

Nutritional models for grazing animals

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SUMMARY

The purpose of simulation modeling and critical considerations for developing models are discussed. A theoretical nutritive model for grazing animals is presented that contains the essential components found in most models of this system. Factors affecting transfer between compartments are discussed. Diet selection and methods for calculating transfers at the plant-animal interface are reviewed. It is suggested that transfers at the plant-animal interface are the most critical processes in the system, but biologically they are the least understood. The use of artificial intelligence and neural networks is suggested as new approaches to modeling diet selection. It is concluded that nutritive models of grazing animals are currently available that are useful tools for investigating management alternatives but that lack of user friendly interfaces will limit their application.

Key words: foraging behavior, plant-animal interface, simulation.

YFIRLIT

Fóðurfræðilíkon fyrir dýr á beit

Fjallað er um markmið hermílikanagerðar og þau vandamál sem almennt koma upp við gerð hermílikana. Kynnt er fræðilegt líkan af næringarbúskap dýra á beit sem felur í sér flesta þá þætti sem almennt eru teknir með í líkón af þessu tagi. Þættir sem ráða flæði milli eininga í kerfinu eru ræddir. Farið er yfir það helsta sem vitað er um plöntuval beitardýra og þær boðleiðir sem ráða í samspili plantna og dýra. Færð eru rök fyrir því að þessar boðleiðir ráði mjög miklu og að líffræðilegar hliðar þeirra séu það sem minnst er vitað um af öllum þáttum sem snerta fóðurfræði beitardýra. Lagt er til að gervigreind og tauganet séu notuð við gerð hermílikana af plöntuvali beitardýra.

Niðurstaðan er sú að ekki skorti góð líkón af fóðurfræði beitardýra sem nýst gætu við samanburð á leiðum við beitarstjórnun. Þessi líkón eru hins vegar ekki nægjanlega auðveld í notkun til þess að þau verði almennt notuð.

INTRODUCTION

Models are abstract representations of reality (Grant, 1986). They are useful because models help to organize and quantify knowledge about a subject. Scientific investigation normally begins as a conceptual thought model of the factors that influence the behavior of a system. Traditionally this led to experimental designs that kept all factors constant except the ones under investigation, and the effect of imposed treatments was evaluated

using statistical models. Implicit in the use of statistical models is the assumption that there are unaccounted for sources of variation (i.e. random error). Unfortunately, in large scale field trials (e.g. grazing experiments) the random error can be greater than the variation caused by experimental treatments. Furthermore, the number of factors that influence the behavior of large scale systems can be so great that the availability

of resources to test all factors is quickly overwhelmed. Systems analysis offers an alternative to traditional experimental procedures. As the complexity of a system increases the value of quantitative systems models increases.

Although, a model is often evaluated based on its predictive ability simulation models can provide useful insight into problems regardless of their predictive ability. Simulation models help: (1) define problems, (2) organize thoughts, (3) understand data and theory, and (4) make predictions. It is inappropriate to expect that biological models will ever have the predictive or theoretical value of physical models. This is because the emergent properties of hierarchically organized biological systems preclude the reduction of biological systems to physical laws (Popper, 1974; Mayr, 1988).

One of the most important aspects of modeling is first to state the objectives of the model. Objectives should be specific, measurable, and realistic. The objectives provide a basis for deciding what should be included or excluded from the model, and it is vital that they be clearly stated at the beginning (Starfield and Bleloch, 1986). Objectives will include necessary evaluation criteria (Forbes and Oltjen, 1986). This will determine the appropriate type of model and the level of resolution necessary if a simulation model is used. A model can only be evaluated by comparing model output to objectives established when construction began.

The resolution of a model determines what aspects of the system will be included in it. Model objectives help determine its resolution, and it is important to understand how resolution affects construction and application. High resolution models that explicitly quantify every detail of the process being modeled have the greatest potential for wide spread application. However, there are several disadvantages that accompany the broad applicability of high resolution models. As

resolution increases so does the cost of model development and operation. Furthermore, as model complexity increases the ability to interpret results becomes more difficult. Extremely complex models may lose the ability to accomplish some of the reasons for modeling such as helping to understand how a system functions. As complexity increases comprehension of how changes in inputs affect model output is compromised. The simplest model that will accomplish the objects will be the most useful one (Starfield and Bleloch, 1986).

This review will present a generalized nutrient model for grazing animals. The model presented is considered theoretical because it has not been constructed and verified but represents the structure found in most published models. Approaches used by other investigators to calculate transfers will be presented and discussed, and emphasis will be given to modeling the plant-animal interface. Emphasis is placed on modeling the plant-animal interface because this is the process that normally limits production of grazing animals.

The theoretical model presented in this review might be considered an average single animal model. The objective of the model is to simulate the response in terms of animal production (i.e. meat, milk or fiber production) in response to variations in forage conditions. Reproduction is not considered because this is a herd level process.

MODEL DESCRIPTION

A conceptual grazing animal nutritive model is presented in Figure 1. This model represents the components found in most published grazing animal simulation models. An attempt was made to simplify the structure of this conceptual model, yet maintain the essence of other published models. The model represents, albeit simplified, the way herbivores are generally considered to interact with their environment to obtain nutrients and how these nutrients are metabolized by the ani-

mal. The model will be examined by describing the processes that regulate transfers between compartments.

Nutrient models of grazing animals should contain compartments representing: (1) available forage, (2) forage consumed and (3) animal tissue and products. Transfer of nutrients between these compartments is controlled by complex interactions between the compartments and information from the preference and environment auxiliary variables. The complexity of the system is a function of the interaction of the factors that control the rates of transfer between compartments and between compartments and sources or sinks.

Plant animal interface

The transfer of nutrients from the forage compartment to the animal (Figure 1, T1) is the plant animal interface (Forbes and Oltjen, 1986). This transfer is a function of the nutrient intake of the animal and dietary preferences of the animal. Models for grazing animals must include logic to interface forage availability with animal grazing behavior. Simulation of the plant animal interface in-

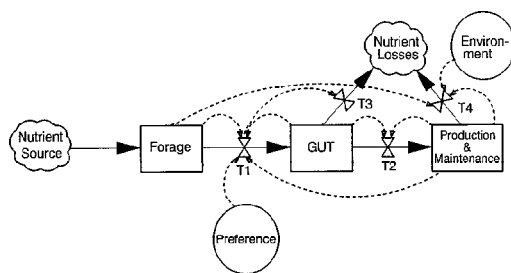


Figure 1. A generalized nutrient model for grazing animals. This model represents the most parsimonious structure that can adequately describe the transfers and processes necessary to simulate nutrient consumption and use in a grazing animal.

1. mynd. Almenn líkan af næringarbúskap beitardýra. Þetta er fátæklegasta uppbyggingin sem þó felur í sér þann tilflutning og þá ferla sem taka verður tillit til svo herma megi eftir því hvernig beitardýr nýta næringarefni.

volves allocating forage from various forage classes to consumption, based on the availability of the forage and the preference for the forage by the animal. Although, these processes are complex and poorly understood models that do not accurately simulate processes at the plant animal interface are of little value for grazing animals (Whelan *et al.*, 1984). Simulation of the plant-animal interface is the last process to be rigorously simulated in animal production models and is the weakest link in all animal production models. Because of the importance of this process it will be examined in detail later in this review.

Nutrient intake

Nutrient intake in most models is a function of available forage, nutrient density of diet, physical fill limitations of the animal and chemostatic limitations (Sanders and Cartwright, 1979; Loewer *et al.*, 1983ab; Blackburn and Cartwright, 1987a; MacNeil *et al.*, 1987) in addition under tropical and subtropical conditions high body temperatures may restrict feed intake (Loewer *et al.*, 1987). Regardless of forage quality or animal nutrient demand all models restrict forage intake when availability falls below a critical level. Procedures for restricting intake because of inadequate forage vary from a linear relationship between forage availability and demand (Sanders and Cartwright, 1979) to complex sets of logic that sequentially allocate forage of lower desirability classes when forages of higher desirability are depleted (Loewer *et al.*, 1987; Blackburn and Kothmann, 1991).

Nutrient density of the selected diet determines whether the amount of intake will be limited by physical fill or by chemostatic mechanisms. Physical limits on intake are calculated as a function of animal size and diet digestible dry matter (DDM) (Sanders and Cartwright, 1979; Loewer *et al.*, 1983ab; Blackburn and Cartwright, 1987a; MacNeil *et al.*, 1987). Chemostatic limits are a func-

tion of diet DDM and nutrient demands for maintenance and production (Loewer *et al.*, 1983ab; Blackburn and Cartwright, 1987a). When dietary nutrient density exceeds a preset concentration or nutrient intake exceeds nutrient demands dry matter intake is restricted to simulate chemostatic control of intake.

Digestion and assimilation of nutrients

After forage intake is simulated forage must be digested into the different nutrients being modeled, and partitioned to meet the nutrient demands of the animal. Digestion is indirectly dealt with at the plant animal interface because forage consumed is generally represented in terms of nutrients that can be used by the animal. Simulation of digestion involves converting consumed forages to units that are flowed through the compartments (e.g. usually net energy (kcal) and digestible protein (g)) and transferring indigestible fractions and metabolic by products to a nutrient sink. The calculations for these conversions are straight forward and based on equations derived from data from many metabolism studies (ARC, 1980; NRC, 1984, 1985). Environmental influences that might be considered at this point in the model are whether the heat increment is a nutrient loss or is used to maintain thermal neutrality and any affect that temperature may have on efficiency of digestion.

Simulation of the digestion of consumed forages is usually done at a low level of resolution because there is a large data base to relate feed of a known chemical composition to quantities of nutrients that can be assimilated by the animal. Information is available to simulate in detail the processes of digestion and have been incorporated in models whose objective is to simulate digestion (Graham *et al.*, 1976; Swift, 1983). But this level of resolution is not necessary or appropriate for animal production models.

Calculated nutrient pools are transferred to a production compartment or lost to a nu-

trient sink if they are used for maintenance. The model must allocate the available nutrients to these demands. This is usually done by prioritizing nutrient demands and fulfilling all the demand for the function with the highest priority then progressively allocating nutrients to demands with lower priorities until all available nutrients have been used. Maintenance and production demands are normally prioritized as follows: maintenance > pregnancy > fiber > lactation > growth > body stores. Blackburn and Cartwright (1987a) presented an empirical system for simultaneously allocating available nutrients to various production demands after maintenance requirements were met. If nutrient demands are not met by forage intake then lean and fat must be catabolized to meet maintenance, pregnancy, fiber and lactation demands.

Maintenance costs are simulated as nutrient transfers out of the system to a sink. Maintenance includes basal metabolism, energy used to harvest forage, and energy required to maintain homeostasis when the animal is not in the thermal neutral zone. The cost of harvesting forage depends on forage standing crop, pasture size and topography. In general the energetic cost of harvesting forage has not been explicitly modeled. Most grazing models have included a parameter that allows additional energy requirements for forage harvesting but this has been an empirical adjustment used to tune the model to validation data (Graham *et al.*, 1976; Blackburn and Cartwright, 1987a).

However, Smith (1988) presented a model of sheep distribution and movement that was linked to a sheep production model (Noble, 1975). This model integrated physiological needs to maintain homeostasis, environmental conditions and spatial location of resources in a pasture. Walker *et al.* (1989) developed a simulation model that included empirical data on the energetic cost of harvesting forage. Sensitivity analysis of the model to variation in diet DDM fecal output, and grazing

activity indicated that grazing activity accounted for less than 0.5% of the variation in average simulated cow weight. This suggests that while livestock distribution may be an important process affecting ecological processes in a pasture it may not be important for predicting livestock performance.

Energetic cost of maintaining thermal balance have been included as the major source of variation in maintenance energy requirements in many grazing nutrition models. This energy expenditure is usually modeled as a function of environmental conditions and insulatory value of the animals skin and hair (Graham *et al.*, 1976; Loewer *et al.*, 1983a).

PLANT ANIMAL INTERFACE

The plant animal interface (T1, Figure 1 and Figure 2) is the least understood of the transfers and interactions in the generalized grazing animal nutritional model. Processes at the plant animal interface determine diet quality (i.e. nutrient density) and level of intake. Sensitivity analysis of nutrient models of grazing animals is generally lacking. Therefore, it is difficult to estimate the importance of modeling this interface on overall model performance. However, sensitivity analysis of a grazing model in which diet DDM fecal output and grazing activity were driving variables indicated that relative to the other driving variables DDM accounted

for 95% of the variation in simulated animal response (Walker *et al.*, 1989). Doyle *et al.* (1989) also reported that simulated beef production was most sensitive to parameters that affected pasture growth and forage quality, which directly affect DDM intake. Because processes at the plant animal interface affect the quantity and quality of the diet, it is postulated that they have a greater effect on simulated and actual animal response than on any other transfer in the system.

The effect of decisions by the grazing animal or calculated transfers in the simulation model determines the composition of the diet. This controls the quality of the diet, changes the forage availability at the next time step thereby affecting subsequent diet selection, and over time will influence the ecological condition of the vegetation complex. Before discussing simulation approaches to modeling the plant-animal interface the processes that conceptually affect this interface will be considered.

Diet selection is a stimulus response behavior (Booth, 1990) of the grazing animal that is the result of three factors: (1) animal preference, (2) forage palatability and (3) forage availability. Palatability is a plant characteristic that stimulates a selective response by the animal (Heady, 1964). Preference refers to selection by the animal and is essentially behavioral (Heady, 1964). The ability of the animal to express its preference will be determined by the quantity and structure of the vegetation complex. If the objective of the model is to have wide applicability across vegetation types and changing forage conditions then it will need to simulate the effects of preference, palatability and availability on diet selection.

Preference is affected by innate and learned components and their interaction. The most obvious source of innate variation in diet selection is the difference among species of herbivores (van Dyne *et al.*, 1980). However, within a species differences between breeds have been shown (Herbel and Nel-

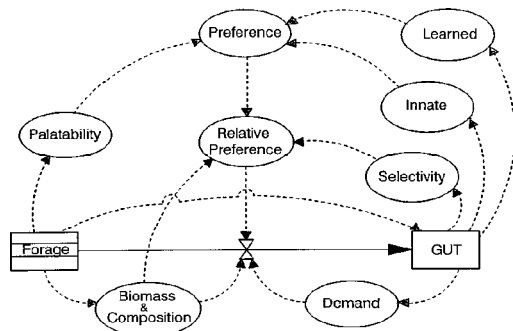


Figure 2. Model of factors that affect transfers at the plant animal interface.
 2. mynd. Líkan af þeim þáttum sem ráða flæði milli plantna og dýra.

son, 1966; Langlands, 1968, 1969). There is also genetic influence of foraging behavior at the individual animal level (Hancock, 1952). Innate factors affecting diet selection are modified *via* learning to decide the ultimate dietary preference of the animal (Provenza and Balph, 1987).

Forage palatability is in the domain of the plant. It is the chemical, structural and visual attributes of the plant that elicit the grazing response of the animal. The response elicited to palatability attributes depends and interacts with the state of the animal. Food preferences and aversions are dependent on the momentary conditions of testing. Thus, to understand the sensory influences on diet intake and selection we must test and retest choices from the start to the finish of a meal (Booth, 1990). Because research on cue-consequence specificity of diet selection by herbivores is just beginning our understanding of and ability to pair sensory (palatability) attributes of the plant with a behavioral response (i.e. acceptance or rejection) is currently very inadequate (Arnold and Hill, 1972; Marten, 1969). However, most grazing animal models use an algorithm that maximizes the rate of DDM intake. The implied assumption is that DDM and harvestability are the palatability factors that are influencing intake.

Plants that make up the diet of the grazing animal must be considered within the context of the environment from which the diet is selected. This environment has the attributes of spatial and structural variation, total forage biomass and species composition. These additional sources of variation that the animal must cope with result in a hierarchy of decisions that the grazing animal must make to select a diet (Senft, 1989). However, because the frequency of these decisions is so high 10 million/year only molar (aggregate result of many decisions) behaviors are measured and therefore simulated in a model (Senft, 1989).

Because preference, palatability and avail-

ability interact and are affected by many other factors, many grazing models use a low level of resolution to model the plant animal interface. In the low resolution models preference is often expressed as a vector of preference indices (one element for each forage species or category). This information is normally user supplied and the simulated diet is the product of relative preference and available forage composition (Senft and Rittenhouse, 1983; MacNeil *et al.*, 1987). Such models may actually do a better job of simulating diet composition than more detailed models but they are limited in their ability to increase understanding of processes that affect diet selection and to simulate the animal's response to changes in forage conditions. Because of the importance of the plant animal interface in simulating the nutrient status of the grazing animal and because forage conditions are constantly changing this review will consider the structure of a high resolution plant animal interface model.

GENERALIZED PLANT-ANIMAL INTERFACE SIMULATION MODEL

The goal of the generalized plant-animal interface model presented in Figure 2 is to dynamically simulate selection of plants and plant parts and provide insight into the processes that influence diet selection and intake. Preference is a function of innate and learned factors of the animal interacting with the palatability (i.e. sensory cues) of the plant. Absolute preference represents the preferred composition of the diet if availability of potential food items is unlimited. Absolute preference is modified by actual forage availability and the internal state of the animal (e.g. satiety) that represents its desire to express selectivity. The result of these two factors interacting with absolute preference is relative preference. Relative preference can be calculated several ways (Lechowicz, 1982); however, in simulation models the most common method is to divide the pro-

portion of a forage category in the diet by the proportion of that item in the vegetation standing crop (equation 1):

$$RP_i = \frac{f_i}{b_i} \quad (1)$$

where RP_i = relative preference for forage category i , f_i = proportion of forage category i in the diet, b_i = proportion of forage category i in standing group.

The product of relative preference, forage composition and animal demand will determine the amount of forage transferred from each category to the animal (equation 2) assuming that quantities of desired forages are not limiting:

$$F_i = RP_i \cdot b_i \cdot d \quad (2)$$

where F_i = quantity of forage category i (kg), RP_i = relative preference for forage category i , b_i = proportion of forage category i in standing group, d = total animal forage demand (kg).

All models reviewed determined transfers from the forage pool to the animal pool as a function of forage availability, animal preference and animal demand for nutrients (Figure 2). Differences among models resulted from the way they determined preference and allocated forage when the available amount did not meet the animal demand. In reviewing how the various models dealt with these problem similarities will be emphasized. The reader is referred to the original articles for the details and differences among the actual algorithms used to calculate transfers.

Community selection

Before a herbivore can consume it must make many decisions within a hierarchical framework that will position it to begin harvesting forage (Senft *et al.*, 1987). Thus the herbivore must first select the plant community in which to graze and then locate a feeding station before it can select food items to consume. Within this hierarchy selection for individual plants is most commonly modeled although Smith (1988) contends that spatial

choices have a greater ecological impact than selection of plants or plant parts. With few exceptions, selection of plant communities has been treated similar to selection of plant species. MacNeil *et al.*, (1987) and Senft (1989) used a preference index to simulated spatial distribution in a manner similar to the distribution of grazing pressure to functional groups of forage. Smith (1988) simulated spatial distribution of sheep based on environmental, topographic and physiological parameters. None of the other models reviewed explicitly addressed spatial distribution.

Regression has most often been used to predict spatial distribution (Cook, 1966; Senft *et al.*, 1983, 1985; Smith, 1988) but these models have not been incorporated into a grazing animal nutritive model. More recently artificial intelligence and object oriented programming have been used to simulate habitat selection by herbivores (Saaremaa *et al.*, 1988; Hyman *et al.*, 1991).

Simulating preference

Three of the seven models reviewed employed a constant, user supplied value for relative preference (Ellis *et al.*, 1976; MacNeil *et al.*, 1987; Senft, 1989) (Table 1 and 2). This implies the modelers assumed the relationship between animal and plant factors that determine preference were too poorly understood to have utility for predicting diet composition. This is apparent in the model developed by Ellis *et al.* (1976). These authors discussed many factors affecting diet selection and then proceeded to model relative preference with a user supplied value. Senft (1989) advanced the concept and use of relative preference by developing a model that dynamically varies relative preference in relation to forage availability. Senft's model still requires user supplied estimates of relative preference but uses them with a matching model derived from the psychological literature (Staddon, 1983) to vary relative preference as a continuous function of forage availability.

Table 1. Factors used to calculate preference in models that simulate diet selection.
1. tafla. Þættir sem notaðir eru til að reikna val í líkönum sem herma eftir beitaval.

Citation	Factors used to calculate preference
Ellis <i>et al.</i> , 1976 Sibbald <i>et al.</i> , 1979 Loewer <i>et al.</i> , 1987	Relative preference f (DDM, grazing pressure) MAX (intake rate of DDM) where $\text{DDM}/\text{time} = f$ (dry matter/t, DDM, proportion of new, dead and old tissue in dry matter, forage availability)
MacNeil <i>et al.</i> , 1987 Demment and Greenwood, 1988	Plant preference • Community preference MAX (intake rate of DE) where $\text{DE}/\text{time} = f$ (bite size, chew rate, movement rate, rumination requirement, grazing time per bout)
Senft, 1989 Blackburn and Kothmann, 1991	Relative preference & Over matching f (DDM, crude protein, palatability factor, avoidance factor)

The remaining four models reviewed assumed that preference was related to the rate of nutrient capture (Sibbald *et al.*, 1979; Loewer *et al.*, 1987; Demment and Greenwood, 1988; Blackburn and Kothmann, 1991) (Table 1 and 2). The currency in these models was usually DDM or digestible energy (DE); however, Blackburn and Kothmann (1991) also included crude protein and anti-quality factors. Models that assume preference is a function of nutrient density satisfy the animals demand for a food item based on its absolute rather than relative availability.

Assumptions and algorithms for calculating preference vary among the four models that derive a preference value from some nutrient or palatability factor of the plant. Sibbald *et al.* (1979) modeled preference for discrete DDM classes as an empirically derived linear relationship between DDM and grazing pressure. In that model preference increased with increasing levels of DDM and the slope increased as grazing pressure declined. Loewer *et al.* (1987) assumed that animals would select the food item that maximized rate of intake. Rate of dry matter intake was a function of the composition and DDM of new, old and dead material of a food item and a forage availability factor. It is assumed that the intake rate is highest for new and lowest for old material. The forage

availability factor limits intake rate when forage availability falls below a critical level. Demment and Greenwood (1988) developed a model that maximized DE per unit time using a search algorithm to solve for the optimal combination of bite size, chew rate and movement rate. Diet composition (percent cell wall) was determined by bite size assuming that changes in bite size are caused by the level within the sward that plants are severed. Blackburn and Kothmann (1991) calculate a desirability index for each food item as a function of DDM, CP and an avoidance factor that is designed to reflect chemical or physical deterrents in the plant that will limit palatability. The maximum proportion of the diet that any food item can contribute is further constrained by a palatability factor that limits potential intake of a food because of anti-quality compounds such as phenolics. Both the avoidance and palatability factors are supplied by the user.

Forage allocation

The second problem of a plant-animal interface model is to adjust the simulated diet when forage availability will not meet animal demand for one or more of the potential food items. Two different solutions to this problem have been used. One approach is to vary preference for a food item as continu-

Table 2. Factors used to allocate forage when animal demand for a food item exceeds the availability of that item.

2. tafla. Þættir sem notaðir eru til að skipta niður fódri þegar ásókn dýra í fódur gerð er meiri en framboðið.

Citation	Limiting forage function
Ellis <i>et al.</i> , 1976 Sibbald <i>et al.</i> , 1979 Loewer <i>et al.</i> 1987	Relative preference f (DDM, grazing pressure) if $DDM_i/t > DDM_{i+1}$ then graze DDM_i else graze DDM_i and DDM_{i+1} where DDM_i/t = intake rate of the highest ranked food item, DDM_{i+1}/t = intake rate of the second highest ranked food item
MacNeil <i>et al.</i> , 1987 greater is propor- com-	If forage demand for the i^{th} species on the j^{th} community is greater than the availability of that forage resource the deficiency is composed of forage resources in excess of demand and proportional to the product of the preference for the species and community where the excess is available
Demment and Greenwood, 1988	MAX (intake rate of DE) where $DE/time = f$ (bite size, chew rate, movement rate, rumination requirement, grazing time per bout)
Senft, 1989	Relative preference & Over matching
Blackburn and Kothmann, 1991	f (biomass, lower critical availability)

ous function of its availability. Thus the proportion of a food item in the diet constantly declines below the preferred level but the food is generally not depleted. When this approach is used the algorithm that calculates preference constantly adjusts diet composition for changing forage availabilities (e.g. Ellis *et al.*, 1976; Sibbald *et al.*, 1979; Demment and Greenwood, 1988; Senft, 1989).

The other approach for calculating diets when forage availability is limiting consumption of a forage category is to add new food items or restrict consumption of a food item when the rate of nutrient capture falls below a critical level. This method of calculating diet composition under conditions of limiting forage supply uses the tactical approach hypothesized by optimal foraging (Pyke, 1984). The model of Loewer *et al.* (1987) assumed animals would consume one food item exclusively until its rate of DDM intake equaled the food item with the next highest rate of DDM intake. At this point both food items would be consumed indiscriminately. This logic is clearly suited only for monocultures. If forage demand for the

i^{th} species on the j^{th} community was greater than the availability of that forage resource, MacNeil *et al.* (1987) satisfied the forage deficiency from forage resources that were in excess of animal demand. Excess forage was allocated to meet the deficiency from each category in proportion to the product of the preference for the species and community where the excess was available. If animal demand for a food item would deplete that resource below a critical availability that would interfere with the animal's ability to harvest the desired proportion of the food item, Blackburn and Kothmann (1991) used an iterative procedure to calculate the diet. A harvestability coefficient (range 0–1) was computed based on a saturation curve and multiplied by the desired proportion of the forage category in the diet. The preferred diet was again calculated based on a reduced proportion of the limiting food item in the diet. This procedure was repeated until the demand for all food items was met or for a maximum of three iterations. After three iterations if the animals demand cannot be met then intake is reduced.

Critique of diet selection models

The applicability and usefulness of these diet selection models will depend on the system to be simulated. Compared to natural rangelands monoculture pastures present a much different challenge to both the grazing animal and the modeler. Except for the model developed by Blackburn and Kothmann (1991) all models developed to simulate diet selection on rangelands have used a user supplied preference index to calculate diet composition (Ellis *et al.*, 1976; MacNeil *et al.*, 1987; Senft, 1989). Blackburn and Kothmann's (1991) model while apparently more mechanistic may in practice be similar to the preference index models as users adjust the palatability and avoidance factors in the former to obtain reasonable predictions of diet composition. Models that base diet selection solely on units of DDM or DE (Sibbald *et al.*, 1979; Loewer *et al.*, 1987; Demment and Greenwood, 1988) do not characterize all factors affecting diet selection on rangelands but appear to simulate diet selection adequately on monocultures.

Attempts to simulate diet selection and forage allocation have not progressed much during the 15 year period covered by the models reviewed in this paper. This is because of the complexity of the processes involved and because the biology of diet selection (see Hughes, 1990). Provenza and Balph (1990) reviewed five conceptual models used to explain diet selection. The models were: (1) endogenously-generated hungers (euphagia), (2) immediate sensory consequences (hedyphagia), (3) body morphophysiology and size (morpho-physiology), (4) learning through foraging consequences (learning), and (5) nutritional optimization (optimal foraging). It is of interest to compare which of these biological models of diet selection are simulated by the mathematical models. The model developed by Senft (1989) is the only model using relative preference that had biological implications. The simulation of a matching response to vary preference in response to changes in forage avail-

ability is a mathematical representation of the learning model. The models of Sibbald *et al.* (1979), Loewer *et al.* (1987) and Blackburn and Kothmann (1991) that calculate preference as a function of nutrient density can be considered to simulate the euphagia and hedyphagia models on the tactical level and optimal foraging on the strategic level. Demment and Greenwood's (1988) model clearly is simulating the morphophysiology model but also includes aspects of the optimal foraging model because its objective function maximizes DE intake. The fact that there are five biological models competing to explain foraging behavior (Provenza and Balph, 1990) suggests the difficulty of developing mathematical solutions to diet selection.

The use of artificial intelligence and neural networks may provide techniques to assist in simulation diet selection if not the understanding of the biology of this process. Effective use of these techniques will require a better understanding of the rules of thumb that livestock use to select diets. Sheep have been shown to discriminate between forages based on height and brightness (Bazely, 1990; Illius and Gordon, 1990).

CONCLUSIONS

Simulation models of grazing animals are now commonly used by researchers to evaluate the outcome of management alternatives. Doren *et al.* (1985) evaluated the effect of varying calving date and supplementation on biological and economic efficiency of beef cattle production. Blackburn and Cartwright (1987b) simulated sheep production under varying climatic conditions in Kenya and determined that it was important to match body size and potential milk production. Many other practical applications could be listed. The major factor limiting the use of available models is their difficulty of use. Currently there is a greater need for developing user friendly interfaces for existing nutritive models of grazing animals than to improve the logic and algorithms that drive them.

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