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AGE-SEX DIFFERENCES IN THE DIETS OF WINTERING ROCKY MOUNTAIN BIGHORN SHEEP¹

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Abstract. The winter diets of Rocky Mountain bighorn sheep in Banff National Park were studied to determine whether the age-sex classes have evolved differences in food exploitation patterns under selective pressure to reduce intrapopulation competition. Rams remained primarily on the north end of the study area while the "non-ram" superclass (ewes, lambs, yearlings) occupied primarily the south end. Vegetation analysis indicated that the southern part of the range was characterized by relatively more *Bromus*, *Carex*, *Koeleria*, *Poa*, *Oxytropis*, and *Juniperus* and less *Festuca*, *Fragaria*, *Hedysarum*, *Arctostaphylos*, and *Rosa* than the northern portion. In addition, the southern part of the range was typified by less soil, more xeric conditions, lower plant biomass and apparently overgrazed conditions relative to the more northern parts. Ewes, lambs, and yearlings were found to have diets more similar to each other than to that of adult rams. Class effects in multivariate statistical analysis were significant; the major univariate differences were that non-rams ate more *Carex* and less *Festuca* than did rams. This class effect was found to be wholly attributable to the fact that rams and non-rams segregate onto separate portions of the range which contain different availabilities of forage plants. It was considered to be unlikely that the spatial separation arose from diet preferences but rather from some unrelated factor. The observed differences should not be considered as an adaptation for competition reduction.

Key words: age-sex differences; Banff; bighorn sheep; Canada; diet; habitat selection; intra-specific competition; Ovis; winter behavior.

INTRODUCTION

Competition is generally most intense between individuals that are ecologically similar (Darwin 1859). Intraspecific competition is, therefore, likely to be the most severe ecological constraint felt by any individual. Some workers have suggested that the sexes may differ ecologically and thus reduce intrapopulation competition. This suggestion is attributable originally to Darwin (1872). It was revived in the 1950's by Rand (1952) and Amadon (1959), elaborated in the 1960's (review in Selander 1972), and was recently the subject of a major review (Keast 1977). Niche differences between the sexes have been documented in such diverse groups as vascular plants, fish, reptiles, birds, and mammals (see Shank 1979 for a partial review).

Geist and Petocz (1977) showed that Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in Banff National Park, Canada, segregate sexually onto separate portions of their winter range and occupy cliff and meadow terrains in different proportions. They suggested that this segregation might entail ecological separation for the purpose of competition reduction. During the winters of 1975-76 (October-April) and 1978 (January-April), I investigated the same population studied by Geist and Petocz (1977) in an attempt

to determine the following: (1) sexual preferences in occupied portions of the common winter range, (2) vegetative differences in areas preferred by primarily unisexual groups, (3) the relative proportions of plant taxa eaten by the age-sex classes, and (4) the relationship between availability and choice of forage plants.

THE STUDY AREA AND POPULATION

All observations were made on the Palliser Range in the southeast corner of Banff National Park (51°22'N, 115°35'W). This population has been the subject of studies by several workers (Geist 1966, 1968, 1971, Petocz 1973, Shackleton 1973, Stelfox 1976, Geist and Petocz 1977) whose publications contain full descriptions of the study area and the local sheep population.

Briefly, the study area is a 7-km segment of continuous, southwesterly-facing slopes rising from ≈1650 m above sea level on the valley floor to 2850 m at the ridge's high point. The midslopes, from ≈1830 m to 2135-2285 m, are vegetated by disclimax *Elymus in-novatus*-*Festuca* subalpine meadows. From the meadow zone to the ridge top are steep but broken limestone cliffs. The meadow zone is sharply dissected, resulting in exposed spurs which are rapidly blown clear of snow.

The sheep population has been stable in number since at least 1965 with some 40 "non-rams" (ewes, lambs, yearlings) and 30 rams wintering on the range. The quality of the population has been characterized

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as "poor" by Shackleton (1973) and "medium" by Stelfox (1976) using different criteria.

METHODS

The range was divided into 12 spatial units which were subsequently combined to form three "aggregated spatial units" of differing sizes and characteristics. These areas are termed the northern, southern, and middle portions of the range.

Sheep were censused from one to four times weekly from standardized points on the valley floor in much the same manner as employed by Geist and Petocz (1977). A total of 75 censuses were completed yielding 2153 sheep sightings.

At 5-min intervals, the exact location of every sheep visible from standardized positions on the valley floor was recorded on a fine-scale grid system (accurate to $\approx \pm 5$ m) together with the age-sex class of each individual and its activity type. A total of 11 390 feeding location records were compiled over the winter. Those grid locations having the highest cumulative frequency of feeding records were considered favored feeding areas.

To determine the relative availabilities of forage plant species on the feeding areas of rams and non-rams, I performed standard vegetation analyses on the two most favored ram and non-ram feeding areas on each of the three range portions. Daubenmire's (1959) canopy cover method of vegetation analysis was employed using actual percentage cover rather than the six-point scale advocated. The plot frame was 20×50 cm (0.1 m^2). Quadrats were placed at 1-m intervals along three 10-m lines placed parallel to the contour and 2 m apart vertically. This close configuration of points was necessitated by the restricted areas defined as favored feeding areas. The vegetation of the Palliser Range and the surrounding area is well known (see Stringer 1972, Stelfox 1976, Hamer et al. 1977).

Differences in the forage species ingested by the age-sex classes were determined by analysis of plant fragments in the feces. Controversy still exists concerning the validity of the technique. However, Vavra et al. (1978) suggest it may usefully be employed when (a) wild animals are being studied, (b) when all individuals occupy the same range, and (c) where relative values are of interest. Each of these conditions is met in this study. Todd and Hansen (1973) tested the fecal analysis technique on bighorn sheep and found no significant differences between fecal and rumenal samples.

A total of 272 fecal samples from rams, ewes, lambs, and yearlings were collected between 16 November 1975 and 6 April 1976 and between 26 January and 16 April 1978. Analysis was done by the Composition Analysis Laboratory, Colorado State University, Fort Collins, Colorado using Sparks and Malecheck's (1968) method. One slide was made per sample and 20 fields per slide were examined under a binocular mi-

croscope. Species presence was expressed as relative density (Hansen and Reid 1975).

To determine if major forage species differed in quality, weathered samples were collected from various parts of the range on 23 March 1978. The collection procedure simulated actual grazing; the plant was grasped close to the ground with the thumb and forefinger and pulled sharply upwards, thereby producing the distinctive, squeaky "pop" heard as bighorns graze. Samples were dried for 24 h at 60°C and analyzed by the Alberta Department of Agriculture for crude protein, acid detergent fiber (ADF), calcium and phosphorus. Estimated digestible energy was calculated as $-1.921 \times \% \text{ADF} + 124.78$ (E. S. Redshaw, personal communication).

In all statistical tests, the 5% level of probability was used to indicate significance.

RESULTS

Spatial occupation patterns

Fig. 1 shows that the percentages of rams and non-rams observed on the northern, middle, and southern portions of the range exhibit an inverse relationship. Clearly, rams preferentially occupy the north end of the range while non-rams remain largely on the southern end. These findings are similar to those of Geist (1971) and Geist and Petocz (1977).

Use of plant communities

To determine if there were associations of plant taxa on the Palliser Range, ordination tests were made using principal components analysis based on correlations between percentage covers of plant genera (*Q*-type analysis in Pielou 1977). Three factors were calculated using the Statistical Package for the Social Sciences (SPSS) factor analysis library program (Kim 1975). Fig. 2 plots these factor values in three-dimensional factor space. To make associations and disassociations clearer, dotted lines are drawn between associated genera which are arbitrarily defined as being closer than 0.70 factor units through three-space.

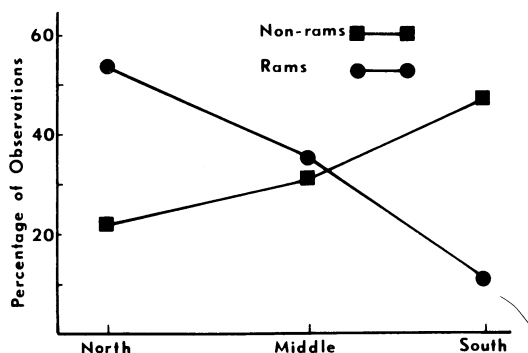


FIG. 1. Percentage occupation by rams and non-rams on the north, south, and middle portions of the Palliser Range over the entire winter of 1975–1976.

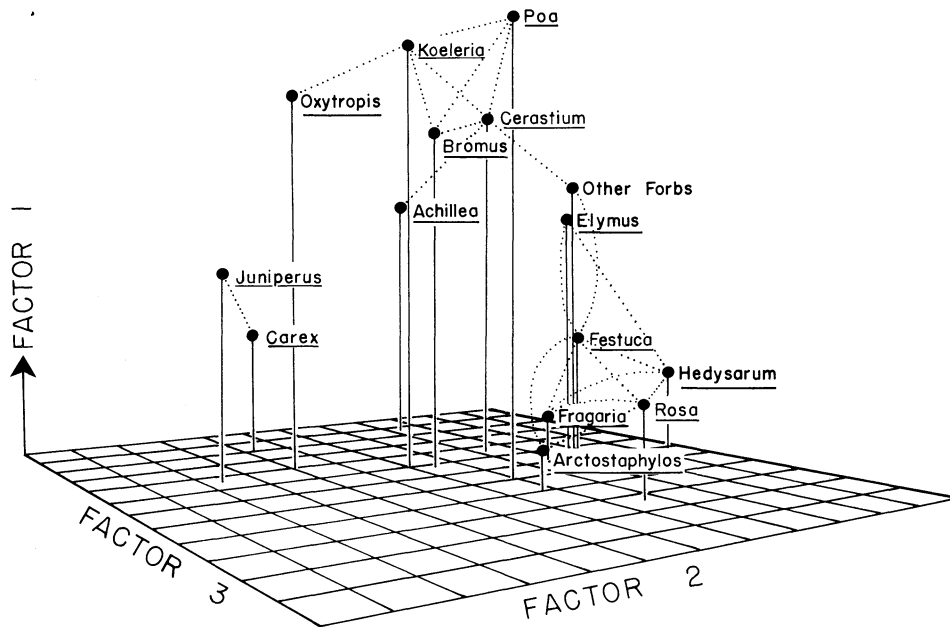


FIG. 2. Representation of the spatial relations of plant taxa in three-dimensional factor space as determined by principal component analysis. Dotted lines indicate taxa closer to each other than 0.70 units.

Three relatively discrete groupings are present: the "Carex type" comprised of *Juniperus* and *Carex*, the "Koeleria type" containing *Oxytropis*, *Koeleria*, *Poa*, and *Bromus*, and the "Festuca type" comprised of *Festuca*, *Rosa*, *Hedysarum*, *Fragaria*, and *Arctostaphylos*. The ubiquitous taxa (*Cerastium*, *Achillea*, Other forbs, and *Elymus*) form a bridge between the latter two groups but are not fully integrated into either group. Subjectively, the three vegetative types have distinct ecological relationships. The *Festuca* type is associated with sheltered conditions indicating winter snow cover, good soil formation, and mesic conditions. It is characterized by high biomass values. By contrast, the *Koeleria* type is associated with exposed slopes, much scree and little soil, more xeric conditions, and low biomass values. The *Carex* type is similar to the *Koeleria* type but occurs in more rocky and more exposed locations.

Smoliak (1974) reported that under conditions of heavy grazing by domestic sheep, *Festuca* decreased or disappeared while *Koeleria* increased in abundance. Stelfox (1976) found overgrazed bighorn sheep ranges to carry more *Koeleria* and less *Festuca* than more lightly grazed areas. On the Palliser, the *Koeleria* type seems clearly associated with localized areas of overgrazing relative to the *Festuca* type.

Table 1 presents the results of analysis of variance testing for differences in plant cover on the three portions of the range. For both sexes combined, feeding areas on the northern portions of the range contain, relative to the southern Palliser, significantly more

Festuca, *Fragaria*, *Hedysarum*, *Arctostaphylos*, and *Rosa*, and less *Bromus*, *Carex*, *Koeleria*, *Poa*, *Oxytropis*, and *Juniperus*. These taxa fall out quite clearly into the "types" defined by principal components analysis. The northern part of the range, preferentially occupied by rams (Fig. 1), is characterized by the *Festuca* type, whereas the southern portion, occupied mostly by non-rams, is characterized by the *Koeleria*

TABLE 1. Mean percent cover (\pm SD) of the 15 most common taxa on the North, South, and Middle portions of the Palliser Range. Table shows values in standard numerical form; statistical tests were based on arcsine-transformed data. Asterisks (*) indicate significant differences among the three portions, with $\alpha = .05$.

Taxon	Percent cover ($\bar{x} \pm$ SD)		
	North	Middle	South
<i>Bromus</i>	.63 \pm 1.69	3.29 \pm 5.29	4.67 \pm 4.75*
<i>Carex</i>	.04 \pm .45	1.41 \pm 4.06	3.23 \pm 8.63*
<i>Elymus</i>	9.54 \pm 9.96	6.79 \pm 7.24	10.08 \pm 12.95*
<i>Festuca</i>	10.21 \pm 9.41	6.16 \pm 9.54	.92 \pm 6.45*
<i>Koeleria</i>	1.45 \pm 2.70	.21 \pm 1.00	2.91 \pm 3.47*
<i>Poa</i>	1.70 \pm 2.78	.83 \pm 2.18	4.58 \pm 6.94*
<i>Achillea</i>	1.04 \pm 2.12	.63 \pm 2.00	1.75 \pm 6.60
<i>Cerastium</i>	1.41 \pm 2.37	.75 \pm 2.01	1.67 \pm 2.70*
<i>Fragaria</i>	2.88 \pm 4.27	2.00 \pm 3.91	1.08 \pm 6.55*
<i>Hedysarum</i>	6.87 \pm 7.61	7.08 \pm 7.29	2.08 \pm 4.13*
<i>Oxytropis</i>	3.00 \pm 6.50	.25 \pm 1.26	4.41 \pm 5.51*
Other forbs	7.92 \pm 5.18	8.12 \pm 6.21	7.58 \pm 7.30
<i>Arctostaphylos</i>	5.38 \pm 11.39	8.42 \pm 13.35	.83 \pm 6.43*
<i>Juniperus</i>	0 \pm 0	.63 \pm 3.34	3.78 \pm 7.96*
<i>Rosa</i>	.96 \pm 2.77	1.04 \pm 2.89	.83 \pm 6.43*

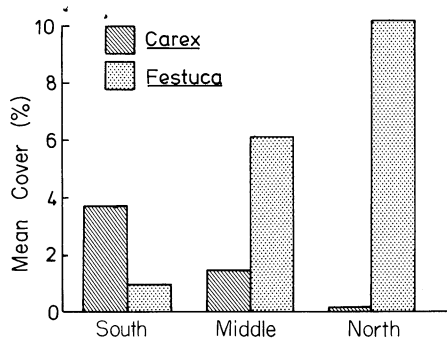


FIG. 3. Percentage mean cover of *Festuca* and *Carex* on favored feeding areas on the southern, northern, and middle portions of the range.

and *Juniperus-Carex* types. Therefore, rams are concentrating their feeding on productive, mesic, and probably lightly grazed areas whereas the non-rams are utilizing drier and putatively overgrazed areas. The effect of area on the relative availability of the two most important forage taxa, *Festuca* and *Carex*, is shown in Fig. 3.

Diet analysis

A total of 32 forage taxa were identified in the fecal analysis. The means (\pm SE) of percentage presence of the 10 most common taxa are presented as Table 2. A complete list can be found in Shank (1979).

A calculation of the similarity between two diets is often useful in comparative studies. Most such studies have been based on Kulczynski's similarity index (Oosting 1954, Gauch 1973) which compares only shared diet components and can therefore lead to spurious results. A more robust index is represented by Cavalli-Sforza and Edwards' (1967) measure of "genetic distance" as described by Batschelet (1976). This latter index treats each diet as a "unit vector" on n possible diet components which in concert define a

TABLE 3. Cavalli-Sforza's index of similarity comparing mean diets of ewes, lambs, yearlings, and rams. Smaller values indicate greater similarity.

	Lamb	Yearling	Ram
Ewe	7.1	9.2	12.7
Lamb		7.0	13.4
Yearling			15.7

unique point in an n -dimensional hyperspace. The similarity between two diets is expressed simply as the cosine of the angle between the pair of lines connecting the origin with the points defining the two diets.

Table 3 presents the Cavalli-Sforza and Edwards' index of similarity comparing the diets of the four classes based on all 32 forage taxa identified. It shows that ewes, lambs, and yearlings (i.e., non-rams) represent a cluster of high diet similarity, in contrast to rams, whose diet differs from those of each of the non-ram classes (larger values in Table 3).

More detailed statistical analyses are required to answer the questions (a) do the diets of the classes differ?, and (b) what single forage items contribute most to observed diet differences? Only the 10 most common forage taxa were treated statistically (Table 2). Combined, these taxa comprise between 96.6 and 97.5% of the ram and non-ram diets; little information is lost by failing to treat the other 22 identified taxa. The SPSS MANOVA program (Cohen and Burns 1977) was employed for both multi- and univariate tests.

There are four factors which might be expected to affect the proportion of forage species in an animal's diet: year of fecal collection, month of collection, area of collection (North, South, Middle), and the age-sex class of sheep concerned. The effects of these four factors on diet composition were tested in a four-way multivariate analysis of variance. This analysis shows

TABLE 2. Summary of percentages of the 10 most common forage taxa ingested by ewes, lambs, yearlings, and rams during the winters of 1975–1976 and 1978. Parenthetical values are SE's.

Taxon	Diet composition (%)				
	Ewe (N = 85)	Lamb (N = 78)	Yearling (N = 18)	Ram (N = 91)	All classes (N = 272)
<i>Bromus</i> sp.	4.14 (0.62)	4.63 (0.60)	3.73 (1.30)	3.78 (0.51)	4.13 (0.32)
<i>Carex</i> sp.	11.94 (1.34)	11.73 (1.75)	12.38 (2.60)	3.71 (0.49)	9.16 (0.73)
<i>Elymus</i> sp.	2.16 (0.48)	3.29 (0.84)	1.28 (0.84)	3.16 (0.81)	2.76 (0.40)
<i>Festuca</i> sp.	68.70 (2.24)	68.56 (2.62)	68.02 (3.76)	77.18 (2.03)	71.45 (1.28)
<i>Koeleria cristata</i>	4.83 (0.77)	5.47 (0.72)	3.55 (1.18)	3.96 (0.66)	4.64 (0.41)
<i>Poa</i> sp.	2.37 (0.37)	1.72 (0.36)	3.36 (1.36)	1.27 (0.27)	1.88 (0.20)
<i>Astragalus</i> sp.	0.75 (0.27)	1.00 (0.28)	0.96 (0.50)	0.14 (0.06)	0.63 (0.12)
<i>Picea</i> sp.	0.27 (0.25)	0.0 (0.0)	0.12 (0.12)	1.54 (0.67)	0.61 (0.21)
Unknown composite	0.85 (0.26)	0.39 (0.17)	1.56 (0.60)	0.64 (0.20)	0.69 (0.12)
Unknown forb	1.35 (0.29)	0.69 (0.26)	1.89 (0.75)	1.26 (0.30)	1.17 (0.16)

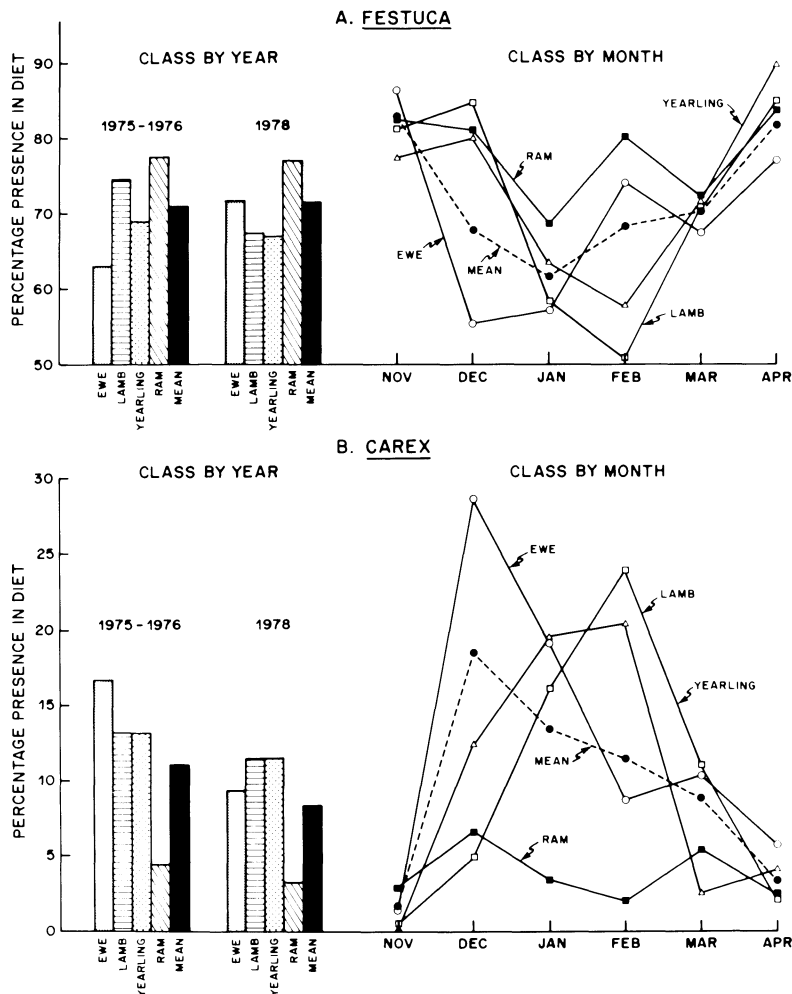


FIG. 4. *Festuca* (A) and *Carex* (B) contents of age-sex class diets broken down by month and by year.

statistically significant effects of year, month, and area (plus interaction effects) but none for age-sex class. If, however, the area effect is removed and a three-way analysis performed, significant class effects emerge. In other words, rams and non-rams do indeed eat a diet composed of different proportions of plant taxa but these differences are solely attributable to differential use of areas (Fig. 1) which are characterized by different forage plant availabilities (Table 1, Fig. 3).

The pattern is particularly striking with respect to the two most commonly used forages, *Carex* and *Festuca*. Fig. 4 shows that rams ate more *Festuca* and less *Carex* than the non-ram classes. Fig. 5 shows that *Festuca* use was low on the southern part of the range and high on the northern end. *Carex* shows exactly the opposite relationship. Use of these taxa on the various portions of the range mirrors their availability (Fig. 3) and range use by rams and non-rams (Fig. 1).

A question remains as to whether non-rams occupy

the south end of the range simply because *Carex* is a preferred food and readily available there. That seems unlikely for a number of reasons. First, the south end of the range exhibits all the characteristics of a poor, overgrazed range with low plant biomass, little soil, low availability of *Festuca*, and much *Koeleria*. Secondly, those non-rams which do enter the rams' favored range shift their diets so as to ingest even more *Festuca* than do resident rams (Fig. 5A). Such behavior would be an unlikely occurrence if *Festuca* were not highly favored by non-rams. And lastly, the estimated digestible energy of *Festuca* (10.4 MJ/kg) exceeds that of *Carex* (8.70 MJ/kg). *Festuca* is clearly a superior forage in terms of useable energy, the major winter requirement.

DISCUSSION

It seems clear that there are significant differences in the "food niche" of Palliser rams and non-rams during the winter. These differences do not arise as a

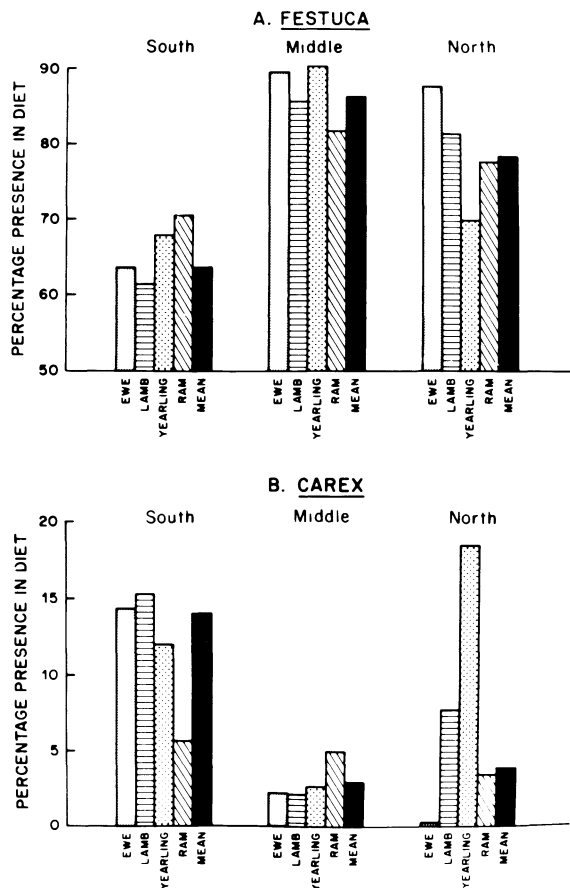


FIG. 5. *Festuca* (A) and *Carex* (B) contents of age-sex class diets broken down by area of collection.

function of differential "preference," but rather as a result of segregation of rams and non-rams onto portions of the range containing distinct forage plant availabilities. Why this spatial segregation should occur is not clear but probably cannot be related to the energy content of the diet. These observations suggest that there has been no natural selection for winter diet differences as a means for reducing intraspecific competition as suggested by Geist and Petocz (1977); that is, the observed diet differences probably do not represent an adaptation. The dietary differences are the result of separate, but poorly understood, forces selecting for sexual segregation. Gould and Lewontin (1979) have warned against the "adaptationist program" of proposing separate adaptive stories for each observed trait. As Williams (1969:261) stated, "One should never imply an effect is a function unless he can show it is produced by design and not by happenstance."

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