

Food Resource Partitioning by Sympatric Ungulates on Great Basin Rangeland

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Abstract

The usefulness of a conceptual framework for understanding food selection by ungulates, based on four morphological parameters (body size, type of digestive system, rumino-reticular volume to body weight ratio, and mouth size), was tested by applying discriminant analysis to 194 monthly diet determinations based on microhistological fecal analysis for five sympatric species of ungulates in northeastern California and northwestern Nevada. In each season, the group means were located in the hypothesized order along the axis described by the first discriminant function: feral horse, domestic cow, domestic sheep, pronghorn, mule deer. Horse and cow diets consisted primarily of grasses. Pronghorn and mule deer diets consisted primarily of browse. Sheep diets were intermediate. Four browses (*Artemisia* spp., *Cercocarpus ledifolius*, *Purshia tridentata*, and *Juniperus occidentalis*) were selected as the most useful species for discriminating between animal species. The data and analyses support the hypothesized food selection framework.

A conceptual framework for understanding the nutritional basis for food selection by ungulates has been outlined (Hanley 1982) and is based on four ungulate morphological parameters: (1) body size and (2) type of digestive system (cecal or ruminant) determine the overall time-energy constraints within which the ungulate may forage selectively; (3) rumino-reticular volume to body weight ratio determines the type of forage the ruminant is most efficient in processing; and (4) mouth size determines the ability of the ungulate to harvest selectively plant parts or individuals. Each of these parameters may be considered an important factor in determining an ungulate's relative position along a gradient ranging from highly selective browse diets to less selective graminoid diets.

The framework was presented as a means of further understanding the diet selection process of large, generalist herbivores. An understanding of the reasons why ungulates select the kinds of foods that they do will yield predictive insight into problems involving competition and food resource partitioning in ungulate communities. On the basis of that framework, one should be able to predict not only the types of foods that will be selected by the members of a given array of ungulate species but also the rank of each species along a gradient reflecting the differences in degree of selectivity and types of foods selected. We were able to test the theory in this way, using diet composition data collected from five species of sympatric North American ungulates (Table 1). The specific hypothesis tested was that when ordered along a mathematically defined gradient based on plant species composition of their diets, the five ungulate species would appear in the following order: feral horse (*Equus caballus*), domestic cow (*Bos* spp.), domestic sheep (*Ovis aries*), pronghorn antelope (*Antilocapra*

americana), mule deer (*Odocoileus hemionus*). The reasons are as follows.

From Table 1, it can be seen that we had two basic groups of animals in terms of body weight, very large animals (horse and cow) and relatively small animals (sheep, pronghorn, and mule deer). Furthermore, the horse is a cecal digester, while the others are ruminants. The time-energy constraints should be much more restrictive for the horse and cow than for the other species, especially so for the horse. The horse should have the least amount of time to forage selectively, followed by the cow and then the three small ruminants, which also have small mouths that enable them to be selective of plants parts and individuals consumed.

Cattle and domestic sheep have very large rumens in proportion to their body weight (rumino-reticular volume to body weight ratio of about 0.250) and therefore should be well adapted to digesting a high cellulose (i.e., grass) diet. Pronghorn and mule deer, on the other hand, have relatively small rumens (rumino-reticular volume to body weight ratio of about 0.110) and therefore should be well adapted to digesting a high cell soluble and/or high lignin (i.e., forb and browse) diet. For these reasons, sheep diets should be more similar to cattle and horse diets than should pronghorn or mule deer diets. Pronghorn and mule deer diets should be very similar. However, due to differences in stomach structure, pronghorn were expected to be more similar to sheep than mule deer were. "Pronghorn antelope have a rumen somewhat more similar to sheep than that of deer in relative shape and size" (Church 1975:24).

The predicted ordering of the ruminants along a food selection gradient can be related to their ordering along a gradient of ratio of rumino-reticular volume (1) to metabolic body weight ($W_{kg}^{0.75}$). Metabolic body weight incorporates both the absolute and relative costs of body weight; and if mouth size is correlated with body weight via the time-energy constraints, then effects of mouth size also are taken into account with the use of this ratio. Rumino-reticular volume to metabolic body weight ratios for the four ruminants are 1.120, 0.665, 0.338, and 0.289, for cow, sheep, pronghorn, and mule deer, respectively. Thus, the very large cecal digester (horse) and the small ruminant with the small rumino-reticular volume (mule deer) should be positioned at opposite ends of a less selective graminoid diet to highly selective browse diet gradient, respectively, with the cow, sheep, and pronghorn positioned between these extremes. This hypothesis was tested with data from 194 determinations of plant species composition of diets selected by these 5 species of ungulates.

Methods

Study Area and Data Collection

Diet composition data were obtained by microhistological analysis of fecal samples (Sparks and Malechek 1968, Ward 1970, Hansen and Dearden 1975) collected monthly from July 1976 through June 1977, in northeastern California and northwestern Nevada near Cedarville, California. The study area was typical of the intermountain Great Basin rangeland, consisting of habitat types ranging from shadscale (*Atriplex confertifolia*) and grease-

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Table 1. Estimated body weight, rumino-reticular volume to body weight ratio, and weight of rumino-reticular contents of the five ungulate species involved in the present study. Range of values are in parentheses.

Species	Body weight of adults (kg)	Rumino-reticular volume (l) to body weight ratio	Weight of fresh rumino-reticular contents as proportion of body weight	Source
Horse	500 (410-636)	—	—	3
Cow	475 (308-600)	0.240 (0.160-0.264)	0.134 (0.100-0.150)	5,7,9,12,13,14
Sheep	50 (29-76)	0.250 (0.160-0.333)	0.120 (0.069-0.150)	1,4,5,7,8,9,11
Pronghorn	50 (44-58)	0.127 (0.126-0.128)	0.077 —	6,11
Mule deer	60 (56-74)	0.104 (0.103-0.105)	0.075 (0.073-0.078)	2,7,10

Sources:

- 1 Allo et al. 1973
- 2 Anderson et al. 1974
- 3 Jurgens 1974
- 4 Leng and Brett 1966
- 5 Moir 1968
- 6 O'Gara 1970 and personal correspondence

- 7 Prins and Geelen 1971
- 8 Purser and Moir 1966
- 9 Short 1963
- 10 Short et al. 1963
- 11 Sundstrom et al. 1973
- 12 Thomas et al. 1961
- 13 Tulloh and Hughes 1965a
- 14 Tulloh and Hughes 1965b

wood (*Sarcobatus vermiculatus*) dominated communities to white fir (*Abies concolor*) forest. Most of the area, however, was characterized by sagebrush species (*Artemisia tridentata* and *A. arbuscula*, principally) and perennial bunchgrasses—bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), and Sandberg bluegrass (*Poa secunda*). Western juniper (*Juniperus occidentalis*) and curl-leaf mountain mahogany (*Cercocarpus ledifolius*) woodlands formed a transition zone between the white fir forests at the higher elevations and the shrub-steppe below. The study area encompassed about 350,000 ha. Elevation ranged from 1500–2700 m. Average annual precipitation ranged from about 30 mm at the lowest elevations to about 600 mm at the highest elevations, mostly occurring as winter snow and spring rain (Summerfield and Bagley 1974). The winter of 1976–1977 was unusually dry.

Domestic stock were turned out on the range in April and were taken off the range in November. Pronghorn, mule deer, feral horses, and cattle were free-roaming. Sheep were herded. Pronghorn, cattle, and horses were distributed over a wide elevational range, whereas deer and sheep were most abundant in the juniper-

mountain mahogany woodlands. All animals selected their diets voluntarily. No animals received supplemental rations.

Four major fecal collection areas were designated within the study area. The collection areas were further subdivided into shrubland and woodland vegetation types. Fresh fecal pellet collections were made in each study area and each vegetation type monthly for all species which were present. Cattle, horse, sheep, and pronghorn generally occurred in groups. Therefore, fecal collections were made in areas recently used by such groups. Deer, on the other hand, were much more solitary, so fecal collections were made by clearing permanently marked transects monthly. A single diet sample consisted of a composite collection of 2 g (fresh weight) samples from at least 50 pellet groups for an animal species in such a localized collection area.

A total of 194 diet samples were collected (Table 2). The plant species composition of each diet sample was determined by the Composition Analysis Laboratory, Department of Range Science, Colorado State University, Fort Collins. Diet composition was based on readings of 100 microscope fields per sample. Data were expressed as percent relative density of recognizable plant frag-

Table 2. Stratification of diet samples. One sample equals a composite collection from more than 50 fecal pellet groups. S = shrubland; W = woodland.

Season/ Month	Horse		Cow		Sheep		Pronghorn		Mule deer	
	S	W	S	W	S	W	S	W	S	W
Spring										
March	3	2	—	—	—	—	4	1	—	2
April	2	2	1	2	—	1	2	2	—	4
May	1	2	3	1	—	1	2	3	—	3
Summer										
June	1	3	2	4	—	1	2	2	—	4
July	2	4	3	5	—	1	2	3	—	1
August	2	4	3	5	—	2	2	3	—	4
Fall										
September	2	3	3	4	—	1	2	3	—	4
October	2	3	1	3	—	2	2	3	—	4
November	3	3	1	1	—	1	3	2	—	4
Winter										
December	2	2	—	—	—	—	1	2	—	—
January	3	1	—	—	—	—	2	—	—	3
February	2	2	—	—	—	—	2	—	—	3

ments. Although forages differ in their digestibility and identifiability, it was believed that these data were adequate for gross diet comparisons between the five ungulates under study. Highly digestible or poorly identifiable forages would be underestimated in all diets.

Data Analysis

Since ungulate diets change seasonally, the data were stratified by four seasons of 3 months each (Table 2). Data for cattle and sheep were not available for the winter period, as these animals were not on the range at that time.

Diet relationships during each season were subjected to discriminant analysis (Cooley and Lohnes 1971, Klecka 1975), a multivariate statistical technique useful for investigating within and between group variability, testing differences in the composition of groups, and identifying variables most useful in determining the most likely group membership of individual cases. All diets of each animal species in each season were considered a group. Groups therefore were composed of a number of cases, each being one diet determination for that particular animal species during that particular season. Each case was described by the percent relative density of identifiable plant fragments. A total of 76 variables (plant species) were identified in the diets and were used in the discriminant analysis.

The test of the hypothesis involved the location of group means ("centroids") along the axis defined by the first discriminant function. The first discriminant function is that function which accounts for the greatest proportion of the total variance within and between groups. It therefore provides an objective means of ranking the animal species along a single gradient, each position being determined by the plant species composition of the diets comprising the group.

A stepwise selection procedure was utilized to select the variables (plant species) most useful in defining the discriminant functions. Variables were chosen by the criterion of minimizing Wilks' lambda, a measure of group discrimination, thus maximizing the overall multivariate *F* ratio for the test of differences among group centroids. For each season, the stepwise selection procedure was stopped at 10 steps. This was a subjective determination but was believed appropriate because it provided a high degree of discriminating power, yet remained general enough to avoid centering on the personality of these particular data. For each season this provided a canonical correlation for the first discriminant function that when squared was >0.95 (i.e., $>95\%$ of the variance in the discriminant function was explained by the groups). It also ensured that the relative percentage of the eigenvalue associated with the first function was >75.0 and that for the sum of the first two functions was >95.0 (i.e., that the first function accounted for $>75\%$ and that the first two functions accounted for $>95\%$ of the

Table 3. Location of group centroids along the axis described by the first discriminant function. In each season horse and cow are not significantly different ($p>0.50$); all other pairs are highly significantly different ($p<0.01$).

Species	Spring	Summer	Fall	Winter
Horse	-7.96	-4.62	-4.08	20.02
Cow	-8.36	-4.05	-3.45	-
Sheep	-1.01	-3.33	-2.09	-
Pronghorn	6.27	7.59	2.23	18.76
Mule Deer	7.57	7.79	7.08	-61.92
Canonical Correlation	0.99	0.99	0.98	0.99
Relative percentage of the eigenvalue associated with the first discriminant function	84.1	88.3	76.7	95.0

total variance existing in the discriminating variables). Differences in group centroids were tested for statistical significance by calculating an *F* ratio for the Mahalanobis distance between each pair of groups. Variables most important in defining the discriminant functions were determined on the basis of the magnitude of their standardized discriminant function coefficient.

Therefore, discriminant analysis provided a means of ordering the five animal species along a single gradient on the basis of the plant species composition of their diets. Discriminant analysis also provided a means of identifying the plant species that were most useful in differentiating between animal species.

Results

Test of the Hypothesis

For each season the hypothesis was not rejected, that when the animal species were ranked along a gradient based on diet composition, they would appear in the following order: horse, cow, sheep, pronghorn, deer (Table 3). The only possible exception was Spring, where horse and cow appeared in reversed order. However, the locations of horse and cow centroids were not significantly different ($P>0.50$). The locations of all other possible pairs of centroids were highly significantly different ($P<0.01$) from one another. As hypothesized, pronghorn and deer diets were most similar to each other, and sheep diets were intermediate between the large ungulates on one side and the small rumen volume ruminants on the other side. The locations of the centroids of horse and pronghorn were surprisingly similar in Winter. This reflected similarities in habitat use, however, and not similarities in types of foods selected (see below).

Diet Composition

Differences in diet composition in terms of forage classes also were as expected. Horse and cattle primarily consumed graminoids

Table 4. Summary of percent relative density of identifiable plant fragments occurring in feces during each season—equally weighted by month.

	Horse	Cow	Sheep	Pronghorn	Mule deer
Spring (March, April, May)					
graminoids	86.2	94.3	46.6	2.0	9.1
forbs	9.4	3.5	12.3	16.1	6.2
browse	4.3	2.2	41.1	81.9	84.7
Summer (June, July, August)					
graminoids	95.2	91.3	68.2	4.6	8.4
forbs	3.9	2.7	21.8	27.0	4.0
browse	1.0	5.9	10.1	68.4	87.6
Fall (September, October, November)					
graminoids	94.9	92.8	47.3	1.7	4.0
forbs	2.1	4.1	12.0	10.8	3.5
browse	3.0	3.1	40.7	87.6	92.5
Winter (December, January, February)					
graminoids	81.5	—	—	1.0	3.2
forbs	6.7	—	—	7.7	3.0
browse	11.8	—	—	91.4	93.8

in all seasons, whereas browse was much more apparent in the diets of pronghorn and deer (Table 4). Sheep diets were intermediate. These data provide further credibility to the food selection framework, since they demonstrate the hypothesized gradient in forage classes as well as plant species. Despite the dissimilarity in plant species composition of pronghorn and deer winter diets (as indicated by relative locations of group centroids) for example, it is apparent that these animals nevertheless were selecting the same *types* of foods. Browse constituted >90% of pronghorn and deer winter diets, as compared to only 11.8% of horse diets.

Analysis of the discriminant function coefficients revealed the most valuable plant species for discriminating between the diet composition of the various ungulate species. It therefore was possible to name the discriminant functions on this basis. The first discriminant function for Spring was an *Artemisia* spp., *Cercocarpus ledifolius*, *Juniperus occidentalis* gradient (Fig. 1), the main effect of which was to separate the pronghorn and deer diets, which were high in these species, from the horse and cattle diets, which were very low in these species. Although sheep diets were intermediate in these species, they were relatively high in *Peraphyllum ramosissimum*, *Muhlenbergia richardsoni*, and *Iva axillaris*, this being demonstrated by the second discriminant function. *Peraphyllum ramosissimum* grew in localized patches in the study area. *Muhlenbergia richardsoni* and *Iva axillaris* were most common in the periodically flooded *Artemisia cana* communities. The high occurrences of these species in the Spring sheep diets probably was an artifact of the sheep being herded, and thus concentrated in localized areas, and a small sample size (only two diets for sheep were available in Spring).

The first discriminant function for the Summer diets represented a *Purshia tridentata*, *Artemisia* spp., *Cercocarpus ledifolius* gradient, the effect of which, again, was to separate the pronghorn and deer diets, which were high in these species, from the horse, cattle, and sheep diets, which were low in these species (Fig. 2). The second discriminant function again was strongly influenced by *Peraphyllum ramosissimum*, and again reflected the localized distribution of sheep. The strong *Oenothera tenacetifolia* component of the second axis reflected the herding of sheep onto large, dry *Juncus balticus* meadows during summer. Thus, the first axis again

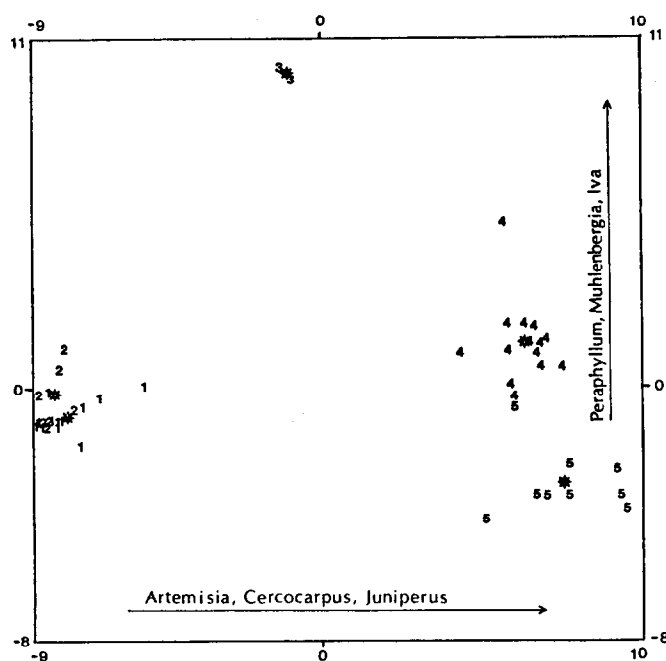


Fig. 1. Plot of discriminant scores of Spring (March, April, May) diets. The first (abscissa) and second (ordinate) discriminant functions have been given biological interpretation as indicated. 1 = horse; 2 = cow; 3 = sheep; 4 = pronghorn; 5 = mule deer; * indicates a group centroid.

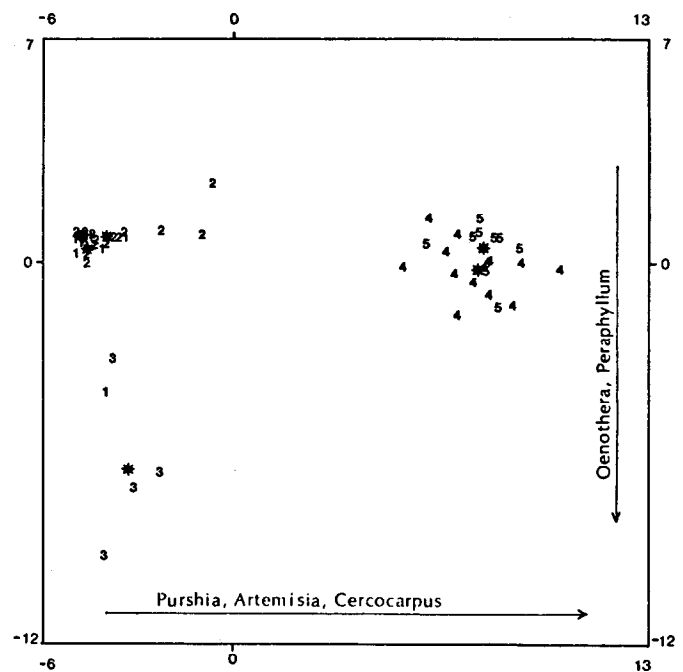


Fig. 2. Plot of discriminant scores of Summer (June, July, August) diets. The first (abscissa) and second (ordinate) discriminant functions have been given biological interpretation as indicated. 1 = horse; 2 = cow; 3 = sheep; 4 = pronghorn; 5 = mule deer; * indicates a group centroid.

was most strongly determined by forage selection, while the second axis again reflected the herding influence on forage available to sheep.

During Fall, sheep no longer were concentrated on and around the dry meadows. The first discriminant function represented a *Purshia tridentata*, *Cercocarpus ledifolius* gradient, whereas the *Artemisia* spp. component of the diets was represented by the second discriminant function (Fig. 3). The second discriminant

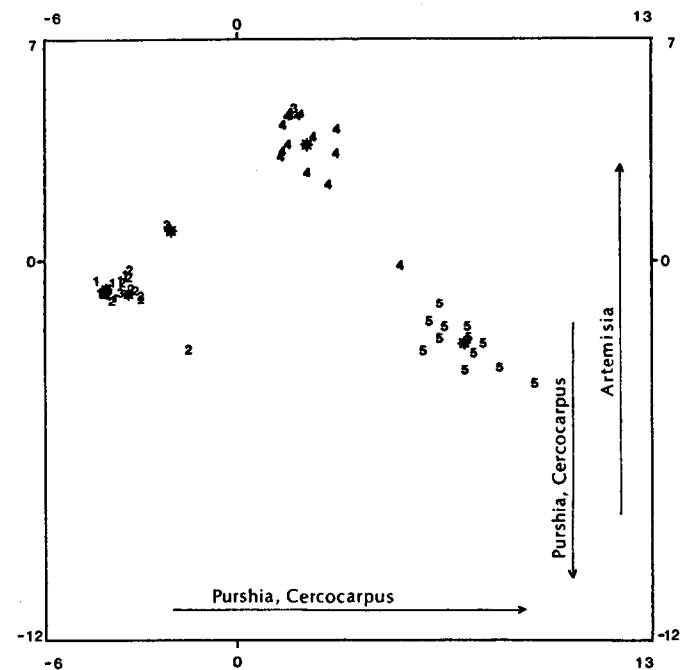


Fig. 3. Plot of discriminant scores of Fall (September, October, November) diets. The first (abscissa) and second (ordinate) discriminant functions have been given biological interpretation as indicated. 1 = horse; 2 = cow; 3 = sheep; 4 = pronghorn; 5 = mule deer; * indicates a group centroid.

function for Fall diets was therefore less strongly influenced by herding and forage availability to sheep than had been the second function for Spring and Summer diets. The relative percentage of the eigenvalue associated with the first discriminant function was lowest for Fall diets (Table 3). However, the within and between group dietary relationships are easily seen in the plot of diet locations along the first two axes (Fig. 3), the eigenvalues of which together accounted for 98.1% of the trace. During Fall, deer diets were high in *Purshia tridentata* and *Cercocarpus ledifolius*, whereas pronghorn diets were high in *Artemisia* spp. Horse and cattle diets continued to consist primarily of grasses. Sheep diets were again intermediate but contained very little *Purshia tridentata* or *Cercocarpus ledifolius*.

The first discriminant function for the Winter diets was strongly controlled by *Cercocarpus ledifolius*, *Purshia tridentata*, and *Juniperus occidentalis* (Fig. 4). It primarily reflected differences in habitat use during the winter of 1976–1977. Snowfall was relatively light that year, and deer did not seasonally migrate. Pronghorn and horse, however, moved to lower elevations as snow began to accumulate in late December. Therefore, although deer and pronghorn continued to select the same types of forage (primarily browse; Table 4), differences in forage species availability strongly influenced the plant species composition of their diets and, therefore, the discriminant functions. The second function represented an *Artemisia* spp. gradient and separated pronghorn from horse diets.

Discussion

The diet composition data determined in this study are supported by similar results obtained by numerous other investigators using a variety of techniques (McMahan 1964, Mackie 1970, Beale and Smith 1970, Boeker et al. 1972, Wallmo et al. 1973, Sundstrom et al. 1973, Kufeld et al. 1973, Hansen and Reid 1975, Bishop et al. 1975, Rosiere et al. 1975, Hansen and Dearden 1975, Harniss et al. 1975, Dusek 1975, Hubbard and Hansen 1976, Uresk and Richard 1976, Schwartz and Nagy 1976, Papez 1976, Olsen and Hansen 1977, Stuth and Winward 1977, Hansen et al. 1977, Hansen and Clark 1977, Schwartz et al. 1977, Short et al. 1977, Salter and Hudson 1979, Deschamp et al. 1979). All of these studies show that

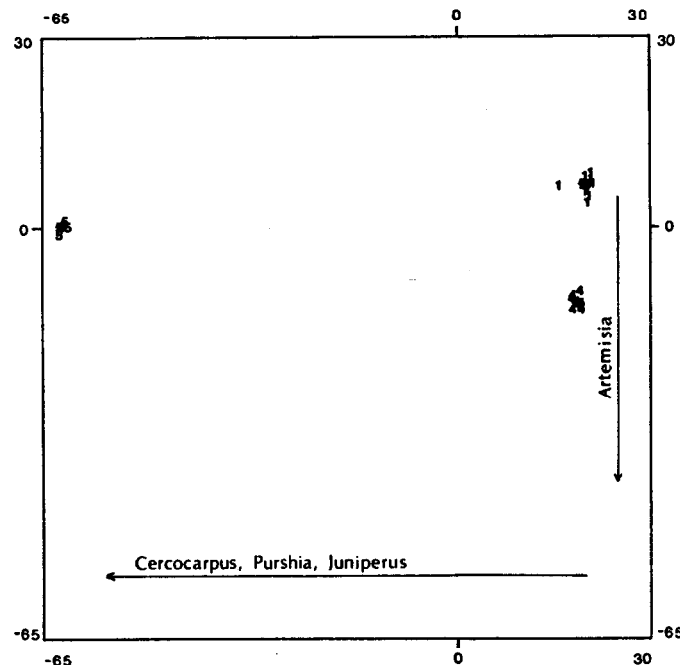


Fig. 4. Plot of discriminant scores of Winter (December, January, February) diets. The first (abscissa) and second (ordinate) discriminant functions have been given biological interpretation as indicated. 1 = horse; 4 = pronghorn; 5 = mule deer; * indicates a group centroid.

in habitats similar to those involved in the present study, the diets of cattle and horse are composed primarily of graminoids, while those of pronghorn and mule deer are composed primarily of browse and forbs. Sheep diets are generally intermediate, being composed primarily of graminoids and forbs but also containing appreciable proportions of browse. Results obtained by microhistological fecal analysis and rumen analysis tend to show lower proportions of forbs in the diet of all these animal species, particularly so for spring and summer pronghorn and deer diets, than do results obtained by esophageal fistula or visual observations of tame animals. The difference is due to differential digestibility and identifiability of forages. Diet composition of highly digestible forages (particularly forbs) is consistently underestimated while that of graminoids and shrubs is generally overestimated by rumen and microhistological fecal analysis (Bergerud and Russell 1964, Dearden et al. 1975, Vavra et al. 1978, Havstad and Donart 1978). Therefore, it is likely that the present data underestimate the true proportion of the diets that was composed of forbs and other highly digestible forages (e.g., very young leaves of grasses and browse). The overall pattern evident in the analysis of these data, however, is supported by the literature.

These data and the patterns produced by discriminant analysis of the data are consistent with the ungulate food selection framework (Hanley 1982) and therefore support its validity. Additional support is provided by the literature on chemical composition of forage types, chemical composition of diets selected by ungulates, and degree of selectivity exhibited by these ungulates. The chemical composition of forage types and the advantages and disadvantages of eating them have been discussed elsewhere (Hanley 1982). That large rumen volume ruminants select a diet high in cell walls while small rumen volume ruminants select a diet low in cell walls is supported by data reported by Schwartz et al. (1977) and Wallmo et al. (1977). Schwartz et al. compared the chemical composition of diets selected by sympatric bison (*Bison bison*), cattle, sheep, and pronghorn. In all seasons pronghorn diets were lower in cell walls than cattle or bison diets were. They were also lower in cell walls than sheep diets were during spring through fall; but sheep diets were lower in cell walls during winter. Sheep diets, however, were obtained by esophageal fistula samples while pronghorn diets were obtained by hand clipping species in proportion to their use. The ability of sheep to select a higher quality diet than that available on offer has been shown by numerous investigators (Cook and Harris 1950; Milton 1953; Meyer et al. 1957; Weir and Torell 1959; Arnold 1960, 1962a, 1962b, 1964; Bland and Dent 1964; Heady 1964; Fontenot and Blaser 1965; Eadie 1969). The importance of the difference in diet collection methods may have been particularly great during winter when browse constitutes a greater proportion of the diet. Mule deer diets collected by hand by Wallmo et al. (1977) in a different study area were very similar in terms of proportion of cell walls to the pronghorn diets reported by Schwartz et al. (1977). The deer diets were lower in total cell walls and higher in lignin than the pronghorn diets were (which is consistent with theory), but this may have reflected differences in habitats.

It is particularly interesting that browse species were so important in determining the discriminant functions in the present diet analysis. All four of the most important species controlling the discriminant functions, *Artemisia* spp., *Cercocarpus ledifolius*, *Purshia tridentata*, and *Juniperus occidentalis*, are browse species. *Artemisia* spp. and *Juniperus* spp. are known to be highly variable in volatile oil content (Smith 1950, Nagy and Regelin 1977); and *Cercocarpus ledifolius* and *Purshia tridentata* both take on club-shaped or mushroom-shaped, heavily hedged growth forms when grazed heavily by cattle (Hormay 1943, personal observation). The majority of individuals of these latter two species within the reach of ungulates in the study area existed in heavily hedged growth forms while the present data were being collected (personal observation; U.S. Dep. of Interior, Bureau of Land Management, Susanville, California District, unpublished data). These four browse species apparently were of relatively high value to deer and

pronghorn. Efficient exploitation of these forage resources, however, is dependent on a relatively small rumen capacity (for efficient digestion of browse), small body size (for relaxed time-energy constraints to permit intraspecific "shopping"), and a small mouth size (for harvesting only the current annual growth). Whereas deer and pronghorn diets were consistently relatively high in these four species, cattle and horse diets were not consistently high in any particular species; rather they were dominated by a variety of grasses and varied from location to location (hence the failure of any grass species to be useful as a discriminator indicative of horse and cattle diets). The other species for which discriminant functions were named, *Peraphyllum ramosissimum*, *Muhlenbergia richardsoni*, *Iva axillaris*, and *Oenothera tenacetifolia*, were of much less importance (controlling the second discriminant function) and were presumed to be of local significance only.

The investigated ungulates exhibited diets consisting of the expected types of forages; and the discriminant analysis indicated a gradient of forage selectivity associated with the differences in diet composition. Horses and cattle have the least time and ability to forage selectively but are physically able to efficiently exploit the relatively abundant and easily recognizable high cellulose forage resource (i.e., grasses). Pronghorn and deer, on the other hand, have both the time and ability to be highly selective foragers and are physically able to most efficiently exploit the high cell solubles forage resource (i.e., forbs and browse). Sheep have the time and ability to be highly selective foragers as well as being physically able to efficiently exploit the high cellulose forage resource. Sheep selectively harvest the most choice portions of the grasses while supplementing their diet with high cell soluble forbs and browse.

Conclusions

The ungulate food selection framework was useful in predicting diet relationships between the ungulates investigated in the present study. It is consistent with current knowledge of the nutrition of ungulates and diet selection by ungulates of other ecosystems as well (e.g., see Hofmann 1973). It is based on two basic premises: (1) that the degree of selectivity that can be exercised by foraging animals is restricted by time-energy constraints, and (2) that ungulates have evolved a variety of digestive systems enabling them to efficiently utilize fibrous forage resources, heterogeneous with regard to plant cell wall thickness and extent of lignification. Within the ruminants, large body size and large rumen volume are adaptations to exploitation of high cellulose diets (i.e., grassy environments). Small body size and small rumen volume, on the other hand, are adaptations to exploitation of high cell soluble and lignin diets (i.e., woody environments). Of native North American species these extremes are probably best represented by bison (*Bison bison*) and black-tailed deer (*Odocoileus hemionus columbianus*), bison being adapted to the Great Plains and black-tailed deer being adapted to the dense coniferous forests of the coastal Pacific Northwest. Elk (*Cervus elaphus*) is probably the most generalized North American species in these respects. Among African ungulates, the extremes are represented by the African buffalo (*Syncerus caffer*) and suni (*Nesotragus moschatus*), while Grant's gazelle (*Gazella granti*) is an intermediate species.

Knowledge of the values of the four morphological parameters (body size, type of digestive system, rumino-reticular volume to body weight ratio, and mouth size) involved in the food selection framework is sufficient for prediction of the kind of diet that will be selected by an ungulate given a free choice. This provides a basis for assessing relative habitat quality for various species of ungulates and an understanding of potential competitive (or facilitative) relationships among them. Such an understanding is much more valuable than simple measures of dietary overlap or similarity. A few implications for competition theory and habitat management have been addressed by Hanley (1982); and elsewhere (Hanley 1980) the food selection framework has been extended to include habitat patch selection. A deeper understanding of food resource partitioning by ungulates awaits to be revealed by a knowledge of

the reasons why ungulates select the plant species that they do, a subject beyond the framework investigated here.

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