

APPLICATION OF OPTIMAL FORAGING THEORY
FOR BIGHORN SHEEP HABITAT EVALUATION

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ABSTRACT

Characteristics of forage resources commonly used in evaluating forage quality are palatability, based on food habits and preferences, and chemical compositions of forages in relation to nutrient requirements of animals. An additional characteristic of a forage resource is the distribution and sizes of potential bites. This attribute influences the efficiency with which a forage may be harvested by a herbivore. Concepts of optimal foraging theory related to this characteristic of forage resources are reviewed. A method for measuring foraging efficiency of bighorns is presented. Preliminary results, comparing efficiencies of bighorns when browsing vs. grazing and when browsing shrub resprouts vs. older shrub growth, are presented.

INTRODUCTION

Studies of bighorn sheep (*Ovis canadensis*) feeding ecology have included habitat selection, food habits, and forage preferences (Constan 1972, Todd 1972, Stelfox 1976, Wikeem and Pitt 1979, Johnson 1980, and others). Chemical-physical compositions of bighorn forages have also been studied (Demarchi 1968, Hebert 1973). Nutritional requirements of ruminants are fairly well known. Using such information, valuable bighorn forages can be identified as those forages in appropriate habitats, preferred by bighorns, and containing high levels of digestible energy and nutrients.

Risenhoover (1981) demonstrated that habitat visibility and distance from escape terrain influenced bighorn foraging efficiency. He measured foraging efficiency as the percent of time spent foraging as opposed to being alert or social. Bighorn preferred habitats wherein they foraged most efficiently. Thus, occurrence in a habitat that does not require bighorns to divert time from foraging activity is a factor influencing the value of bighorn forages.

Another characteristic of a forage resource may influence its value to sheep. This characteristic is harvestability and is a function of the spatial arrangement and sizes of potential bites. Therefore, valuable forages must be available in suitable habitats, palatable, nutritious, and distributed so they may be efficiently harvested. A desirable food which cannot be harvested efficiently may be eaten only incidentally during foraging activities dictated by less nutritious, but more easily harvested foods.

Objectives of this paper are to briefly review concepts and literature in optimal foraging theory applicable to large generalist herbivores and to present a method for measuring bighorn foraging efficiency which may provide insight into herbivore diet selection as it relates to the spatial arrangement and sizes of food items.

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REVIEW

OPTIMAL FORAGING THEORY

A complete discussion of optimal foraging theory is beyond the scope of this paper and only a cursory review is presented. For a more complete review, see Schoener (1971), Pyke et al. (1977), and Krebs (1978).

Although optimal foraging theory was originally conceived to predict foraging behavior (search and acquisition) and diet selection (food choice) of granivores (Emlen 1966) and insectivores (MacArthur and Pianka 1966), recent developments have provided insight to factors influencing diet selection by large generalist herbivores (Westoby 1974, Pulliam 1975, Ellis et al. 1976). Optimal foraging theory assumes natural selection has produced animals which efficiently exploit their food resources and that inefficient foragers suffer a decrease in fitness. Animals maximize their efficiency in obtaining energy and nutrients through decisions concerning foraging behavior and diet selection. These decisions are made under constraints placed on each animal by its behavior, morphology, physiology, and environment. Thus, maximizing foraging efficiency is actually an optimization process. If animals forage optimally, and if costs and benefits of foraging are measured accurately, the observed cost-benefit ratio represents the most efficient exploitation of available food resources.

OPTIMAL FORAGING AND HERBIVORES

Most conceptual models of optimal foraging by herbivores have dealt with diet selection as the sole process for maximizing energy intake within

constraints of meeting nutrient demands (Westoby 1974, Pulliam 1975, Ellis et al. 1976) or minimizing ingestion of toxins (Freeland and Janzen 1974). For the most part, these models assume all potential foods are equally harvestable.

Belovsky (1978) suggested that poor harvestability of aquatic plants that were necessary for meeting sodium requirements of moose (Alces alces) constrained the animal's ability to maximize its energy intake. His model for moose on Isle Royale assumed sodium from aquatic plants to be the limiting nutrient and terrestrial forbs and browse to be the most profitable sources of energy in a moose's summer diet.

In his study of the foraging efficiency of greater kudu (Tragelaphus strepsiceros), Owen-Smith (1979) recognized a difference between "potential" and "accepted" foods and suggested differences in phenology accounted for this discrepancy. More recently, Owen-Smith and Novellie (1982) suggested that not only nutritive quality, a function of phenology, but also food bite size affect herbivore foraging efficiency.

Trudell and White (1981) investigated the effect of plant structure and availability on reindeer (Rangifer tarandus) feeding and foraging behavior. They found both structure and availability influence reindeer biting rate, and bite size.

Based on observations of bighorn foraging behavior and diet selection in Waterton Canyon, Colorado, we believe the following factors influence foraging efficiency of the animals: (1) visibility and distance from escape terrain; (2) group size; (3) forage nutritional quality; (4) sizes of the available forage items; and (5) the spatial arrangement of forage items. We are currently measuring bighorn foraging efficiency in a variety of environments, using a method described below. We expect results will provide insight to how the above factors affect bighorn foraging efficiency.

STUDY AREA

Bighorn sheep in Waterton Canyon provide a unique opportunity to study foraging efficiency because they are habituated to humans, allowing relatively close observations, and they seasonally exhibit 2 distinct feeding strategies (browsing leaves of shrubs during summer-fall and grazing grasses and forbs during winter-spring). Waterton Canyon is a shrubland environment located approximately 40 km southwest of Denver in Colorado's front range (elevation - 1700-2345 m). The lower portion of the canyon is dominated by Gambel oak (Quercus gambelii) on north-facing slopes and true mountainmahogany (Cercocarpus montanus) on south-facing slopes. Grassy openings are interspersed throughout the lower canyon and are larger on the higher slopes. Prominent species in these openings are Indian ricegrass (Oryzopsis hymenoides), wheat grass (Agropyron spp.), bluegrass (Poa spp.), needlegrass (Stipa spp.), cheatgrass brome (Bromus tectorum), hairy goldenaster (Chrysopsis villosa), and numerous other forbs. These species are also found in lesser densities in the understories of

mountainmahogany stands. Understories of oak stands are dominated by sedges (*Carex* spp.). In the upper portion of the canyon, coniferous species including ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) replace Gambel oak on north-facing slopes and oak dominates the south-facing slopes. For a more complete description of the Canyon, see Risenhoover (1981) and Rominger (1983).

METHODS

For this study, 4 measures of bighorn foraging efficiency are being obtained.

1. Digestible dry matter intake/step while foraging;
2. Digestible dry matter intake/minute foraging;
3. Crude protein intake/step while foraging;
4. Crude protein intake/minute foraging.

These necessitate measuring 3 components of bighorn foraging efficiency:

1. Field observations of foraging behavior to measure bite-intake rates;
2. Estimation of bite sizes for each forage species eaten;
3. Nutritional analyses of bighorn forages.

OBSERVATIONS OF BEHAVIOR

Feeding bighorn ewes are observed through binoculars or a spotting scope. Their foraging behavior is described into a tape recorder during 2-10 minute observation periods for each sheep. Information recorded includes the number of bites of each species ingested, the number of steps taken while foraging (a step is defined as movement of a particular foot), and any interruptions of foraging and feeding behavior.

These data provide indices of foraging efficiency in terms of bites/step and bites/minute of foraging. A sheep is considered foraging only when feeding or searching for food. (Searching for food is defined here as whenever an animal is interpreted to be looking at food or moving toward food.) Additional information recorded with each observation includes date, time, and habitat characteristics.

ESTIMATION OF BITES

Immediately following an observation period, the feeding site is visited to verify the species consumed and obtain duplicate bites of each species by hand-plucking samples. Each sample represents 20 bites.

Samples are field weighed and frozen within 24 hours. Prior to nutritional analyses, samples are oven-dried at 50C for 48 hours and reweighed.

LABORATORY ANALYSES

Samples are analyzed for in vitro digestible dry matter and crude protein content (Kjeldahl N X 6.25). Upon completion of analyses, coefficients of nutritional value will be applied to bite/size estimates to obtain digestible dry matter/bite and crude proteir/bite for each major forage. These estimates will then be applied to the observed intake rates to calculate the above measures of foraging efficiency.

EXAMPLE RESULTS

Since nutritional analyses of forages are pending, results presented here are preliminary and intended only to illustrate potential applications of the technique. Foraging efficiency is expressed at a cursory level in bites/step and bites/minute.

For this study, bighorns were considered "browsing" when 75% or more of their bites during an observation period were on shrubs, and "grazing" when 75% or more of their bites during an observation period were on forbs and/or grasses. Comparison of bighorn ewes browsing versus grazing was based on 261 observation periods for a total of 1400 minutes (mean obs. = 5.4 minutes, Table 1). Sheep browsed most during June through October 1981 and grazed most during November 1981 through February 1982. When foraging efficiency was measured as bites/step and as bites/minute, sheep were more efficient while browsing ($P < 0.001$). However, these results do not address differences in bite sizes between forage classes. Biomass intake/bite was lower when sheep were browsing true mountainmahogany than when grazing mature grasses and forbs. Ultimately, conclusions will be based on digestible dry matter and protein intake per step and per minute.

A comparison of bighorns browsing year-old regrowth on clearcut true mountainmahogany stands versus browsing on uncut stands of the same species is not confounded by variation in bite sizes (Table 2). This comparison was based on 92 observation periods for a total of 520 minutes (means obs. = 5.6 minutes). Sheep foraged more efficiently while browsing on clearcut shrubs, however, the difference may well have been due to sampling variation ($P < 0.12$ for bites/minute, Table 2). Resprouting on clearcut shrubs concentrated many harvestable leaves into a small volume. Also harvest of leaves on the resprouting shrubs was not impeded by large stems which occurred on uncut shrubs.

Bites/minute appears to be about 3 times as precise a measure of foraging efficiency as its bites/step. When foraging efficiency was measured as bites/step, coefficients of variation (St. Dev./mean) for browsing and for grazing were 0.94 and 0.93, respectively (Table 1). In contrast, when foraging efficiency was measured as bites/minute, coefficients of variation were 0.26 and 0.32, respectively. A similar

trend occurs in Table 2. Although measurements of bites/minute appear to be more sensitive to changes in foraging efficiency, measurements for bites/step may provide a better indication of energy or nutrient intake per energy expended for harvesting food.

Table 1. Foraging efficiencies of ewes browsing leaves of shrubs versus grazing grasses and forbs in Waterton Canyon, Colorado.

Feeding Strategy	Observations (No.)	Foraging Efficiency					
		Bites/Step			Bites/Minute		
		Mean	St.Dev.	Coef. Var.	Mean	St.Dev.	Coef. Var.
Browsing ^{1/}	98	10.4*	9.8	0.94	18.0*	4.7	0.26
Grazing ^{2/}	163	6.0*	5.6	0.93	14.9*	4.8	0.32

1/ Sheep were considered browsing when 75% or more of their bites were of browse species during an observation period. Sheep browsed most during June-October 1981.

2/ Sheep were considered grazing when 75% or more of their bites were of grasses and forbs during an observation period. Sheep grazed most during November 1981 - February 1982.

* Difference between browsing and grazing significant at P 0.001.

Table 2. Foraging efficiencies of ewes browsing clearcut versus uncut true mountainmahogany (Cercocarpus montanus) in Waterton Canyon, Colorado, June-November 1981.

Forage Type	Observations (No.)	Foraging Efficiency					
		Bites/Step			Bites/Minutes		
		Mean	St.Dev.	Coef. Var.	Mean	St.Dev.	Coef. Var.
Clearcut	12	14.1	15.3	1.08	20.2*	4.8	0.24
Uncut	80	9.9	8.8	0.88	17.7*	4.5	0.25

*Difference significant at P 0.12

CONCLUSION

The value of a forage resource to bighorns is determined by its nutritional composition, palatability, the habitats in which it occurs, and its availability for efficient harvest by bighorns. This 4th characteristic, harvestability, is dependent upon the sizes and spatial arrangement of potential bites. Harvestability of forages is often overlooked in range evaluations.

Optimal foraging theory assumes animals have evolved foraging behaviors and diets which maximize their efficiencies in exploiting their food resources. Most applications of the theory to ungulates have dealt with predicting optimal diets from an array of potential forages. The potential effects of differing forage harvestabilities on diet selection have been largely neglected.

A method for measuring foraging efficiency of bighorns has been described. The method has promise for providing insight into the effects of the sizes and spatial arrangements of potential bites on bighorn foraging efficiencies. Such knowledge should help identify valuable bighorn forage resources and increase our understanding of bighorn habitat requirements.

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