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INTRODUCTION

There has been very little plant synecological work done in the Canadian Rocky Mountains, particularly on alpine communities and their environments. Biological studies of population dynamics of wild ungulates and their ranges designed to determine forage production, utilization and carrying capacities are hampered by a lack of knowledge on biotic-abiotic interactions. Cain (1969:41) referred to this problem by stating "The physical structure of the biotic communities is not constant in an absolute sense over any considerable distance; and the abiotic factors of climate, soil, and topography which influence the biotic members also show different mixtures over space.... Any biological system will of necessity have associated physical determinants in the climatic, geological, and pedological conditions and will itself be a consequence of the historical record of migrations and evolution."

The author has often been perplexed over the problem of estimating grazing capacities of native ungulate ranges when certain forage species have been found to be preferred on some ranges but ignored on others by the same ungulate species. For example, bighorn sheep exhibit a moderate-high preference for bluebunch wheatgrass (Agropyron spicatum) in south-western Alberta. However, they left this species relatively untouched in Kootenay National Park in British Columbia, both prior to and during a 75 per cent population mortality attributed to malnutrition during the period 1966 to 1968. Similarily, although bighorn sheep utilize Idaho fescue (Festuca idahoensis) in southwestern Alberta, they appear to prefer the green color phase of this species in preference to the blue color phase. Elk have been observed to utilize silver willow (Eleagnus commuta) extensively on some winter ranges and to leave it untouched on other winter ranges.

This problem has been discussed by several authors. Cook and Stoddart (1953) in an article entitled "The Quandry of Utilization and Preference" stated that only occasionally do animals actually seek a preferred species; rather they merely spend greater time foraging upon, the preferred plant upon which they chance to come. Heady (1964) concluded that "... in general there seems to be no consistent correlation between chemical composition of forage and its preference. More important is the combination of chemical components." Young (1948) suggested that three interrelated systems exist which regulate food acceptance, namely:

1. within the animal body, including nerve stimuli initiated by energy release, blood sugar level, body temperature, movements in the digestive tract, fatigue of mouth parts, the senses, and others. These are mainly associated with the stopping of eating.
2. the conditioning of an organism by previous feeding habits.
3. the nutritive and physical environment of an animal.

The three systems are interrelated in a stimulus-response chain of events that includes recognition of food, movement to the food, appraisal, initial eating, and cessation of eating.

This paper is a compilation and summary of several articles encompassing the field of Soil - Vegetation - Climate - Ungulate Interrelationships. It is hoped that such a review will provide a clearer understanding of the numerous biotic - abiotic interactions that influence forage preference, palatability, and ultimately range carrying capacities.

DEFINITIONS

Palatability - This term has been defined by Heady (1964) as the plant conditions or characteristics which stimulate a selective response by animals. It has also been described (Cook *et al.*, 1962) as that quality in a forage plant that makes it preferred when a choice of various plants are available.

Preference - This term is reserved for selection by the animal and is essentially behavioral. Relative preference indicates proportional choice among two or more foods.

Grazing Capacity - This term is used in this paper to be synonymous with Range Carrying Capacity, and refers to the optimum number of ungulates, or animal-unit-months, that a range can support on a long-term basis without suffering regression in condition and trend.

PROBLEMS IN ESTIMATING PREFERENCE, UTILIZATION AND GRAZING CAPACITY

Probably the most important and universal factor affecting palatability is succulence, closely followed by the nutrient content of the forage (Mitchel, 1963). Some authors say that it is the succulence of the plant which makes it preferred, others say it is the nutrient content, or the tenderness of the stems, or the instinct of the animal to graze plants. Probably these are the most important factors influencing preference but each situation is different and the plant species grazed are dependent upon the environment of the range and the conditions under which the animal is grazing. Several other factors affecting palatability are actually only functions of the main factors mentioned above, that is, they influence succulence, mineral content etc. Some of these factors are soil fertility, fertilization, season, plant maturity, burning, and possibly the presence of fecal material and urine spots. Factors which affect forage availability are important, as an animal can only eat what is there and available, and if there is a variety of plant species, he choses what he likes best (Holscher et al.,1953, Peterson and Wollfolk, 1955).

Variability has been mentioned as one of the most important factors influencing grazing capacities (Stoddart and Smith,1955). Much of this variability can be attributed to factors which influence palatability such as kind of animal, age, degree of plant maturity, stage of pregnancy, physical condition of the animal, hunger, familiarity an animal has with a plant, availability and relative abundance of associated plants, and chemical composition of plants (Green etal.,1951; Jones 1952; Tribe 1952; Stoddart and Smith 1955; Cook 1962; May and Severson 1963; Heady 1964). One of the most important of these is the availability or relative abundance of associated plant species. Cook and Stoddart (1953) emphasized this point when they stated that "Many plants of low palatability frequently make up a great portion of the grazing ungulates diet when abundant in the floral composition. This does not necessarily occur only when other, more palatable, species are scarce or are all closely grazed, but results merely from the greater frequency with which the more abundant species comes before the animal in the normal process of grazing." An example of this, is the use of ninebark in the Missoula, Montana area where it is abundant.

Under the canopy of an open forest, the palatability of grasses declines significantly from what it is on a treeless plain (Cook and Harris,1950; Harris,1954). Other factors influencing utilization are the ungulate stocking rate, the animals history and the time of day (Holscher et al.,1953; Peterson and Wollfolk,1955; Springfield and Reynolds, 1951; Wagnon et al.,1960).

The primary tastes (salty, sweet, sour bitter) are not adequate to determine palatability and preference because taste results from combined stimulations and there are no corresponding rigidly specific taste cells. A continually changing body chemistry undoubtedly influences taste.

Determining grazing capacity is a quandry because of tremendous annual fluctuations in forage production. On perennial forage, production may be three times as great, and on annual vegetation production may be ten times as great, from one year to another (Morris, 1967). Grazing capacity has come to be regarded as the maximum number of ungulates which can graze each year on a given area of range, for a specific number of days, without inducing a downward trend in forage production, forage quality, or soil (Stoddart,1967).

Another important factor influencing grazing capacity is the lack of uniform distribution of grazing ungulates, hence, grazing capacity must be based upon the capacity of important, accessible "key areas" rather than upon the forage produced over the entire range. Correct grazing should be judged after considering the percentage removed from major forage species, soil stability, topography, uniformity of grazing, and animal response (Stoddart,1967).

Utilization measurements in plant response studies should consider 1. the portions of the plant being utilized, 2. whether or not the plants were grazed during the growing season, after maturity, or both. The composition of the diet is not an accurate index to palatability because relative abundance of species as well as per cent utilization determines the amount of each plant consumed (Cook and Stoddart, 1953).

BIOTIC FACTORS INFLUENCING RANGE PRODUCTION, UTILIZATION AND GRAZING

1. Succulence of Forage

The youngest plants, the leaves, and in most cases the most succulent plants, are also the most nutritious (see section on nutrition). That succulence is important in species preference was shown on a ponderosa pine range in New Mexico (Springfield and Reynolds, 1951) where Hereford cattle grazed less discriminately when the grasses were wet from rain or heavy dew. A regression correlation of $r = .69$ was obtained correlating per cent diet with per cent moisture. The following are some results of this study.

Plant Species	% Diet	% Moisture
Orchard grass	26	57
Smooth brome	24	48
Tall oatgrass	9	47
Kentucky bluegrass	9	46
Slender wheatgrass	21	38
Bluestem wheatgrass and Big bluegrass	3	37 34
Crested wheatgrass	9	38

Bluestem wheatgrass and big bluegrass were relatively untouched until the other species had been fully utilized.

A study in Eastern Montana (Holscher *et al.*, 1953, Peterson and Wollfolk, 1955) showed that twice as many bluegrama plants were grazed along the fringes of coulees as on the uplands and fifty per cent more than in the hills. Buffalo-grass and bluestem wheatgrass also showed a similar higher preference when grazed in the valley bottoms. Increased succulence was reported an important factor in this differential use.

A similar study in Kansas shortgrass prairie produced similar results (Moorfield and Hopkins, 1951). However, a study in Southern Arizona (Coble and Bohning, 1959) on native grass species showed no correlation between preference and moisture content. This indicates that biological exceptions are common place.

The grazing and regrazing of certain plants within a species by cattle and sheep is intimately connected with preference for tender and juicy forage. Plants grazed the previous year have no dead material about them; only new growth. On grass-legume pastures, Cowlishaw and Alder (1960) found a negative correlation between per cent dried matter and preference for grazed patches of forage. On crested wheatgrass pasture which had been fifty per cent utilized, forty per cent of the plants were unused and thirty per cent were grazed down to two inches or less. New growth from grazed patches is not only more succulent but contains one to five per cent more protein than other forage (Allred, 1951). No doubt these examples indicate a combined preference for succulence, tenderness and nutritious forage.

2. Nutritive Value of Forage

The preference for leafy parts of plants by cattle and sheep is beneficial in that protein, phosphorus, cellulose, and gross energy are generally higher in forage consumed than in total current growth (Cook et al., 1956). The seasonal shift in preference due to protein content was illustrated in a study on bunchgrass and pine - bunchgrass ranges in Oregon (Allred, 1951). In this study Sandberg bluegrass was little used except in the spring and early summer. The protein content declined steadily from 5.41 per cent on June 25 to 2.96 per cent on August 20. Several inches of rain fell in early September resulting in an increase in protein content (5.64 per cent) on September 16, and in some renewed use of the species. Bluebunch wheatgrass was found especially nutritious throughout the grazing season with an average protein content of 6.93 per cent for the season. It maintained the five per cent minimum protein allowance for cows with calves until mid-October and was the most preferred species with sixty per cent utilization on untimbered areas. The average protein content of Sandberg bluegrass was 4.41 per cent while its average herbage utilization over the season was sixteen per cent.

Livestock often turn their attention to shrub forage as grass species mature and dry. Since most browse species store carbohydrate reserves in the current annual growth (Cook, 1956) it appears that extra nutrition, and perhaps succulence supplied by the browse species causes the change in diet.

To understand the changes in nutritive value and corresponding responses in preference by cattle and sheep from spring to fall, the remarks by Cook (1956) are worth quoting verbatum (pages 18 and 19) "... the individual forage classes are inherently different in the content of the various nutrients and furthermore, show seasonal changes among the separate nutrients with advancing stages of maturity. Grasses are the lowest in protein and phosphorus but are the highest in energy-yielding cellulose. Browse plants are highest in protein and lowest in cellulose. Forbs are intermediate in most respects. Grasses lose about one half their protein content and increase decidedly in lignin and cellulose with the advancement of season. However, protein content of forbs and browse decreases only slightly and lignin and cellulose increase only slightly as the season advances. For these reasons the grazing animal can more nearly satisfy its requirements if it has access to an assortment of species from all three forage classes.

Both sheep and cattle changed their preference for the various forage classes as the summer season advanced. For both, the grasses were relatively high in the diet during early summer but were less readily eaten in the late summer. Sheep and cattle ate little browse during the early season but browse consumption increased decidedly later. These changes were more pronounced for sheep than cattle. The percentage of forbs in the diet increased only slightly as the season advanced.

As a result of the reduction of grass and an increase in forbs and browse in the diet as the season advances, the nutrient intake is maintained at a relatively high level since forbs and browse do not decrease as decidedly in nutrient content as grasses.

Browse and forbs furnish ample protein and phosphorus late in the season but are somewhat deficient in energy supplying qualities, whereas grass is deficient in both protein and phosphorus late in the season but is still high in energy. All three forage classes are high in carotene (vitamin A) during the entire season.

Late summer or fall rains may produce regrowth somewhat comparable in nutrient content to spring growth if these fall growing plants are present. In the event the forage remains dry and dormant throughout the fall grazing period, all critical nutrients may be borderline or slightly deficient. Figure 2 below illustrates some of the above points."

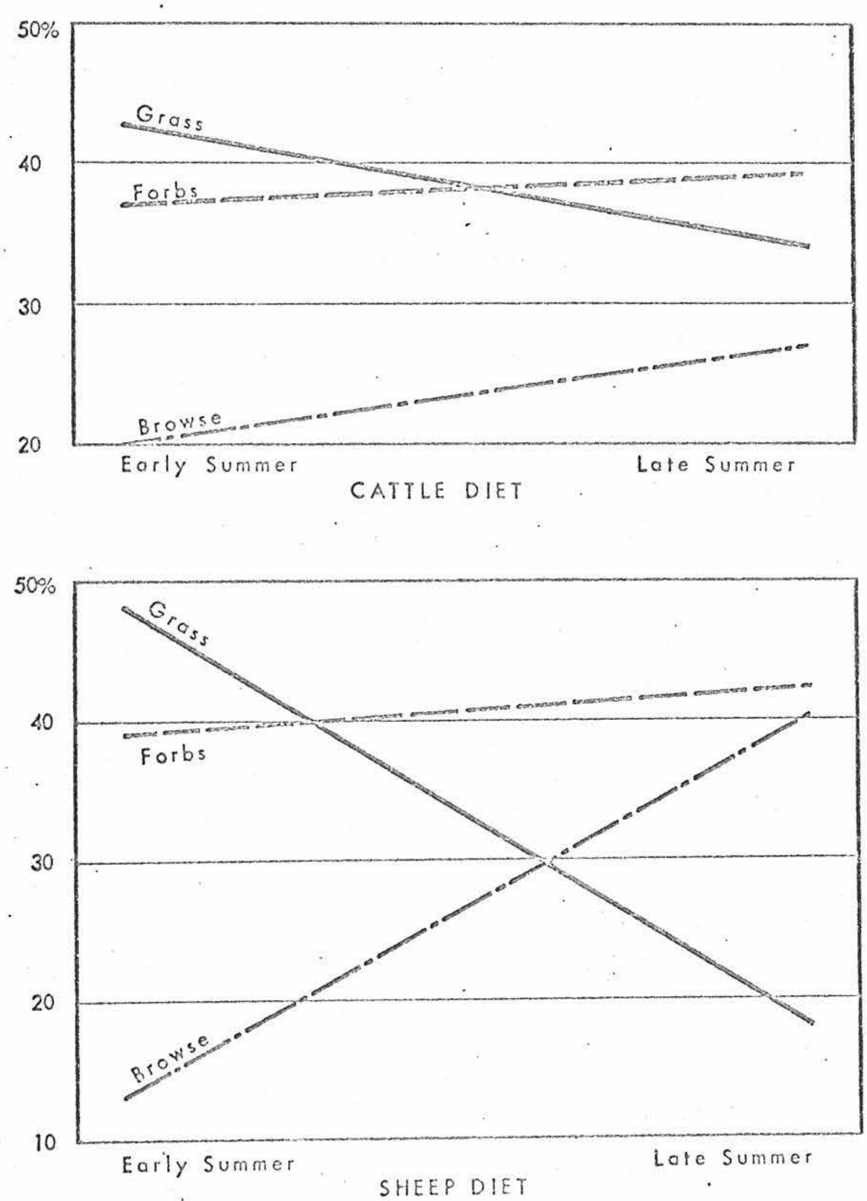

Fig. 2. *The composition of the diet for cattle and sheep by forage classes from early summer (July 1) to late summer (September 1) on typical summer range in northern Utah. The range where sheep diets were studied consisted of 65 percent grass, 20 percent forbs, and 15 percent browse, and the range where cattle were studied consisted of 25 percent grass, 40 percent forbs and 35 percent browse.*

In winter, grasses are markedly deficient in protein, phosphorus, and carotene but are a good source of energy. Therefore, a mixture of browse and grass more nearly balances the diet than either forage class alone. Forbs are generally unimportant in the diet during winter grazing.

Site conditions and stage of growth were important factors affecting the nutritive value of range forage. Sites indirectly affected the chemical content of plants through soil and plant development, water runoff, intensity of shade, and other environmental factors. Individual chemical constituents of the plants were affected differently by various sites. The effects of site also presented marked differences in the stem - leaf ratio in various species, thereby affecting the palatability of forage and nutrient content of the diet since leaves are more preferred than stems and are decidedly different in chemical composition. Environmental factors and soil moisture are more important in determining the nutrient content of range forage plants under various site conditions than the chemical content of the soil as determined by standard methods (Cook, 1950).

There is a high positive correlation between protein content and preference by cattle and sheep. Foods high in sugars, or with sugars added, are preferred by cattle, pigs, calves and deer. High total ether extract indicates high preference. Grasses highest in phosphate and potash are the most acceptable to livestock.

As proteins, sugars, fats, and preferred components of ether extract increase in percentage composition, lignin and crude fiber decrease. Therefore negative correlations of lignin and crude fiber with increased preference have been shown. Tannins, coumarins, and nitrates decrease preference. However, in general there seems to be no consistent correlation between chemical composition of forage and its preference. More important is the combination of chemical components. Total nutritive value of the plant may be a better indicator of palatability, although chemical composition is the most important palatability factor. As grasses and broad-leaved herbs mature, they decrease in crude protein and increase in crude fiber, lignin, cellulose, and other carbohydrates. Palatability decreases as grass forage becomes tall, coarse and dry (Cook and Harris, 1950; Cook, 1959; Stoddart and Smith, 1955).

Cook (1959) summarized "In general, chemical composition is the most important palatability factor. Other factors such as proportion of leaves, stems, and fruits, plant growth stages; past grazing use; climate; topography; soil moisture; and fertility have been related to palatability mainly through their influence on chemical components. Little information is available on external form, texture, and odor as they may influence preference."

3. Plant Species Composition

The quantity of feed consumed by the grazing animal is influenced by the plant species present, stage of growth, abundance of forage, and general climatic conditions. Therefore, the intake and composition of the diet vary from day to day and from one range to another (Cook, 1956).

Clarke and Tisdale (1945) reported (page 47) that "palatability is influenced by a number of factors, including class of livestock, intensity of grazing, growth stage of the plants, time of year and relative abundance of other species.... Pastures containing a mixture of species usually are preferred to those composed of pure stands of one species. The various native and introduced pasture forages vary considerably in chemical composition, palatability and growth development. Hence, a mixed stand usually will produce a more desirable type of feed throughout the whole season. For example, in the Shortgrass Prairie, early species such as junegrass and niggerwool are valuable especially for early spring pasture, while speargrass and western wheatgrass are excellent for late spring and summer. Grama grass, which is later in growth development than any of these is of little use for spring grazing but makes good feed for late summer and fall. In winter, species such as pasture sage which are unpalatable during the summer are grazed considerably and provide valuable nutrients. McCall (31) at Pullman, Washington, found that a mixture of ten per cent of sagebrush and other non-grasses with 90 per cent of bluebunch wheatgrass was more palatable, digestable and nutritious for lambs than was cured grass alone." Cowlishaw and Alder (1960) found that white clover by itself was not relished by cattle, but when grown with ryegrass was taken with the grass readily: The relation works both ways in that the amount of grass growing in the clover influenced the palatability of the mixture. Similarly, a mixture of orchardgrass and white clover was preferred to orchardgrass alone, and a mixture of fescue and white clover was more readily taken than just the grass (Voisin, 1961).

Some species are grazed heavily when they occur in small quantities throughout a "better" forage, whereas in dense stands the use is light. This situation was shown for Agropyron smithii on lowland sites by Tomanek et al. (1958). Hurd and Pond (1958) concluded that utilization was not influenced by frequency, abundance, or amount of herbage produced.

4. Ungulate Species and Stocking Rates

As grazing pressure increases, the use of forbs increases and relatively undesirable species such as silvery lupine become important forage (Hurd, 1969).

Hyder, D. N. et al. (1966) concluded that summer-long (May 1 to November 1) grazing at different intensities for 23 years in Colorado had not affected species frequencies to any great extent. He felt that the most important effect of heavy grazing was a reduction in herbage yields. In discussing winter-range utilization by elk and mule deer in southeastern Washington, Bueckner (1952) reported that Idaho fescue ranked high in preference for elk and mule deer and was morepalatable than bluebunch wheatgrass (85% utilization compared to 50% respectively). The higher utilization of Idaho fescue was correlated with higher production compared to bluebunch wheatgrass (13 compared to 6 lbs. per acre respectively) and reflected the influence of availability upon utilization. Idaho fescue is also a choice forage plant relished by all classes of livestock (Range Plant Handbook, 1937).

Severson et al. (1968) showed the diet of antelope and sheep in the Wyoming Red Desert varied greatly with seasons. Figure 4 from their publication illustrates the seasonal preference changes.

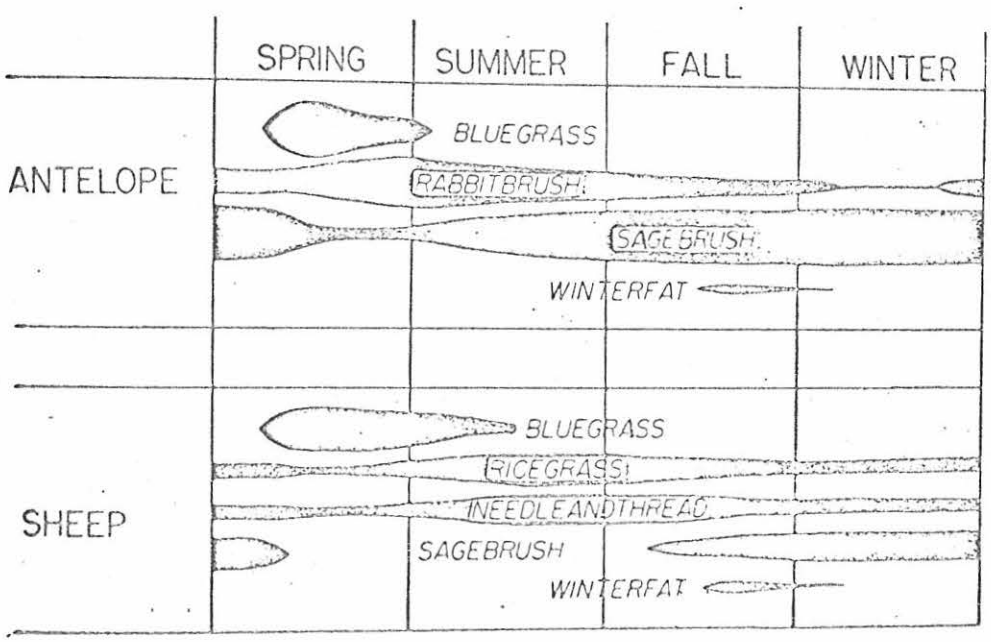

Figure 4. Seasonal Preference for Forage by Antelope and Sheep on the Sagebrush-grass Vegetation Type in the Red Desert Region

Bueckner (1952) found that elk fed avidly on cheatgrass in early May when the forage was green and fairly abundant in patches on benches and ridges. It was not utilized in a cured-state. Bluebunch wheatgrass withstood heavy fall and winter utilization provided it did not receive spring and summer use. Under a stocking rate of 4 acres per elk-month during the fall to spring period including some spring use the grassland range remained in an overgrazed, abused condition. Nine acres per elk-month and 7 acres per deer-month appeared to be the approximate proper stocking rates for the southeastern Washington range for fall to spring use, providing no livestock use occurred. At a population density of 41 elk and 11 deer per square mile (4 acres per elk-month and 11 acres per deer-month), 78 per cent of the bluebunch wheatgrass was removed. This utilization declined to 49 per cent at a population density of 16 elk and 21 deer per square mile (9 acres per elk-month and 7 acres per deer-month).

5. Instinct of the Ungulate to Select Most Nutritious and Balanced Diet

Stapleton (in Grass Productivity by A. Voisin, 1961) commented that "The cow has an appetite instinct which allows her to select the foods which best satisfy her physiological requirements." This instinct is modified by many factors, but if conditions permit an animal to be selective in feeding this statement is true. A study in England by Cowlishaw (1960) showed that the closest correlation to preference rank was the content of soluble dry matter (total nutrient material except liquids). Water soluble ash and carbohydrates were also closely related to preference rank.

In another study at Cornell University (Voisin, 1961), two steers were fed from a mixed orchardgrass - clover pasture. One of these was stall-fed from pasture clippings and the other grazed on the pasture. Analysis showed that the nitrogen content of the grass eaten by the stall-fed steer was always lower than that of the grazing animal, with the latter always chosing a diet richer in protein.

A similar study by Meyer, et al. (1957) showed no difference in total digestible nutrients (TDN) of the clippings consumed from alfalfa or clover-orchard grass pastures when fed as silage to cattle and sheep, from that of the TDN content of the clippings themselves. However, when the animals were allowed to graze, the TDN content of consumed forage was definitely higher than that of the total vegetation (60.7 versus 56.5 per cent of dry weight respectively).

Cattle foraging on very young and succulent pasture will also utilize older, coarser plants along fence rows to gain roughage (Wagnon et al., 1960). Conversely, cattle on older pasture will seek out younger plants in search of added succulence and tenderness (Voisin, 1961).

Thomas (1947) relates that cattle will supplement grasses deficient in minerals, with weeds such as nettle or dandelion that have a higher mineral content. The instinctive knowledge of a need for roughage is also revealed by observations of cattle eating a great deal of straw and coarse grasses when being fed protein supplements (Allred et al., 1951). A somewhat different view is taken by Wagnon et al. (1960) who contend that livestock have no a priori knowledge or instinct as to what they can or cannot eat. Grazing animals have a taste for juicy, tender forage. Cattle which have been raised on grass and cereal hays and have never seen alfalfa will eat bedding straw before trying alfalfa hay. Even though ungulates have the ability to select the most nutritious and balanced diet it takes time for them to become accustomed to unfamiliar forage plants.

The general concensus by most range specialists is that animal species have innate preferences for certain plants, parts of plants, or plants in particular growth stages. Grazing animals exhibit variation in preferred foods from one location to another, from one season to another, over a period of a few days, within the same day, and among individuals. Reducing the available feed supply by grazing has altered preference. On the other hand, relative utilization of a species does not appear to be influenced by frequency, abundance, or amount of herbage.

6. Animal Physiology

Cook (1956) remarked (page 11) that "Feed requirements for livestock vary according to age and stage of development of the animal and phase of production such as maintenance, gestation, growth, fattening, and lactation." In addition to the above, sight, smell, touch, taste, hunger, instinct and experience probably all affect preference.

7. Animal Waste Deposits

It has been observed many times that ungulates will not graze forage growing close to or on their own droppings (Allred _et al._, 1951; Plice, 1953; Thomas, 1947; Voisin, 1961). The reason for this has not been satisfactorily determined, but odor seems to be a factor while the rankness of the forage may also be involved. Voisin (1961) relates an interesting sidelight concerning the tolerance of one class of livestock for the dung of another species. Cattle will not feed upon grass where their own manure lies but will graze next to horse manure, and the converse is also true. Cattle will eat next to sheep droppings, but not where sheep have lain. The fact that bighorn sheep decline in numbers and often disappear completely after domestic sheep and cattle have been introduced to their range (Bueckner, 1960) may be in part due to the intolerance of bighorn sheep to graze on range where the droppings of livestock are present.

There is some controversy over the influence of urine spots on forage utilization. Voison (1961) states that according to Dr. A. G. Etter that both horses and cattle seek out grass which is growing where they have urinated, seeking instinctively to recover the nitrogen, potassium and trace elements contained in the urine. On the other hand Allred (1951) maintains that urine spots are shunned as are manure piles.

8. Sweetness of Forage

Plice (1953) found that the sweetness of forage influenced palatability. Artificial sweeteners, containing no food value, as well as natural sugars (molasses) when sprayed on unpalatable forage causes it to be taken readily.

Pastures fertilized with phosphate fertilizers are especially preferred. Phosphorus is an essential element in the sugar synthesis process and if more is available, to a limit, more sugar is produced thus making the forage sweeter. Plice (1953) showed that in alfalfa hay which is not allowed to cure before bailing, that fermentation takes place which lowers the nutritive content but doubles the sugar content. This forage is much preferred by livestock over freshly cut or properly cured alfalfa hay.

9. Fibrosity

That cattle are influenced by fibrosity in their preferences for certain forage species is shown by the results of a study done in Arizona (Cranfield, 1942). Fine-stemmed species such as spruce top grama, slender grama, and hairy grama were highly preferred while coarse or stiff-stemmed species such as side oats, grama and black grama were less preferred. Cowlishaw (1960) found that lignin content was negatively correlated to preference rank. Since fiber (lignin) content increases as the plant matures (Cook et al., 1956; Cowlishaw, 1960) there is little doubt that fiber content is connected with decreased palatability as the season progresses.

ABIOTIC FACTORS

1. Soil - Vegetation - Climate Interactions

Scott and Billings (1964) remarked, page 266 " [plant] species are frequently correlated (positively or negatively) with available potassium, calcium, magnesium, and phosphorus.... Ecotypes within a species may differ in their nutrient requirements. For example, Snayden and Bradshaw (1961) have demonstrated ecotypes in *Festuca ovina* that differ in their calcium requirements, and that these ecotypes may exist within a mile or so of each other.... The conclusion seems to be that nitrogen availability is not usually limiting in the Medicine Bow alpine environment." Further on page 267 they stated "Both the range of conditions within which a plant can survive, and the rate of energy gain or loss under particular conditions will be determined by the genotype of the plant. However, the actual response of a plant at some particular instant will be considerably smaller than its genotypic potential and would probably be past growing conditions or pretreatment of the plant.... The correlation between above-ground summer standing crop for individual species and 55 environmental factors was tested. Different factors were significant for different species. The factors most frequently significant were: altitude, winter snow cover, moisture regime, soil movement, percentage clay, extractable potassium, and available water in subsoil. Factors that were occasionally significant: 30 cm. soil temperature, bulk density, pH, extractable phosphorus, difference between extractable calcium of topsoil and subsoil."

It is possible that native range carrying capacities may often be influenced by soil nutrition and that in some cases ranges may be judged suitable or unsuitable by wild ungulates on the basis of the presence, absence, or proximity to, essential nature soil licks. This may be especially true where the forage is deficient in essential macro, micro, or trace elements. Bighorn sheep, mountain goats, elk, mule deer and moose frequent natural licks especially during certain periods of the summer, apparently to satisfy physiological needs. McCrory (1967) showed that mountain goats in Jasper National Park extracted proportionately high amounts of calcium and copper from a soil lick during a period in the summer when these elements were in great demand to meet location and hair development needs. The presence of a natural lick may be the controlling factor in determining the carrying capacity of many native ungulate ranges.

It has been shown that cattle, at least in some cases, graze plants containing more of a mineral or minerals that they need (Thomas, 1947). This can result in selective grazing of plants which have a greater ability to extract this substance from the soil. A study made in Montana showed that on high mountain pastures when there existed a phosphorus deficiency, cattle tended to graze larkspur which contained more phosphorus than the other species (Morris, 1967). Cattle fed a supplement of phosphorus before being taken onto the area showed no abnormal preference for this species. Lovvorn and Wood (1962) showed that soil fertility affects the rate of plant growth toward maturity. Phosphorus deficiency frequently delays maturity, as does excess nitrogen. As previously shown there is a definite correlation between plant maturity and preference, and in this way also soil fertility may influence preference, even though indirectly.

Fertilization of pastures and ranges affects palatability mainly by increasing succulence. Burton, et al. (1956, 1958) found that an increase in the amount of nitrogen per acre resulted in an increase in succulence and palatability.

Alkalinity suppresses the solubility of some elements required by plants, for example the insolubility of phosphates in a soil containing calcium carbonate. As phosphorus has a great affect upon the ability of a plant to withstand adverse conditions such as overgrazing, its lack is an important factor in the condition of ranges. In general, high alkalinity tends to limit the supply of many nutrients as negatively charged ions are absorbed with difficulty by plants when the soil reaction exceeds pH 7.6.

Potassium plays an important part in many of the vital physiological processes of the plant, and a deficiency has decided effects, such as lowering disease resistance, photosynthetic functions, and reproductive capacity.

Soil texture is important because of the differential water holding capacities of the various textural classes. The water retention capacity of a coarse soil such as sand is much less than for a fine soil such as clay. Ellis (1938) demonstrated this by showing that sands provided only 0.25 to 0.50 inches of water available to plants per foot of soil compared to 1.0 inch for sandy loams, 2.0 inches for loams, and 3.5 inches for clays.

The chemical activity of a soil is greatly influenced by the size of the separates. Thus sand separates take an almost negligible part in the chemical and physical activities unless the particles are composed of $CaCO_3$ or some other soluble compound. Clay particles, on the other hand are synthesized in the soil and are very active chemically. The comparative nutrient content of soil separates from five soils derived from limestone and shales were shown as follows (Millar, 1943):

P_2O_5			Ca O			MgO			K_2O		
Sand	Silt	Clay	Sand	Silt	Clay	Sand	Silt	Clay	Sand	Silt	Clay
0.19	0.17	0.49	7.55	6.82	6.67	0.44	0.52	1.84	1.49	1.95	2.67

2. Climate

The phosphorus content of forage plants is usually lessened under drought conditions (Clarke and Tisdale, 1945). In pastures of more humid areas and where the grass is kept in the leaf stage, they reported that protein often decreased as well as phosphorus under dry conditions, although this pattern was not evident in drier regions.

Climate, soil, and topography also have a direct bearing on animal behavior and thereby further influence food preference. Grazing animals change their preferences with differences in temperature and rainfall and wetness of foliage. Animal movements change with drought cycles, soil texture (heavy clay is avoided in wet weather), and steepness of slope (Cook and Stoddart, 1953; Stoddart and Smith, 1955).

Climate may be the most important physical feature determining vegetation, by its action in forming soils and through its direct effect upon the plants. The relative rates of activity of the different forces of weathering and soil formation are determined by climate, which also limits the extent to which soil development proceeds. In arid regions, the lack of water prevents soil development from ever progressing to a mature type.

Among the factors which comprise climate, the most important single influence in range productivity is precipitation. This influence is largely determined by the amount and seasonal distribution of precipitation.

Precipitation also directly affects the winter ungulate use of various ranges due to the varying depths of snow. This factor combines with the direction and velocity of wind to determine the distribution, depth and hardness of snow pack conditions on winter ranges. Snow pack conditions in northern latitudes and on mountainous ranges are important regulators of winter forage availability and play a major role in determining range carrying capacities.

Temperature is an important climatic factor with respect to both plants and animals. The growing season of plants is determined by temperature, while a combination of temperature and wind appear to be important in determining the behavior of ungulates on both summer and winter ranges. A combination of frequent high winds, a semi-arid climate and light - moderate grazing may result in considerable soil retrogression.

3. Fire

Another factor which seems to act as a function of succulence and mineral content in affecting palatability is fire. It has long been observed that cattle, sheep, and deer prefer burned-over areas to adjacent undisturbed pastures (Aldous, 1934; Love and Jones, 1947; Shephard, 1953). This is largely due to increased succulence and nutrient content although ease of grazing and availability of forage are other probable factors.

On two Kansas bluestem pastures, burning increased the leaf area of big bluestem plants by 23 per cent compared to that on unburned pastures.

In little bluestem a 64 per cent increase resulted and succulence was increased (Aldous, 1934). Under stands of longleaf pine, burning resulted in phosphorus and protein increases of two to three times in grasses during the spring months (Shephard, 1953).

4. Degree of Shade or Sunlight

Cattle do not care to graze in timbered areas as much as in the open, evidently the forage in the former type is less palatable, even though it may consist of the same species. On summer bunchgrass and pine - bunchgrass ranges in Eastern Oregon, species common to both types generally showed a decrease in palatability on the pine - bunchgrass type (Pickford and Reid, 1948). Preference and utilization in the open and timbered areas are shown below:

Species	% Herbage Utilization		% Herbage Production Per Acre	
	Open	Timbered	Open	Timbered
Idaho fescue	54	22	2.8	113.8
Bluebunch wheatgrass	60	59	113.2	23.6
Prairie junegrass	55	30	46.6	73.0
Mountain brome	44	16	3.6	19.2

Bluebunch wheatgrass is the exception to the rule. The decline in the palatability of most of the species is evidently not due to nutritional factors as chemical analysis showed the forage in the timbered area to be as nutritious as that in the open.

5. Season and Photoperiod

Grazing for succulence and tender parts, combined with instinct, results in an important factor which must be taken into consideration in range management: the seasonal use of species. Livestock preference changes from one species to another as one becomes more mature and the other flourishes into maximum growth. As the grasses mature, ungulates prefer those that stay most nutritious after maturity. The following excerpt from a study in Utah (Cook, et al., 1956) illustrates this point well, where preference is manifested as utilization.

Dates	Per cent Utilization By Cattle		
	Crested Wheatgrass	Tall Wheatgrass	Intermediate Wheatgrass
May 15	10	2	20
" 21	20	2	25
" 30	10	5	35
June 7	7	9	40
" 15	15	11	55
" 21	25	18	67
" 29	25	25	80
August 5	1	15	12
" 12	3	27	30
" 24	5	38	52

Most of the variation in seasonal preference shown above is due to differential maturity, commencement of growth and nutrient content. Crested wheatgrass begins growth about a week and a half before the other grasses, but matures at a much faster rate. Correspondingly, it receives little use late in the season when its nutrient content is low. Tall wheatgrass starts growth later, regulting in less utilization early in the season compared to crested wheatgrass. It matures slowly, retaining sufficient protein to maintain high forage value late into the season, resulting in greater usage later in the season. Intermediate wheatgrass has about the same growth rate as tall wheatgrass, but retains a greater proportion of total digestible nutrients, making it an excellent forage throughout the spring and summer periods.

Sometimes even the time of day will influence species preference. Springfield and Reynolds (1951) found cattle to be highly selective in their grazing during the middle of the day. In the open parks of the ponderosa pine type in New Mexico, they found that orchardgrass was grazed mostly during the morning and evening with bromegrass grazed mostly in the afternoon. Kentucky bluegrass and crested wheatgrass were taken in greatest amounts in the early morning. Succulence evidently influenced this usage as the per cent moisture of forage declined appreciably during mid-day.

Hickman (1968) in a study of seasonal trends in the nutritive content of important range forage species near Silver Lake, Oregon compared values for Idaho fescue, junegrass, bluebunch wheatgrass, Sandberg's bluegrass, bottlebrush squirreltail, and Thurber's stipa. He found that late in the season, Idaho fescue and Thurber's needlegrass were highest in crude protein, phosphorus and digestibility. Bluebunch wheatgrass was lowest in these constituents and also had a wide calcium:phosphorus ratio.

On perennial ryegrass - subclover and tall fescue - subclover forage mixtures, grazing cattle preferred grass to clover during the spring - summer period. Sheep selected a consistently high amount of subclover in both pasture mixtures during spring. In summer, sheep preferred tall fescue to subclover but on ryegrass - subclover pastures they retained or increased their preference for dry subclover over ryegrass. Light and heavy stocking induced no large differences in forage selection patterns for either cattle or sheep (Bedell, 1968).

Following a study of chemical composition and digestibility of forage species by mule deer in Colorado, Dietz, et al. (1962) summarized that the various nutrients contained in summer range species were affected significantly by the season when they were collected. Protein, ash, and phosphorus percentages were highest in the late spring, while fat, fiber, nitrogen-free extract, and calcium percentages were highest in the fall. On the summer range, interactions between species and seasons were highly significant for calcium and phosphorus; significant for protein, fat, and nitrogen-free extract; and non-significant for crude fiber and ash. The interaction of species with years had a significant effect only on the calcium percentages of the plants, while the season years interaction showed no significant effect on any of the nutrients. The effect of years on the nutritive content of browse species was highly significant for fiber, nitrogen-free extract, and calcium, but not significant for protein, fat, ash and phosphorus. Forage species from summer range were closer to the desired 2:1 ratio in calcium and phosphorus than winter range forage species during the summer-use period.

Johnston, et al. (1967) analysed principal forage species of the alpine tundra zone in southwestern Alberta for crude protein, calcium, phosphorus, ash, silica, and cellulose. They also determined digestibility coefficients of cellulose *in vitro* as well as Nutritive Value Indices (N.V.I.). This involved a study of seven grass and grass-like species at five stages of growth and 12 herbaceous and shrubby species at three stages of growth. They found that percentages of crude protein and phosphorus of all species decreased with advancing maturity while calcium and cellulose contents increased. Digestible coefficients and N.V.I. decreased with advancing maturity. High percentages of crude protein and phosphorus, a low calcium to phosphorus ratio, and a high N.V.I. were determined for alpine vegetation at all stages of growth. The vegetation was found to provide a nutritious forage for bighorn sheep during the summer months.

SUMMARY AND CONCLUSIONS

A number of biotic and abiotic factors influence ungulate forage palatability and preference, and indirectly range carrying capacities. The quandry of accurately evaluating range carrying capacities arises from the dynamic conditions of plants, soil, animals and climate that change not only seasonally, but daily and even within the day. The numerous combinations and permutations possible as a result of this dynamic interplay of biotic - abiotic factors indicate that one cannot assign characteristic palatability, preference and nutritive values for individual forage species. However, it is now possible to quite accurately predict the type of utilization each forage species will receive under a given set of conditions.

The main biotic - abiotic factors which determine forage utilization and range carrying capacities through their influence on forage nutrition, palatability and preference are:

BIOTIC	ABIOTIC FACTORS
1. Succulence of Forage	1. Soil-Vegetation-Climate Interactions
2. Nutritive Value of Forage	2. Climate
3. Plant Species Composition	3. Fire
4. Ungulate Species & Stocking Rates	4. Degree of Shade or Sunlight
5. Ungulate Instinct	5. Season and Photoperiod
6. Ungulate Physiology	
7. Animal Waste Deposits	
8. Sweetness of Forage	
9. Fibrosity.	

As the interaction of each of the above factors influences forage utilization, and as there are 14! (factorial) or 95 permutations possible, the magnitude of the problem in accurately predicting range use and grazing capacity can be seen.

Some generalizations that are helpful in assessing forage preference by ungulates, are:

1. There are four groups of factors which influence preference. One is palatability which includes attributes of the plant that the animal can recognize. The second includes conditions surrounding available herbage such as microclimate, soil conditions, relative abundance, contamination, and mixture of species. These factors play a dual role in affecting palatability and animal behavior. Third, is the previous history of the animal in both the sense of evolution of food habits and learning by the individual through repeated experience. The fourth includes the physiological state of the animal. The act of selecting food is influenced by all four and can only be finally understood in terms of interactions among them.
2. Vegetational changes resulting from grazing seem to be correlated more with intensity of range stocking and use than with preference.
3. Although ungulates usually graze instinctively on plants which supply their nutritive needs, at times they feed solely for taste or succulence.
4. Native forage may be deficient in some elements at certain times of the year, for instance during periods of molt and lactation. Unless the native ungulates can make up this nutritive deficit from natural soil or water licks the carrying capacity of the range will be reduced or may even fail to maintain any native ungulates.

5. Chemical composition of forage is one of the most important palatability factors. Other factors such as proportion of leaves, stems, and fruits; plant growth stages; past grazing use; climate; topography; soil moisture; and fertility have been related to palatability mainly through their influence on chemical components. There is little information available on the manner in which external plant form, texture, and odor influence preference.
6. Most variation in seasonal preference is due to differential species maturity, commencement of growth and nutritive content. Succulence influences the degree of within-day variation in use of a species as the per cent moisture of forage declines appreciably during mid-day.
7. Protein, ash and phosphorus percentages of mule deer and bighorn sheep forage were highest in the late spring, while fat, fiber, nitrogen-free extract, and calcium percentages were highest in the fall.
8. Factors which affect forage availability, such as snowpack conditions and species composition, are important as an animal can only eat what is there and available, and if a variety of species are available, he choses what he likes best.
9. Important factors which influence palatability of forage are: kind of animal, degree of plant maturity, stage of pregnancy, physical condition of the animal, hunger, familiarity of an animal with a plant, availability and relative abundance of associated plants, and chemical composition of plants.
10. Under the canopy of an open forest, the palatability of grasses declines significantly from what it is on a treeless plain.

11. The primary tastes (salty, sweet, sour, bitter) influence palatability but are not adequate to determine palatability and preference because taste results from combined stimulations and there are no corresponding, rigidly specific taste cells. A continually changing body chemistry undoubtedly influences taste.

12. Determining grazing capacity is difficult because perennial forage production may vary threefold, while annual forage production may vary tenfold, from one year to another.

13. Because of the general lack of uniform distribution of grazing ungulates, grazing capacity must be based upon the capacity of important, accessible "key areas" rather than upon the forage produced over the entire range.

14. Correct grazing should be judged on the utilization of major forage species, soil stability, topography, uniformity of grazing, and animal response.

15. Grasses are the lowest, of the three forage classes, in protein and phosphorus but are the highest in energy-yielding cellulose. They lose about half their protein content and increase decidedly in lignin and cellulose as the grazing season advances. Browse plants are highest in protein and lowest in cellulose. Forbs are intermediate in most respects but are generally always high in phosphorus. The protein content of forbs and browse decreases only slightly, and lignin and cellulose increase only slightly, as the season advances.

16. Livestock and native ungulates change their preference for three forage classes throughout the year. Generally, the preference for grass in the spring declines as the summer advances while the preference

for forbs and browse increases. In the fall there is a definite preference for browse which at this time is usually more nutritious than grasses or forbs.

17. Site conditions indirectly affect the chemical content of plants through soil and plant development, water runoff, intensity of shade, and other environmental factors.

18. There is a high positive correlation between protein content of plants and preference by cattle and sheep.

19. Grasses highest in phosphate and potash are the most acceptible to livestock.

20. Forage high in sugars, or with sugars added, are preferred by cattle, calves, deer and pigs.

21. Tannins, nitrates and coumarins decrease preference.

22. Ranges containing a mixture of species are usually preferred to those composed of pure stands of one species.

23. Grazing of native forage at various intensities of ungulate stocking has little affect on species frequency. Heavy grazing has its most important affect in reducing herbage yields.

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