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IMPLICATIONS OF DIETARY OVERLAP TO MANAGEMENT OF FREE-RANGING LARGE HERBIVORES[1]

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Introduction

In North America, rangelands support mixtures of ungulate species that neither co-evolved nor evolved with the vegetation. Wild herbivores, due to the presence of the large human population and concomitant land uses incompatible to wildlife, are forced to exist in ecologically incomplete habitats (Cole, 1971). That is, animals are not free to exist where they once did because many of the habitats have been altered or no longer exist. Low elevation winter ranges particularly have become private crop or range lands, and have high density human populations including cities. Deer or elk on winter and spring range that is private land are perceived as reducing the forage available for livestock to be turned out later in the spring. Sportsmen resent the presence of livestock in areas they hunt and envision that livestock consume forage that otherwise would be available to increased numbers of game animals.

Free-ranging large herbivores are faced with the dilemma of extracting sufficient nutrients and energy from rangeland vegetation to meet their minimum requirements for growth and reproduction. The forage base from which animals select their diets is frequently limited in amount and constantly changing in quality. Various species of large herbivores have evolved to meet their specific nutrient requirements by adapting feeding strategies that tend to optimize levels of energy and nutrient intake, and minimize feeding time (Ellis et al., 1976).

By selecting some plant foods and rejecting others, herbivores influence structure and composition of vegetation, potentially impacting their own population dynamics and those of sympatric herbivores. Under production systems in which a single species of herbivore is maintained, management efforts can be designed to maximize single-product outputs. For example, on private lands grazed only by cattle, rangeland vegetation can be altered to maximize nutrient intake for growth and reproductive capabilities of bovines.

When other species of herbivores are added to the system, as in multiple-use management on public lands or fee-hunting situations on private lands grazed concurrently by livestock, vegetation management becomes increasingly complex. Because nutrient requirements of different species usually vary, consideration must be given to providing adequate nutrition to each. When feeding strategies of various herbivores parallel one another and dietary habits converge, the potential for forage competition may increase.

The objective of this paper is to review factors which influence dietary selection by free-ranging large herbivores and discuss management implications of convergent dietary habits.

Diets of Large Herbivores are Constrained by Four Morphological Characteristics

Diet selection by ungulates has been examined on the basis of (1) body size, (2) type of digestive system (ruminant vs cecal), (3) rumino-reticular volume, and (4) mouth size (Van Soest 1982, Hanley 1982, Demment and Van Soest 1985). Larger animals require more nutrients per day than smaller animals but the larger animal's relative requirements (per unit weight of body tissue) are less. Since larger animals require greater amounts of dry matter intake per day, they have less time to spend selectively foraging. Conversely, since their relative requirements are less they have less need to be selective (Demment and Van Soest, 1985) and can meet their nutritional requirements with relatively lower forage quality (Hanley, 1982). Forage situations where quantity of material available is the limiting factor should favor the small herbivore's success in a competitive situation whereas limited quality of forage available would favor larger herbivores.

Animals of similar body size may still have dissimilar food habits if their digestive tracts are different. Ruminants are time-limited in regard to rate of passage of forages and are therefore intake-limited. They are quite efficient in terms of absolute digestion. Cecal digestors on the other hand are only 70% as efficient as ruminants in absolute digestion of cellulose but are not intake-limited and meet their nutritional requirements by passing larger amounts of dry matter through their gastro-intestinal tracts (Janis, 1976). Therefore, in situations of limiting forage quantity the ruminant should prevail, but where quality is limited the cecal digester with the ability to process more material per unit of time should prevail.

Ruminant species outnumber those of cecal digestors in the modern world (Janis, 1976). However, within ruminants distinct differences occur due to rumino-reticular volume to body size ratio. As has been mentioned, rate of passage is a critical factor in the foraging success of a ruminant. Animals with small rumens are particularly sensitive to forages of high cell wall content. Foods are retained in the reticulo-rumen until digestion allows particles to be reduced to sufficient size to pass through the rumen-omasal orifice. Therefore, passage rate decreases with increasing dietary fiber. For an animal with a small rumen, fill is reached in a short time and intake is restricted. An animal with a large rumen could better cope with the problems of

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physical characteristics, succulence and maturation, and genotype (Marten, 1973). Herbivores probably select food items that maximize sensory pleasure and minimize gastric or sensory discomfort (Arnold and Dudzinski, 1978). Some plant species have been consistently documented as being relatively unpalatable (Marten, 1978) because of objectionable chemical or morphological characteristics (Muegglar, 1970). However, preference for most plant species is situation-specific, and traits such as concentrations of sugar or soluble carbohydrates, protein, ether extract, mineral content, succulence, and morphological traits cannot be relied upon as repeatable palatability criteria in diverse situations (Marten, 1978).

Among environmental factors influencing palatability of forages are soil fertility, animal dung, plant diseases, climatic variation, seasonal or diurnal variations, and relative availability of plant species (Marten, 1978). In the west, seasonal and annual variation in precipitation, and the consequences on forage production are important and recurring variables influencing wild and domestic herbivores.

Holechek et al. (1982a and b) restricted yearling heifers to either grassland or forest pastures for a June to October grazing season for 4 years. Similarity indices were developed from dietary information between grazing periods within pastures and years (table 1); and between years within pastures and grazing periods (table 2). When diet similarities were compared between grazing periods within year or between years within grazing periods little consistency was observed on the forest pastures which contained more diverse plant communities and therefore a greater variety of plant species available. Shrub use was particularly variable among years and periods, and seemed to depend on the availability of green grass. Cattle diets on grasslands were less diverse than those on the forest reflecting less diversity in vegetation availability. Diets in spring on the grassland were less similar than other seasons because diversity in availability would be greatest during the growing season.

TABLE 1. THE PERCENT SIMILARITY OF CATTLE DIETS COMPARING GRAZING PERIODS WITHIN YEARS

Food comparison	Year 1976	1977	1978
Grassland			
LS-ESu[a]	46	78	59
LS-LSu	51	71	48
LS-F	51	61	49
ESu-LSu	76	75	68
ESu-F	74	65	66
LSu-F	82	74	74
Forest			
LS-ESu	47	52	55
LS-LSu	42	37	52
LS-F	41	40	44
ESu-LSu	66	54	54
ESu-F	52	61	42
LSu-F	46	67	45

[a]LS = late spring, ESu = early summer, LSu = late summer, F = fall

TABLE 2. THE PERCENT SIMILARITY OF CATTLE DIETS COMPARING YEARS WITHIN EACH GRAZING PERIOD

Year Comparison	Grazing Period Late spring	Early summer	Late summer	Fall
Grassland				
1976-1977	48	70	76	72
1976-1978	46	45	66	67
1977-1978	38	44	65	72
Forest				
1976-1977	42	56	56	53
1976-1978	43	51	42	48
1977-1978	51	53	41	54

Given all the variables previously discussed, those inherent to the animals, those found in forage and those of the environment plus the interactions; defining dietary overlap and from that competition, is no easy task. If cattle restricted to specific study pastures (grassland or forest) consume diets of limited repeatability, defining dietary overlap between or among different herbivore species free to select a variety of feeding sites form a diverse landscape over several years does not seem practical. However, land managers are faced with the task of identifying the correct mix of herbivores so that the forage resource is not degraded.

Applying Food-Habits Information to Management of Large Herbivores

Dietary information has been used to determine nutritional adequacy of the forage base (Westoby, 1974), animal performance (Svejcar and Vavra, 1985; Hobbs et al., 1982), suitability of improved forages (Truscott and Currie, 1983), and habitat preference estimations (Jenkins and Wright, 1983). Knowledge of food-habits can aid managers in assessing the potential of forage competition among sympatric herbivores, and provide a basis for allocating forage in multi-herbivore production systems. Information on the dietary preferences of herbivores can also provide useful insights for using animals as environmental tools to alter plant community composition and structure.

Although in the practical sense interspecific competition between sympatric herbivores may appear to be obvious and may indeed exist, relationships between large herbivores are not necessarily competitive and may often benefit one or the other or both herbivores. The existence of interspecific competition is difficult to determine scientifically from empirical data. Interspecific competition must be judged on the basis of two criteria (Wagner, 1969): (1) two species compete when they share a resource that is present in short supply, and (2) in using the resource, each species reduces the other's population performance to levels below what these measures would be in the absence of other species. Much of the literature on competition between organisms focuses on measurement of niche and niche overlap. Hurlbert (1978) defined niche overlap as the degree to which frequency of interspecific encounter is higher or lower than it would be if each species utilized each resource in proportion to its abundance. Measures of niche overlap are designed to establish the degree that two species share a set of resources or utilize the same part of shifted on the different study areas with overall less similarity of food habits on most study areas.

Lesperance et al. (1970) used rumen fisculated steers and rumen excreta from collected mule deer to examine competitive use of the range forage resource in Nevada. Examination of food habits indicated cattle had the potential to compete with mule deer for bitterbrush (Purshia tridentata) during fall. Potential competition between cattle and mule deer during the spring season when both herbivores had high consumption of grass was alleviated by use of different range types. During other seasons, food habits of the two herbivores were separated by the high selectivity of cattle for grasses and mule deer for browse. Over utilization of a range areas by either herbivore resulted in an increasingly less desirable plant population for that species but tended to produce and ecological shift in plant population more favorable for utilization by the other species. Periodic grazing of bitterbrush by cattle was thought to benefit mule deer by increasing browse availability through alterations in morphological characteristics of shrub canopy. The authors also suggested spring competition could be avoided by delaying cattle turnout on deer ranges until May, and early removal of cattle to prevent browse use on deer winter ranges.

Hanley and Hanley (1982) used diet composition data obtained from horses, cattle, sheep, pronghorn, and mule deer, analyzed by discriminant analysis, to predict an ungulate food selection framework associated with herbivore morphological parameters (body size, type of digestive tract, rumino-reticular volume to body weight ratio, and mouth size). With this knowledge, prediction of the kind of diet that would be selected by a herbivore can be projected. In their study, diets of cattle and horses were composed primarily of graminoids, while those of pronghorn and mule deer were composed primarily of browse and forbs. Sheep diets were intermediate between the former herbivore groups.

Nelson (1977), using Smith's (1965) data on vegetative composition and utilization by mule deer and sheep developed formulations for calculating maximum stocking rates, carrying capacities and trade-offs among herbivore species based on key species in the diets of the two herbivores. Knowledge of food habits using this methodology provides a means of calculating a reasonable optimum stocking rate combination that would be expected to result in maximum allowable use of key species in the diets of the two herbivores.

Sheehy (1988) used diet composition of elk, cattle and mule deer to develop a similarity index of large herbivore diets on seasonal rangeland in northeastern Oregon (table 4).

The similarity indices of dietary overlap indicated there was a high probability diets of elk in the winter and spring consisted of many of the same food items as diets of cattle in the fall. The indices also indicated food habits of cattle and elk were generally more similar to each other than with food habits of mule deer. Although food habits indicated the potential for competition among herbivores, especially cattle and elk, indices of herbivore distributional overlap indicated the probability of herbivore competition for habitat on this seasonal rangeland was less than would be indicated solely from dietary overlap (table 5).

TABLE 4. INDICES OF DIET OVERLAP OF CATTLE, ELK AND DEER ON A SEASONAL RANGELAND IN NORTHEASTERN OREGON.

Herbivore (Season)	Cattle (Summer)	Cattle (Fall)	Elk (Winter)	Elk (Spring)	Deer (Win-Spr)
Cattle (Summer)		61.6	75.8	55.0	37.5
Cattle (fall)			67.5	76.4	46.0
Elk (Winter)				77.3	44.0
Elk (Spring)					50.0
Deer (Win-Spr)					

TABLE 5. PROBABILITY OF DISTRIBUTIONAL OVERLAP OF 3 LARGE HERBIVORES ON SEASONAL GRASS STEPPE RANGELAND

Overlap	Plant Comm	X	Edge	X	Elevation
Elk-Cattle	.043		.518		.600
Cattle-Elk	.280		.343		.381
Deer-Cattle	.874		.851		.880
Cattle-Deer	1.000		1.000		.939
Deer-Elk	.366		.766		.355
Elk-Deer	.663		.736		.596

Probability of deer and cattle distributional overlap was highest among the three herbivores but dietary overlap of these two herbivores was low. Cattle and elk had high probability of overlap in food habits but distributional overlap was moderate to low. Deer and elk had low probability of distributional overlap and dietary overlap. Timing of distribution of the three herbivores on seasonal rangeland was also a factor ameliorating the potential for herbivore competition. Elk and deer had highest occupancy in winter and early spring before cattle turnout. In years with normal or above average spring and early summer precipitation, dietary items common to diets of the three herbivores had opportunity for regrowth. Sheehy (1988) also used that food habit information to determine association of herbivores with plant communities present on seasonal rangeland in northeastern Oregon. By comparing rank correlation of food items occurring in the diet of herbivores and the same forage species in plant communities, association of herbivores with specific plant communities could be assigned. Food habit information indicated diets of elk and cattle had highest correlation with different plant communities. Cattle and mule deer diets had highest correlation with the same plant community but diet composition of the two herbivores indicated less than 50% dietary overlap indicating the use of different plant species within the same community. In general the potential for a competitive relationship

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