

# Large Herbivore Foraging and Ecological Hierarchies

## *Landscape ecology can enhance traditional foraging theory*

R. L. Senft, M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift

**A**pplications of optimal foraging theory (Pyke 1984, Schoener 1971) to large herbivores have been problematic (Owen-Smith and Novellie 1981, Westoby 1974), partly because optimal foraging theory has been developed for predators and nectar feeders rather than large herbivores. Predators generally seek spatially scattered prey of nearly constant and high nutritional value. Large herbivores, on the other hand, confront an apparent food surplus, which is of low and highly variable nutritive quality (Belovsky 1984, Westoby 1978). Compared with the prey consumed by predatory animals, the food of large herbivores is much more likely to be widely dispersed over the landscape, rather than concentrated in discrete patches.

Large herbivores interact with forage resources at several levels of ecological resolution. The animals confront a series of interrelated foraging problems, each on a different tempo-

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**While predators seek scattered prey of high nutritional quality, large herbivores confront widely dispersed, lower quality food**

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ral and spatial scale. The fundamentally spatial nature of this problem suggests that landscape ecology, the science that studies the development and dynamics of spatial heterogeneity in ecosystems (Risser et al. 1984), may be a very useful tool.

We have found that many of the problems of applying traditional optimal foraging theory to large herbivores, including ruminant and nonruminant ungulates (Artiodactyla, Perissodactyla, and Proboscidea) and marsupials (Macropodidae), can be solved by blending elements of foraging theory, landscape ecology, and hierarchy theory. Our approach is different from traditional optimal foraging theory in that we are more concerned with behavioral processes and patterns than with theoretical or evolutionary outcomes. Our conceptual framework spans patch to regional levels of ecological resolution. We invoke hierarchy theory to integrate foraging decisions at different spatio-temporal scales. In this article, we present hypotheses pertaining to the different scales in this ecological hierarchy.

### Ecological hierarchies

Food resources of large generalist herbivores can be considered to be micropatches (or feeding stations or plants), plant communities, landscapes, and regional systems (Figure 1). Boundaries between the subunits within each hierarchical scale must be defined ultimately by animal perceptions and foraging responses.

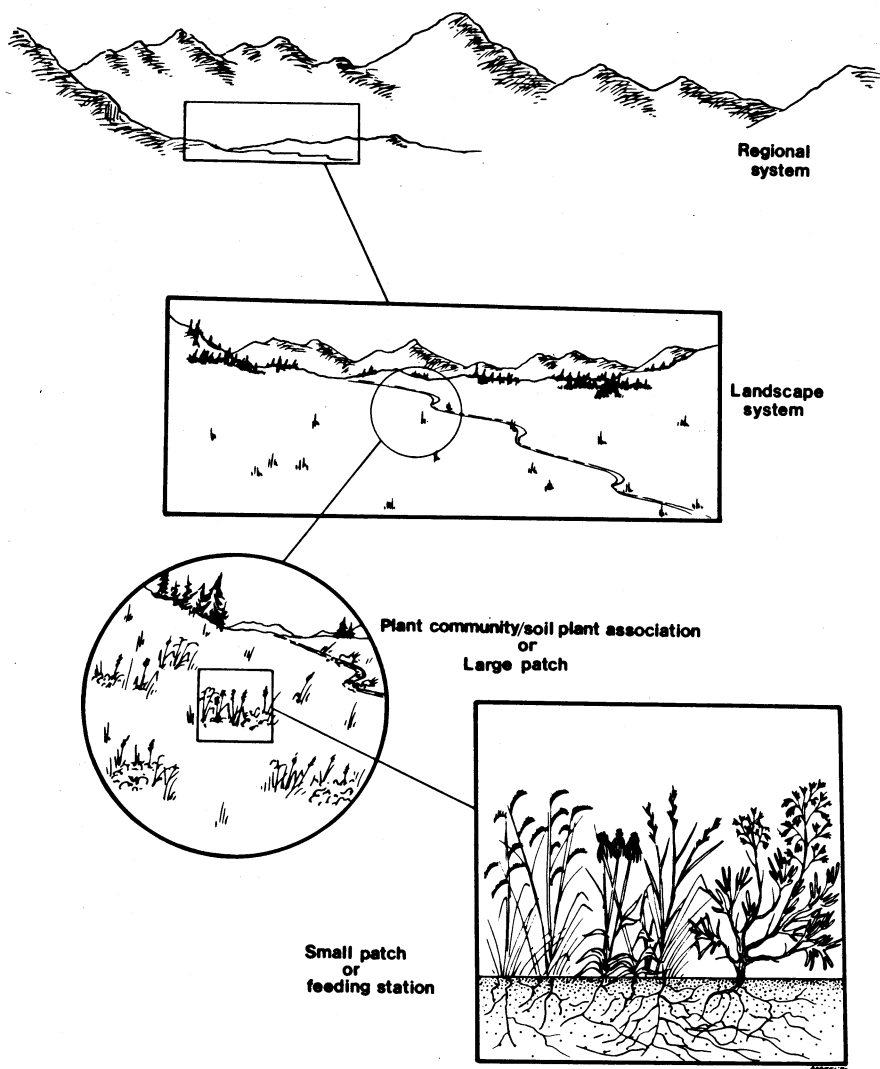
While ecologists usually define such plant communities by species composition or physiognomy (McNaughton 1983, Whittaker 1971), these criteria do not necessarily coincide with an animal's ecological requirements or perceptions of resource pattern (Wiens 1976). We posit that animals often perceive relatively consistent assemblages of plant populations that are clustered in conjunction with soils or patterns of disturbance.

Communities, in turn, cluster in conjunction with geomorphic features to form landscape systems (Forman and Godron 1981). Regional systems are large-scale assemblages of landscapes (Rowe 1961). Boundaries of a home range or of a fenced pasture often delineate a landscape system, while the annual range of migration of wild herbivores can define a regional system.

A basic postulate of hierarchy theory is that functional parameters, the frequencies and rates of activities, are often more useful for defining hierarchical scales than are physical structures (Allen and Starr 1982). Scales in an ecological hierarchy are separated by identifying frequencies or rates of pertinent processes (Table 1). Ungu-

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**Figure 1.** An ecological hierarchy encountered by large herbivores while foraging. Scales are defined by rates of foraging processes and ecosystem processes. Boundaries between units at each scale are defined by animal behavior.

lates eat approximately  $10^7$  bites/yr (Chacon et al. 1976), and each bite represents a decision about what plant or plant part to eat. Large herbivores cross plant-community boundaries as many as 50 times/day,<sup>1</sup> which implies a decision frequency of  $10^4$ /yr. At the regional scale, animals switch among landscape systems as often as several times per year or as seldom as once in several years.

### Foraging patterns

Different foraging response patterns are displayed at different scales (Table 1). In a manner analogous to the emergence of deterministic gas laws

from large numbers of stochastic molecular interactions, molar foraging patterns are the aggregate results of many individual molecular foraging decisions (Staddon 1983). The type of behavior that is observed depends upon the relationship between frequency of observation and frequency of the behavior (Allen and Starr 1982). Diet selection decisions, for example, often occur at such high frequency that only molar patterns are generally measured. On the other hand, regional-scale movements occur at such low frequency that molecular decisions are easily observed.

There are three basic molar response patterns: matching, overmatching, and undermatching (Staddon 1983). Matching occurs when an

animal adjusts its foraging behavior in proportion to changing dietary rewards (Herrnstein 1970, Staddon 1983). Overmatching results from a disproportionately large foraging response to a change in reward; undermatching from a disproportionately small response.

**Community scale.** Overmatching is the pattern most prominent when a large herbivore selects plants either from a community or from locations within a community (i.e., micro-patches) (Table 1). To maximize nutrient intake (Belovsky 1984), the generalist herbivore employs tactics in which preferences are nonlinearly related to forage abundance and quality. Diet selection is based in part on palatability, the aggregate sensory image of a potential food. However, palatability is only weakly correlated with nutritive quality and may be modified by plant physical characteristics, presence of secondary compounds, and prior feeding experience (Arnold and Hill 1972, Cooper and Owen-Smith 1986).

Where the sensory cues for forage selection reinforce each other, relative preference (the ratio of the proportion of an item in the diet to the proportion of available herbage) may be a positive exponential function of relative nutritive quality (Senft 1984) (Figure 2a). Conversely, negative exponential relationships may arise between preference and negative reinforcements, such as phytochemical deterrents (Bryant and Kuropat 1980, Reichardt et al. 1987). Both these conditions produce overmatching.

**Landscape scale.** Matching is the prominent pattern when large herbivores interact with landscape systems by selecting plant communities and other landscape components for feeding (Table 1). Animals' relative preference for plant communities (the ratio of the proportion of total feeding time to the proportion of home range area) is generally a linear function of the relative abundance and/or nutritive quality of the preferred plants in the communities (Figure 2b). A wide array of herbivores exhibit landscape-scale matching, including domestic sheep and cattle, mule deer, wapiti, feral horses, North American bison, eastern grey kangaroos, and walla-

<sup>1</sup>R. L. Senft, 1981. Unpublished data.

roos (Coppock et al. 1983, Duncan 1983, Hanley 1984, Hunter 1962, Senft et al. 1985, Taylor 1984).

Selection of feeding areas is modified from a pure matching pattern by several factors, including topography and proximity to water or salt licks (Valentine 1947). Because watering points and salt licks act as attractants, foraging intensity nearby is not affected by declining forage availability. Escape from insect harassment and selection of favorable microclimates further modify the basic matching pattern. Animals may avoid otherwise attractive feeding areas to escape discomfort.

**Regional scale.** If animals or human herders switch among landscapes on the basis of forage availability, then the regional molar response pattern will be matching. Thus, we hypothesize that in the absence of overriding constraints, foraging behavior should produce a landscape stocking rate that is a linear function of landscape productivity (Figure 2c).

Regional-scale foraging tactics include migration, transhumance, nomadism, and home-range behavior (Table 1). Transhumance is a repeatable, patterned response to predictable seasonal shortages in forage availability (Bremen et al. 1978, Gulliver 1955, Tucker 1986). In contrast, nomadism, whether natural or caused by human herders, is an adaptation to unpredictable forage production (Baker 1978, Dyson-Hudson and Dyson-Hudson 1980).

In the Serengeti regional ecosystem, nomadic herds opportunistically follow spatially distributed rainfall-related production pulses (McNaughton 1985, Pennycuik 1975, Sinclair 1985). Thus, ungulate herds move among landscape units on a contingency basis, as forage distributions vary. A similar regional response pattern has been suggested for the North American bison (England and DeVos 1969). Under unfenced, unherded conditions, domestic livestock also move to new grazing areas when forage intake or availability decreases to some critical threshold (Squires 1982).

Home-range behavior is the regional-scale response wherein subpopulations restrict their movements to a subset of the potentially available

**Table 1.** Summary of a conceptual model of large herbivore foraging in an ecological hierarchy.

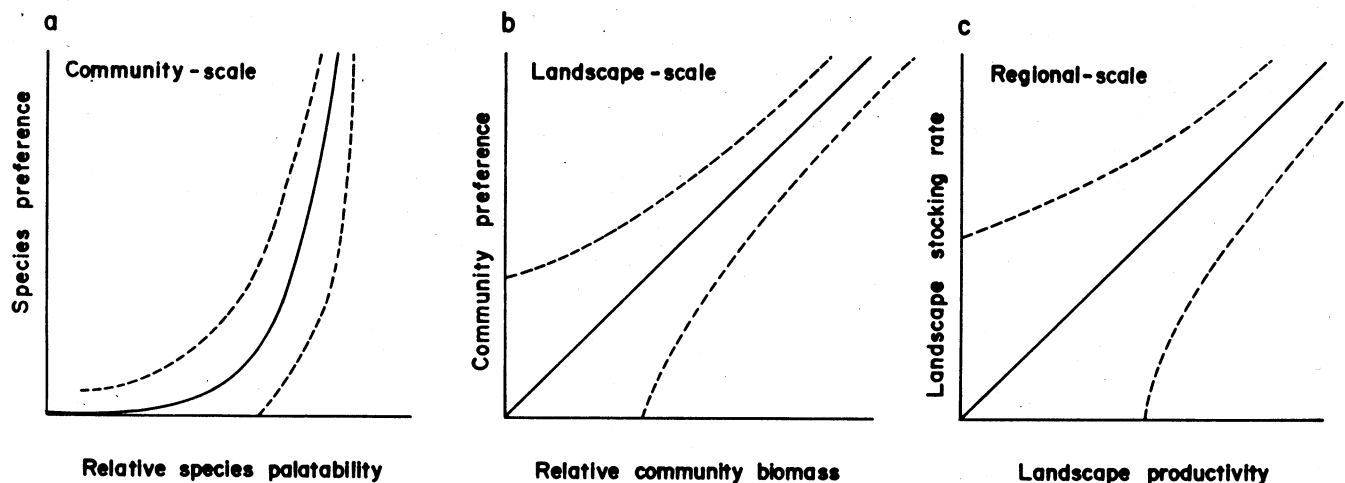
Foraging Component	Scale in Ecological Hierarchy		
	Plant Communities	Landscape	Region
Units of selection	Plants, feeding stations, or micropatches	Communities or large patches	landscape
Foraging behavior	Diet selection	Feeding-area selection	Migration Nomadism Transhumance Home range
Behavior frequency (decisions/yr)	10 <sup>7</sup>	10 <sup>4</sup>	10 <sup>-1</sup> –10 <sup>1</sup>
Aggregate response pattern	Overmatching	Matching	Matching
Alternative hypothetical foraging mechanisms	Momentary maximization Feeding station processes Micropatch-level processes	Turning frequency Boundary contrast Transit rate Patch-selection processes	Boundary contrast Calculated migration Noncalculated migration Genetically programmed migration
Hypothetical foraging goals	Nutrient maximization Toxin minimization Nutrient balance	Optimize foraging efficiency	Maintain intake Avoid physical stressor
Interactive factors	Forage biomass Nutritive quality Plant morphology	Forage biomass Nutritive quality	Forage biomass
Noninteractive factors	Microsite variables	Substrate Topography Water location Microclimate	Geomorphology Regional climate Physical barriers Water location

range. Ungulate home ranges are centered on best foraging habitat and watering areas (Hunter 1964). Although carrying capacities of home ranges are directly related to proportions of higher-quality plant communities, responses may deviate from that shown in Figure 2c. Where animal numbers are increasing, more favorable home ranges are often occupied first (Hunter 1964). Low-status animals and juvenile herds may be forced onto low-quality ranges, resulting in densities higher than expected from forage availability (Van Horne 1983); conversely, when pop-

ulations are depressed, the lowest-quality home ranges may be abandoned first (Arnold and Dudzinski 1978).

## Foraging mechanisms

**Community scale.** Foraging ungulates must solve two problems at the plant community scale: which plants or plant parts should be selected from the array of immediately available material (diet selection) and how they should move through the community (location selection). Direct application of optimal foraging theory mod-



**Figure 2.** Foraging response patterns observed at three hierarchical scales. **a.** Community scale. Species preference equals a plant's percentage in the animal's diet divided by the plant's percentage in the community. Relative species palatability is a measure of the desirability of a given species with respect to the average desirability of all the species available. **b.** Landscape scale. Community preference equals percentage of total grazing time spent in a community. Relative community biomass is community biomass divided by the area-weighted mean community biomass. **c.** Regional scale. Landscape stocking rate equals animal numbers times duration divided by landscape area. Landscape productivity is mass per unit area. Theoretical confidence bands (—) have been drawn to be broader at larger scales where nonforage factors have more importance. These confidence bands become narrower as rewards and responses increase.

els to field situations may encounter several major problems (Pyke 1984).

Optimal foraging theory models predict outcomes of processes on an evolutionary time scale and assume the existence of appropriate decision-making mechanisms on a behavioral time scale. Thus, optimal foraging theory predicts molar behavioral patterns that ought to evolve, but operational molecular mechanisms remain poorly conceptualized. Optimal foraging theory must necessarily assume either that animals integrate formidable amounts of information about forage resource distributions, or it must assume natural selection for simple behavioral rules-of-thumb that yield approximately optimal solutions, but require far less cognitive function (Cowie and Krebs 1979, Janetos and Cole 1981, Krebs and McCleery 1984). Unfortunately, very few studies either support or distinguish between these two assumptions (Pyke 1984).

Diet selection by large herbivores requires the solution of two opposing problems: obtaining maximal quality and adequate quantity. Since the vast majority of an herbivore's available food material is of low nutritive value, selection for quality is at the expense of quantity. Additionally, herbivores' diet selection is constrained by body size, gut type and capacity,

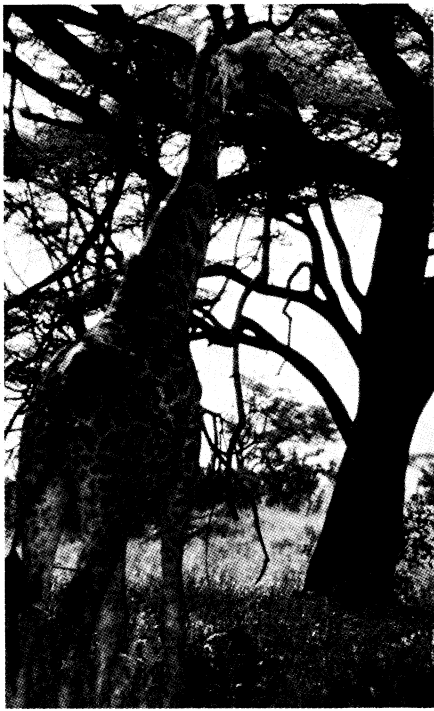
ability toprehend forage, and available feeding time (Belovsky 1984, Demment 1982, Hanley 1982, Owen-Smith 1982).

Herbivores may utilize momentary maximization to solve the quality-quantity problem. Momentary maximization dictates sequential acceptance of the most palatable items encountered at each feeding location until palatability decreases to some threshold level (Staddon 1983). Threshold of acceptance is presumably conditioned by recent experience. Each encounter with a high-quality item raises the threshold, while encounters with low-quality items lower the acceptance level. However, the herbivore must consume some items regardless of quality to maintain total intake and to sample for temporal changes in relative palatability (Westoby 1974). Therefore, there is usually a low, nonzero probability that any item will be consumed. This probability need not be constant but may vary with level of satiation (Ellis et al. 1976, Ivlev 1966).

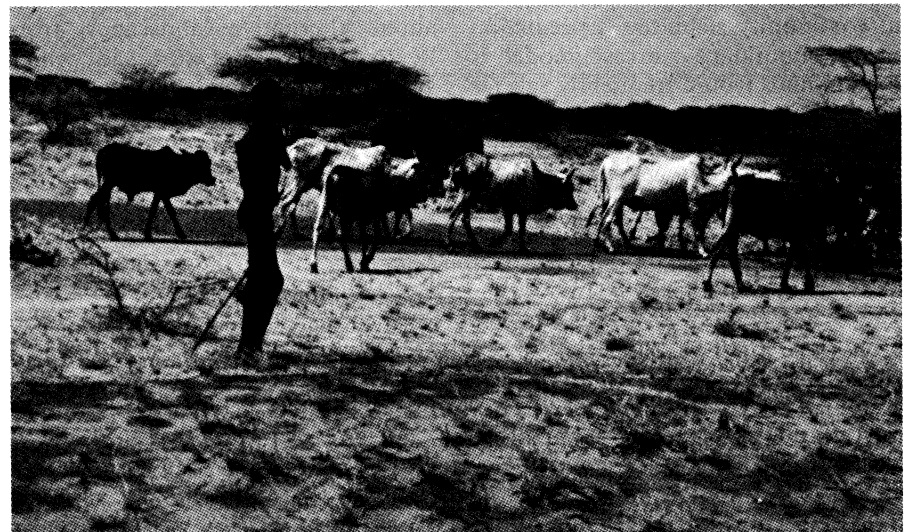
Movement through the community, or selection of a grazing location within it, can be explained in a variety of ways. Perhaps the most parsimonious is to assume that the grazing animal selects a diet by momentary maximization from a sensorially de-

fined (Arnold 1966a,b) array of plants larger than it can reach without moving. Selection of the best available plant from those sensed will eventually require that the animal move forward to obtain it. Once the animal has changed location and the boundary of the array under consideration has changed, further movement is possible. A single mechanism—diet selection by momentary maximization—thus solves the diet-selection and location problems simultaneously.

Alternative hypotheses explaining foraging behavior within a plant community can be erected but require adding to the spatial hierarchy an additional level intermediate between the plant and the plant community. One such hypothesis assumes that ungulates feed at a series of "feeding stations," consisting of the forage immediately available when the forefeet are stationary (Novellie 1978). Diet selection proceeds at that station by momentary maximization, as before. In this case, however, no movement results from the diet-selection decision process, and an additional rule must be postulated. The simplest rule is a simple giving-up rule. When the best remaining item at the station is below some threshold, or when the rate of forage acquisition at that station falls below a threshold, the ani-



Large herbivores may determine their own foraging strategies or be directed by humans. A giraffe grazing on a tree in the Serengeti Plain. Zebras graze on the Serengeti Plain. A Turkana herdsboy watches over his livestock in Kenya. Photos: M. Coughenour.



mal moves forward, establishing a new feeding station at which diet selection again proceeds.

Rather than introduce feeding stations as the intermediate scale, one may consider that the plant community consists of an array of patches, rather than individual plants, that are sensed by the grazing animal. Within a patch, diet selection is again a process of momentary maximization but movement among patches must be accomplished by assessing the "marginal value" of the patch relative to all others (Charnov 1976).

The decision to leave a patch and to select a new patch may be based on the rate of forage intake at the present patch, the expected rate at other patches, and the cost of moving to a new patch. Foragers should remain in a patch until forage is depleted below some threshold, until a certain amount of forage has been taken, until a certain time has passed in the patch (Charnov 1976), until a certain time has passed since a food item has been procured (McNair 1982), or un-

til intake rate falls to some level (Cowie and Krebs 1979). Thresholds are reached more quickly in poor patches than in rich ones. Thus, patch residence times will be proportional to relative food availability, resulting in a matching pattern.

**Landscape scale.** Landscape matching may be a simple outcome of community-scale foraging. Some biologists have hypothesized that ungulates move through a community from plant to nearest plant, or from patch to nearest patch, changing direction with each move. The animals may turn more frequently when foraging in more productive and more diverse communities (Crawley 1983). Thus, animals will stay longer in communities with higher densities of preferred forage. On the other hand, animals would turn less frequently in poor

stands, resulting in faster transit.

The turning-frequency hypothesis is in conflict with some features of observed ungulate behavior. Animals often follow topographic contours when feeding, with little evidence of zigzagging (Arnold and Dudzinski 1978). In addition, gregarious species may form grazing fronts (McNaughton 1984, Sinclair 1985), which would be disrupted by random-walk behavior of individual animals. Browsing animals (e.g., deer) often follow established trails, physical boundaries, and topographic contour lines. Finally, empirical and computer-simulation studies of foraging directionality have indicated that animals should and actually do tend to maintain foraging direction (Pyke 1978).

Alternatively, landscape matching could result from ungulate herds

moving more slowly across more productive, nutrient-rich communities. This behavior also can be modeled from simple community-level feeding-station processes. If time spent at each station is positively related to biomass (Ruyle and Dwyer 1985), then foragers will move slowly across rich communities and rapidly across poor ones. This model is attractive because it does not assume behaviors, such as frequent changes of foraging direction, that conflict with observed ungulate behavior.

In a third scenario, animals evaluate the relative attractiveness of vegetation types at community boundaries. The probability of animals' returning to a given type is proportional to community richness. A prediction of the boundary-contrast model is that animals would frequently reverse direction of movement when moving from a high-quality to a low-quality community. However, animals rarely reverse direction of grazing after crossing community boundaries.<sup>2</sup> The boundary-contrast model may require sharp boundaries between communities, a condition that is uncommon for most large herbivore habitats; otherwise, it would require animals to have the capacity to recognize gradual changes in community composition.

**Regional scale.** Regional-scale foraging behavior is the result of a wide array of tactics and movement cues. Movements are more likely to be dictated by factors beyond the scope of simple optimization. For example, animals may be forced to move during dry periods or when forage is buried by snow. Thus, there is a greater likelihood that herbivores obey landscape-departure rather than landscape-selection rules. Further, genetically coded responses to nonforage cues, such as photoperiod, may trigger long-range migrations in some species that do not have direct information about distant resources.

Hypothetical regional mechanisms parallel landscape-level mechanisms, but with important distinctions. Not all landscape-level mechanisms are appropriate at the regional level. Migratory and nomadic ungulates exhibit landscape switching, an all-or-

nothing response triggered by a cue (Murdoch 1969). Turning frequency and rate-of-transit rules acting at the landscape level cannot generate a switching response; boundary-contrast and marginal value-based decisions among landscapes could, however. Regional moves of nomadic and migratory herds may stem from a simple dissatisfaction rule; however, there is evidence that some species sample areas outside the habitual range in anticipation of a move (Franklin et al. 1975).

Information gained by sampling allows implementation of powerful selection rules. Baker (1978) distinguished "noncalculated" migration, in which there is no information about alternative landscapes, from "calculated" migration, in which some regional knowledge is assumed. Noncalculated switches require only a departure decision, whereas calculated migration also requires selection. Ungulates employ a number of mechanisms that may increase the ratio of calculated to noncalculated migration, including contact among adjacent social groups and exploratory migration.

### Foraging goals

Proximal foraging goals arise within two systems: natural selection acting over generations (Krebs and McCleery 1984, Mayr 1983) and new rules or strategies that an animal learns within its lifetime. Evolution of rule-based behavior can be numerically simulated by staging "contests" between alternative rules (Holland 1986), provided there is a mechanism for selection based on contest results. The scales of such contests may range from individual foraging events to the fate of a population over generations.

Decision-making goals at different scales in the ecological hierarchy relate to specific aspects of the overall problem of obtaining an adequate and balanced diet (Table 1). The immediate goals of one scale differ from those of another because resource distributions, foraging costs, and risks vary with scale. Decision making at larger spatial scales occurs less frequently than decision making at smaller scales. However, the consequences of each individual decision for the animal are likely to be more

significant at larger spatial and longer temporal scales.

A proximal goal of diet selection is to maximize dietary nutrient concentration (Belovsky 1984, Pyke 1984). Nutrient maximization is a very efficacious goal at the community scale, because nutrient concentrations of individual plants and plant parts vary greatly (Mattson 1980). Rate of protein intake is generally more important for large herbivores than rate of digestible-energy intake (Belovsky 1984). However, the degree to which energy or protein is maximized depends upon body size and digestive physiology (Demment 1982, Janis 1976).

Landscape-scale decision-making goals are less easily defined. While there may be differences in nutrient content of diets selected from different communities, these may in some circumstances be overshadowed by the time and energy costs of travel. Further, significant amounts of foraging time may be lost if animals do not feed in some suboptimal habitats while moving among watering, feeding, and sheltering sites. Thus, a goal of dietary maximization cannot suffice at the landscape scale because the importance of other, nondietary goals has increased. Available time must be used efficiently to satisfy multiple objectives.

Regional-scale decision making is invoked when forage intake cannot be maintained or when climatic stress becomes limiting. Minimal dissatisfaction can suffice as the goal of a landscape departure rule, whereas minimization of travel costs relative to gain is a more prudent goal for a landscape-selection rule.

Although ecological scales appear somewhat discrete (Allen and Starr 1982), interactions among foraging goals at different scales may be important. For example, when different food items are differentially distributed among communities, goals of diet selection interact with, and even become synonymous with, goals of landscape use.

Another example is central-place foraging from water or shelter, where nonfood resources such as water, shelter, salt licks, and protection from predators are highly localized on landscapes, but forage resources are dispersed. Water is often concentrated

<sup>2</sup>See footnote 1 above.



at discrete locations, and selection for watering points occurs less frequently than does diet or community selection. Thus, community- and landscape-scale foraging goals can be nested within goals of seeking water, and water becomes a major constraint on regional movement.

### Interactive versus noninteractive resources

The degree to which a foraging animal is capable of modifying its behavior in response to foraging-induced environmental change depends on the scale of change. Animals tend to interact more with resource systems at low to intermediate scales than at larger scales (Figure 3). Animals have the largest effects on resource variables that change at rates similar to their own behavioral frequencies (Allen and Starr 1982).

In direct contrast, factors with slower rates of change act as constraints upon environments of faster processes. These noninteractive factors are essentially driving variables, as they affect forage resources, but are not affected by forage use. An analogous distinction between interactive and noninteractive plant herbivore systems (Caughley 1976) addresses controls on population dynamics rather than controls on foraging behavior.

While localized forage removal produces variability, which then affects animals' subsequent foraging decisions, it is also important to consider plants' active responses, such as regrowth. At the plant scale, maximal growth is achieved at low to intermediate grazing intensities (Coughenour 1984, McNaughton 1979). At community and landscape scales, ungulate herds may actively maintain specific areas of short, rapidly growing plants in otherwise tall coarse vegetation (grazing lawns) and thereby actually facilitate rates of resource renewal greater than those in ungrazed or lightly grazed areas (McNaughton 1984).

Interaction strength may also depend upon the way herbivore mobility compares with rates of plant processes. At the level of diet selection, plants cannot respond before animals move to the next plant or small patch. Significant plant responses do occur

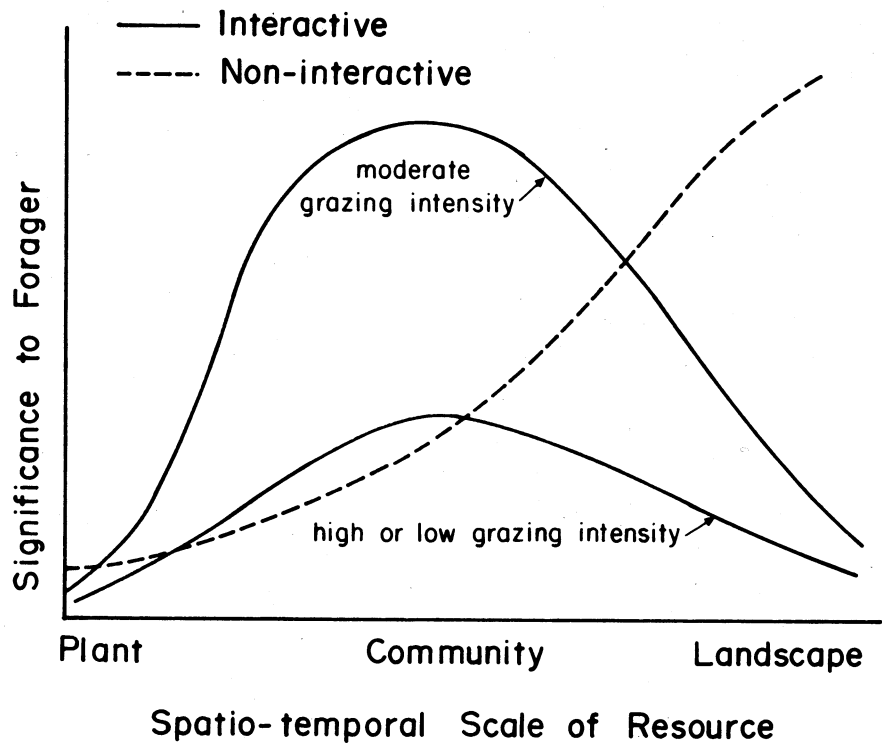


Figure 3. Conceptual model of the way the significance of interactive and noninteractive variables change with scale and grazing intensity. "Significance" refers to the extent to which foraging decisions are influenced by plant, community, and landscape or regional-scale variability. Interactions between foragers and resources prevail at smaller scales; noninteractive constraints, such as of topography and macroclimate, dominate at larger scales. Interactions are stronger at moderate grazing intensities than at low or high intensities.

over a time scale comparable with that of movements among landscapes. In some ecosystems herbivores may induce a shifting mosaic of patches (Ring et al. 1985). Regionally, however, herbivore movements occur over a timespan similar to, or slightly greater than, a single plant-growth cycle, so interactive effects are still present but weak.

Plant-herbivore interactions decline in relative importance at very large scales, as foraging decisions increasingly involve tradeoffs with nonforaging decisions. Variations in these factors may also dictate the form and strength of interactive processes (Coughenour 1984, 1985). With increasing spatial scale, the frequencies of animal decisions become less similar to the frequency of environmental changes (Allen and Starr 1982). Consequently, we suggest that the confidence bands around relationships between forage factors and animal response should become increasingly wide as the spatial scale increases (Figure 2).

### Conclusions

A theory of large herbivore foraging must first be based on actual decision-making mechanisms. Decision making is governed by specific rules, which can be postulated and tested. To approach foraging optimality (Janetos and Cole 1981, Pyke 1984), learning or natural selection must act upon these mechanisms. Second, a useful foraging theory must explain how foraging behavior varies with ecological scale. We have proposed that an ecological hierarchy be used as a framework for such investigation. Third, the theory must invoke realistic goals applicable to various ecological scales in order to explain the objectives of foraging behavior. Fourth, a mechanism for goal evolution must be provided. Finally, the theory needs to be put into an ecosystem context, by considering the responses of plants on the various ecological and evolutionary time scales and identifying how the relative significance of interactive and noninter-

active processes varies.

We also have presented alternative hypotheses for foraging decision-making rules. Critical experimentation is necessary to select among these possibilities.

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