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Applying the Concept of Feeding Stations to the Behavior of Cattle Grazing Variable Amounts of Available Forage

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APPLYING THE CONCEPT OF FEEDING STATIONS TO THE BEHAVIOR OF CATTLE GRAZING VARIABLE AMOUNTS OF AVAILABLE FORAGE

by

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ABSTRACT

Applying the Concept of Feeding Stations to the Behavior of Cattle Grazing Variable Amounts of Available Forage

by

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Utah State University, 1983

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A quantitative description of the foraging process is necessary for effective planning and execution of intensive grazing schemes. Foraging behavior is defined as having two components: feeding and moving. At intervals the foraging animal walks a number of steps searching for food and then pauses to feed at a new position here termed a feeding station. Five behavioral variables were analyzed under this framework: 1) time spent at a feeding station; 2) number of bites at a feeding station; 3) steps taken between stations; 4) rate of steps; and 5) foraging time. The experimental design consisted of grazing small adjacent, approximately 7-ha paddocks for periods lasting 8 days. Animals significantly ($P<0.01$) increased the probability of taking 1 to 2 bites at a station as the season progressed. Regression analysis relating foraging time (in days) on a paddock revealed that the regression coefficients were statistically significant ($P<0.05$) suggesting that heifers were appreciably increasing foraging time as the grazing periods progressed. Analysis of moving behavior indicated that animals most often took 1 step between feeding stations and moved at approximately the same rate regardless of sward conditions. The significance of the behavioral measurements is discussed.

(68 pages)

INTRODUCTION

The question of how large, free-ranging, herbivores relate behaviorally to their food resource is both practically important and theoretically interesting. Such animals are known to exhibit an array of behavior-compensating responses to changes in food supply, some of which are perhaps more sensitive than others and therefore better indicators of forage conditions. The literature, for instance, has identified a variety of feeding behaviors relating such aspects as biting rate and bite size (Chacon and Stobbs 1976), feeding station interval (Goddard 1968), step rate (Novillie 1978), eating time per unit distance covered (Owen-Smith 1979) and foraging time (Arnold and Dudzinski 1978). The extent to which these foraging indices might be incorporated into the design and management of grazing systems is difficult to answer because the interrelationships between such behaviors and plant-related factors that are useful in preserving the condition of the range are not clearly understood. In addition, the associations between structural and chemical components of the vegetation and the nutritional status of the grazing animal are also relevant to animal production. Research to elucidate these associations may suggest ways of altering the biotic and abiotic environment for the welfare of the animals.

How cattle vary their feeding strategies is also of theoretical interest. The literature has provided some examples where a high degree of experimental manipulation has been applied to assess the nutritional status of grazing animals by determining the intake of digestible energy and nutrients (Nastis 1979). However, these techniques involved are expensive, time-consuming and difficult. Behavioral approaches are simple and relatively inexpensive. In addition, they might illustrate how an animal perceives its food resource. The work of Allden and Whittaker (1970) and Chacon et al. (1976) are examples of this approach. Determining changes in the feeding tactics of grazing cattle (i.e. bites per feeding station) in response to increasing levels of forage availability may be one way to evaluate how an animal perceives food abundance.

Delineation of the Problem

While actively foraging, an animal typically walks a certain number of steps in search of food and then pauses to feed at a new position termed a "feeding station" by Goddard (1968). At this location the animal can adopt one of two different tactics: it can take a certain number of bites which will vary in proportion to the time spent at a feeding station, or it can spend the same amount of time at a feeding station but lower the rate of biting to allow more time for discrimination among those plant components which provide the greatest amount of favorable sensory stimuli. Theoretically, the latter course would be the most advantageous if the average quality of the potential harvestable forage drops below the animal's nutritional requirement or if the time required for other activities (e.g. rumination) allows for such behavior. In addition to these tactics, an animal can increase the number of steps between stations to broaden the searching area and therefore increase the probability of encountering the most rewarding food items.

The above decisions can conceivably take place with or without changes in total daily foraging time. An increase in time spent foraging will be profitable if the increase in nutrients harvested in all feeding stations compensates for the increase in energy cost of greater movement between stations and if adequate time is left for other necessary activities.

Feeding station intervals, number of steps between stations and step rate have been measured in African ungulates (Novillie 1978). Foraging time and biting rate have been determined on mature crested wheatgrass stands in late summer (Nastis 1979 and Scarnecchia 1980). Daily foraging time and biting rate of Angus heifers grazing mature crested wheatgrass increased significantly as forage available was depleted from 919 to 143 kg dry matter/ha (Nastis 1979) and from 366 to 297 kg dry matter/ha (Scarnecchia 1980). However, there is a lack of corresponding information for cattle grazing young early-season forage or for animals managed in rotational grazing systems.

In spring, forage conditions differ markedly from those of mid and late summer. Bulk density, green:dead and leaf:stem ratios present different situations for selection. Presumably, changes in foraging strategies can provide clues to help determine how much early spring forage an animal needs to fulfill its intake requirements, and how forage availability relates to intake. If there are behavioral variables that are consistent with a decline in foraging efficiency (i.e. low rate of intake per feeding station and a greater number of steps between stations), this would be very helpful for management purposes.

Purpose of the Study

The purpose of the study was to establish, first, if a relationship exists between feeding station interval, bites per feeding station, number of steps between stations, and foraging time of cattle and the quantity of available forage on semiarid crested wheatgrass. (Agropyron desertorum) range. Secondly, if such relationships were found to exist, it would then be necessary to quantify them in order to prepare a basis for subsequent studies that would measure forage intake and relate it to these behaviors.

Objectives

1. To determine if feeding station interval, bites at a station, steps between stations, and step rate vary according to different levels of forage availability.

2. To determine how total daily foraging time varies in relation to level of available forage as crested wheatgrass ranges are grazed in early spring.

3. To determine if the behaviors listed in objectives 1 and 2 are responsive to changes in structural and nutritional characteristics of the forage, including leaf:stem ratios, green:dead ratios, nitrogen content and cell wall content.

Hypotheses

The following are stated as null hypotheses:

1. The time spent per feeding station declines as available forage increases.

2. The number of bites per feeding station increases as forage availability increases.

3. The number of steps between feeding stations increases as forage availability increases.

4. Heifers increase their step rate as the amount of available forage decreases.

5. As the forage supply increases, the heifers decrease their time spent foraging.

Definition of Terms

Available forage

The amount of plant material (crested wheatgrass) present per unit of area at a point in time as determined by harvest and weight techniques.

Forage allowance

Available forage (kg/ha) per number of animals or mass of animals liveweight.

Foraging

The combined processes of moving in search of food and eating at a feeding station.

Foraging strategy

The entire set of feeding-related decisions and resultant behaviors made by the animal to cope with changes in the environment. It does not carry implications as to whether these decisions are made consciously or not.

Foraging tactics

The individual decisions that constitute a foraging strategy.

Feeding station

The hypothetical semicircle in front of the animal within which a certain number of plants become available without the animal moving its front feet.

Feeding station interval

The time spent at a station (seconds).

Biting rate at station

The number of bites taken per feeding station interval.

Set of steps

The number of steps taken between feeding stations.

Step set interval

The time spent moving between feeding stations (seconds).

Foraging speed

The distance covered per unit of time when foraging without interruption of more than 30 seconds as estimated from the number of steps taken per unit of time.

Foraging time

The time spent foraging by an animal as measured by vibracorders.

LITERATURE REVIEW

Large herbivores are generally surrounded by an apparent surfeit of potential food items. The quality of this material drops below the nutritional requirements of the animal at least for part of the year. In copying with this situation an ungulate can adapt by taking random bites from the nearest plant in whatever vegetation type it finds itself, but the animal would likely die as the quality of its diet would be almost certainly be too low during part of the year (Jarman and Sinclair 1979). However, this does not occur as animals definitely exercise selectivity on at least three different levels: a) the plant community, b) plant species, and c) plant parts eaten (Pyke et al. 1977). The emphasis expressed on each of these levels will depend on seasonal and spatial differences between plant communities as well as the herbivore's intrinsic characteristics (Van Soest 1982 and Charles et al. 1981).

Components of the Feeding Process

The process of feeding could be viewed as a two-phase process involving "site" (i.e. feeding station) and "bite" selection (i.e. number of bites per feeding station) (Hodgson and Jamieson 1981). At intervals the animal moves and then pauses to feed at a particular location termed a "feeding station." Goddard (1968) has used the term "station interval" to refer to the time spent eating at a hypothetical semicircle in front of the animal in which it can reach all the plants available in that semicircle without moving its front feet. Between feeding stations the animal takes a certain number of steps and then pauses to feed at a new "site." In the course of moving, the animal can take some bites to perhaps sample a variety of plant types to assess the relative "profitability" of feeding by each (Ellis et al. 1976). As little eating generally takes place while moving between stations (Owen-Smith and Novillie 1982), large herbivores spend most of their foraging time in places where food acquisition is most profitable (Royama 1970), thus displaying long feeding stations intervals.

Eating at a station usually involves prehension, ingestion and deglutition of food items. The quality and amount of parts eaten will depend on the way an animal emphasizes different foraging tactics. Biting rate, size of bites and foraging time are among the main set of decisions that cattle and sheep modify in response to changes in plant quantity and quality (Arnold and Dudzinski 1978 and Stobbs 1975).

Alterations of the movement pattern between stations are also part of the animal strategy to compensate for the considerable variation in structure and biochemical composition displayed by plant species at different phenological stages (Novillie 1978). For instance, steps between stations, step rate and total number of steps taken per day can be considered as subcomponents of the movement process. From the latter viewpoint the feeding strategy can also be regarded as consisting of a series of step sets alternated with feeding stations (Novillie 1978).

Effects of the Feeding Process on Intake and Nutrition

The number and size of bites taken at a station may have a regulatory function on the amount and quality of food harvested per station (Novillie 1978). Increases in movement rate between stations will increase the foraging cost, because the increase in rate of energy expenditure (c) with increasing speed (v) is linear (i.e. $c(v) = a + b.v.$, Pyke 1981).

In general, foraging activity has costs and benefits (Sih 1980). The costs include stress from adverse physical conditions and reduced time available for other fitness-enhancing activities. Benefits consist of greater nutrient acquisition rates (i.e. intake of digestible protein and energy per feeding station) and therefore, better animal performance.

Research experience on feeding behavior reveals that daily consumption of herbage by a grazing animal (I) can be viewed as the product of three variables: the time spent foraging (FT), the rate of biting during foraging (RB) and herbage intake per bite (IB); thus: $I = FT \times RB \times IB$ (Arnold and Dudzinski 1978). Two additional variables can be calculated from the components of the above equation. They are: a) the total number of foraging bites per day (B), the product of FT and RB; and b) the rate of herbage intake (RI), the product of RB and IB (Hodgson 1982a). The latter variables could also be calculated using some shorter time interval (i.e. intake at a feeding station as the product of the number of bites at a station and IB). A similar approach could be followed to determine the total number of bites over a 24-hour period.

Modifications of these seven variables, in addition to other aspects of behavior (i.e. locomotion and rumination), can be seen as compensating animal responses to sward conditions (Hodgson 1982b). The balance between the cost and benefits of variations in feeding tactics will largely determine animal performance. If animals have difficulty consuming large quantities of fibrous feed and, when grazing some swards, have difficulty satisfying intake requirements, animal performance will be reduced. Conversely, if feed is eaten in excess of that required for maintenance, relatively small increases in the quality of diet will lead to large increases in production (Stobbs 1975).

Factors that Limit the Compensating Response of Cattle

Although grazing animals adjust the above behavioral variables in response to variation in the vegetation, these operate within certain limitations (Arnold and Dudzinski 1978). The anatomy and physiology of the animal as well as its social and vegetative environment set a limit to the emphasis that could be put in each of the foraging tactics examined. These sets of interacting factors can at the same time be artificially grouped in two categories: a) animal related factors and b) vegetation factors.

Animal-related factors

The anatomy of cattle imposes certain constraints on the animals' ability to select at a particular site. Having no upper incisors, cattle use their highly mobile tongues as prehensile organs to encircle small quantities of herbage which are then grasped between the tongue and lower teeth and torn off. Tongue size and mobility and the lack of upper incisors may increase the difficulty of prehensing and ingesting herbage as the vegetation is grazed down in height (Leight 1972). The prehension pattern may also alter the balance between intake (I) and selection (S) under circumstances where shrubs make up a significant proportion of the accepted food items. Low growth forms (i.e. bryophytes) require rapid mouth and lip movements while biting, and pulling movements are useful in removing leaves from branches (Trudell and White 1981). The anatomy of the harvesting apparatus of a cow is not perfectly adapted to such feeding.

Fatigue may also set an effective upper limit to the number of bites required when intake per bite is reduced. Stobbs (1975), working with tropical swards, suggested that the number of grazing bites taken by cows during a 24 h period (RB x FT) rarely exceeds 36,000 because exhaustion limits the grazing time to approximately 720 min/24 h, particularly where feed is limited and where swards are very mature and leaves inaccessible.

The stability of quality and amount ingested (RB x IB) over a certain period of time may also be influenced by experience and social interactions. Jamieson and Hodgson (1979) have suggested that observed differences in grazing time between continuous and rotational grazing may involve an element of conditioning to the effects of strip grazing. For example, the animal may be capable of anticipating a new allowance of herbage in the next pasture it is scheduled to enter, and this influences the amount of time spent grazing in the pasture it presently occupies. This may explain why cattle have been observed to reduce grazing time in certain circumstances rather than increase it, such as at low forage availability, as commonly suggested (Arnold and Dudzinski 1978, Stobbs 1975, Nastis 1979, and Scarnecchia 1980). The fact that under certain circumstances social interactions may either inhibit or enhance the compensatory response of grazing animals certainly adds more complexity to the understanding of feeding behavior of domestic herbivores.

Social facilitation does not appear to have been studied in grazing animals except when they were given a supplementary source of food. Tribe (1950, cited by Lynch and Hedges 1979) suggested that social facilitation may have caused a group of sheep which was fed a supplement to graze for the same length as an unsupplemented group; suggesting that synchronization among animals in a group has an effect on the activity rhythms of each animal and would act as a confounding factor in behavioral studies.

Factors of the vegetation

It is difficult to separate the confounding effects of concomitant changes in physical and nutritive characteristics of the vegetation upon the feeding behavior of cattle. Animals apparently respond to variation in sward structure. Bulk density of herbage within the sward (weight per unit of volume) exerted an influence upon intake per bite (Hodgson, 1982b). Biting rate was more highly correlated with plant height (r^2 = 0.95) than with forage biomass availability (r^2 = 0.80) (Nastis 1979). Grazing time was inversely correlated with forage available (Scarnecchia 1980).

As forage plants mature, there is usually an increase in the proportion of fiber and a reduction in the protein and non-structural carbohydrates of the cell contents (Van Soest 1965). A similar decline in nutritive value has been observed as leaves are depleted faster than stems and the sward is grazed down (Stobbs 1975). These two depletion processes can reduce the nutritional value of the highest quality diet which can be selected from the sward (Stobbs 1975) and increase the rumination time (Balch 1971). Since the total diurnal time is fixed (24 hr), an increase in time spent ruminating necessarily decreases the time spent eating (i.e. shorter feeding station interval) and other activities. Competition for time thus becomes a possible factor limiting feed consumption (Van Soest 1982).

Influence of Selective Feeding

It is frequently difficult to separate the independent effects of intake or selection upon the emphasis put on a particular feeding strategy. Also the degree to which some improvement in the nutrient content of the diet can be equated with variations in bite number or size have not been reported in the literature.

Though it would be logical to expect that selective foraging would tend to increase both the time searching for stations (ST) and the feeding station interval (FSI), evidence of these effects is scarce. Novillie (1978) associated mean FSI with chemical and structure nature of the vegetation. High FSI's were associated with mature and dry coarse swards of relatively poor nutritional value. Yet one might expect that selection at a station would limit intake per bite (IBS) and the rate of intake per feeding station (RIS), but information in this respect is also lacking. However, these considerations indicate the need for a higher degree of experimental manipulation and research in this area.

Relationship Between Social Structure and Forage Condition

The social structure and stability of an animal system may also reflect the pattern and structure of a plant community as well as the quality of its components. Jarman (1974) stated that the feeding style of a species influences its typical group size and hence its social organization. Large groups of selective feeders, defined by Jarman (1974) as those whose diet differs sharply from the available herbage, would soon become scattered and thus small group sizes are characteristic of selective feeders and large groups of unselective feeders. Dudzinski et al. (1982) monitored dispersion of cattle grazing in five major vegetation communities over time, using four forage-condition classes. Herd sizes in a free-ranging situation were more clumped than would be expected if they followed a random distribution. As forage conditions deteriorated, herd separation tended to increase. These aspects of cattle behavior were not as sensitive to changes in forage conditions as the same behavior in sheep (Dudzinski et al. 1978, cited by Dudzinki et al. 1982). Whether group cohesion differences could be due to alterations in patterns of movement between stations and time spent feeding at station has not yet been determined.

Determining the sensitivity of site selection (i.e. feeding station) and bite selection (i.e. biting rate per feeding station) to different forage conditions (i.e. leaf:stem and green:dead ratios) is relevant to grazing management. If the behavioral parameters as hypothesized are sensitive to increasing amounts of forage available, behavioral approaches can be used as a basis for assessing the nutritional welfare of free-ranging cattle.

METHODS AND PROCEDURES

Study Area

The study was conducted at the Tintic pastures research facility located 8 km south of Eureka in Juab County. The facility is divided into 24 pastures each 28 ha in area of which Pasture No. 18 was selected for this study.

Pasture 18 was previously described in detail (Scarnecchia 1980). The vegetation is predominantly crested wheatgrass (*Agropyron desertorum*) from a seeding established approximately 20 years ago. Western wheatgrass (*Agropyron smithii*) and big sagebrush (*Artemisia tridentata*), along with some other native grasses, forbs, and the tree *Juniperus spp.*, are minor components.

The average precipitation over the period from October 1978 to March 1981 was characterized as having 88 percent of the precipitation fall during the winter months (October 1 to May 1) with the remaining falling during the active growing season.

Table 1 reports the daily maximum and minimum temperatures over the experimental period (April and May, 1982).

Vegetation Analysis

Pasture 18 was subdivided using electric fences into three approximately equal homogenous sections based on vegetation, distance from the water point, and topography.

Table 1. Maximum and minimum temperatures (C^{o}) at Eureka, Utah, during April and May, 1982.

	Early				Intermediate				Late		
	Date	Max	Min		Date	Max	Min		Date	Max	Min
April	24	15	1	May	2	22	9	May	22	22	7
	25	18	2		3	17	8		23	19	9
	26	15	7		4	13	5		24	19	5
	27	16	3		5	13	-2		25	22	6
	28	20	3		6	14	-1		26	26	8
	29	20	0		7	17	3		27	24	14
	30	18	1		8	18	7		28	21	-2
May	1	20	8		9	13	1		29	15	4
Average		17.7	3.1			15.9	3.7			21.0	6.4

Forage available in each sub-unit was determined by randomly locating an average of twenty, 0.5-m^2 plots in a stratified fashion. Soil series and topography were used as a criteria to subdivide each sub-unit into strata. Standing grass vegetation was clipped to a height of about 1.5 cm, 1 to 2 days before and after each grazing trial. After clipping, the material was separated into green and dead fractions and the two portions were oven dried at 60 to 65 C for 24 hours and then weighed.

A 10 percent aliquot was taken from the green herbage harvested in each sample plot and pooled. This material was then divided into two equal subsamples. The two subsamples were then randomly assigned for either chemical or structural analysis. Standard procedures as outlined by Harris (1970) were used to respectively estimate crude protein and cell wall content. Structural components such as dried leaf and stem parts were separated manually and weighed. The ratio between leaf and stem was calculated by dividing their dried weight. A similar approach was followed to determine dry:green ratios.

Grazing and Animal Management

The experimental design consisted of grazing the small adjacent, approximately 7-ha paddocks for periods lasting 8 days. The particulars of the grazing treatments are shown in Table 2.

As forage grew and availability increased through the three successive trials, stocking density was adjusted to provide in all studies an average of 6.3 kg dry matter per heifer per day for 8 days (Table 2).

Table 2. Grazing management variables.

Variables	Trial 1 Early	Trial 2 Intermediate	Trial 3 Late
Dates	24 Apr-1 May	2 May-9 May	22 May-29 May
Area of Pasture Unit (ha)	7.06	7.06	6.28
Number of Heifers	23	64	86
Length of Grazing Period (days)	8	8	8
Stocking Density (heifers/ha)	3.26	9.06	13.69
Forage Allowance (kg DM per heifer per day)	6.30	6.30	6.30
Target utilization (%)	60	60	60

Foraging Behavior

Four categories of activities were considered: 1) foraging, defined as the amount of time spent either moving with the head down between feeding stations or eating at a station. Eating at a station was described by four subcomponents: selection, gathering, masticating and swallowing of food items; 2) walking, defined as those steps taken with the head up for a bout longer than 30 seconds; 3) resting, either lying or standing for periods longer than one minute; and 4) others, which included social interactions and short spells of interruptions of other activities for periods longer than 15 seconds while foraging.

Eating and moving

Observations on eating and moving behavior were begun the second day after the heifers entered a particular pasture and were conducted daily thereafter, during the mornings, until the last day of each grazing period.

Animals were systematically selected and focally observed. The systematic-focal procedure consisted of systematically selecting the third animal from the left side of the herd; and then, moving right, selecting the fifth, seventh, ninth animals etc., until a total of 14 heifers were observed. Focal observations on individual animals were continued until a predetermined number of feeding stations intervals and set of steps between stations (10 of each class) were completed (Hodgson 1982a). The number of bites per feeding station interval was determined visually using an electronic stopwatch that allowed time spent per feeding station to be recorded with an approximate sensitivity of 0.01 seconds.

Observations on step rate were done on focal animals over periods of five minutes, with the watch being stopped when animals were involved in non-foraging activities (Lehner 1979). Sessions usually started at dawn and finished with the beginning of the first afternoon period of resting.

Foraging time

Elapsed foraging time as well as the scheduling of foraging activities were assessed by using vibracorders[1] on five heifers (Figure 1). The methodology of recording grazing time by this technique has been described in detail by Stobbs (1970) and Scarnecchia (1980).

Animals wearing the vibracorders were gathered and corraled every two or three days so that the recording charts could be changed. During this period necessary adjustments were made on halter ties and vibracorders mounts. This period generally lasted less than one hour.

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[1]Servis Model TRT, Servis Recorder Co., Marion, Ohio.

Figure 1. Foraging time being measured with a vibracorder.

RESULTS AND DISCUSSION

Sward Characteristics

Neither protein nor cell wall levels varied much between the first (early), and second (intermediate) trials of the study (Table 3). However, by late spring, both protein and cell wall had begun to change. Crude protein had declined to 13.69 percent at pregrazing with a subsequent decline to 8.22 percent at the time of the post-grazing measurement. Cell wall levels followed similar but inverse trends to those observed for protein levels. The relatively high protein values were within the limits of those reported by Cook and Harris (1968) suggesting that protein content did not pose a major limitation to forage quality for grazing animals. In the vegetative growth stage, protein levels in grasses are usually high. Crested wheatgrass remained vegetative through the first two trials of the study and only during the third trial did stem elongation occur.

Table 3. Nutritive content of pre- and post-grazing samples of green crested wheatgrass at three stages of maturity.

Nutrient Component	Early		Intermediate		Late	
	Pre[a]	Post[a]	Pre	Post	Pre	Post
Crude Protein (%)	18.06	15.94	18.00	15.91	13.69	8.22
Cell Wall (%)	45.44	55.84	48.75	56.63	54.09	63.10

[a]Designates pre- and post-grazing.

Correlation analysis between selected pasture components and nutrient content indicated that structural features of the vegetation such as amount of leaf and green material were major components exerting a controlling influence on nutrient content (Table 4).

Table 4. Correlations between structural and chemical components of the vegetation.

	Available Forage (kg/ha)	Crude Protein (%)	Cell Wall (%)	Stem:Leaf Ratio
Cell Wall	-.25	-.88*	-	-
Stem:Leaf	-.26	-.91*	.73	-
Green:Dead	.60	-.61	.48	.51

*P = 0.05

Leafiness in pasture plants is commonly associated with forage quality because there is usually a positive correlation between leaf percentage in a given plant species and the protein and mineral composition, and dry matter digestibility (Fagan and Jones 1924; Reid et al. 1959, cited by Norton 1982).

Heifers did not appreciably alter the relationship between leaf and stem as indicated by the relative similarity between pre- and post-grazed samples of the first two trials (Table 5). Apparently heifers ate with little discrimination for leaves when leaves were highly abundant, as suggested by the high proportion of leaves remaining after the early and intermediate grazing trials. Conversely heifers notably depleted leaves over stems during the late trial (Figure 2). During this same trial, protein declined from 13.06 to 8.22 percent and cell

Table 5. Structural components of crested wheatgrass forage pre- and post-grazing at three stages of maturity.

Factors	Early		Intermediate		Late	
	Pre[a]	Post[a]	Pre	Post	Pre	Post
Structure Ratios						
Stem:Leaf	.00	.00	.02	.03	.06	1.05
Green:Dead	.33	.19	1.09	1.10	1.73	1.60
Forage Availability (kg/ha)	196	86	643	193	1021	153

[a]Designates pre- and post-grazing.

wall increased from 54.09 to 63.10. The latter process could be attributed to the combined effects of heifers selecting leaves over stems and to the fact that a major share of stem growth occurred during the last trial. Cattle exhibit considerable preference when grazing. It is not merely restricted to the selection of one plant species over another, but also operates within plants at the level of plant parts. The diets of grazing animals consistently contain more leaf and less stem, and more live and less dead material than the average vegetation to which animals have access (Chacon and Stobbs 1976, Van Dyne et al. 1980, and Arnold 1981).

Foraging Behavior

Eating at a feeding station

The overall trend in number of bites per feeding station (NBS), feeding station interval (FSI) and the biting rate at a station (BRS) is presented in Table 6. The seasonal trend indicates that mean NBS declined from 4.6 to 3.3 bites/station as the grazing season progressed.

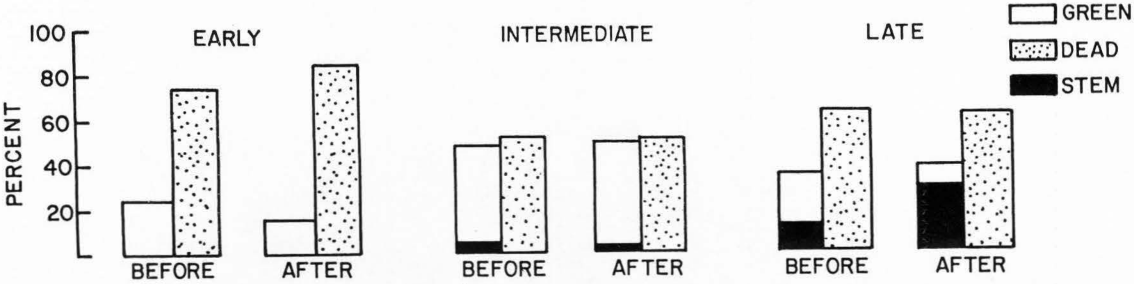

Figure 2. Mean green leaf, dead, and green stem components of the sward during spring before and after grazing.

Table 6. Means and standard deviation of number of bites per feeding station, feeding station interval and biting rate at a station.

	Early	Intermediate	Late
Number of Observations	420	420	580
Number of Bites per Feeding Station	4.59 ± 2.91	3.95 ± 2.99	3.32 ± 2.46
Feeding Station Interval (sec)	4.88 ± 3.47	4.73 ± 4.14	4.53 ± 3.67
Bites/sec[a]	.94	.83	.73

[a]Calculated by dividing the average feeding interval (FSI) into the average number of bites per feeding station (NBS).

This is an agreement with the findings of Allden and Whittker (1970) who worked with grazing sheep, and Chacon and Stobbs (1976) and Scarnecchia (1980) who studied cattle. The reduction of biting activity as forage availability increased might indicate that fewer bites per feeding station were required to satisfy intake requirements. It might also relate to a greater difficulty of prehending leaf tissue with more stem material interfering. There was no evidence, however, of statistical significance, though the declining trend through the study was consistent. The relatively large standard deviations associated with NBS and FSI may have contributed to the lack of statistical significance.

The histograms in Figure 3 are plots of bites per station in various frequency class intervals. For example, the first bar of each histogram shows the percentage of bites in the 1 to 2 bites-per-station category, the second those of the 3 to 4 category and so on. This presentation is similar to that of Novillie (1978) for foraging behavior of blesbock and

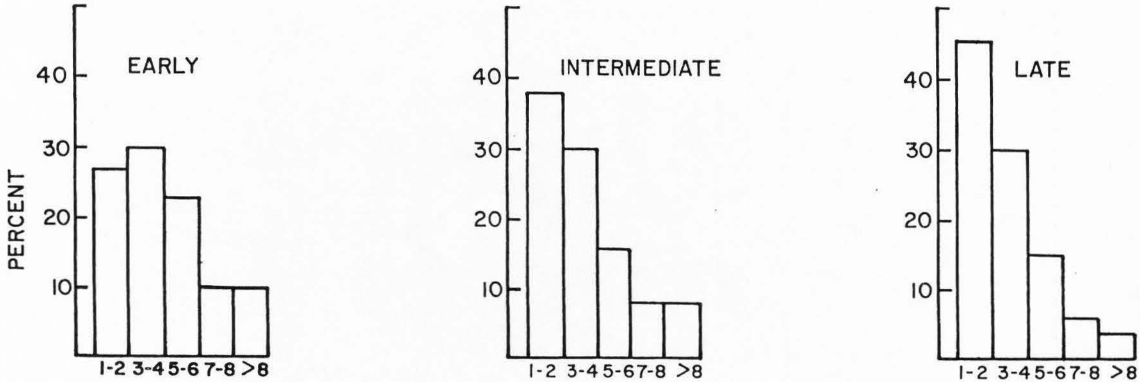

Figure 3. Frequency histograms of number of bites at a feeding station.

Springbock in Africa. In Figure 4 histograms of FSIs are plotted in the same way as for NBSs. These histograms reveal that heifers adjusted their feeding behavior in response to increasing levels of forage by varying the number of bites in much greater proportion than the time spent at a station. The chi-square test indicated that the probability of an eating behavioral event, NBS or FSI, being classified in the 1 to 2, 3 to 4, 5 to 6 category and so on was independent of seasonal influences; however, the amount of variation associated with NBSs was higher than FSI. Hence the level of significance for the test on NBS was low ($P = .23$) compared to that for FSI ($P = .96$).

The difference between the observed and expected proportions of NBSs and FSIs categories are illustrated in Figures 5 and 6 (see also Appendix Tables 11 and 12). These differences show that in addition to the same features described above, animals remarkably increased the frequency of bites in the 1 to 2 bite/station category from 27 to 45 percent.

To assess the statistical significance of this later feeding tactic, a Z-test (based on the difference between proportions) was conducted (Christensen 1977). The results of this test revealed that such increases were significant at $P<.01$.

Two possible reasons could be proposed to account for the increase in the frequency of bites in the 1 to 2 category and the subsequent decline in the mean number of bites per feeding station, assuming NBS and FSI remained constant and competition for time and food was not limiting.

Firstly, animals might respond to increasing levels of forage availability by lowering the number of bites at a station (NBS), thus

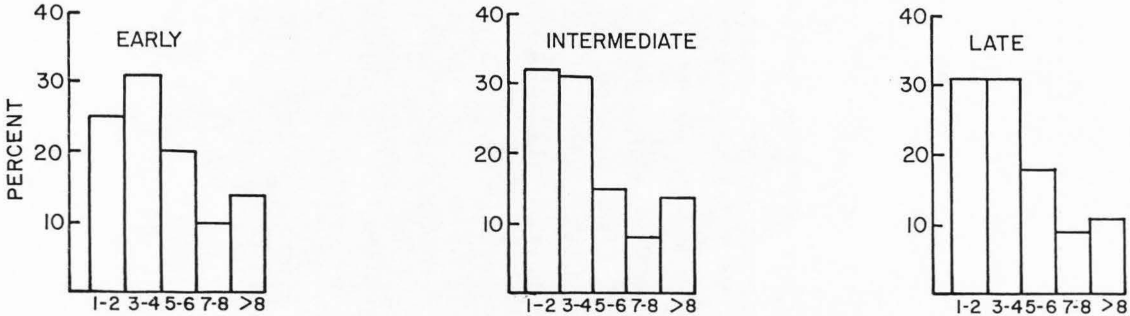

Figure 4. Frequency histograms of eating seconds spent at a feeding station.

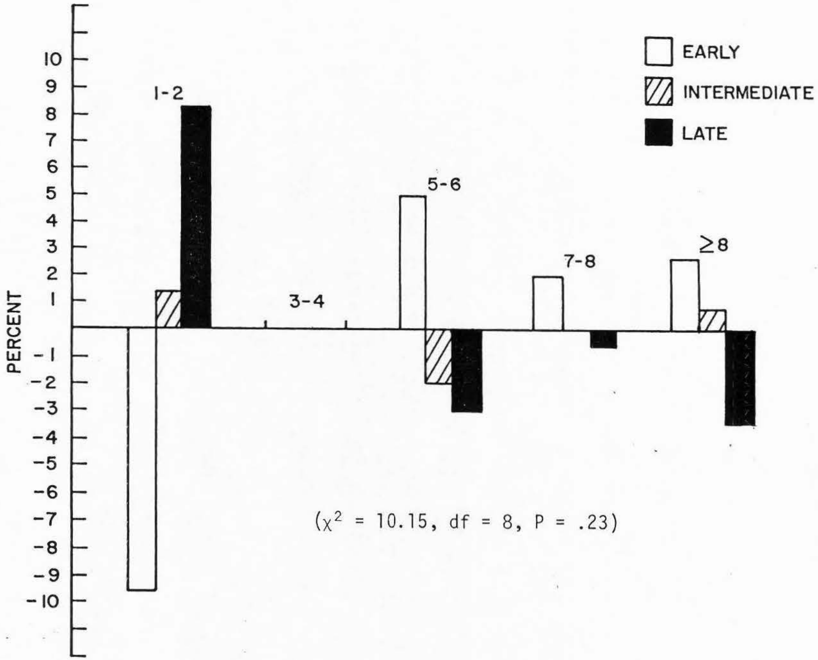

Figure 5. Percent difference between observed and expected bites at a feeding station assuming that NBS follows a χ^2 distribution. For example, in early season bites in the 1-2 category were about 10% fewer than would be predicted.

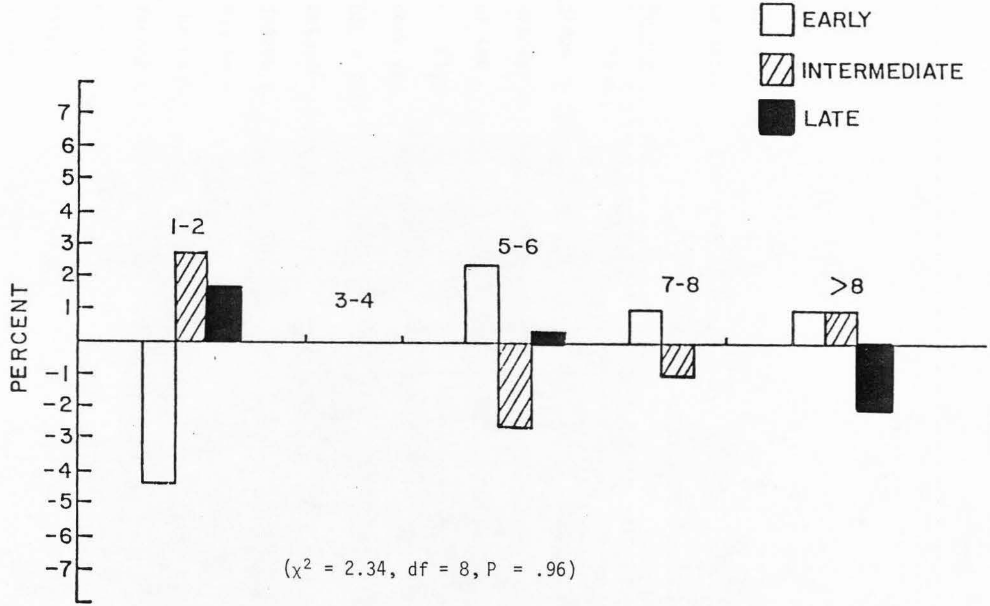

Figure 6. Percent difference between observed and expected time spent at a feeding station assuming that FSI follows a χ^2 distribution. For example, in early season time spent at stations in the 1-2 category were about 4.2% fewer than would be predicted by the χ^2 distribution.

allowing more time to discriminate between the most preferred food items. Alternatively, animals might feed less selectively and increase the number of bites per unit of time, thereby accepting relatively more food from each feeding station. The results of this experiment suggest that Angus heifers probably employed the first approach, particularly during the last trial when protein content declined from 13.69 to 8.22 percent and cell wall increased from 54.09 to 63.10 percent as a result of increased stem content on the sward.

Moving between stations

Seasonal patterns in steps between stations are shown in Figure 7. Steps in the 1-step category were the most frequent in all trials. The average probability of taking steps did not change significantly for any of the categories as forage availability increased (Appendix Table 13).

Figure 8 shows that the difference between the percentage of observed and expected values was not significant (X^2 = 2.16, df = 14, OSL = .99). Angus heifers took approximately 3 steps while moving between stations (Table 7), irrespective of stage of maturity. This suggests that searching strategies were not emphasized. This feature may have reflected the pattern of food distribution and abundance within the paddocks. The three paddocks were quite homogenous with respect to forage composition and distribution. However, under different conditions, the distance covered between stations (average length of steps, LST x STS) as well as the time searching for stations (ST) could be very large in any situation where food is sparse (Scarnecchia 1980).

These features relating to moving behavior could be also analyzed using information on step rate. There is a negative correlation between

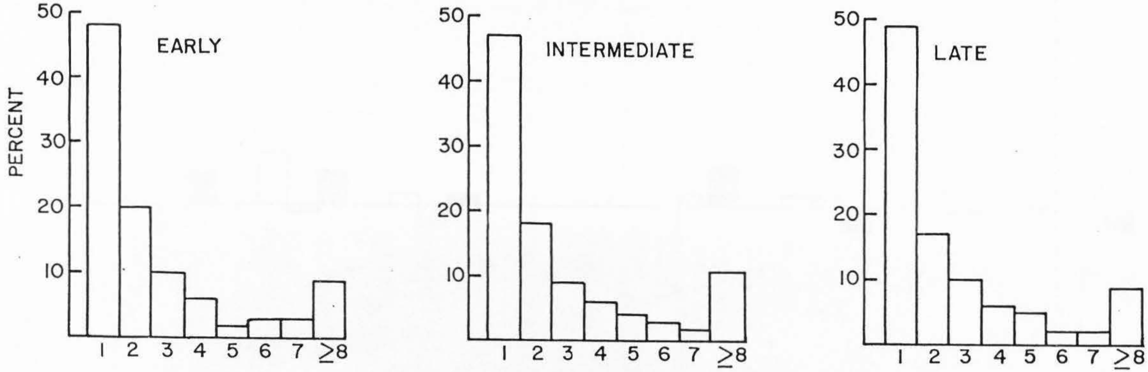

Figure 7. Frequency histograms for number of steps taken between feeding stations.

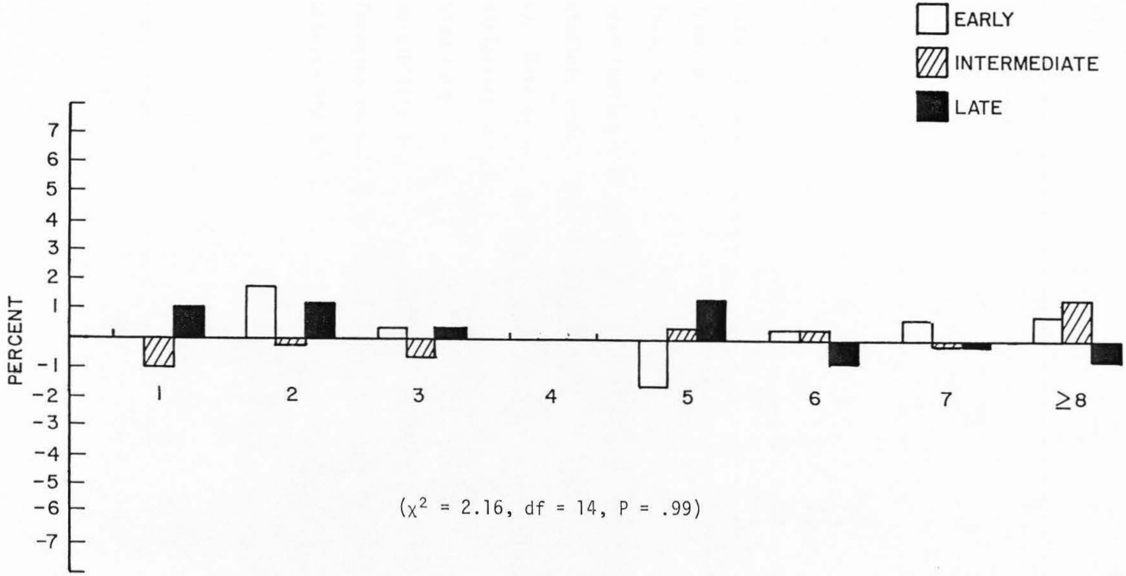

Figure 8. Percent difference between observed and expected steps between stations assuming that STS follows a χ^2 distribution. For example, in early season the number of steps between stations in the 1 category were equal to that predicted by the χ^2.

Table 7. Mean and standard deviation of number of steps between stations, step rate and step set interval[a].

	Early	Intermediate	Late
Steps Between Stations	3.22 $\pm$ 4.50	3.19 $\pm$ 4.07	2.95 $\pm$ 3.59
Step Rate (steps $\cdot$ min^{-1})	17.09 $\pm$ 6.23	19.63 $\pm$ 8.22	19.67 $\pm$ 9.18
Step Set Interval (sec)	2.72	2.69	2.52

[a]Step set interval (STI) was estimated from the equation STI = 0.359 + 0.733 (STS), which explained 89 percent of the variation in STI.

step rate and mean FSI; the longer a foraging animal spends at each feeding station the lower its overall movement rate (Novillie 1978). Thus, one would expect animals to move at approximately the same rate when feeding station interval and the number of steps taken between stations remain approximately constant as occured in this study (Table 6). Data on step rate indicated that there was not a statistical difference ($P<.05$) between the average number of steps per unit foraging time taken in any particular trial (Appendix Table 14). This possibility has been suggested by Pyke (1981) who has hypothesized that foraging animals should minimize foraging speed because the relationship between energetic cost and speed is positive and linear.

Foraging Time

Although there was not a significant difference in the average time spent foraging between early (9.70 hr/da), intermediate (9.96 hr/da) and late trials (9.72 hr/da), foraging time (FT) increased continuously as the grazing period progressed in any particular trial. The regression coefficient relating grazing time to days on a paddock (Figure 9) was

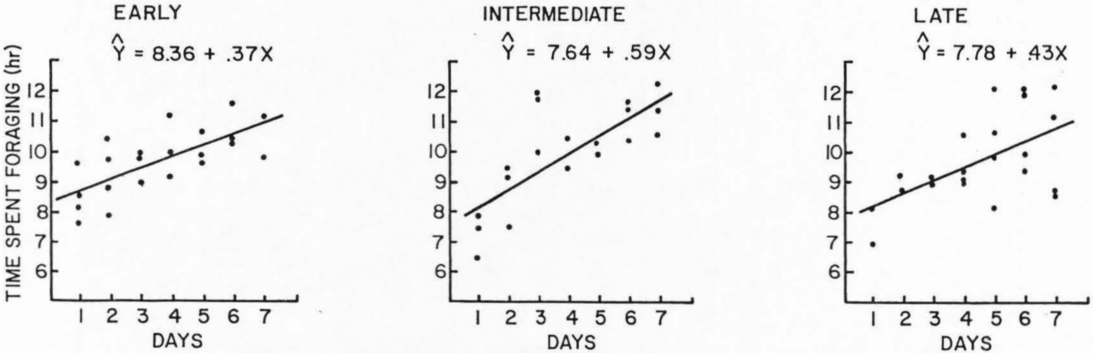

Figure 9. Regression of daily foraging time (FT) on the number of days on a paddock (DP).

significant in all trials at the 0.05 probability level (Table 8). Heifers compensated for changing sward conditions by increasing FT at an average rate of .46 hr/da. Arnold (1960) also reported a linear increase in foraging time from 7.0 to 10.3 hr/da when forage availability decreased from 3000 to 1000 kg DM/ha in Phalaris pasture. Similar compensating responses to decreasing levels of forage were reported by Nastis (1979) and Scarnecchia (1980) at the Tintic study area in late summer.

Table 8. Simple regression analysis of daily foraging time (FT) on number of days on a paddock (DP).

	Early	Intermediate	Late
Number of Observations	22	19	22
Avg.	9.70	9.96	9.72
SD	1.06	1.66	1.45
Max.	11.53	12.28	12.25
Min.	7.67	6.48	6.92
b	.37	.59	.43
T ratio	4.38*	4.76*	11.38*

When an analysis of variance was performed in a split plot statistical design using heifers as blocks, trials as units and days and subunits (Appendix Table 15), the inferences from such analysis confirmed the results described above. The compensating response varied significantly (P<.05) from day to day while the time at which spring grazing commenced (i.e. stage of forage maturity) does not affect the average time spent foraging.

The average investment in grazing was 17 percent more than that reported by Nastis (1979) and 6.4 percent more than that reported by Scarnecchia (1980). Both of the earlier studies conducted were in summer. This suggests that more forage was required to satisfy intake requirements during spring. Later in the season animals eat less because bulk in the rumen effectively limits forage intake. Presumably, the observed differences in foraging time can be attributed to a greater percentage of the forage biomass being green leaves in this experiment than in Nastis' study. Similar causes might determine higher investment in foraging time when this research was compared to the work conducted by Scarnecchia because stems are retained in the rumen for relatively longer periods of time than are leaves as demonstrated by Poppi et al. (1981).

Chacon and Stobbs (1976) have indicated that low foraging time during the early stages of defoliation or subsequent declines in the later stages could be due to a lack of desire to harvest feed when leaf density is low, to nitrogen or mineral deficiencies, or to bulk in the rumen. As indicated previously foraging time increased linearly over the course of a particular trial. In the present experiment stem:leaf ratios were very low as leaves made up most of the green available forage. Protein also appeared sufficient for maximum intake from the standpoint of efficient ruminal turnover and rate of passage of digesta through the gastro-intestinal tract. Thus none of the factors listed, except perhaps fatigue, presumably limited the compensating response, considering that grazing times were close to the maximum 12 hr/da reported by Stobbs (1975).

Theoretically a decrease in time spent foraging would be expected under a negative energy balance (Nastis 1979) or if progressive defoliation reduces the scope for selection and prevents the animals from harvesting adequate amounts of herbage (Chacon and Stobbs 1976). Since no evidence of a decrease in foraging time was observed on any of the trials, it can be speculated that energetic balance was positive. The paddocks were stocked to provide adequate quantities of forage (6.30 kg DM heifer day^{-1}) for seven days.

Relationship Between Foraging Behavior Measurements and Sward Characteristics

In order to further investigate relationships between animal and plant factors and because some of sward characteristics were significantly correlated to behaviors, behavioral data were further analyzed by simple correlation and stepwise multiple regression procedures. For both analyses, the individual animal behaviors from either the beginning or end of all grazing trials were correspondly paried with the average sward characteristics before and after grazing. Table 9 summarizes the findings of these analyses. Although roughly half of the correlations tested were significant, none were considered high. Four factors could possibly account for these low correlation coefficients: 1) high variability of the behavior variables, 2) poor linear relationships between some foraging behavior measurements and sward characteristics, 3) high dependance of feeding behavior on more

Table 9. Simple correlation coefficients (r) between foraging behaviors and vegetation variables.[a]

	Available Forage (kg/ha)	Green:Dead Ratio	Stem:Leaf Ratio	Crude Protein (%)	Cell Wall (%)
Bites per Feeding Station (NBS)	-0.04	0.42**	-0.37**	0.37*	0.36**
Feeding Station Interval (FSI)	-0.22*	-0.11	0.05	0.04	0.04
Steps Between Stations (STS)	0.19	-0.03	-0.13	0.19	-0.29**
Step Rate (SR)	.21	.21	-0.06	-0.10	0.23
Foraging Time (hr/da)	-0.66**	0.03	0.41	0.69**	0.64**

[a]Based on 84 eating or moving observations and 18 foraging time records.

* $P<0.05$

** $P<0.01$

than one vegetation variable and 4) dependance of feeding behavior on other environmental factors such as temperature.

Stepwise mutliple regression analysis, which allows for selecting a useful subset from a large collection of pasture predictors, showed that foraging time (FT) was largely determined by FAV, CW percent and S:L ratio of the sward; FT = .222 - .00269 FAV + 0.20 CW% - 1.38 S:L, r^2 = .81. Similar analysis relating number of bites at station (NBS) to sward characteristics suggest that among the predictors studied, FAV and G:D ratio mainly determined NBS, as indicated by the equation NBS = 4.974 + 0.0012 FAV - 1.36 G:D. However, this relationship accounted for only 24 percent of the variation. Thus NBS was low in those stations where dead material was abundant since FAV contributed little (.06) to increase the low power of the regression for predicting NBS; conversely, FAV added 27 percent to the power of the equation predicting FT. Poor relationships were found when the other behavioral measurements were related to sward characteristics (Appendix Table 16).

Evaluation of the Foraging Strategy

The correlation between behavioral measurements and forage availability (FAV) are of particular relevance to this study. It was hypothesized that there was no relation between the number of bites per feeding station (NBS), feeding station interval (FSI), steps between stations (STS), step rate (SR), foraging time (FT) and FAV. However significant but low correlations were found only for FSI and FT. Consequently, the hypotheses that no relationships existed between the latter two tactics and FAV was rejected.

Significance of the Behavioral Measurements

Although the foregoing framework for testing hypotheses relating forage supply and feeding behavior confirmed the sensitivity of the number of bites per feeding station, and foraging time to sward characteristics, there is a pressing need to better define behavioral characteristics and relations which provide additional biological significance. Short-term measurements of feeding tactics such as NBS, FSI, STS, STI when combined with FT allow further analysis of the foraging strategy from a completely different prospective than that used by Allden and Whittaker (1970), Chacon et al. (1976) and Scarnecchia (1980). The main difference is that grazing time recorded by the vibracorder is subdivided into: a) time spent moving between stations (ST), b) time spent eating at a station (ET), and c) minor amounts of time spent engaged in standing or other activities (OA) for periods of less than 30 seconds.

Subjective observations indicated that, when actively grazing on crested wheatgrass pasture, Angus heifers seldom raised their heads or became involved in agonistic activities while moving from station to station. Thus it can be assumed that ET + ST + OA is approximately equal to ET + ST because OA was generally a minor component. Under this assumtion, the vibracorder would effectively measure $FT_{ET\ +\ ST}$. Even under ideal conditions the vibracorder is not sensitive to interruptions in harvesting of less than about 30 seconds (Scarnecchia 1980). Measurements of feeding behavior on a time scale of less than a half minute will certainly compensate for the lack of sensitivity of the vibracorder to very short interruptions in feeding activity.

Table 10 illustrates how NBS, FSI and STI in combination with FT can be used to generate additional information on daily time spent at feeding stations, daily time spent moving between stations, biting rate and total daily bites. These results reveal that while daily time eating at a station (ET) and daily time spent moving between stations (ST) did not notably vary from trial to trial, the total daily bites declined from 21,010 bites early to 16,350 later in the season, implying that fewer bites were required to satisfy intake requirements as forage availability increased from 196 to 1021 kg $\cdot$ ha^{-1}, probably because the concomitant increase in bite size that usually occurs as biting rate declines (Arnold 1981). These trends could also be interpreted as if greater discrimination was necessary to select leaves from a mixture of reproductive culms and leaves as plants grew and became reproductive, because greater discrimination was necessary to select leaves from stems. Similar trends were observed on a similar area by Nastis (1979) and Scarnecchia (1980).

A similar approach to that designed to estimate daily number of eating bites could be used to assess the area harvested and the distance covered while foraging. Figure 10 shows some physiognomic characteristics of the animal that permit one to estimate the average area per feeding station (AS) and the average length per step (LST). Mathematically, the following relationships show how area harvested (AH) as well as the average distance covered while foraging (DC) can be calculated:

$$AS = \pi r^2/360$$

$$AH = FT \times AS \times RE$$

$$DC = FT \times LST \times MR$$

Table 10. Calculation of time spent feeding at station, time spent moving between stations, biting rate (BR) and total daily bites (TB) using short-term estimates of eating behavior.

Behavioral Variable	Grazing Trial Early	Intermediate	Late
Time Spent Feeding at Station (hr/da)[a]	6.21	6.37	6.22
Time Spent Moving Between Stations (hr/da)[b]	3.49	3.59	3.50
Foraging Time (hr)	9.70	9.96	9.72
Biting Rate (bites/min)[c]	36	32	26
Total Daily Bites (x 10^3)[d]	21.01	19.03	16.35

[a] Foraging time x $\frac{\text{feeding station interval}}{\text{feeding station int. + step set int.}}$

[b] Foraging time x $\frac{\text{step set interval}}{\text{feeding station int. + step set int.}}$

[c] Number of bites at a station x $\frac{60}{\text{feeding station int. + step set int.}}$

[d] Biting rate x foraging time

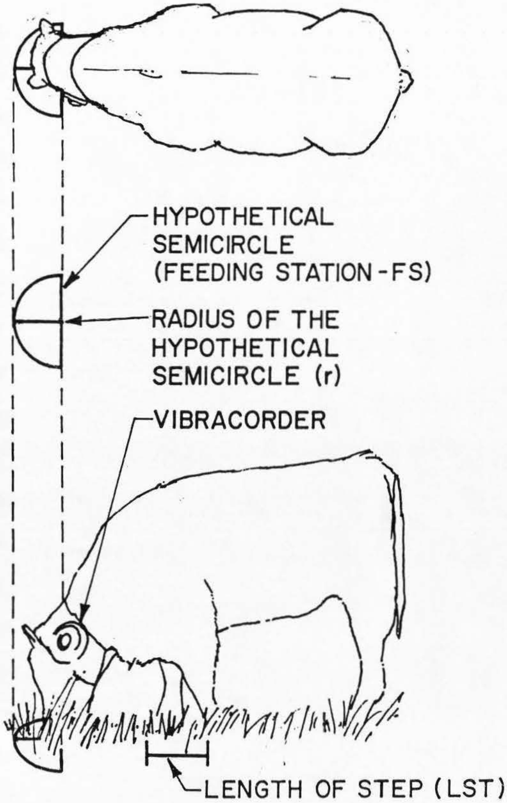

Figure 10. Idealized depiction of the feeding station, defined as the hypothetical semicircle containing forage available to the animal without moving its front feet.

where:

AS = the average area of a feeding station (m^2)

α = eating arc (degrees)

r = radius of the hypothetical semicircle (m)

AH = daily area harvest (m^2)

FT = foraging time (min)

AS = average area per feeding station (m^2)

RE = rate of food encounter (FSIs $\cdot$ min^{-1})

DC = daily distance covered (m)

LST = average length per step (m)

MR = movement rate (m $\cdot$ min^{-1})

DC = distance covered (m)

LST = average length of a foraging step (m)

MR = movement rate (steps $\cdot$ min^{-1})

To further illustrate the theoretical significance of the feeding events investigated in this experiment, let us assume that data on bite size is given from determinations on esophageally fistulated animals (Hodgson 1982a). Then the total daily intake (I) can be calculated as the product of average bite size at a feeding station (BSS) and the number of daily feeding stations (RE x FT). In addition, separate estimates of nutrient intake could be generated from extrusa samples to develop a behavioral index of feeding efficiency such as:

$$HE = \frac{I \times NVI}{AH}$$

where:

HE = harvesting efficiency

I = intake

NVI = nutrient value of intake

AH = daily area harvest

Hypothetically the above "index of efficiency" could potentially reflect the efficiency of a grazing management strategy. It has been hypothesized that the best way of integrating livestock needs to plant needs is by designing grazing systems which allow for high intensity of grazing use but low frequency of defoliation (Kothmann 1980). Thus the proposed index may reflect that trend as HE would be high where nutrient intake is adequate (animal requirement = I x NVI) and the area harvested small.

CONCLUSIONS AND RECOMMENDATIONS

Analysis of foraging behavior of Angus heifers revealed that the number of bites per feeding station, and foraging time were the variables most sensitive to sward characteristics. Foraging time was the most sensitive to total forage availability, while the number of bites per feeding station was mainly sensitive to green and dead proportions of forage at a station, presumably because leaf made up most of the green material in all trials except the third one. Other findings of the study included: a significant increase on the 1 to 2 bites/station category as forage quality declined as a result of the increase in the intensity of leaf depletion during the last grazing trial; and a significant linear increase in foraging time in all trials as the grazing periods progressed from day to day.

The latter compensanting tactic was mainly explained by variations in forage availability (FAV), stem leaf ratio (S:L), and cell wall content (CW percent); R^2 = .81. It was not possible to fully explain that animals were intensifying their selective activities later in the season because of the lack of information on bite size and quality of food taken at a station. High variability in the behavioral observations and a possible over-estimation of the time spent moving between stations (because of difficulties involved in accurately estimating the time required to take one step) were among the main limitations of the study.

Main recommendations for future research follow:

1. Use of tame animals fitted with oesophageal fistula to provide data on average bite size and quality of the food selected at a station.

2. Observations of a marked set of tame animals through all trials so that the variability among animals could be adequately blocked. This would increase the statistical efficiency of future behavioral studies in this area.

3. Use of motion picture photography to allow the precise recording of time involved moving between stations, particularly those involving the 1 to 2 step category where hand-held stop watches have limited sensitivity.

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APPENDIXES

Table 11. Percent difference between observed and expected number of bites per feeding station and calculation of X^2.

Trials		Bites per Feeding Station Category 1-2	3-4	5-6	7-8	>8	Total
Early	Observed	27	30	23	10	10	100
	Expected	36.7	30.0	18.0	8.0	7.3	
	Deviation	9.7	0.0	+5.0	+2.0	+2.7	
		2.55	0.00	1.39	0.50	0.97	
Intermediate	Observed	38	30	16	8	8	100
	Expected	36.7	30.0	18.0	8.0	8.3	
	Deviation	+1.3	0.0	-2.0	0.0	-0.3	
		0.05	0.00	0.22	0.00	0.06	
Late	Observed	45	30	15	6	4	100
	Expected	36.7	30.0	18.0	8.0	7.3	
	Deviation	+8.3	0.0	-3.0	-2.0	-3.3	
		1.89	0.00	0.50	0.50	1.52	
Total		110	90	54	24	22	300
		4.49	0.00	2.11	1.00	2.55	10.15

X^2 = 10.15 with 8 df, P = .24.

Table 12. Percent difference between observed and expected feeding station interval (sec) and calculation of χ^2.

		Bites per Feeding Station Category					
Trials		1-2	3-4	5-6	7-8	>8	Total
Early	Observed	25	31	20	10	14	100
	Expected	29.3	31.0	17.7	9.0	13.0	
	Deviation	-4.3	0.0	+2.3	+1.0	+1.0	
		0.64	0.00	0.31	0.11	0.08	
Intermediate	Observed	32	31	15	8	14	100
	Expected	29.3	31.0	17.7	9.0	13.0	
	Deviation	+2.7	0.0	-2.7	-1.0	+1.0	
		0.24	0.00	0.40	0.11	0.08	
Late	Observed	31	31	18	9	11	100
	Expected	29.3	31.0	17.7	9.0	13.0	
	Deviation	+1.7	0.0	+0.3	0.0	-2.0	
		0.09	0.00	0.01	0.00	0.31	
Total		88	93	53	27	39	300
		0.97	0.00	0.72	0.22	0.47	2.38

χ^2 = 2.38 with 8 df, P = .96.

Table 13. Percent difference between observed and expected steps between stations and calculation of χ^2.

Trials		Steps Between Stations Category 1	2	3	4	5	6	7	>8	Total
Early	Observed	48	20	10	6	2	3	2	9	100
	Expected	48.0	18.3	9.7	6.0	3.7	2.7	2.0	9.7	
	Deviation	0.0	+1.7	+0.3	0.0	-1.7	-0.3	0.0	-0.7	
		0.00	0.15	0.01	0.00	0.76	0.04	0.00	0.05	
Intermediate	Observed	47	18	9	6	4	3	2	11	100
	Expected	48.0	18.3	9.7	6.0	3.7	2.7	2.0	9.7	
	Deviation	-1.0	-0.3	-0.7	0.0	+0.3	0.3	0.0	1.3	
		0.02	0.01	0.05	0.00	0.03	0.04	0.00	0.18	
Late	Observed	49	17	10	6	5	2	2	9	100
	Expected	48.0	18.3	9.7	6.0	3.7	2.7	2.0	9.7	
	Deviation	+1.0	-1.3	+0.3	0.0	+1.3	-0.7	0.0	+0.7	
		0.02	0.10	0.01	0.00	0.48	0.17	0.00	0.05	
Total		144	55	29	18	11	8	6	29	300
		0.04	0.26	0.07	0.00	1.27	0.25	0.00	0.28	2.16

χ^2 = 2.38 with df 14, P = 0.99.

Table 14. Analysis of variance of step rate.

Source	DF	Sum of Squares	Mean Squares	F Ratio
Trials	2	1,285	643	.94
Error	87	59,456	683	
Total	89	60,742		

[a]Calculated using the ranks rather than the original observations.

Table 15. Analysis of variance for daily foraging time as related to time of grazing and days on a paddock.

Source	DF	Sum of Squares	Mean Squares	F Ratio
Cows	3	10.56	3.52	
Days	6	59.05	9.84	10.95*
Error a	17	15.28	0.90	
Trials	2	0.73	0.36	0.33NS
Trials x days	12	13.22	1.10	1.20NS
Error b	22	20.07	0.91	

*Significant ($P < 0.05$).