

Diet Optimization in a Generalist Herbivore: The Moose

GARY E. BELOVSKY

Society of Fellows, 16 Holyoke Street, Cambridge, Massachusetts 02138

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In an attempt to understand the foraging of a generalist herbivore, a linear programming optimization model was constructed to describe moose feeding in summer. The model attempts to predict the amounts of aquatic vegetation, deciduous leaves, and forbs a moose should consume each day; and to determine whether or not its feeding is constrained by the maximum feeding time available each day, its daily rumen processing capacity, its sodium requirements, and its energy metabolism. The model can be solved for two alternative strategies: time minimization and energy maximization. The energy-maximizing strategy appears to predict the observed diet chosen by an average moose very well. Also, the diets selected by moose of each sex and various reproductive states appear to fit the energy-maximizing strategy. In addition, it is demonstrated that a moose's body size at weaning, size at first reproduction, and maximum size are related to foraging efficiency. Furthermore, there appears to exist an optimum adult body size for feeding. The general conclusion arrived at is that the foraging of a generalist herbivore can be predicted in a quantitative manner, at least in this case, as has been shown for other types of consumers (carnivores and granivores).

The theory of optimal foraging (MacArthur and Pianka, 1966; MacArthur, 1972; Schoener, 1969a,b, 1971; Covich, 1973; Pulliam, 1974; Cody, 1974; Katz, 1974; Emlen, 1966, 1968, 1973) has been successfully applied to a number of animals, both under controlled laboratory conditions and in the field (Wolf and Hainsworth, 1971; Wolf *et al.*, 1972; Pulliam and Enders, 1971; Schoener, 1969b; Menge, 1975; Charnov, 1976; Werner and Hall, 1974; Emlen and Emlen, 1975). This theory, however, has not been applied to herbivores, those animals eating leaves and twigs, because their diets are very complex:

- (1) Different parts of plants (i.e., leaves, buds, twigs, etc.) are of different digestibilities at any one time and the digestibilities vary from season to season.
- (2) The digestibility varies among individual plants within the same species and among species.
- (3) Different plants are thought to be selected to meet different nutritive requirements (i.e., one plant may be selected to meet protein requirements, and another to meet mineral requirements; still another may be selected because it is high in energy, although it may be low in these other components).

Two recent studies (Westoby, 1974; Freeland and Janzen, 1974) have considered herbivore feeding strategies. Their general conclusion is that animals select food plants in an effort to avoid overingestion of any one plant toxin and to achieve nutrient and energy requirements. These authors list a series of alternative hypotheses for herbivore feeding strategies, but do not define an optimal strategy. Their hypotheses are too complex to be tested in terms of a simple foraging model, such as those presented previously for other types of consumers.

In this paper, I have developed a very simplified optimization model for a foraging herbivore, using the moose (*Alces alces*), as an example. The model is based upon only two nutrient requirements for a moose: sodium, which is found in aquatic plants that are low in energy content; and energy, which is reasonably abundant in all other food plants that are low in sodium. Two alternative hypotheses are solved for in the model: the moose as an energy-intake maximizer or a feeding-time minimizer (Schoener, 1969a,b). Using these alternative hypotheses, the model makes relatively simple predictions which can be tested with field observations. Observations of moose feeding during the summer indicate that the model's predictions are validated for the conditions faced by a moose at Isle Royale National Park, Michigan. It is, therefore, concluded that the situation faced by some herbivores in selecting a diet is not as complex as has been previously supposed.

THE MODEL

The optimization technique of linear programming has long been used by livestock producers to determine the diet for cattle which produces the greatest growth rate or milk production at the lowest possible cost. Recently, Westoby (1974) suggested that this technique might be applied to determine whether or not an animal forages in an optimal manner.

To employ linear programming to an optimization problem, one must be able to (1) specify some quantity to be maximized or minimized (goal); (2) identify limits in achieving this goal (constraints). After doing this, one needs to establish equations for the goal and constraints, in terms of variables which are responsible for the process in question; e.g., in feeding, the variables are quantities of different foods. This requires an ability to measure the interrelationships between the quantity of a variable and the achievement of a constraint or goal.

The equations in a linear program must be linear and of the form

$$C \leq \text{or} \geq \sum_i a_i x_i,$$

for constraints, where x_i is the quantity of variable i , and a_i transposes x_i into the units of the constraint, C ; and

$$P = \sum_i b_i x_i,$$

for the goal, where b_i transposes x_i into the units of the goal, P . Using these equations, the basic theorem of linear programming states that the optimal solution for our goal, if one exists, occurs at the intersection of at least two constraint equations. The linear programming algorithm finds the values of the i variables at each intersection, calculates P for these values, and compares all such intersections to find the one which gives the optimum P value. It is possible, however, depending upon the equations, to have no optimal solution (constraints do not intersect) or infinite solutions (the goal equation intersects a constraint equation along a line segment). Strum (1972) gives a detailed description of the linear programming algorithm.

For the purposes of this paper, only the summer feeding of moose will be analyzed (June 3–September 15). This period is important because it is then that moose bear their young and store fat for the lean winter period. During the summer feeding period, moose consume aquatic macrophytes in beaver ponds, the leaves of deciduous plants, and forbs. The model does not distinguish among species of plants in each of the above three food classes. Therefore, the moose as portrayed in the model need only decide on which and how much of each food class it will consume.

In constructing the linear programming model for moose feeding, it was assumed that the animal had two alternative goals (symbols listed in Table I):

(1) *Energy maximization* is a potential goal, since the more food available, the greater its potential for reproduction and fat storage. This goal is written as

$$E = \sum_i (K_i D_i - S_i) x_i, \quad (1)$$

where E is the energy available to a moose, K_i is the gross caloric content of food i per unit dry weight, D_i is the dry matter digestibility of food class i , S_i is the energetic cost of cropping a unit dry weight of food i , and x_i is the dry matter weight of food class i consumed. Therefore, K_i , D_i , and S_i must be measured for a moose's various foods.

(2) *Feeding time minimization* is a possible goal for two reasons. One, the less time that a moose feeds, the lower its exposure to predation by wolves (*Canis lupus*) and to environmental conditions that would lead to thermal imbalance. Second, the less time a moose spends feeding, the more time it can spend selecting mates, caring for offspring, etc. The time-minimization goal is written as

$$T = \sum_i t_i x_i, \quad (2)$$

TABLE I
A Glossary of Terms Used in the Text

a_i	A linear program constant pertaining to food class i
B_i	The bulkiness of food class i (g-wet wt/g-dry wt)
b_i	A constant transposing the quantity of food class i in the diet into the quantity to be optimized
C	A linear programming constraint
D_i	The percentage digestibility of food class i
K_i	The gross caloric content of food class i
M	The animal's basal metabolism (kcal/day)
M_M	The animal's maintenance metabolism (kcal/day)
M_R	The animal's metabolism for maintenance, growth and reproduction (kcal/day)
N_M	The animal's sodium requirements for maintenance (g-dry wt of aquatics consumed/day)
N_R	The animal's sodium requirements for maintenance, growth, and reproduction (g-dry wt of aquatics consumed/day)
NE	The net energy intake by the animal
P	The optimum value of concern
R	The daily rumen processing capacity (g-wet wt/day)
S_i	The energy expended by an animal in moving from food plant i to food plant i to crop a unit weight of food i (kcal/g-dry wt)
s	The sex specific variable transposing the bull's R value into the cow's
t_i	The time spent in cropping a unit weight of food class i (min/g-dry wt)
E	The maximum energy intake goal (kcal/day)
T	The minimum time spent feeding (min/day)
T_T	The time available for feeding on land (min/day)
T_A	The time available for feeding in water (min/day)
I	The terrestrial consumption by the animal (g-dry wt/day)
TE	The energy supplied to an animal by consuming terrestrial plants (kcal/day)
W	The animal's weight in kilograms
x_i	The quantity of food class i in the animal's diet (g-dry wt/day)
Y	The number of calves being raised by a cow

where T is the time spent feeding, and t_i is the time required to crop a unit dry weight of food class i . In this case, t_i must be measured by observing moose feed.

The next step in constructing the linear programming model is to determine what constraints operate upon a moose's feeding. Four constraints are assumed to be important:

(1) An animal must satisfy its *energy requirements*. Two alternative energy demand terms can be used in the model: the metabolic demands for maintenance, M_M (including the necessary energy storage for the winter period), and the metabolic demands for maintenance, increased body size, and reproduction, M_R . If M_M is not surpassed or equaled, the individual will perish, while the failure to achieve M_R leads to the extinction of the population, since reproduction will not equal mortality. The constraint equation can be written

$$M_M \text{ or } M_R \leq \sum_i (K_i D_i - S_i) x_i. \quad (3)$$

In this constraint, we are measuring the amount of a moose's energy demand supplied by each food class and the variables are the same as those required in the energy goal equation.

(2) *Sodium* is a potentially limiting mineral for a moose and it has been demonstrated that sodium is in short supply for moose at Isle Royale (Botkin *et al.*, 1973; Jordan *et al.*, 1973). Lack of this mineral can prevent reproduction and lead to death (Church *et al.*, 1971). Aquatic macrophytes are the only significant source of sodium for moose. These plants are available only during the summer and moose are never seen feeding in ponds during any other season. This time limitation is believed to arise from the moose's problem of excessive heat loss to cold water during periods other than summer. As a result of this time limitation, the moose must satisfy its annual sodium requirements during the summer or perish.

The quantity of sodium required by a moose depends upon whether the moose is simply maintaining itself, N_M , or reproducing, N_R . This difference is due to the large quantities of sodium required for growth and reproduction (Jordan *et al.*, 1973). Therefore, this constraint can be written

$$N_M \text{ or } N_R \leq x_1, \quad (4)$$

where N_M and N_R are the quantities of aquatic vegetation which must be consumed each day if the moose is to satisfy its sodium requirements and x_1 is the quantity (dry weight) of aquatics consumed. For this constraint, one must be able to measure N_M and N_R .

(3) The amount of *feeding time available* to a moose each day is another potential constraint. This arises from two problems: the avoidance of excessive heat loads during certain portions of the day and a time investment in rumination to achieve some desired digestibility of food plants. First, the moose, like other animals, must limit its activity to times and habitats which allow it to maintain thermal homeostasis. Second, a moose as a ruminant must spend time regurgitating its food and remasticating it for the symbiotic microorganisms in its rumen, to achieve some level of digestibility. This second rationale for

time limitation is an assumption which is addressed in the Appendix. The feeding time limitation, both thermal and ruminating, has been worked out and presented in another paper (Belovsky, 1977). In this study, it was found that the moose's available time for feeding in aquatic and terrestrial sites is independent, owing to the high thermal conductivity of water.

The time constraint is written as

$$T_A \geq t_1 x_1 \quad (5)$$

for aquatic plants, and

$$T_T \geq \sum_i t_i x_i, \quad i = 2, 3, \quad (6)$$

for terrestrial plants, where T_A is the time available each day for feeding on aquatics, T_T is the time available for feeding on land during each day, and t_1 is the amount of time it requires to crop a unit dry weight of aquatic plants. t_i and t_1 are identical to the variables in the time-minimization goal. Therefore, in this constraint, we must measure T_A , T_T , and t_i , including t_1 .

(4) The last constraint is the moose's *daily rumen* capacity, since it is generally thought that a food plant's physical qualities determine its passage rate through the rumen (Baile and Forbes, 1974; Blaxter, 1967; Church *et al.*, 1971). The rumen, the first of four stomachs, is a container of fixed volume in which plant tissues are fermented. Furthermore, the rumen is constructed to control food passage depending upon the breakdown of these foods. The term "rumen capacity" refers to the quantity of food in the rumen, since a large portion of the structure's volume contains saliva, water, and various digestive fluids. Also, it is assumed that a moose's rumen capacity fills as a function of the wet weight of plants contained in it (see the Appendix for a discussion).

The rumen constraint is written as

$$R \geq \sum_i B_i x_i, \quad (7)$$

where R is the amount of food (wet weight) which passes through the rumen each day and B_i is the amount of rumen capacity taken up by a quantity of food i . Both R and B_i must be measured. This constraint is season dependent since R and B_i vary with the physical qualities of plants that change between seasons.

Now that we have hypothesized alternative goals and potentially limiting factors for a moose's feeding (constraints); we need to measure (1) the parameters in the goal and constraint equations and (2) the moose's actual feeding behavior. By using the feeding model to predict the moose's behavior, we can compare the result to a moose's observed behavior. If the model's predictions compare poorly with the observed behavior, we can be fairly confident that the model's

constraints or goals are not important for a moose's feeding. On the other hand, if the model's predictions agree with a moose's behavior, one can say that there exists strong evidence that a moose's foraging operates in the manner specified by the model. The only way to truly test the model, however, is to change the values of the parameters in the constraint and goal equations by studying moose in a different environment and determine whether or not the model is still predictive.

DATA REQUIRED FOR THE MODEL

The majority of parameter values in this model were obtained from field and laboratory measurements made at Isle Royale National Park, Michigan, between 1972 and 1974 (Belovsky and Jordan, 1978). All parameter values refer to an upland forest dominated by *Betula alleghaniensis* and are presented with their confidence intervals (95%).

t_i : The time required to crop a quantity of food ($i = 1$, aquatics; $i = 2$, deciduous leaves; and $i = 3$, forbs) was found to be 0.05 ± 0.01 min/g-dry wt of aquatics, 0.06 ± 0.01 min/g-dry wt for deciduous leaves, and 0.12 ± 0.02 min/g-dry wt for forbs (Belovsky and Jordan, 1978).

S_i : The cost of acquiring a quantity of food was found to equal 0.01 ± 0.01 kcal/g-dry wt for deciduous leaves, 0.01 ± 0.01 kcal/g-dry wt for forbs, and 0.03 ± 0.02 kcal/g-dry wt for aquatics (Belovsky and Jordan, 1978).

B_i : The bulkiness of a quantity of food was found to be 4.0 g-wet wt/g-dry wt for deciduous leaves (3.7 to 4.5), 4.4 g-wet wt/g-dry wt for forbs (3.3 to 10.0), and 20.0 g-wet wt/g-dry wt for aquatics (5.3 to 100.0) (Belovsky and Jordan, 1978).

D_i : The dry matter digestibility of each food was measured to be 72% for deciduous leaves, 86% for forbs, and 94% for aquatics (Belovsky and Jordan, 1978).

K_i : The gross caloric value of food is 4.2 kcal/g-dry wt for deciduous leaves (Golley, 1961), 4.8 kcal/g-dry wt for forbs (Golley, 1961), and 4.1 kcal/g-dry wt for aquatics (Boyd, 1970). It is assumed that these average values are adequate, since the variations in caloric value for similar plants are small (Golley, 1961).

T_A and T_T : To avoid circularity, we need an estimate of a moose's maximum potential daily feeding time. Through measurements of thermal parameters in the moose's environment, an optimization model was developed to predict the amount of feeding time available to a moose each day. This model predicts, on the basis of a moose's thermal balance, when, where, and for how long a moose should feed. The model is presented elsewhere (Belovsky, 1977); it predicts that a moose has 256 min/day to feed on land (T_T) and 150 min/day to feed in water (T_A).

M_M and M_R : A moose's basal energy metabolism (M : kcal/day) can be calculated using Kleiber's (1961) formula

$$M = 70W^{0.75}, \quad (8)$$

where W is a moose's weight in kilograms. Moen (1974) and Gasaway and Coady (1974) assume that an animal's maintenance (M_M) and reproductive (M_R) metabolic requirements can be presented as a multiple of M ; using their values for these multiples, I estimated:

- (1) M_M for bulls and cows is 1.8 times M ;
- (2) M_R for bulls and barren cows is 2 times M , since an energy reserve is required for the fall mating;
- (3) M_R for cows with calves is 2.7 times M , primarily because of the energetic costs of lactation.

N_M and N_R : A moose's sodium demand was measured by accounting for a moose's output of feces, urine, body growth, fat deposition, reproduction, and lactation (Belovsky, 1977); and then multiplying by the appropriate sodium content. Although this does not necessarily provide the minimum amount of sodium required by a moose, we can say that since a moose is losing this quantity of sodium it must replace this amount to remain in steady state. Furthermore, this sodium measure may be a minimum quantity, since Botkin *et al.* (1973) have shown sodium to be exceptionally rare at Isle Royale.

For an average moose at Isle Royale (358 kg), it was found that a bull or a barren cow requires 1.34 g/day of sodium during the summer to satisfy its annual maintenance requirement, since aquatics, the only source of sodium, are available only in summer (Belovsky, 1977). A bull or a barren cow requires 1.88 g/day of sodium to satisfy reproduction requirements, while a cow with calf requires an additional 1.18 g/day/calf of sodium (Belovsky of 1977). Since the aquatic vegetation consumed by moose is 0.00295 g- Na^+ /g-dry wt, these sodium requirements become 454 g/day of aquatics for maintenance, 636 g/day for a bull or barren cow's reproduction, and an additional 401 g/day of aquatics for each calf a cow is raising. Assuming that sodium requirements are a constant fraction of body weight (Church *et al.*, 1971) and the sodium expenditure for a calf is constant because of some minimum to ensure calf survival, we can write sodium demand (g-dry wt of aquatics/day) as

$$N_M = (1.27 \text{ g/day/kg})(W) \quad (9)$$

for both sexes,

$$N_R = (1.78 \text{ g/day/kg})(W) \quad (10)$$

for bulls and barren cows, and

$$N_R = (1.78 \text{ g/day/kg})(W) + (401 \text{ g/day/calf})(Y), \quad (11)$$

for cows with young, where Y is the number of calves. Since cows do not generally grow or deposit fat, while lactating (Knorre, 1959), the N_R value can be reduced by this unrealized increase in tissue:

$$N_R = (1.27 \text{ g/day/kg})(W) + (401 \text{ g/day/calf})(Y). \quad (12)$$

R : The last parameter required for the model is the amount of food processed each day in the rumen, as a function of the moose's weight. Values for the wet weight of food in the moose's four stomachs and the weight of the moose were taken from the literature (Egorov, 1964; Schladweiler and Stevens, 1973; unpublished data from Isle Royale). To convert these stomach values to wet weight of food only in the rumen, the first stomach, Short's (1964) study of deer (*Odocoileus virginianus*) rumen development was applied to moose, such that:

- (1) A moose weighing less than 100 kg is assumed to have a rumen which composes 44% of the entire stomach,
- (2) a moose weighing between 100 and 200 kg has a stomach which is 62% rumen, and
- (3) a moose weighing 200 kg or more has a stomach which is 75% rumen.

To convert the weight of food in the rumen into the daily quantity processed by the rumen, one needs to know the turnover time. This turnover time was estimated to be 1.14 (24 hr/21 hr) from Mautz's (1971) radioisotope study of deer digestion.

Since it was found that a cow moose has a stomach which is 1.2 times larger than that of a bull of the same size (Egorov, 1964; Schladweiler and Stevens, 1973; unpublished data from Isle Royale), the daily quantity of food processed by the rumen was standardized by dividing female values by 1.2. These standardized values are then regressed against body weight:

$$R = 35047 \log_{10} W - 57993 \quad (13)$$

($r = 0.96$, $N = 21$, $P \leq 0.01$). Therefore, Eq. (13) can be used to compute the daily quantity of food processed by a bull's rumen, while a cow's value is 1.2 times the bull's.

All constraint values (M_N , M_R , N_M , N_R , T_A , T_T , R) are summarized in Table II and all parameter values (t_i , B_i , K_i , D_i , S_i) are shown in Fig. 1.

TABLE II
A Summary of the Constraint Values Used in the Moose Feeding Model

Constraint	Bull	Barren cow	Cow with calf
M_M (kcal/day)	$126W^{0.75}$	$126W^{0.75}$	$126W^{0.75}$
M_R (kcal/day)	$140W^{0.75}$	$140W^{0.75}$	$189W^{0.75}$
N_M (g-dry wt of aquatics/day)	$1.27W$	$1.27W$	$1.27W$
N_R (g-dry wt of aquatics/day)	$1.78W$	$1.78W$	If growing: $1.78W + 401Y$ Nongrowing: $1.27W + 401Y$
T_A (min/day)	150	150	150
T_T (min/day)	256	256	256
R (g-wet wt/day)	$35,047 \log_{10} W - 57,993$	$42,056 \log_{10} W - 69,592$	

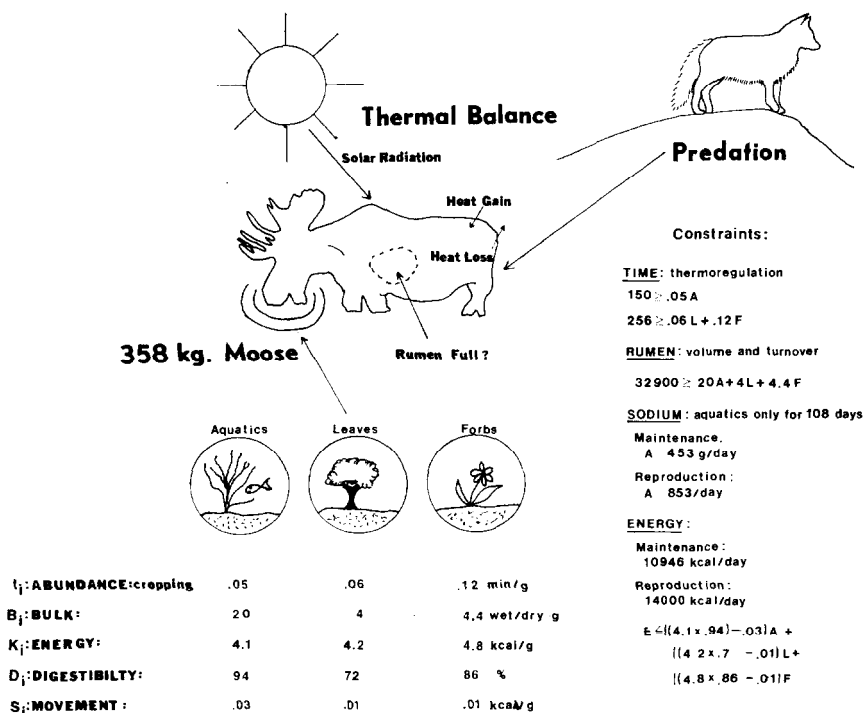


FIG. 1. A presentation of the food characteristics and constraints used to model optimal foraging for an average adult moose. The constraint equations used in the linear program appear on the right side of the figure. (The R value is an average R for moose weighing between 300 and 400 kg, using the data employed to calculate the R - W equation in the text).

RESULTS AND DISCUSSION

The optimization model for moose feeding is solved for three situations of increasing specificity, each with different constraints: (1) average Isle Royale moose's feeding, (2) feeding of average bull, barren cow, and cow with calf, and (3) feeding changes with changes in body size. This scheme starts with the simplest model and proceeds to the most complex.

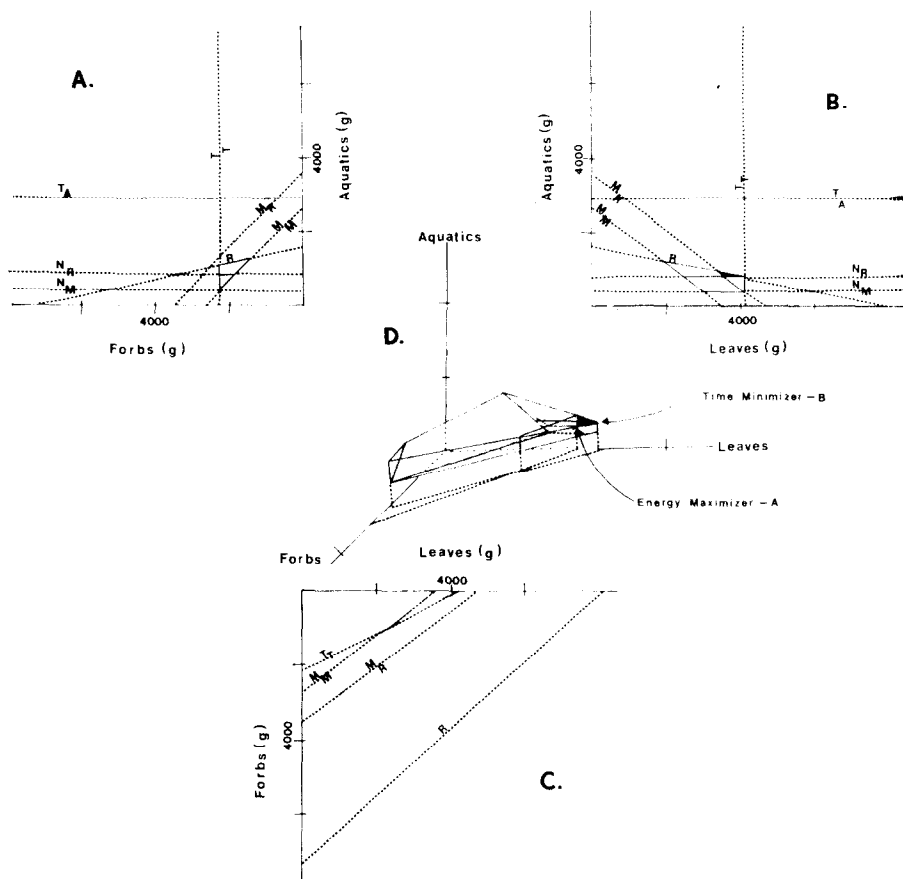


FIG. 2. The linear program constraints solved for a 358-kg average adult moose. The pairwise solutions for food classes appear in (A), (B), and (C). Each of these graphs represents the solution of the linear programming constraints, assuming that the third food class is not consumed. Figure 2D presents the three-dimensional portrayal of the solution for all food classes simultaneously (each of the pairwise graphs represents x - y , y - z , or x - z planes). The area or volume encompassed by solid lines represents the set of feasible diets satisfying the moose's maintenance requirements, while the darkened region also satisfies reproductive needs. The symbols describing the various constraints are defined in Table I. Point A, the energy maximizer, comes the closest to the observed behavior of moose in the wild.

Average Isle Royale Moose

The average Isle Royale moose is assumed to weigh 358 kg, is 50% bull and 50% cow and in terms of reproduction, it is 54% with calf and 46% bull or barren (due to twinning in the population) (Jordan *et al.*, 1971). The reason for choosing to work with such a hypothetical animal is that the observed diet for an Isle Royale moose was measured for an average individual (amount of food removed/day/area divided by the number of moose/area (Belovsky and Jordan, 1978)). Therefore, to be able to compare the observed diet with that predicted by the model, we must work with the hypothetical average individual.

Figure 1 presents the constraint equations for our average moose and their graphical solution appears in Table II. The graphical solution is presented in a pairwise manner, assuming that the third food class is not consumed (Figs. 2a-c). Regions surrounded by solid lines represent combinations of the two food classes which supply maintenance requirements, while darkened regions provide reproductive requirements. The two-way representation shows that:

- (1) aquatic plants must always be consumed to supply sodium requirements,
- (2) forbs and aquatic plants cannot satisfy reproductive energy requirements, because of the amount of time it takes to crop forbs and the bulkiness of aquatics which fill the rumen; and
- (3) deciduous leaves and aquatics can supply both maintenance and reproductive requirements, which indicates that some quantity of deciduous leaves must be consumed for reproduction, since they are less time consuming to crop and less bulky than forbs.

These are interesting results, since they point out that aquatics must be consumed to supply sodium, but deciduous leaves, the food with the lowest dry weight gross caloric value, are the main and essential source of reproductive energy.

Each of the two-way solutions for the constraint equations can now be combined into a three-dimensional solution, where each two-way solution represents the x - y , y - z , z - x planes (Fig. 2d). The corners of the darkened volume must now be tested to determine which provides the energy maximized diet and the time minimization diet. It is found, using the linear programming algorithm, that point *A* represents the energy-maximized diet and point *B*, the time-minimized diet. The quantities of each food class in these diets appear in Table III, along with the observed diet.

Although the energy-maximized diet appears to be closer to the observed diet in every class, than does the time-minimized diet, one would like to make some statement about the relative closeness of fit. Two methods can be employed if we ignore the potential error in the predicted consumption values

TABLE III

The Predicted Diets (Energy Maximized and Time Minimized) for an Average Isle Royale Moose Compared with the Observed Food Consumption^a

	Energy maximized	Time minimized	Observed
Aquatics	853 (17.8 %)	958 (21.8 %)	868 (17.7 %)
Deciduous leaves	3585 (75.0 %)	3435 (78.2 %)	3656 \pm 81 (74.6 %)
Forbs	342 (7.2 %)	0 (0 %)	374 (8.0 %)
Energy intake (kcal/day)	15,458	14,000	15,861
Feeding time (min/day)	299	254	307

^a All food consumption values are measured in g-dry wt/day and the values in parentheses are the percentages of each food in the diet.

which will be examined in detail in a later section. First, a χ^2 goodness-of-fit test can be used to compare the predicted with observed diet. This was done by first converting the predicted and observed diets from units of grams consumed per day to bites per day, as a discrete unit is required for a χ^2 test (aquatics: 0.10 bites/g; leaves: 0.68 bites/g; forbs: 3.34 bites/g). Using the fraction of the predicted diets composed of aquatic and terrestrial plants (forbs and leaves combined, since the time minimization diet predicts no forb intake), one can compute the expected quantity of each food class in the observed diet based upon the total measured food consumption (1194 bites/day). Then by knowing the density of moose (no./m²) and sample area for each food type (m²), a predicted quantity of food consumed can be calculated and compared with the observed food removed (Belovsky and Jordan, 1978). This test shows that the time-minimization diet is significantly different from the observed diet ($\chi^2 = 152.80$, $df = 1$, $P \leq 0.005$), while the energy-maximization diet is not significantly different from the observed diet ($\chi^2 = 0.42$, $df = 1$, $P \leq 0.55$). These χ^2 tests assume that the bites in each food class are equivalent, which may or may not be the case; but the tests serve as one of the two ways of comparing the model with the observed feeding in a somewhat objective manner.

Second, a t test can be used to test whether or not the predicted consumption of deciduous leaves is significantly different from the observed mean consumption with its standard deviation. This test indicates that the time-minimization diet is almost significantly different ($t = 2.37$, $P \leq 0.15$), while the energy-maximization diet is not significantly different ($t = 0.76$, $P \leq 0.65$). Therefore, in each of the two tests, the energy-maximized diet is not significantly different from the observed diet, while in at least one case, the time-minimization diet is significantly different from the observed. This provides evidence that a moose forages in an energy-maximizing manner.

If moose do maximize the energy in their diet, then several important points become evident. First, the synthesis of time, sodium, and rumen processing constraints leads to the inclusion of all three food types in the moose's diet. Second, the energy-maximizing diet would provide 11% more energy than required for reproduction metabolism and only 3% of the diets providing maintenance requirements also satisfy reproductive needs. Therefore, this limited feeding flexibility would seem to suggest that moose cannot afford very much error in their behavior or environmental variation; this may account for the very small coefficient of variation observed for the consumption of deciduous leaves, 2.2%.

Sex Differentiation

The next step is to distinguish between cow moose with calves and adults expending little energy and minerals for reproduction; i.e., males and barren

TABLE IV
The Predicted Diets of Moose (358 kg) of Different Reproductive States Compared to the Observed Food Consumption (g-dry wt/day)^a

	Energy maximizer	Time minimizer	Observed
Bull			
Aquatics	642	978	655
Deciduous leaves	4267	2586	(3967) (2791)
Forbs	0	0	150
Cow with calf			
Aquatic	1038	1038	1081
Deciduous leaves	3191	3506	(2910) (2910) ^b
Forbs	538	252	598
Barren Cow			
Aquatic	941	1379	1081
Deciduous leaves	4277	2078	(2910) (1634)
Forbs	0	0	598

^a The values in parentheses are estimated deciduous consumption values, with the first representing the intake if the moose is an energy maximizer, and the second the intake if the moose is a time minimizer (see text for further explanation).

^b The energy-maximizing and time-minimizing solutions are the same since neither satisfies the cow's 15,555-kcal/day requirement. Approximately 60 g of leaf intake is required above what the rumen can hold. This indicates that the 1081-g intake of aquatics may be a slight overestimate.

cows. Substituting the sex and reproductive specific constraint values (Table II) for the average values in Fig. 1, still using a 358-kg individual, we can solve the model for the two alternative goals: energy-maximizing diet and time-minimizing diet. Although cows with young bear the brunt of increased dietary requirements (energy, sodium), they also possess larger rumens than do bulls. This enables the cow to compensate for the added sodium demand, satisfied only by bulky aquatics. The predicted diets for each of the three demographic classes (bull, barren cow, cow with young) and their observed diets appear in Table IV.

It is much more difficult in this case to compare the predicted and observed diets, since the observed diets are known only for aquatics and forbs. Deciduous leaves are absent from the observed diets since these are eaten primarily at night in thick cover; so it is impossible to determine the ratio of time spent by males feeding on leaves to time spent by cows, as was done for the other food classes (Belovsky and Jordan, 1978). Nevertheless, on the basis of a limited observed diet, it appears that:

(1) Bulls are energy maximizers, since their aquatic consumption is very close to that predicted in the energy-maximized diet and aquatics are the least costly food to crop in terms of time, which would indicate a greater consumption of this food if the moose minimized feeding time. Forbs, on the other hand, fit either goal equally, since both predict that this food should not be consumed. But the fact that forbs have the highest energy content may suggest that some consumption, as observed, fits an energy-maximizing strategy. In addition, I have observed moose feeding on herbaceous plants, the only food in reach, while bedded. If this were the case, then periods of inactivity may not be totally food-free and an energy-maximizing moose would be expected to consume the small quantity of herbs surrounding its beds. Bulls may be energy maximizers by necessity since they lose up to 17% of their body weight during the fall breeding season and consequently require an energy reserve from their summer feeding.

(2) Cows with young appear to be energy maximizers, since the predicted forb consumption for energy maximization agrees very well with the observed consumption, even though forbs are the most costly to feed on in terms of time. Aquatic consumption, however, fits either goal equally well, since the two diets predict the same consumption of this food.

(3) Barren cows have an observed diet which is identical with that for a cow with calf, even though both predicted diets deviate substantially from the observed. It is thought that barren cows and cows with calves have identical diets, since no statistical difference between the two could be found and their respective diets differ by less than 0.1%. For these reasons, their diet data were combined (Belovsky and Jordan, 1978). This suggests that a cow moose

always feeds in a manner which is consistent with the presence of young, even though she may be barren. Therefore, cows are either "programmed" for the bearing of and caring for young or they anticipate future pregnancies and store sodium and energy.

The observed and predicted diets can be compared in a second way, by estimating deciduous consumption. This is done by two methods:

(1) If the moose is an energy maximizer, it should fill its rumen, which allows us to compute deciduous intake as the rumen processing capacity (R) less the known bulk intake of aquatics and forbs.

(2) If the moose is a time minimizer, it should feed until it satisfies its energy requirements, in which case the deciduous intake is computed as the difference between the daily energy requirements (M_R) and the energy supplied by the known consumption of aquatics and forbs. These estimates of deciduous consumption appear in Table IV in parentheses. We can then use a χ^2 goodness-of-fit test to compare the observed and predicted diets, as was done in the average moose analysis. In this case, however, the predicted removals by bulls and cows with calves are combined and divided by 2, since the sex ratio is 1:1. This is required, since the observed consumption (bites/m²) could not be allocated to each sex (Belovsky and Jordan, 1978). This allows us to compare a predicted utilization of the plants in the environment with the observed utilization and various combinations of each sex's strategies leads to different predicted utilizations.

If bulls and cows are both energy maximizers, the observed and predicted utilizations are not significantly different ($\chi^2 = 3.01$, $df = 1$, $P \leq 0.09$); however, all other strategy combinations do differ significantly from the observed consumption (bull time minimizer—cow time minimizer: $\chi^2 = 7.04$, $df = 1$, $P \leq 0.006$; bull time minimizer—cow energy maximizer: $\chi^2 = 13.34$, $df = 1$, $P \leq 0.005$; and bull energy maximizer—cow time minimizer: $\chi^2 = 31.54$, $df = 1$, $P \leq 0.005$). Therefore, it appears that both males and females attempt to maximize their energy intake during the summer.

It appears, at least superficially, that bulls and cows with young are energy maximizers rather than time minimizers. If this is true, several points can be made. First, if a cow with a calf is to achieve its energy requirements, it must include forbs in the diet, since a diet of deciduous leaves alone will not provide sufficient energy. Second, bulls and barren cows have great flexibility in their feeding, since 35% of a bull's diet combinations permit reproduction, while 44% of a barren cow's provide for reproductive requirements. On the other hand, less than 2% of the potential diet combinations of a cow with calf permit the successful rearing of young; it is no wonder that over 60% of the calves perish each year (Jordan *et al.*, 1971). This may also explain why a barren cow chooses a diet identical to that chosen by a cow with calf, as a means of storing sodium and energy for future calf production.

Body Size Variation

The final level of complexity to be added to the model will be changes in optimal foraging with body weight. By examining changes in net energy intake with changes in body size, one might hope to ascertain whether there exists an adult size which leads to a maximum net energy intake and whether size at weaning and size at first reproduction depend upon feeding capabilities. Also, there may exist a maximum body size for moose, beyond which feeding does not satisfy energy and sodium requirements. The premise employed here is that energy intake is an important determinant of a moose's capability of surviving and reproducing and therefore, body size which influences feeding should be linked to life history parameters. By comparing the various observed body sizes at different stages of the moose's life history to those predicted on the basis of net energy intake we can determine whether or not feeding is an important factor.

How the model is varied. By allowing each of the constraint values for M_M , M_R , N_M , N_R , and R to become continuous functions of body size (Table II), we can begin to modify the model. Several simplifying assumptions were made and were later tested to determine their validity:

(1) Forbs and deciduous leaves were combined into a single food class, terrestrials, which is composed of 9% forbs and 91% leaves, based upon the previously presented energy-maximized solutions. And all terrestrial traits are weighted averages based upon these values (Table V).

TABLE V

The Food Parameters Obtained by Combining Deciduous Leaves and Forbs into a Single Class, Terrestrials

$B_T = 4.04$ g-wet wt/g-dry wt
$K_T = 4.25$ kcal/g-dry wt
$D_T = 73\%$
$S_T = 0.01$ kcal/g-dry wt
$t_T = 0.065$ min/g

(2) Changes in daily feeding time and cropping rates with body size were assumed to occur at the same rate. This allows us to ignore these variations and to treat T_A , T_T and t_i as constants, since the changes with size would cancel. Furthermore, if this is the case and we utilize the assumption which combines the deciduous leaves and herbs into a single food class, then the time constraint can be dropped since it is already operating implicitly in the determination of the relative proportions of leaves and herbs in the diet.

(3) The model was only solved for energy maximization, since all observed diets in previous sections compared the best with the predicted energy-maximized diet. Finally, for simplicity, the model was solved graphically.

From the parameters in Table II, an equation can be constructed to measure a moose's net energy intake. The daily rumen processing capacity (R) less the bulk of aquatic intake needed to supply sodium demands determines the rumen capacity remaining for terrestrial intake (I):

$$I = R - B_1(N_R), \quad (14)$$

where N_R is the appropriate equation from Table II and B_1 is the bulk constant for aquatics. Using the quantity, I , we can determine the energy supplied by terrestrials (TE):

$$TE = (I)(K_T D_T - S_T)/B_T, \quad (15)$$

where B_T , K_T , D_T , and S_T are the terrestrial's bulk, gross caloric content, digestibility, and energetic cost to crop, respectively. Adding to the energy intake from terrestrials (TE) the energy supplied by aquatics, we obtain the total net energy intake by a moose (NE):

$$NE = TE + N_R(K_1 D_1 - S_1). \quad (16)$$

By combining Eqs. (14)–(16) and using the parameters in Tables II and III and Fig. 2, we obtain

$$NE = \frac{s(35047 \log_{10} W - 57993) - (20 \text{ g-wet wt/g-dry wt})(N_R)}{4.04 \text{ g-wet wt/g-dry wt}} \\ \cdot 3.09 \text{ kcal/g} + (3.82 \text{ kcal/g})(N_R), \quad (17)$$

where s is 1 for bulls and 1.2 for cows.

The calculation of a moose's NE at a specific weight, sex, and reproductive state enables us to compare this value with the animal's weight specific M_R (Table II). If NE is greater than or equal to M_R , the moose is capable of surviving since it can satisfy its energy demands; otherwise, it perishes. Furthermore, when NE equals M_R , we have found either a moose's maximum or its minimum body size. Figure 3 contains the comparison of the NE and M_R functions for bulls and barren cows, while Fig. 4 shows the relationship for cows with calves. The differences in the NE functions for bulls and barren cows are due to the sex specific differences in rumen volume.

By solving the NE equations for the critical weights at which NE equals M_R , we can determine when individuals should be capable of self-sufficiency.

These critical points are satisfied by the equations

$$26806 \log_{10} W - 44356 - 20.4W = 140W^{0.75} \quad (18)$$

for bulls,

$$32167 \log_{10} W - 53227 - 20.4W = 140W^{0.75} \quad (19)$$

for barren cows,

$$32167 \log_{10} W - 59361 - 20.4W = 189W^{0.75} \quad (20)$$

for growing cows with a calf, and

$$32167 \log_{10} W - 59361 - 14.6W = 189W^{0.75} \quad (21)$$

for nongrowing cows with calves. Finally, the assumptions (see above) used in constructing these simplified models can be tested by comparing the simple

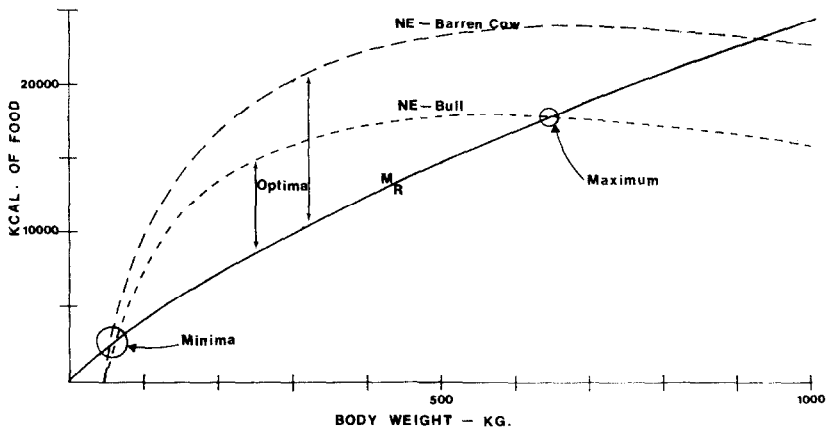


FIG. 3. A graphical determination of a bull's and a barren cow's body weight at weaning, a bull's optimum size, and a bull's maximum body weight. The optimum body size for the cow is presented, but the maximum cow size is not relevant since the cow in this case is barren and moose cows in the wild generally bear young. The NE and M_R functions are defined by the formulas in the text. The intersections of the net energy curves (NE) with the energy metabolism curve (M_R) define maximum and minimum body sizes. If the NE curve lies below the M_R curve, the moose perishes since it cannot satisfy its energy and sodium demands. The body weight at which the NE curve lies the greatest distance above the M_R curve defines the optimum body size. The sizes at weaning are 62 kg for cows and 67 kg for bull's, since below these weights the moose cannot satisfy their energy and sodium demands without a nutritional supplement, milk. Bulls have an optimum body size of 250 kg and a maximum size of 645 kg. The barren cow has an optimum size of 307 kg.

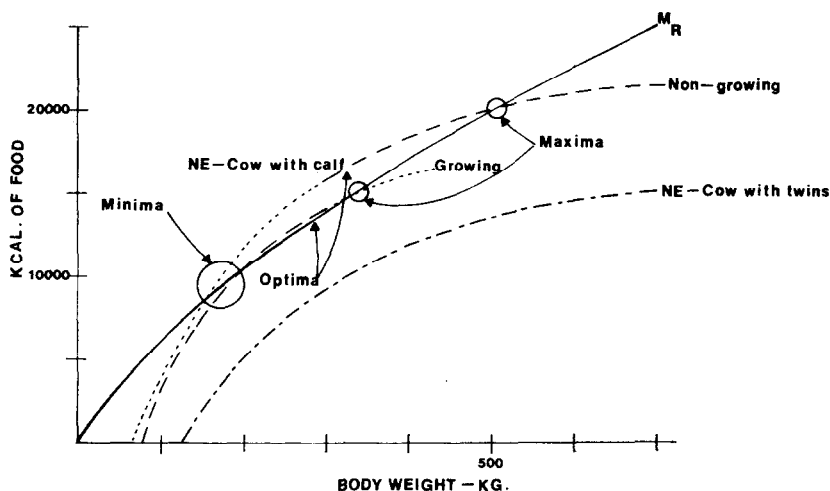


FIG. 4. A graphical determination of a cow with calf's minimum, optimum, and maximum body sizes. The NE and M_R functions are defined by the formulas in the text. The intersections of the net energy curve (NE) with the energy metabolism curve (M_R) defines the maximum and minimum sizes. If the NE curve lies below the M_R curve, the moose perishes since it cannot satisfy its energy and sodium demands. The body weight at which the NE curve lies the greatest distance above the M_R curve defines the optimum body size. A cow can satisfy her energy and sodium demands along with those of her calf at a weight of 141 kg, if she forgoes her own growth, and 167 kg, if she continues to grow. Cows have an optimum body weight of 285 kg and a maximum of 514 kg.

models' results for energy intake with those obtained from a detailed solution of the linear programs at different body sizes. The energy intakes predicted by the energy-maximizing linear programs are very close to those obtained from the simplified equations (deviation less than 9%) and the simplified form generally provides a larger value.

We can also find the optimum body size which allows the moose to feed at the greatest surplus of energy over the M_R value. This body size should provide the moose with the greatest possible survival and reproductive output, since the moose will have the greatest amount of energy for producing young and fat storage. This body size can be found by setting the derivative of the function, $NE - M_R$, with respect to body weight, equal to zero:

$$d/dW (NE - M_R) = 0.$$

The derivatives of Eqs. (18)–(21) with respect to W and set equal to zero have the general form

$$c_1(\log_{10} e)(1/W) - c_2 - c_3(0.75)W^{-0.25} = 0,$$

where c_1 , c_2 , and c_3 are the specific constants from Eqs. (18)–(21).

Size at weaning. In Fig. 3, the M_R function is intersected for the first time by the NE function at 62 kg for barren cows and 67 kg for bulls. Below these weights, the moose is unable to satisfy its energy demands and take in sufficient aquatic macrophytes to fulfill its sodium requirements. The model asserts that the moose should not be able to survive unless it attains a nutritional supplement high in sodium and energy. The supplement comes in the form of a moose cow's milk. Data obtained from Knorre (1959) show that a calf weighs on the average 11.2 kg at birth and gains 0.25 kg/day during its first month of life, 0.55 kg/day in the second, 0.90 kg/day during the third, and 1.2 kg/day during the fourth. Using these figures for calf growth and assuming that all calves are born on June 1, the midpoint of the calving season, we calculate that a calf should attain a weight of 62 to 71 kg in early September (Sept. 1-7). At this time, the calf should be independent of its mother's milk as a nutritional supplement. Knorre (1959) claims that weaning of moose calves occurs in early September. This indicates that this important life history event depends upon the calf's ability to feed itself and obtain sufficient sodium on its own.

Size at first reproduction for cows and their optimum size for feeding. In Fig. 4, the NE functions of a cow with calf and a cow with twins are compared to the M_R function of a cow with a single calf. The first intersection of the NE and M_R lines of a cow with a single calf occurs at 141 kg for nongrowing cows and 169 kg for growing cows. The reason for this much higher intersection than the already stated 62 kg for barren cows arises from a greater aquatic intake needed to supply sodium to calves. Knorre (1959) cites data on domestic moose in Siberia which indicate that a cow moose will not reproduce, regardless of her age, unless her weight is from 292 to 335 kg. Therefore, it appears that the age at first reproduction for a cow depends upon some critical weight. However, the comparison of the NE and M_R functions shows that the size at which a cow can first successfully bear a calf is much smaller than this empirical size.

By referring to Fig. 3 again, one can see that the optimum body size for a barren cow is 307 kg; in Fig. 4, it is 285 kg for a nongrowing cow with calf. The first of these optimal sizes falls within the range of body weights for a cow's first reproduction presented above, and the second just misses. This indicates that cows begin to reproduce only when they have first maximized the energy available to them. Furthermore, it is interesting that the average weight asymptotically approached by cows with calves is 330 kg and by barren cows, 370 kg (Skuncke; vide Peterson, 1955). These weights are very close to the optimum sizes predicted, indicating that growth either terminates or is negligible after the optimum is reached. The reason for this delay in female reproduction, until net energy intake is maximized, will be analyzed in a later paper.

A cow's ability to twin. At no point in Fig. 4 does the NE line for cows with twins intersect the M_R line for a cow with a single calf. This indicates that a cow cannot successfully raise twins unless she was barren the previous year and had stored an excess of sodium from aquatic feeding. The above result explains why it is beneficial for barren cows to consume a quantity of aquatics that is greater than the amount required to supply the necessary sodium. This assertion could be tested if we had information on whether or not cow moose can successfully raise twins in consecutive years, but this information is not available. Also, this result explains why cows that bear twins generally lose one of the young in the first two months after parturition.

Optimum body size for bulls and their size at first reproduction. Bull moose present an anomaly. The optimum bull size is 250 kg, which is smaller than that predicted for cows. But, it is a well-known fact that bulls are larger than cows, a case of sexual dimorphism. As is characteristic of all cervids (Trivers, 1972), bulls compete with each other for mates. Knorre (1959) provides data which indicate that the bull which physically intimidates its opposition achieves a greater number of mates. Therefore, bulls may become larger than the optimum feeding size, as a result of sexual selection. This will be examined further in a later paper.

Bulls are known to become sexually active when they have attained a weight of 300 kg (Knorre, 1959), which is close to the optimum body size predicted in Fig. 3. This indicates that bulls may maximize their survival before they begin to reproduce, which is the same strategy employed by cows. In this case, however, maximum reproductive success does not accompany maximum net energy intake since bulls compete for mates and success depends upon the relative body sizes of the competitors. The fact that bulls on the average approach a weight of 450 kg (Skuncke; vide Peterson, 1955), which is larger than the size for optimal feeding, may be due to the above-mentioned sexual selection. Furthermore, they can achieve this size because their feeding constraints enable them to reach maximum weights greater than those of reproducing females (645 kg vs 514 kg; see next section).

Maximum body sizes for moose. It is interesting that bulls in Fig. 3 and cows in Fig. 4 show a second, higher intersection of the NE and M_R curves. The second point of intersection predicts a maximum weight, beyond which the moose is unable to satisfy its M_R requirements. This maximum is approximately 645 kg for bulls and 514 kg for cows with calves. The higher intersection for barren cows in Fig. 3 is ignored, since cows generally bear calves after they reach 300 kg in the wild. The upper limit for bull size compares favorably with the maximum recorded weight for a bull from Ontario, 630 kg (Peterson, 1955). Although there exist only a few records of cow moose weights, since hunters are generally concerned with the larger bulls, the largest female record found was 447 kg from Sweden (Skuncke; vide Peterson, 1955).

The trends observed for minimum, maximum, and optimum body sizes in a population are similar to Schoener's (1969b) hypothesis concerning body size selection for feeding. To determine the impact of food availability upon body size, food quality, or quantity, changes can be approximated by raising or lowering the M_R line, but keeping it parallel to the original function (see Schoener (1969a) for a detailed discussion of this technique). In this way, Schoener's (1969b) argument that as food diminishes in an animal's environment (M_R is raised) large consumers are selected against faster than small consumers is substantiated. This is predicted here, however, without making Schoener's (1969b) assumption that food for large animals is rarer than food for small animals.

Sensitivity of the Model to Perturbations

There exist two ways to test the model's sensitivity; vary the parameters to determine how the solution changes and apply the model to moose in a different environment. First, we can vary the constraint values (N_R , T_T , T_A , R) to see how they affect the solution for the energy-maximized diet, since this predicted diet was found to come closest to the observed moose feeding behavior. For simplicity, this sensitivity analysis will be restricted to the average moose model, the least complex case. Leaves and forbs will be combined into a single food class for convenience, since the two-dimensional optimization model is much easier to solve than the three-dimensional case (Figs. 5A-D). By simplifying this model, we find:

(1) A unit change in N_R creates a decrease of 4.95 g-dry wt in terrestrial consumption as N_R increases from the constraint used above (853 g) to 938 g. Any further intake of aquatics above 938 g will lead to the moose's failing to satisfy its energy requirements because of the rumen constraint. If N_R declines below the 853-g constraint used in the model the energy-maximized diet will not change since the linear programming solution is found at the intersection of the R and T_T constraint lines. Therefore, changes in N_R affect the problem (maintaining a biologically feasible solution) only in the range of 853 to 938 g (Fig. 5A).

(2) A unit change in T_T creates a change of 15.4 g-dry wt in terrestrial consumption until 938 g of aquatics is consumed (the greatest aquatic consumption still permitting M_R to be satisfied) or until the R , T_T , and N_R constraint lines all intersect at the same point, at which point T_T no longer acts as a constraint. Therefore, T_T can only vary over the range of 228 to 258 min and still have the model feasible (Fig. 5B).

(3) Changes in T_A are of little consequence, since it is much larger than the time required by a moose to satisfy N_R . Furthermore, if T_A were to enter into the problem (T_A equal to the time required to crop N_R), it would have to decrease by more than 55% (Fig. 5C).

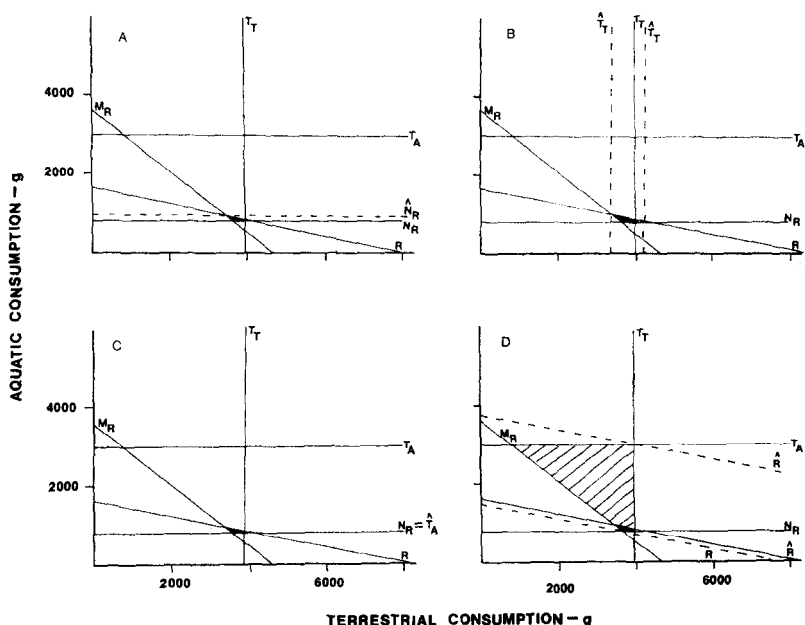


FIG. 5. Two-dimensional plots (aquatic plant consumption and terrestrial plant consumption; herbs and leaves combined; see text) of the diet linear programming constraints for an average adult moose are presented. In each graph one of the four constraints (N_R in (A), T_T in (B), T_A in (C), and R in (D)) involved in determining an energy-maximizing diet is allowed to vary until it no longer affects the solution to the model. The dashed lines represent the maximum variations in the constraint (noted also by a \wedge over the appropriate constraint symbol). The regions containing feasible solutions for the diet model, when the constraints are unaltered, are darkened, while any additional feasible diets arising from the variations in the constraints are denoted as striped regions (see the section on the model's sensitivity for a complete discussion).

(4) A unit change in R leads to a change of 0.05 g-dry wt in aquatic consumption, as long as the aquatic consumption is greater than N_R , since the T_T - R constraints appear to determine the energy-maximized diet. However, when the N_R - R constraints determine the diet, terrestrial consumption changes by 0.25 g-dry wt/g-wet wt in R (Fig. 5D).

Variations in the N_R and T_T constraints lead to the greatest per unit change in the diet. However, if N_R and T_T are only allowed to vary separately, their total maximum effect on terrestrial consumption is an 11% decrease with an increase in N_R or a decrease in T_T and a 1% increase when T_T is increased. Although changes in R have the smallest per unit effect on terrestrial consumption, variation in this constraint has the greatest potential cumulative effect since R can vary over a very large range. Of all the constraints, R is the only one for which we have confidence intervals (95%) and these (± 2513.00)

rule out this constraint from any important variation at any given body size (variation in terrestrial consumption less than 16%).

As mentioned above, the confidence intervals for the constraint values are unknown, except for R . If we could vary the constraints within their confidence intervals, as was done above for R , a much better picture of sensitivity could be achieved. In this way, we could also determine the maximum deviation from the model's predictions if all of the constraints varied simultaneously. Nevertheless, the above discussion does provide us with a feel for the accuracy of the model's predictions. Finally, variations in the constraints appear to maintain the energy-maximizing strategy as the better description of the observed diet, except when the energy-maximizing and time-minimizing solutions are the same.

Changes in the parameters in the constraint equations, other than the constraint values, would have to be larger than the confidence intervals (95%) presented in the data section before any large changes in the predicted diet would be observed. Therefore, I conclude that, although a linear program model could be very sensitive to parameter changes; this model's parameter values, given their confidence intervals, are unlikely to account for large deviations in the predicted diets.

The second means of testing the model is to use it to predict an average moose's diet in a different environment. This was done for an Isle Royale forest bordering Lake Superior, with a canopy dominated by *Abies balsamea* and *Betula papyrifera*. In this environment, moose need only consume 172 g-dry wt of aquatics each day to satisfy their sodium demand (N_R), since the aquatics average 0.0146 g of Na^+ /g-dry wt (Belovsky, 1977). These aquatic plants, however, are bulkier ($B_1 = 92.1$ g-wet wt/g-dry wt) and require more time to crop ($t_1 = 0.21$ min/g-dry wt) than those already used in the model (Belovsky and Jordan, 1978). Solving the model for deciduous and aquatic consumption, since forb feeding in this forest was not studied (Belovsky and

TABLE VI

The Predicted and Observed Diets for an Average Isle Royale Moose in an Environment Different from the First Examined^a

	Energy maximizer	Time minimizer ^b	Observed
Aquatics	172	—	161
Deciduous leaves	4267	—	4609

^a All food consumption values are presented in terms of g-dry wt/day, and forbs and leaves are combined into a single class, terrestrials.

^b There exists no solution to the time-minimized diet, since even the energy-maximized diet is 499 kcal/day less than M_R .

Jordan, 1978), we find that there exists no solution to the time-minimized diet, since even the energy-maximized diet is 499 kcal/day less than M_R . The inability of the predicted diets for this new area to supply a moose's M_R requirements may arise from applying the original parameter values to this different forest. One suggestion is that the moose have more time to feed in this forest bordering Lake Superior because of the cooler summer climate; this would provide a greater daily terrestrial consumption. Another factor leading to this discrepancy could be that herb feeding was not studied in this region. Nevertheless, the energy-maximized diet is not significantly different from the observed food intake ($\chi^2 = 3.25$, $P \leq 0.08$) (Table VI). Therefore, it appears that the model succeeds in predicting a moose's diet in a completely different environment, which suggests that we initially chose the important constraints for moose feeding.

CONCLUSION: RELATION OF THIS MODEL TO OTHER FORAGING MODELS

This paper demonstrates that a large generalist herbivore, the moose, feeds in a manner which is predicted by an optimization model. Using a series of constraints imposed upon the animal's feeding capabilities, one may predict a precise optimal diet combination and compare it to the observed behavior of the animal. This approach differs from those taken in several other feeding strategy analyses. In contrast to the Freeland and Janzen (1974) argument, the feeding of a generalist herbivore can be analyzed without reference to toxins, innate desires for diet diversity (this will be further substantiated in a later paper), and specific coevolutionary interactions. This enables one to treat the herbivore's feeding in a precise, rigorous manner, comparable to the carnivore models (Schoener, 1969a,b, 1971; MacArthur and Pianka, 1966; MacArthur, 1972; Cody, 1974; Emlen, 1966; Pulliam, 1974). However, these carnivore models assume simultaneous searches for all food classes, which does not occur for the moose and most likely many large herbivores. The ability to use linear programming for such herbivores is a result of the separate search patterns for each food class. Finally, although Westoby (1974) suggests the use of linear programming in the analysis of herbivore feeding, he assumes that the combination of foods in the diet needs to be optimized with respect to many nutritional constraints; whereas the model presented in this paper seems to predict diets very close to those observed with much less complexity.

The model differs in other fundamental ways. First, whereas most studies of optimal feeding attempt to demonstrate instantaneous maximization of energy intake per unit time or the minimization of feeding time, they do not attempt to predict a specific optimum diet and compare it to a specific observed diet (Willson, 1971, 1972; Emlen and Emlen, 1975; Wolf *et al.*, 1971, 1972; Menge, 1975; Rosenzweig and Sterner, 1970; Jenkins, 1975; Charnov, 1976). The

only other study that successfully predicts an animal's diet is that of Werner and Hall (1974) for bluegill sunfish. Another attempt to predict an animal's diet by Emlen and Emlen (1975), using domestic rats, was not very successful. Furthermore, the instantaneous optimization assumption in these studies is supplanted in this paper by the moose's ability to "know" future nutritional requirements (e.g., sodium and energy) and to seek an optimal diet in accord. In this respect, the model is similar to Katz's (1974) optimization of feeding behavior in *Quelea*. Finally, whereas many feeding models have been a simple maximization or minimization of feeding time, this model utilizes the structural constraints of the animal to define optimal feeding, which limits the range of potential solutions.

The model goes beyond the explanation of the feeding behavior of moose to predict the evolutionary factors controlling body size at weaning, first reproduction, and optimal feeding. This indicates that evolution has selected these traits in response to feeding considerations and other factors (e.g., sexual selection for bulls). Therefore, one might suggest that moose could wean earlier and have earlier reproduction if the evolutionary process had "designed" an animal with a larger rumen processing capacity. But, we must also remember that the food in the rumen must be attained at an expenditure of time, limiting other activities and increasing the risk of predation and inadequate thermoregulation. Even more important, one must recall that the food in the rumen increases the animal's mass without contributing to the power output in movement, increasing the chances that a predator can run down the moose. Therefore, in these new circumstances, the moose might become a time minimizer and counter the increased energy-intake capabilities.

The model may be criticized since it makes no pretense to explain seasonal changes in diet or the selection of individual plant species within each food class. These questions, however, will be dealt with in later papers. Modeling of a moose's selection of plant species composing each food class can be accomplished using the more standard instantaneous optimization approach of contingency models. Nevertheless, I believe that we should be encouraged by the ability of a simple model to predict an animal's consumption of major food types.

APPENDIX: RUMEN PROCESSING CAPACITY

The rumen is known to be the location of food plant fermentation by symbiotic microorganisms in ruminants, but many of the particulars of rumen functioning are still uncertain. Using the available literature, the model employs several assumptions to include the daily rumen processing capacity.

Two aspects of rumen functioning are fairly well understood. First, it requires time for the symbiotic microorganisms in the rumen to ferment plant tissues,

which indicates that there exists a positive correlation between the time food remains in the rumen and its breakdown, digestion (Hungate, 1966). Second, the passage rate of food out of the rumen to a large extent depends upon the specific gravity and size of food particles, which is determined by the tissue itself, state of digestion, and amount of mastication (Baile and Forbes, 1974; Blaxter, 1962). The particle size also affects the rate of fermentation through surface-to-volume considerations (Blaxter, 1962; studies of particle size versus digestion over time). Therefore, it appears that passage rate through the rumen and the digestion of foods are in a trade-off situation. One way, however, that a ruminant can increase both processes is to masticate foods very well to reduce the particle size, a method that includes rumination (regurgitation and remastication of foods already ingested). This suggests that for each type of food plant tissue a ruminant should have an optimal passage rate and digestion combination that depends to a certain extent upon a minimum mastication-rumination investment.

The passage rate of food and the volume of the rumen organ determine the daily rumen processing capacity referred to in the model. The filling of this capacity in the model is assumed to depend upon the wet weight of food ingested. Although there are several studies of the effect of food water content on intake, most indicate that there is no effect (Pettyjohn *et al.*, 1963; Davies, 1962; Thomas *et al.*, 1961), until the food water content exceeded 72% (Duckworth and Sherlaw, 1958; Thomas *et al.*, 1961). At water contents greater than 72%, it was found that intake was controlled by the food's wet weight. In the model, we are dealing with foods that are a minimum of 70% and a maximum of 90% water.

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