; *c* $P < 0.01$; *d* $P < 0.001$.

Table 1. Frequency of browsing by bighorn ewes in the winter and alpine ranges during 10-minute focal-animal observations in May–September. Numbers of observations in parentheses

Year	% of observations with browsing		<i>G</i>	<i>P</i>
	Winter range	Alpine range		
1984	11.8 (119)	57.5 (80)	47.85	<0.001
1985	13.8 (58)	80.7 (57)	55.81	<0.001

Table 2. Seconds spent biting vegetation by foraging bighorn ewes during 10-minute observations in May–August. *N* refers to the number of ewes: when ewes were observed more than once, the average of all observations was used for analysis

Year	Winter range			Alpine range			<i>t</i>	<i>P</i>
	<i>N</i>	mean	SD	<i>N</i>	mean	SD		
1984	34	542	26.3	29	488	34.8	5.159	<0.001
1985	34	544	22.3	40	510	36.1	4.106	<0.001

in 1984 and 1985. The subsample analyzed (77 observations) included all data from 1985, data from 1984 for ewes that were not present in 1985, and six repeated observations of ewes that were yearlings in 1984.

The analysis of migration data may be affected to an unknown extent by non-independence of observations resulting from the gregarious nature of the ewes, and should be interpreted with caution. Groups of migrating sheep included from one to ten ewes. Several analyses are limited to data collected in 1984–1985, because in those years the number of marked ewes was the largest.

Results

Demography. The number of ewes and lambs (10-months-old) in March increased from 65 in 1981 to 98 in 1985, then declined during a pneumonia epizootic to 64 in 1986. The population in March 1987 included 48 ewes and 14 lambs.

Fecal analyses. In late May and early June, fecal crude protein content was higher in the winter range than in the alpine range (Fig. 1). Crude protein content of ewe feces was considerably higher in the alpine than in the winter range from late June to late July, and remained higher until September. In 1985, the protein content of feces in the alpine was lower ($P < 0.05$) than in 1984 from early July onward.

Foraging behavior. There were no monthly differences in either range in the frequency of browsing (Festa-Bianchet 1987). Browse was eaten more frequently in the alpine range (Table 1). The main browse plants fed upon by ewes appeared to be willow (*Salix* spp.) in both ranges, spruce (*Picea engelmanni*) in the alpine, and poplar (*Populus* spp.) in the winter range.

While foraging, ewes spent more time biting vegetation in the winter range than in the alpine (Table 2). The number of alert postures and the time spent biting vegetation were correlated (winter range: $r = -0.31$, $N = 50$, $P = 0.01$; alpine range: $r = -0.32$, $N = 51$, $P = 0.01$). There were no differences in the number of alert postures during 10-min samples between the two ranges (1984: $t = 0.06$; 1985: $t = 0.71$, $P > 0.4$). Ewes assumed alert postures 3.8 times ($N = 121$, $SD = 1.9$) every 10 min. The duration of alert postures did not appear to vary between ranges, according to a small sample measured in 1985 (winter range: 6.7 s, $N = 38$; alpine range: 6.9 s, $N = 10$). In this study, 92% of focal-animal observations were of ewes in groups of six or more sheep.

Ewes appeared to spend more time foraging in the alpine than in the winter range from late May to July 1985 (Fig. 2). From late May to July 1984, in the winter range, 15 ewes observed for an average of 7 h (range 4.4–9.3) spent

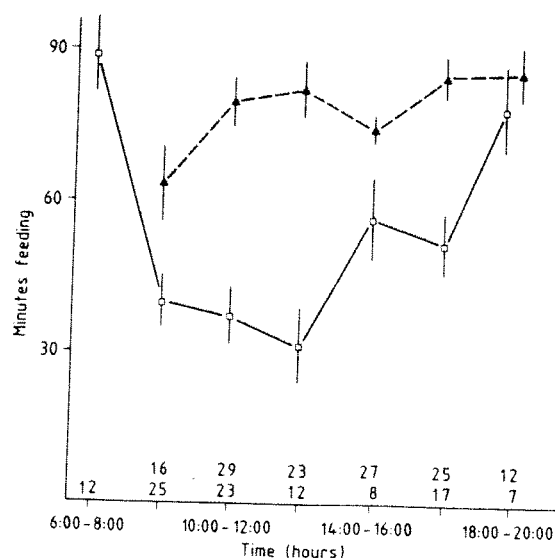


Fig. 2. Minutes spent feeding (mean \pm SE) during 2-h intervals by bighorn ewes in the winter (squares) and alpine (triangles) range from 20 May to 31 July in 1985. The numbers of ewes observed are indicated along the ordinate: alpine range on top, winter range below

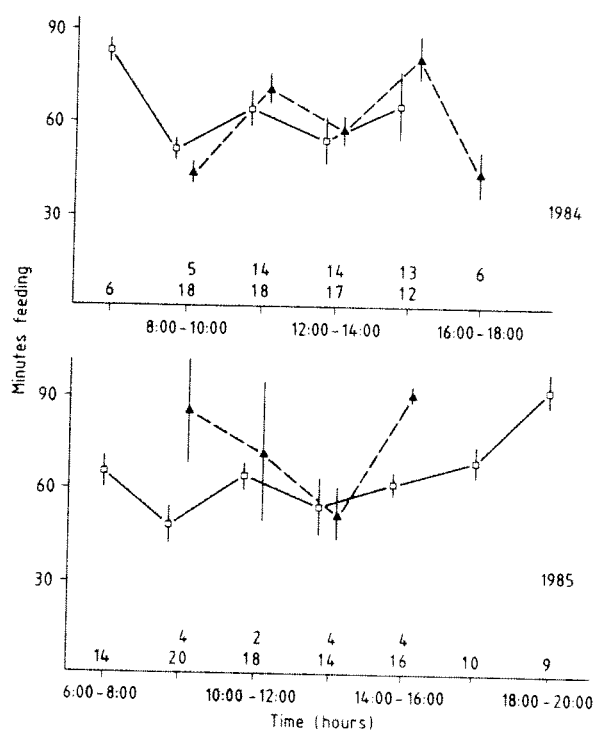


Fig. 3. Minutes spent foraging (mean \pm SE) during 2-h intervals by bighorn ewes in the winter (squares) and alpine (triangles) range from 1 August to 15 September 1984 and 1985. The numbers of ewes observed are indicated along the ordinate: alpine range on top, winter range below

37% of their time foraging (interquartile range: 31–44%), while in the alpine range 16 ewes observed on average for 6.9 h (range 4.3–10.1) foraged for 62% of the time (interquartile range: 59–70%). In August, however, no difference between the two ranges was evident (Fig. 3).

Seasonal migration. Pregnant ewes left earlier than non-pregnant ones. Pregnancy rate and lambing date varied with age (Festa-Bianchet, in press), and the following analysis was limited to ewes three years of age and older. Pregnant ewes ($N=56$) left on average on 18 May (SD=7.8), while non-pregnant ones ($N=10$) left on 24 May (SD=9.0) ($t=1.95$, $P<0.03$ one-tailed). Among two-year-olds, those pregnant ($N=16$) left on average on 24 May, those not pregnant ($N=16$) on 31 May ($t=1.78$, $P<0.05$).

Ewes left the winter range before lambing. Known exceptions were one in 1981 and three in 1986. These four ewes migrated to the alpine range with their lambs within two weeks of giving birth. In 1987, a two-year-old ewe left the winter range in early May, then returned and lambled there in early June. Yearling ewes (never pregnant) often left the winter range with older ewes in May, but returned within 2–8 days and remained until June: at least 16 of 23 (70%) behaved in this way in 1984–1986. In such cases, the date of the second move was used for data analysis. The spring migration dates of ewes aged one, two, three, and four or more years (Table 3) were different ($F_{3,133}=75.47$, $P<0.0001$), and significant pairwise differences existed between yearlings and all other age classes, and between two-year-olds and ewes aged four or more years. These age classes were chosen on the basis of differences in reproduction (Festa-Bianchet, in press). Dates of spring migration in successive years by individual ewes aged three or more years were correlated (for example in 1984–1985, $r=0.41$, $N=38$, $P=0.01$).

There was little variation in timing of spring migration during the first six years of the study (Table 4). In 1983 I was not in the study area from 5 to 29 May, but 38 of 39 ewes three years of age and older were still in the winter range on 4 May, and all but one had left by 30 May. In 1987, the spring migration may have occurred earlier than in other years: 37 of 44 ewes three years of age and older were still in the winter range on 7 May, but only 14 remained there by 11 May. All ewes had left by 26 May.

The spring migration was, except for most yearlings, a discrete event. Each ewe would leave and not return to

Table 3. Date of spring migration from the winter range to the alpine range by bighorn ewes of different ages, 1981–1986. Some ewes are included in more than one age class, and more than once in the >4 years age class

Ewe age	N	Mean	SD	Range
1	35	June 10	14.1	May 10–July 7
2	36	May 27	10.9	May 11–June 19
3	34	May 18	8.1	Apr 30–June 7
4	28	May 17	9.0	Apr 30–June 11
>4	122	May 19	8.2	Apr 30–June 14

Table 4. Date of spring migration from the winter range to the alpine range by bighorn ewes three years of age and older

Year	N	Mean	SD	Range
1981	16	May 15	7.8	Apr 30–June 2
1982	31	May 19	9.5	May 10–June 11
1984	43	May 18	9.6	Apr 30–June 14
1985	49	May 17	5.3	May 10–June 3
1986	43	May 21	7.9	May 2–June 8

Table 5. Days spent in the winter range by bighorn ewes three years of age and older between 20 June and 30 November

Year	N	Mean	SD
1981	17	41.6	29.5
1982	31	61.9	25.5
1983	31	74.4	29.9
1984	42	91.1	28.3
1985	47	97.8	24.9
1986	41	82.1	26.1

Table 6. Days spent in the winter range between 20 June and 30 November by bighorn ewes of different ages in 1984 and 1985. Six ewes were included in both the one- and two-year-old age classes

Ewe age	N	Mean	SD
1	13	113	22.5
2	13	123	19.1
3	10	103	23.4
>3	41	94	26.7

the winter range for several weeks or months. In contrast, the return to the winter range often involved one or more stays of 1–14 days, followed by returns to the alpine before finally settling in the winter range. In June and July, ewes licked salt at the mineral licks in the canyon during short visits to the winter range. A maximum of 28% of 63 ewes in 1984 and 21% of 68 ewes in 1985 apparently undertook a single migration to and from the alpine range. Over 70% of the ewes moved between the two ranges at least twice, and 29% moved three times or more (up to five times).

Ewes appeared to return earlier each year from 1981 to 1985 (Table 5) (e.g. paired test comparing the same ewes in 1984 and 1985, $t=2.34$, $N=45$, $P<0.001$). In 1986, ewes spent less time in the winter range than in either 1984 (paired $t=3.52$, $N=37$, $P=0.001$) or 1985 (paired $t=6.84$, $N=47$, $P<0.001$). These data were not analyzed with ANOVA because of potential non-independence of data collected in different years from the same individuals. Individual ewes were consistent in their relative use of the winter range. For example, the number of days spent there by the same ewes in 1984 and 1985 were correlated ($r=0.65$, $N=40$, $P<0.0001$).

Young ewes spent more time in the winter range than older ewes (Table 6) ($F_{3,73}=5.38$, $P=0.002$). A significant pairwise difference existed between two-year-olds and ewes aged four or more years. Reproductive status did not affect use of the winter range. Ewes three years of age and older that did not produce a lamb in 1984–1985 ($N=7$) spent on average 107 days (SD=29.7) in the winter range from 20 June to 30 November, as opposed to 94 days (SD=25.5) for parous ewes ($N=44$) ($U=211$, $P=0.28$).

Use of the winter range in July–September varied between years. From 7 to 22% of the marked ewes were seen on average during searches in July. The corresponding ranges were 7–36% in August and 8–71% in September.

Discussion

Forage quality was not the only constraint influencing migratory behavior of bighorn ewes. In the spring, pregnant

ewes moved to lambing areas before plant growth had started there, and for two to four weeks fed mostly on low-protein, sparse overwintered forage. At the same time, forage in the winter range was at its peak quality. The weather was likely harsher in the alpine, where snowfalls and freezing temperatures were common. The lambing grounds, however, were rugged, precipitous, and apparently safe from terrestrial predators. Predator avoidance was likely the reason why ewes migrated to these areas before lambing. At least two breeding pairs of coyotes (*Canis latrans*) were found in the winter range, and cougars (*Felis concolor*) were also present. No terrestrial predators were ever seen in the lambing areas. Golden eagles (*Aquila chrysaetos*) were occasionally seen in both ranges. No attacks were ever seen, but eagles may take newborn lambs (Nette et al. 1984). Ewes moved to the lambing grounds a few days before parturition, which occurred on average on 5 June for two-year-olds and 24 May for older ewes (Festa-Bianchet, in press).

An alternative strategy could have been to lamb in the winter range and migrate to the alpine in June. This would have allowed exploitation of the most nutritious forage available in each range, but only four ewes (1.6% of the available ewe-years) behaved in this way. There was no apparent shortage of escape terrain in the winter range, but predators were common, and 8–12 km of travel away from safe terrain were necessary to reach the alpine. At least one lamb was killed by predators while migrating between ranges. Bergerud et al. (1984) reported that calving caribou (*Rangifer tarandus*) in mountainous habitat were faced with a similar trade-off between access to nutritious forage and predator avoidance. Nelson and Mech (1981) found that white-tailed deer (*Odocoileus virginianus*) were more vulnerable to predation while migrating between ranges.

Yearling and non-pregnant adult ewes remained longer in the winter range, presumably to exploit the nutritious forage available there in late May and early June. In early June rams congregate in the winter range, possibly to take advantage of high-quality forage (Festa-Bianchet 1986b).

In late June and through July, fecal crude protein was greater in the alpine range, and most ewes were found there. It is unlikely that the greater consumption of browse in the alpine in June and July had a major effect on fecal crude protein, because ewes selected growing buds, which have a low content of secondary compounds (Bryant et al. 1983; Palo et al. 1985).

The combination of more time spent foraging and less time spent biting vegetation while foraging in the alpine suggests a lower foraging efficiency there than in the winter range. Forage scarcity and a need for salt were the likely reasons why not all ewes were in the alpine in July. In the winter range temperatures often reached 28°C (up to 34°C), and ewes were often seen panting, a likely indication of heat stress. In the alpine, temperatures were seldom above 20°C. Ewes in the winter range in June and July appeared to forage mostly in the early morning and late evening (Fig. 2), possibly to reduce exposure to heat and insects during the day. Ewes in this population do not forage at night (personal observation). Biting insects were a much greater nuisance in the winter range than in the alpine, and so was harassment from people and dogs (Festa-Bianchet 1987). Predation risk also appeared to be greater in the winter range. About two dozen attacks by coyotes

were observed, and up to 10 lambs were eaten (and presumably killed) by coyotes in some years. Coyotes were seen in the alpine range only three times in seven years, and no evidence of predation was ever found there.

In August and September, the difference in fecal crude protein between the alpine and the winter range was small. Given that browsing was more frequent in the alpine, it is possible that there was no difference in forage quality (Mould and Robbins 1981). Seip (1983) reported that in late summer Stone sheep (*O. dalli stonei*) were distributed over the entire range of available elevations, as altitudinal differences in forage quality decreased. At Sheep River, forage availability appeared lower in the alpine range. Possibly, ewes returned to the winter range to exploit the more abundant forage and despite possibly lower protein content, hotter temperatures, insect and human harassment, and greater predation risk. In 1986, following a population decline, many ewes remained in the alpine range until later than in the previous two years, possibly because of greater forage availability. It would be desirable to measure forage production and utilization in both ranges, to test the hypothesis of a density-dependent trade-off between forage quantity and quality.

Ungulates feeding on nutritious new-growth forage show an increased requirement for sodium (Hebert and Cowan 1971; Pletscher 1987), and the only known salt licks in the total range of the Sheep River ewes were in the winter range. It is therefore likely that sodium requirements affected range selection independently of forage characteristics.

Gregariousness affected dispersion. When some ewes migrated between ranges, other ewes in the group likely followed. The temporary move of most yearling ewes to the lambing areas in the alpine range in May appeared to result from reluctance to abandon the group. From an optimal foraging viewpoint, these ewes should not have left the winter range until mid-June. Instead, they followed older ewes to the lambing areas, then returned to the winter range within a few days, presumably because they encountered low-quality forage at higher elevations. Some of the non-pregnant ewes may also have migrated before the optimal time because of unwillingness to remain in the winter range after most of the other ewes had left.

Ewes also appeared to be limited to familiar areas. In the alpine, about 2 km separated the ewe's range from an area utilized by other ewes (the Cliff Creek group in Festa-Bianchet 1986 a). This area included extensive grassy slopes and a mineral lick. Presumably, Sheep River ewes could have exploited these forage and mineral resources instead of returning to the winter range, but did not do so. It is unlikely that they were excluded through social interactions, as three distinct groups of ewes shared the winter range without apparent interference (Festa-Bianchet 1986 a). The need for security from predators may have selected ewes that did not venture into unfamiliar areas (Geist 1971). While this behavior is in most cases advantageous, it may be suboptimal under certain specific circumstances such as the one outlined above.

In conclusion, it appears that the antipredator strategy of bighorn ewes results in a number of foraging costs, because ewes forfeit high-quality forage to move to the lambing areas, yearling ewes follow pregnant ewes to these areas instead of remaining longer in the winter range, and ewes appear reluctant to explore new habitat. The results of this

and other studies (Holmes 1984; Bergerud et al. 1984; Risenhoover and Bailey 1985) suggest that risk of predation in different habitat patches must be taken into account when evaluating the foraging strategy of herbivores.

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