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S. Payne

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1973 PROGRESS REPORT

TERRESTRIAL MODEL: ANIMAL PROCESSES (VERSION III)

S. Payne  
Utah State University

US/IBP DESERT BIOME  
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## COMPARATIVE DESCRIPTION OF ANIMAL MODELS

### GENERAL ECOSYSTEM MODEL

The ecosystem has been partitioned into three main subsystems; the plant, animal and soils communities. The animal community models presented here are designed to be used in conjunction with the models constructed concurrently on soils (Radford, 1973) and on plants (Valentine, 1973) for the US/IBP Desert Biome general purpose modeling effort. The computer representations are to be used with the organizing program designed by Goodall and Gist (1973).

A set of models has been developed for each community, each model varying in the sophistication and complexity of its biology. For example, leaf abscission in the simplest model of the plant community (Version I) occurs at a rate constant in time, independent of the species of the plant. The plant model which is just one step up in complexity (Version II) describes leaf abscission as occurring at a constant rate in time but specific to the species of plant. Leaf abscission in Version III of the plant model occurs at a rate that is plant species-specific. The rates are constant for the duration of each season of the year (a season being a time period defined within the plant model), but may differ from season to season. Other processes have been conceived in different ways, so that one plant model may be extremely simple (most processes being "black-boxed"), another a little more complex, and a third may consider some processes in an extremely complex, physiologically-based manner (see Valentine, 1973, for further discussion on the levels of resolution of the plant community models). This technique of construction of the set of plant models has also been applied to the animal and soils models.

Selecting a model for each of the three subsystems and combining them generates an ecosystem model. Which model is chosen for each subsystem depends on the purpose of the simulation. For example, if the investigator is interested in some aspect of the soil community which is apparently unrelated to the animal community, at least for the time period being considered, he should implement the simulation with a simplified animal model that does not provide and need detailed information on the actions and life history of the animals. The resolution of the plant model needed may be high, so that a relatively complex and detail-structured plant model may be called for. To verify that the animal community is indeed unimportant in this investigation, the simple animal model may be replaced by a more biologically explicit version and the outputs of both simulations compared. Interchangeability of these models is possible due to the use of common state variables, inputs and outputs.

The set of state variables incorporated in the models is shown in Table 1. The variables most frequently used in the animal models represent subcompartments of the total

amounts of live vegetation, shed seeds, dead organic matter and litter, soil organic matter, animals, and animal numbers present in the system. Consider the state variables describing the biomass of live vegetation. This total amount can be subdivided by vegetative groups (plant species, functional groups, structural groups, age-classes, etc.), and further by plant organs. The amounts in these subcompartments can then be subdivided by chemical components. Each of these cross-classified compartments is a state variable concerned with the live vegetation. Thus, for example, there may be state variables representing the amounts of nitrogen in the leaves of grasses, and carbon in the young stems of *Lycium andersonii*. The biomass of shed seeds can be subdivided by seed species and "seed horizons" (layers of soil which partition the non-uniform vertical distribution of seeds within the soil and are not necessarily the same as the soil horizons). The amounts in these subcompartments can then be partitioned into amounts of chemical components. For example, there may be compartments representing the amounts of nitrogen in the grass seeds in seed horizon one (0-10 cm), and phosphorus in the *Lycium* seeds in seed horizon three (30-70 cm). The amount of the dead organic matter and litter (hereafter referred to as organic debris) can be compartmentalized into different categories and chemical components. These state variables generally include animal excreta, soft parts of animal carcasses and skeletons. Also included may be categories such as standing dead, herbaceous litter and dead roots -- material that was once part of living plants and that will now undergo decomposition. Generally, decomposer activity occurs at different rates depending on the type of organic debris. Two organic debris state variables are the amounts of nitrogen in standing-dead litter, and carbon in animal excreta. Soil organic matter may be partitioned into the amounts of each chemical component in each soil horizon. For example, there may be a compartment representing the amount of calcium in the soil organic matter of soil horizon four (40-120 cm). The animal biomass is subdivided into animal groups (see "Comparison of Animal Models, Common Elements") and further into chemical components. The population of animals is subdivided into groups. Hence, there are many cross-classifications available to enable the investigator to describe the system.

The predicted values of the state variables at the end of any time unit are a result of the actions of one, two or all three submodels, depending on the state variable. Table 1 summarizes the actions of the models on the values of the state variables: no one particular level of model resolution is described in this table; it is a general overview of the interactions that occur in some or all of the subsystem models. The processes involved in the animal models will be discussed in detail later ("Structure and Processes").

Table 1. State variables and interacting processes

State variables			Direct actions of models which affect resultant state variable values		
FORTTRAN*	Math**	Definition	Plant	Soils	Animals
CVEG (I,J,K)	$X_{1sgf}$	amounts in live vegetation compartments -- vegetation groups x organs x chemical components	carbon fixation, mineral uptake, organ abscission, leafing out, germination, translocation, fruit maturation		consumption
SEED (I,JH,K)	$X_{2pnf}$	amounts in shed seed compartments -- seed species x "seed horizon" x chemical components	seed shedding, death, germination		consumption
CLIT (L,K)	$X_{21df}$	amounts in dead organic matter and litter compartments -- organic debris categories x chemical components	organ abscission, root death	conversion of one type of debris to another, decomposition, erosion, deposition, crust growth, respiration, loss of nitrogen	consumption, excretion, death
CORG (JH,K)	$X_{22hf}$	amounts in soil organic matter compartments -- soil horizons x chemical components		deposition, erosion, loss of nitrogen, mineralization, decomposition, respiration	consumption, excretion of soil animals
CBIOM (N,K)	$X_{11cf}$	amount in animal compartments -- animal groups x chemical components			consumption, birth, death, growth, metabolism, emigration, immigration, man-management
CMIN (JH,K)		amount in inorganic soil material compartments -- soil horizons x chemical components	uptake	deposition, erosion, nitrogen fixation, nitrogen losses, rain, dust, soil organic matter, decomposition, leaching, uptake, mineralization, solution flows	
POP (N)	$X_{12c}$	populations of animal groups			birth, death, immigration, emigration, man-management

\* FORTRAN symbols used in computer representations of models

\*\* mathematical symbols used in the section "Structure and Processes"

Table 1, continued

State variables			Direct actions of models which affect resultant state variable values		
FORTTRAN*	Math**	Definition	Plant	Soils	Animals
SNOCOV		weight of snow cover		snowfall, snow blowing, melting	
FREWAT		depth of free water over soil surface		rain, runoff/on, evaporation, percolation, snow absorption	
WATABS (JH)		amount of water in each soil horizon		percolation, evaporation, artificial input/output, upward flows	
KOVER (I)		proportion of ground covered by each plant species	biomass of each plant species		
AGAIN (K,P)	$X_{01rf}$	net change in the system -- chemical component x channel (atmosphere, surface flow, subsoil flow)	net carbon fixation	nitrogen fixation, volatilization, denitrification, respiration, decomposition, carbon fixation by crust, dust, deposition, erosion	metabolism
EROD (P)		accumulated net gain or loss of inert particles through each channel		dust, erosion, runoff	
H2O (P)		net gain or loss of water through each channel		rainfall, snowfall, snow blowing, evaporation, evapotranspiration, runoff/artificial input/output, drainage to subsoil	

\* FORTRAN symbols used in computer representations of models

\*\* mathematical symbols used in the section "Structure and Processes"

## COMPARISON OF THE ANIMAL MODELS

### COMMON ELEMENTS

Three models have been designed (and implemented) to simulate the dynamics of the animal community. All are time-varying models and are deterministic. The areas they simulate are assumed to be spatially homogeneous. Animal I is the only linear (within limits) model; the more complex Animal II and III are non-linear.

The models were built on a physiological basis, recognizing protein, fat and structural tissues. In the model, chemical elements are tracked through the interactions between the animals, plants, soil, decomposers, and environment. A maximum of six chemical elements are provided for in the computer programs of the models. Three elements were used in the simulation; nitrogen, ash and carbon. Because of the types of tissues distinguished with the models, carbon was divided into three categories; protein carbon, reserve carbon and structural carbon. Protein carbon makes up the proteinaceous material used in metabolic activities; reserve structural carbon is from tissues such as bone, ligaments, hair, and teeth and regarded as unusable in metabolism. Labile fats in such tissues are not included in the structural tissue compartment. However, protein fibers in the bone (collagen, for example), are included in the compartment. Subsequent reference to "protein tissue" or "protein of animals" will imply a tissue composed of protein carbon and its associated mineral and non-carbonaceous elements (nitrogen, sulphur, etc.), and will exclude the material in the structural tissues. It is actually the protoplasm of cells (excluding lipids and carbohydrates) which can be catabolized. "Diet protein," on the other hand, may contain protein from structural tissues of prey animals, as well as protoplasm of cells which can be catabolized.

The classes of animals to be used in a simulation can be varied according to the needs of the experimenter and the data available for input. On the most detailed level, a species of animal may be chosen and age cohorts specified. For example, three groups may be *Dipodomys merriami* adults, young adults and juveniles. These age cohorts are entirely optional, and could be replaced by the single category of *Dipodomys merriami*. If this is too detailed for the purpose at hand, "kangaroo rats" may be a suitable class. With still more generalization, "rodents" may be the class used in the simulation. No matter what name is given, the rates that correspond to the animal grouping must be appropriate. For example, the consumption rate for *Dipodomys merriami* should be that of that species of animal, while the consumption rate for "kangaroo rats" should be an overall rate that is determined from the species of kangaroo rats grouped under that title.

Each model simulates population numbers and biomasses in terms of the chemical components, per unit area, for each

class of animal defined in the system. Figure 1 is a simple diagram of the major processes involved. The amounts and composition of animal organic debris, such as skeletons and soft parts of carcasses, and excreta, are input to the soils submodels of the general ecosystem model. Interaction with the plant model occurs through animal action on the vegetation and seeds present. Respiration adds carbon dioxide to the environment. The process of growth increments the biomass of the animals within the animal compartments. Reproduction decreases the adult biomass and increases the biomass and numbers of the young. The more advanced models involve processes not included in this general overview.

As mentioned previously, the state variables of every module of the general ecosystem model are the same (Table 1). The parameters that are required for each model vary extensively between models and will be discussed later.

### CONTRASTING ELEMENTS

Because the models were built with different objectives (described below), different parts of the animal community are emphasized in each with varying degrees of mathematical complexity and biological realism. Table 2 is a summary of the major differences between the models.

ANIMAL I was constructed with the objective of providing a gross effect of animal "grazing" on the ecosystem, for simulations of very short or very long time periods. It simulates the action of the animal community as a whole -- there is no differentiation between animal classes. The only advantage in specifying animal classes in a simulation would be to obtain a list of these classes in the output and thus record the animals that were included in the simulated system. The parameters used are not animal group-specific but are considered constant for the community. That is, each parameter has a single community value. For example, the metabolic rate is the same for each class of animal in the simulation and equals the value of the metabolic rate of the whole community per unit biomass. These parameters are considered constant with respect to time. No environmental factors are considered explicitly. For simulations of a short time period, the values of the parameters should reflect the climate and season of this period. For simulations of a long time period, the parameters should have values averaged over the years. Because of the lack of detail in the structure of the animal community as simulated, the model is intended to be used in the whole ecosystem model when the emphasis and interest of the investigation is on the plant or soils compartments. The storage space required for the computer model and the execution time for one pass through the model are small. This is advantageous when the model is coupled with the larger, more complex soils and/or plant models. It allows inclusion of the animal community at small cost to the total operating time and storage space.

The objective of ANIMAL II is to simulate the effects of feeding by different animal groups on the ecosystem. ANIMAL II is more detailed than Version I in that it distinguishes between animal classes, the biomass and numbers of each class being predicted grossly. However, because there is no provision for transfer from one age-group to another, cohorts should not be used, unless the simulated time period is sufficiently short so that transfers do not occur. The parameters are specific to the animal groups in the system, and are time-invariant. Environmental factors are not explicitly used. As for ANIMAL I, this model is intended to be used over very short or very long time periods. In contrast to ANIMAL I, however (as the parameters are specific to each class of animal, and thus more detail is present in the animal community as simulated), ANIMAL II may be of use when it is necessary or of interest to include and manipulate the feeding

dynamics of particular classes of animals as opposed to the community as a whole. The storage space and execution time compare with the other models.

The objectives of ANIMAL III are to simulate the seasonal impact of different animal groups on the ecosystem, and to predict the biomass and numbers of each animal group, reflecting their seasonal changes and nutritional status. The impact could be due to the feeding of the animals or their presence; for example, trampling of vegetation. ANIMAL III thus elaborates on II in that seasons are defined for each class of animals throughout the year. The animals are grouped as desired with time periods delineated during the year, detailing their life history. The parameters are animal group-specific and season-specific. For example, for ground beetles, an overwintering season may be defined. The parameters denoting ground beetle respiration during this

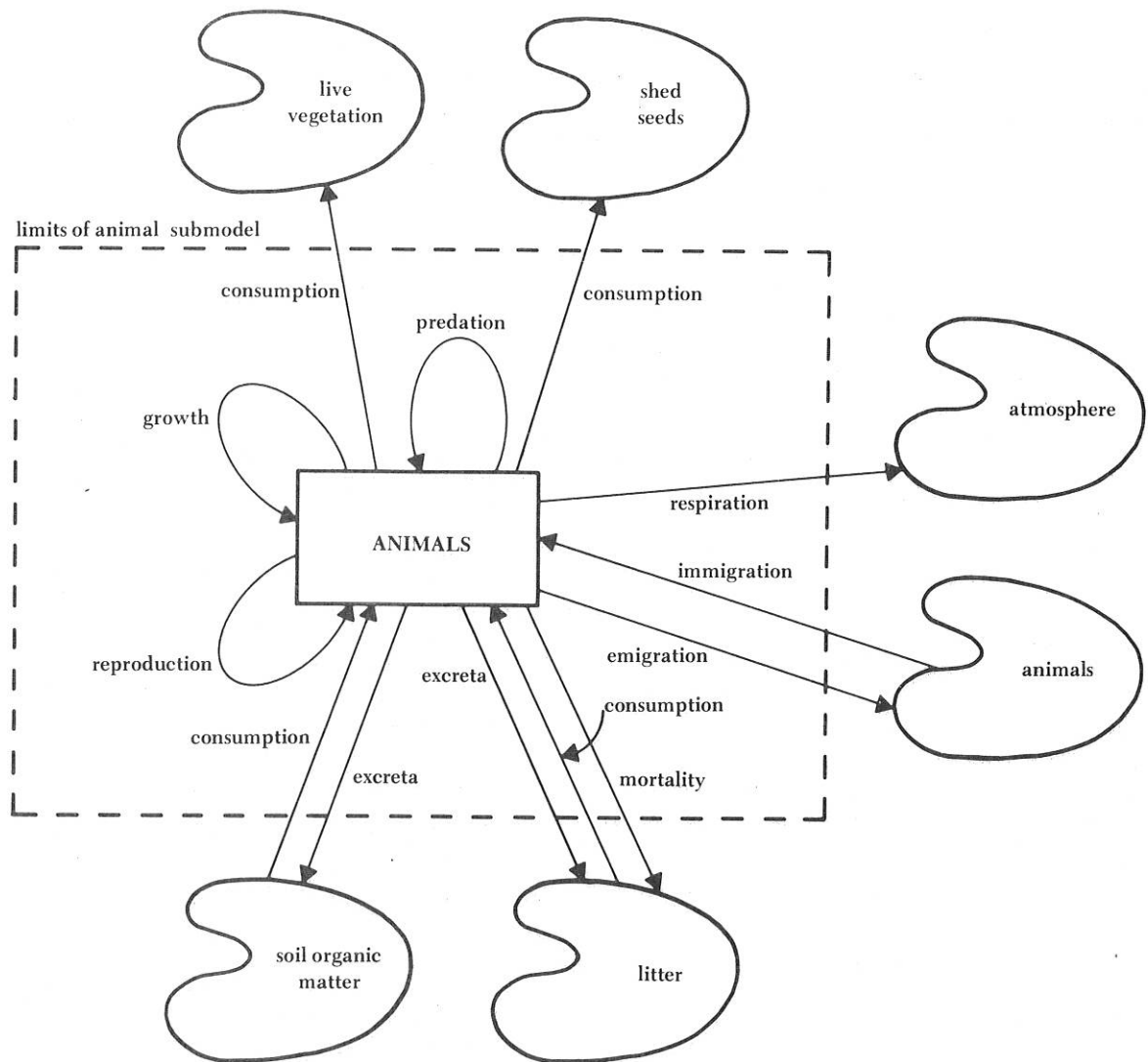


Figure 1. Processes in the animal models.

season will have a different value from that during the active season. Thus temporal factors are explicitly modeled and environmental factors, implicitly modeled.

Version III also included two sets of state variables not in I or II; the biomass of "milk" and "wool" of each animal group subdivided into chemical constituents. "Wool" biomass was specified to provide for inclusion of domestic animals (especially sheep) in the simulation. A large part of the food intake of such animals may go into wool; therefore, monitoring such biomass may be valuable. The term "wool" as used here denotes a product of potentially all age-groups of animals which is periodically shed or removed, including, for example, the wool of sheep and exoskeletons of insect instars. "Milk" biomass was included as an elaboration of the mechanics of ANIMAL II to produce more accuracy in the estimation of biomasses. The term "milk" denotes a product of mature animal groups, manufactured and stored within their bodies for the feeding of juvenile animal groups and including, for example, the milk of mammals and brood food of bees (Chapman, 1969, p. 36). "Milk" provides a high concentration of protein and reserve tissues (none is wasted by the juveniles) and can be assimilated to a high degree. Thus the effect of "milk" as a food for juveniles is considerable. The production of "milk" by the adult group can be costly (Maynard and Loosli, 1969, p. 518). Consideration of these factors prompted the inclusion of the "milk" state variables. Energy costs and equivalents are

explicitly used in this model in contrast to II and I.

This model can be used in simulations of any time period, up to the point at which successional changes in the animal community become too important to ignore. It is expected to be used when it is necessary to include the animal community and obtain seasonally varying demographic and energetic values that are of reasonable accuracy. Since environmental factors are not explicitly used (once the seasons have been defined with the corresponding parameters), the specifications of the whole simulation period have been determined, except as the food sources may vary as predicted by the other submodels.

The models may also differ in the way that each process is handled. This will be apparent as each process is discussed individually.

### STRUCTURE AND PROCESSES

For each process a verbal and mathematical description is given. For explanation of the mathematical symbols refer to Goodall and Gist (1973). If, in a description of one model, a symbol representing a **temporary variable** or **parameter** is identical to a symbol in a description of another model, the meaning of the symbols is not necessarily the same. Because of the large number of symbols used, duplication has been unavoidable. Within a model description, however, each

Table 2. Comparison of animal models

Version	Species/cohort differentiation	Time-varying parameters	Parameters dependent on environmental variables	Simulation time	Objectives and use
one	no	no	no	very short, very long	supportive role; to supply average effect of animal community without detailed input requirements
two	yes	no	no	very short, very long	supportive role; to supply average effect of animal community (differentiated into groups) without detailed input requirements
three	yes	yes	no	years	supportive role; to supply seasonal effect of animal community and to predict seasonal changes in animal biomass composition and population



mathematical symbol has a unique meaning. The symbols representing the state variables, the rates of change of the state variables, prior and posterior subscripts are common to all descriptions. The rates of change of state variables with respect to time are indicated in Goodall and Gist (1973) by "dots" above the state variable symbol. This is not meant to imply that the equations are differential equations -- the model consists of difference equations. This notation is used for brevity.

#### FEEDING

There are five sources of food -- live vegetation, shed seeds, dead organic matter, soil organic matter, and animals. These foods are further compartmentalized as described in Table 1 and in the section "General Ecosystem Model."

#### ANIMAL I

There is a maximum postulated consumption level for the animal community, per time unit, being the sum of the maximum postulated consumption levels of the five sources of food during the time unit. These levels roughly represent the proportion of herbivores, seed eaters, detritivores, and carnivores in the system as simulated. The form of the feeding relationships (if there is sufficient food present) is

$$Y = a\chi$$

where  $\gamma$  is the amount of a food item consumed per time unit,  $a$  is a constant, and  $\chi$  is the animal biomass. These linear (within limits) feeding relationships of ANIMAL I are adequate when the food sources are abundant (DeAngelis, Goldstein and O'Neill, n.d.). Thus an assumption of this model is that the food sources throughout the simulation will not be scarce. If the amount of any of the food sources is less than the maximum postulated consumption level for the populations, the animals will not compensate by eating more of another food source.

For live vegetation, the actual amount consumed per unit animal carbon is a constant (input parameter  $P_1$ ), given that sufficient live vegetation is present during that time unit. If vegetation is insufficient, all the live vegetation is consumed, and there is no compensation for the deficiency by eating of another food source. All compartments of the live vegetation are considered to be equally acceptable to the animals, and so the total amount of vegetation consumed is distributed among the vegetation compartments in proportion to their biomass. Figure 2 is the graph of the relationship.

$$\begin{aligned} Z_1 &= \text{amount of carbon consumed from live vegeta-} \\ &\quad \text{tion per time unit} \\ &= P_1 \cdot Z_3 \text{ if } P_1 \cdot Z_3 \leq Z_2 \\ &= Z_2 \text{ if } P_1 \cdot Z_3 > Z_2 \end{aligned} \quad (I-1)$$

where  $Z_2$  is the amount of carbon in live vege-  
tation ( $\sum_s \sum_{f \in C} X_{1sgf}$ )

and where  $Z_3$  is the amount of carbon in the  
animal community ( $\sum_c \sum_{f \in C} X_{1,cf}$ )

$$\begin{aligned} Z_{4sgf} &= \text{amount of chemical constituent } f \text{ consumed} \\ &\quad \text{from vegetation compartment (s,g), per time} \\ &\quad \text{unit} \\ &= (Z_1/Z_2) \cdot X_{1sgf} \end{aligned} \quad (I-2)$$

$$H\dot{X}_{1sgf} = Z_{4sgf} \quad (I-3)$$

For shed seeds there is a maximum postulated consump-  
tion level of seeds from each seed horizon per time unit, per  
unit animal carbon -- input parameters  $P_{3n}$ . The actual  
amount consumed equals this maximum, providing suffi-  
cient seeds are present in that horizon. If not, the seeds from  
that horizon are all consumed and the animal does not  
compensate for the deficiency. Figure 3 shows the form of  
the relationship.

$$\begin{aligned} Z_{5n} &= \text{amount of carbon consumed from shed seeds in} \\ &\quad \text{seed horizon } n \text{ per time unit} \\ &= P_{3n} \cdot Z_3 \text{ if } P_{3n} \cdot Z_3 \leq Z_{6n} \\ &= Z_{6n} \text{ if } P_{3n} \cdot Z_3 > Z_{6n} \end{aligned} \quad (I-4)$$

where  $Z_{6n}$  is the amount of carbon in seeds of  
seed horizon  $n$  ( $\sum_p \sum_{f \in C} X_{2pnf}$ )

$$\begin{aligned} Z_{7pnf} &= \text{amount of chemical constituent } f \text{ consumed} \\ &\quad \text{from shed seed compartment (p,n) per time} \\ &\quad \text{unit} \\ &= (Z_{5n}/Z_{6n}) \cdot X_{2pnf} \end{aligned} \quad (I-5)$$

$$H\dot{X}_{2pnf} = Z_{7pnf} \quad (I-6)$$

For organic debris, there is a maximum postulated  
consumption level for each category per unit animal carbon  
per unit time (input parameters  $P_{4d}$ ). As for live vegetation  
and seeds, the actual amount consumed equals this  
maximum providing sufficient vegetation is present in the  
category. If not, all that type of organic debris is consumed  
and the animal goes without the deficit. Figure 4 shows the  
relationship.

$$\begin{aligned} Z_{8d} &= \text{amount of carbon consumed from organic} \\ &\quad \text{debris category } d, \text{ per time unit} \\ &= P_{4d} \cdot Z_3 \text{ if } P_{4d} \cdot Z_3 \leq Z_{9d} \\ &= Z_{9d} \text{ if } P_{4d} \cdot Z_3 > Z_{9d} \end{aligned} \quad (I-7)$$

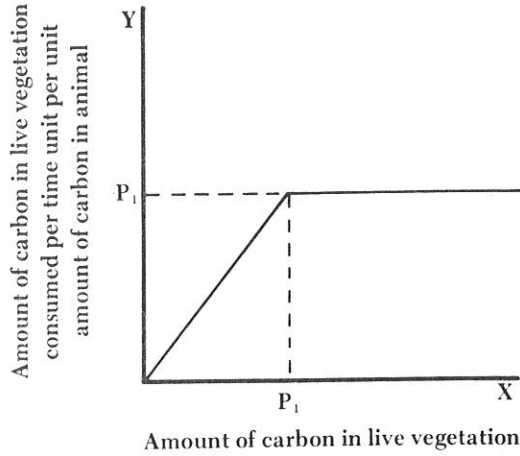


Figure 2. Live vegetation consumption (ANIMAL I).

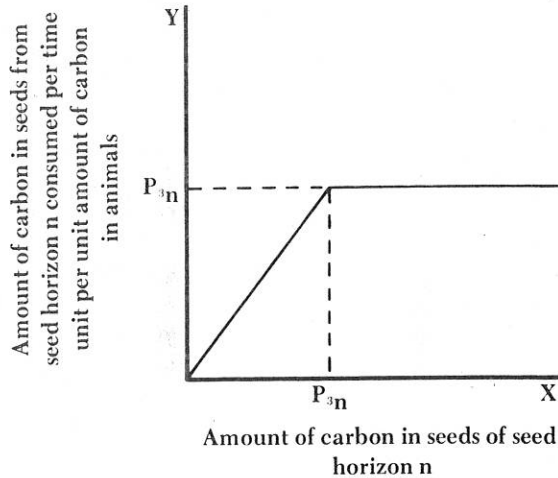


Figure 3. Shed seed consumption (ANIMAL I).

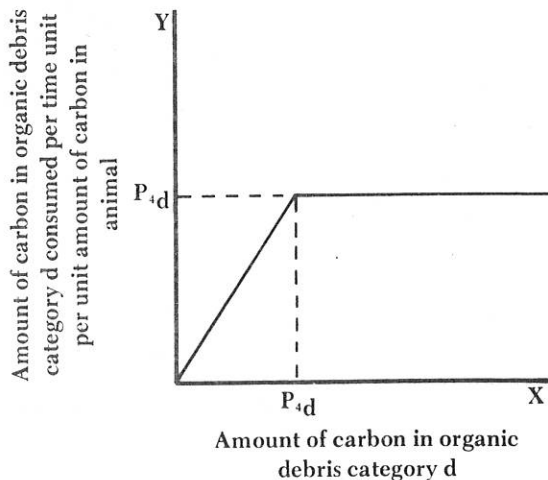


Figure 4. Organic debris consumption (ANIMAL I).

where  $Z_{0d}$  is the amount of carbon of organic debris category  $d$  ( $\sum_{f \in C} X_{21df}$ )

$$\begin{aligned} Z_{10df} &= \text{amount of chemical constituent } f \text{ consumed} \\ & \text{from organic debris category } d, \text{ per time unit} \\ &= (Z_{8d}/Z_{0d}) \cdot X_{21df} \quad (\text{I-8}) \end{aligned}$$

$$H\dot{X}_{21df} = Z_{10df} \quad (\text{I-9})$$

The food source of soil organic matter is handled as for vegetation, shed seeds and organic debris, with maximum postulated consumption levels specified ( $P_{5h}$ ) for the soil organic matter in each soil horizon.

$$\begin{aligned} Z_{11h} &= \text{amount of carbon consumed from soil organic} \\ & \text{matter in soil horizon } h \text{ per time unit} \\ &= P_{5h} \cdot Z_3 \text{ if } P_{5h} \cdot Z_3 \leq Z_{12h} \\ &= Z_{12h} \text{ if } P_{5h} \cdot Z_3 > Z_{12h} \quad (\text{I-10}) \end{aligned}$$

where  $Z_{12h}$  is the amount of carbon in the soil organic matter of soil horizon  $h$  ( $\sum_{f \in C} X_{22hf}$ )

$$\begin{aligned} Z_{13hf} &= \text{amount of chemical constituent } f \text{ consumed} \\ & \text{from each soil organic matter compartment } h \\ & \text{per time unit} \\ &= (Z_{11h}/Z_{12h}) \cdot X_{22hf} \quad (\text{I-11}) \end{aligned}$$

$$H\dot{X}_{22hf} = Z_{13hf} \quad (\text{I-12})$$

With carnivores, only the soft parts of the animals are consumed -- the skeletons are added directly to the organic debris compartment. This simulates the passage of skeletal material through the animals without digestion. It also, of course, simulates action by predators which do not eat skeletons and consume only flesh. It is assumed here that the exoskeletons of invertebrates are totally indigestible, which is not necessarily true (e.g., Chapman, 1969, p. 30). The ratio of each chemical constituent in the soft parts of the body to the total amount of that chemical constituent in the animal is assumed constant (input parameter  $P_{6f}$ ), and thus the amount of each chemical constituent in the skeleton is calculable. The actual amount killed equals the maximum postulated predation level per unit animal carbon (input parameter  $P_{11}$ ). If the animal community as simulated has been divided into groups, each is considered to be an equally acceptable food source and so the total amount of animal prey is distributed among the prey groups in proportion to their biomass.

$$\begin{aligned} Z_{14} &= \text{amount of carbon in prey killed per time unit} \\ &= P_7 \cdot Z_3 \quad (\text{I-13}) \end{aligned}$$

$Z_{15cf}$  = amount of chemical constituent f in prey group c killed per time unit

$$= (Z_{14}/Z_3) \cdot X_{11cf} = P_7 \cdot X_{11cf} \quad (I-14)$$

$$p\dot{X}_{11cf} = Z_{15cf} \quad (I-15)$$

$Z_{16f}$  = amount of chemical constituent f in prey killed per time unit

$$= \sum_c Z_{15cf} \quad (I-16)$$

$Z_{17f}$  = amount of chemical constituent f in prey killed and consumed per time unit (soft parts of carcasses)

$$= Z_{16f} \cdot P_{6f} \quad (I-17)$$

$Z_{18f}$  = amount of chemical constituent f in prey killed and added to the organic debris skeleton category (d = 6) per time unit

$$= Z_{16f} - Z_{17f} \\ = p\dot{X}_{216f} \quad (I-18)$$

The sum of the consumptions of each food source is the intake of the entire animal community as simulated. The amounts eaten are decremented from the values of the relevant state variables at the end of the time unit. If the animal community has been divided into groups, the intake of the community is distributed among the groups in proportion to their biomass. Thus it is that each animal group is considered omnivorous.

$Z_{19c}$  = proportion of carbon in the community from animal group c

$$= \frac{\sum_{f \in C} X_{11cf}}{Z_3} \quad (I-19)$$

$Z_{20cf}$  = amount of chemical constituent f that is consumed by animal group c per time unit from non-animal food sources

$$= \left( \sum_s \sum_g Z_{4sgf} + \sum_p \sum_n Z_{7pnf} + \sum_d Z_{19df} + \sum_h Z_{13hf} \right) \cdot Z_{19c} \quad (I-20)$$

from equations I-2, 5, 8, 11, 19

$Z_{21cf}$  = total amount of chemical constituent f that is consumed by animal group c from animal sources per time unit

$$= Z_{17f} \cdot Z_{19c} \quad (I-21)$$

## ANIMAL II

The approach to this process is adapted from Goodall (1969). The form of the relationship is

$$\gamma = a \chi (1 - e^{-b\psi})$$

where  $\gamma$  is the amount of food consumed per time unit,  $a$  and  $b$  are constants,  $\chi$  is the animal biomass, and  $\psi$  is the amount of food available (Ivlev, 1961; Gallopin, 1971). For each animal group the input parameters dealing with the feeding process are the maximum postulated consumption level per unit animal carbon per time unit ( $P_{1c}$ , or "a" in the above relationship), the searching ability of the group ( $P_{2c}$ , or "b" in the above relationship), and the relative food preferences ( $P_{3sgc}$ ,  $P_{4pnc}$ ,  $P_{5dc}$ ,  $P_{6hc}$ ,  $P_{7yc}$ ).

Since the feeding preferences of each animal group are specified, there is recognition within the model of herbivores, granivores, detritivores, carnivores, and omnivores, unlike ANIMAL I. The "suckling" of juveniles can be approximated by specifying the "mother" group as the prey of the juvenile group, in the preference tables.

If the searching ability of the group is low (i.e.,  $P_{2c}$  is small), then the weighted sum of the amounts of the preferred foods (the weights being the preferences) must be high for the actual consumption level to be near the maximum possible. If the searching ability is high ( $P_{2c}$  is large) then the weighted sum can be lower and the consumption level still be near the maximum level. Figure 5 shows the relationship.

The food preferences are values obtained from field investigations and are factors which weight the amounts of each food item present during each time unit.

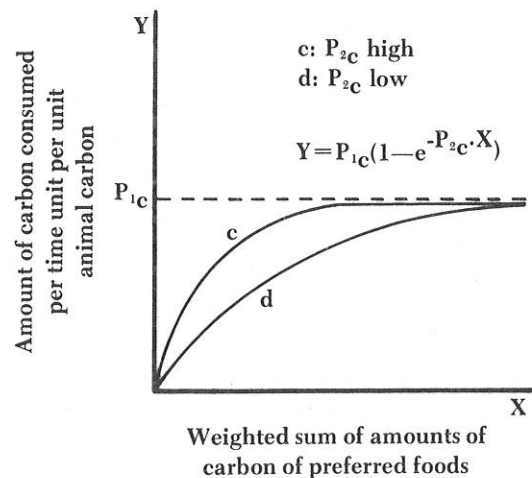


Figure 5. Total carbon consumption (ANIMAL II).

$Z_{1sgc}$  = weighted amount of carbon in plant group  $s$ , organ  $g$ , as related to consumer  $c$

$$= P_{3sgc} \cdot \sum_{f \in C} X_{1sgf} \quad (\text{II-1})$$

$Z_{2pnc}$  = weighted amount of carbon in seed species  $p$  of of seed horizon  $n$  as related to consumer  $c$

$$= P_{4pnc} \cdot \sum_{f \in C} X_{2pnf} \quad (\text{II-2})$$

$Z_{3dc}$  = weighted amount of carbon of organic debris category  $d$  as related to consumer  $c$

$$= P_{5dc} \cdot \sum_{f \in C} X_{21df} \quad (\text{II-3})$$

$Z_{4hc}$  = weighted amount of carbon of soil organic matter in soil horizon  $h$  as related to consumer  $c$

$$= P_{6hc} \cdot \sum_{f \in C} X_{23hf} \quad (\text{II-4})$$

$Z_{5yc}$  = weighted amount of carbon in prey group  $y$  as related to consumer  $c$

$$= P_{7yc} \cdot \sum_{f \in C} X_{11yf} \quad (\text{II-5})$$

$Z_{6c}$  = weighted amount of carbon in preferred food sources of consumer  $c$

$$= \sum_{sg} Z_{1sgc} + \sum_{pn} Z_{2pnc} + \sum_d Z_{3dc} + \sum_h Z_{4hc} + \sum_y Z_{5yc} \quad (\text{II-6})$$

from equations II-1, 2, 3, 4, 5

$Z_{7c}$  = amount of carbon in food sources "taken" per time unit by animal group<sup>1</sup>  $c$

$$= P_{1c} (1 - \exp(-P_{2c} \cdot Z_{6c})) \cdot Z_{8c} \quad (\text{II-7})$$

where  $Z_{8c}$  is the amount of carbon in consumers  $c$  ( $\sum_{f \in C} X_{11cf}$ )

If a preferred food source is present in a very low amount (or is absent) the consumer compensates by eating more of

the other preferred foods.

$Z_{9c}$  = factor to scale the weighted amounts of carbon of preferred foods so that their sum equals the total amount of carbon consumed per time unit, as calculated in II-7

$$= Z_{7c} / Z_{6c} \quad (\text{II-8})$$

$Z_{10sgc}$  = amount of carbon in plant compartment ( $s,g$ ) consumed by animal group  $c$  per time unit

$$= Z_{1sgc} \cdot Z_{9c} \quad (\text{II-9})$$

$Z_{11pnc}$  = amount of carbon in seed compartment ( $p,n$ ) consumed by animal group  $c$  per time unit

$$= Z_{2pnc} \cdot Z_{9c} \quad (\text{II-10})$$

$Z_{12dc}$  = amount of carbon in organic debris category  $d$  consumed by animal group  $c$  per time unit

$$= Z_{3dc} \cdot Z_{9c} \quad (\text{II-11})$$

$Z_{13hc}$  = amount of carbon in soil organic matter of soil horizon  $h$  consumed by animal group  $c$  per time unit

$$= Z_{4hc} \cdot Z_{9c} \quad (\text{II-12})$$

$Z_{14yc}$  = amount of carbon in prey group  $y$  taken by animal group  $c$  per time unit

$$= Z_{5yc} \cdot Z_{9c} \quad (\text{II-13})$$

Having determined the fraction of the amount of carbon from a food compartment that is consumed or killed, the fraction of the amount of each chemical constituent in that compartment that is consumed or killed is calculated. Each food compartment is decremented by the amounts taken by all animal groups of the community.

$Z_{15sgfc}$  = amount of chemical constituent  $f$  in plant compartment ( $s,g$ ) that is consumed by  $c$  per time unit

$$= (Z_{10sgc} / \sum_{f \in C} X_{1sgf}) \cdot X_{1sgf} \quad (\text{II-14})$$

$$H \dot{X}_{1sgf} = \sum_c Z_{15sgfc} \quad (\text{II-15})$$

$Z_{16pnfc}$  = amount of chemical constituent  $f$  in seed compartment ( $p,n$ ) that is consumed by  $c$  per time unit

$$= (Z_{11pnc} / \sum_{f \in C} X_{2pnf}) \cdot X_{2pnf} \quad (\text{II-16})$$

<sup>1</sup>Actually if  $c$  is a predator, then  $Z_{7c}$  also includes the skeleton carbon biomass, which is not consumed but added to the organic debris (see equations II-24, 27).

$$H\dot{X}_{2pnf} = \sum_c Z_{16pnfc} \quad (\text{II-17})$$

$Z_{17dfc}$  = amount of chemical constituent f in organic debris category d that is consumed by c per time unit

$$= (Z_{12dc} / \sum_{f \in C} X_{21df}) \cdot X_{21df} \quad (\text{II-18})$$

$$H\dot{X}_{21df} = \sum_c Z_{17dfc} \quad (\text{II-19})$$

$Z_{18hfc}$  = amount of chemical constituent f in soil organic matter of soil horizon h that is consumed by c per time unit

$$= (Z_{13hc} / \sum_{f \in C} X_{22hf}) \cdot X_{22hf} \quad (\text{II-20})$$

$$H\dot{X}_{22hf} = \sum_c Z_{18hfc} \quad (\text{II-21})$$

$Z_{19yfc}$  = amount of chemical constituent f in prey group y killed by c per time unit

$$= (Z_{14yc} / \sum_{f \in C} X_{11yf}) \cdot X_{11yf} \quad (\text{II-22})$$

$$P\dot{X}_{11yf} = \sum_c Z_{19yfc} \quad (\text{II-23})$$

In predation, only the soft parts of the structural carbon are consumed. All the reserve and protein carbon is eaten. The skeleton parts have associated amounts of non-carbonaceous elements which are also added to the organic debris with the carbonaceous materials. The fraction of the structural carbon that makes up the skeleton is a constant (input parameter  $P_{8c}$ ) for each animal group, the assumption being that the ligaments, tendons and other structural "soft" tissues grow at the same rate as do the bones or "hard" structural tissues. The ratio of the biomass of each mineral element to the structural carbon in the skeleton is also considered constant (input parameters  $P_{9cf}$ ) for each animal group. This enables differentiation between the structural frames of different animal groups. For example, insect cuticles contain a much higher percentage of nitrogen than is found in mammal skeletons, and this fact is able to be expressed in the model. Using these ratios, the amount of prey killed by predators is divided into an edible part and a part that is added directly to the skeletal category of the organic debris. This simulates the passage of skeletal material through the animals without digestion except for labile fats of the skeleton when consumed. It also simulates the actions of

animals which do not ingest skeletons at all, but which crunch up the bones and obtain the fatty deposits within. It neglects the possibility of total or partial assimilation of invertebrate exoskeletons.

$Z_{20y5c}$  = amount of skeleton structural carbon (f = 5) in prey group y killed by c per time unit

$$= P_{8y} \cdot Z_{19y5c} \quad (\text{II-24})$$

$Z_{20yfc}$  = amount of mineral constituent in skeleton of prey group y killed by c per time unit, where  $f \in M$

$$= P_{9yf} \cdot Z_{20y5c} \quad (\text{II-25})$$

$$= 0 \quad (\text{II-26})$$

$Z_{20yfc}$  = amount of carbon constituent (other than structural carbon) in skeleton of prey group y killed by c per time unit that is added to the organic debris skeleton category, where  $f \in C - [5]$

$Z_{21yfc}$  = amount of chemical constituent f in prey group y consumed by c per time unit

$$= Z_{19yfc} - Z_{20yfc} \quad (\text{II-27})$$

from equations II-22, 24, 25, 26

$Z_{22f}$  = amount of chemical constituent f in all prey groups that is added to surface litter skeleton category (d = 6) due to predation per time unit

$$= \sum_c \sum_y Z_{20yfc} = P\dot{X}_{216f} \quad (\text{II-28})$$

The total intake of each animal group is found in terms of the total intake of each chemical constituent from each food compartment.

$Z_{23cf}$  = amount of chemical constituent f consumed by animal c per time unit

$$= \sum_s \sum_g Z_{15sgfc} + \sum_p \sum_n Z_{16pnfc} + \sum_d Z_{17dfc} + \sum_h Z_{18hfc} + \sum_y Z_{21yfc} \quad (\text{II-29})$$

from equations II-14, 16, 18, 20, 27

## ANIMAL III

The feeding process is almost identical to that modeled in II. Here the parameters are seasonally varying. The seasons are defined for each animal group by the investigator prior to simulation, each season beginning on a certain Julian day ( $P_{43cm}$ ). The parameters of the process are the maximum postulated consumption level per unit animal structural carbon per time unit for each animal group and season ( $P_{1cm}$ ), the searching ability of the group in each season ( $P_{2cm}$ ), and the relative food preferences of each animal group in each season ( $P_{3sgem}$ ,  $P_{4pncm}$ ,  $P_{5dcm}$ ,  $P_{6hcm}$ ,  $P_{7ycm}$ ). The food preferences are the factors which weight the amounts of each food item present during each time unit. Note that fetal groups (see "Reproduction and Population Changes") do not consume any food during their development periods ( $P_{1bm} = 0$ ). They are, in this respect, considered to be part of the mother group. The body structural carbon of the breeding group is incremented by the structural carbon of the fetal group, and this total is used in the calculation of the consumption of the breeding group.

Version III also simulates "milk" production by mature animal groups, thus providing another food source for juvenile groups. The amount of "milk" of each animal group is subdivided by chemical constituents, each compartment being a state variable. The preference of the juvenile group for the "milk" of the "mother"<sup>2</sup> group is expressed as an input parameter ( $P_{7ycm}$ ) -- one of the items in the prey preference list. To distinguish the food source as the "milk" of the "mother" group as opposed to the flesh, a further input parameter is specified ( $P_{35cm}$ ). This has either the value 0 if group  $c$  is not being suckled in season  $m$ , or a non-zero value equal to the numerical designation of the "mother" group of group  $c$  in season  $m$ . For the first part of the nursing season, the juvenile group consumes "milk" only, at a rate proportional to the juvenile group's structural carbon. The magnitude of this "part" is determined by input parameter  $P_{42c}$ . All food preferences are ignored during this time period. For the remainder of the period, other foods listed in the input preference arrays are also eaten. As described in the "Growth" section, the production of "milk" decreases linearly with time during the second part of the nursing period, and thus as the "milk" supply for the young dwindles, they compensate by consuming proportionately more of the other preferred foods. This simulates weaning.

In this model, an estimation is made of the fraction of carbon from fat tissues occurring in the total intake of reserve

<sup>2</sup>"Mother" in this context applies to an animal group that feeds "milk" to another group; it is not necessarily the animal group that gave birth to the group being "suckled." For example, worker bees ("mother" group) feed brood food ("milk") to the larvae (Chapman, 1969). In most cases, however, "mother" will apply to the reproductive group, as in mammals.

carbon. It is assumed in this calculation that all reserve carbon of animal origin is carbon from fat tissues, including animal carcass debris, but excluding "milk." It is recognized that "milk" of mammals contains carbohydrates (Kleiber, 1961, p. 312), the proportion of fat to carbohydrate varying widely between animal species. Since "milk" production is modeled here, an input parameter,  $P_{55c}$ , is used to denote the ratio of fat carbon to total reserve carbon in "milk." It is also recognized that fats occur in parts of plant tissues in addition to the carbohydrates (Maynard and Loosli, 1969, p. 20). In these cases, the proportion of carbohydrates is usually much greater than the proportion of fats, and thus the approximation is made here that the fat content can be ignored. To be considerably more accurate, a fat carbon to total reserve carbon ratio could be defined for each food item, with the overall fraction of fat carbon in the reserve carbon intake then being found.

if  $P_{35cm} \neq 0$ ,

$$\begin{aligned} Z_{82c} &= \text{length of nursing season } m \text{ of group } c \\ &= P_{43c(m+1)} - P_{43cm} \text{ if } P_{43c(m+1)} > P_{43cm} \\ &= P_{43c1} + 365 - P_{43cm} \text{ if } P_{43c(m+1)} \leq P_{43cm} \end{aligned} \quad \text{(III-1)}$$

if ( $P_{35cm} = 0$ ) or ( $P_{35cm} \neq 0$  and  $t > P_{42c} \cdot Z_{82c} + P_{43cm}$ ),

$$\begin{aligned} Z_{1sgc} &= \text{weighted amount of carbon in plant groups,} \\ &\text{organ } g, \text{ as related to consumer } c \\ &= P_{3sgem} \cdot \sum_{f \in C} X_{1sgf} \end{aligned} \quad \text{(III-2)}$$

$$\begin{aligned} Z_{2pnc} &= \text{weighted amount of carbon in seed species } p, \\ &\text{of seed horizon } n \text{ as related to consumer } c \\ &= P_{4pncm} \cdot \sum_{f \in C} X_{2pnf} \end{aligned} \quad \text{(III-3)}$$

$$\begin{aligned} Z_{3dc} &= \text{weighted amount of carbon of organic debris} \\ &\text{category } d \text{ as related to consumer } c \\ &= P_{5dcm} \cdot \sum_{f \in C} X_{21df} \end{aligned} \quad \text{(III-4)}$$

$$\begin{aligned} Z_{4hc} &= \text{weighted amount of carbon of soil organic} \\ &\text{matter in soil horizon } h \text{ as related to consumer } c \\ &= P_{6hcm} \cdot \sum_{f \in C} X_{22hf} \end{aligned} \quad \text{(III-5)}$$

$Z_{5yc}$  = weighted amount of carbon of animal food from group  $y$  as related to consumer  $c$

$$\begin{aligned} &= P_{7ycm} \cdot \sum_{f \in C} X_{11yf} \quad \text{if } y \neq P_{35cm} \\ &= P_{7ycm} \cdot \sum_{f \in C} X_{13yf} \quad \text{if } y = P_{35cm} \end{aligned} \quad (\text{III-6})$$

if  $P_{35cm} = y \neq 0$  and  $t \leq P_{42c} \cdot Z_{82c} + P_{43cm}$ ,

$$Z_{1sgc} = Z_{2pnc} = Z_{3dc} = Z_{4hc} = 0 \quad (\text{III-7})$$

$$Z_{5yc} = \sum_{f \in C} X_{13yf} \quad (\text{III-8})$$

$Z_{6c}$  = weighted amount of carbon in preferred food sources of consumer  $c$

$$\begin{aligned} &= \sum_s \sum_g Z_{1sgc} + \sum_p \sum_n Z_{2pnc} + \sum_d Z_{3dc} \\ &\quad + \sum_h Z_{4hc} + \sum_y Z_{5yc} \end{aligned} \quad (\text{III-9})$$

if  $P_{36cm} = 0$  (i.e.,  $c$  is not breeding in season  $m$ ),

$Z_{7c}$  = amount of carbon in food sources "taken" per time unit by animal group  $c$ <sup>3</sup>

$$\begin{aligned} &= P_{1cm} (1 - \exp(-P_{2cm} \cdot Z_{6c})) \cdot \\ &\quad (X_{11c5} - X_{14c5} - X_{13c5}) \end{aligned} \quad (\text{III-10})$$

if  $P_{36cm} \neq 0$  (i.e.,  $c$  is breeding in season  $m$ ),

$$\begin{aligned} Z_{7c} &= P_{1cm} (1 - \exp(P_{2cm} \cdot Z_{6c})) \cdot (X_{11c5} - \\ &\quad X_{14c5} - X_{13c5} + X_{11b5} - X_{14b5} - \\ &\quad X_{13b5}) \end{aligned} \quad (\text{III-10a})$$

where  $b$  is the numerical designation of the fetal group of breeding group  $c$  in this season

If a preferred food source is present in a very low amount (or is absent), the consumer compensates by eating more of the other preferred foods.

$Z_{9c}$  = factor to scale the weighted amounts of carbon of preferred foods so that their sum equals the

total amount of carbon consumed per time unit as calculated in (III-10)

$$= Z_{7c}/Z_{6c} \quad (\text{III-11})$$

$Z_{10sgc}$  = amount of carbon in plant compartment (s,g) consumed by animal group  $c$  per time unit

$$= Z_{1sgc} \cdot Z_{9c} \quad (\text{III-12})$$

$Z_{11pnc}$  = amount of carbon in seed compartment (p,n) consumed by animal group  $c$  per time unit

$$= Z_{2pnc} \cdot Z_{9c} \quad (\text{III-13})$$

$Z_{12dc}$  = amount of carbon in organic debris category  $d$  consumed by animal group  $c$  per time unit

$$= Z_{3dc} \cdot Z_{9c} \quad (\text{III-14})$$

$Z_{13hc}$  = amount of carbon in soil organic matter of soil horizon  $h$  consumed by animal group  $c$  per unit unit

$$= Z_{4hc} \cdot Z_{9c} \quad (\text{III-15})$$

$Z_{14yc}$  = amount of carbon in animal food of group  $y$  taken by animal group  $c$  per time unit

$$= Z_{5yc} \cdot Z_{9c} \quad (\text{III-16})$$

Having determined the fraction of the amount of carbon from a food compartment that is consumed or killed, the fraction of the amount of each chemical constituent in that compartment that is consumed or killed is calculated. Each food compartment is decremented by the amounts taken by all animal groups of the community.

$Z_{15sgfc}$  = amount of chemical constituent  $f$  in plant compartment (s,g) that is consumed by  $c$  per time unit

$$= (Z_{10sgc}/\sum_{f \in C} X_{1sgf}) \cdot X_{1sgf} \quad (\text{III-17})$$

$$H\dot{X}_{1sgf} = \sum_c Z_{15sgfc} \quad (\text{III-18})$$

$Z_{16pnfc}$  = amount of chemical constituent  $f$  in seed compartment (p,n) that is consumed by  $c$  per time unit

$$= (Z_{11pnc}/\sum_{f \in C} X_{2pnf}) \cdot X_{2pnf} \quad (\text{III-19})$$

<sup>3</sup> Actually if  $c$  is a predator, then  $Z_{7c}$  includes the skeleton carbon biomass which is not consumed but added to the organic debris.

$$H\dot{X}_{2pnf} = \sum_c Z_{16pnfc} \quad (\text{III-20})$$

$Z_{17dfc}$  = amount of chemical constituent f in organic debris category d that is consumed by c per time unit

$$= (Z_{12dc} / \sum_{f \in C} X_{21df}) \cdot X_{21df} \quad (\text{III-21})$$

$$H\dot{X}_{21df} = \sum_c Z_{17dfc} \quad (\text{III-22})$$

$Z_{18hfc}$  = amount of chemical constituent f in soil organic matter of soil horizon h that is consumed by c per time unit

$$= (Z_{13hc} / \sum_{f \in C} X_{22hf}) \cdot X_{22hf} \quad (\text{III-23})$$

$$H\dot{X}_{22hf} = \sum_c Z_{18hfc} \quad (\text{III-24})$$

Following determination of the amounts of live vegetation, shed seeds, organic debris, and soil organic matter consumed, the animal component of the diet is ascertained. If the parameter  $P_{35cm}$  equals y (where y is the numerical designation of the "prey" group) and group c is nursing, then the animal food from group y is "milk." If  $P_{35cm}$  does not equal y or animal group c is not nursing, then the animal food from group y is the non-skeletal parts of that group. Consider the latter case first.

Once the biomass of prey killed is determined, it is divided into edible and non-edible parts. The edible part consists of all reserve and protein carbon, together with the carbon from soft structural tissues, and the corresponding non-carbonaceous constituents determined from parameters  $P_{14ft}$ . As for ANIMAL II, a constant fraction of the body structural carbon makes up the skeleton (input parameter  $P_{8c}$ ). Associated with this hard structural carbon are minimum amounts of the non-carbonaceous constituents (parameters  $P_{9cf}$ ) -- the actual amounts per unit hard structural carbon are variable due to the possibility of storage of minerals in the skeleton above these minimums (up to some maximum mineral to hard structural carbon [or collagen carbon] ratios). Since the soft structural carbon is considered to be proteinaceous in origin, there are constant ratios of non-carbon constituents to the soft structural carbon (input parameters  $P_{14c3}$ ). Hence, given the amount of prey killed, the skeletal material to be added to the organic debris can be calculated. As in Version II, this process simulates passage of the skeletal material through the animals without digestion, except for the labile fats which are consumed, and it also

simulates the actions of animals which do not ingest skeletons at all but eat the fatty tissues (marrow) inside the bones. It ignores possible digestion of invertebrate exoskeletons. Version III, as mentioned previously, includes "wool" growth. The amount of "wool" of each animal group is subdivided by chemical constituent, each compartment being a state variable. "Wool" remains from the prey are added to the organic debris. Any "milk" in the prey is considered totally edible.

if  $P_{35cm} \neq y$ ,

$Z_{20yc}$  = proportion of prey group y killed by consumer c per time unit

$$= Z_{14yc} / \sum_{f \in C} X_{11yf} \quad (\text{III-25})$$

$Z_{21yfc}$  = amount of chemical constituent f in prey group y killed by c per time unit

$$= Z_{20yc} \cdot X_{11yf} \quad (\text{III-26})$$

$$p\dot{X}_{11yf} = \sum_c Z_{21yfc} \quad (\text{III-27})$$

$Z_{22yfc}$  = amount of chemical constituent f in "wool" of prey group y killed by c per time unit

$$= Z_{20yc} \cdot X_{14yf} \quad (\text{III-28})$$

$$p\dot{X}_{14yf} = \sum_c Z_{22yfc} \quad (\text{III-29})$$

$Z_{23yfc}$  = amount of chemical constituent f in "milk" of prey group y killed by c per time unit

$$= Z_{20yc} \cdot X_{13yf} \quad (\text{III-30})$$

$$p\dot{X}_{13yf} = \sum_c Z_{23yfc} \quad (\text{III-31})$$

$Z_{24yfc}$  = amount of chemical constituent f (excluding "wool" and "milk") in prey group y killed by c per time unit

$$= (X_{11yf} - X_{14yf} - X_{13yf}) \cdot Z_{20yc} \quad (\text{III-32})$$

$$p\dot{X}_{15y} = \sum_c Z_{24y5c} \quad (\text{III-33})$$



$$p\dot{X}_{16y} = \sum_c (X_{16y} \cdot Z_{20yc}) \quad (\text{III-34})$$

$Z_{25y5c}$  = amount of soft structural carbon ( $f = 5$ ) in prey group  $y$  killed by  $c$  per time unit

$$= Z_{24y5c} (1 - P_{8y}) \quad (\text{III-35})$$

$Z_{25yfc}$  = amount of mineral element  $f$  in soft structural parts of prey group  $y$  killed by consumer  $c$  per time unit where  $f \in M$

$$= Z_{25y5c} \cdot P_{14f3} \quad (\text{III-36})$$

$Z_{25yfc}$  = amount of carbon constituent (other than structural carbon) in soft structural parts of prey group  $y$  killed by  $c$  per time unit where  $f \in C - [5]$

$$= 0 \quad (\text{III-37})$$

$Z_{19yfc}$  = amount of mineral constituent  $f$  in edible parts of prey group  $y$  killed by group  $c$  per time unit, where  $f \in M$

$$= \sum_{t \in C - [5]} Z_{24yfc} \cdot P_{14ft} + Z_{25yfc} + Z_{23yfc} \quad (\text{III-38})$$

$Z_{19y5c}$  = amount of structural carbon ( $f = 5$ ) in edible parts of prey group  $y$  killed by group  $c$  per time unit

$$= Z_{25y5c} + Z_{23y5c} \quad (\text{III-39})$$

$Z_{19yfc}$  = amount of carbon constituent  $f$  in edible parts of prey group  $y$  killed by group  $c$  per time unit, where  $f \in C - [5]$

$$= Z_{24yfc} + Z_{25yfc} + Z_{23yfc} \quad (\text{III-40})$$

$Z_{26f}$  = amount of chemical constituent  $f$  in all prey groups that is added to organic debris, skeleton category ( $d = 6$ ) per time unit due to predation

$$= \sum_c \sum_y (Z_{24yfc} - Z_{19yfc}) = p\dot{X}_{216f} \quad (\text{III-41})$$

$Z_{27f}$  = amount of chemical constituent  $f$  in the "wool" of all prey groups that is added to the organic debris soft animal parts category ( $d = 5$ ) due to predation per time unit

$$= \sum_c \sum_y Z_{22yfc} = p\dot{X}_{215f} \quad (\text{III-42})$$

Now consider the case of one animal group feeding from the "milk" of another group (the programming of the model provides the restriction that if a juvenile group is being "suckled" it can have only one "mother" group). In contrast to the predator-prey relationship discussed previously, there is no waste with this food source; all the "milk" taken from the "mother" is consumed.

if  $P_{35cm} = y$ ,

$Z_{20yc}$  = proportion of "milk" of  $y$  consumed by  $c$  per time unit

$$= Z_{14yc} / \sum_{f \in C} X_{13yf} \quad (\text{III-43})$$

$Z_{19yfc}$  = amount of chemical constituent  $f$  in "milk" of "mother" group  $y$  consumed by  $c$  per time unit

$$= Z_{20yc} \cdot X_{13yf} = s\dot{X}_{11yf} = s\dot{X}_{13yf} \quad (\text{III-44})$$

The total intake of each animal group then, is found in terms of the total intake of each chemical constituent from each food compartment.

$Z_{28cf}$  = amount of chemical constituent  $f$  consumed by group  $c$  per time unit

$$= \sum_s \sum_g Z_{15sgfc} + \sum_p \sum_n Z_{16pnfc} + \sum_d Z_{17dfc} + \sum_h Z_{13hfc} + \sum_y Z_{19yfc} \quad (\text{III-45})$$

from equations III-17, 19, 21, 23, 38-40, 44

$Z_{8c}$  = fraction of carbon from fat tissue in the total reserve carbon intake of group  $c$  per time unit

$$= (Z_{1764c} + Z_{1754c} + \sum_{y \neq P_{35cm}} (Z_{24y4c} + Z_{23y5c} \cdot P_{55y}) + Z_{19y'4c} \cdot P_{55c}) / Z_{28c4} \quad (\text{III-46})$$

where  $y'$  =  $P_{35cm}$

$d = 6$ : skeletons of animals

$d = 5$ : soft parts of animal carcasses

**Discussion**—Suppose that for each animal group ( $c$ ) in the simulation, the rates of consumption of each food item ( $i$ ) are

known. These may have been obtained through stomach analyses or from direct observations in laboratory feeding experiments, for example:

let there be  $n$  animal groups  
 let the rate of consumption of food item  $i$  by animal group  $c$   
 (= amount of carbon in food  $i$  consumed/[amount of carbon in animal·time]) =  $\gamma_{ci}$   
 let the amount of carbon in animal group  $c$  =  $a_c$

then, the community consumption rate of food item  $i$  per unit amount of carbon in animal per unit time =

$$(a_1/c \sum_{c=1}^n a_c) \cdot \gamma_{1i} + (a_2/c \sum_{c=1}^n a_c) \cdot \gamma_{2i} + \dots + (a_n/c \sum_{c=1}^n a_c) \cdot \gamma_{ni} = (\sum_{c=1}^n a_c \cdot \gamma_{ci}) / \sum_{c=1}^n a_c$$

This relationship will provide the feeding parameters for ANIMAL I. The parameter  $P_1$  (equation I-1) can be found by summing the community consumption rates for all live vegetation food items. It would not be possible to tell from examination of the consumed seeds which came from which seed horizon. To determine parameter  $P_{3n}$  (equation I-4) knowledge of the activity of the animal groups could solve this problem. For example, it might be assumed that an animal that spent 50% of its active period on the surface and 50% in burrows and tunnels in the first seed horizon, might obtain 50% of its seeds from the surface of the soil and 50% from the first seed horizon. Thus the overall seed consumption rate for the group may be divided into consumption rates for seeds from each seed horizon. These would be the  $\gamma_{ci}$  values mentioned above, and the parameters  $P_{3n}$  could be obtained from the community consumption rate relation above. For organic debris, certain types would probably be recognizable in stomach analyses, and certainly in laboratory feeding trials. Thus the  $\gamma_{ci}$  values would be available, and hence values of parameters  $P_{4d}$  (equation I-7) could be obtained. Soil organic matter consumption poses the same problem as seed consumption -- it would have to be assumed that during the active period of the animal group, it could be feeding at any point in the soil profile where it is observed. Thus the total consumption rate of soil organic matter for the animal group could be subdivided into consumption rates of soil organic matter by soil horizons in proportion to the percentage of activity in that horizon. These rates would be the  $\gamma_{ci}$  values, and thus the community  $P_{5h}$  parameters (equation I-10) could be obtained as in the above relationship. In determining the parameter  $P_7$  (equation I-13) the amount of prey biomass killed by each animal group per time unit is needed. By summing the community consumption rates for all animal prey items,  $P_7$  can be found.

It has been assumed that the amount consumed by each animal group is known. For the simulation, the amount of

each food item present in the system also needs to be known in order to set up the initial state variable values. Feeding parameters for ANIMAL II can be obtained from these data, when collected at times of different food densities.

let amount of carbon in food  $i$  be  $\beta_i$ ; then the preference of animal group  $c$  for food item  $i$ ,

$$\psi_{ci} = (a_c \cdot \gamma_{ci} / \beta_i)$$

which is calculable since  $a_c$ ,  $\gamma_{ci}$ ,  $\beta_i$  are known. Parameters  $P_{4pnc}$  (II-2),  $P_{5dc}$  (II-3),  $P_{6hc}$  (II-4),  $P_{7yc}$  (II-5), and  $P_{3sgc}$  (II-1) of II are thus obtained.

$$P_{1c} = \lim_{(\sum_i \psi_{ci} \cdot \beta_i \rightarrow \infty)} \sum_i \gamma_{ci}$$

Through non-linear multiple regression on the points  $(\sum_i \psi_{ci} \cdot \beta_i, \sum_i \gamma_{ci})$ , parameters  $P_{1c}$  (the asymptote) and  $P_{2c}$  (the curvature constant) are obtainable.

ANIMAL III feeding parameters follow the same calculations except that data for each season defined for each animal group must be available so that seasonally varying parameters are calculable.

#### ASSIMILATION

##### ANIMAL I

Two assimilation efficiencies are defined (input parameters  $P_8$ ,  $P_9$ ); one is applied to the non-animal foods and the other to the animal foods. Each efficiency parameter is a fraction representing that proportion of food consumed that is assimilated (Odum, 1971). The remainder is expelled from the consumer without digestion occurring, and increments the organic debris category of excreta. Figure 6 illustrates the relationships.

$Z_{22cf}$  = amount of chemical constituent  $f$  assimilated by animal group  $c$  per time unit

$$= Z_{20cf} \cdot P_8 + Z_{21cf} \cdot P_9 \quad (I-22)$$

from equations I-20, 21

$Z_{23cf}$  = amount of chemical constituent  $f$  egested by  $c$  per time unit

$$= Z_{20cf} + Z_{21cf} - Z_{22cf} \quad (I-23)$$

$Z_{24f}$  = amount of chemical constituent  $f$  egested per time unit

$$= \sum_c Z_{23cf} = E \dot{X}_{21f} \quad (I-24)$$

## ANIMAL II

An assimilation efficiency is defined for each chemical constituent (input parameters  $P_{10cf}$ ) for each animal group. Each efficiency is a fraction representing that proportion of the chemical constituent consumed that is assimilated. The remainder is excreted without digestion and is added to the organic debris excreta category. These fractions are the same for each food item -- that is, each chemical constituent in each food item is assimilated with the same efficiency. Assimilation efficiencies for chemical constituents have been obtained for domestic herbivores (Cook et al., 1967). The assumption is made that the assimilation efficiencies for the chemical constituents in herbage are also applicable to chemical constituents in other food sources. Also it is assumed that such principles apply to all types of animals. The assimilation efficiency for structural carbon would be low in contrast to that for reserve carbon and protein carbon (Maynard and Loosli, 1969, p. 19). Thus diets that were high in structural carbon would be less digestible than diets that were high in protein and reserve carbon. Since the composition of the diets depends on the preferences and the amount of the food supply, these compositions may change with time. The overall digestibility of the diet would also change with the composition, and therefore with time. Figure 7 illustrates the relationships.

$$\begin{aligned} Z_{24cf} &= \text{amount of chemical constituent } f \text{ assimilated by} \\ &\quad \text{animal group } c \text{ per time unit} \\ &= Z_{23cf} \cdot P_{10cf} \end{aligned} \quad (\text{II-30})$$

$$\begin{aligned} Z_{25cf} &= \text{amount of chemical constituent } f \text{ egested by} \\ &\quad \text{animal group } c \text{ per time unit} \\ &= Z_{23cf} - Z_{24cf} \end{aligned} \quad (\text{II-31})$$

$$\begin{aligned} Z_{26f} &= \text{amount of chemical constituent } f \text{ egested per} \\ &\quad \text{time unit} \\ &= \sum_c Z_{25cf} = E \dot{X}_{21,7f} \end{aligned} \quad (\text{II-32})$$

## ANIMAL III

Since an animal may consume proteinaceous structural material (from foods of animal origin), the total amount of carbon from dietary protein consumed is not given by the protein carbon intake. Assuming that all nitrogen occurs in the form of amino acids, the total dietary protein carbon intake is estimated from the nitrogen intake (if there are no limiting conditions). If there is insufficient carbon in the protein carbon and structural carbon intakes (i.e., carbon is limiting) to account for the carbon amount in the protein predicted by the nitrogen intake, then nitrogen must have been ingested in the a non-proteinaceous form. This excess nitrogen is excreted. Animals with microorganisms in their

gut are thought to be able to utilize non-protein nitrogen -- this has been proven in ruminants (Maynard and Loosli, 1969, p. 135), but it is uncertain in insects (Chapman, 1969, p. 81). For the majority of animals, it appears that the only useful nitrogen is that associated with protein.

The fat carbon intake is the calculated fraction of the reserve carbon intake, described in the feeding section. The carbon from digestible carbohydrates makes up the remainder of the reserve carbon intake. The carbon from structural carbohydrates, such as lignin and cellulose, constitutes the remainder of the structural carbon intake.

As in Version II, an assimilation efficiency is defined for each chemical constituent (input parameters  $P_{10cf}$ ) for each animal group. These parameters are not seasonally varying in this case: it was thought that the collection of data to fill such a seasonally varying data list would be an overwhelming task, and that there would not be an increase in accuracy of

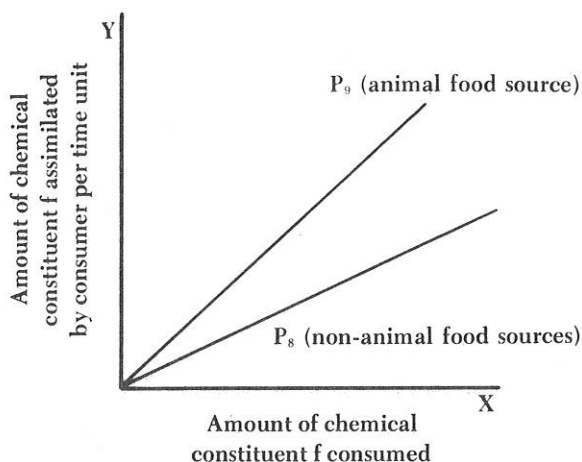


Figure 6. Assimilation process (ANIMAL I).

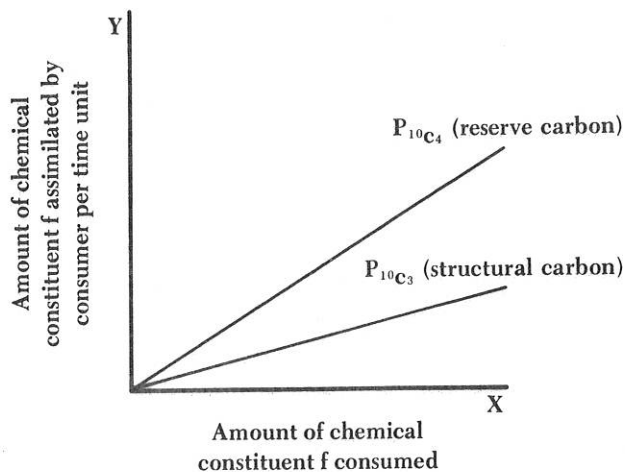


Figure 7. Assimilation process (ANIMAL II).

prediction concomitant with the difficulty of data collection. In this model, the assimilation efficiency for protein carbon is applied to the proteinaceous structural carbon as well, and to the accompanying nitrogen and mineral constituents (given by parameters  $P_{14f3}$ ).

$$\begin{aligned} Z_{29c} &= \text{amount of carbon in protein intake, predicted} \\ &\text{from the non-carbon constituents of the intake} \\ &= \min(Z_{28cf}/P_{14f3}) \quad (\text{III-47}) \\ &f \in M \end{aligned}$$

if  $Z_{29c} > Z_{28c3} + Z_{28c5}$  (carbon limiting),

$$\begin{aligned} Z_{30c3} &= \text{amount of carbon in protein intake} \\ &= Z_{28c3} + Z_{28c5} \quad (\text{III-48}) \end{aligned}$$

if  $Z_{29c} \leq Z_{28c3} + Z_{28c5}$ ,

$$\begin{aligned} Z_{30c3} &= Z_{29c} \\ Z_{30cf} &= \text{amount of non-carbon constituent } f \text{ in protein} \\ &\text{intake, where } f \in M \\ &= Z_{30c3} \cdot P_{14f3} \quad (\text{III-49}) \end{aligned}$$

Excess nitrogen is excreted:

$$EN\dot{X}_{17c1} = Z_{28c1} - Z_{30c1} \quad (\text{III-50})$$

$$\begin{aligned} Z_{31c} &= \text{amount of proteinaceous structural carbon} \\ &= Z_{30c3} - Z_{28c3} \quad (\text{III-51}) \end{aligned}$$

let  $Z_{28c1}$  now represent the value  $Z_{30c1}$ ,

$$\begin{aligned} Z_{32cf} &= \text{amount of chemical constituent } f \text{ assimilated} \\ &\text{by animal group } c \text{ per time unit} \\ &= P_{10c3} \cdot Z_{30cf} + P_{10cf}(Z_{28cf} - Z_{30cf}) \quad (\text{III-52}) \\ &\text{where } f \in M \end{aligned}$$

$$Z_{32cf} = P_{10cf} \cdot Z_{28cf}, \text{ where } f \in C-[5] \quad (\text{III-53})$$

$$Z_{32c5} = P_{10c3} \cdot Z_{31c} + P_{10c5}(Z_{28c5} - Z_{31c}) \quad (\text{III-54})$$

$$E\dot{X}_{17cf} = Z_{28cf} - Z_{32cf} \quad (\text{III-55})$$

$$\begin{aligned} Z_{33c} &= \text{amount of carbon from assimilated protein for} \\ &\text{group } c \text{ per time unit} \\ &= Z_{32c3} + P_{10c3} \cdot Z_{31c} \quad (\text{III-56}) \end{aligned}$$

$$Z_{34c} = \text{amount of carbon from assimilated fats for group } c \text{ per time unit}$$

$$= Z_{8c} \cdot Z_{32c4} \quad (\text{III-57})$$

$$\begin{aligned} Z_{35c} &= \text{amount of carbon from assimilated carbohy-} \\ &\text{drates for group } c \text{ per time unit} \\ &= (Z_{32c4} - Z_{34c}) + (Z_{32c5} - P_{10c3} \cdot Z_{31c}) \\ &\quad (\text{III-58}) \end{aligned}$$

**Discussion**—Suppose that the assimilation efficiencies of ash, protein, fats and labile carbohydrates, and structural carbohydrates are known ( $p_{c2}$ ,  $p_{c3}$ ,  $p_{c4}$ ,  $p_{c5}$ ) for each animal group. Since it is assumed in Version III that all nitrogen is in the form of amino acids, the assimilation efficiency for nitrogen  $p_{c1}$  can be equated to  $p_{c3}$ , the assimilation efficiency of protein. Thus parameters  $P_{10cf}$  (III-52 to 54) of III are obtained.

In II, no distinction is made between the assimilation of animal structural carbon (proteinaceous in origin) and the plant structural carbon (carbohydrate in origin). Thus the overall assimilation efficiency for structural carbon must be determined by considering the ratio of animal structural carbon to total structural carbon in the diet.

Suppose animal structural carbon in diet of group  $c$ :total structural carbon in diet of  $c = \lambda_c$ ,

let  $\mu_{cf}$  = assimilation efficiency of constituent  $f$  by group  $c$

then  $\mu_{c5} \cdot (\text{total structural carbon}) = p_{c5} \cdot (\text{total structural carbon} - \text{animal structural carbon}) + p_{c3} \cdot (\text{animal structural carbon})$ ,

$$\text{i.e., } \mu_{c5} = p_{c5}(1 - \lambda_c) + p_{c3} \lambda_c$$

$$\text{also } \mu_{c3} = \mu_{c1} = p_{c3}$$

$$\mu_{c4} = p_{c4}$$

Since only a small amount of mineral elements are associated with protein, only a small error is introduced if the protein-associated minerals are ignored and the assimilation efficiency for ash ( $p_{c2}$ ) is used for the value  $\mu_{c2}$ . Thus if  $\lambda_c$  is known, parameters  $P_{10cf}$  of Version II (II-30) are obtained.  $\lambda_c$  can be estimated from the composition of the foods and the preferences for these foods.

Suppose  $\omega_i$  = amount of structural carbon in food source  $i$  and  $\psi_{ci}$  = preference of group  $c$  for food source  $i$

then  $\lambda_c = (\sum_{i \in I} \psi_{ci} \cdot \omega_i) / (\sum_{i \in I} \psi_{ci} \cdot \omega_i)$  where  $I = [i: i \text{ is of animal origin}]$

This ratio will not be exact if one or more of the foods are limiting (i.e., present in insufficient amounts relative to the group's requirement), or if there are large changes in  $\omega_i$ .

Taking these assimilation efficiencies  $\mu_{cf}$ , the overall

community assimilation efficiencies ( $P_8, P_9, I-22$ ) of  $I$  can be estimated.

Let

amount of carbon in food  $i$  consumed by  $c$  per unit animal carbon =  $\gamma_{ci}$

amount of each chemical constituent  $f$  in food  $i$  per unit carbon =  $\lambda_{fi}$

amount of carbon in group  $c = a_c$

$I = [i:i \text{ is of animal origin}]$

$J = [i:i \text{ is not of animal origin}]$

then

amount of  $f$  in food  $i$  consumed by  $c = \gamma_{ci} \cdot \lambda_{fi} \cdot a_c$

amount of  $f$  consumed by  $c$  from foods  $i \in S =$

$$\sum_{i \in S} (a_c \gamma_{ci} \cdot \lambda_{fi}) = \chi_{sf}, \text{ where } S = I \text{ or } S = J$$

for animal foods ( $S = I$ ),

amount of  $f$  assimilated from animal foods by community

$$= \sum_{i \in I} \sum_c \gamma_{ci} \cdot \lambda_{fi} \cdot a_c \cdot p_{cf}, \text{ where } f \in C-[5]$$

$$= \sum_{i \in I} \sum_c \gamma_{ci} \cdot \lambda_{5i} \cdot a_c \cdot p_{c3}, \text{ where } f = 5$$

then

assimilation efficiency of community for constituent  $f$  from animal foods =  $\mu'_{I_f}$

$$= (\sum_{i \in I} \sum_c a_c p_{cf} \lambda_{fi} \gamma_{ci}) / \chi_{I_f}, \text{ where } f \in C-[5]$$

$$\mu'_{I_5} = (\sum_{i \in I} \sum_c a_c p_{c3} \lambda_{5i} \gamma_{ci}) / \chi_{I_5}, \text{ where } f = 5$$

for non-animal foods ( $S = J$ ),

$$\mu'_{J_f} = (\sum_{i \in J} \sum_c a_c p_{cf} \lambda_{fi} \gamma_{ci}) / \chi_{J_f}$$

Now a compromise has to be made to find total assimilative efficiencies for the animal and non-animal foods. That is, the assimilation efficiencies for each chemical constituent have to be combined to give the "best" overall efficiency. One method suggested is to sum the weighted efficiencies for each chemical constituent, the weights being the proportions of the total amount assimilated that the chemical constituents make up.

Thus,

the total amount consumed by the community =  $\sum_f \chi_{sf}$   
from food  $S$

the community assimilation efficiency =

$$\sum_f (\chi_{sf} / \sum_f \chi_{sf}) \cdot \mu'_{sf}$$

The parameters ( $P_8, P_9$ ) are time-invariant, and hence the initial values of each, calculated on the composition of the food items at the beginning of the simulation, will not change during the simulation. If the chemical composition of the foods changes during the time period, then the overall assimilation efficiencies should also change according to the equations above.

#### RESPIRATION/METABOLISM

##### ANIMAL I

The animal community respire at a constant rate (input parameter  $P_{10}$ ); the amount of carbon respired as carbon dioxide, and the amount of mineral elements excreted as by-products, are constant proportions of the animal biomass of these chemical elements. Figure 8 shows the relationships. Carbon dioxide is lost from the system to the atmosphere and the mineral elements increment the organic debris excreta category. Included in these losses from the animals are the costs of activity, maintenance, reproduction, and growth.

$Z_{25cf}$  = amount of chemical constituent  $f$  respired or excreted per time unit

$$= P_{10} \cdot X_{11cf} = R \dot{X}_{11cf} \quad (I-25)$$

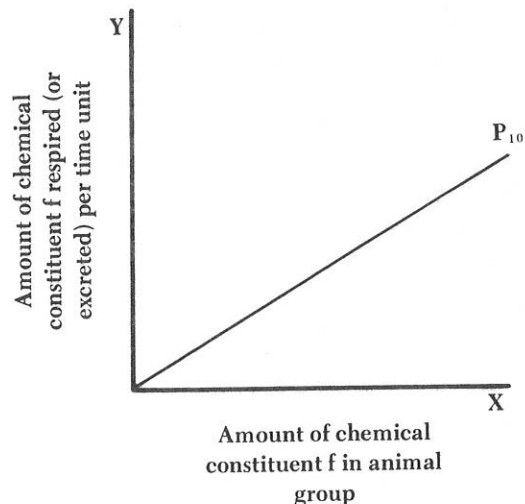


Figure 8. Respiration (ANIMAL I).

$Z_{26}$  = total carbon lost from system to atmosphere by respiration per time unit

$$= \sum_c \sum_{f \in C} Z_{25cf} = R\dot{X}_{01,13} \quad (\text{I-26})$$

$$R\dot{X}_{217f} = \sum_c Z_{25cf}, \text{ where } f \in M \quad (\text{I-27})$$

$$R\dot{X}_{217f} = 0, \text{ where } f \in C \quad (\text{I-28})$$

### ANIMAL II

The amount of carbon respired per day by an animal is a non-linear function of the animal's carbon biomass. The relationship is of the form  $aX^b$ , after Brody (1945) and Reichle (1968). Figures 9a and 9b illustrate the function. For each animal group,  $a$  and  $b$  are input parameters ( $P_{11c}$ ,  $P_{12c}$ ). The amount of carbon respired per day by an animal group is then the amount respired by an individual of that group times the population of the group. This function includes the costs of activity, reproduction, growth, and maintenance (as in Weins and Innis, 1973). A constant fraction of the carbon ( $P_{13c}$ ) is supposed to come from "protein tissue" metabolism while the remainder is from reserves (Maynard and Loosli, 1969, Chap. 14). Associated with the "protein tissue" breakdown is the excretion of mineral elements ["endogenous urinary nitrogen," in mammals (Maynard and Loosli, 1969, p. 415), for example]. "Protein" is considered to have a constant ratio of mineral elements to carbon, while reserve tissues contain no mineral elements and are considered to consist only of carbon, hydrogen and oxygen (input parameters  $P_{14ft}$ ; Kleiber, 1961, p. 43).

$Z_{27c}$  = carbon respired per time unit by  $c$

$$= P_{11c} (Z_{8c}/X_{12c})^{P_{12c}} \cdot X_{12c} \quad (\text{II-33})$$

where  $Z_{8c}$  is amount of carbon in  $c$  — equation II-7

$Z_{28c3}$  = Protein carbon ( $f = 3$ ) potentially metabolized by  $c$  per time unit

$$= P_{13c} \cdot Z_{27c} \quad (\text{II-34})$$

$Z_{28c4}$  = reserve carbon ( $f = 4$ ) potentially metabolized by  $c$  per time unit

$$= Z_{27c} - Z_{28c3} \quad (\text{II-35})$$

If there are insufficient reserves to supply the required amount of reserve carbon, then "protein tissue" is broken down to supply this needed carbon. If there is insufficient protein carbon then the animal group dies.

$Z_{29c4}$  = reserve carbon ( $f = 4$ ) metabolized by  $c$  per time unit

$$= \min(X_{11c4}, Z_{28c4}) \quad (\text{II-36})$$

$Z_{29c3}$  = protein carbon ( $f = 3$ ) metabolized by  $c$  per time unit

$$= Z_{27c} - Z_{29c4} \quad (\text{II-37})$$

$$Z_{29c5} = 0 \quad (\text{II-38})$$

$Z_{29cf}$  = amount of mineral element  $f$  excreted as by-product of respiration of group  $c$  per time unit, where  $f \in M$

$$= Z_{29c3} \cdot P_{14f3} + Z_{29c4} \cdot P_{14f4} \quad (\text{II-39})$$

( $P_{14ft}$  = ratio of  $f$ 'th constituent  $f \in M$  to the  $t$ 'th constituent [ $t = 3$ , protein carbon;  $t = 4$ , reserve carbon;  $t = 5$ , structural carbon;  $P_{143t} = 1 \forall t$ ])

$$R\dot{X}_{01,13} = \sum_c Z_{27c} \quad (\text{II-40})$$

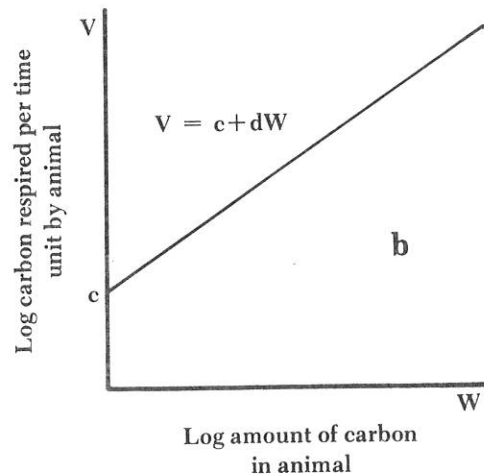
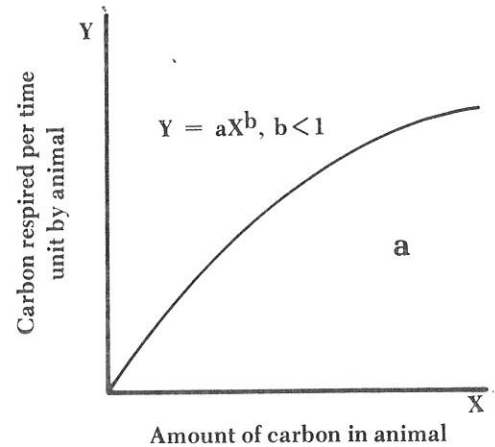


Figure 9. (a and b) respiration -- ANIMAL II.

$$R\dot{X}_{11cf} = Z_{29cf} \quad (\text{II-41})$$

$$R\dot{X}_{217f} = \sum_c Z_{29cf}, \text{ where } f \in M \quad (\text{II-42})$$

$$R\dot{X}_{217f} = 0, \text{ where } f \in C \quad (\text{II-43})$$

### ANIMAL III

Even if it is assumed that all intake nitrogen is in the form of amino acids, it does not necessarily follow that all the assimilated nitrogen is able to be used in protein synthesis. Some of the essential amino acids may not be present at the time of attempted protein synthesis, and thus synthesis will not occur. Each protein has a biological value indicating the proportion of digested protein that is used to satisfy body protein needs (Crampton, 1965, p. 158), the remainder being excreted and used as an energy source. Hence, following assimilation, there is a further loss of nitrogen, mainly in the form of urea ( $\text{CO}[\text{NH}_2]_2$ ) for mammals, or uric acid ( $\text{C}_5\text{H}_4\text{O}_3$ ) for invertebrates, reptiles and birds (Maynard and Loosli, 1969, p. 125; Chapman, 1969, p. 496; Welty, 1963, p. 132). Parameter  $P_{43c}$  represents the weight ratio of nitrogen to carbon in the nitrogenous excretions of group c. An input parameter,  $P_{44c}$ , is defined for each animal group to represent the fraction of assimilated protein that is unusable in protein synthesis due to the biological value properties of the group's diet. The energy released from the breakdown of this assimilated protein is used to meet the maintenance requirements of the animal. The carbon not in urea or uric acid is respired.

$$\begin{aligned} Z_{36c} &= \text{amount of dietary protein carbon lost through} \\ &\quad \text{biological value considerations from group c} \\ &\quad \text{per time unit} \\ &= Z_{33c} \cdot P_{44c} \quad (\text{III-59}) \end{aligned}$$

$$BV\dot{X}_{17cf} = Z_{36c} \cdot P_{14f3}, \text{ where } f \in M \quad (\text{III-60})$$

$$BV\dot{X}_{17c3} = Z_{36c} \cdot P_{14_{13}}/P_{45c} \quad (\text{III-61})$$

$$BV\dot{X}_{01_{13}} = Z_{36c} (1 - P_{14_{13}}/P_{45c}) \quad (\text{III-62})$$

If, in a season, an animal group is producing "milk" and the population of the group being nursed becomes zero, then the stored "milk" is reabsorbed by the lactating group and is available for use in growth and maintenance (see "Growth" for further discussion on "milk" production). There are no digestive processes involved in the reabsorption and thus the assimilation efficiencies are not applied. The protein is considered to have a biological value of 100%, and there is no waste.

$$\text{if } P_{35c} \neq c \text{ for some } c^l, m^l, \text{ and } X_{12c} = 0: Z_{60c} = 1$$

$$\text{if } P_{35c} \neq c \text{ for any } c^l, m^l, \text{ or } X_{12c} \neq 0: Z_{60c} = 0 \quad (\text{III-62a})$$

Furthermore, tissues from fetal deaths are assumed to be reabsorbed and to thus become available for use in maintenance and growth. The amounts reabsorbed are given by  $Z_{102cf}$  (III-219 to 221). The assimilation efficiencies are not applied and the biological value of the protein is assumed to be 100%.

$$\begin{aligned} Z_{37cf} &= \text{amount of constituent f available for maintenance} \\ &\quad \text{and production by group c per time unit,} \\ &\quad \text{where } f \in M \\ &= Z_{32cf} - Z_{36c} \cdot P_{14f3} + Z_{60c} \cdot X_{13cf} + Z_{102cf} \quad (\text{III-63}) \end{aligned}$$

$$\begin{aligned} Z_{37c3} &= \text{amount of dietary protein carbon available for} \\ &\quad \text{maintenance and production by group c per} \\ &\quad \text{time unit} \\ &= Z_{33c} - Z_{33c} \cdot P_{44c} + Z_{60c} (X_{13c3} + X_{13c5}) + \\ &\quad \quad \quad Z_{102c3} \quad (\text{III-64}) \end{aligned}$$

$$\begin{aligned} Z_{37c4} &= \text{amount of dietary fat carbon available for} \\ &\quad \text{maintenance and production by group c per} \\ &\quad \text{time unit} \\ &= Z_{34c} + Z_{60c} \cdot X_{13c4} \cdot P_{55c} + Z_{102c4} \quad (\text{III-65}) \end{aligned}$$

(where  $P_{55c}$  is the ratio of fat carbon to reserve carbon in "milk")

If the animal is a ruminant, there is an appreciable loss of energy and carbon through methane production (Kleiber, 1961, p. 262). Input parameter  $P_{46c}$  represents the fraction of carbon from digested carbohydrates that is lost as methane, for each animal group.

$$\begin{aligned} Z_{38c} &= \text{amount of carbon respired in methane production} \\ &\quad \text{by group c per time unit} \\ &= P_{46c} \cdot Z_{35c} \quad (\text{III-66}) \end{aligned}$$

$$\begin{aligned} Z_{37c5} &= \text{amount of dietary carbohydrates carbon available} \\ &\quad \text{for maintenance and production by group} \\ &\quad \text{c per time unit} \\ &= Z_{35c} - Z_{38c} + Z_{60c} \cdot X_{13c4} (1 - P_{55c}) + \\ &\quad \quad \quad Z_{102c5} \quad (\text{III-67}) \end{aligned}$$

$$MP\dot{X}_{013} = Z_{38c} \quad (\text{III-67a})$$

$$MR\dot{X}_{13cf} = MR\dot{X}_{11cf} = X_{13cf} \cdot Z_{60c} \quad (\text{III-67b})$$

To determine the amount of carbon respired in maintenance by an animal of a group per time unit, the same functional form as in II is used;  $a\chi^b$  (Brody, 1945; Kleiber, 1961; Maynard and Loosli, 1969), where  $a$  and  $b$  are constants and  $\chi$  is the weight of the animal in terms of carbon. This predicts the amount of energy respired per time unit; the amount of carbon respired depending on the types of tissues that are catabolized to meet this energy. In contrast to II, therefore, parameter  $a$  ( $P_{11cm}$  in III) is the amount of energy per unit of metabolic size of an animal of group  $c$ , used in maintenance per time unit during season  $m$ . It includes a factor which compensates for the inefficiency of catabolism of nutrients. Parameter  $b$  ( $P_{12cm}$ ) also has seasonal values. Thus the average environments of the seasons are incorporated into the simulation by their effects on the respiration rates and maintenance requirements of the animal groups. The costs of basal metabolism and activity are included in these calculations. If group  $c$  is breeding, then  $\chi$  contains the amount of fetal carbon. As in "Feeding," the fetal group ( $b$ ) is considered to be a part of the mother group in this process. Group  $b$  does not carry out any respiration directly ( $P_{11bm} = 0$ ).

Associated with basal metabolism there is a urinary nitrogen excretion (called endogenous urinary nitrogen, or EUN in mammals; Maynard and Loosli, 1969, p. 415). There is also a fecal nitrogen excretion (called metabolic fecal nitrogen, or MFN, in mammals; Maynard and Loosli, 1969, p. 140; Kleiber, 1961, p. 258), due to breakdown of digestive enzymes in the body. The latter excretion may be related to dietary intake (Maynard and Loosli, 1969, p. 142) as well as metabolic size of the animal, but it is assumed here that, at least for a first approximation, the total nitrogen excretion due to basal metabolic reactions can be expressed as the amount of nitrogen excreted per unit or energy respired in basal metabolism (parameter  $P_{13cm}$ ). This nitrogen originates from protein tissue in the animal's body. It is assumed here that the energy released in the catabolism is available to meet the maintenance requirements. Input parameter  $P_{47c3}$  represents the energy released per unit of protein carbon. The associated protein carbon is partly respired, the remainder being excreted in the urea or uric acid. The associated mineral elements are excreted.

if  $P_{36cm} = 0$  (i.e.,  $c$  is not breeding),

$$\begin{aligned} Z_{39c} &= \text{energy for maintenance requirements of group } c \\ &\text{per time unit} \\ &= P_{11cm} \cdot \left( \sum_{f \in C} X_{11cf} / X_{12c} \right)^{P_{12cm}} \cdot X_{12c} \quad (\text{III-68}) \end{aligned}$$

if  $P_{36cm} \neq 0$  (i.e.,  $c$  is breeding),

$$Z_{39c} = P_{11cm} \cdot \left( \sum_{f \in C} (X_{11cf} + X_{11bf}) / X_{12c} \right)^{P_{12cm}} \cdot X_{12c} \quad (\text{III-68a})$$

where  $b$  is the numerical designation of the fetal group of  $c$  in this season

$$\begin{aligned} Z_{40c1} &= \text{EUN and MFN excreted by } c \text{ per time unit} \\ &= Z_{39c} \cdot P_{13cm} \quad (\text{III-69}) \end{aligned}$$

$$\begin{aligned} Z_{40c3} &= \text{carbon from protein associated with the} \\ &\text{EUN and MFN excretions of } c \text{ per time unit} \\ &= Z_{40c1} / P_{143} \quad (\text{III-70}) \end{aligned}$$

$$\begin{aligned} Z_{40cf} &= \text{non-carbon constituents associated with the} \\ &\text{EUN and MFN excretions of } c \text{ per time unit} \\ &= Z_{40c3} \cdot P_{14f3}, \text{ where } f \in M \quad (\text{III-71}) \end{aligned}$$

$$Z_{40cf} = 0, \text{ where } f \in C - [3] \quad (\text{III-72})$$

$$MN\dot{X}_{17cf} = Z_{40cf}, \text{ where } f \in M \quad (\text{III-73})$$

$$MN\dot{X}_{11cf} = Z_{40cf} \quad (\text{III-74})$$

$$MN\dot{X}_{17c3} = Z_{40c1} / P_{45c} \quad (\text{III-75})$$

$$MN\dot{X}_{013} = Z_{40c3} - Z_{40c1} / P_{45c} \quad (\text{III-76})$$

$$\begin{aligned} Z_{41c} &= \text{energy remaining to be respired to sustain the} \\ &\text{maintenance requirement of group } c \text{ per time} \\ &\text{unit} \\ &= Z_{39c} - (Z_{36c} + Z_{40c3}) \cdot P_{47c3} \quad (\text{III-77}) \end{aligned}$$

The energy needed (expressed by  $Z_{41c}$ , III-77) is supplied first by the dietary fats and carbohydrates. If these are exhausted, the reserves of the body are catabolized, followed by the dietary protein, and then a portion of the animal's body protein; synthesis of protein takes priority if possible over catabolism of protein (Maynard and Loosli, 1969, p. 143). Each of these compounds, protein, fat and carbohydrates, has an energy to carbon ratio indicated by parameters  $P_{47cf}$ ,  $f = 3, 4, 5$ , respectively (Kleiber, 1961, p. 125). Protein catabolism causes nitrogen and mineral element excretion to occur, according to parameters  $P_{14f3}$ . All the carbon except for that occurring in urea or uric acid is respired. It is assumed that fats and carbohydrates are used in proportion to their abundance if they are present in excess.

The protein tissue of the animal, as mentioned above, can be used in maintenance up to a certain point, depending on the protein status of the animal. Each animal has an optimum protein level which grows with a juvenile animal and is a constant for adults (parameter  $P_{18c}$ ; Bailey and Zobrisky, 1968, pp. 108-111; Schoenheimer, 1965, p. 25). It



is assumed that there is no protein tissue storage to supplement any deficiency, although it is true that in reality, small storage may occur (Maynard and Loosli, 1969, p. 148). Comparison of the actual protein carbon content of the animal group to the optimum level is an indicator of the well-being of the group; a protein carbon level that is less than this steady state level is an indicator of malnourishment and reflects on the animal's fitness. Any protein in "milk" or "wool" is not included in the level. Any "excess" body protein present above a certain fraction of this optimum level (parameter  $P_{48c}$ ) is the amount able to be catabolized.

$$\begin{aligned} Z_{42c} &= \text{energy in dietary carbohydrates and fats of} \\ &\quad \text{group } c \text{ during this time unit} \\ &= Z_{37c4} \cdot P_{47c4} + P_{47c5} \cdot Z_{37c5} \quad (\text{III-78}) \end{aligned}$$

$$\begin{aligned} Z_{43c} &= \text{energy in body reserves of } c \text{ during this time} \\ &\quad \text{unit} \\ &= (X_{11c4} - X_{13c4} - X_{14c4}) \cdot P_{47c4} \quad (\text{III-79}) \end{aligned}$$

$$\begin{aligned} Z_{44c} &= \text{catabolizable energy in the dietary protein of} \\ &\quad \text{group } c \text{ at this time unit} \\ &= Z_{37c3} \cdot P_{47c3} \quad (\text{III-80}) \end{aligned}$$

$$\begin{aligned} Z_{45c} &= \text{catabolizable energy in available body protein} \\ &\quad \text{of } c \text{ at this time unit} \\ &= (X_{11c3} - X_{13c3} - X_{14c3} - P_{48c} \cdot X_{16c}) \cdot \\ &\quad \quad \quad \quad \quad \quad \quad \quad \quad \quad P_{47c3} \quad (\text{III-81}) \end{aligned}$$

$$\text{if } Z_{41c} \leq Z_{42c},$$

$$\begin{aligned} Z_{46c4} &= \text{amount of dietary fat carbon remaining for use} \\ &\quad \text{in production by group } c \text{ during this time} \\ &\quad \text{unit} \\ &= Z_{37c4} - (Z_{41c}/Z_{42c}) \cdot Z_{37c4} \quad (\text{III-82}) \end{aligned}$$

$$\begin{aligned} Z_{46c5} &= \text{amount of dietary carbohydrate carbon re-} \\ &\quad \text{maining for use in production by group } c \\ &\quad \text{during this time unit} \\ &= Z_{37c5} - (Z_{41c}/Z_{42c}) \cdot Z_{37c5} \quad (\text{III-83}) \end{aligned}$$

$$R\dot{X}_{01,13} = (Z_{41c}/Z_{42c}) \cdot (Z_{37c4} + Z_{37c5}) \quad (\text{III-84})$$

$$Z_{46cf} = Z_{37cf}, \text{ where } f \in M \quad (\text{III-84a})$$

$$\text{if } Z_{43c} + Z_{42} \geq Z_{41c} > Z_{42c},$$

$$R\dot{X}_{11c4} = (Z_{41c} - Z_{42c})/P_{47c4} \quad (\text{III-85})$$

$$R\dot{X}_{01,13} = (Z_{41c} - Z_{42c})/P_{47c4} + Z_{37c4} + Z_{37c5} \quad (\text{III-86})$$

$$Z_{46c4} = Z_{46c5} = 0 \quad (\text{III-87})$$

$$Z_{46cf} = Z_{37cf}, \text{ where } f \in M \quad (\text{III-87a})$$

$$\text{if } Z_{44c} + Z_{43c} + Z_{42c} \geq Z_{41c} > Z_{43c} + Z_{42c},$$

$$Z_{46c4} = Z_{46c5} = 0 \quad (\text{III-88})$$

$$R\dot{X}_{11c4} = (X_{11c4} - X_{13c4} - X_{14c4}) \quad (\text{III-89})$$

$$\begin{aligned} Z_{46c3} &= \text{amount of dietary protein carbon remaining} \\ &\quad \text{for use in production by group } c \text{ during this} \\ &\quad \text{time unit} \\ &= Z_{37c3} - (Z_{41c} - Z_{42c} - Z_{43c})/P_{47c3} \quad (\text{III-90}) \end{aligned}$$

$$\begin{aligned} Z_{46cf} &= \text{amount of non-carbon constituent } f \text{ remaining} \\ &\quad \text{for use in production by group } c \text{ during this} \\ &\quad \text{time unit, where } f \in M \\ &= Z_{37cf} - (Z_{41c} - Z_{42c} - Z_{43c})/P_{47c3} \cdot P_{14f3} \\ &\quad \quad \quad \quad \quad \quad \quad \quad \quad \quad (\text{III-91}) \end{aligned}$$

Urea and mineral elements are excreted:

$$R\dot{X}_{17cf} = (Z_{41c} - Z_{42c} - Z_{43c})/P_{47c3} \cdot P_{14f3}, \text{ where } f \in M \quad (\text{III-92})$$

$$R\dot{X}_{17c3} = (Z_{41c} - Z_{42c} - Z_{43c})/P_{47c3} \cdot P_{14,13}/P_{45c} \quad (\text{III-93})$$

The remainder of the carbon is respired:

$$\begin{aligned} R\dot{X}_{01,13} &= X_{11c4} - X_{13c4} - X_{14c4} + Z_{37c4} + Z_{37c5} + \\ &\quad (Z_{41c} - Z_{42c} - Z_{43c})/P_{47c3} \cdot (1 - P_{14,13}/P_{45c}) \\ &\quad \quad \quad \quad \quad \quad \quad \quad \quad \quad (\text{III-94}) \end{aligned}$$

$$\text{if } Z_{45c} + Z_{44c} + Z_{43c} + Z_{42c} \geq Z_{41c} > Z_{44c} + Z_{43c} + Z_{42c},$$

$$Z_{46c4} = Z_{46c3} = Z_{46c5} = 0 \quad (\text{III-95})$$

$$R\dot{X}_{11c4} = (X_{11c4} - X_{13c4} - X_{14c4}) \quad (\text{III-96})$$

$$Z_{46cf} = Z_{37cf} - Z_{37c3} \cdot P_{14f3}, \text{ where } f \in M \quad (\text{III-97})$$

$$R\dot{X}_{11c3} = (Z_{41c} - Z_{42c} - Z_{43c} - Z_{44c} - Z_{45c})/P_{47c3} \quad (\text{III-98})$$

$$\begin{aligned} R\dot{X}_{11cf} &= (Z_{41c} - Z_{42c} - Z_{43c} - Z_{44c} - Z_{45c})/P_{47c3} \cdot \\ &\quad \quad \quad \quad \quad \quad \quad \quad \quad \quad P_{14f3}, \text{ where } f \in M \quad (\text{III-99}) \end{aligned}$$

$$\begin{aligned} R\dot{X}_{17cf} &= Z_{37c3} \cdot P_{14f3} + (Z_{41c} - Z_{42c} - Z_{43c} - \\ &\quad \quad \quad \quad \quad \quad \quad \quad \quad \quad Z_{44c} - Z_{45c})/P_{47c3} \cdot P_{14f3} \quad (\text{III-100}) \end{aligned}$$

$$R\dot{X}_{17C3} = Z_{37C3} \cdot P_{14_{13}}/P_{45C} + (Z_{41C} - Z_{42C} - Z_{43C} - Z_{44C} - Z_{45C})/P_{47C3} \cdot P_{14_{13}}/P_{45C} \quad (\text{III-101})$$

$$R\dot{X}_{01_{13}} = X_{11C4} - X_{13C4} - X_{14C4} + Z_{37C4} + Z_{37C3}(1 - P_{14_{13}}/P_{45C}) + (Z_{41C} - Z_{42C} - Z_{43C} - Z_{44C} - Z_{45C})/P_{47C3} \cdot (1 - P_{14_{13}}/P_{45C}) \quad (\text{III-102})$$

if  $Z_{41C} > Z_{45C} + Z_{44C} + Z_{43C} + Z_{42C}$ , animal group c dies.

If the animal group is in aestivation or hibernation, there is a reduced respiration rate for that season (Schmidt-Nielsen, 1961, p. 45; Wood, 1971, p. 128), which is able to be simulated by reducing parameter  $P_{11CM}$  for that season.

**Discussion**—Extensive studies have been performed on the equation  $aX^b$  for homeotherms and it has been found that in basal metabolism, the metabolic size exponent for mammals is approximately 0.75 (Kleiber, 1961, p. 212; Maynard and Loosli, 1969, p. 414), while the proportionality coefficient equals 70 kcals per day per unit metabolic size when X is the wet weight of the animal in kilograms. This constant can be adjusted so that the relation holds when X is measured in grams of carbon.

let  $\psi$  = fraction of protein in the animal

$\beta$  = fraction of fat in the animal

then using an average carbon to protein ratio of 0.53, and an average carbon to fat ratio of 0.76 (Kleiber, 1961, p. 43),

weight of carbon in X =  $(\psi(0.53) + \beta(0.76))X = \phi X$

The composition of normal and starved animals is similar with respect to the relative percentages of fat and protein in the body (Kleiber, 1961, p. 58), and thus this conversion factor  $\phi$  should not vary greatly with the nutritional standing of the animal.

let  $X_w$  = wet weight of animal in kilograms

$X_c$  = weight of animal in grams of carbon

then,  $70 X_w^{0.75} = 70 (X_c/\phi \cdot 1000)^{0.75}$

Thus the basal metabolism coefficient =  $70/(1000 \cdot \phi)^{0.75}$  kcals per  $(gC)^{3/4}$ .

Now, to obtain the coefficient a, an activity cost and inefficiency cost of catabolism must be multiplied with the basal metabolism coefficient. For other animal groups, the same types of calculations can be carried through. Thus the

coefficients  $P_{11CM}$ ,  $P_{12CM}$  of III (III-68) are determined. The coefficient  $P_{12C}$  of II (II-33) is exactly the same as  $P_{12CM}$  of III in value. To obtain  $P_{11C}$  of II (II-33) the energy respired per unit metabolic size, in carbon, ( $P_{11CM}$  of III) must be converted to grams of carbon respired per unit metabolic size (measured in carbon). Here it is necessary to make an assumption regarding the type of tissue the animal is catabolizing for energy (Kleiber, 1961, p. 89).

Consider fat; there are 0.76 g of carbon per gram of fat, and 9.5 kcal of energy per gram of fat. Thus there are 0.76/9.5 (= 0.079) g of carbon respired per kcal of energy released. Similarly for carbohydrates, there is 0.42/4.0 (= 0.105) g of carbon respired per kcal of energy. For protein, 0.53/4.8 (= 0.110) g of carbon are respired per kcal of energy released (Kleiber, 1961, pp. 43, 83, 125).

Since the protein and carbohydrate values are very close, the estimate of the amount of carbon respired per unit of energy respired, has to be based on the amount of fat the animal will use. Observation of the type of diet and whether or not the animal will be fasting (e.g., hibernation) should guide the choice. Once an overall ratio of grams of carbon respired per kcal of energy is obtained, this can be multiplied by  $P_{11CM}$  of III to obtain  $P_{11C}$  of II.

The linear relationship in ANIMAL I is an approximation to the curvilinear form used in II. If the amount of carbon respired per time unit by an animal of each group of the simulation is known ( $\nu_c$ ) when that animal has a biomass approximately equal to that at the beginning of the simulation (perhaps determined by  $aX^b$  relationship of II), then  $P_{10}$  (I-25) of ANIMAL I can be determined.

$$\text{total carbon respired by community} = \sum_c \nu_c \cdot \eta_c$$

$$P_{10} = \left( \frac{\sum_c \nu_c \eta_c}{\sum_c a_c} \right)$$

where the amount of carbon in the animal group =  $a_c$

population of the animal group =  $\eta_c$

This parameter should be calculated when the average weights of the animals are close to those occurring at the start of the simulation. This is because the linear approximation of the respiration relation overestimates the amount of carbon respired for animals with biomasses higher than those used in the above relation, and underestimates the amount respired for those with lower biomasses. In a short simulation the biomasses would not be expected to fluctuate rapidly, and so the amount of carbon respired as predicted by the linear relation from I would be close to reality. In a very long simulation over years, there are likely to be as many instances when the individual's biomass is higher than the initial value, as there are instances when the individual's biomass is lower than the initial value. Therefore, the calculation above is a reasonable compromise.

## GROWTH

Foods cannot be used in the form in which they are consumed; they undergo enzymatic hydrolysis to simpler substances such as simple sugars, fatty acids and amino acids. These simple compounds can be oxidized (deaminated or transaminated in the case of amino acids) to supply energy, releasing carbon dioxide and nitrogenous wastes (Wood, 1971, pp. 17-26; Schmidt-Nielsen, 1961, p. 39; Maynard and Loosli, 1969, p. 143; Chapman, 1969, Chap. VI). They can also be used as "building blocks" to form new tissues. Consider protein digestion. The nitrogen assimilated is considered to be totally from food protein and is thus found, in the course of digestion, combined with carbon and other elements in amino acids. These amino acids are essential to protein synthesis which is, in essence, the linking of amino acids. The carbon in amino acids is labeled "protein carbon" in the intake, if the foods consumed are only of plant origin. With animal foods, structural tissues of the prey are proteinaceous and thus, in these cases, "structural carbon" can also be in compound with nitrogen in the form of amino acids. It can be assumed that the nitrogen content of food proteins and animal body proteins is approximately the same (Kleiber, 1961, p. 42), so that the carbon (be it labeled "protein carbon" or "structural carbon") assimilated with the nitrogen as protein, is present in the nitrogen:carbon ratio needed in synthesis of proteinaceous animal material. Any excess amino acids not used in protein synthesis are deaminated (or transaminated) with the nitrogen being excreted in urea, uric acid or occasionally other nitrogenous compounds. The carbon from the deaminated amino acids enters the tricarboxylic acid cycle. Consider lipid and carbohydrate digestion where the reserve carbon in the intake is an element. These compounds are digested to fatty acids, glycerol and simple sugars which can be further catabolized to compounds in the tricarboxylic acid cycle (acetyl coA). The structural carbon from plant foods is largely found in carbohydrates which are broken down to simple sugars and later acetyl coA, entering the tricarboxylic acid cycle. The structural carbon assimilated from animal foods is protein and the digestive reactions undergone are described above.

The following paragraphs refer to ANIMAL I and II only.

All the nitrogen assimilated is potentially available for use in the growth process. The protein carbon and/or structural carbon are used in conjunction with the nitrogen (since they would be part of the amino acids prior to deamination) for protein synthesis. The reserve carbon, structural carbon and the amount of protein carbon remaining after protein synthesis all enter the tricarboxylic acid cycle where no distinction is made between their origins. Since, in Versions I and II, the energetic differences between proteins, fats and carbohydrates are not considered, these three carbon components can be considered to form a "pool" of carbon which can be used in all tissue building occurring in these

two versions. The synthesis of animal fats begins with acetyl coA in the tricarboxylic acid cycle. Thus all the assimilated carbon remaining (not used in synthesis of proteinaceous material or in combination with the nitrogenous wastes) is available for fat synthesis in I and II (Maynard and Loosli, 1969, pp. 107, 84, 105, 135, 147; Chapman, 1969, p. 67).

The assimilated ash can be used in synthesis of tissues in growth. The mineral elements needed for protein synthesis are assumed to be associated with the nitrogen and carbon in the amino acids. The skeleton in mammals is not, in I and II, considered to be a storage area of mineral elements. Thus, the "pool" of minerals is only decremented by use of the minerals in the synthesis of proteinaceous and structural tissues during growth. The remainder is excreted. This implies that the dynamic exchange of minerals between the skeleton and the tissues, in mammals, is at equilibrium. That is, there is no net loss or gain of minerals from the body of an adult animal (except if protein deficiencies should occur; Maynard and Loosli, 1969, p. 165).

## ANIMAL I

In this model the chemical composition of the animal community remains constant -- there are constant ratios of each chemical constituent to the total carbon. Any addition of chemical constituents to the animal biomass must be done so as not to change these proportions.

The maximum weight gain per unit of carbon assimilated will occur when the ratios of minerals assimilated to the carbon assimilated are the same as, or greater than, those of the animal composition. In these cases there are no mineral-limiting conditions and the gain equals the amount of carbon assimilated together with the amount of minerals that leave the animal composition unchanged. But in certain cases, insufficient minerals will be assimilated so that if the assimilated carbon was added to the biomass with these amounts of minerals, the animal composition would change. So the weight gain is reduced and will be less than the maximum. It will consist of the amount of carbon and other minerals that with the limiting mineral can be added to the biomass and not change the relative chemical composition of the animal community.

$Z_{27f}$  = ratio of chemical constituent f to total carbon in animal chemical composition

$$= (X_{11cf} / \sum_{f \in C} X_{11cf}) \text{ (for any group c)} \quad \text{(I-29)}$$

$Z_{28cf}$  = amount of chemical constituent f that (in the absence of limiting conditions) will be added to c per time unit

$$= Z_{27f} \cdot \sum_{f \in C} Z_{22cf} \quad \text{(I-30)}$$

from equation I-22

$$Z_{29} = \text{factor by which weight gain is reduced, if a mineral is limiting}$$

$$= \min_{f \in M} (1, (Z_{22cf}/Z_{28cf})) \quad (\text{I-31})$$

$$Z_{30cf} = \text{amount of chemical constituent } f \text{ that is added to } c \text{ per time unit}$$

$$= Z_{29} \cdot Z_{28cf} = G\dot{X}_{11cf} \quad (\text{I-32})$$

If there are any amounts of mineral elements remaining that have been assimilated but not incorporated into the weight gain these are excreted. Any excess carbon is respired.

$$G\dot{X}_{217f} = \sum_c (Z_{27cf} - Z_{30cf}), \text{ where } f \in M \quad (\text{I-33})$$

$$G\dot{X}_{217f} = 0, \text{ where } f \in C \quad (\text{I-34})$$

$$G\dot{X}_{0113} = \sum_c \sum_{f \in C} (Z_{22cf} - Z_{30cf}) \quad (\text{I-35})$$

### ANIMAL II

In this model, the reserve carbon constituent of the animal group is able to be used in the building of new tissues, together with the assimilated carbon and mineral elements (Schmidt-Nielsen, 1961, p. 10). Synthesis of "protein tissue" to replace that which was respired is the first part of this process. As mentioned previously ("Respiration") the "protein tissue" is considered to have constant ratios of mineral elements to carbon (protein carbon); input parameters  $P_{14f3}$ . Thus an inadequate diet, either in quantity or quality, could affect "protein" synthesis. Insufficient mineral(s) to combine with the carbon necessary to replace that protein carbon respired results in a "protein" deficiency. Insufficient carbon available for the synthesis in comparison to the amount of protein carbon respired also would result in a deficiency of "protein." The assumption is made that there is no storage of "protein" in the animals, which is a close approximation to reality (Maynard and Loosli, 1969, p. 145; Wood, 1971, p. 80). Thus, if the animal is not producing a special nitrogenous product (e.g., body tissue, milk, fetus) the only need for "protein" synthesis is to replace that which was respired in maintenance.

$$Z_{30c3} = \text{amount of carbon available for building of new tissues in } c \text{ per time unit} \quad (\text{II-44})$$

$$= X_{11c4} + \sum_{f \in C} Z_{24cf} \quad (\text{II-44})$$

from equation II-30

$$Z_{30cf} = \text{amount of mineral element } f \text{ available for building of new tissues in } c \text{ per time unit, where } f \in M$$

$$= Z_{24cf} \quad (\text{II-45})$$

$$Z_{31c3} = \text{amount of carbon synthesized to "protein tissue" by } c \text{ in response to respiration losses, per time unit}$$

$$= \min_{f \in [M,3]} (Z_{27c3}, (Z_{30cf}/P_{14f3})) \quad (\text{II-46})$$

from equations II-37, 39

$$Z_{31cf} = \text{amount of mineral element } f \text{ synthesized to "protein tissue" by } c \text{ in response to respiration losses per time unit, where } f \in M$$

$$= Z_{31c3} \cdot P_{14f3} \quad (\text{II-47})$$

$$Y\dot{X}_{31cf} = Z_{31cf}, \text{ where } f \in [M,3] \quad (\text{II-48})$$

$$Z_{32cf} = \text{amount of mineral element } f \text{ available to } c \text{ for growth following respiratory "protein" synthesis per time unit, where } f \in M$$

$$= Z_{30cf} - Z_{31cf} \quad (\text{II-49})$$

$$Z_{32c3} = \text{amount of carbon available to } c \text{ for growth following respiratory "protein" synthesis per time unit}$$

$$= Z_{30c3} - Z_{31c3} \quad (\text{II-50})$$

For each animal group, growth of each constituent occurs at a constant rate providing there are sufficient chemical reserves. This growth rate is input parameter  $P_{15c}$ . If there are insufficient raw materials (carbon and minerals) the growth is less than the potential maximum designated by the input parameter.

$$Z_{33cf} = \text{maximum amount of constituent } f \text{ that can be added as growth per time unit, to } c$$

$$= P_{15c} \cdot X_{11cf} \quad (\text{II-51})$$

$$Z_{34c} = \text{maximum amount of carbon that can be added as growth to } c \text{ per time unit}$$

$$= \sum_{f \in C} Z_{33cf} \quad (\text{II-52})$$

$$Z_{35c} = \text{factor by which growth is reduced if there are insufficient raw materials}$$

$$= \min_{f \in [M]} (1, (Z_{32cf}/Z_{33cf}), (Z_{32c3}/Z_{34c})) \quad (\text{II-54})$$

$$Z_{36cf} = \text{amount of constituent } f \text{ added to group } c \text{ in growth per time unit}$$

$$= Z_{35c} \cdot Z_{33cf} \quad (\text{II-55})$$

Any excess mineral constituents are excreted. These represent the by-products of oxidation of the foodstuffs -- e.g., urea, salts (Schmidt-Nielsen, 1961, p. 59; Wood, 1971). Any carbon left in the "pool" is added to the reserves of the animal group as fat (reserve carbon; Schmidt-Nielsen, 1961, p. 10).

$$G\dot{X}_{217f} = \sum_c (Z_{32cf} - Z_{36cf}), \text{ where } f \in M \quad (\text{II-57})$$

$$G\dot{X}_{217f} = 0, \text{ where } f \in C \quad (\text{II-58})$$

$$G\dot{X}_{11cf} = Z_{36cf} \quad (\text{II-59})$$

$$F\dot{X}_{11c4} = Z_{32c3} - \sum_{f \in C} Z_{36cf} \quad (\text{II-60})$$

### ANIMAL III

In this model there are four growth processes simulated; juvenile body growth, fetal tissue growth, "milk" production, and "wool" production. Protein re-synthesis, described below, fattening and mineral storage may also occur. The four types of growth mentioned above are able to occur concurrently in an animal group in any season. The actual amounts which are produced depend on the amounts of raw materials -- dietary fats, carbohydrates and proteins, reserve tissues from the animal's body, and, as mentioned in "Respiration," a part of the labile protein tissue of the animal. The amount of energy available also determines the actual amount of production, as does the nutritional standing of the animal group. Since the three basic compounds, fat, carbohydrates and proteins, yield differing amounts of energy per unit of compound catabolized, and since energy is being explicitly traced in Version III, the carbon from the raw materials is not considered to form a "pool" from which carbon is available for synthesis, as happens in Versions I and II. The production process is described later in this section.

First, consider each type of growth and the potential amounts to be produced each time unit, beginning with fetal tissue growth. The fetuses are considered to be animal groups separate from the breeding groups although respiration of the fetuses is included in the mother group's respiration (refer to the "Respiration" section). The reproductive process is described in "Reproduction and Population Changes." The fetal growth period in viviparous animals is the development time of the embryo up to birth. In oviparous animals, it is the period during which the eggs form prior to deposition, while in ovoviparous animals it is the time during which eggs form prior to any development of the embryo within. In this latter case, mortality of adults after the "fetal period" should also reflect mortality in the egg group, since the eggs would actually be developing with the mother animal, and death in the breeding group would infer death in the egg group. The fetal growth period may constitute several seasons of the breeding group, but the

restriction is made that the maximum potential growth rate for each carbon constituent per unit steady state protein carbon (input parameters  $P_{16cfm}$ ) be constant over the successive fetal growth seasons. This is an approximation to reality, since different parts of an animal's body develop at different rates (Bailey and Zobrisky, 1968, p. 108). However, since it is unlikely that there will be much data on fetal growth rates, the simpler approach of constant growth rates was taken. These may be calculated as described in the following "Discussion" section. On the first day of the fetuses' growth, i.e., the first day of the season when parameter  $P_{36cm}$  has the value one, a very small amount of protein carbon (parameter  $P_{49}$ ) is transferred from the mother group to the fetal group, causing the fetal steady state protein level to be set at this amount of protein carbon. During this time unit, the population of the fetal group is set at the maximum postulated number of fetuses per individual gravid animal for this season ( $P_{25cm}$ ).

if  $t = P_{43cm}$  and  $P_{36cm} = 1$ ,

$$C\dot{X}_{11b3} = P_{49} = C\dot{X}_{11c3} = C\dot{X}_{16b} \quad (\text{III-103})$$

where b is the numerical designation of the group that constitutes the fetuses of c

$$C\dot{X}_{11bf} = P_{49} \cdot P_{14f3} = C\dot{X}_{11cf}, \text{ where } f \in M \quad (\text{III-103a})$$

$$C\dot{X}_{12\Sigma} = P_{25cm} \cdot X_{12c} \quad (\text{III-104})$$

The potential growth increments per time unit are calculated on the fetal group's steady state protein level, modified by the number of fetuses per individual gravid animal. The more fetuses born per breeding individual, the less each weighs (Maynard and Loosli, 1969, p. 498). Figure 10 illustrates the relationship (parameter  $P_{50c}$  indicates the "curvature" of the relationship). Thus the growth rates must be calculated so as to predict the birthweight of a single individual (see "Discussion" section following). This birthweight is the maximum weight at which an individual can be born, or in the case of eggs, the maximum weight that an egg will weigh upon formation. The actual birthweight will depend on the nutritional status of the mother group, as well as the number born.

A breeding group whose protein carbon level is lower than that of the optimum level (protein deficient) will have less labile protein tissue available for potential use by the fetuses, and thus may have undersized young and/or a reduced number of young. The number of young born, or in the case of eggs, the number deposited, does not necessarily equal the maximum postulated number. Malnutrition, judged by the protein carbon deficit of the fetuses, may cause death and reabsorption (Maynard and Loosli, 1969, p. 499). See the "Mortality" section for further details.

If during a period of malnutrition, the growth of the fetus is slowed, it can potentially compensate once food becomes plentiful; the potential growth increments are adjusted so that the fetus regains its optimum weight and chemical composition. Each carbon constituent has accompanying amounts of non-carbon constituents in the ratios given by the parameters  $P_{14ft}$ . Thus the potential amounts of each constituent are calculated. The protein steady state level of the fetal group is increased during each time unit. Figures 10b and 10c illustrate the form of the growth curve, when the number of fetuses is constant.

$$Z_{47bf} = \text{amount of constituent } f \text{ by which animal group } b \text{ is below the level of } f \text{ corresponding to maximum growth, where } f \in C$$

$$= \max(0, (X_{16b} - X_{11b3} + X_{13b3} + X_{14b3}) \cdot P_{16bfm'} / P_{16b3m'}) \quad (\text{III-105})$$

where  $m'$  is the numerical designation of the season of fetal group  $b$  corresponding to season  $m$  of mother group  $c$

$$Z_{48b} = \text{factor by which growth increments of } b \text{ are decreased due to the number of fetuses per breeding individual of } c$$

$$= \exp(-P_{50c} \cdot \max(0, X_{12b}/X_{12c} - 1)) \quad (\text{III-106})$$

$$Z_{49bf} = \text{potential growth increment of constituent } f \text{ in fetal group } b \text{ per time unit, when } f \in C$$

$$= (X_{16b} \cdot P_{16bfm'} + Z_{47bf}) \cdot Z_{48b} \quad (\text{III-107})$$

$$Z_{49bf} = \sum_{t \in C} Z_{49bt} \cdot P_{14ft}, \text{ where } f \in M \quad (\text{III-108})$$

$$G\dot{X}_{16b} = X_{16b} \cdot P_{16b3m'} \cdot Z_{48b} \quad (\text{III-109})$$

There is a constant amount of energy per unit carbon associated with each of the potential increments of carbon constituents ( $P_{51f}$ ). Thus the total amount of energy incorporated in the potential growth is calculable. The amount of energy needed to produce this growth (excluding the energy in the tissue) is the energy needed to overcome the inefficiency of anabolism, given by parameter  $P_{52c}$ .

$$Z_{50c} = \text{energy needed by breeding group } c \text{ to form the potential growth increments (excluding the energy in the tissue) of fetal group } b, \text{ per time unit}$$

$$= \left( \sum_{f \in C} Z_{49bf} \cdot P_{51f} \right) \cdot P_{52c} \quad (\text{III-110})$$

The second form of growth is juvenile tissue growth. This may occur in an animal group while fetal tissues are also being formed. The amounts of each carbon constituent per

time unit that will potentially be added to the juvenile group biomass, are constant fractions (parameters  $P_{16cfm}$ ) of the difference between the group's current steady-state protein level, and the optimal steady-state protein level

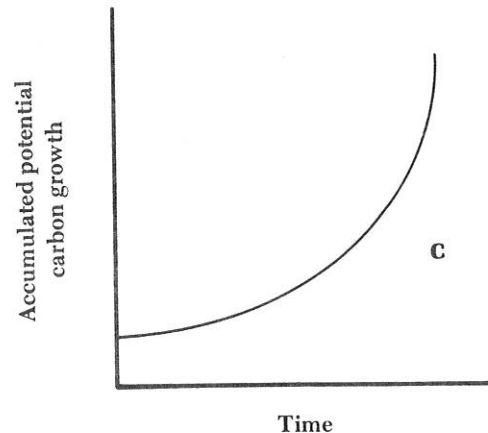
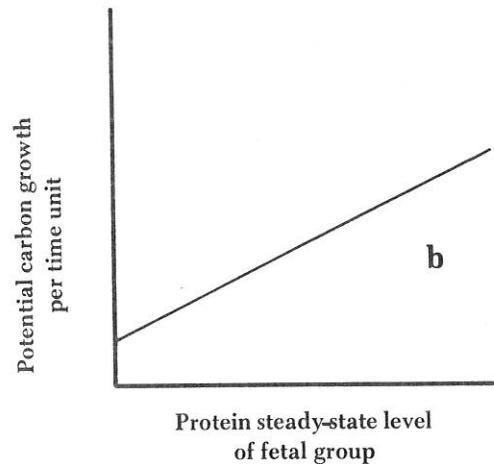
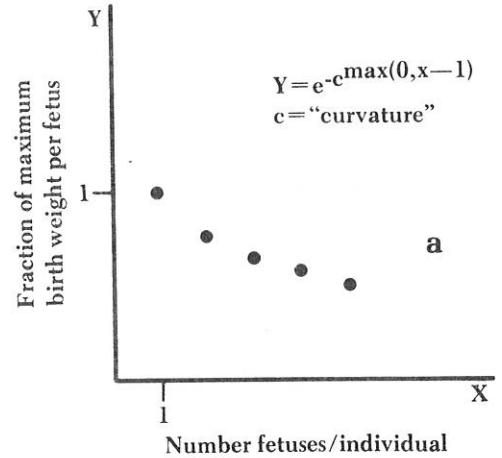


Figure 10. (a) birth weight vs. fetus numbers, ANIMAL III; (b and c) fetal growth, ANIMAL III.

( $P_{18c}$ ) it will have when mature. When the juvenile group is very young this difference is large; therefore the potential growth increments per time unit are large. As the animals grow, the difference decreases and the potential increments become smaller, until they are approximately zero (if the animals reach mature size prior to the end of the growth period). The restriction is made that the relative growth rates of each carbon constituent remain constant over the growth seasons. However, it is recognized that different tissues mature at different rates (Widdowson, 1968), and this situation can be approximated by appropriately adjusting the growth parameters, since the approach to optimal mature size and composition is asymptotic. The following "Discussion" section amplifies this point. Figures 11a and 11 b illustrate the growth relationships, given that there are no limiting conditions.

As with fetuses, malnutrition may stunt growth because the potential increments desired per time unit cannot be produced due to the lack of raw materials and energy. If later during the designated juvenile growth season(s), food becomes plentiful, the juvenile group can regain the weight and chemical composition that it would have had if the potential increments had been met (Maynard and Loosli, 1969, p. 445). It is assumed that once the growth period is over, an underweight juvenile group remains undersized with no further structural growth. However, since the greater proportion of structural growth occurs early in the development period of the juvenile (Maynard and Loosli, 1969, p. 439), the undernourished animal has the majority of this period in which to regain full structural growth (the growth parameters can be set to accomodate this feature). For mammals at least, several studies have reported that in cases of undernutrition, the growth period is extended with the undernourished animals eventually reaching the normal size and weight. Early, severe malnutrition has been noted to cause permanent stunting (Maynard and Loosli, 1969, p. 445). Thus this model approximates the observed situation in that the growth period is limited. It would take severe stunting (i.e., large differences between actual increments of growth and the potential increments) in the early phases of growth to cause the individual to be permanently stunted since it is early in the growth period that the largest increments in structural tissue growth occur.

The potential increments in the non-carbon constituent growth are calculated from the carbon constituent increments through use of the ratios  $P_{14ft}$  -- each carbon constituent having a constant amount of non-carbon constituents associated with it.

The protein steady state level of the juvenile group grows with it, and equals the sum of the birth protein steady state level and the potential growth increments of protein carbon. At the end of the growing period, the steady state level per individual is made equal to the input parameter  $P_{18c}$ .

let  $P_{53c'm'}$  = numerical designation of the fetal group of mother group  $c'$  in season  $m'$

$Z_{51cf}$  = 0 if birth of  $c$  has not occurred yet, where  $f \in C$   
 = amount of carbon constituent  $f$  in an individual of group  $c$  at birth if birth has occurred

if  $P_{16cfm} \neq 0$  and  $c \neq P_{53c'm'}$  for any  $c', m'$ ,

$$Z_{51cf} = 0 \tag{III-111}$$

The growth occurring in this season is fetal growth.

if  $P_{16cfm} \neq 0$  and  $c \neq P_{53c'm'}$  for any  $c', m'$ ,

if  $t = P_{43cm}$ ,

$$Z_{51cf} = (X_{11cf} - X_{13cf} - X_{14cf})/X_{12c}, \text{ where } f \in C \tag{III-112}$$

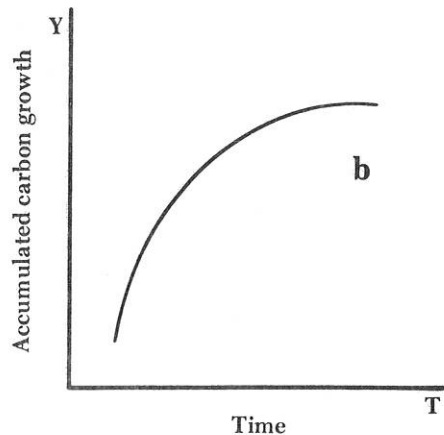
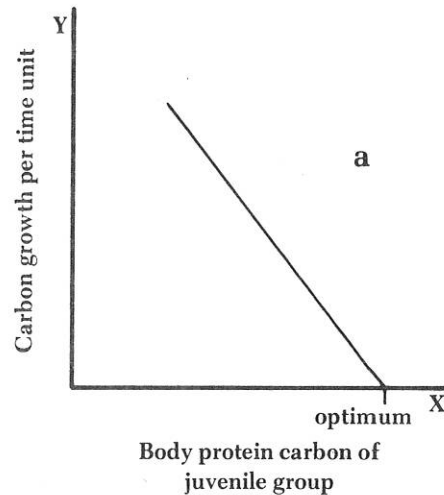


Figure 11. (a and b) juvenile growth, ANIMAL III.

The growth occurring in this season is juvenile growth.

$$Z_{52cf} = \text{amount of constituent } f \text{ by which group } c \text{ is below the level of } f \text{ corresponding to maximum growth, where } f \in C$$

$$= \max(0, (P_{16cfm}/P_{16c3m}) \cdot (X_{16c} - Z_{51c3} \cdot X_{12c}) + Z_{51cf} \cdot X_{12c} - (X_{11cf} - X_{13cf} - X_{14cf}))$$

(III-113)

$$Z_{53cf} = \text{potential growth increment of constituent } f \text{ in juvenile group } c \text{ per time unit, where } f \in C$$

$$= P_{16cfm}(X_{12c} \cdot P_{18c} - X_{16c}) + Z_{52cf} \quad \text{(III-114)}$$

$$Z_{53cf} = \sum_{t \in C} Z_{53ct} \cdot P_{14ft}, \text{ where } f \in M \quad \text{(III-115)}$$

As in the fetal growth process, there is a constant amount of energy per unit carbon associated with each of the potential increments of carbon constituents ( $P_{51f}$ ). The amount of energy needed to produce the juvenile growth increments (excluding the energy in the tissue) is the energy needed to overcome the inefficiency of anabolism, given by parameter  $P_{52c}$ . In this model it is assumed that the inefficiencies of growth, maintenance and tissue production are equal (Kleiber, 1961, p. 291).

$$Z_{54c} = \text{energy needed by group } c \text{ to form the potential growth increments (excluding the energy in the tissue) per time unit}$$

$$= \left( \sum_{f \in C} Z_{53cf} \cdot P_{51f} \right) \cdot P_{52c} \quad \text{(III-116)}$$

$$G \dot{X}_{16c} = P_{16c3m} \cdot (X_{12c} \cdot P_{18c} - X_{16c}) \quad \text{(III-117)}$$

The production of "milk" is also simulated in Version III. The restriction is made that an animal group ( $c'$ ) can be nursed over one season ( $m'$ ) only, due to the method of calculation of the length of the nursing period (see III-1). For the first part of the nursing period (designated by parameter  $P_{42c'}$ ) the potential amount of "milk" produced depends on the demand of the group being nursed (Elsley, 1971, p. 396). This demand is a constant fraction ( $P_{1c'm'}$ ) of the body structural carbon of this group. As the juvenile group grows, the body structural carbon increases, and thus the "milk" demand increases until the end of the first part of the nursing period, when it reaches a maximum. From this maximum potential production level, there is a linear decrease to zero in the amount of "milk" produced per unit body structural carbon over the rest of the nursing period. There is an upper limit to the production level of an animal, equal to a constant fraction ( $P_{54c}$ ) of the animal's body structural carbon. This implies that this limit is dependent on the size of the animal. Figure 12a represents the relationship between potential production and time if the population of the group being nursed does not change. Figure 12b represents the

relationship between the potential production per unit body structural carbon of the young animal group and time.

As mentioned in the "Feeding" section, the decrease in "milk" production stimulates weaning of the young.

if  $P_{35c'm'} = c$  for any  $c', m'$ ,

Group  $c$  is suckling group  $c'$  during its season  $m'$ .

if  $t \leq P_{42c'} \cdot Z_{52c'} + P_{43c'm'}$  (refer to "Feeding" section),

$$Z_{55c} = \text{amount of carbon potentially produced in "milk" by group } c \text{ per time unit}$$

$$= \min(P_{1c'm'} \cdot (X_{11c'5} - X_{13c'5} - X_{14c'5}), P_{54c} \cdot (X_{11c5} - X_{13c5} - X_{14c5})) \quad \text{(III-118)}$$

if  $t > P_{42c'} \cdot Z_{52c'} + P_{43c'm'}$ ,

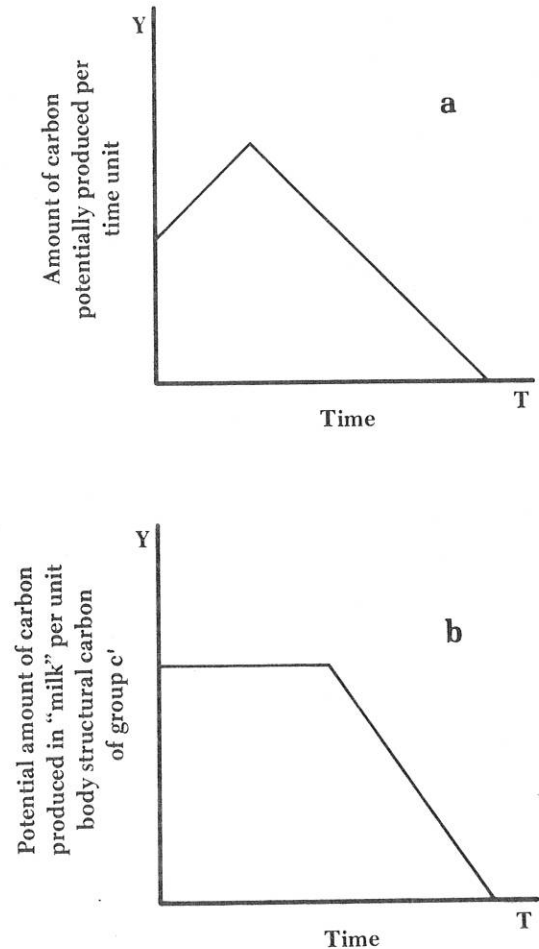


Figure 12. (a and b) "milk" production -- ANIMAL III.



$$Z_{55c} = \min[(P_{1c'm'} - P_{1c'm'}(t - P_{42c'} \cdot Z_{82c'} - P_{43c'm'}) / ((1 - P_{42c'}) Z_{82c'}) \cdot (X_{11c'5} - X_{13c'5} - X_{14c'5}), P_{54c} \cdot (X_{11c'5} - X_{13c'5} - X_{14c'5})] \quad (\text{III-119})$$

Note that the "stimulation" for the beginning of "milk" production is the presence of the young. If there were no individuals to nurse, no "milk" production would occur. If in the decline period, there are no young to consume the "milk" produced, production stops (Maynard and Loosli, 1969, p. 523), and any "milk" stored in the nursing animal is reabsorbed. The actual amounts of "milk" produced depend upon the nutritional status of the nursing group. Protein deficiencies may cause a lowering of production, as may undernourishment (Maynard and Loosli, 1969, p. 547). The demand for non-carbon constituents is usually relatively high in "milk" production, and thus it is in this process that significant amounts of mineral constituents may be withdrawn from the storage in the skeleton of the animal group, at least in the case of mammals (Maynard and Loosli, 1969, p. 550).

The composition of "milk" is considered constant for each animal group ( $P_{21cf}$ ); i.e., the ratio of each chemical constituent to the total carbon is constant.

$$\begin{aligned} Z_{56cf} &= \text{amount of constituent } f \text{ potentially produced in} \\ &\quad \text{"milk" per time unit, by group } c \\ &= Z_{55c} \cdot P_{21cf} \end{aligned} \quad (\text{III-120})$$

There is energy associated with each unit of carbon potentially produced as "milk." If the reserve carbon in the "milk" was all fat, then the amount of energy per unit carbon constituent would be the same as those for the body tissues ( $P_{51f}$ ). However, as mentioned in the "Feeding" section, the reserve carbon in "milk" is partially from carbohydrates and partially from fats. Thus the energy per unit reserve carbon in "milk" is smaller than the energy per unit reserve carbon in body tissues. Knowing the ratio of carbon from fats to total carbon from carbohydrates and fats ( $P_{55c}$ ), the former ratio of energy to reserve carbon can be computed. The anabolism inefficiency is assumed to be the same as for maintenance and growth ( $P_{52c}$ ).

$$\begin{aligned} Z_{57c} &= \text{amount of energy needed by } c \text{ to produce the} \\ &\quad \text{potential amounts of "milk" per time unit} \\ &\quad \text{(excluding the energy in the tissue)} \\ &= \left[ \sum_{f \in C} Z_{56cf} \cdot P_{51f} + Z_{56c4} \cdot P_{55c} \cdot P_{514} + Z_{56c4} \cdot \right. \\ &\quad \left. (1 - P_{55c}) \cdot P_{516} \right] \cdot P_{52c} \end{aligned} \quad (\text{III-121})$$

where

$P_{516}$  = energy per unit of carbon from carbohydrates

$P_{514}$  = energy per unit of carbon from fats

The fourth type of growth is that of "wool". The amount of carbon in "wool" potentially produced per time unit is a constant fraction of the body structural carbon of the animal group ( $P_{56cm}$ ). Thus the production is dependent on the size of the animal group, as measured by its structural weight. The composition of "wool" is considered constant for each animal group; i.e., the ratio of each chemical constituent to the total carbon is constant ( $P_{19cf}$ ).

$$\begin{aligned} Z_{58cf} &= \text{amount of constituent } f \text{ potentially produced in} \\ &\quad \text{"wool" per time unit by group } c \\ &= (P_{56cm} \cdot (X_{11c'5} - X_{13c'5} - X_{14c'5})) \cdot P_{19cf} \end{aligned} \quad (\text{III-122})$$

As was the case for "milk", any reserve carbon in "wool" may not be purely carbon from fat tissues in the "wool" -- there may be some carbohydrates. Thus with the ratios of fat carbon to total reserve carbon for "wool" of the animal group ( $P_{57c}$ ), and using the ratios of energy per unit carbon constituent defined in the previous growth processes ( $P_{51f}$ ), the total energy needed to form the "wool" can be estimated. The inefficiency of anabolism is considered to be the same as for all the previous growth processes ( $P_{52c}$ ).

$$\begin{aligned} Z_{59c} &= \text{amount of energy needed by } c \text{ to produce the} \\ &\quad \text{potential amounts of "wool" per time unit} \\ &\quad \text{(excluding the energy in the tissue)} \\ &= \left[ \sum_{f \in C} Z_{58cf} \cdot P_{51f} + Z_{58c4} \cdot P_{57c} \cdot P_{514} + \right. \\ &\quad \left. Z_{58c4} \cdot (1 - P_{57c}) \cdot P_{516} \right] \cdot P_{52c} \end{aligned} \quad (\text{III-123})$$

Thus, the maximum amounts of each chemical constituent and the energy needed to synthesize the maximum amounts of tissues are calculated. Since amino acids are the precursors of proteins, only digested proteins can be used to synthesize the protein components of the tissues (microbial production of protein being ignored). Reserve tissues (fat or carbohydrate) can be synthesized from any of the three components -- protein, fat or carbohydrate. Energy can be obtained for any or all of these compounds.

$$\begin{aligned} Z_{61cf} &= \text{total amount of constituent } f \text{ needed to} \\ &\quad \text{satisfy all potential amounts of growth and} \\ &\quad \text{production by } c \text{ per time unit, where } f \in M \\ &= Z_{49bf} + Z_{53cf} + Z_{56cf} + Z_{58cf} \end{aligned} \quad (\text{III-124})$$

from equations III-108, 115, 120, 122 (where b is the fetal group of c in this season)

$$Z_{61c3} = \text{total amount of carbon from proteinaceous tissue needed to satisfy all potential amounts of proteinaceous growth and production by c per time unit}$$

$$= \sum_{f=3,5} (Z_{49bf} + Z_{53cf} + Z_{56cf} + Z_{58cf}) \quad (\text{III-125})$$

from equations III-107, 114, 120, 122

$$Z_{61c4} = \text{total amount of carbon from fats or proteins or carbohydrates needed to satisfy all potential amounts of reserve tissue growth or production by c per time unit}$$

$$= Z_{49b4} + Z_{53c4} + Z_{56c4} + Z_{58c4} \quad (\text{III-126})$$

from equations III-107, 114, 120, 122

$$Z_{62c} = \text{amount of energy needed to synthesize the potential amounts of growth and production (excluding energy in the tissues) of c per time unit}$$

$$= Z_{50c} + Z_{54c} + Z_{57c} + Z_{59c} \quad (\text{III-127})$$

from equations III-110, 116, 121, 123

The four types of growth discussed previously all occur concurrently, but the extent to which each occurs is dependent on the amounts of available raw materials and the condition of the animal group. The potential increments are calculated assuming the animal group to be in optimum condition, i.e., to have a protein carbon level equal to the optimum protein carbon level of the group. If this is so, and the protein intake of the animal group is sufficient to meet the potential growth increment requirements, the potential increments are the actual increments, assuming no other limiting conditions such as lack of energy, minerals or carbon. If the animal group is not in optimum condition, the protein intake has to exceed the requirements for the potential production by the amount of protein carbon deficit in order to attain the maximum growth increments (once again supposing that there are no other limiting conditions). However, when protein does become limiting, i.e., the animal begins to draw upon its body protein tissue without replacement occurring, there is an allocation of the available protein to the different forms of growth which is only partially dependent on the calculated potential increments. Embryo growth, for example, is only slightly affected by parental malnutrition, unless it is very severe (Montsgaard, 1969). "Wool" production is not shut off during periods of negative protein balance in the animal

although it is somewhat reduced (Maynard and Loosli, 1969, p. 475; Lorin Harris, pers. comm.; Mitchell, 1962, p. 365). "Milk" production is quickly affected by lack of available protein (Maynard and Loosli, 1969, p. 522; Flatt and Moe, 1971, p. 341). Figure 13 represents the form of the relationships between the proportion of maximum growth (as given by the potential increments) desired, and the factor indicating the protein status of the animal, assuming there are no other limiting conditions. The protein carbon available is the dietary protein carbon plus the "excess" protein carbon of the animal group above a certain fraction ( $P_{48c}$ ) of the optimum protein carbon level.

$$Z_{63c} = \text{available protein carbon of group c per time unit}$$

$$= Z_{46c3} + (X_{11c3} - X_{13c3} - X_{14c3} - P_{48c} \cdot X_{16c}) \quad (\text{III-128})$$

$$Z_{64c} = \text{factor indicating the protein status of animal group c during this time unit}$$

$$= \min (1, Z_{63c} / [(1 - P_{48c}) \cdot X_{16c} + Z_{61c3}]) \quad (\text{III-129})$$

The curves of Figure 13 are assumed to be of the form  $Y = X^k$  where k is a parameter less than one, dependent on the growth type and animal group ( $P_{58ca}$ , where a = 1, embryo growth; a = 2, juvenile growth; a = 3, "milk" production; a = 4, "wool" production). Now, the pro-

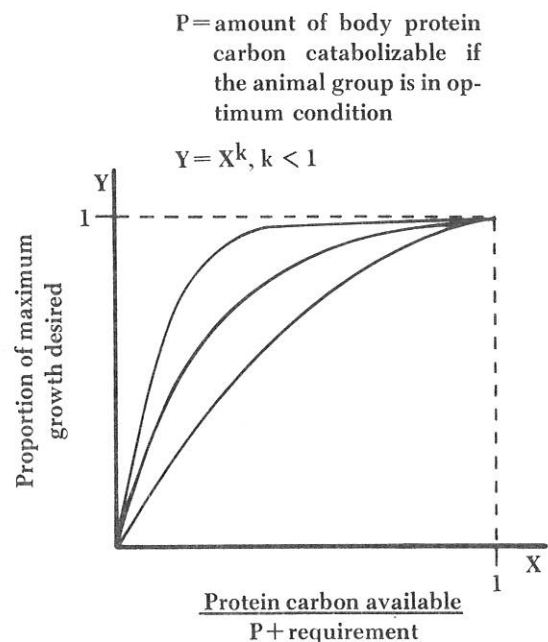


Figure 13. Growth reduction (ANIMAL III).

portions of maximum growth (as given by the potential increments) desired are determined. These are applied to the potential increments and to the associated energy requirements, to obtain the current desired growth increments. The protein carbon needed to satisfy these increments is compared with the available protein, and if there is insufficient available, it is arbitrarily decided to decrease each growth increment by 10% repeatedly, until the protein carbon requirement is satisfied.

The first time through this iterative procedure,  $n = 0$ , where  $n$  is the number of times the potential growth increment is decreased by 10%.

$Z_{65bf}$  = amount of constituent  $f$  to be produced in fetal growth of group  $b$  (when  $b$  is the fetal group of  $c$ ) per time unit

$$= Z_{64C} P_{58cl} \cdot Z_{49bf} \cdot (0.9)^n \quad (\text{III-130})$$

$Z_{66C}$  = amount of energy needed to produce the fetal growth increments in  $c$  per time unit

$$= Z_{64C} P_{58cl} \cdot Z_{50C} \cdot (0.9)^n \quad (\text{III-131})$$

$Z_{67cf}$  = amount of constituent  $f$  to be produced in juvenile growth of  $c$  per time unit

$$= Z_{64C} P_{58c2} \cdot Z_{53cf} \cdot (0.9)^n \quad (\text{III-132})$$

$Z_{68C}$  = amount of energy needed to produce the juvenile growth increments of  $c$  per time unit

$$= Z_{64C} P_{58c2} \cdot Z_{54C} \cdot (0.9)^n \quad (\text{III-133})$$

$Z_{69cf}$  = amount of constituent  $f$  to be produced in "milk" by  $c$  per time unit

$$= Z_{64C} P_{58c3} \cdot Z_{56cf} \cdot (0.9)^n \quad (\text{III-134})$$

$Z_{70C}$  = amount of energy needed to produce "milk" increments in  $c$  per time unit

$$= Z_{64C} P_{58c3} \cdot Z_{57C} \cdot (0.9)^n \quad (\text{III-135})$$

$Z_{71cf}$  = amount of constituent  $f$  to be produced in "wool" of  $c$  per time unit

$$= Z_{64C} P_{58c4} \cdot Z_{58cf} \cdot (0.9)^n \quad (\text{III-136})$$

$Z_{72C}$  = amount of energy needed to produce "wool" increments in  $c$  per time unit

$$= Z_{64C} P_{58c4} \cdot Z_{59C} \cdot (0.9)^n \quad (\text{III-137})$$

$Z_{73cf}$  = total amount of  $f$  needed to satisfy all the

growth and production increments of  $c$  per time unit, where  $f \in M$

$$= Z_{65bf} + Z_{67cf} + Z_{69cf} + Z_{71cf} \quad (\text{III-138})$$

$Z_{73C3}$  = total amount of carbon from proteinaceous tissues needed to satisfy all the growth and production increments of protein of  $c$  per time unit

$$= \sum_{f=3,5} (Z_{65bf} + Z_{67cf} + Z_{69cf} + Z_{71cf})$$

$$(\text{III-139})$$

$Z_{73C4}$  = total amount of carbon needed to satisfy all growth and production increments of reserve tissues, by  $c$  per time unit

$$= Z_{65b4} + Z_{67c4} + Z_{69c4} + Z_{71c4} \quad (\text{III-140})$$

$Z_{74C}$  = amount of energy needed to synthesize the growth and production increments (excluding energy in the tissues) of  $c$  per time unit

$$= Z_{66C} + Z_{68C} + Z_{70C} + Z_{72C} \quad (\text{III-141})$$

if  $Z_{63C} \geq Z_{73C3}$ , protein carbon requirements for the growth increments are satisfied;

if  $Z_{63C} < Z_{73C3}$ , increase  $n$  by 1 and resume iteration from equation III-130.

There is now determined to be sufficient protein carbon available to satisfy the growth increments designated in III-130, 132, 134, 136. The question of whether there is sufficient carbon available for formation of reserve tissues now has to be resolved. This carbon originates from the dietary fats and carbohydrates, the reserve tissues of the animal's body and any available protein that is not used to satisfy the proteinaceous growth increments. If the amount of carbon needed ( $Z_{73C4}$ ) is less than the amount of carbon available, no reduction of the growth increments occurs. If, however, carbon is limited, then each growth increment is reduced repeatedly by 10% until the reserve tissue carbon requirement is met. This means that the protein carbon requirement is decreased also, thus causing more carbon to be made available for reserve tissue synthesis.

$Z_{75C}$  = amount of available carbon for group  $c$  per time unit

$$= Z_{46c4} + Z_{46c5} + (X_{11c4} - X_{13c4} - X_{14c4}) + (Z_{63C} - Z_{73C3}) \cdot (1 - P_{1413}/P_{45C}) \quad (\text{III-142})$$

Note that not all the carbon from catabolism of protein is usable; the nitrogen must be excreted as urea or uric acid,

compounds which contain carbon. Thus the amount of carbon available for synthesis of reserve tissues from the proteins is the protein carbon less the carbon in the nitrogenous wastes.

if  $Z_{73c4} \leq Z_{75c}$ , carbon requirements for growth of reserve tissues are met;

if  $Z_{73c4} > Z_{75c}$ , the growth increments must be decreased by 10%; i.e.,  $n$  is increased by 1, and the growth increments are recalculated, resuming iteration from equation III-130.

There is now determined to be sufficient protein carbon and carbon for reserve tissues to satisfy the growth increments designated in III-130, 132, 134, and 136 for the value of  $n$ . It now remains to be seen whether there are sufficient amounts of non-carbon constituents available to satisfy the growth increments. First, consider the case of nitrogen. The nitrogen requirement is for the synthesis of proteinaceous materials; therefore the nitrogen must be a part of amino acids. Thus, the available nitrogen is the dietary nitrogen (since it was assumed that all nitrogen ingested is from protein sources) plus the nitrogen corresponding to the amount of non-dietary protein catabolized to fulfill the protein carbon requirements.

$$\begin{aligned} Z_{76c1} &= \text{available nitrogen for group } c \text{ per time unit} \\ &= Z_{46c1} + \max[0, (Z_{73c3} - Z_{46c3}) P_{14_{13}}] \end{aligned} \quad \text{(III-143)}$$

if  $Z_{73c1} \leq Z_{76c1}$ , nitrogen requirements for growth of tissues are met;

if  $Z_{73c1} > Z_{76c1}$ , the growth increments must be decreased by 10%; i.e.,  $n$  increased by 1, and the growth increments are recalculated, resuming iteration from equation III-130.

There is now determined to be sufficient protein carbon, carbon for reserve tissues and nitrogen to satisfy the growth increments designated in III-130, 132, 134, and 136 for the value of  $n$ . Now the same procedure has to be followed through for mineral constituents. The amounts of available minerals are the amounts consumed, plus the amounts stored in the hard, structural tissues of the animal (Mitchell, 1962, p. 261). It is assumed that any minerals associated with protein tissues that are catabolized for protein growth are also available. The methods of determining the amounts of minerals associated with the hard structural carbon (i.e., the minimum amounts needed to form the skeleton) and the amounts associated with the soft body structural carbon (proteinaceous material) are described in the "Feeding" process.

$$Z_{76cf} = Z_{46cf} + \max[0, (Z_{73c3} - Z_{46c3}) \cdot P_{14_{13}}] +$$

$Z_{91cf}$ , where  $f \in M - [1]$

where

$$\begin{aligned} Z_{91cf} &= \text{amount of constituent } f \text{ stored in the skeleton of} \\ &\quad c \text{ during this time unit} \\ &= (X_{11cf} - X_{13cf} - X_{14cf}) - P_{14f3} [(1 - P_{8c}) \cdot \\ &\quad (X_{11c5} - X_{13c5} - X_{14c5}) + (X_{11c3} - X_{13c3} - \\ &\quad X_{14c3})] - P_{9cf} \cdot P_{8c} (X_{11c5} - X_{13c5} - X_{14c5}) \end{aligned} \quad \text{(III-144a)}$$

if  $Z_{73cf} \leq Z_{76cf}$ , mineral requirements for growth of tissues are met;

if  $Z_{73cf} > Z_{76cf}$ , the growth increments must be decreased by 10%; i.e.,  $n$  is increased by 1 and the growth increments are recalculated, resuming iteration from equation III-130.

At this point, all the material requirements for the growth increments designated in III-130, 132, 134, and 136 for the final value of  $n$  are satisfied. It only remains to test if the available energy is present in sufficient quantity for the proposed production. This energy may be produced by catabolism of various compounds -- dietary fats, protein, carbohydrates, reserve tissues, and labile protein tissues to a certain extent. The non-proteinaceous material is utilized first, with protein being catabolized only if necessary. For each compound (fat, protein, carbohydrate) there is a constant amount of energy per unit of carbon ( $P_{47cf}$ ).

if  $Z_{73c4} < Z_{46c4} + Z_{46c5}$  (i.e., if all the reserve tissue can be synthesized from the dietary fats and carbohydrates, then part of these compounds are available for energy use, plus all the reserve tissue of the animal, and the rest of the available protein not used in protein synthesis),

$$\begin{aligned} Z_{77c} &= \text{available energy for group } c \text{ per time unit} \\ &= (Z_{46c5} - Z_{46c5} / (Z_{46c4} + Z_{46c5}) \cdot Z_{73c4}) \cdot P_{47c5} \\ &\quad + [(Z_{46c4} - Z_{46c4} / (Z_{46c4} + Z_{46c5}) \cdot Z_{73c4}) + \\ &\quad (X_{11c4} - X_{13c4} - X_{14c4})] \cdot P_{47c4} + (Z_{63c} - \\ &\quad Z_{73c3}) \cdot P_{47c3} \end{aligned} \quad \text{(III-144b)}$$

$$\begin{aligned} \text{if } Z_{46c4} + Z_{46c5} + (X_{11c4} - X_{13c4} - X_{14c4}) > Z_{73c4} \\ \geq Z_{46c4} + Z_{46c5} \end{aligned}$$

i.e., if all the dietary fats and carbohydrates, and part of the body reserve tissues are used in synthesizing reserve tissue, then the available energy is determined from the body reserve tissue remaining plus the unused available protein,

$$Z_{77c} = [(X_{11c4} - X_{13c4} - X_{14c4}) + Z_{46c4} + Z_{46c5} - Z_{73c4}] \cdot P_{47c4} + (Z_{63c} - Z_{73c3}) \cdot P_{47c3} \quad (\text{III-144c})$$

$$\text{if } Z_{73c4} \geq Z_{46c4} + Z_{46c5} + (X_{11c4} - X_{13c4} - X_{14c4})$$

i.e., some of the unused available protein tissue must be catabolized to supply the needed energy, since all reserve tissue and dietary fats and carbohydrates are used to synthesize the growth increments of reserve tissue,

$$Z_{77c} = (Z_{63c} - Z_{73c3}) - [Z_{73c4} - Z_{46c4} - Z_{46c5} - (X_{11c4} - X_{13c4} - X_{14c4})] / [1 - (P_{14c3} / P_{45c})] \cdot P_{47c3} \quad (\text{III-145})$$

If insufficient energy can be made available for the growth increments, the increments must be decreased.

If  $Z_{77c} \geq Z_{74c}$ ; energy requirements for growth are met,

if  $Z_{77c} < Z_{74c}$ ; n is increased by 1 and the growth increments recalculated, resuming iteration from equation III-130.

Now the growth increments designated in III-130, 132, 134, 136 for the final value of n, are the *actual* increments for this time unit.

$$G\dot{X}_{11cf} = Z_{67cf} + Z_{69cf} + Z_{71cf} \quad (\text{III-146})$$

$$G\dot{X}_{13cf} = Z_{69cf} \quad (\text{III-147})$$

$$G\dot{X}_{14cf} = Z_{71cf} \quad (\text{III-148})$$

$$G\dot{X}_{11bf} = Z_{65cf}, \text{ where } b \text{ is the numerical designation of the fetal group of } c \text{ during this season} \quad (\text{III-149})$$

The amounts of constituents used to produce this growth must be subtracted from the original totals. Consider the proteinaceous material first;

if  $Z_{73c3} \leq Z_{46c3}$ ; i.e., if the protein synthesis was accomplished from dietary protein only,

$$Z_{80c} = \text{amount of dietary protein carbon remaining in } c \text{ per time unit after accounting for use in protein synthesis} \\ = Z_{46c3} - Z_{73c3} \quad (\text{III-150})$$

if  $Z_{73c3} > Z_{46c3}$ ; i.e., labile protein tissue of the animal was used in protein synthesis,

$$Z_{80c} = 0 \quad (\text{III-151})$$

$$PS\dot{X}_{11cf} = (Z_{73c3} - Z_{46c3}) \cdot P_{14f3}, \text{ where } f \in M + [3] \quad (\text{III-152})$$

The tissues that were used to synthesize the reserve tissue growth increments, are now decremented.

if  $Z_{73c4} \leq Z_{46c4} + Z_{46c5}$ ; i.e., if reserve tissue synthesis was accomplished from dietary fats and carbohydrates only,

$$Z_{78c4} = \text{amount of dietary fat carbon remaining in group } c \text{ per time unit after accounting for use as material in growth} \\ = Z_{46c4} - [Z_{46c4} / (Z_{46c4} + Z_{46c5})] \cdot Z_{73c4} \quad (\text{III-153})$$

$$Z_{78c5} = \text{amount of dietary carbohydrate carbon remaining in group } c \text{ per time unit after accounting for use as material in growth} \\ = Z_{46c5} - [Z_{46c5} / (Z_{46c4} + Z_{46c5})] \cdot Z_{73c4} \quad (\text{III-154})$$

$$Z_{78c3} = \text{amount of dietary protein carbon remaining in group } c \text{ per time unit after accounting for use as material in growth} \\ = Z_{80c} \quad (\text{III-154a})$$

$$Z_{82c} = \text{amount of reserve tissue catabolized by } c \text{ per time unit to supply carbon for reserve tissue synthesis in growth} \\ = 0 \quad (\text{III-154b})$$

$$\text{if } Z_{46c4} + Z_{46c5} + (X_{13c4} - X_{13c4} - X_{14c4}) \geq Z_{73c4} \\ > Z_{46c4} + Z_{46c5}$$

i.e., reserve body tissue must be used to synthesize the reserve growth increments,

$$Z_{78c4} = 0 = Z_{78c5} \quad (\text{III-155})$$

$$Z_{82c} = Z_{73c4} - (Z_{46c4} + Z_{46c5}) = RS\dot{X}_{11c4} \quad (\text{III-156})$$

$$Z_{78c3} = Z_{80c} \quad (\text{III-156a})$$

$$\text{if } Z_{73c4} > Z_{46c4} + Z_{46c5} + (X_{11c4} - X_{13c4} - X_{14c4})$$

i.e., some carbon from the available protein must be used in the reserve tissue synthesis; more protein than the amount indicated by the carbon need must be catabolized due to the loss of some of the carbon in the nitrogenous wastes,

$$Z_{78c4} = Z_{78c5} \quad (\text{III-157})$$

$$RS\dot{X}_{11c4} = X_{11c4} - X_{13c4} - X_{14c4} = Z_{82c} \quad (\text{III-158})$$

$Z_{79c}$  = amount of available protein carbon from protein catabolized to provide carbon for reserve tissue increments of  $c$  per time unit

$$= [Z_{73c4} - Z_{46c4} - Z_{46c5} - (X_{11c4} - X_{13c4} - X_{14c4})] / (1 - P_{14,13}/P_{45c}) \quad (\text{III-159})$$

$$RS\dot{X}_{17c3} = Z_{79c} \cdot P_{14,13}/P_{45c} \quad (\text{III-160})$$

if  $Z_{79c} \leq Z_{80c}$ ; i.e., the amount of remaining dietary protein carbon is sufficient to supply the needed carbon,

then

$$Z_{78c3} = Z_{80c} - Z_{79c} \quad (\text{III-161})$$

if  $Z_{79c} > Z_{80c}$ ; i.e., the amount of remaining dietary protein carbon is insufficient to supply the needed carbon,

then

$$Z_{78c3} = 0 \quad (\text{III-162})$$

$$RS\dot{X}_{11cf} = (Z_{79c} - Z_{80c}) \cdot P_{14f3}, \text{ where } f \in M[3] \quad (\text{III-163})$$

$$RS\dot{X}_{17cf} = (Z_{79c} - Z_{80c}) \cdot P_{14f3}, \text{ where } f \in M \quad (\text{III-164})$$

The sources from which the non-carbon constituents are taken are decremented. When body protein is catabolized to provide amino acids for protein synthesis, the corresponding non-carbon constituents are available for incorporation into the growth increments. However, if body protein is catabolized to provide energy or carbon for reserve tissue growth, the corresponding non-carbon constituents are excreted (III-164). If dietary protein, on the other hand, is catabolized for any reason, the non-carbon constituents are available for use in synthesis.

if  $Z_{73cf} \leq \max [0, (Z_{73c3} - Z_{46c3}) \cdot P_{14f3}] + Z_{46cf}$ , where  $f \in M$ ; if no minerals need to be taken from storage in the skeleton to supply the needed amounts for synthesis,

$Z_{78cf}$  = amount of non-carbon constituent  $f$  remaining in group  $c$  per time unit after accounting for use as material in growth, where  $f \in M$

$$= Z_{46cf} + \max[0, (Z_{73c3} - Z_{46c3}) \cdot P_{14f3}] - Z_{73cf} \quad (\text{III-165})$$

$Z_{92cf}$  = amount of  $f$  available to group  $c$  per time unit after accounting for use as material in growth, where  $f \in M$

$$= Z_{91cf} + Z_{78cf} \quad (\text{III-165a})$$

if  $Z_{73cf} > \max [0, (Z_{73c3} - Z_{46c3}) \cdot P_{14f3}] + Z_{46cf}$ ,

$$Z_{78cf} = 0, \text{ where } f \in M \quad (\text{III-166})$$

$$MS\dot{X}_{11cf} = Z_{73cf} - \max [0, (Z_{73c3} - Z_{46c3}) \cdot P_{14f3}] - Z_{46cf}, \text{ where } f \in M \quad (\text{III-166a})$$

$$Z_{92cf} = Z_{78cf} + Z_{91cf} - [Z_{73cf} - \max [0, (Z_{73c3} - Z_{46c3}) \cdot P_{14f3}] - Z_{46cf}], \text{ where } f \in M \quad (\text{III-167})$$

The sources from which the energy is obtained must now be decremented.

$Z_{83c}$  = amount of energy able to be produced from the remaining dietary fats, carbohydrates and body reserve tissue of  $c$  per time unit

$$= Z_{78c4} \cdot P_{47c4} + Z_{78c5} \cdot P_{47c5} + (X_{11c4} - X_{13c4} - X_{14c4} - Z_{82c}) P_{47c4} \quad (\text{III-167a})$$

if  $Z_{74c} \leq Z_{78c4} \cdot P_{47c4} + Z_{78c5} \cdot P_{47c5}$ ; i.e., the energy is supplied by the remaining dietary carbohydrates and fats,

$Z_{81c4}$  = amount of dietary fat carbon remaining in  $c$  per time unit after all the decrements for growth have been accounted for

$$= Z_{78c4} - Z_{78c4} \cdot Z_{74c} / (Z_{78c4} \cdot P_{47c4} + Z_{78c5} \cdot P_{47c5}) \quad (\text{III-168})$$

$Z_{89c}$  = amount of reserve body tissue used in energy production by  $c$  per time unit

$$= 0 \quad (\text{III-168a})$$

$Z_{81c5}$  = amount of dietary carbohydrate carbon remaining in  $c$  per time unit after all the decrements for growth have been accounted for

$$= Z_{78c5} - Z_{78c5} \cdot Z_{74c} / (Z_{78c4} \cdot P_{47c4} + Z_{78c5} \cdot P_{47c5}) \quad (\text{III-169})$$

$Z_{81c3}$  = amount of dietary protein carbon remaining in c per time unit after all the decrements for growth have been accounted for

$$= Z_{78c3} \quad (\text{III-169a})$$

$$G\dot{X}_{01_{13}} = (Z_{78c4} + Z_{78c5}) \cdot Z_{74c} / (Z_{78c4} \cdot P_{47c4} + Z_{78c5} \cdot P_{47c5}) \quad (\text{III-170})$$

if  $Z_{83c} \geq Z_{74c} > Z_{78c5} \cdot P_{47c5} + Z_{78c4} \cdot P_{47c4}$ ; i.e., part of the energy is supplied by the remaining reserve tissue of the body,

$$Z_{81c3} = Z_{78c3}$$

$$Z_{81c4} = Z_{81c5} = 0 \quad (\text{III-171})$$

$$G\dot{X}_{01_{13}} = Z_{78c4} + Z_{78c5} + (Z_{74c} - Z_{78c5} \cdot P_{47c5} - Z_{78c4} \cdot P_{47c4}) / P_{47} \quad (\text{III-172})$$

$$ES\dot{X}_{11c4} = (Z_{74c} - Z_{78c5} \cdot P_{47c5} - Z_{78c4} \cdot P_{47c4}) / P_{47c4} \\ = Z_{89c} \quad (\text{III-173})$$

if  $Z_{74c} > Z_{83c}$ ; i.e., part of the energy is supplied by the remaining available protein of the group,

$$ES\dot{X}_{11c4} = X_{11c4} - X_{13c4} - X_{14c4} - Z_{82c} = Z_{89c} \quad (\text{III-174})$$

$$Z_{81c4} = Z_{81c5} = 0 \quad (\text{III-175})$$

$Z_{84c}$  = amount of remaining available protein carbon that must be catabolized to yield the energy needed by c per time unit

$$= (Z_{74c} - Z_{83c}) / P_{47c3} \quad (\text{III-176})$$

$$ES\dot{X}_{17c3} = Z_{84c} \cdot P_{14_{13}} / P_{45c} \quad (\text{III-177})$$

$$G\dot{X}_{01_{13}} = Z_{78c4} + Z_{78c5} + (X_{11c4} - X_{13c4} - X_{14c4} - Z_{82c}) + Z_{84c} \cdot (1 - P_{14_{13}} / P_{45c}) \quad (\text{III-178})$$

if  $Z_{78c3} \geq Z_{84c}$ ; i.e., the remaining dietary protein supplies the rest of the energy needed,

$$Z_{81c3} = Z_{78c3} - Z_{84c} \quad (\text{III-179})$$

if  $Z_{78c3} < Z_{84c}$ ; i.e., some of the energy comes from labile body tissues,

$$Z_{81c3} = 0 \quad (\text{III-180})$$

$$ES\dot{X}_{11cf} = (Z_{84c} - Z_{78c3}) \cdot P_{14f3}, \text{ where } f \in M + [3] \quad (\text{III-181})$$

$$ES\dot{X}_{17cf} = (Z_{84c} - Z_{78c3}) \cdot P_{14f3}, \text{ where } f \in M \quad (\text{III-182})$$

As mentioned at the beginning of the description of this process for ANIMAL III, "protein resynthesis," fattening and mineral storage may also occur in the animals following allocation of the resources to the four main types of growth.

"Protein resynthesis" is the synthesis of protein to replace that which was used as materials for growth, i.e., to replace the labile protein tissue which was catabolized. Only dietary protein can be used in the synthesis, while the remaining dietary fats, carbohydrate reserve body tissue and dietary protein can be used to provide the energy needed for the production of the system. The corresponding mineral constituents needed in the synthesis may be supplied by the dietary mineral intake or the minerals in the skeleton storage.

$$Z_{85c} = \text{amount of protein carbon by which group c is below the optimum level during the time unit} \\ = X_{16c} - (X_{11c3} - X_{13c3} - X_{14c3}) \quad (\text{III-183})$$

$Z_{86c}$  = proposed amount of carbon to be added to c in protein synthesis per time unit, if sufficient energy is available

$$= \min [1, Z_{81c3} / Z_{85c}, Z_{92cf} / (Z_{85c} \cdot P_{14f3})] \cdot Z_{85c}, \\ \text{where } f \in M \quad (\text{III-184})$$

$Z_{87c}$  = energy needed to produce the proposed synthesis of protein tissue by c per time unit

$$= Z_{86c} \cdot P_{52c} \cdot P_{513} \quad (\text{III-185})$$

$Z_{88c}$  = energy available to produce the proposed synthesis of protein tissue by c per time unit

$$= Z_{81c4} \cdot P_{47c4} + Z_{81c5} \cdot P_{47c5} + P_{47c4} (X_{11c4} - X_{13c4} - X_{14c4} - Z_{82c} - Z_{89c} + (Z_{81c3} - Z_{86c}) \cdot P_{47c3}) \quad (\text{III-186})$$

$Z_{90cf}$  = actual amount of constituent f added to c in protein synthesis per time unit

$$= Z_{86c} \cdot P_{14f3} \text{ if } Z_{88c} \geq Z_{87c} \\ = [(Z_{88c} + Z_{86c} \cdot P_{47c3}) / (Z_{87c} + Z_{86c} \cdot P_{47c3})] \cdot Z_{86c} \cdot P_{14f3} \text{ if } Z_{88c} < Z_{87c} \quad (\text{III-187})$$

$$Y\dot{X}_{11cf} = Z_{90cf}, \text{ where } f \in M + [3] \quad (\text{III-188})$$

$$Z_{93cf} = \text{amount of } f \text{ remaining for the dietary intake after all growth and protein resynthesis demands have been met, for group } c \text{ per time unit}$$

$$= \max [Z_{78cf} - Z_{90cf}, 0] \quad (\text{III-189})$$

The amount of mineral elements used from bone storage, if any, must be decremented.

$$MY\dot{X}_{11cf} = \max(0, Z_{90cf} - Z_{78cf}), \text{ where } f \in M \quad (\text{III-190})$$

The compounds which were catabolized to yield the necessary energy are now decremented.

$$Z_{94c} = \text{energy needed to produce the actual synthesis of protein tissue by } c \text{ per time unit}$$

$$= Z_{90c3} \cdot P_{52c} \cdot P_{513} \quad (\text{III-191})$$

$Z_{94c} \leq Z_{81c4} \cdot P_{47c4} + Z_{81c5} \cdot P_{47c5}$ ; i.e., the energy is supplied by breakdown of the dietary fats and carbohydrates

$$Z_{95c4} = \text{amount of remaining dietary fat in } c \text{ per time unit following all growth and "protein synthesis"}$$

$$= Z_{81c4} - Z_{81c4} \cdot Z_{94c} / (Z_{81c4} \cdot P_{47c4} + Z_{81c5} \cdot P_{47c5}) \quad (\text{III-192})$$

$$Z_{95c5} = \text{amount of remaining dietary carbohydrate in } c \text{ per time unit following all growth and "protein resynthesis"}$$

$$= Z_{81c5} - Z_{81c5} \cdot Z_{94c} / (Z_{81c4} \cdot P_{47c4} + Z_{81c5} \cdot P_{47c5}) \quad (\text{III-193})$$

$$Z_{95c3} = \text{amount of remaining dietary protein in } c \text{ per time unit following all growth and "protein resynthesis"}$$

$$= Z_{81c3} - Z_{90c3} \quad (\text{III-193a})$$

$$Y\dot{X}_{0113} = (Z_{81c4} + Z_{81c5}) \cdot Z_{94c} / (Z_{81c4} \cdot P_{47c4} + Z_{81c5} \cdot P_{47c5}) \quad (\text{III-194})$$

if  $(X_{11c4} - X_{13c4} - X_{14c4} - Z_{82c} - Z_{89c}) \cdot P_{47c4} \geq Z_{94c} - Z_{81c4} \cdot P_{47c4} - Z_{81c5} \cdot P_{47c5} > 0$ ; i.e., part of the remaining reserve body tissue of the animal group must be used,

$$Y\dot{X}_{11c4} = (Z_{94c} - Z_{81c4} \cdot P_{47c4} - Z_{81c5} \cdot P_{47c5}) / P_{47c4} \quad (\text{III-195})$$

$$Y\dot{X}_{0113} = Z_{81c4} + Z_{81c5} + (Z_{94c} - Z_{81c4} \cdot P_{47c4} - Z_{81c5} \cdot P_{47c5}) / P_{47c4} \quad (\text{III-196})$$

$$Z_{95c4} = 0 = Z_{95c5} \quad (\text{III-197})$$

$$Z_{95c3} = Z_{81c3} - Z_{90c3} \quad (\text{III-197a})$$

if  $Z_{94c} > (X_{11c4} - X_{13c4} - X_{14c4} - Z_{82c} - Z_{89c}) \cdot P_{47c4} + Z_{81c4} \cdot P_{47c4} + Z_{81c5} \cdot P_{47c5}$ ; i.e., part of the dietary protein must be used to supply the energy,

$$Y\dot{X}_{11c4} = X_{11c4} - X_{13c4} - X_{14c4} - Z_{82c} - Z_{89c} \quad (\text{III-198})$$

$$Z_{95c4} = 0 = Z_{95c5} \quad (\text{III-199})$$

$$= Z_{81c3} - Z_{90c3} - [Z_{94c} - (X_{11c4} - X_{13c4} - X_{14c5} - Z_{82c} - Z_{89c}) \cdot P_{47c4} - Z_{81c4} \cdot P_{47c4} - Z_{81c5} \cdot P_{47c5}] / P_{47c3} \quad (\text{III-199a})$$

$$Y\dot{X}_{17c3} = [Z_{94c} - (X_{11c4} - X_{13c4} - X_{14c5} - Z_{82c} - Z_{89c}) \cdot P_{47c4} - Z_{81c4} \cdot P_{47c4} - Z_{81c5} \cdot P_{47c5}] / P_{47c3} \cdot (P_{1413} / P_{45c}) \quad (\text{III-200})$$

$$Y\dot{X}_{0113} = Z_{81c4} + Z_{81c5} + (X_{11c4} - X_{13c4} - X_{14c4} - Z_{82c} - Z_{89c}) + [Z_{94c} - (X_{11c4} - X_{13c4} - X_{14c5} - Z_{82c} - Z_{89c}) \cdot P_{47c4} - Z_{81c4} \cdot P_{47c4} - Z_{81c5} \cdot P_{47c5}] / P_{47c3} \cdot (1 - P_{1413} / P_{45c}) \quad (\text{III-200a})$$

Fattening is the process whereby reserve tissues are produced in the group. This only occurs with "excess" carbon intake; i.e., when the amount of carbon ingested exceeds the maintenance and growth requirements of the animal. Reserve tissues are considered to be only fat (no carbohydrate), and to consist of carbon, hydrogen and oxygen, with no mineral constituents. Carbon from dietary fats and carbohydrates can be used in this process, as well as dietary proteins. The inefficiency of fat anabolism is usually greater than for maintenance and growth (Kleiber, 1961, p. 291; parameter  $P_{56c}$ ). All the dietary carbon remaining at this point is used or respired.



$Z_{96C}$  = fraction of remaining dietary carbohydrate that is used in fattening by c per time unit (also equals fraction of remaining dietary fat that is used in fattening)

$Z_{97C}$  = fraction of remaining dietary protein that is used in fattening by c per time unit

$Z_{98C}$  = energy available for production of the fat synthesized from dietary compounds by c per time unit

$$= (1 - Z_{96C}) \cdot Z_{95C4} \cdot P_{47C4} + (1 - Z_{96C}) \cdot Z_{95C5} \cdot P_{47C5} + (1 - Z_{97C} / (1 - [P_{14,13} / P_{45C}])) \cdot Z_{95C3} \cdot P_{47C3} \quad (\text{III-201})$$

$Z_{99C}$  = energy needed to produce the fat by c per time unit

$$= [Z_{96C} \cdot Z_{95C4} + Z_{96C} \cdot Z_{95C5} + Z_{97C} \cdot Z_{95C3}] \cdot P_{56C} \cdot P_{514} \quad (\text{III-202})$$

To use all the carbon present from the diet, the energy available is equal to the energy needed. Then an equation in  $Z_{97C}$ ,  $Z_{96C}$  can be found. Supposing that the carbohydrate and fats are all used before the protein is catabolized,  $Z_{97C}$  and  $Z_{96C}$  can be found and thus the amount of fat produced can also be determined.

$$Z_{96C} [Z_{95C4} \cdot P_{56C} \cdot P_{514} + Z_{95C4} \cdot P_{47C4} + Z_{95C5} \cdot P_{47C5} + Z_{95C5} \cdot P_{56C} \cdot P_{514}] + Z_{97C} [Z_{95C3} \cdot P_{47C3} / (1 - P_{14,13} / P_{45C}) + Z_{95C3} \cdot P_{56C} \cdot P_{514}] = Z_{95C4} \cdot P_{47C4} + Z_{95C5} \cdot P_{47C5} \quad (\text{III-203})$$

if  $(Z_{95C4} \cdot P_{56C} \cdot P_{514} + Z_{95C4} \cdot P_{47C4} + Z_{95C5} \cdot P_{47C5} + Z_{95C5} \cdot P_{56C} \cdot P_{514}) \geq \text{RHS of III-203}$ ; i.e., if the coefficient of  $Z_{96C}$  is greater than the RHS of III-203,

$$Z_{96C} = \text{RHS} / \text{coefficient of } Z_{96C} \\ = (Z_{95C4} \cdot P_{47C4} + Z_{95C5} \cdot P_{47C5} + Z_{95C3} \cdot P_{47C3}) / (Z_{95C4} \cdot P_{56C} \cdot P_{514} + Z_{95C4} \cdot P_{47C4} + Z_{95C5} \cdot P_{47C5} + Z_{95C5} \cdot P_{56C} \cdot P_{514}) \quad (\text{III-204})$$

$$Z_{97C} = 0 \quad (\text{III-205})$$

if

$$(Z_{95C4} \cdot P_{56C} \cdot P_{514} + Z_{95C4} \cdot P_{47C4} + Z_{95C5} \cdot P_{47C5} + Z_{95C5} \cdot P_{56C} \cdot P_{514}) < \text{RHS of III-203}$$

$$Z_{96C} = 1 \quad (\text{III-206})$$

$$Z_{97C} = (\text{RHS} - \text{coefficient of } Z_{96C}) / (\text{coefficient of } Z_{97C})$$

$$= (Z_{95C3} \cdot P_{47C3} - Z_{95C4} \cdot P_{56C} \cdot P_{514} - Z_{95C5} \cdot P_{56C} \cdot P_{514}) / (Z_{95C3} \cdot P_{56C} \cdot P_{514} + Z_{95C3} \cdot P_{47C3} / (1 - P_{14,13} / P_{45C})) \quad (\text{III-207})$$

$$F\dot{X}_{11C4} = Z_{96C} (Z_{95C4} + Z_{95C5}) + Z_{97C} \cdot (Z_{95C3}) \quad (\text{III-208})$$

$$F\dot{X}_{17C3} = Z_{97C} [Z_{95C3} / (1 - P_{14,13} / P_{45C})] \cdot (P_{14,13} / P_{45C}) \quad (\text{III-209})$$

$$F\dot{X}_{01,13} = Z_{95C4} (1 - Z_{96C}) + Z_{95C5} (1 - Z_{96C}) + Z_{95C3} (1 - Z_{97C} / (1 - P_{14,13} / P_{45C})) \quad (\text{III-210})$$

$$U\dot{X}_{17C1} = Z_{93C1} \quad (\text{III-210a})$$

Any non-nitrogenous mineral elements remaining may be stored in the skeleton of the animal, depending on its current status (Mitchell, 1962, p. 226). An input parameter ( $P_{57cf}$ ) defines the maximum amount of each mineral that can be associated with each unit of hard structural carbon. Another parameter ( $P_{9cf}$ ) defines the minimum amount of each mineral that is associated with each unit of hard structural carbon (or collagen carbon; Eames and Posner, 1970, p. 21).

$$Z_{98cf} = \text{maximum amount of mineral f able to be stored by c per time unit, where } f \in M - [1] \\ = P_{8C} \cdot (X_{11C5} - X_{13C5} - X_{14C5}) \cdot (P_{57cf} - P_{9cf}) \quad (\text{III-211})$$

$$Z_{99cf} = \text{amount of mineral f added to skeleton storage per time unit in c, where } f \in M - [1] \\ = \min (Z_{98cf} - Z_{91cf}, Z_{93cf}) \quad (\text{III-212}) \\ = SM\dot{X}_{11cf}$$

$$U\dot{X}_{17cf} = Z_{93cf} - Z_{99cf}, \text{ where } f \in M - [1] \quad (\text{III-213})$$

**Discussion**—For fetal growth in Version III, the following calculations provide a method to obtain parameters  $P_{1\text{cfm}}$  (III-105-109).

Suppose that the length of the growth period =  $\eta$ ; let the maximum growth rates of protein carbon, reserve carbon and structural carbon =  $\gamma_1, \gamma_2, \gamma_3$ , respectively ( $\gamma_i, i = 1, 2, 3$ ); let the maximum birth weights of protein carbon, reserve carbon and structural carbon per individual =  $\pi_1, \pi_2, \pi_3$ , respectively ( $\pi_i, i = 1, 2, 3$ ).

Then, for some small  $\epsilon$

steady-state protein carbon level at end of first day =  $\epsilon$   
 steady-state protein carbon level at end of second day =  $\epsilon(1 + \gamma_1)$   
 steady-state protein carbon level at end of third day =  $\epsilon(1 + \gamma_1)^2$   
 steady-state protein carbon level at end of  $n$ th day =  $\epsilon(1 + \gamma_1)^{n-1}$

and thus the growth increments (maximum) are calculated,

amount  $i$  added on first day = 0  
 amount  $i$  added on second day =  $\gamma_i \epsilon$   
 amount  $i$  added on third day =  $\gamma_i \epsilon(1 + \gamma_i)$   
 amount  $i$  added on  $n$ th day =  $\gamma_i \epsilon(1 + \gamma_i)^{n-2}$

thus the total amount of  $i$  added over the growth period

$$\begin{aligned} &= \gamma_i \epsilon [1 + (1 + \gamma_i) + \dots + (1 + \gamma_i)^{\eta-2}] \\ &= \gamma_i \epsilon [((1 + \gamma_i)^\eta - 1) / \gamma_i] \\ &= (\gamma_i / \gamma_i) \epsilon [(1 + \gamma_i)^\eta - 1] \end{aligned}$$

For  $i = 2, 3$  (reserve carbon, structural carbon)

$$\pi_i = (\gamma_i / \gamma_i) \epsilon [(1 + \gamma_i)^\eta - 1]$$

For  $i = 1$  (protein carbon)

$$\pi_1 - \epsilon = \epsilon [(1 + \gamma_1)^\eta - 1]$$

Now  $\pi_i, \eta$  are known with  $\epsilon$  chosen very small, so  $\gamma_1$  can be determined,

$$\begin{aligned} ((\pi_1 - \epsilon) / \epsilon) + 1 &= (1 + \gamma_1)^\eta - 1 \\ \ln[(\pi_1 - \epsilon) / \epsilon + 1] &= (\eta - 1) \ln(1 + \gamma_1) \\ \ln(1 + \gamma_1) &= (1 / (\eta - 1)) \ln[(\pi_1 - \epsilon) / \epsilon + 1] = \\ &= (1 / (\eta - 1)) \ln(\pi_1 / \epsilon) \\ 1 + \gamma_1 &= e^{1 / (\eta - 1) \ln(\pi_1 / \epsilon)} \\ \gamma_1 &= e^{1 / (\eta - 1) \ln(\pi_1 / \epsilon)} - 1 \end{aligned}$$

$\gamma_i$  can be determined,

$$\begin{aligned} \pi_i \gamma_i / (\epsilon \gamma_i) &= (1 + \gamma_i)^\eta - 1 \\ \gamma_i &= \pi_i \gamma_i / [\epsilon ((1 + \gamma_i)^\eta - 1)] \end{aligned}$$

For juvenile growth rates in III, parameters  $P_{1\text{cfm}}$  (III-113) can be calculated as follows,

Suppose the birth protein steady-state carbon level =  $\beta$  and the adult optimal steady-state level =  $\rho$  and the length of the growing season =  $\eta$

let the maximum rates of growth of protein carbon, reserve carbon, structural carbon =  $\gamma_1, \gamma_2, \gamma_3$  ( $i = 1, 2, 3$ ), respectively,

then, steady-state protein level at day one =  $\beta = \rho - (\rho - \beta)(1 - \gamma_1)$ ,  
 steady-state protein level at day two =  $\beta + (\rho - \beta)\gamma_1 = \rho - (\rho - \beta)(1 - \gamma_1)$   
 steady-state protein level at day three =  $\rho - (\rho - \beta)(1 - \gamma_1) + [\rho - \rho + (\rho - \beta)(1 - \gamma_1)]\gamma_1 = \rho - (\rho - \beta)(1 - \gamma_1)^2$   
 steady-state protein level at day  $\eta = \rho - (\rho - \beta)(1 - \gamma_1)^{\eta-1}$

the growth increments of carbon type  $i$  are,

amount of  $i$  added on first day =  $\gamma_i(\rho - \beta)(1 - \gamma_i)^0$   
 amount of  $i$  added on day 2 =  $\gamma_i(\rho - \beta)(1 - \gamma_i)$   
 amount of  $i$  added on day  $\eta = \gamma_i(\rho - \beta)(1 - \gamma_i)^{\eta-1}$

thus the total amount added over the growth period

$$\begin{aligned} &= \gamma_i(\rho - \beta) [1 + (1 - \gamma_i) + \dots + (1 - \gamma_i)^{\eta-1}] \\ &= \gamma_i(\rho - \beta) [(1 - \gamma_i)^\eta - 1] / (-\gamma_i) \\ &= (\gamma_i / \gamma_i) (\rho - \beta) [1 - (1 - \gamma_i)^\eta] \end{aligned}$$

For protein carbon the total amount added should equal  $(\rho - \beta)$  since these rates are calculated on the assumption that the growing animal is well nourished and reaches optimal condition. However, since the approach to the steady-state level of  $\rho$  is asymptotic, the total growth can never equal  $\rho - \beta$  exactly. Thus an amount less than  $\rho - \beta$  must be accepted with an error  $\epsilon$  % of the total to be added.

$$\begin{aligned} \rho - \beta - (\epsilon / 100)(\rho - \beta) &= (\gamma_i / \gamma_i) (\rho - \beta) [1 - (1 - \gamma_i)^\eta], \text{ i.e., } 1 - (\epsilon / 100) = 1 - (1 - \gamma_i)^\eta \\ \gamma_i &= 1 - e^{\ln(\epsilon / 100) / \eta} \end{aligned}$$

Now  $\eta$  is known from the assumptions made as to the length of the growing period. As was mentioned in the description of the juvenile growth, the choice of  $\epsilon$  causes the growth rate to vary so by choosing  $\epsilon$  very small, the major part of the growth of protein carbon can occur in the early parts of the growth period and thus the accompanying reserve and structural carbon also occur in major proportions during the early phases.

The amount of structural carbon added over the growth period is assumed to be known by the investigator. For reserve carbon addition, the amount added should not include the amounts of fat put on by the animal due to the fattening process, i.e., due to the process that occurs when dietary carbon intake is higher than that needed for maintenance and growth. The reserve carbon growth is that of marrow in the bones, for example. It should be a very small amount (Maynard and Loosli, 1969, p. 436).

let the amount of structural carbon added =  $\phi_3$   
 amount of reserve carbon added =  $\phi_2$

then  $\phi_i = (\gamma_i / Y_i) (\rho - \beta) [1 - (1 - \gamma_i)^\eta]$

$$\gamma_i = \phi_i Y_i / ((\rho - \beta) [1 - (1 - \gamma_i)^\eta])$$

The  $\phi_i$ ,  $\rho$ ,  $\beta$ ,  $\gamma_i$ ,  $\eta$  are known and so  $\gamma_i$  are determinable.

The energy:carbon ratios for each of the compounds, proteins, fats and carbohydrates, are probably applicable over many species of animals, since an "average" composition of each compound can be assumed. For example, Kleiber (1961, pp. 43, 83) gives "average" composition data as follows: protein, 53% carbon, 16% nitrogen, 1% ash; carbohydrate, 42% carbon; fat, 76% carbon. Kleiber (1961, p. 125) also gives energetic values: protein, 5.7 kcal per gram; carbohydrate, 4.0 kcal per gram; fat, 9.5 kcal per gram.

Thus parameters  $P_{5if}$  of Version III are calculable,

$$P_{513} = (\text{energy/carbon}) \text{ for protein} = (5.7/.53) \text{ kcal per gram of protein carbon} = 10.7$$

$$P_{514} = (\text{energy/carbon}) \text{ for fats} = (9.5/0.76) \text{ kcal per gram of fat carbon} = 12.5$$

$$P_{515} = (\text{energy/carbon}) \text{ for carbohydrates} = (4.0/0.42) \text{ kcal per gram of carbohydrate carbon} = 9.5$$

The parameters  $P_{47cf}$  of Version III (III-143) differ from  $P_{5if}$  in that the latter are the heats of combustion energy per unit carbon, and the former are the catabolizable energy per unit carbon. For fats and carbohydrates these ratios are the same. For protein,  $P_{47cf}$  does not include the energy lost

in the nitrogenous compound excreted (Kleiber, 1961, pp. 125, 264).

for mammals:

$$P_{47c3} = (4.8/0.53) \text{ kcal per gram of protein carbon catabolized} = 9.06$$

for birds, reptiles, insects:

$$P_{47c3} = (4.36/0.53) \text{ kcal per gram of protein carbon catabolized} = 8.23$$

Parameter  $P_{45c}$  of III has the value of the ratio of the weight of nitrogen in urea or uric acid to the weight of carbon. Urea has chemical formula  $(\text{NH}_2)_2\text{CO}$ ; uric acid has chemical formula  $\text{C}_5\text{H}_4\text{O}_3\text{N}_4$  (Kleiber, 1961, p. 265), thus

$$\text{urea: (N weight/C weight)} = (28/12) = 2.33 = P_{45c} \quad (c \in [\text{mammals}])$$

$$\text{uric acid: (N weight/C weight)} = (56/60) = 0.93 = P_{45c} \quad (c \in [\text{non-mammals}])$$

For the parameters denoting the composition of a product, for example "milk" or "wool" ( $P_{21cf}$ , III-120;  $P_{89cf}$ , III-122;  $P_{55c}$ , III-121;  $P_{57c}$ , III-123), the following example illustrates the method of calculation.

Kleiber (1961, p. 312) and Maynard and Loosli (1969, p. 524) give the composition of rat's milk as: fat, 9.3%; lactose, 3.7%; protein, 8.7%; ash, 2%. Using the composition data above, 100 g of milk consists of:

fat	$9.3 \times 0.76 \text{ g carbon} = 7.08 \text{ g carbon}$
lactose	$3.7 \times 0.42 \text{ g carbon} = 1.56 \text{ g carbon}$
protein	$8.7 \times 0.53 \text{ g carbon} = 4.61 \text{ g carbon}$
	$8.7 \times 0.16 \text{ g nitrogen} = 1.39 \text{ g nitrogen}$
	$8.7 \times 0.1 \text{ g ash} = 0.87 \text{ g ash}$
ash	2 g

$$\text{So } P_{55c} = \text{carbon from fats/total fat and carbohydrate carbon} = 7.08/(7.08 + 1.56) = 0.82$$

$$P_{21c1} = 1.39/(7.08 + 1.56 + 4.61) = 1.39/13.25 = 0.105$$

$$P_{21c2} = 2.87/13.25 = 0.216$$

$$P_{21c3} = 4.61/13.25 = 0.348$$

$$P_{21c4} = (7.08 + 1.56)/13.25 = 8.64/13.25 = 0.652$$

$$P_{21c5} = 0$$

The parameters  $P_{14ft}$  of II and III represent the ratio of chemical constituent  $f$  to carbon constituent  $t$  such that

$$P_{141t} = (\text{nitrogen weight})/(\text{carbon constituent weight})$$

$$P_{142t} = (\text{ash weight})/(\text{carbon constituent } t \text{ weight})$$

$$P_{143t} = 1 \forall t$$

Note that if  $t$  refers to the reserve carbon constituent then  $P_{14ft} = 0$  ( $f \in M$ ) since it is assumed that all reserve tissues consist of no other elements but carbon, hydrogen and oxygen. From the composition data above, and since protein carbon refers to carbon in labile protein tissues,

$$P_{14_{13}} = 16/53 = 0.302$$

$$P_{14_{23}} = 1/53 = 0.0189$$

$$P_{1433} = 1$$

If  $t$  refers to structural carbon, the situation is a little more complicated. Parameters  $P_{8c}$  and  $P_{9cf}$  of III (III-144a) are related to  $P_{14f5}$  in the following manner:

$$\begin{aligned} P_{14f5} &= (\text{minimum weight of mineral } f)/(\text{total structural carbon weight}) \\ &= (\text{hard structural carbon})/(\text{total structural carbon}) \cdot (\text{minimum weight of mineral } f \text{ in skeleton})/(\text{hard structural carbon}) + (\text{soft structural carbon})/(\text{total structural carbon}) \cdot (\text{weight of mineral } f \text{ in proteinaceous tissue})/(\text{proteinaceous tissue}) \\ &= P_{8c} \cdot P_{9cf} + (1 - P_{8c}) \cdot P_{14f3} \end{aligned}$$

#### MORTALITY

Death due to predation has already been accounted for in the feeding process in which the predator group expresses a preference for the prey group.

The mortality discussed here is death due to non-predatory causes such as parasites, disease, old age, and malnutrition. It also includes predatory deaths caused by animals not in the simulated system. The carcasses are divided into soft and hard parts to enable the soils model to decompose these categories at different rates.

#### ANIMAL I

Death occurs at a constant rate proportional to the biomass of the animals (input parameter  $P_{11}$ ). Figure 14 illustrates the relationship. The carcasses are divided into soft and hard parts and added to the organic debris. The fractions of each constituent occurring in the soft parts of

the animal body are constant (input parameter  $P_{16f}$ ), and these fractions of the chemical constituents that die constitute the soft parts of the carcasses.

$$\begin{aligned} Z_{31cf} &= \text{amount of constituent } f \text{ from } c \text{ dying per time unit} \\ &= P_{11} \cdot X_{11cf} = D \dot{X}_{11cf} \end{aligned} \quad (\text{I-36})$$

$$\begin{aligned} Z_{32f} &= \text{amount of } f \text{ from all animal groups dying per time unit} \\ &= \sum_c Z_{31cf} \end{aligned} \quad (\text{I-37})$$

$$\begin{aligned} Z_{33f} &= \text{amount of } f \text{ added to organic debris soft animal parts category (d = 5) per time unit} \\ &= Z_{32f} \cdot P_{8f} = D \dot{X}_{215f} \end{aligned} \quad (\text{I-38})$$

$$D \dot{X}_{216f} = Z_{32f} - Z_{33f} \quad (\text{I-39})$$

#### ANIMAL II

For each animal group, there is a constant mortality rate (input parameter  $P_{16c}$ ). The protein and reserve carbon with the accompanying mineral elements constitute the soft parts of the carcasses. This includes the fats in the marrow of the bones. The fraction of structural carbon that makes up the skeleton is a constant for each animal group (input parameter  $P_{8c}$ ). The amounts of each mineral element per unit of skeleton structural carbon are also constants (input parameters  $P_{9cf}$ ).

$$\begin{aligned} Z_{37cf} &= \text{amount of constituent } f \text{ of } c \text{ dying per time unit} \\ &= P_{16c} \cdot X_{11cf} = D \dot{X}_{11cf} \end{aligned} \quad (\text{II-61})$$

$$Z_{38c5} = \text{amount of skeleton structural carbon in } c \text{ dying per time unit}$$

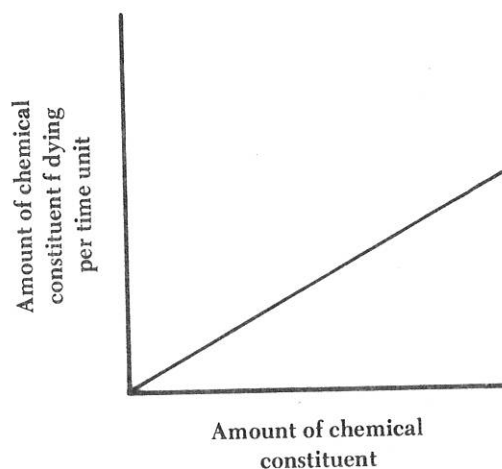


Figure 14. Mortality (ANIMAL I, II).

$$= P_{8c} \cdot Z_{37c5} \quad (\text{II-62})$$

$Z_{38cf}$  = amount of mineral element  $f$  in skeleton of  $c$  dying per time unit, where  $f \in M$

$$= P_{9cf} \cdot Z_{38c5} \quad (\text{II-63})$$

$Z_{38cf}$  = amount of carbon constituent  $f$  (other than structural carbon) in skeleton of  $c$  dying per time unit that is added to the organic debris skeleton category, where  $f \in C-[5]$

$$= 0 \quad (\text{II-64})$$

$$D\dot{X}_{215f} = \sum_c (Z_{37cf} - Z_{38cf}) \quad (\text{II-65})$$

$$D\dot{X}_{216f} = \sum_c Z_{38cf} \quad (\text{II-66})$$

### ANIMAL III

For each animal group there is a constant mortality rate (input parameter  $P_{23cm}$ ) representing the deaths due to non-predatory causes. For fetuses this rate represents the deaths due to prenatal cause -- it does not include the fetal losses associated with pregnant adult losses. In addition to these constant rates, a calculated mortality rate is obtained based on the "condition" of the animals. The index of "condition" is the ratio of the protein carbon level to the steady-state protein carbon level. When this has the value one, i.e., when the animal is in optimum condition, the mortality rate due to malnutrition is zero. As the index decreases, the mortality rate increases until it reaches one. The relationship that is hypothesized is

$$\text{mortality rate} = 1 - \exp[a \cdot \ln((X - \rho)/(1 - \rho))]$$

where  $a$ ,  $\rho$  are parameters, and  $X$  is the condition index. Parameter  $a$  controls the curvature of the function and  $\rho$  is the index at which mortality is one. The form of the curve is depicted in Figure 15. In this description, parameters  $P_{58c}$  represent  $a$  and  $P_{48c}$  represent  $\rho$ .

If the animal group is pregnant, the combined mortality rate of that group due to all non-predatory causes and malnutrition is also applied to the fetal group. The amounts of tissues that die are added to the surface litter. If the animal group is a fetal group the tissues that die are reabsorbed by the parental group.

As in I and II, the carcasses are divided into soft and hard parts (except in the case of resorption). "Wool" is added to the soft animal parts debris category, as is "milk." All reserve carbon and protein carbon are also added to the soft parts debris category. The body structural carbon is divided into "soft" structural carbon and "hard" structural carbon. The former is the carbon which forms part of the proteinaceous non-skeleton tissues such as ligaments and

tendons. The latter is the carbon which forms part of the skeleton. Using the ratios  $P_{14f3}$  and considering the soft structural carbon to be totally proteinaceous, the amounts of nitrogen and minerals associated with these soft tissues can be estimated. The remainder, after accounting for the nitrogen and minerals corresponding to the protein carbon, is then assumed to be part of the hard structural tissues.

$Z_{100c}$  = condition index of group  $c$

$$= (X_{11c3} - X_{13c3} - X_{14c5})/X_{16c} \quad (\text{III-214})$$

$Z_{101c}$  = fraction of animal group  $c$  dying per time unit due to malnutrition and non-predatory causes

$$= P_{23cm} \text{ if } Z_{100c} \geq 1$$

$$= 1 \text{ if } Z_{100c} \leq P_{48c}$$

$$= P_{23cm} + (1 - P_{23cm}) [1 - \exp(P_{58c} \cdot \ln((Z_{100c} - P_{48c})/(1 - P_{48c})))] \text{ if } P_{48c} < Z_{100c} < 1 \quad (\text{III-215})$$

if  $P_{16cfm} \neq 0$  and  $c = P_{53c'm'}$  for some  $c'$ ,  $m'$ ; i.e.,  $c$  is a fetal group,  $c'$  the parent group, resorption of the dead tissues occurs:

$$FR\dot{X}_{11cf} = X_{11cf} \cdot Z_{101c} \quad (\text{III-216})$$

$$FR\dot{X}_{13cf} = X_{13cf} \cdot Z_{101c} \quad (\text{III-217})$$

$$FR\dot{X}_{14cf} = X_{14cf} \cdot Z_{101c} \quad (\text{III-218})$$

$$FR\dot{X}_{16cf} = X_{16cf} \cdot Z_{101c} \quad (\text{III-218a})$$

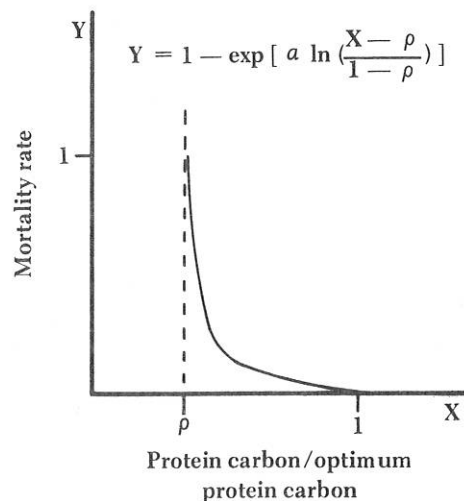


Figure 15. Mortality due to malnutrition (ANIMAL III).

$$FR\dot{X}_{15c} = (X_{11c5} - X_{13c5} - X_{14c5}) \cdot Z_{101c} \quad (\text{III-218b})$$

$Z_{102c'f}$  = amount of constituent  $f$  resorbed into adult group  $c'$  from fetal tissue group  $c$ , per time unit, where  $f \in M$

$$= X_{11cf} \cdot Z_{101c} \quad (\text{III-219})$$

$Z_{102c'3}$  = amount of carbon from protein tissues resorbed into adult group  $c'$  from fetal tissue group  $c$ , per time unit

$$= (X_{11c3} + X_{11c5}) \cdot Z_{101c} \quad (\text{III-220})$$

$Z_{102c'4}$  = amount of carbon from fat tissues resorbed into adult group  $c'$  from fetal tissue group  $c$  per time unit

$$= (X_{11c4} - X_{13c4} - X_{14c4}) \cdot Z_{101c} + X_{13c4} \cdot P_{55c} + X_{14c4} \cdot P_{57c} \quad (\text{III-221})$$

$Z_{102c'5}$  = amount of carbon from carbohydrate tissues resorbed into adult group  $c'$  from fetal tissue of group  $c$  per time unit

$$= X_{13c4} (1 - P_{55c}) + X_{14c4} \cdot (1 - P_{57c}) \quad (\text{III-221a})$$

if  $P_{36cm} \neq 0$ ; i.e., group  $c$  is pregnant in season  $m$ ,  $b$  is the numerical designation of the fetal group of  $c$ ;

if  $j$  is the numerical designation of the animal group with mortality rate  $Z_{101c}$ , equations III-222 to III-235 are applied to  $j = c$  and  $j = b$ ;

if  $P_{36cm} = 0$  or  $P_{16cfm} = 0$  or  $c \neq P_{53c'm}$  for any  $c'$ ,  $m'$ ; i.e., group  $c$  is not pregnant nor is it a fetal group,

$j = c$  only, in III-222 to III-235

$Z_{103jf}$  = amount of  $f$  of  $j$  dying per time unit

$$= X_{11jf} \cdot Z_{101c} = D\dot{X}_{11jf} \quad (\text{III-222})$$

$$D\dot{X}_{14jf} = X_{14jf} \cdot Z_{101c} \quad (\text{III-223})$$

$$D\dot{X}_{13jf} = X_{13jf} \cdot Z_{101c} \quad (\text{III-224})$$

$$D\dot{X}_{16jf} = X_{16jf} \cdot Z_{101c} \quad (\text{III-225})$$

$Z_{104jf}$  = amount of  $f$  (excluding "milk" and "wool") in  $j$  dying per time unit

$$= (X_{11jf} - X_{14jf} - X_{13jf}) \cdot Z_{101c} \quad (\text{III-226})$$

$$D\dot{X}_{15j} = Z_{104j5} \quad (\text{III-227})$$

$Z_{105j}$  = amount of soft structural carbon of  $j$  dying per time unit

$$= (1 - P_{8j}) \cdot Z_{104j5} \quad (\text{III-228})$$

$Z_{106jf}$  = amount of mineral  $f$  of  $j$  dying per time unit in soft tissues, where  $f \in M$

$$= \sum_{t \in C-[5]} Z_{104jt} \cdot P_{14ft} + Z_{105j} \cdot P_{14f3} \quad (\text{III-229})$$

$Z_{107jf}$  = amount of mineral  $f$  of  $j$  dying per time unit in hard skeletal tissues

$$= Z_{104jf} - Z_{106jf} \quad (\text{III-230})$$

$$D\dot{X}_{215f} = \sum_c \sum_j [X_{14jf} \cdot Z_{101c} + X_{13jf} \cdot Z_{101c} + Z_{106jf}], \text{ where } f \in M \quad (\text{III-231})$$

$$D\dot{X}_{215f} = \sum_c \sum_j [X_{14jf} \cdot Z_{101c} + X_{13jf} \cdot Z_{101c} + Z_{104jf}], \text{ where } f \in C-[5] \quad (\text{III-232})$$

$$D\dot{X}_{2155} = \sum_c \sum_j [X_{14jf} \cdot Z_{101c} + X_{13jf} \cdot Z_{101c} + Z_{105j}] \quad (\text{III-233})$$

$$D\dot{X}_{216f} = \sum_c \sum_j Z_{107jf}, \text{ where } f \in M \quad (\text{III-234})$$

$$D\dot{X}_{2165} = \sum_c \sum_j P_{8j} \cdot Z_{104j5} \quad (\text{III-235})$$

**Discussion**—Suppose the percentage of the initial population of each animal group that dies (due to causes other than system predation) during a time period  $\eta$  is known and equals  $\rho_c$ . The following calculations yield the mortality parameters of the three models ( $P_{11}$ , I-36;  $P_{16c}$ , II-61;  $P_{23cm}$ , III-98). For III, the percentage dying should not include deaths due to malnutrition.

let the number of animals in group  $c$  at the beginning of the period  $\eta = \nu_c$

let the fraction dying per time unit =  $\pi_c$

then,

$$\text{number dying on time unit one} = \pi_c \nu_c = \pi_c \nu_c (1 - \nu_c)^0$$

$$\text{number dying on time unit two} = \pi_c (\nu_c - \pi_c \nu_c) = \pi_c \nu_c (1 - \nu_c)$$

$$\text{number dying on time unit } \eta = \pi_c \nu_c (1 - \nu_c)^{\eta-1}$$

$$\begin{aligned}
 \text{thus, the total number dying during time period} &= \rho_c \nu_c \\
 &= \pi_c \nu_c + \pi_c \nu_c (1 - \nu_c) + \dots + \pi_c \nu_c (1 - \nu_c)^{\eta-1} \\
 &= \pi_c \nu_c [(1 - (1 - \pi_c)^\eta) / \pi_c] = \nu_c [1 - (1 - \pi_c)^\eta]
 \end{aligned}$$

therefore,

$$\begin{aligned}
 \rho_c &= 1 - (1 - \pi_c)^\eta \\
 (\ln(1 - \rho_c) / \eta) &= \ln(1 - \pi_c)
 \end{aligned}$$

and

$$\pi_c = 1 - e^{\ln((1 - \rho_c) / \eta)}$$

If the time period  $\eta$  is within a season of group  $c$  defined for III, then parameters  $P_{23cm}$  (III-98) are calculated. If this time period encompasses the simulation period of II, then parameters  $P_{16c}$  of II (II-61) are defined. The parameter  $P_{11}$  (I-36) of I can be calculated from the previous  $P_{16c}$  values as follows:

suppose the initial populations of each group in the community, as simulated in I, are known and equal  $\nu_c$

and suppose the fraction of group  $c$  dying per time unit =  $\pi_c$

then,

$$\text{total number dying per time unit} = \sum_c \pi_c \cdot \nu_c$$

percent of total population dying =

$$\begin{aligned}
 &(\sum_c \pi_c \nu_c / \sum_c \nu_c) \\
 &= P_{11}
 \end{aligned}$$

Since in I the ratios of the size of each population to the total numbers are constant, the calculation above applies to the community throughout the simulation period.

#### REPRODUCTION AND POPULATION CHANGES

##### ANIMAL I

The size distribution of the community is considered to be constant so that any decrease or increase in biomass reflects a decrease or increase in the population size. The population is proportional to the total amount of carbon. Reproduction is therefore not explicitly modeled but it is implicitly included through biomass increases.

$$\begin{aligned}
 Z_{34cf} &= \text{change in amount of chemical constituent } f \text{ of} \\
 &\text{animal group } c \text{ due to all processes, per time} \\
 &\text{unit} \\
 &= P\dot{X}_{11cf} + R\dot{X}_{11cf} + G\dot{X}_{11cf} + D\dot{X}_{11cf}
 \end{aligned} \tag{I-40}$$

(from equations I-15, 25, 32, 36)

$$\begin{aligned}
 Z_{35c} &= \text{average carbon per individual of group } c \\
 &= \sum_{f \in C} X_{11cf} / X_{12c}
 \end{aligned} \tag{I-41}$$

$$\dot{X}_{12c} = \sum_{f \in C} Z_{34cf} \cdot Z_{35c} \tag{I-42}$$

##### ANIMAL II

Reproduction is not modeled explicitly. There is an input parameter,  $P_{17c}$ , which determines whether the amount of structural carbon per individual of group  $c$  remains constant over the simulation, or whether it can vary. If the length of the simulation period is less than or equal to the time required for the development and subsequent transfer of the animal group to another group (i.e., the generation time;  $P_{17c}$ ), the structural carbon per individual is not constant. The growth process in this case represents the development of the individuals of the group. The proportion of each chemical constituent remains nearly constant with possible variations occurring in the reserve carbon due to fattening and in the protein carbon (and associated minerals) due to malnutrition. During each time unit the average structural carbon per individual is calculated so that any loss in structural carbon due to mortality can be translated into a loss of population. Thus, there can be no increases in the population of the group during the simulation, but decreases may occur due to deaths.

When the length of the simulation is greater than the generation time, the population of the group is considered to be proportional to the structural carbon of the group, thus assuming the structural carbon per individual to be constant. The growth process, in this case, is a reproduction process -- increases in structural carbon imply increases in the population. The amount of reserve carbon and protein carbon (with the accompanying minerals) per individual may vary due to fattening and malnutrition (respectively). Thus the size distribution of the group is considered to be approximately constant.

$$\begin{aligned}
 Z_{39c} &= \text{change in the amount of structural carbon of} \\
 &\text{group } c \text{ per time unit which causes a popula-} \\
 &\text{tion change} \\
 &= P\dot{X}_{11c5} + D\dot{X}_{11c5} + G\dot{X}_{11c5} \\
 &\text{if } P_{17c} < \text{simulation time period}
 \end{aligned}$$

$$= p\dot{X}_{11c5} + D\dot{X}_{11c5} \text{ if } P_{17c} \geq \text{simulation time period} \quad (\text{II-67})$$

(from equations II-23, 59, 61)

$$Z_{40c} = \text{average structural carbon per individual of group c}$$

$$= X_{11c5}/X_{12c} \text{ where } X_{11c5}, X_{12c} \text{ have the initial state variable values if } P_{17c} < \text{simulation time period}$$

$$= X_{11c5}/X_{12c} \text{ where } X_{11c5}, X_{12c} \text{ have the current state variable values if } P_{17c} \geq \text{simulation time period} \quad (\text{III-68})$$

$$\dot{X}_{12c} = Z_{39c} \cdot Z_{40c} \quad (\text{II-69})$$

### ANIMAL III

In this model, reproduction is treated explicitly. For each pregnant group of animals there is a corresponding fetal group into which embryo growth increments are channeled. There is a fixed gestation period; conception occurs on a set date with birth on a set date -- one birthday at most occurring in a season. For each birth, there is a potential maximum number of young per adult able to be born ( $P_{25cm}$ , III-104), each with a potential maximum weight. Malnutrition of the adult group may cause the number of young and/or the average weight per offspring to be less than the maximum (see "growth" process description for further details).

On the day of conception the population of the embryo group is set at the maximum, with a transfer of protein carbon and the corresponding mineral elements, from the breeding group. This causes the fetal group to enter into the simulation. However, the respiration, "feeding" and growth processes of the fetal group are controlled by the breeding group. The death process is also partially influenced by that of the breeding group. Hence, although the embryo group is separate from the parental group, there are still interactions between the two groups, as would be expected.

As mentioned in "Growth", animals need not be of mature size to reproduce -- juvenile growth can occur concurrently with embryo growth.

Changes in the population of a cohort can occur due to transfer into this cohort from another, transfer out of the cohort, migration (see later discussion of these processes), reproduction, death, and predation. For each time unit of simulation there is an average structural carbon biomass per individual of each cohort. By accumulating the decrements in structural carbon due to death and predation per time unit for each animal group, the numbers dying per time unit can be determined.

$$Z_{122c} = \text{changes in structural carbon of c due to death and system predation per time unit}$$

$$= p\dot{X}_{15c} + D\dot{X}_{15c} + FR\dot{X}_{15c} =$$

$$\dot{X}_{15c} \quad (\text{III-236})$$

(from equations III-33, 227, 218b)

$$Z_{123c} = \text{average structural carbon per individual of animal class c}$$

$$= [(X_{11c5} - X_{13c5} - X_{14c5})/X_{12c}] \quad (\text{III-237})$$

$$Z_{124c} = \text{change in population due to death and system predation of c per time unit}$$

$$= (Z_{122c}/Z_{123c}) = D\dot{X}_{12c} \quad (\text{III-238})$$

For discussion on the transfer process see "Transfer: ANIMAL III" and for immigration/emigration see "Migration: ANIMAL III."

$$\dot{X}_{12c} = D\dot{X}_{12c} + C\dot{X}_{12c} + T\dot{X}_{12c} + V\dot{X}_{12c} + I\dot{X}_{12c} + A\dot{X}_{12c} \quad (\text{III-239})$$

(from equations III-238, 104, 246, 265, 256, 247)

### EXCRETION

There is no separate process for excretion. It is a by-product of the respiration, assimilation and growth processes.

### ANIMAL I

$$\dot{X}_{217f} = E\dot{X}_{217f} + R\dot{X}_{217f} + G\dot{X}_{217f} \quad (\text{I-43})$$

(from equations I-24, 27, 28, 33, 34)

### ANIMAL II

$$\dot{X}_{217f} = E\dot{X}_{217f} + R\dot{X}_{217f} + G\dot{X}_{217f}$$

(II-70)

(from equations II-32, 42, 57, 58)

### ANIMAL III

In this model, an animal group's excreta can be distributed throughout the soil profile. If it is added to the surface of the soil it increments the amount of the excreta category of the organic debris. If added to the soil horizons



it increments the amounts of soil organic matter in these horizons. An input parameter ( $P_{27chm}$ ) apportions the excreta throughout the soil profile, for each season and animal group. This parameter is an indicator of the area of activity of the animal group.

$Z_{109cf}$  = amount of f in the excreta of c per time unit

$$= \dot{X}_{17cf}$$

$$= E\dot{X}_{17c1} + BV\dot{X}_{17c1} + E\dot{X}_{17c1}$$

$$+ MN\dot{X}_{17c1} + R\dot{X}_{17c1} + RS\dot{X}_{17c1}$$

$$+ ES\dot{X}_{17c1} + U\dot{X}_{17c1}, \text{ where } f=1$$

(from equations III-50, 60, 55, 73, 92, 93, 100, 101, 164, 182, 210a)

$$= BV\dot{X}_{17cf} + E\dot{X}_{17cf} + MN\dot{X}_{17cf}$$

$$+ R\dot{X}_{17cf} + RS\dot{X}_{17cf} + ES\dot{X}_{17cf}$$

$$+ U\dot{X}_{17cf}, \text{ where } f \in M - [1]$$

(from equations listed above, excluding III-50, 210 a, and including III-213)

$$= BV\dot{X}_{17c3} + E\dot{X}_{17c3} + MN\dot{X}_{17c3}$$

$$+ R\dot{X}_{17c3} + RS\dot{X}_{17c3} + ES\dot{X}_{17c3}$$

$$+ Y\dot{X}_{17c3} + F\dot{X}_{17c3}, \text{ where } f=3$$

(from equations III-61, 55, 75, 92, 93, 100, 101, 160, 177, 201, 209)

$$= E\dot{X}_{17cf}, \text{ where } f \in C - [3] \quad (\text{III-240})$$

(from equation III-55)

$Z_{110cfh}$  = amount of f added to soil horizon h by excretion of c per time unit

$$Z_{109cf} \cdot P_{27chm} \quad (\text{III-241})$$

$Z_{111cf}$  = amount of f added to soil surface by excretion of c per time unit

$$= Z_{109cf} - \sum_h Z_{110cfh} \quad (\text{III-242})$$

$$E\dot{X}_{217f} = \sum_c Z_{111cf} \quad (\text{III-243})$$

$$E\dot{X}_{22hf} = \sum_c Z_{110cfh} \quad (\text{III-244})$$

**Discussion**—The parameters  $P_{27chm}$  (III-121) of III may be obtained through knowledge of each animal group's activity regime. For example, if an animal spends 50% of its time on the surface, 30% in the first soil horizon and 20% in the second soil horizon, then it may be assumed that the amount of excreta is deposited in these areas in proportion to the time it spent in each. Thus  $P_{27c1m} = 0.3$  and  $P_{27c2m} = 0.2$ .

#### TRANSFERS

This process involves transfer of animals from one animal class to another.

#### ANIMAL I

There is no provision for transfers in this model. Consequently division of groups of animals into age-classes should be avoided unless the time period of the simulation is such that there is no need for transfers to occur.

#### ANIMAL II

As for I, there is no provision for transfers in this model and age-classes should not be specified unless the time period of the simulation covers a period during which no transfers occur.

#### ANIMAL III

For every animal class (except the oldest) there is a day on which the whole biomass and population of the class are transferred to another group. These dates are input parameters  $P_{28c}$ . The group to which the class is transferred is also determined by an input parameter ( $P_{29c}$ ).

let  $Z_{112cr} = 1$  if group c transfers to r during this time unit; i.e.,  $P_{29c} = r$  and this time unit =  $P_{28c}$

$$= 0 \text{ if not} \quad (\text{III-245})$$

$Z_{113c}$  = change in population of c due to group transfers, per time unit

$$= Z_{112cr} \cdot X_{12c} = T\dot{X}_{12c} \quad (\text{III-246})$$

$A\dot{X}_{12r}$  =  $\sum_{c \in Tr} Z_{113c}$ , where Tr = groups that transfer during this time unit (III-247)

$Z_{114cf}$  = amount of constituent f taken from c in group transfers per time unit

$$= Z_{112cr} \cdot X_{11cf} = T\dot{X}_{11cf} \quad (\text{III-248})$$

$$A\dot{X}_{11rf} = \sum_{c \in Tr} Z_{114cf} \quad (\text{III-249})$$

$$T\dot{X}_{14cf} = X_{14cf} \cdot Z_{112Cr} \quad (\text{III-250})$$

$$A\dot{X}_{14rf} = \sum_{c \in Tr} T\dot{X}_{14cf} \quad (\text{III-251})$$

$$T\dot{X}_{13cf} = X_{13cf} \cdot Z_{112Cr} \quad (\text{III-252})$$

$$A\dot{X}_{13cf} = \sum_{c \in Tr} T\dot{X}_{13cf} \quad (\text{III-253})$$

$$T\dot{X}_{16c} = X_{16c} \cdot Z_{112Cr} \quad (\text{III-254})$$

$$A\dot{X}_{16r} = \sum_{c \in Tr} T\dot{X}_{16c} \quad (\text{III-255})$$

## MIGRATION

## ANIMAL I

There is no process to simulate migration in this model.

## ANIMAL II

There is no process to simulate migration in this model.

## ANIMAL III

This process can also include man-management. The times of the year during which the animals immigrate or are brought into the system can be specified as the starting dates of seasons ( $P_{40cm}$ ). The time they emigrate or are taken out of the system can also be specified as the starting dates of other seasons ( $P_{41cm}$ ). Thus there are seasons when certain groups of animals may not be present, in which case, the model ignores all processes except for that of checking for the animals return. Consider immigration; input parameters  $P_{30cfi}$ ,  $P_{31ci}$ ,  $P_{32ci}$ ,  $P_{33ci}$ ,  $P_{34ci}$  designate the carbon constituent biomasses, "wool," "milk" carbon, the protein steady-state level, and the population of the successive arrivals of each animal group over the period of simulation. Thus, for example, during one year the grazing pressure of cattle brought onto a winter range may be light, whereas the next year it may be heavy. Each spring, a constant number of migrating birds may return to their breeding grounds within the system. The model records the arrival of the animals as a gain of chemical constituents to the system. For emigration, all the animals of those migrating groups leave the system at the start of the designated seasons. Migration of birds in fall from the system to overwintering grounds outside the system would be an example of such a process. Removal of cattle with the advent of summer can also be included. If it is necessary to simulate removal of only a portion of the animal group present, leaving a fixed population density, the starting dates of the seasons can be adjusted so that this situation can be approximated; during one time unit (beginning of the emigration season) all the group can leave. During the next time unit (beginning of the

immigration season) a number of them equal to the fixed population density can "return."

let  $Z_{118ci} = 1$  if this is the  $i$ th immigration of group  $c$  since the simulation began, and if this time unit is a day of immigration; i.e., equals  $P_{40cm}$

= 0 if not

$$I\dot{X}_{12c} = P_{31ci} \cdot Z_{118ci} \quad (\text{III-256})$$

$Z_{115cf}$  = amount of mineral  $f$  in immigrants to  $c$ , during the  $i$ th immigration (excluding "milk" and "wool"), where  $f \in M$

$$= \sum_{t \in C} P_{30cti} \cdot P_{14ft} \cdot Z_{118ci} \quad (\text{III-257})$$

$Z_{115cf}$  = amount of carbon  $f$  in immigrants to  $c$  during the  $i$ th immigration (excluding "milk" and "wool"), where  $f \in C$

$$= P_{30cfi} \cdot Z_{118ci} \quad (\text{III-258})$$

$Z_{116cf}$  = amount of chemical constituent  $f$  in "wool" of immigrants to  $c$  during the  $i$ th immigration

$$= P_{32ci} \cdot P_{19cf} \cdot Z_{118ci} = I\dot{X}_{14cf} \quad (\text{III-259})$$

$Z_{117cf}$  = amount of chemical constituent  $f$  in "milk" of immigrants to  $c$  during  $i$ th immigration

$$= P_{33ci} \cdot P_{21cf} \cdot Z_{118ci} = I\dot{X}_{13cf} \quad (\text{III-260})$$

$$I\dot{X}_{16c} = P_{34ci} \cdot Z_{118ci} \quad (\text{III-261})$$

$$I\dot{X}_{0113} = \sum_c \left( \sum_{f \in C} Z_{115cf} + P_{32ci} + P_{33ci} \right) \cdot Z_{118ci} \quad (\text{III-262})$$

$$I\dot{X}_{011f} = \sum_c (Z_{115cf} + Z_{116cf} + Z_{117cf}), \text{ where } f \in M \quad (\text{III-263})$$

$$I\dot{X}_{11cf} = Z_{115cf} + Z_{116cf} + Z_{117cf} \quad (\text{III-264})$$

let  $Z_{119ci} = 1$  if this is the  $i$ th emigration of group  $c$  since the simulation began and if this time unit is a day of emigration; i.e., equals  $P_{41cm}$

= 0 if not

$$V\dot{X}_{12c} = X_{12c} \cdot Z_{119ci} \quad (\text{III-265})$$

$$V\dot{X}_{11cf} = X_{11cf} \cdot Z_{119ci} \quad (\text{III-266})$$

$$\dot{V}\dot{X}_{01f} = \sum_c X_{11cf} \cdot X_{119ci}, \text{ where } f \in M \quad (\text{III-267})$$

$$\dot{V}\dot{X}_{013} = \sum_c \sum_{f \in C} X_{11cf} \cdot Z_{119ci} \quad (\text{III-268})$$

$$\dot{V}\dot{X}_{14cf} = X_{14cf} \cdot Z_{119ci} \quad (\text{III-269})$$

$$\dot{V}\dot{X}_{13cf} = X_{13cf} \cdot Z_{119ci} \quad (\text{III-270})$$

$$\dot{V}\dot{X}_{16c} = X_{16c} \cdot Z_{119ci} \quad (\text{III-271})$$

OVERWINTERING -- WINTER HIBERNATION --  
SUMMER AESTIVATION

### ANIMAL I

None of these processes is modeled explicitly in I. The effects of such behavior can be included in the simulation if the period of simulation spans the time when hibernation or aestivation is in progress. That is, the simulation must begin during the hibernation and end during the hibernation, so that the time-invariant parameters of this model will apply throughout the whole time period. If an animal group emerges from or goes into hibernation during the simulation, the parameters must initially be given values that are averaged over the simulation period. Then gross estimates of the total biomass and population will be obtained without showing the fluctuations due to these periods of inactivity.

### ANIMAL II

In this model, the animals can be dealt with group by group, and so the fact that one group may be in hibernation while another is not need not affect the parameter values of both, as it does in I. For the group that does hibernate, a simulation of a time period encompassing the term of hibernation would necessitate an averaging of the parameters. Thus it would appear that in the non-hibernating periods, the animal group was less active than in reality, while in its hibernating seasons, it was more active than in reality.

### ANIMAL III

Hibernation and aestivation can be modeled explicitly. As mentioned previously, for each animal group a number of seasons are defined over the year. The investigator can define a season during which the animal group will be inactive. The parameters for these seasons can be set accordingly. Thus the type of year as regards environmental stresses upon the animal group is set prior to the simulation. During the periods of inactivity, the animals are still regarded as being within the system -- they are available to predators, if such preferences are expressed by other animal groups in those seasons. Respiration and death are the only processes that the hibernating groups take part in. Animals that retire underground during periods of stress and live off their stores, can, somewhat inadequately, be simulated in

this model. In these seasons if the foods that they express preferences for are available, according to the plant and soils models, then they will eat these. For example, rodents living in their burrows during winter may not be hibernating but living off their stores of seeds. To simulate this, the preference for seeds in this season would be satisfied by feeding on the shed seeds on the surface. Thus, instead of "physically" transporting the seeds to caches during the active period of the year, the model uses the seeds left on the surface, as if the rodents stored only what they would eat during winter. This underestimates the impact of the rodents on the seed reserves, as they customarily remove more seeds than they use during the winter months. Periods of torpor, or short-term hibernation or aestivation are not able to be simulated because of the lack of direct environmental cues.

### "WOOL" REMOVAL

#### ANIMAL I and ANIMAL II

This process is not included in these versions.

#### ANIMAL III

This process simulates removal of "wool" at specified dates of the year for each animal group. As mentioned previously, "wool" can refer to several structures; for example, sheep wool and exoskeletons of insect instars. The shedding of an exoskeleton or the shearing of sheep is thus modeled here. Input parameters  $P_{37ci}$  indicate the proportion of "wool" to be removed at each date which is specified by an input parameter ( $P_{38ci}$ ).

$$\begin{aligned} \text{let } Z_{120c} &= 1 \text{ if this time unit} = P_{38ci} \\ &= 0 \text{ if not} \end{aligned}$$

$$Z_{121cf} = \text{amount of chemical constituent } f \text{ in the "wool" of } c \text{ removed}$$

$$= Z_{120c} \cdot P_{37ci} \cdot X_{14cf} = K\dot{X}_{11cf} = K\dot{X}_{14cf}$$

(III-272)

$$K\dot{X}_{01f} = \sum_c Z_{121cf}, \text{ where } f \in M \quad (\text{III-273})$$

$$K\dot{X}_{013} = \sum_c \left( \sum_{f \in C} Z_{121cf} \right) \quad (\text{III-274})$$

### EFFECT OF ANIMALS ON THE SYSTEM

#### ANIMAL I

The only effects that animals have on the simulated system in this model are those due to actual consumption of food materials, excretion of compounds and respiration of carbon.

## ANIMAL II

As in I, consumption, respiration and excretion are the only processes that affect the system.

## ANIMAL III

Without inclusion of animal-caused transfers of materials to organic debris categories, the effects of certain animal groups are grossly underestimated. For example, tree-girdling insects may consume relatively small amounts of food, but they damage and kill vast amounts of living tissue. In this model, a process is included that transfers an amount of one state variable (i) to another state variable (k), the amount transferred being proportional to the amount of the first state variable consumed (parameters  $P_{59ijkcm}$ ). Thus clipping of vegetation by jackrabbits can be included in the simulation as can trampling of vegetation by large herbivores while they feed, and the killing of sheep by coyotes which consume only a small part of their prey before running off, can also be included in the simulation. The state variable into which the transfer is made need not be a state variable representing an organic debris category. For example, seed dispersal by rodents can be simulated by transferring seeds from the soil surface to different seed horizons within the soil. Here, the state variables into which transfers are made represent the amounts of seeds in various seed horizons.

The transfer of amounts from a set of state variables representing the amounts of all the chemical constituents of the subcompartment must not change the relative proportions of these chemical constituents in the subcompartment. For example, transfers from the plant #3, organ #4 subcompartment must occur at the same rate for each chemical constituent of that subcompartment.

let  $Z_{108ci}$  = amount of state variable i consumed by c per time unit

$$= Z_{15sgfc} \text{ (from equation III-17)}$$

$$\text{or} = Z_{16pnfc} \text{ (from equation (III-19))}$$

$$\text{or} = Z_{17dfc} \text{ (from equation III-21)}$$

$$\text{or} = Z_{18hfc} \text{ (from equation III-23)}$$

$$\text{or} = Z_{21yfc} \text{ (from equation III-26)} \quad \text{(III-275)}$$

$$AL\dot{X}_i = \sum_c \sum_k P_{59ikcm} \cdot Z_{108ci} \quad \text{(III-276)}$$

$$AG\dot{X}_k = \sum_c \sum_i P_{59ikcm} \cdot Z_{108ci} \quad \text{(III-277)}$$

## SUMMARY OF PROCESSES

The total changes in the state variables due to animal-related processes are listed in this section.

## ANIMAL I

Vegetation—Herbivory.

$$\dot{X}_{1sgf} = H\dot{X}_{1sgf} \text{ (from equation I-1)} \quad \text{(I-44)}$$

Shed seeds—Consumption.

$$\dot{X}_{2pnf} = H\dot{X}_{2pnf} \text{ (from equation I-6)} \quad \text{(I-45)}$$

Organic debris—Consumption,  $d \neq 5, 6, 7$ .

$$\dot{X}_{2idf} = H\dot{X}_{2idf} \text{ (from equation I-9)} \quad \text{(I-46)}$$

Consumption, death (excluding system predation).

$$\dot{X}_{215f} = H\dot{X}_{215f} + D\dot{X}_{215f} \text{ (from equations I-9, 38)} \quad \text{(I-47)}$$

Consumption, death (including system predation).

$$\dot{X}_{216f} = H\dot{X}_{216f} + D\dot{X}_{216f} + P\dot{X}_{216f} \text{ (from equations I-9, 39, 18)} \quad \text{(I-48)}$$

Consumption, excretion, respiration, growth.

$$\dot{X}_{217f} = H\dot{X}_{217f} + E\dot{X}_{217f} + R\dot{X}_{217f} + C\dot{X}_{217f} \text{ (from equations I-43, 9, 24, 27, 28, 33, 34)} \quad \text{(I-49)}$$

Soil organic matter—Consumption.

$$\dot{X}_{22hf} = H\dot{X}_{22hf} \text{ (from equation I-12)} \quad \text{(I-50)}$$

Animal biomass—System predation, respiration, growth, death (excluding system predation).

$$\dot{X}_{11cf} = P\dot{X}_{11cf} + R\dot{X}_{11cf} + G\dot{X}_{11cf} + D\dot{X}_{11cf} \text{ (from equations I-40, 15, 25, 32, 36)} \quad \text{(I-51)}$$

Animal populations—

$$\dot{X}_{12c} \text{ (see equation I-42)}$$

Atmospheric interactions (gain or loss to system)—Respiration, growth.

$$\dot{X}_{0113} = R\dot{X}_{0113} + G\dot{X}_{0113} \text{ (from equations I-26, 35)} \quad \text{(I-52)}$$

## ANIMAL II

**Vegetation**—Consumption.

$$\dot{X}_{1sgf} = H\dot{X}_{1sgf} \text{ (from equation II-15)} \quad (\text{II-71})$$

**Shed seeds**—Consumption.

$$\dot{X}_{2pnf} = H\dot{X}_{2pnf} \text{ (from equation II-17)} \quad (\text{II-72})$$

**Organic debris**—Consumption,  $d \neq 5, 6, 7$ .

$$\dot{X}_{21df} = H\dot{X}_{21df} \text{ (from equation II-19)} \quad (\text{II-73})$$

Consumption, death (excluding system predation).

$$\dot{X}_{215f} = H\dot{X}_{215f} + D\dot{X}_{215f} \text{ (from equations II-19, 65)} \quad (\text{II-74})$$

Consumption, death (including system predation).

$$\dot{X}_{216f} = H\dot{X}_{216f} + D\dot{X}_{216f} + P\dot{X}_{216f} \text{ (from equations II-19, 66, 28)} \quad (\text{II-75})$$

Consumption, excretion, respiration, growth.

$$\dot{X}_{217f} = H\dot{X}_{217f} + E\dot{X}_{217f} + R\dot{X}_{217f} + G\dot{X}_{217f} \text{ (from equations II-70, 32, 42, 44, 57, 58)} \quad (\text{II-76})$$

**Soil organic matter**—Consumption.

$$\dot{X}_{22hf} = H\dot{X}_{22hf} \text{ (from equation II-21)} \quad (\text{II-77})$$

**Animal biomasses**—System predation, respiration, protein resynthesis, growth, death,  $f \neq 4$ .

$$\dot{X}_{11cf} = P\dot{X}_{11cf} + R\dot{X}_{11cf} + Y\dot{X}_{11cf} + G\dot{X}_{11cf} + D\dot{X}_{11cf} \text{ (from equations II-23, 41, 48, 59, 61)} \quad (\text{II-78})$$

System predation, respiration, protein resynthesis, growth, death, fattening.

$$\dot{X}_{11c4} = P\dot{X}_{11c4} + R\dot{X}_{11c4} + Y\dot{X}_{11c4} + G\dot{X}_{11c4} + D\dot{X}_{11c4} + F\dot{X}_{11c4} \text{ (from equations II-23, 41, 48, 59, 61, 60)} \quad (\text{II-79})$$

**Animal populations**—

$$\dot{X}_{12c} \text{ (see equation II-69)}$$

**Atmosphere interactions (gain or loss from the system)**—Respiration.

$$\dot{X}_{0113} = R\dot{X}_{0113} \text{ (from equation II-40)} \quad (\text{II-80})$$

## ANIMAL III

**Vegetation**—Herbivory, clipping/wastage.

$$\dot{X}_{1sgf} = H\dot{X}_{1sgf} + AL\dot{X}_i \text{ (from equations III-18, 276)} \quad (\text{III-278})$$

**Shed seeds**—Consumption, movement through horizons by animals.

$$\dot{X}_{2pnf} = H\dot{X}_{2pnf} + AL\dot{X}_i + AG\dot{X}_i \text{ (from equations III-20, 276, 277)} \quad (\text{III-279})$$

**Organic debris**— $d \neq 5, 6, 7$ . Consumption, transfers into and out of by animal action.

$$\dot{X}_{21df} = H\dot{X}_{21df} + AL\dot{X}_i + AG\dot{X}_i \text{ (from equations III-22, 276, 277)} \quad (\text{III-280})$$

$d = 5$ , consumption, predation, mortality.

$$\dot{X}_{215f} = H\dot{X}_{215f} + P\dot{X}_{215f} + D\dot{X}_{215f} \text{ (from equations III-22, 42, 231, 233)} \quad (\text{III-281})$$

$d = 6$ , consumption, predation, mortality.

$$\dot{X}_{216f} = H\dot{X}_{216f} + P\dot{X}_{216f} + D\dot{X}_{216f} \text{ (from equations III-22, 41, 234, 235)} \quad (\text{III-282})$$

$d = 7$ , consumption, excretion.

$$\dot{X}_{217f} = H\dot{X}_{217f} + E\dot{X}_{217f} \text{ (from equations III-22, 243)} \quad (\text{III-283})$$

**Soil organic matter**—Consumption, excretion, transfers into and between horizons through animal action.

$$\dot{X}_{22hf} = H\dot{X}_{22hf} + E\dot{X}_{22hf} + AL\dot{X}_i + AG\dot{X}_i \text{ (from equations III-24, 244, 276, 277)} \quad (\text{III-284})$$

**Animal biomass—**

$Z_{128cf}$  = change in chemical constituent f of c from all processes except fattening; transfers into and from the cohort; immigration; emigration; mortality; predation; respiration; nursing; growth; protein resynthesis; "wool" removal; "milk" resorbption; metabolic nitrogen loss; conception; fetal resorbption; storage of minerals

$$\begin{aligned} Z_{128cf} = & A\dot{X}_{11cf} + T\dot{X}_{11cf} + I\dot{X}_{11cf} \\ & + V\dot{X}_{11cf} + D\dot{X}_{11cf} + P\dot{X}_{11cf} \\ & + R\dot{X}_{11cf} + S\dot{X}_{11cf} + \\ & G\dot{X}_{11cf} + Y\dot{X}_{11cf} + K\dot{X}_{11cf} \\ & + MR\dot{X}_{11cf} + MN\dot{X}_{11cf} + \\ & C\dot{X}_{11cf} + FR\dot{X}_{11cf} + SM\dot{X}_{11cf} \\ & + PS\dot{X}_{11cf} + RS\dot{X}_{11cf} + MS\dot{X}_{11cf} \\ & + ES\dot{X}_{11cf} + MY\dot{X}_{11cf} + AL\dot{X}_i \end{aligned} \quad (\text{III-285})$$

(from equations 249, 248, 264, 266, 222, 27, 85, 89, 96, 98, 99, 44, 146, 149, 188, 198, 272, 67b, 74, 103, 103a, 216, 212, 152, 158, 163, 166a, 173, 174, 181, 190, 276).

$$\dot{X}_{11cf} = Z_{128cf}, \text{ where } f \neq 4 \quad (\text{III-286})$$

$$\dot{X}_{11c4} = Z_{128c4} + F\dot{X}_{11c4} \text{ (from equations III-285, 208)} \quad (\text{III-287})$$

**Atmosphere interactions (gain to or loss from the system)—**

Carbon: immigration, emigration, respiration, "wool" removal, loss due to biological value considerations, methane production, loss associated with metabolic nitrogen loss; anabolism inefficiencies; catabolism of tissues for energy in protein resynthesis; inefficiency of fat production.

$$\begin{aligned} \dot{X}_{0113} = & I\dot{X}_{0113} + V\dot{X}_{0113} + R\dot{X}_{0113} \\ & + K\dot{X}_{0113} + BV\dot{X}_{0113} + MP\dot{X}_{0113} \\ & MN\dot{X}_{0113} + G\dot{X}_{0113} + Y\dot{X}_{0113} \\ & + F\dot{X}_{0113} \end{aligned} \quad (\text{III-288})$$

(from equations III-262, 268, 84, 86, 94, 102, 274, 62, 67a, 76, 172, 178, 196, 202, 210)

Immigration, emigration, "wool" removal, where  $f \in M$ .

$$\dot{X}_{0113} = I\dot{X}_{011f} + V\dot{X}_{011f} + K\dot{X}_{011f} \quad (\text{III-289})$$

"Wool"—Predation, mortality, transfer from and into the cohort, emigration, immigration, "wool" removal, growth, fetal resorbption.

$$\begin{aligned} \dot{X}_{14cf} = & P\dot{X}_{14cf} + D\dot{X}_{14cf} + A\dot{X}_{14cf} + \\ & T\dot{X}_{14cf} + V\dot{X}_{14cf} + I\dot{X}_{14cf} + \\ & K\dot{X}_{14cf} + C\dot{X}_{14cf} + FR\dot{X}_{14cf} \end{aligned} \quad (\text{III-290})$$

(from equations III-29, 223, 251, 250, 269, 259, 272, 148, 217)

"Milk"—Predation, nursing, mortality, transfers into and between cohorts, emigration, immigration, resorbption, production, fetal resorbption.

$$\begin{aligned} \dot{X}_{13cf} = & P\dot{X}_{13cf} + S\dot{X}_{13cf} + D\dot{X}_{13cf} + \\ & A\dot{X}_{13cf} + T\dot{X}_{13cf} + I\dot{X}_{13cf} + \\ & V\dot{X}_{13cf} + MR\dot{X}_{13cf} + C\dot{X}_{13cf} \end{aligned} \quad (\text{III-291})$$

(from equations III-31, 44, 224, 253, 252, 260, 270, 676, 147)

**Excreta**—Egestion; respiration; loss due to biological value considerations; metabolic nitrogen; protein catabolism for reserve tissue synthesis, and for energy needs in synthesis of new tissues and protein resynthesis and fattening; unused mineral constituents; non-proteinaceous nitrogen.

$$\begin{aligned} \dot{X}_{17cf} = & E\dot{X}_{17cf} + R\dot{X}_{17cf} + BV\dot{X}_{17cf} + \\ & MN\dot{X}_{17cf} + RS\dot{X}_{17cf} + ES\dot{X}_{17cf} + \\ & Y\dot{X}_{17cf} + F\dot{X}_{17cf} + U\dot{X}_{17cf} + \\ & EN\dot{X}_{17cf} \end{aligned} \quad (\text{III-292})$$

(from equations III-55, 92, 93, 100, 101, 60, 61, 73, 75, 160, 164, 177, 182, 201, 209, 210a, 213, 50)

**Protein steady-state level**—Growth; predation; mortality; fetal resorbption; transfer into and out of the cohort; emigration and immigration; conception.

$$\begin{aligned} \dot{X}_{16c} = & C\dot{X}_{16c} + P\dot{X}_{16c} + D\dot{X}_{16c} + \\ & FR\dot{X}_{16c} + T\dot{X}_{16c} + A\dot{X}_{16c} + \\ & V\dot{X}_{16c} + I\dot{X}_{16c} + C\dot{X}_{16c} \end{aligned} \quad (\text{III-293})$$

(from equations III-117, 109, 34, 225, 218, 254, 255, 271, 261, 104)

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**APPENDIX 1**  
SYMBOL EQUIVALENCE TABLE

The symbols used in the text are listed here with their definitions. The units used are  $\text{wt} \cdot \text{area}^{-1} \cdot \text{time}^{-1}$  except when indicated as follows:

<p>* <math>\text{wt} \cdot \text{area}^{-1}</math>  <math>\uparrow \text{time}^{-1}</math>  <math>\downarrow \text{area}^{-1} \cdot \text{time}^{-1}</math>  <math>\star \text{area}^{-1}</math>  ** <math>\text{wt}</math></p>	<p><math>\uparrow\uparrow \text{energy} \cdot \text{area}^{-1} \cdot \text{time}^{-1}</math>  *** <math>\text{wt} \cdot \text{wt}^{-1} \cdot \text{time}^{-1}</math>  <math>\uparrow\uparrow\uparrow \text{wt} \cdot \text{wt}^{-1}</math>  <math>\uparrow\uparrow\uparrow \text{wt} \cdot \text{energy}^{-1}</math>  <math>\uparrow\uparrow\uparrow \text{energy} \cdot \text{area}^{-1}</math></p>
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Symbol	Definition
<i>ANIMAL I</i>	
$Z_1$	amount of carbon consumed by the community from live vegetation per time unit
$Z_2$	* amount of carbon in live vegetation
$Z_3$	* amount of carbon in animal community
$Z_{4sgf}$	amount of chemical constituent f consumed by the community from vegetation compartment (s,g) per time unit
$Z_{5n}$	amount of carbon consumed by the community from the shed seeds in seed horizon n per time unit
$Z_{6n}$	* amount of carbon in seeds of seed horizon n
$Z_{7pnf}$	amount of chemical constituent f consumed by community from shed seed compartment (p,n) per time unit
$Z_{8d}$	amount of carbon consumed by the community from the organic debris category d per time unit
$Z_{9d}$	* amount of carbon in organic debris of category d
$Z_{10df}$	amount of chemical constituent f consumed by the community from organic debris category d per time unit
$Z_{11h}$	amount of carbon consumed by the community from soil organic matter in soil horizon h per time unit
$Z_{12h}$	* amount of carbon in soil organic matter in soil horizon h
$Z_{13hp}$	amount of chemical constituent f consumed by community from each soil organic matter compartment h per time unit
$Z_{14}$	amount of carbon in prey killed by predators in the system per time unit
$Z_{15cf}$	amount of chemical constituent f of prey group c killed by predators in the system per time unit
$Z_{16c}$	amount of chemical constituent f in prey killed by predators in the system per time unit
$Z_{17f}$	amount of chemical constituent f in prey killed by predators in the system and consumed per time unit
$Z_{18f}$	amount of chemical constituent f in prey killed by predators in the system and added to organic debris skeleton category (d=6) per time unit
$Z_{19c}$	proportion of carbon in the community from animal group c
$Z_{20cf}$	amount of chemical constituent f consumed by c per time unit, from non-animal food sources



Symbol	Definition
$Z_{21cf}$	total amount of chemical constituent f consumed by c per time unit from animal sources
$Z_{22cf}$	amount of chemical constituent f assimilated by c per time unit
$Z_{23cf}$	amount of chemical constituent f egested per time unit by c
$Z_{24f}$	amount of chemical constituent f egested per time unit
$Z_{25cf}$	amount of chemical constituent f respired or excreted per time unit by c
$Z_{26}$	total carbon lost from system to atmosphere per time unit due to respiration
$Z_{27f}$	ratio of chemical constituent f to total carbon in animal composition
$Z_{28cf}$	amount of chemical constituent f that (in absence of limiting conditions) will be added to c per time unit
$Z_{29}$	factor by which weight gain is reduced if a mineral is limiting
$Z_{30cf}$	amount of chemical constituent f added to c per time unit
$Z_{31cf}$	amount of chemical constituent f from c dying (excluding system predation) per time unit
$Z_{32f}$	amount of chemical constituent f in all animals dying per time unit (excluding system predation)
$Z_{33f}$	amount of chemical constituent f added to organic matter soft animal parts category ( $d=5$ ) per time unit from the death of animals (excluding system predation)
$Z_{34cf}$	change in amount of chemical constituent f in group c due to all processes, per time unit
$Z_{35c}$	average carbon per individual of group c
$P_1$	† maximum postulated amount of live vegetation carbon consumed per unit animal carbon biomass per time unit
$P_{3n}$	† maximum postulated amount of carbon consumed from the $n$ th horizon per unit animal carbon biomass per time unit
$P_{4d}$	† maximum postulated amount of carbon consumed from the $d$ th category of the organic debris per unit animal carbon biomass per time unit
$P_{5h}$	† maximum postulated amount of carbon consumed from soil organic matter of the $h$ th soil horizon per unit animal carbon biomass per time unit
$P_{6f}$	fraction of the total biomass of chemical constituent f that makes up the soft part of the body (no units)
$P_7$	† maximum postulated predation level of animal prey per unit animal biomass per time unit (fraction of animal biomass that is killed by predators in the system per time unit)
$P_8$	fraction of consumed non-animal food that is assimilated (no units)
$P_9$	fraction of consumed animal food that is assimilated (no units)
$P_{10}$	† fraction of animal biomass respired per time unit
$P_{11}$	fraction of animal biomass dying (excluding system predation) per time unit

Symbol	Definition
$X_{1sgf}$	* amount of chemical constituent f in plant group s organ g per area
$X_{2pnf}$	* amount of chemical constituent f in shed seed species p in seed horizon n per area
$X_{11cf}$	* amount of chemical constituent f in animal group c per area
$X_{21df}$	* amount of chemical constituent f in organic debris category d per area
$X_{22hf}$	* amount of chemical constituent f in soil organic matter horizon h per area
$\dot{X}_{0113}$	total loss of carbon from the system per time unit due to animal action
$G\dot{X}_{0113}$	loss of carbon from the system per time unit due to animal growth
$R\dot{X}_{0113}$	loss of carbon from the system per time unit due to animal respiration
$\dot{X}_{1sgf}$	total change in the amount of chemical constituent f in plant group s organ g per time unit due to animal action
$H\dot{X}_{1sgf}$	change in chemical constituent f in plant group s organ g per time unit due to animal consumption
$\dot{X}_{2pnf}$	total change in chemical constituent f in shed seed species p in seed horizon n per time unit due to animal action
$H\dot{X}_{2pnf}$	change in chemical constituent f in shed seed species p in seed horizon n per time unit due to animal consumption
$\dot{X}_{11cf}$	total change in chemical constituent f in animal group c per time unit due to animal actions
$D\dot{X}_{11cf}$	change in chemical constituent f in animal group c due to death (excluding system predation)
$G\dot{X}_{11cf}$	change in chemical constituent f in animal group c per time unit due to growth
$p\dot{X}_{11cf}$	change in chemical constituent f in animal group c due to predation in the system per time unit
$p\dot{X}_{11cf}$	change in chemical constituent f in animal group c due to respiration per time unit
$\dot{X}_{12c}$	‡ total change in population of animal group c per time unit
$\dot{X}_{21df}$	total change in chemical constituent f in organic debris category d per time unit due to animal action
$H\dot{X}_{21df}$	change in chemical constituent f in organic debris category d per time unit due to animal consumption
$D\dot{X}_{215f}$	change in chemical constituent f in organic debris soft parts of carcasses category (d=5) per time unit due to the death of animals (excluding system predation)
$D\dot{X}_{216f}$	change in chemical constituent f in organic debris skeleton category (d=6) per time unit due to death of animals (excluding system predation)
$p\dot{X}_{216f}$	change in chemical constituent f in organic debris skeleton category (d=6) per time unit due to death from predation within the system
$E\dot{X}_{217f}$	change in chemical constituent f in organic debris excreta category (d=7) per time unit due to egestion
$G\dot{X}_{217f}$	change in chemical constituent f in organic debris excreta category (d=7) per time unit due to growth
$R\dot{X}_{217f}$	change in chemical constituent in organic debris excreta category (d=7) per time unit due to respiration

Symbol	Definition
$\dot{X}_{22hf}$	total change in chemical constituent in soil organic matter horizon per time unit due to animal action
$H\dot{X}_{22hf}$	change in chemical constituent in soil organic matter horizon per time unit due to animal consumption
<i>ANIMAL II</i>	
$Z_{1sgc}$	*weighted amount of carbon in plant group s organ g as related to animal group c
$Z_{2pnc}$	*weighted amount of carbon in seed species p of seed horizon n as related to animal group c
$Z_{3dc}$	*weighted amount of carbon in organic debris category d as related to animal group c
$Z_{4hc}$	*weighted amount of carbon of soil organic matter in soil horizon h as related to animal group c
$Z_{5yc}$	*weighted amount of carbon of prey group y as related to animal group c
$Z_{6c}$	*weighted amounts of carbon of all preferred food sources of animal group c
$Z_{7c}$	amount of carbon in food sources "taken" per time unit by animal group c
$Z_{8c}$	amount of carbon in animal group c
$Z_{9c}$	factor to scale the weighted amounts of carbon of preferred foods so that their sum equals the total amount of carbon consumed per time unit by animal group c
$Z_{10sgc}$	amount of carbon in plant compartment (s,g) consumed by animal group c per time unit
$Z_{11pnc}$	amount of carbon in seed compartment (p,n) consumed by animal group c per time unit
$Z_{12dc}$	amount of carbon of organic debris category d consumed by animal group c per time unit
$Z_{13hc}$	amount of carbon in soil organic matter in soil horizon h consumed by animal group c per time unit
$Z_{14yc}$	amount of carbon in prey group y taken by animal group c per time unit
$Z_{15sgfc}$	amount of chemical constituent f in plant compartment (s,g) consumed by animal group c per time unit
$Z_{16pnfc}$	amount of chemical constituent f in seed compartment (p,n) consumed by animal group c per time unit
$Z_{17dfc}$	amount of chemical constituent f in organic debris category d consumed by animal group c per time unit
$Z_{18hfc}$	amount of chemical constituent f in soil organic matter of soil horizon h consumed by animal group c per time unit
$Z_{19yfc}$	amount of chemical constituent f in prey group y killed by animal group c per time unit
$Z_{20yfc}$	amount of chemical constituent f in skeleton of prey group y killed by animal group c per time unit that is added to the organic debris skeleton category
$Z_{21yfc}$	amount of chemical constituent f in prey group y consumed by animal group c per time unit
$Z_{22f}$	amount of chemical constituent f in all prey groups added to skeleton organic debris category due to predation per time unit
$Z_{23cf}$	amount of chemical constituent f consumed by animal group c per time unit

Symbol	Definition
$Z_{24cf}$	amount of chemical constituent f assimilated by animal group c per time unit
$Z_{25cf}$	amount of chemical constituent f egested by animal group c per time unit
$Z_{26f}$	amount of chemical constituent f egested per time unit
$Z_{27c}$	carbon respired by animal group c per time unit
$Z_{28cf}$	amount of chemical constituent f potentially metabolized by animal group c per time unit
$Z_{29cf}$	amount of chemical constituent f metabolized in respiration by animal group c per time unit
$Z_{30cf}$	amount of chemical constituent f available for building new tissue of animal group c per time unit
$Z_{31cf}$	amount of chemical constituent f synthesized to "protein tissue" by animal group c in response to respiration losses per time unit
$Z_{32cf}$	amount of chemical constituent c available for building new tissues of animal group c following resynthesis of "protein" per time unit
$Z_{33cf}$	maximum amount of constituent f that can be added to animal group c as growth per time unit
$Z_{34c}$	maximum amount of carbon that can be added to animal group c as growth per time unit
$Z_{35c}$	factor by which growth of animal group c is reduced if there are insufficient raw materials
$Z_{36cf}$	amount of chemical constituent f added to animal group c in growth per time unit
$Z_{37cf}$	amount of chemical constituent f of animal group c dying (excluding system predation) per time unit
$Z_{38cf}$	amount of chemical constituent f in skeleton of animal group c dying (excluding system predation) per time unit that is added to the organic debris skeleton category
$Z_{39c}$	change in the amount of structural carbon in animal group c per time unit which determines population $\Delta s$
$Z_{40c}$	**average structural carbon per individual of animal group c
$P_{1c}$	†maximum postulated amount of carbon consumed per unit amount of carbon in animals per time unit by animal group c
$P_{2c}$	†coefficient of searching ability of animal group c
$P_{3sgc}$	preference of animal group c for plant group s organ g (no units)
$P_{4pnc}$	preference of animal group c for seed species p in seed horizon n (no units)
$P_{5dc}$	preference of animal group c for organic debris d category (no units)
$P_{0hc}$	preference of animal group c for soil organic matter in soil horizon h (no units)
$P_{7yc}$	preference of animal group c for prey group y (no units)
$P_{8c}$	fraction of the structural carbon that occurs in the skeleton of animal group c (no units)
$P_{9cf}$	ratio of mineral constituent f in the skeleton to the structural carbon of the skeleton of animal group c (no units)

Symbol	Definition
$P_{10cf}$	fraction of the amount of chemical constituent $f$ consumed by animal group $c$ that is assimilated (no units)
$P_{11c}$	proportionality constant for animal group $c$ in the respiration relation (amount of carbon respired per time unit by an animal with carbon content equal to 1)
$P_{12c}$	power constant for animal group $c$ in the respiration relation (no units)
$P_{13c}$	fraction of respired carbon of animal group $c$ that originates in "protein tissue" (no units)
$P_{14ft}$	ratio of the $fth$ constituent to the $tth$ constituent ( $f \in M + [3]$ , $t \in C$ ), e.g., $P_{14_{13}}$ , ratio of mineral 1 to carbon in "protein tissue" $P_{14_{23}}$ , ratio of mineral 2 to carbon in "protein tissue" $P_{14_{33}}$ , ratio of carbon to carbon in "protein tissue" (= 1) $P_{14_{f4}} = 0 \forall f$ (reserve tissue contains no minerals) $P_{14_{3t}} = 1 \forall t$ (no units)
$P_{15c}$	† maximum proportion of each carbon constituent that can be added to animal group $c$ in growth per time unit per unit animal structural carbon
$P_{16c}$	† fraction of animal group $c$ dying (excluding system predation) per time unit
$P_{17c}$	† time required for development and subsequent transfer of group $c$

The following 14 variables are defined exactly as in ANIMAL I:

$X_{1sgf}$	$X_{12c}$	$\dot{X}_{0_{13}}$	$H\dot{X}_{1sgf}$	$\dot{X}_{11cf}$
$X_{2pnf}$	$X_{21df}$	$R\dot{X}_{0_{13}}$	$\dot{X}_{2pnf}$	$D\dot{X}_{11cf}$
$X_{11cf}$	$X_{22hf}$	$\dot{X}_{1sgf}$	$H\dot{X}_{2pnf}$	

$F\dot{X}_{11c4}$  change in reserve carbon in animal group  $c$  due to excess carbon being available for fattening, following growth per time unit

The following three variables are defined exactly as in ANIMAL I:

$G\dot{X}_{11cf}$

$F\dot{X}_{11cf}$

$P\dot{X}_{11cf}$

$Y\dot{X}_{11cf}$  change in chemical constituent  $f$  in animal group  $c$  due to synthesis of "protein" to replace that which was metabolized in respiration per time unit

The following 11 variables are defined exactly as in ANIMAL I:

$\dot{X}_{12c}$	$D\dot{X}_{215f}$	$E\dot{X}_{217f}$	$\dot{X}_{22hf}$
$\dot{X}_{21df}$	$D\dot{X}_{216f}$	$G\dot{X}_{217f}$	$H\dot{X}_{22hf}$
$H\dot{X}_{21df}$	$P\dot{X}_{216f}$	$R\dot{X}_{217f}$	

Symbol	Definition
$P_{1cm}$	***maximum postulated carbon consumption per unit structural carbon of animal group c per time unit in season m
$P_{2cm}$	**"searching ability" of animal group c in season m; interacts with available foods to cause deviation of consumption from maximum level
$P_{3sgcm}$	reference of animal c for plant group s organ g in season m (no units)
$P_{4pncm}$	preference of animal c for seed group p occurring in seed horizon n in season m (no units)
$P_{5dcm}$	preference of animal c for organic debris category d in season m (no units)
$P_{6hcm}$	preference of animal c for soil organic matter in soil horizon h in season m (no units)
$P_{7ycm}$	preference of animal c for animal prey group y in season m (no units)
$P_{8c}$	ratio of structural carbon in skeleton:total structural carbon in animal group c (no units)
$P_{9cf}$	†††minimum ratio of non-carbonaceous constituent f to structural carbon in skeleton of animal group c
$P_{10cf}$	fraction of intake of chemical constituent f that is assimilated by animal group c; assimilation efficiency. f=3: assimilation efficiency for protein tissue; f=4: reserve tissue (fats and carbohydrates); f=5: structural tissue (lignin) (no units)
$P_{11cm}$	††energy per unit of metabolic size that is respired per time unit by animal group c in season
$P_{12cm}$	exponent of the weight of an animal of group c -- an expression which gives the metabolic size of the animal (no units)
$P_{13cm}$	†††amount of nitrogen excreted per unit of energy respired in basal metabolism by animal group c in season m
$P_{14ft}$	(f=1, nitrogen; f=2, ash; f=3, carbon; t=3, protein; t=4, reserve; t=5 structural) ratio of constituent f to carbon in tissue t: $P_{14_{33}} = P_{14_{34}} = P_{14_{35}} = 1$ . Reserve tissues are assumed to be totally carbon (excluding hydrogen, oxygen considerations): $P_{14_{12}} = 0 = P_{14_{24}}$ (no units)
$P_{16cfm}$	††maximum potential growth rate for carbon constituent f in group c, season m per unit steady-state protein carbon (if c is a fetal group); amount of carbon constituent f added per time unit to group c per unit difference between the optimal adult steady-state protein level and the current steady-state protein level (if c is a juvenile group)
$P_{18c}$	*optimum protein carbon level of an adult animal from group c
$P_{19cf}$	ratio of chemical constituent f to total carbon in the wool of group c (no units)
$P_{21cf}$	ratio of chemical constituent f to total carbon in milk of group c (no units)
$P_{23cm}$	†fraction of group c in season m that dies per time unit (excluding system predation)
$P_{25cm}$	maximum postulated number of fetuses per individual gravid animal of group c in season m (no units)
$P_{27chm}$	fraction of the excreta of animal group c in season m that is added to soil organic matter in soil horizon h (no units)
$P_{28c}$	Julian date upon which animal group c is transferred to another group (no units)

Symbol	Definition
$P_{29C}$	the numerical designation of the animal group to which animal group $c$ is transferred (no units)
$P_{30cfi}$	amount of carbon constituent $f$ in group $c$ (excluding wool and milk) that immigrates into the system per time unit for the $i$ th immigration since the simulation began (occurs only if the Julian day equals $P_{40cM}$ ) ( $f \in C$ )
$P_{31Ci}$	amount of wool carbon in group $c$ that immigrates into the system per time unit for the $i$ th immigration since the simulation began (occurs only if the Julian day equals $P_{40cM}$ )
$P_{32Ci}$	amount of milk carbon in group $c$ that immigrates into the system per time unit for the $i$ th immigration since the simulation began (occurs only if the Julian day equals $P_{40cM}$ )
$P_{33Ci}$	the protein steady-state level of group $c$ that immigrates into the system per time unit for the $i$ th immigration since the simulation began (occurs only if the Julian day equals $P_{40cM}$ )
$P_{34Ci}$	† population of group $c$ that immigrates into the system per time unit for the $i$ th immigration since the simulation began (occurs only if the Julian day equals $P_{40cM}$ )
$P_{35cM}$	equals 0 if animal group $c$ is not being suckled in season $m$ ; equals numerical designation of the animal group suckling group $c$ in season $m$ (no units)
$P_{36cM}$	equals 0 if animal group $c$ is not pregnant in season $m$ ; non-zero otherwise (no units)
$P_{37Ci}$	proportion of wool removed from group $c$ at the $i$ th time unit designated by $P_{38Ci}$ (no units)
$P_{38Ci}$	$i$ th day on which wool is removed (no units)
$P_{40cM}$	beginning Julian date of a season on which immigration into the system occurs (no units)
$P_{41cM}$	beginning Julian date of a season on which emigration from the system occurs (no units)
$P_{42C}$	fraction of the nursing period during which animal group $c$ consumes only milk (no units)
$P_{43cM}$	beginning Julian day of season $m$ of animal cohort $c$ (no units)
$P_{44C}$	fraction of protein assimilated by animal group $c$ that is not used in protein synthesis due to the biological value properties of the diet (no units)
$P_{45C}$	††† ratio of nitrogen to carbon (by weight) in the urea (or uric acid) excreted by animal group $c$
$P_{46C}$	fraction of carbon from digested carbohydrates that is lost as methane from animal group $c$ (no units)
$P_{47Cf}$	††† energy per unit of carbon constituent $f$ in animal group $c$ available when catabolized
$P_{48C}$	fraction of body protein carbon (total milk-wool protein carbon) of group $c$ is able to be catabolized to meet maintenance needs (no units)
$P_{49}$	*initial amount of protein carbon transferred to a fetal group when pregnancy period begins
$P_{50C}$	curvature constant in relation between fraction of maximum fetal birth weight and number of fetuses per female (no units)
$P_{51f}$	amount of energy per unit carbon constituent $f$ in that tissue ( $f=3$ , protein; $f=4$ , fat; $f=5$ , structural tissues; $f=6$ , carbohydrates) (no units)
$P_{52C}$	inefficiency of growth and production anabolism: fraction of the energy in the tissue produced that is needed to carry out the production (and which is wasted) (no units)

Symbol	Definition
$P_{53cm}$	numerical designation of the fetal group of mother group c in season m (no units)
$P_{54c}$	† maximum milk carbon produced per unit body structural carbon of group c per time unit
$P_{55c}$	ratio fat carbon: total reserve carbon (fat and carbohydrate carbon) in milk of animal group c (no units)
$P_{56cm}$	† rate of wool carbon production per unit body structural carbon of animal group c in season m
$P_{57c}$	ratio fat carbon: total reserve carbon in wool of animal group c (no units)
$P_{58ca}$	exponent of the protein status factor of group c for growth type a (a = 1, embryo growth; a = 2, juvenile growth; a = 3, milk production; a = 4, wool production) (no units)
$P_{59ikc}$	fraction of the amount of state variable i consumed per time unit by group c that is transferred to state variable k (i: any food item variable; k: shed seed horizons, organic debris categories) (no units)
$P_{60c}$	fraction of females in the population of group c (no units)
$P_{61c}$	inefficiency of fat anabolism (no units)
$P_{62cf}$	††† maximum ratio of non-carbonaceous constituent f to hard (skeleton) structural carbon in group c
$P_{63c}$	parameter indicating the curvature of the malnutrition mortality curve (no units)
$X_{1sgf}$	* amount of chemical constituent f in plant group s, organ g
$X_{2pnf}$	* amount of chemical constituent f in seed group p in seed horizon n
$X_{11cf}$	* amount of chemical constituent f in animal group c
$X_{12c}$	☆ population of animal group c per unit area
$X_{13cf}$	* amount of chemical constituent f in milk of animal group c
$X_{14cf}$	* amount of chemical constituent f in wool of animal group c
$X_{16c}$	* protein steady-state level of animal group c
$X_{21df}$	* amount of chemical constituent f in organic debris category d
$X_{22hf}$	* amount of chemical constituent f in soil organic matter in soil horizon h
$BV\dot{X}_{0113}$	loss of carbon from the total system due to catabolism of assimilated protein because of biological value considerations of the animal groups per time unit
$F\dot{X}_{0113}$	loss of carbon from the total system due to respiration of carbon from the inefficiencies of production of fat per time unit by the animal groups
$G\dot{X}_{0113}$	loss of carbon from the total system due to respiration of carbon from the inefficiencies of production per time unit in the animal groups
$I\dot{X}_{011f}$	gain of constituent f to the total system due to the immigration of animals per time unit
$K\dot{X}_{011f}$	loss of constituent f from the total system due to wool removal per time unit



Symbol	Definition
$MN\dot{X}_{01,13}$	loss of carbon from the total system due to losses of carbon associated with the production of endogenous urinary nitrogen by the animal groups per time unit
$MP\dot{X}_{01,13}$	loss of carbon from the total system due to methane production per time unit by the animal groups
$R\dot{X}_{01,13}$	loss of carbon from the total system due to respiration of animal groups in maintenance
$V\dot{X}_{01,1f}$	loss of chemical constituent f per time unit from the total system due to emigration of animals
$Y\dot{X}_{01,13}$	loss of carbon from the system due to respiration of carbon from animal groups following the inefficiency of protein resynthesis
$H\dot{X}_{1sgf}$	change in amount of chemical constituent f per time unit in plant group s organ g due to consumption by animals
$H\dot{X}_{2pnf}$	change in amount of chemical constituent f per time unit in seed group p in seed horizon n due to consumption by animals
$A\dot{X}_{1,1cf}$	change in amount of chemical constituent f per time unit in group c due to arrival of animals from another group
$C\dot{X}_{1,1cf}$	change in the amount of chemical constituent f per time unit in animal group c due to conception (transfer of protein from mother group to fetal group)
$D\dot{X}_{1,1cf}$	change in the amount of chemical constituent f per time unit in animal group c due to mortality (excluding system predation)
$ES\dot{X}_{1,1cf}$	change in the amount of chemical constituent f in animal group c per time unit due to catabolism to provide energy for production and growth
$F\dot{X}_{1,1c4}$	change in the amount of chemical constituent f = 4 (reserve carbon) per time unit in group c due to fat deposition
$FR\dot{X}_{1,1cf}$	change in the amount of chemical constituent f per time unit in group c (where c is a fetal group) due to resorption into the mother group following death due to malnutrition and prenatal causes
$G\dot{X}_{1,1cf}$	change in the amount of chemical constituent f per time unit in animal group c due to growth and production increments
$I\dot{X}_{1,1cf}$	change in the amount of chemical constituent f per time unit in animal group c due to immigration of animals into the system
$K\dot{X}_{1,1cf}$	change in the amount of chemical constituent f per time unit in animal group c due to wool removal
$MN\dot{X}_{1,1cf}$	change in amount of chemical constituent f per time unit in animal group c due to losses associated with the excretion of endogenous urinary nitrogen
$MR\dot{X}_{1,1cf}$	change in amount of chemical constituent f per time unit in animal group c due to milk being resorbed and becoming available for use in production and maintenance
$MS\dot{X}_{1,1cf}$	change in amount of chemical constituent f per time unit in animal group c due to minerals being withdrawn from storage in the skeleton for use in production

Symbol	Definition
$MY\dot{X}_{11cf}$	change in amount of mineral element f in group c per time unit due to withdrawal of minerals from bone storage for use in protein resynthesis
$P\dot{X}_{11cf}$	change in amount of chemical constituent f in animal group c due to system predation
$PS\dot{X}_{11cf}$	change in amount of chemical constituent f in animal group c due to use of labile protein tissue in protein synthesis
$R\dot{X}_{11cf}$	change in amount of chemical constituent f in animal group c per time unit due to catabolism of body tissues for energy for maintenance
$RS\dot{X}_{11cf}$	change in amount of chemical constituent f in animal group c per time unit due to catabolism of body tissues to provide material for synthesis of reserve growth increments
$S\dot{X}_{11cf}$	change in amount of chemical constituent f per time unit in animal group c due to the consumption of milk by dependent animal groups
$SM\dot{X}_{11cf}$	change in amount of chemical constituent f per time unit in animal group c due to storage of minerals in the skeleton
$T\dot{X}_{11cf}$	change in the amount of chemical constituent f per time unit in animal group c due to transfer of animals to another group
$V\dot{X}_{11cf}$	change in the amount of chemical constituent per time unit in animal group c due to emigration of animals out of the system
$Y\dot{X}_{11cf}$	change in chemical constituent f per time unit in animal group c due to resynthesis of protein to make up for deficiencies
$A\dot{X}_{12c}$	‡change in population of animal group c per time unit due to arrival of animals from another group
$C\dot{X}_{12c}$	‡change in the population of animal group c due to conception
$D\dot{X}_{12c}$	‡change in the population of animal group c per time unit due to all mortality
$I\dot{X}_{12c}$	‡change in the population of animal group c per time unit due to immigration from the system
$T\dot{X}_{12c}$	‡change in population of animal group c per time unit due to transfer to another animal group
$V\dot{X}_{12c}$	‡change in population of animal group c per time unit due to emigration of animals into the system
$A\dot{X}_{13cf}$	change in the amount of chemical constituent f in the milk of animal group c due to arrivals of animals from another group
$D\dot{X}_{13cf}$	change in the amount of chemical constituent f in the milk of group c per time unit due to mortality (excluding system predation)
$G\dot{X}_{13cf}$	change in the amount of chemical constituent f in the milk of group c per time unit due to production
$I\dot{X}_{13cf}$	change in the amount of chemical constituent f in the milk of group c immigrating into the system per time unit

Symbol	Definition
$MR\dot{X}_{13cf}$	change in amount of chemical constituent f in the milk of animal group c due to milk resorption per time unit
$p\dot{X}_{13cf}$	change in amount of chemical constituent f in the milk of animal group c due to predatory losses of animals in group c per time unit
$S\dot{X}_{13cf}$	change in amount of chemical constituent f in the milk of animal group c due to suckling per time unit
$T\dot{X}_{13cf}$	change in amount of chemical constituent f in the milk of animal group c due to the transfer of animals to another group
$V\dot{X}_{13cf}$	change in amount of chemical constituent f in the milk of animal group c due to the emigration of animals from the system
$A\dot{X}_{14cf}$	change in the amount of chemical constituent f in the wool of group c due to arrival of animals from another group per time unit
$D\dot{X}_{14cf}$	change in the amount of chemical constituent f in the wool of group c per time unit due to mortality (excluding system predation)
$FR\dot{X}_{14cf}$	change in the amount of chemical constituent f in the wool of fetal group c per time unit that is resorbed due to death from malnutrition and prenatal causes
$G\dot{X}_{14cf}$	change in the amount of chemical constituent f in the wool of group c per time unit due to production
$I\dot{X}_{14cf}$	change in the amount of constituent f in the wool of animals of group c that immigrate into the system per time unit
$K\dot{X}_{14cf}$	change in the amount of constituent f in the wool of animals of group c due to removal per time unit
$p\dot{X}_{14cf}$	change in the amount of chemical constituent f in the wool of animal group c due to system predation
$T\dot{X}_{14cf}$	change in the amount of chemical constituent f in the wool of animal group c per time unit due to transfer of animals to another group
$V\dot{X}_{14cf}$	change in the amount of chemical constituent f in the wool of animal group c per time unit due to emigration of the animals from the system
$D\dot{X}_{15c}$	change in the body structural carbon of animal group c per time unit due to mortality (excluding system predation)
$FR\dot{X}_{15c}$	change in the body structural carbon of animal fetal group c per time unit due to resorption into the maternal group following death due to malnutrition and prenatal causes
$p\dot{X}_{15c}$	change in the body structural carbon of animal group c due to system predation per time unit
$A\dot{X}_{16c}$	change in the protein steady-state level of group c due to arrival of animals from another animal group
$C\dot{X}_{16c}$	change in the protein steady-state level of group c per time unit, due to conception
$D\dot{X}_{16c}$	change in the protein steady-state level of group c per time unit due to mortality (excluding system predation)

Symbol	Definition
$FR\dot{X}_{16c}$	change in the protein steady-state level of fetal group c per time unit due to resorption because of death from malnutrition and prenatal mortality
$G\dot{X}_{16c}$	change in the protein steady-state level of group c per time unit due to growth
$I\dot{X}_{16c}$	change in the protein steady-state level of group c immigrating into the system per time unit
$P\dot{X}_{16c}$	change in the protein steady-state level of animal group c due to system predation per time unit
$T\dot{X}_{16c}$	change in the protein steady-state level of animal group c due to transfer of animals to another group per time unit
$V\dot{X}_{16c}$	change in the protein steady-state level per time unit of animal group c due to emigration of the animals
$BV\dot{X}_{17cf}$	change in amount of chemical constituent f in the excreta of animal group c per time unit due to excretion of protein constituents because of biological value considerations
$E\dot{X}_{17cf}$	change in amount of chemical constituent f in the excreta of animal group c due to the excretion of non-assimilated constituents
$EN\dot{X}_{17c1}$	change in the amount of nitrogen in the excreta of animal group c due to the excretion of non-proteinaceous nitrogen
$ES\dot{X}_{17cf}$	change in the amount of constituent f in the excreta of animal group c due to the excretion of constituents associated with protein catabolized to yield energy for growth and production
$F\dot{X}_{17c3}$	change in the amount of constituent f in the excreta of animal group c due to excretion of constituents associated with the catabolism of dietary protein to yield energy for fattening
$MN\dot{X}_{17cf}$	change in the amount of chemical constituent f in the excreta of animal group c due to the excretion of constituents associated with endogenous urinary nitrogen per time unit
$R\dot{X}_{17cf}$	change in the amount of chemical constituent f per time unit in the excreta of animal group c due to wastes produced by catabolism of protein body tissues for maintenance
$RS\dot{X}_{17cf}$	change in the amount of chemical constituent f per time unit in the excreta of animal group c due to wastes produced by catabolism of protein for reserve tissue synthesis
$U\dot{X}_{17cf}$	change in the amount of chemical constituent f per time unit in the excreta of animal group c due to excretion of unused dietary mineral constituents ( $f \in M$ )
$Y\dot{X}_{17cf}$	change in the amount of chemical constituent f per time unit in the excreta of animal group c due to wastes produced by catabolism of dietary protein to provide energy for protein resynthesis
$D\dot{X}_{21df}$	change in the amount of chemical constituent f per time unit in organic debris category d ( $d=5$ , soft animal parts; $d=6$ , skeleton) due to mortality (excluding system predation)
$E\dot{X}_{217f}$	change in the amount of chemical constituent f per time unit in organic debris category 7 (excreta) due to animal excretion

Symbol	Definition
$H\dot{X}_{21df}$	change in amount of chemical constituent f per time unit in organic debris category d due to consumption by animals
$P\dot{X}_{21df}$	change in amount of chemical constituent f per time unit in organic debris category d due to system predation
$E\dot{X}_{22hf}$	change in amount of chemical constituent f per time unit in the soil organic matter in soil horizon h due to animal excretion
$H\dot{X}_{22hf}$	change in amount of chemical constituent f per time unit in soil organic matter in soil horizon h due to consumption by animals
$AG\dot{X}_k$	change in state variable k per time unit due to the addition of damaged, clipped or wasted foods by animal groups
$AL\dot{X}_i$	change in state variable i per time unit due to the loss because of damaging, clipping or wasting this food source by animal groups
$Z_{1sgc}$	*preference weighted amount of carbon in plant group s organ g as related to consumer group c
$Z_{2pnc}$	*preference weighted amount of carbon in seed group p in seed horizon n as related to consumer group c
$Z_{3dc}$	*preference weighted amount of carbon in organic debris category d as related to consumer c
$Z_{4hc}$	*preference weighted amount of carbon in soil organic matter in soil horizon h as related to consumer c
$Z_{5yc}$	*preference weighted amount of carbon in animal prey group y if c is not being nursed by y; in milk of group y if c is being nursed by y
$Z_{6c}$	*preference weighted amount of carbon in food sources of consumer c
$Z_{7c}$	amount of carbon in food sources "captured" per time unit by consumer c
$Z_{8c}$	†fraction of carbon from fat tissues in the total reserve carbon intake of group c per time unit
$Z_{9c}$	†factor to scale the weighted amounts of preferred foods so that their sum equals the total amount of carbon consumed per time unit by consumer c
$Z_{10sgc}$	amount of carbon in plant group s organ g consumed by animal group c per time unit
$Z_{11pnc}$	amount of carbon in seed group p in seed horizon n consumed by animal group c per time unit
$Z_{12dc}$	amount of carbon in organic debris category d consumed by animal group c per time unit
$Z_{13hc}$	amount of carbon in soil organic matter in soil horizon h consumed by animal group c per time unit
$Z_{14yc}$	amount of carbon in the food from animal group y (prey or milk) captured by group c per time unit
$Z_{15sgfc}$	amount of chemical constituent f in plant group s organ g consumed by animal group c per time unit
$Z_{16pnfc}$	amount of chemical constituent f in seed group p in seed horizon n consumed by animal group c per time unit
$Z_{17dfc}$	amount of chemical constituent f in organic debris category d consumed by animal group c per time unit
$Z_{18hfc}$	amount of chemical constituent f in soil organic matter in soil horizon h consumed by animal group c per time unit

Symbol	Definition
$Z_{19}yfc$	amount of chemical constituent f in edible parts of prey group y killed by consumer c per time unit; amount of chemical constituent f in milk of mother group y consumed by c per time unit
$Z_{20}yc$	† proportion of prey group y killed by consumer c per time unit; proportion of milk of group y consumed by animal group c per time unit
$Z_{21}yfc$	amount of chemical constituent f in prey group y killed by consumer c per time unit
$Z_{22}yfc$	amount of chemical constituent f in wool of prey group y killed by consumer c per time unit
$Z_{23}yfc$	amount of chemical constituent f in the milk of prey group y killed by animal group c per time unit
$Z_{24}yfc$	amount of chemical constituent f in prey group y (excluding milk and wool) killed by animal group c per time unit
$Z_{25}yfc$	amount of chemical constituent f in soft structural parts of prey group y killed by consumer c per time unit
$Z_{26}f$	amount of chemical constituent f in all prey groups that is added to the organic debris skeleton category per time unit, due to system predation
$Z_{27}f$	amount of chemical constituent f in the wool of all prey groups that is added to the organic debris soft animal parts category, per time unit due to system predation
$Z_{28}cf$	amount of chemical constituent f consumed by animal group c per time unit
$Z_{29}c$	amount of protein carbon that would correspond to the amounts of non-carbonaceous constituents consumed per time unit
$Z_{30}cf$	amount of chemical constituent f consumed in protein tissues by animal group c per time unit
$Z_{31}c$	amount of carbon that is ingested as proteinaceous structural carbon by animal group c per time unit
$Z_{32}cf$	amount of chemical constituent f assimilated by animal group c per time unit
$Z_{33}c$	amount of carbon from protein tissues assimilated by animal group c per time unit
$Z_{34}c$	amount of carbon from fat tissues assimilated by animal group c per time unit
$Z_{35}c$	amount of carbon from carbohydrates assimilated by animal group c per time unit
$Z_{36}c$	amount of assimilated protein carbon excreted and respired per time unit by animal group c due to biological value considerations
$Z_{37}cf$	amount of chemical constituent f available for maintenance and production by animal group c per time unit
$Z_{38}c$	amount of carbon expelled in methane production by animal group c per time unit
$Z_{39}c$	†† energy for maintenance of animal group c per time unit
$Z_{40}cf$	amount of chemical constituent f excreted by animal group c per time unit associated with endogenous urinary nitrogen loss
$Z_{41}c$	†† energy needed for maintenance after energy supplied by EUN and biological value protein catabolism has been accounted for in group c per time unit
$Z_{42}c$	†† energy in dietary fats and carbohydrates of group c per time unit

Symbol	Definition
Z <sub>43C</sub>	††††energy in body fat reserves of group c
Z <sub>44C</sub>	††catabolizable energy in the dietary protein of group c per time unit
Z <sub>45C</sub>	††††catabolizable energy in available body protein of group c
Z <sub>46Cf</sub>	amount of dietary tissue (f=3, protein; 4, fat; 5, carbohydrate) carbon remaining for production by group c per time unit after maintenance has been satisfied
Z <sub>47Cf</sub>	* amount of constituent f by which animal group c is below the level that would be achieved with maximum growth
Z <sub>48C</sub>	factor by which the growth increments of group c are decreased due to the size of the litter (no units)
Z <sub>49Cf</sub>	potential growth increment of constituent f in fetal group c per time unit
Z <sub>50C</sub>	††energy needed by breeding group c to form the potential growth increments of the fetal group per time unit (excluding the energy in the tissues)
Z <sub>51Cf</sub>	** amount of carbon constituent f in an individual of group c at birth; equals 0 if birth has not occurred yet
Z <sub>52Cf</sub>	* amount of carbon constituent f by which group c is below the level of f corresponding to given juvenile growth rates
Z <sub>53Cf</sub>	potential growth increment of constituent f in juvenile group c per time unit
Z <sub>54C</sub>	††energy needed by group c to form potential growth increments (excluding energy in the tissue) per time unit
Z <sub>55C</sub>	amount of carbon potentially produced in milk by group c per time unit
Z <sub>56Cf</sub>	amount of constituent f potentially produced in milk per time unit by group c
Z <sub>57C</sub>	††amount of energy needed by group c to produce the potential amounts of milk per time unit (excluding the energy in the tissue)
Z <sub>58Cf</sub>	amount of constituent f potentially produced in wool per time unit by group c
Z <sub>59C</sub>	††amount of energy needed by group c to produce the potential amount of wool per time unit (excluding the energy in the tissue)
Z <sub>60C</sub>	†equals 1 if milk produced by animal group c is reabsorbed; equals 0 otherwise (fraction of milk reabsorbed per time unit)
Z <sub>61Cf</sub>	total amount of constituent f needed to satisfy all the potential amounts of growth and production by group c per time unit
Z <sub>62C</sub>	††amount of energy needed to synthesize the potential amounts of growth and production (excluding energy in the tissues) of group c per time unit
Z <sub>63C</sub>	available protein carbon of group c per time unit
Z <sub>64C</sub>	factor indicating the protein status of animal group c during a time unit (no units)
Z <sub>65Cf</sub>	amount of constituent f to be produced in fetal growth of group c per time unit

Symbol	Definition
$Z_{66c}$	†† amount of energy needed to produce the growth increment in the fetuses of mother group c per time unit
$Z_{67cf}$	amount of constituent f to be produced in juvenile growth of group c per time unit
$Z_{68c}$	†† amount of energy needed to produce the juvenile growth increments of group c per time unit
$Z_{69cf}$	amount of constituent f to be produced in milk by group c per time unit
$Z_{70c}$	†† amount of energy needed to produce milk increments in group c per time unit
$Z_{71cf}$	amount of constituent f to be produced in wool of group c per time unit
$Z_{72c}$	†† amount of energy needed to produce wool increments in group c per time unit
$Z_{73cf}$	total amount of constituent f needed to satisfy all the growth and production increments of group c per time unit ( $f \in \text{minerals}$ ); $f=3$ , total amount of carbon from proteinaceous tissues needed to satisfy all the growth and production increments of protein of c per time unit; $f=4$ , total amount of carbon needed to satisfy all growth and production increments of reserve tissues by c per time unit
$Z_{74c}$	†† amount of energy needed to synthesize the growth and production increments (excluding energy in the tissues) of c per time unit
$Z_{75c}$	amount of available carbon for group c per time unit following the meeting of the protein requirements
$Z_{76cf}$	available mineral f for group c per time unit
$Z_{77c}$	†† available energy for group c per time unit following the meeting of the protein, reserves and mineral requirements
$Z_{78cf}$	amount of dietary minerals ( $f \in M$ ), protein carbon ( $f=3$ ), fat carbon ( $f=4$ ), carbohydrate carbon ( $f=5$ ) remaining in group c per time unit after accounting for use as material in growth
$Z_{79c}$	amount of available protein carbon from protein catabolized to provide carbon for reserve tissue increments in group c per time unit
$Z_{80c}$	amount of dietary protein carbon remaining in group c per time unit after accounting for uses in protein synthesis
$Z_{81cf}$	amount of dietary carbon ( $f=3$ , protein; $f=4$ , fat; $f=5$ , carbohydrate) remaining in group c per time unit after all the decrements for growth and energy have been accounted for
$Z_{82c}$	amount of reserve tissue catabolized by c per time unit to supply carbon for reserve tissue synthesis in growth and production
$Z_{83c}$	†† amount of energy able to be produced from the remaining dietary fats and carbohydrates and from body reserve tissue of animal group c per time unit
$Z_{84c}$	amount of remaining available protein carbon that must be catabolized to yield the energy needed by c per time unit to meet the inefficiencies of growth and production
$Z_{85c}$	* amount of protein carbon by which animal group c is below the optimum level
$Z_{86c}$	proposed amount of carbon to be added to group c in protein synthesis per time unit (to account for protein deficiencies) if sufficient energy is available to meet the costs of inefficiency of anabolism



Symbol	Definition
$Z_{87c}$	††energy needed to produce the proposed synthesis of protein tissue (to account for protein deficiencies) by group c per time unit
$Z_{88c}$	energy available to produce the proposed synthesis of protein tissue (to account for protein deficiencies) by group c per time unit
$Z_{89c}$	amount of reserve body tissue used for energy to produce growth increments per time unit for group c
$Z_{90cf}$	amount of constituent f added to group c in protein synthesis (to account for protein deficiencies) per time unit
$Z_{91cf}$	* amount of constituent f stored in the skeleton of c
$Z_{92cf}$	amount of chemical constituent f available to group c per time unit after accounting for use as material in growth (includes stored minerals) ( $f \in M$ )
$Z_{93cf}$	amount of constituent f remaining from dietary intake after all growth and protein resynthesis demands have been met for group c per time unit
$Z_{94c}$	††energy needed to produce the protein synthesized in response to the protein deficiency in group c per time unit
$Z_{95cf}$	amount of remaining dietary protein ( $f=3$ ), fat ( $f=4$ ), carbohydrate ( $f=5$ ) in group c per time unit after all growth and protein resynthesis
$Z_{96c}$	fraction of remaining dietary carbohydrate and dietary fat used in fattening of group c following all growth and protein resynthesis (no units)
$Z_{97c}$	fraction of remaining dietary protein used in fattening of group c, following all growth and protein resynthesis (no units)
$Z_{98c}$	††energy available for production of the fat synthesized from the remaining dietary compounds following growth and protein resynthesis by group c per time unit
$Z_{99c}$	††energy needed to produce fat in group c per time unit
$Z_{100c}$	condition index of group c; fraction of the optimal protein carbon level of group c at this time instant (no units)
$Z_{101c}$	†fraction of animal group c dying per time unit due to malnutrition and non-predatory causes
$Z_{102cf}$	amount of chemical constituent f resorbed into adult group c from fetal deaths per time unit
$Z_{103cf}$	amount of constituent f in animal group c dying per time unit (excluding system predation)
$Z_{104cf}$	amount of constituent f in group c (excluding wool and milk) dying per time unit (excluding system predation)
$Z_{105c}$	amount of soft structural carbon of group c dying per time unit
$Z_{106cf}$	amount of mineral constituent f in animal group c dying per time unit excluding the constituents in the skeleton
$Z_{107cf}$	amount of mineral constituent f in the skeleton of animal group c dying per time unit
$Z_{108ci}$	amount of state variable i consumed by animal group c per time unit
$Z_{109cf}$	amount of constituent f in the excreta of animal group c per time unit

Symbol	Definition
$Z_{110cfh}$	amount of chemical constituent f added to soil horizon h by excretion of animal group c per time unit
$Z_{111cf}$	amount of chemical constituent f added to soil surface by excretion of animal group c per time unit
$Z_{112Cr}$	†equals 1 if group c transfers to group r during this time unit; equals 0 otherwise (fraction transferred to r per time unit)
$Z_{113c}$	‡change in population of group c due to transfer to another group per time unit
$Z_{114cf}$	amount of constituent f taken from group c in transfers to another group per time unit
$Z_{115cf}$	amount of constituent f in animals of group c immigrating into the system per time unit (excluding wool and milk)
$Z_{116cf}$	amount of chemical constituent f in wool of animals of group c that immigrate into the system per time unit
$Z_{117cf}$	amount of chemical constituent f in the milk of animals of group c that immigrate into the system per time unit
$Z_{118ci}$	equals 1 if this is the <i>ith</i> immigration of group c since the simulation began, and if this time unit is the day of immigration ( $P_{40cM}$ ); 0 otherwise (no units)
$Z_{119ci}$	equals 1 if this is the <i>ith</i> emigration of group c since the simulation began, and if this time unit is the day of emigration ( $P_{41cM}$ ); 0 otherwise (no units)
$Z_{120c}$	equals 1 if this time unit is the date of wool removal; 0 otherwise (no units)
$Z_{121cf}$	amount of chemical constituent f in the wool of group c removed per time unit
$Z_{122c}$	change in structural carbon of group c due to all mortality per time unit
$Z_{123c}$	**average structural carbon per individual of animal group c
$Z_{124c}$	‡change in population of group c per time unit due to all mortality
$Z_{125cm}$	length of nursing season m of group c (no units)
$Z_{126cf}$	maximum amount of mineral f able to be stored in the skeleton by animal group c per time unit
$Z_{127cf}$	amount of mineral f added to skeleton storage in group c per time unit
$Z_{128cf}$	change in chemical constituent f of group c due to all processes except fattening



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247 K1=ILVADD(N+NS)
248 IF (NS.EQ.NSEAS(N)) GO TO2100
249 K2=ILVADD(N+NS+1)-1
250 GO TO2105
251 2100 K2=ILVADD(N+1,1)-1
252 C
253 C.....THE FIRST COLUMN IN 'ILVPRF' DENOTES THE IND X NUMBER OF
254 C.....PLANT COHORT, THE SECOND COLUMN DENOTES THE INDEX NUMBER OF
255 C.....THE PLANT ORGAN
256 2105 DO2110 K=K1,K2
257 T=ILVPRF(K,1)
258 J=ILVPRF(K,2)
259 C
260 C.....THE PREFERRED FOOD ITEMS ARE WEIGHTED BY PREFERENCES SPECIFIC
261 C.....FOR THE COHORT IN THE SEASON
262 C.....PRAV(I,J)=PREF(LV(K)+AVEG(I,J)
263 *F (AVEG(I,J),LE.O.) PRAV(I,J) = 0.
264 2110 FFFVEG=EFFVEG+PRAV(I,J)
265 C
266 C.....SHED SEED CONSUMPTION
267 C
268 C.....THE PROCEDURE IS AS ABOVE FOR LIVE VEGETATION CONSUMPTION
269 C.....2115 IF (ASEED,LE.O.,OR..NOT.NFOOD(2,NS,N)) GO TO213*
270 K1=ISDAD(N+NS)
271 IF (NS.EQ.NSEAS(N)) GO TO2120
272 K2=ISDAD(N+NS+1)-1
273 GO TO2125
274 2120 K2=ISDAD(N+1,1)-1
275 C
276 C.....THE FIRST COLUMN OF 'ISDPRF' DENOTES THE SPECIES OF PLANT
277 C.....FROM WHICH THE SEED COMES, THE SECOND COLUMN DENOTES THE
278 C.....SEED HORIZON FROM WHICH IT IS GATHERED
279 2125 DO2130 K=K1,K2
280 T=ISDPRF(K,1)
281 JH=ISDPRF(K,2)
282 PPDV(I,JH)=PREFSD(K)+ASEED(I,JH)
283 IF (ASEED(I,JH),LE.O.) PPDV(I,JH) = 0.
284 2130 FFFVEG=EFFVEG+PPDV(I,JH)
285 C
286 C.....DEAD ORGANIC MATTER CONSUMPTION
287 C
288 C.....THE PROCEDURE IS AS ABOVE FOR LIVE VEGETATION CONSUMPTION
289 C.....2135 IF (ALIT,LE.O.,OR..NOT.NFOOD(3,NS,N)) GO TO2155
290 K1=ILITAD(N+NS)
291 IF (NS.EQ.NSEAS(N)) GO TO2140
292 K2=ILITAD(N+NS+1)-1
293 GO TO2145
294 2140 K2=ILITAD(N+1,1)-1
295 C
296 C.....'ILITPR' LISTS THE INDEX NUMBERS OF THE DEAD ORGANIC MATTER
297 C.....CATEGORIES
298 2145 DO2150 K=K1,K2
299 L=ILITPR(K)
300 PRE(L)=PREFLT(K)+ALIT(L)
301 IF (ALIT(L),LE.O.) PRE(L) = 0.
302 2150 FFFVEG=EFFVEG+PRE(L)
303 C
304 C.....SOIL ORGANIC MATTER CONSUMPTION
305 C.....2155 IF (AORH,LE.O.,OR..NOT.NFOOD(4,NS,N)) GO TO2175
306 K1=IORGAD(N+NS)
307 IF (NS.EQ.NSEAS(N)) GO TO2160
308 K2=IORGAD(N+NS+1)-1
309 GO TO2165
310 2160 K2=IORGAD(N+1,1)-1
311 C
312 C.....'IORGPR' LISTS THE INDEX NUMBERS OF THE SOIL HORIZONS
313 C.....FROM WHICH THE SOIL ORGANIC MATTER IS CONSUMED
314 2165 DO2170 K=K1,K2
315 JH=IORGPR(K)
316 PORGI(JH)=PREFORG(K)+AORGI(JH)
317 IF (AORGI(JH),LE.O.) PORGI(JH) = 0.
318 2170 FFFVEG=EFFVEG+PORGI(JH)
319 C
320 C.....CONSUMPTION OF OTHER ANIMALS, INCLUDING SUCKLING BY YOUNG
321 C.....2175 IF (.NOT.NFOOD(5,NS,N)) GO TO2195
322 K1=ICARAD(N+NS)
323 IF (NS.EQ.NSEAS(N)) GO TO2180
324 K2=ICARAD(N+NS+1)-1
325 GO TO2185
326 2180 K2=ICARAD(N+1,1)-1
327 C
328 C.....'ICARPR' LISTS THE INDEX NUMBERS OF THE PREY COHORTS
329 2185 DO2190 K=K1,K2
330 N=ICARPR(K)
331 IF (NN.NE.SUCKLN(NS,N)) GO TO2186
332 SMILK = 0.
333 DO2197KK = NFRAC1,NFRELH
334 2187 SMILK = SMILK + SMILKPR(N,KK)
335 PCV(NN) = PCARN(K) + SMILK
336 IF (SMILK,LE.O.) PCV(NN) = 0.
337 GO TO2190
338 2196 PCV(NN) = PCARN(P) + ABIN(NN)
339 IF (ABIN(NN),LE.O.) PCV(NN) = 0.
340 2190 FFFVEG=EFFVEG+PCV(NN)
341 2195 IF (EFFVEG,LE.O.) GO TO 2205
342 C
343 C.....THE ACTUAL AMOUNT CONSUMED IS CALCULATED - 9 CH COHORT
344 C.....HAS A MAXIMUM CONSUMPTION CAPACITY, THE ACTUAL AMOUNT
345 C.....CONSUMED DEPENDS ON THIS PARAMETER AND THE PARAMETER WHICH
346 C.....DESCRIBES THE SEARCHING ABILITY OF THE COHORT - 'B'
347 IF (BEST(NS,N),EQ.O.) GO TO2200
348 NHARV = ABY(NS,N)
349 CONSUM = AINS(N) * (1.-EXP(-BINS,N) + EFFVEG) *
350 (CBION(N,NFRELH) - SWOOL(N,NFRELH)-SMILKPR(N,NFRELH)
351 + CBION(NHARV,NFRELH) - SWOOL(NHARV,NFRELH) -
352 SMILKPR(NHARV,NFRELH))
353 GO TO2202
354 2201 CONSUM = AINS,N) * (1.-EXP(-BINS,N)+EFFVEG) *
355 (CBION(N,NFRELH) - SWOOL(N,NFRELH) - SMILKPR(N,NFRELH))
356 2202 IF (CONSUM,GT.O.) GO TO 225
357 2205 DO2200 J=1,NORGAN
358 DO2200 I=1,NVECOH
359 2200 PRAV(I,J)=0.
360 DO 205 JH=1,NSEEDH
361 DO 205 I=1,NSPECV
362 205 PRAV(I,JH)=0.
363 DO 210 L=1,NOLIT
364 210 PRE(L)=0.
365 DO 215 JH=1,NHORIZ
366 215 PORGI(JH)=0.
367 DO 220 NN=1,NPCOH
368 220 PCV(NN)=0.
369 GO TO 203
370 C
371 C.....THE WEIGHTED AMOUNTS OF FOOD AVAILABLE ARE NOW SCALED DOWN
372 C.....BY 'RATIO' TO DETERMINE THE ACTUAL AMOUNTS CONSUMED FROM
373 C.....EACH FOOD COMPARTMENT
374 C.....THE PROPORTION OF CARBON CONSUMED FROM EACH COMPARTMENT
375 C.....DETERMINES THE PROPORTION OF EACH CONSTITUENT THAT IS
376 C.....CONSUMED FROM THAT COMPARTMENT
377 225 RATIO=CONSUM/FFVEG
378 C
379 C.....LIVE VEGETATION
380 DO 235 J=1,NORGAN
381 DO 235 I=1,NVECOH
382 IF (PRAV(I,J),GT.O.) GO TO 236
383 PRAV(I,J) = 0.
384 236 PEC = PRAV(I,J) * RATIO
385 PRAV(I,J) = PEC
386 DO 230 K=1,NFRELH
387 IF (CVEG(I,J,K),LE.O.) GO TO 230
388 PEV=PEC+CVEG(I,J,K)/AVEG(I,J)
389 CVEG(I,J,K)=CVEG(I,J,K)-PEV
390 TAL(K)=TAL(K)+PEV
391 230 CONTINUE
392 235 CONTINUE
393 C
394 C.....SHED SEEDS
395 DO 245 JH=1,NSEEDH
396 DO 245 I=1,NSPECV
397 IF (PROV(I,JH),GT.O.) GO TO 246
398 PRDV(I,JH) = 0.
399 GO TO 245
400 246 PEC = PROV(I,JH) * RATIO
401 PRDV(I,JH) = PEC
402 DO 240 K=1,NFRELH
403 IF (SEED(I,JH,K),LE.O.) GO TO 240
404 PEV=PEC+SEED(I,JH,K)/ASEED(I,JH)
405 SEED(I,JH,K)=SEED(I,JH,K)-PEV
406 TAL(K)=TAL(K)+PEV
407 240 CONTINUE
408 245 CONTINUE
409 C
410 C.....DEAD ORGANIC MATTER
411 DO 255 L=1,NOLIT
412 IF (PRE(L),GT.O.) GO TO 256
413 PRE(L) = 0.
414 GO TO 255
415 256 PEC = PRE(L) * RATIO
416 PRE(L) = 0.
417 DO 250 K=1,NFRELH
418 IF (CLIT(L,K),LE.O.) GO TO 250
419 PEV=PEC+CLIT(L,K)/ALIT(L)
420 CLIT(L,K)=CLIT(L,K)-PEV
421 IF (L,LE.O.,LITAN1,OR,L,LE.O.,LITAN2).AND,K,LE.O.,NELEM2) FRAFAT=FRAFAT +
422 1 * PEV
423 TAL(K)=TAL(K)+PEV
424 250 CONTINUE
425 255 CONTINUE
426 C
427 C.....SOIL ORGANIC MATTER
428 DO 265 JH=1,NHORIZ
429 IF (PORGI(JH),GT.O.) GO TO 266
430 PORGI(JH) = 0.
431 GO TO 265
432 266 PEC = PORGI(JH) * RATIO
433 PORGI(JH) = PEC
434 DO 260 K=1,NFRELH
435 IF (CORGI(JH,K),LE.O.) GO TO 260
436 PEV=PEC+CORGI(JH,K)/AORGI(JH)
437 CORGI(JH,K)=CORGI(JH,K)-PEV
438 TAL(K)=TAL(K)+PEV
439 260 CONTINUE
440 265 CONTINUE
441 C
442 C.....ANTHAL PREY
443 DO 285 NN=1,NSPCOH
444 IF (PCV(NN),GT.O.) GO TO 286
445 PCV(NN) = 0.
446 GO TO 285
447 286 PEC = PCV(NN) * RATIO
448 PCV(NN) = 0.
449 C
450 C.....IF THE COHORT IS SUCKLING IN THIS SEASON THE FOOD CONSUMED
451 C.....FROM THE 'PREY' (MOTHER) COHORT IS MILK
452 IF (SUCKLN(NS,N),EQ.NN) GO TO 270
453 C
454 C.....IF THE COHORT IS NOT SUCKLING AND IS A PREGNANT, THE AMOUNT
455 C.....OF EACH ELEMENT CONSUMED IS PARTITIONED INTO SOFT AND HARD
456 C.....PARTS, WITH THE SOFT PARTS BEING CONSUMED AND THE HARD PARTS
457 C.....BEING ADDED TO THE LITTER
458 PCV(NN) = PEC
459 AMORT=PEC/ABIOM(NN)
460 CALL HORTLY (NN,AMORT,1)
461 GO TO 285
462 270 DO 280 K = 1,NFRELH
463 IF (SMILKPR(NN,K),LE.O.) GO TO 280
464 PEV=SMILKPR(NN,K)/SMILK+PEC
465 SMILKPR(NN,K)=SMILKPR(NN,K)-PEV
466 CBION(NN,K)=CBION(NN,K)-PEV
467 IF (K,EQ,NELEM2) FRAFAT = FRAFAT + PEV * FATMLK(NN)
468 TAL(K)=TAL(K)+PEV
469 280 CONTINUE
470 285 CONTINUE
471 DO 290 K=NFRAC1,NFRELH
472 IF (TAL(K),GT.O.) GO TO 295
473 GO TO 203
474 295 IF (TAL(NELEM2),GT.O.) FRAFAT=FRAFAT+TAL(NELEM2)
475 IF (TAL(NELEM2),LE.O.) FRAFAT = 0.
476 DO 700 J=1,NORGAN
477 DO 700 I=1,NVECOH
478 LLN = I + (J-1)*NVECOH
479 P = PRAV(I,J) + TRANS(LLN,1,N)
480 PRAV(I,J) = 0.
481 IF (P,LE.O.) GO TO 700
482 DO 701 K=1,NFRELH
483 IF (CVEG(I,J,K),LE.O.) GO TO 701
484 PP(K) = CVEG(I,J,K)/AVEG(I,J) + P
485 CVEG(I,J,K) = CVEG(I,J,K) - PP(K)
486 GO TO 701
487 701 PP(K) = 0.
488 CONTINUE
489 NOTR = TRANS(LLN,2,N)
490 CALL POSITN(PP,NOTR)
491 700 CONTINUE
492 DO 702 JH=1,NSEEDH
493 DO 702 I=1,NSPECV
494 LLN = I + (JH-1) * NSPECV + NTSYED
495 P = PRDV(I,JH) + TRANS(LLN,1,N)
496 PRDV(I,JH) = 0.

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517 TF (P,LE,0.) GO TO 702
518 DO 703 K=1,NFRELH
519 IF (SEEDI(JH,LE,0.) GO TO 705
520 PP(K) = SFEDI(JH,K)/ASEEDI(JH) *P
521 SFED00(I,JH,K) = SEED00(I,JH,K) - PP(K)
522 GO TO 703
523 PP(K) = 0.
524 703 CONTINUE
525 NOTR = TRANSIL(L,2,N)
526 CALL POSTN(PP,NOTR)
527 702 CONTINUE
528 DP 706 L=1,NOLIT
529 P = PRELI + TRANS(L+NSTLIT,I,N)
530 PRELI = 0.
531 TF (P,LE,0.) GO TO 706
532 DO 707 K=1,NFRELH
533 IF (CLIT(L,K),LE,0.) GO TO 708
534 PP(K) = CLIT(L,K)/ALIT(L) + P
535 CLIT00(L,K) = CLIT00(L,K) - PP(K)
536 GO TO 707
537 PP(K) = 0.
538 707 CONTINUE
539 NOTR = TRANS(L+NSTLIT,2,N)
540 CALL POSTN(PP,NOTR)
541 706 CONTINUE
542 DO 709 JH=1,NHOR7
543 P = PORGI(JH) * TRANS(JH+NSTOR0,I,N)
544 PORGI(JH) = 0.
545 TF (P,LE,0.) GO TO 709
546 DO 710 K=1,NFRELH
547 IF (CORGI(JH,K),LE,0.) GO TO 711
548 PP(K) = CORGI(JH,K)/ADPGI(JH) + P
549 CORGI00(JH,K) = CORGI00(JH,K) - PP(K)
550 GO TO 710
551 PP(K) = 0.
552 710 CONTINUE
553 NOTR = TRANS(JH+NSTOR0,2,N)
554 CALL POSTN(PP,NOTR)
555 709 CONTINUE
556 DO 712 NN=1,NSPCOH
557 P = PCVIN(N) * TRANS(NN+NSTPPY,I,N)
558 PCVIN(N) = 0.
559 TF (P,LE,0.) GO TO 712
560 AMORT = P/ABTOM(N)
561 CALL MORTLY(NN,AMORT,2)
562 712 CONTINUE
563 -----
564 C.....DETERMINE THE AMOUNT OF PROTEIN CONSUMED
565 C-----
566 C
567 DIETPR(NFRAC1) = TAL(NITRO)/CONST(NITRO,NFRAC1)
568 DO 5 K = 1,NELEMS
569 IF (CONST(N,NFRAC1),LE,0.) GO TO 1
570 DIETPR(NFRAC1) = AMINI(DIETPR(NFRAC1),TAL(K)/CONST(K,NFRAC1))
571 1 CONTINUE
572 T = TAL(NFRAC1) + TAL(NFRELH)
573 TF (DIETPR(NFRAC1),LE, T) GO TO 4
574 DIETPR(NFRAC1) = T
575 GO TO 2
576 4 IF (DIETPR(NFRAC1),GE,TAL(NFRAC1)) GO TO 2
577 EXCRET(NFRAC1) = EXCRET(NFRAC1)*TAL(NFRAC1) - DIETPR(NFRAC1)
578 TAL(NFRAC1) = DIETPR(NFRAC1)
579 EXCRET(NITRO) = EXCRET(NITRO) + TAL(NITRO) - DIETPR(NFRAC1) +
580 2 CONST(NITRO,NFRAC1)
581 TAL(NITRO) = DIETPR(NFRAC1) * CONST(NITRO,NFRAC1)
582 SCPROT = DIETPR(NFRAC1) - TAL(NFRAC1)
583 C-----
584 C.....ASSIMILATION
585 C-----
586 C
587 C
588 DO 5 K = 1,NELEMS
589 DIETPR(K) = DIETPR(NFRAC1) + CONST(K,NFRAC1)
590 ASSIM(K) = COEFF(NFRAC1,N) + DIETPR(K) + (COEFF(K,N)+ITAL(K)-
591 1 DIETPR(K))
592 5 EXCRET(K) = EXCRET(K) + TAL(K) - ASSIM(K)
593 DO 6 K = NFRAC1,NFRELH
594 TF (K,EG,NFRELH) GO TO 7
595 ASSIM(K) = COEFF(K,N) + TAL(K)
596 GO TO 3
597 7 T = COEFF(NFRAC1,N) + SCPROT
598 ASSIM(NFRAC1) = T + COEFF(NFRELH,N) + (TAL(NFRELH) - SCPROT)
599 3 EXCRET(K) = EXCRET(K) + (TAL(K) - ASSIM(K))
600 6 CONTINUE
601 FAT = FRAT + ASSIM(NFRELH)
602 CHO = ASSIM(NELEM2) - FAT + ASSIM(NFRELH) - T
603 PROTEIN = ASSIM(NFRAC1) + T
604 C-----
605 C.....DETERMINE HOW MUCH PROTEIN IS UNUSABLE DUE TO BIOLOGICAL
606 C.....VALUF CONSIDERATIONS
607 C-----
608 C
609 T = PROTEIN + BVPROT(N)
610 DO 8 K = 1,NELEMS
611 EXCRET(K) = EXCRET(K) + T * CONST(K,NFRAC1)
612 8 ASSIM(K) = ASSIM(K) - T * CONST(K,NFRAC1)
613 EXCRET(NFRAC1) = EXCRET(NFRAC1) + T * CONST(NITRO,NFRAC1)/UREA
614 ENERGY = CATPR + T
615 AGAINO(1,*) = AGAINO(1,*) - T * (1-CONST(NITRO,NFRAC1)/UREA)
616 PROTEIN = PROTEIN - T
617 C-----
618 C.....METHANE PRODUCTION BY RUMINANTS
619 C-----
620 C
621 TF (INCLASS(N),NE,2) GO TO 803
622 T = CHO * RUMEN
623 CHO = CHO - T
624 AGAINO(1,*) = AGAINO(1,*) - T
625 C-----
626 C.....MILK REABSORPTION
627 C-----
628 C
629 C
630 803 NHARV = NURSE(NS,N)
631 TF (NHARV,EG,0,AND,IYRDAY,NE,SEASON(NS,N)) GO TO 804
632 TF (NHARV,EG,0) GO TO 805
633 TF (POP(NHARV),GT,0.) GO TO 801
634 805 DO 802 K = 1,NFRELH
635 IF (SMILKP(N,K),LE,0.) GO TO 802
636 IF (K,LE,NELEMS) ASSIM(K) = ASSIM(K) + SMILKP(N,K)
637 CBIOHQ(N,K) = CBIOHQ(N,K) - SMILKP(N,K)
638 SMILK0(N,K) = SMILK0(N,K) + SMILKP(N,K)
639 802 CONTINUE
640 PROTEIN = PROTEIN + SMILKP(N,NFRAC1) + SMILKP(N,NFRELH)
641 FAT = FAT + SMILKP(N,NELEM2) + FATL(K,N)
642 CHO = CHO + SMILKP(N,NELEM2) + (1- FATHL(K,N))
643 801 CONTINUE
644 C-----
645 C.....FETAL RESORPTION
646 C-----
647 C
648 CHO = CHO + STORES(NFLEMS,N)
649 PROTEIN = PROTEIN + STORES(NFRAC1,N)
650 FAT = FAT + STORES(NELEM2,N)
651 DO 80N K = 1,NELEMS

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652 80N ASSIM(K) = ASSIM(K) + STORES(K,N)
653 DO 806 K=1,NELEM2
654 806 STORES(K,N) = 0.
655 C-----
656 C.....RESPIRATION
657 C-----
658 C
659 C
660 IF (RKINS,N),LE,0.) GO TO 12
661 IF (GESTINS,N),EG,0) GO TO 17
662 NHARV = BABY(NS,N)
663 E = RKINS,N) + (ABIOM(N) + ABTOM(NHARV))/POP(N)
664 1 = *RBINS,N) + POP(N)
665 GO TO 18
666 17 E = RKINS,N) + (ABIOM(N)/POP(N))*RBINS,N) + POP(N)
667 18 EUN = RA(NS,N) + E
668 T = EUN/CONST(NITRO,NFRAC1)
669 DO 19 K = 1,NELEMS
670 EXCRET(K) = EXCRET(K) + T * CONST(K,NFRAC1)
671 19 CBIOHQ(N,K) = CBIOHQ(N,K) - T * CONST(K,NFRAC1)
672 CBIOHQ(N,NFRAC1) = CBIOHQ(N,NFRAC1) - T
673 TMP = T
674 EXCRET(NFRAC1) = EXCRET(NFRAC1) + FUN/UPFA
675 AGAINO(1,*) = AGAINO(1,*) - (T * EUN/UREA)
676 E = AMAX(10.,E - T + CATPR-ENERGY)
677 T = FAT + CATFAT + CHO + CATCHO
678 TF (T,LE,0) GO TO 9
679 F = T/7
680 AGAINO(1,*) = AGAINO(1,*) - FAT + F - CHO + F
681 CHO = CHO - CHO + F
682 FAT = FAT - F + FAT
683 THR=0.
684 GO TO 12
685 T = E + T
686 9 AGAINO(1,*) = AGAINO(1,*) - FAT - CHO.
687 FAT = 0.
688 CHO = 0.
689 TF ((CBIOHQ(N,NELEM2)-SWOOL(N,NELFM2) - SHLKP(N,NELEM2))/CAT'AT,
690 1 LT,T) GO TO 10
691 CBIOHQ(N,NELEM2)=CBIOHQ(N,NELEM2) - T/CAT'AT
692 THR = T/CATFAT
693 AGAINO(1,*) = AGAINO(1,*) - T/CATFAT
694 GO TO 12
695 10 T = -(CBIOHQ(N,NELEM2)-SWOOL(N,NELFM2)-SHLKP(N,NELEM2))/CAT'AT
696 IF (CBIOHQ(N,NELEM2)-SWOOL(N,NELFM2)-SHLKP(N,NELEM2),LE,0.) GO TO
697 1 552
698 CBIOHQ(N,NELEM2)=CBIOHQ(N,NELFM2) - (CBIOHQ(N,NELFM2)-SWOOL(N,NELEM2)
699 1 ) - SHLKP(N,NELEM2)
700 THR = CBIOHQ(N,NELEM2)-SWOOL(N,NELFM2)-SHLKP(N,NELEM2)
701 AGAINO(1,*) = AGAINO(1,*) - (CBIOHQ(N,NELFM2)-SWOOL(N,NELFM2)-
702 1 SHLKP(N,NELEM2))
703 552 T = (PROTEIN-CATPR,LT,T) GO TO 11
704 MORE = 0
705 E = T/CATPR
706 GO TO 14
707 11 E = PROTEIN
708 MORE = 1
709 14 PROTEIN = PROTEIN - E
710 DO 13 K = 1,NELEMS
711 EXCRET(K) = EXCRET(K) + E * CONST(K,NFRAC1)
712 13 ASSIM(K) = ASSIM(K) - E * CONST(K,NFRAC1)
713 TT = E * CONST(NITRO,NFRAC1)/UREA
714 EXCRET(NFRAC1) = EXCRET(NFRAC1) + TT
715 AGAINO(1,*) = AGAINO(1,*) - (E-TT)
716 TF (MORE,EG,0) GO TO 12
717 T = T - PROTEIN-CATPR
718 IF ((CBIOHQ(N,NFRAC1)-SWOOL(N,NFRAC1)-SHLKP(N,NFRAC1) - PKIN)*
719 1 PLEVEL(N)-THP)/CATPR,GT,T) GO TO 15
720 C-----
721 C.....ENTIRE COHORT DEATH
722 C-----
723 C
724 C
725 C.....IF THERE IS INSUFFICIENT PROTEIN TISSUE CARBON, THE COHORT
726 C.....DIES
727 551 CALL MORTLY(N,1,0,2)
728 DO 553 K=1,NELEMS
729 553 CLIT00(LITAN1,K) = CLIT00(LITAN1,K) + AS*TM(K)
730 CLIT00(LITAN1,NFRAC1)=CLIT00(LITAN1,NFRAC1)+PPOT'N
731 CLIT00(LITAN1,NELEM2) = CLIT00(LITAN1,NELEM2)+FA*1-CHO
732 INDEX = 1
733 GO TO 475
734 C-----
735 C.....
736 C
737 15 E = T/CATPR
738 CBIOHQ(N,NFRAC1)= CBIOHQ(N,NFRAC1) - E
739 TMP = TMP + E
740 DO 16 K = 1,NELEMS
741 EXCRET(K) = EXCRET(K) + E * CONST(K,NFRAC1)
742 16 CBIOHQ(N,K) = CBIOHQ(N,K) - E * CONST(K,NFRAC1)
743 TT = E * CONST(NITRO,NFRAC1)/UREA
744 EXCRET(NFRAC1)= EXCRET(NFRAC1) + TT
745 AGAINO(1,*) = AGAINO(1,*) - (E-TT)
746 12 CONTINUE
747 C-----
748 C.....GROWTH
749 C-----
750 C
751 C.....THE POTENTIAL AMOUNT OF EACH CONSTITUENT TO BE ADDED
752 C.....IS CALCULATED
753 C-----
754 C
755 C.....FETAL GROWTH
756 DO 20 KK = 1,NFRELH
757 20 BRENB(KK) = 0.
758 EMBEY = 0.
759 IF (GESTINS,N),EG,0) GO TO 25
760 NHARV = BABY(NS,N)
761 IF (LGESTP(N),NE,0,AND,IYRDAY,NE,SEASON(NS,N)) GO TO 24
762 IF (NS,EG,NSEASIN)) LGESTP(N) = SEASON(I,N) + 36 - SEASON(NS,N)
763 24 IF (IYRDAY,NE,SEASON(NS,N),OR,GESTINS,N),GT,-1) GO TO 21
764 DO 23 K= NFRAC1,NFRELH
765 23 START(K-NELEMS,NHARV) = 0.
766 X = BIRTH(NS,N) + POP(N)
767 POP00(NHARV) = POP00(NHARV) + X
768 DO 22 K = 1,NFRAC1
769 CBIOHQ(NHARV,K) = CBIOHQ(NHARV,K) + WINIT + CONST(K,NFRAC1)*X
770 CBIOHQ(N,K) = CBIOHQ(N,K) - WINIT + CONST(K,NFRAC1)*X
771 22 CONTINUE
772 CBIOHQ(NHARV) = PLEV(NHARV) + WINIT*X
773 21 IF (POP(NHARV),LE,0.) GO TO 25
774 IF (PLEVEL(NHARV),LE,0.) GO TO 25
775 CALL SESSUB(NHARV,NSS,IYRDAY)
776 BWFC = ( EXP(-TK(N))+AMAX(10.,POP(NHARV)/(POP(N)+X*RTAT(N) - 1.)
777 1 / (FLOAT(LGESTP(N)) - 1.) ) * (1. + POP(1,NSS,NHARV) - 1.))
778 2 GROW(1,NSS,NHARV)
779 DO 27 K = NFRAC1,NFRELH
780 GRENB(K) = (PLEVEL(NHARV)+GROW(K-NELEMS,NSS,NHARV) +
781 1 AMAX(10.,PLEVEL(NHARV)-CBIOHQ(NHARV,NFRAC1) *SWOOL(NHARV,
782 2 NFRAC1)+SHLKP(NHARV,NFRAC1)) / (GROW(K-NELEMS,NSS,NHARV) /
783 3 GROW(1,NSS,NHARV)) +
784 4 BWFC
785 DO 26 KK = 1,NELEMS
786 26 GRENB(KK) = GRENB(KK) + CONST(K,N,K) + GRENB(KK)

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787 EMBEGY = EMBEGY + GREMB(K)*ENBODY(K-NELEMS)*EFFIC(N)
788 CONTINUE
789 PLEVQ(NHARV) = PLEVQ(NHARV) + PLEVEL(NHARV)*GROWL(NSS,NHARV)
790 + BUFC
791 25 CONTINUE
792 C
793 C.....JUVENILE GROWTH
794 DO 37 K = 1,NFRELH
795 37 GRJUV(K) = 0.
796 AJUVEY = 0.
797 IF (GRDVI(1,NSS,N) LE 0.) GO TO 35
798 NHARV = HUMIN(1)
799 IF (NHARV.EQ.0) GO TO 36
800 CALL SESSUB(NHARV,NSS,IYRDAY)
801 TF (N.EQ.BABY(NSS,NHARV)) GO TO 35
802 DO 30 K = NFRA(1,NFRELH)
803 30 CONTINUE
804 DO 32 K = NFRA(1,NFRELH)
805 32 START(K-NELEMS,N) = (CBION(N,K) - SWOOL(N,K) - SHILK(N,K))/POPIN
806 31 DO 33 K = NFRA(1,NFRELH)
807 GRJUV(K) = GROWIK-NELEMS,NSS,N) + (PMEVL(N) + POPIN) - PLEVEL(N)
808 1 + AMAX1(0.,GROWIK-NELEMS,NSS,N) + (PMEVL(N) + POPIN) +
809 (PLEVEL(N) - START(1,N) + POP(N))
810 3 + START(K-NELEMS,N) + POP(N) - CBION(N,K) + SWOOL(N,K)
811 4 + SHILK(N,K)
812 DO 34 KK = 1,NELFK
813 GRJUV(KK) = GRJUV(KK) + GRJUV(K) + CONST(N,K,K)
814 AJUVEY = AJUVEY + GRJUV(K) + ENBODY(K-NELEMS)*EFFIC(N)
815 CONTINUE
816 PLEVQ(N) = PLEVQ(N) + GROWI(NSS,N) + (PMEVL(N) + POPIN)
817 - PLEVEL(N)
818 35 CONTINUE
819 C
820 C.....MILK PRODUCTION
821 DO 42 K=1,NFRELH
822 42 GRMILK(K) = 0.
823 AMLKEY = 0.
824 TF (NURSE(NSS,N).EQ.0) GO TO 45
825 NHARV = NURSE(NSS,N)
826 TF (ARTOM(NHARV).LE.0.) GO TO 45
827 CALL SESSUB(NHARV,NSS,IYRDAY)
828 TF (IYRDAY.NE.SEASON(NSS,NHARV).AND.NLACT(NHARV).NE.0) GO TO 43
829 TF (NSS.EQ.NSEAS(NHARV).NLACT(NHARV).SEASON(1,NHARV).365-SEASON(1,
830 NSS,NHARV)
831 TF (NSS.NE.NSEAS(NHARV).NLACT(NHARV).SEASON(NSS,NHARV) -
832 SEASON(NSS,NHARV)) GO TO 46
833 IF (IYRDAY.GE.SEASON(NSS,NHARV)) IYR365 = IYRDAY
834 IF (IYRDAY.LT.SEASON(1,NHARV)) IYR365 = IYRDAY + 365
835 GO TO 47
836 IYR365 = IYRDAY
837 IT = MEAN(NHARV) + NLACT(NHARV) + SEASON(NSS,NHARV)
838 TF (IYR365.LE.IT) T = (NSS,NHARV) + (CBION(NHARV,NFRELH)
839 - SWOOL(N,NFRELH) - SHILK(N,NFRELH))
840 1 TF (IYR365.GT.IT) T = AMAX1(0.,(NSS,NHARV) - (NSS,NHARV) +
841 (IYR365-IT)/(NLACT(NHARV) + (1 - MEAN(NHARV)))) +
842 2 ( CBION(NHARV,NFRELH) - SWOOL(NHARV,NFRELH) - SHILK(NHARV,NFRELH))
843 T = AMIN1(T,SHILK(N) + (CBION(N,NFRELH) - SWOOL(N,NFRELH) - SHILK(N,
844 NFRELH)))
845 DO 40 K = 1,NFRELH
846 GRMILK(K) = T * AMLTK(N,K)
847 TF (K.LE.NELEMS) GO TO 40
848 TF (K.EQ.NELEMS2) GO TO 41
849 AMLKEY = AMLKEY + GRMILK(K) + ENBODY(K-NELEMS)*EFFIC(N)
850 GO TO 40
851 AMLKEY = AMLKEY + GRMILK(K) + (FATMLK(N) + ENBODY(K-NELEMS) +
852 1 (1 - FATMLK(N)) + ENBODY(NFRELH-NELEMS+1)) * EFFIC(N)
853 40 CONTINUE
854 45 CONTINUE
855 C
856 C.....WOOL PRODUCTION
857 DO 56 K=1,NFRELH
858 56 GRWOOL(K) = 0.
859 WOLEGY = 0.
860 TF (GROWOL(NSS,N).LE.0.) GO TO 55
861 GROWOL(N) = CBION(N,NFRELH) - SWOOL(N,NFRELH) - SHILK(N,NFRELH)
862 DO 50 K=1,NFRELH
863 50 GRWOOL(K) = T * AWOOL(N,K)
864 TF (K.LE.NELEMS) GO TO 50
865 TF (K.EQ.NELEMS2) GO TO 51
866 WOLEGY = WOLEGY + GRWOOL(K) * EFFIC(N) + ENBODY(K-NELEMS)
867 GO TO 50
868 51 WOLEGY = WOLEGY + GRWOOL(K) + (FATWOL(N) + ENBODY(K-NELEMS) +
869 1 (1 - FATWOL(N)) + ENBODY(NFRELH-NELEMS+1)) * EFFIC(N)
870 50 CONTINUE
871 55 CONTINUE
872 DO 57 K = 1,NELEMS
873 57 CONTINUE
874 TF (K.EQ.NITRO) GO TO 58
875 ASHSTO(K) = CBION(N,K) - SWOOL(N,K) - SHILK(N,K)
876 1 - CONST(K,NFRA(1)) + (1 - SOFTSK(N)) + (CBION(N,NFRELH) - SWOOL(N)
877 2 - NFRELH) - SHILK(N,NFRELH) + CBION(N,NFRA(1)) - SWOOL(N,NFRA(1))
878 3 - SHILK(N,NFRA(1)) - (CBION(N,NFRELH) - SWOOL(N,NFRELH)
879 4 - SHILK(N,NFRELH)) * SOFTSK(N) + BONE(K,N)
880 ASHSTO(K) = AMAX1(0.,ASHSTO(K))
881 AVELH(K) = ASSH(K) + ASHSTO(K)
882 GO TO 57
883 58 AVELH(K) = ASSH(K)
884 57 CONTINUE
885 TTT = 0.
886 NLC = 0.
887 NONCE = 0.
888 POTPR = 0.
889 POTRES = 0.
890 DO 60 K = 1,NFRELH
891 60 TF (K.GT.NELEMS) GO TO 72
892 POTE(M,K) = GREMB(K) + GRJUV(K) + GRMILK(K) + GRWOOL(K)
893 GO TO 60
894 72 IF (K.EQ.NELEMS2) GO TO 61
895 POTPR = POTPR + GREMB(K) + GRJUV(K) + GRWOOL(K) + GRMILK(K)
896 GO TO 60
897 61 POTRES = GREMB(K) + GRJUV(K) + GRWOOL(K) + GRMILK(K)
898 60 CONTINUE
899 TF (POTPR.LE.0.) GO TO 80
900 POTEGY = EMBEGY + AJUVEY + AMLKEY + WOLEGY
901 TF (NONCE.EQ.1) GO TO 67
902 TF (NONCE.EQ.3) GO TO 71
903 TF (NONCE.EQ.4) GO TO 92
904 TF (NONCE.EQ.5) GO TO 100
905 TF (NONCE.EQ.6) GO TO 115
906 C
907 C.....IN SOME CASES, INSUFFICIENT MATERIALS MAY BE AVAILABLE IN
908 C.....THE 'POOL' OF RAW MATERIALS TO SATISFY THE MAXIMUM RATE OF
909 C.....GROWTH, AND SO THE ACTUAL AMOUNTS ADDED TO THE BIONOMASS ARE
910 C.....DECREASED
911 C.....ANY SCALING DOWN THAT IS NECESSARY IS PERFORMED
912 C
913 PROTAV = PROTEN + (CBION(N,NFRA(1)) - SWOOL(N,NFRA(1)) - SHILK(N,NFRA(1))
914 1 - PK(N) + PLEVEL(N)) - TMP

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922 PFACTO = AMIN1(PROTAV/(1-PK(N)) + PLEVEL(N) + POTPR),1.)
923 IF (PFACTO.GE.1.) GO TO 67
924 TF (PFACTO.LE.0.) GO TO 75
925 DECRSE = 1.
926 NONCE = 1
927 70 IF (NLC.LT.20) GO TO 73
928 75 DO 74 K=1,NFRELH
929 GREMB(K) = 0.
930 GRJUV(K) = 0.
931 GRMILK(K) = 0.
932 74 GRWOOL(K) = 0.
933 GO TO 80
934 73 DO 62 K = 1,NFRELH
935 Y = PFACTO * GKIN(1) + DECRSE
936 GREMB(K) = GREMB(K) * Y
937 62 EMBEGY = EMBEGY * Y
938 DO 63 K=1,NFRELH
939 Y = PFACTO * GKIN(2) + DECRSE
940 GRJUV(K) = GRJUV(K) * Y
941 63 AJUVEY = AJUVEY * Y
942 DO 64 K=1,NFRELH
943 Y = PFACTO * GKIN(3) + DECRSE
944 GRMILK(K) = GRMILK(K) * Y
945 64 AMLKEY = AMLKEY * Y
946 DO 65 K=1,NFRELH
947 Y = PFACTO * GKIN(4) + DECRSE
948 GRWOOL(K) = GRWOOL(K) * Y
949 65 WOLEGY = WOLEGY * Y
950 GO TO 66
951 C
952 C.....PROTEIN NEEDS
953 NT = 0
954 67 NT = 0
955 69 TF (POTPR.LE.PROTAV) GO TO 68
956 DECRSE = 0.9
957 NT = NT + 1
958 TF (NT.EQ.20) GO TO 75
959 POTPR = POTPR * DECRSE
960 GO TO 69
961 68 TF (NT.EQ.0) GO TO 71
962 PFACTO = 1.
963 DECRSE = DECRSE * NT
964 NONCE = 3
965 NLC = NLC + NT
966 GO TO 70
967 71 CONTINUE
968 C
969 C.....RESERVE GROWTH TISSUE NEEDS
970 NT = 0
971 91 RESAV = CHO + FAT + CBION(N,NELM2) - SWOOL(N,NELM2) - SHILK(N,NELM2)
972 1 + (PROTAV - POTPR) * (1 - CONST(NITRO,NFRA(1)) / (JFA) - TMP
973 TF (POTRES.LE.RESAV) GO TO 90
974 DECRSE = 0.9
975 NT = NT + 1
976 TF (NT.EQ.20) GO TO 75
977 POTRES = POTRES * DECRSE
978 POTPR = POTPR * DECRSE
979 GO TO 91
980 90 TF (NT.EQ.0) GO TO 97
981 PFACTO = 1.
982 DECRSE = DECRSE * NT
983 NONCE = 4
984 NLC = NLC + NT
985 GO TO 70
986 92 CONTINUE
987 C
988 C.....NONCARBON CONSTITUENT NEEDS
989 MK1
990 94 NT = 0
991 105 T = AVELH(MK) + AMAX1(0.,(POTPR-PROTEN) + CONST(MK,NFRA(1)))
992 DECRSE = 0.9
993 TF (POTEL(MK).LE.T) GO TO 103
994 NT = NT + 1
995 TF (NT.EQ.20) GO TO 75
996 POTE(MK) = POTE(MK) * DECRSE
997 POTPR = POTPR * DECRSE
998 GO TO 105
999 103 TF (NT.EQ.0) GO TO 100
1000 PFACTO = 1.
1001 DECRSE = DECRSE * NT
1002 NONCE = 5
1003 NLC = NLC + NT
1004 GO TO 70
1005 100 AVELH(MK) = T
1006 IF (MK.EQ.NELEMS) GO TO 97
1007 MK = MK + 1
1008 GO TO 94
1009 93 CONTINUE
1010 C
1011 C.....ENERGY NEEDS
1012 NT = 0
1013 114 TF (POTRES.GE.CHO + FAT) GO TO 110
1014 FNEGAV = (CHO - CHO / (CHO + FAT) + POTRES) * CATPR +
1015 1 (CBION(N,NELM2) - SWOOL(N,NELM2) - SHILK(N,NELM2) - TMP + FAT - FAT /
1016 3 (CHO + FAT) + POTRES) * CATFAT + (PROTAV - POTPR) * CATPR
1017 GO TO 117
1018 110 TF (POTRES.GE.CHO + FAT + CBION(N,NELM2) - SWOOL(N,NELM2) - SHILK(N,
1019 1 NLELM2) - TMP) GO TO 111
1020 FNEGAV = (CBION(N,NELM2) - SWOOL(N,NELM2) - SHILK(N,NELM2) - TMP + CHO
1021 1 + FAT - POTRES) * CATFAT + (PROTAV - POTPR) * CATPR
1022 GO TO 117
1023 111 FNEGAV = ((PROTAV - POTPR) - (POTRES - CHO - FAT - CBION(N,NELM2) + TMP +
1024 1 SWOOL(N,NELM2) - SHILK(N,NELM2)) / (1 - CONST(NITRO,NFRA(1)) / (JFA)
1025 2 * CATPR
1026 112 TF (POTEGY.LE.FNEGAV) GO TO 113
1027 DECRSE = 0.9
1028 NT = NT + 1
1029 TF (NT.EQ.20) GO TO 75
1030 POTEGY = POTEGY * DECRSE
1031 POTPR = POTPR * DECRSE
1032 POTRES = POTRES * DECRSE
1033 GO TO 114
1034 113 TF (NT.EQ.0) GO TO 115
1035 PFACTO = 1.
1036 DECRSE = DECRSE * NT
1037 NONCE = 6
1038 NLC = NLC + NT
1039 GO TO 70
1040 115 CONTINUE
1041 C
1042 C.....THE ACTUAL AMOUNTS OF EACH CONSTITUENT PRODUCED ARE ADDED
1043 NHARV = BABY(NSS,N)
1044 DO 120 K = 1,NFRELH
1045 CBION(N,K) = CBION(N,K) + GRJUV(K) + GRMILK(K) + GRWOOL(K)
1046 SWOOL(N,K) = SWOOL(N,K) + GRWOOL(K)
1047 SHILK(N,K) = SHILK(N,K) + GRMILK(K)
1048 120 CBION(NHARV,K) = CBION(NHARV,K) + GREMB(K)
1049 C
1050 C.....DECREMENT SOURCES THAT PROVIDED MATERIALS FOR PROTEIN
1051 C.....GROWTH

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1057 TF (POTPRY,GT,PROTEN) GO TO 121
1058 PROTEN = PROTEN - POTPRY
1059 GO TO 123
1060
1061 121 Y = POTPRY - PROTEN
1062 DO 122 K = 1,NFRAC1
1063 CBIOH(N,K) = CBIOH(N,K) - TT + CONST(K,NFRAC1)
1064 TF (K,NE,NFRAC1) ASSIM(K) = ASSIM(K) + TT*CONST(K,NFRAC1)
1065 PROTEN = D.
1066
1067 C
1068 C.....DECREMENT SOURCES THAT PROVIDED MATERIALS FOR FAT AND CMB
1069 C.....GROWTH
1070 123 TF (POTRES,GT,CHO + FAT) GO TO 124
1071 CHO = CHO - CHO/(CHO + FAT)*POTRES
1072 FAT = FAT - FAT/(CHO+FAT)*POTRES
1073 GO TO 125
1074
1075 124 Y = CHO + FAT + CBIOH(N,NELM2) - SHILKP(N,NELM2) - SWOOL(N,NELM2) - THR
1076 YF (POTRES,GT,Y) GO TO 126
1077 YTT = POTRES - CHO - FAT
1078 CBIOH(N,NELM2) = CBIOH(N,NELM2) - YTT
1079 CHO = D.
1080 FAT = D.
1081 GO TO 125
1082
1083 126 TIV = (POTRES/(1.-CONST(NITRO,NFRAC1)/UREA)
1084 TTT = CBIOH(N,NELM2) - SWOOL(N,NELM2) - SHILKP(N,NELM2) - THR
1085 CHO = D.
1086 FAT = D.
1087 EXCRET(NFRAC1) = EXCRET(NFRAC1) + TIV*CONST(NITRO,NFRAC1)/UREA
1088 YF (CBIOH(N,NELM2),GT,0) CBIOH(N,NELM2) = CBIOH(N,NELM2) - TTT
1089 TF (TIV,GT,PROTEN) GO TO 127
1090 PROTEN = PROTEN - TIV
1091 GO TO 127
1092
1093 127 DO 129 K=1,NFRAC1
1094 CBIOH(N,K) = CBIOH(N,K) - (TIV-PROTEN)*CONST(K,NFRAC1)
1095 TF (K,EO,NFRAC1) GO TO 129
1096 EXCRET(K) = EXCRET(K) + (TIV-PROTEN)*CONST(K,NFRAC1)
1097
1098 129 CONTINUE
1099 PROTEN = D.
1100
1101 C
1102 C.....DECREMENT SOURCES THAT PROVIDED MATERIALS FOR MINERAL AND
1103 C.....NITROGEN GROWTH
1104 125 DO 130 K=1,NELEMS
1105 TF (POTELM(K),GT,ASSIM(K)) GO TO 131
1106 ASSIM(K) = ASSIM(K) - POTELM(K)
1107 GO TO 132
1108
1109 131 CBIOH(N,K) = CBIOH(N,K) - (POTELM(K)-ASSIM(K))
1110 ASSIM(K) = D.
1111
1112 132 AVELM(K) = AVELM(K) - POTELM(K)
1113
1114 130 CONTINUE
1115
1116 C
1117 C.....DECREMENT SOURCES THAT PROVIDED ENERGY FOR GROWTH
1118 E = CHO+CATCHO + FAT+CATFAT
1119 TF (POTEGY,GT,E) GO TO 140
1120 T = POTEGY/E
1121 AGAINQ(1,3) = AGAINQ(1,3) - CHO*T - FAT*T
1122 CHO = CHO - CHO * T
1123 FAT = FAT - FAT * T
1124 GO TO 141
1125
1126 140 AGAINQ(1,3) = AGAINQ(1,3) - CHO - FAT
1127 CHO = D.
1128 FAT = D.
1129 IF (POTEGY,GT,E + (CBIOH(N,NELM2) - SHILKP(N,NELM2) - SWOOL(N,NELM2)
1130 - THR - TTT) * CATFAT) GO TO 142
1131 AGAINQ(1,3) = AGAINQ(1,3) - (POTEGY-E)/C*FAT
1132 Z = (POTEGY-E)/CATFAT
1133 CBIOH(N,NELM2) = CBIOH(N,NELM2) - Z
1134 GO TO 141
1135
1136 142 Z = CBIOH(N,NELM2) - SWOOL(N,NELM2) - SHILKP(N,NELM2) - TTT - THR
1137 TF (CBIOH(N,NELM2),GT,0) CBIOH(N,NELM2) = CBIOH(N,NELM2) - Z
1138 AGAINQ(1,3) = AGAINQ(1,3) - Z
1139 E = E + Z*CATCHO
1140 Y = (POTEGY-F)/CATPR
1141 EXCRET(NFRAC1) = EXCRET(NFRAC1) + Y * CONST(NITRO,NFRAC1)/UREA
1142 AGAINQ(1,3) = AGAINQ(1,3) + Y*(1.-CONST(NITRO,NFRAC1)/UREA)
1143 TF (PROTEN,GT,Y) GO TO 152
1144 DO 153 K=1,NFRAC1
1145 CBIOH(N,K) = CBIOH(N,K) - (Y-PROTEN)*CONST(K,NFRAC1)
1146 DO 156 K = 1,NELEMS
1147 EXCRET(K) = EXCRET(K) + (Y-PROTEN)*CONST(K,NFRAC1)
1148 PROTEN = D.
1149 GO TO 141
1150
1151 152 PROTEN = PROTEN - Y
1153 CONTINUE
1154 DO RESAV=CBIOH(N,NELM2) - SWOOL(N,NELM2) - SHILKP(N,NELM2) - TTT - Z - THR
1155
1156 C
1157 C.....PROTEIN SYNTHESIS
1158 DEFICT = AMAX(D.,PLEVEL(N) - (CBIOH(N,NFRAC1) - SWOOL(N,NFRAC1) -
1159 SHILKP(N,NFRAC1)))
1160 TF (DEFICT,GT,PROTEN) DEFICT = PROTEN
1161 IF (DEFICT,LE,0.) GO TO 168
1162 F = 1.
1163 DO 160 K = 1,NELEMS
1164 F = AMIN(F,AMAX(1,DEFICT*CONST(K,NFRAC1)))
1165 DEFICT = DEFICT * F
1166 IF (DEFICT,LE,0.) GO TO 168
1167 TT = CHO+CATCHO + (FAT+RESAV)*CATFAT
1168 ENEGAV = TT*(PROTEN-DEFICT)*CATPR
1169 FNEED = DEFICT*EFFIC(N)+ENBODY(1)
1170 TF (FNEED,GT,ENEGAV) DEFICT = (PROTEN+TT/CATPR)/(1.+EFFIC(N))
1171 ENBODY(1)/CATPR
1172 DO 162 K=1,NFRAC1
1173 T = DEFICT*CONST(K,NFRAC1)
1174 CBIOH(N,K) = CBIOH(N,K) + T
1175 TF (K,NE,NFRAC1) GO TO 163
1176 PROTEN = PROTEN - DEFICT
1177 GO TO 162
1178
1179 163 CBIOH(N,K) = CBIOH(N,K) - AMAX(D.,T - ASSIM(K))
1180 ASSIM(K) = AMAX(1,ASSIM(K) - T)
1181 AVELM(K) = AVELM(K) - T
1182 CONTINUE
1183 ENEGAV = DEFICT*EFFIC(N)+ENBODY(1)
1184 IF (ENEGAV,GT,CHO+CATCHO+FAT+CATFAT) GO TO 164
1185 CHO = CHO - CHO*FNEED/(CHO+CATCHO + FAT+CATFAT)
1186 FAT = FAT - (CHO+CATCHO+FAT+CATFAT)*FNEED
1187 AGAINQ(1,3) = AGAINQ(1,3) - (CHO+FAT)*FNEED/(CHO + CATCHO+FAT+CATFAT)
1188 GO TO 169
1189
1190 164 AGAINQ(1,3) = AGAINQ(1,3) - CHO - FAT
1191 TF (FNEED,GT,TT) GO TO 165
1192 T = (ENEGAV - CHO+CATCHO+FAT+CATFAT)/CATFAT
1193 CBIOH(N,NELM2) = CBIOH(N,NELM2) - T
1194 AGAINQ(1,3) = AGAINQ(1,3) - T
1195 CHO = D.
1196 FAT = D.
1197 GO TO 168
1198
1199 165 AGAINQ(1,3) = AGAINQ(1,3) - RESAV
1200 CHO = D.
1201 FAT = D.
1202 TF (CBIOH(N,NELM2),GT,0) CBIOH(N,NELM2) = CBIOH(N,NELM2) - RESAV
1203 PROTEN = PROTEN - (ENEGAV)/CATPR
1204 AGAINQ(1,3) = AGAINQ(1,3) - (ENEGAV-TT)/CATPR + (1.-CONST(NITRO,NFRAC1)
1205 )/UREA
1206 EXCRET(NFRAC1) = EXCRET(NFRAC1) + (ENEGAV-TT)/CATPR

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1193 1 CONST(NITRO,NFRAC1)/UREA
1194 168 CONTINUE
1195
1196 C-----
1197 C FATTENING
1198 C-----
1199 C
1200 T = FATEFF(N)+ENBODY(2)
1201 TT = CHO+CATCHO + FAT+CATFAT + PROTFN*CATPR
1202 IF (TT,LE,0.) GO TO 172
1203 XT = CHO*Y + FAT*Y + CHO+CATCHO + FAT+CATFAT
1204 YT = PROTFN*Y + PROTFN*CATPR/(1.-CONST(NITRO,NFRAC1)/UREA)
1205 TF (XT,GE,TT) GO TO 170
1206 X = 1.
1207 Y = (TT-XT)/YT
1208 GO TO 171
1209
1210 170 X = TT/XT
1211
1212 171 CBIOH(N,NELM2) = CBIOH(N,NELM2) + X*(CHO+FAT) + Y*PROTFN
1213 CHO = CHO * (1.-X)
1214 FAT = FAT * (1.-X)
1215 TF = Y*PROTFN/(1.-CONST(NITRO,NFRAC1)/UREA)
1216 PROTFN = PROTFN - Y
1217 EXCRET(NFRAC1) = EXCRET(NFRAC1) + Y*CONST(NITRO,NFRAC1)/UREA
1218 AGAINQ(1,3) = AGAINQ(1,3) - CHO - FAT - PROTFN
1219 172 EXCRET(NITRO) = EXCRET(NITRO) + ASSIM(NITRO)
1220 DO 190 K = 1,NELEMS
1221 TF (K,EO,NITRO) GO TO 190
1222 T = SOFTSK(N) + (CBIOH(N,NFREL) - SWOOL(N,NFREL) - SHILKP(N,NFREL))
1223 1 = (STORSK(N) - PONE(K,N))
1224 TF = AMIN(1, -ASHTO(K), ASSIM(K))
1225 CBIOH(N,K) = CBIOH(N,K) + TF
1226 EXCRET(K) = EXCRET(K) + ASSIM(K) - TF
1227
1228 190 CONTINUE
1229
1230 C-----
1231 C NON-PREDATORY DEATHS
1232 C-----
1233 Y = (CBIOH(N,NFRAC1) - SWOOL(N,NFRAC1) - SHILKP(N,NFRAC1))/PLEVEL(N)
1234 TF (Y,GE,1) AMORT = D.
1235 TF (Y,LE,PK(N)) AMORT = 1.
1236 TF (Y,GT,PK(N),AND,AL,LT,1) AMORT = 1. - EXP(PK(N) *
1237 Y)
1238 ALDQ (Y - PK(N))/(1.-PK(N))
1239 AMORT = DEATH(NS,N) + AMORT - AMORT*DEATH(NS,N)
1240 IF (AMORT,LE,0.) GO TO 202
1241 IF (GEST(NS,N),EQ,0) GO TO 200
1242 NHARY = PABY(NS,N)
1243 CALL HORTLY(NHARY,AMORT,?)
1244 CALL HORTLY(N,AMORT,?)
1245 GO TO 207
1246
1247 200 TF (GROWTH * NS,N) - LE,0.) GO TO 201
1248 NHARY = MUM(N)
1249 IF (NHARY,EO,0) GO TO 201
1250 CALL SESSUB(NHARY,NSS,IYRDAY)
1251 TF (N,NE,NHARY,NSS,IYRDAY) GO TO 201
1252 CALL HORTLY(N,AMORT,?)
1253 GO TO 202
1254
1255 201 CALL HORTLY(N,AMORT,?)
1256 202 CONTINUE
1257
1258 C-----
1259 C EXCRETION
1260 C-----
1261 C.....THE EXCRETED CONSTITUENTS ARE DIVIDED AMONG THE SURFACE AND
1262 C.....SOIL HORIZONS ACCORDING TO AN INPUT PARAMETER
1263 475 DO 485 JH=1,NH1
1264
1265 C.....THE CONSTITUENTS ARE ADDED DIRECTLY TO SOIL ORGANIC MATTER
1266 C.....IF ADDED TO A SOIL HORIZON, ELSE THEY ARE ADDED TO THE
1267 C.....SURFACE LITTER
1268 TF (JH,EO,NH1) GO TO 490
1269 DO 480 K=1,NFREL
1270 480 CORGO(JH,K) = CORGO(JH,K) + EXCRET(K) * TFRFF (JH,NS,N)
1271 485 CONTINUE
1272 490 DO 495 K=1,NFREL
1273 495 CLITGO(LITEX,K) = CLITGO(LITEX,K) + EXCRET(K) * TFRFF (JH,NS,N)
1274 TF (INDEX,NE,1) GO TO 508
1275 INDEX = 0
1276 IF (POP(N),LE,0.) GO TO 505
1277 POPQ(N) = POPQ(N) - POP(N)
1278 GO TO 505
1279
1280 C-----
1281 C WOOL REMOVAL
1282 C-----
1283 598 DO 599 K=1,MAXURT
1284 IF (IYRDAY,NE,NDATE(K,N)) GO TO 599
1285 NT = K
1286 GO TO 605
1287 599 CONTINUE
1288 GO TO 630
1289 605 WRITE(6,20) N,NDATE(N,N)
1290 620 FORMAT(' WOOL REMOVAL FROM GROUP ',I3,' AT TIME UNIT ',I5)
1291 DO 610 K = 1,NFREL
1292 T = PROPT(N,N) * SWOOL(N,K)
1293 WRITE(6,621) T
1294 621 ORMT (6,3)
1295 SWOOL(N,K) = SWOOL(N,K) - T
1296 TF (K,GT,NELEMS) GO TO 615
1297 AGAINQ(1,K) = AGAINQ(1,K) - T
1298 GO TO 610
1299 615 AGAINQ(1,3) = AGAINQ(1,3) - T
1300 610 CONTINUE
1301
1302 C-----
1303 C POPULATION CHANGES
1304 C-----
1305 C.....THE POPULATION IS PROPORTIONAL TO THE STRUCTURAL CARBON LESS
1306 C.....ANY WOOL CARBON AND MILK CARBON
1307 C.....IN JUVENILES, GROWTH OF STRUCTURAL TISSUE IS NOT COUNTED
1308 C.....IN THIS RECKONING. FETAL GROWTH IN ADULT COHORTS IS ALSO NOT
1309 C.....COUNTED IN THIS RECKONING
1310 630 POPQ(N) = POPQ(N) - TBOM(N) + GAMAX(N)
1311 GO TO 505
1312 501 IF (NN(N),NE,1) GO TO 505
1313 NPLACE(N) = NPLACE(N) + 1
1314 NN(N) = 0
1315 DO 502 K = 1,NFREL
1316 IF (CBIOH(N,K),LE,0.) GO TO 581
1317 IF (K,LE,NELEMS) AGAINQ(1,K) = AGAINQ(1,K) - CBIOH(N,K)
1318 TF (K,GT,NELEMS) AGAINQ(1,3) = AGAINQ(1,3) - CBIOH(N,K)
1319 CBIOH(N,K) = CBIOH(N,K) - CBIOH(N,K)
1320 581 TF (SWOOL(N,K),LE,0.) GO TO 582
1321 SWOOL(N,K) = SWOOL(N,K) - SWOOL(N,K)
1322 582 IF (SHILKP(N,K),LE,0.) GO TO 502
1323 SHILKP(N,K) = SHILKP(N,K) - SHILKP(N,K)
1324 502 CONTINUE
1325 TF (PLEVEL(N),LE,0.) GO TO 583
1326 PLEV(N) = PLEV(N) - PLEV(N)
1327 583 IF (POP(N),LE,0.) GO TO 505
1328 POPQ(N) = POPQ(N) - POP(N)
1329 505 CONTINUE
1330
1331 C-----
1332 C DEBUG ROUTINE
1333 C-----

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1329 IF (NDEBUN, EQ, 0) RETURN
1330 WRITE (6,525) IYDAY
1331 WRITE (6,530) ((CVE000(I,J,K), I=1, NVFCOH, J=1, NORGAN), K=1, NFRELMI)
1332 WRITE (6,535) ((SEED00(I,JH,K), I=1, NSPECV), JH=1, NSEEDH), K=1,
1333 NFRELMI)
1334 WRITE (6,540) ((COR000(JH,K), JH=1, NHORIZ), K=1, NFRELMI)
1335 WRITE (6,545) ((CLIT00(L,K), L=1, NOLIT), K=1, NFRELMI)
1336 WRITE (6,550) ((CBIOH0(N,K), N=1, NSPCOH), K=1, NFRELMI)
1337 WRITE (6,555) ((POP000(N), N=1, NSPCOH)
1338 WRITE (6,560) ((AGAIN0(I,J), I=1, 3), J=1, 3)
1339 RETURN
1340 C-----
1341 C READ IN DATA FOR THE NAMELIST
1342 C-----
1343 F*RYRY ATINPUT
1344 READ (5,PUTT)
1345 RETURN
1346 525 FORMAT (' ANIMAL DEBUGGING', 5X, 'IYRDAY =', I4)
1347 530 FORMAT (' CVF000 =', 10F12.6)
1348 535 FORMAT (' SEED00 =', 10F12.6)
1349 540 FORMAT (' COR000 =', 10F12.6)
1350 545 FORMAT (' CLIT00 =', 10F12.6)
1351 550 FORMAT (' CBIOH0 =', 10F12.6)
1352 555 FORMAT (' POP000 =', 10F12.6)
1353 560 FORMAT (' AGAIN0 =', 10F12.6)
1354 END

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Subroutine SESSUB

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1 SUBROUTINE SESSUB (N, NS, IYDAY)
2 INTEGER SEASON
3 COMMON /PARAM/ PARVE(4000), TERR(6, 6, 30), PREFLV(100), PRESD(200),
4 IPREFL(6), PRFRO(16), PCAPN(70), SEASON(6, 10), NSF(6, 30),
5 CCOEFF(5, 30), CROW(3, 6, 30), RK(6, 30), RP(6, 30), RA(6, 30),
6 3 R(6, 30), MUM(30), SOFTK(30), FATMLK(10), FATWOL(30), BTRYH(6, 30),
7 4CONST(3, 5), PMLVEL(30), EFFC(30), PUMEN, WINIT, HAMMR, HAMMUR, BIRDPR
8 5, BIRDUR, CATCHO, CATFAT, LITANI, LITAN2
9 N=NSFAC(N)
10 DO 20 I=1, NS
11 TF (I, EQ, NS) RETURN
12 TF (IYDAY, LT, SEASON II+1, N) I, AND, (IYDAY, GE, SFA(ONIT, N))
13 1 GO TO 15
14 DO TO 20
15 NS=I
16 RETURN
17 20 CONTINUE
18 RETURN
19 END

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Subroutine MORTLY

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1 SUBROUTINE MORTLY (N, AMORT, IP)
2 C
3 C
4 C----- *M* TRANSMITS THE INDEX NUMBER OF THE COHORT IN WHICH THE
5 C----- MORTALITY OCCURS
6 C----- *AMORT* TRANSMITS THE FRACTION OF EACH CONSTITUENT THAT DIES
7 C----- *IP* TRANSMITS THE TYPE OF MORTALITY INVOLVED -
8 C----- TP = 1 PREDATORY DEATH (SOFT PARTS CONSUMED)
9 C----- TP = 2 NON-PREDATORY DEATH (ALL PARTS ADDED TO LITTER)
10 C----- TP = 3 RESORTION
11 C
12 C THE COMMON BLOCKS MUST BE COMPATIBLE WITH THE SUBROUTINE *ANIMAL*
13 C-----
14 COMMON /DEATHS/ TAL(5), TBIOH(30), NELEM2, NELEMS, FRAFAT, STOPE(5, 30)
15 COMMON /SPEC/ NCHAM, INSTUR(20), NSPECV, NSPECA, NORGAN, NFRACT, NRAY,
16 INELEM, NOLIT, NCHECK, IDAY, IYDAY, NREFP(120), NDRUG, NHORIZ, NCOM(10),
17 2LTSCH(30), NCHOCU(10), NCOHOR, NFRELMI, NFRACL, NSPCOH, MONTH, HORDEP(6),
18 3LITRUM(5), NREP(20), IYR, DRYFV(3, 6), LITCAT(15), NVFCOH, LISVCO(15),
19 4NVCCH(10), NVCOCU(10), NSECS, TRUN, NUNLIT, TS TO, JST D, ILIT, JLT, ILH,
20 5JLH, SEEDPE(6), NSEEDH, NELEMS, JSTATE, JDAY
21 COMMON /STAT/ CVE00(15, 10, 6), SEED00(10, 6, 6), POP(10), TBIOH(30, 6),
22 1CLIT(15, 6), CORG(5, 6), CHN(5, 6), SNOCOV, WATARS(5), ANCOV, PERCOV,
23 2TCOV, COVER(10), FREVAT, DUMHY(30)
24 COMMON /CHANGE/ CVE00(15, 10, 6), SEED00(10, 6, 6), POP(10),
25 1CBIOH(30, 6), CLIT00(15, 6), CORG00(15, 6), CHN00(5, 6), SNOCOV, WATARQ(5)
26 2, ANNCOV, PERCOV, TC0V00, COVFRQ(10), FREVAT, DUMHY(30)
27 DIMENSION PLEVEL(10), PLFVQ(10)
28 DIMENSION SWOOL(20, 5), SWOOLQ(20, 5)
29 DIMENSION SHILKP(30, 5), SHILKQ(30, 5)
30 COMMON /PARAM/ PARVE(4000), TERR(6, 6, 30), PREFLV(100), PRESD(200),
31 IPREFL(6), PRFRO(16), PCAPN(70), SEASON(6, 10), NSF(6, 30),
32 CCOEFF(5, 30), CROW(3, 6, 30), RK(6, 30), RP(6, 30), RA(6, 30),
33 3 R(6, 30), MUM(30), SOFTK(30), FATMLK(10), FATWOL(30), BTRYH(6, 30),
34 4CONST(3, 5), PMLVEL(30), EFFC(30), PUMEN, WINIT, HAMMR, HAMMUR, BIRDPR
35 5, BIRDUR, CATCHO, CATFAT, LITANI, LITAN2
36 EQUIVALENCE (DUMHY, PLEVEL), (DUMHYQ, PLEVQ)
37 EQUIVALENCE (DUMHY(31), SHILKP), (DUMHYQ(11), SHILKQ)
38 EQUIVALENCE (DUMHY(11), SWOOL), (DUMHYQ(11), SWOOLQ)
39 DIMENSION S(2)
40 SOFT = 0.
41 DO 25 K=1, NELEMS
42 S(K) = 0.
43 C
44 C
45 TF (IP, NE, 3) GO TO 1
46 NHARV = MUM(N)
47 DO 29 K = 1, NELEMS
48 STORES(K, NHARV) = 0.
49 PLEVQ(N) = PLEVQ(N) - AMORT * PLEVEL(N)
50 DO 26 K = 1, NFRELMI
51 TF (CBIOH(N, K), LE, 0.) GO TO 26
52 Y = CBIOH(N, K) * AMORT
53 YO = AMORT * (CBIOH(N, K) - SWOOL(N, K) - SHILKP(N, K))
54 TF (K, EQ, NELEM2) TBIOH(N) = TBIOH(N) + YO
55 Y = AMORT * SWOOL(N, K)
56 Y = AMORT * SHILKP(N, K)
57 CBIOH(N, K) = CBIOH(N, K) - Y
58 TF (SWOOL(N, K), LE, 0.) GO TO 28
59 SWOOL(N, K) = SWOOL(N, K) - Y
60 TF (SHILKP(N, K), LE, 0.) GO TO 27

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61 SHILKQ(N, K) = SHILKQ(N, K) - Y
62 TF (K, LE, NELEMS) STORES(K, NHARV) = Y
63 IF (K, EQ, NFRAC1, OR, K, EQ, NFRELMI) STORES(NFRAC1, NHARV) = STORES(
64 NFRAC1, NHARV) + Y
65 TF (K, NE, NELEM2) GO TO 26
66 STORES(NELEM2, NHARV) = YO + Y * FATVOL(N) + Y * F * F * MLK(N)
67 STORES(NFLEMS, NHARV) = Y * (1 - FATVOL(N)) + Y * (1 - FATMLK(N))
68 CONTINUE
69 RETURN
70 C
71 C
72 C----- DECREMENTING WOOL BIOMASS
73 1 DO 10 K = 1, NFRELMI
74 IF (SWOOL(N, K), LE, 0.) GO TO 5
75 Y = SWOOL(N, K) * AMORT
76 CBIOH(N, K) = CBIOH(N, K) - Y
77 SWOOL(N, K) = SWOOL(N, K) - Y
78 CLIT00(LITANI, K) = CLIT00(LITANI, K) + Y
79 5 IF (SHILKP(N, K), LE, 0.) GO TO 10
80 Y = SHILKP(N, K) * AMORT
81 CBIOH(N, K) = CBIOH(N, K) - Y
82 SHILKQ(N, K) = SHILKQ(N, K) - Y
83 TF (IP, EQ, 1) GO TO 7
84 CLIT00(LITANI, K) = CLIT00(LITANI, K) + Y
85 DO TO 10
86 7 TAL(K) = TAL(K) + Y
87 TF (K, EQ, NELEM2) FRAFAT = FRAFAT + FATMLK(N) * Y
88 10 CONTINUE
89 C
90 C
91 C----- DECREMENTING STRUCTURAL CARBON BIOMASS (EXCLUDING WOOL)
92 TF (CBIOH(N, NFRELMI) - SWOOL(N, NFRELMI) - SHILKP(N, NFRELMI), LE, 0.)
93 1 GO TO 15
94 Y = AMORT * (CBIOH(N, NFRELMI) - SWOOL(N, NFRELMI) - SHILKP(N, NFRELMI))
95 TBIOH(N) = TBIOH(N) + Y
96 CBIOH(N, NFRELMI) = CBIOH(N, NFRELMI) - Y
97 C
98 C
99 C----- DETERMINE THE AMOUNT OF STRUCTURAL TISSUE CARBON THAT IS
100 C----- CONSIDERED *HARD*
101 C
102 C
103 SOFT = Y * (1 - SOFTS(K))
104 CLIT00(LITAN2, NFRELMI) = CLIT00(LITAN2, NFRELMI) + Y - SOFT
105 PLEVQ(N) = PLEVQ(N) - AMORT * PLEVEL(N)
106 DO 30 K = 1, NFRAC1, NFRELMI
107 TF (K, NE, NFRELMI) GO TO 37
108 Y = SOFT
109 GO TO 33
110 32 TF (CBIOH(N, K) - SWOOL(N, K) - SHILKP(N, K), LE, 0.) GO TO 30
111 Y = AMORT * (CBIOH(N, K) - SWOOL(N, K) - SHILKP(N, K))
112 CBIOH(N, K) = CBIOH(N, K) - Y
113 DO 31 KK = 1, NELEMS
114 TF (K, NE, NFRELMI) GO TO 34
115 YY = Y * CONST(KK, K)
116 GO TO 35
117 34 Y = Y * CONST(KK, K)
118 35 S(KK) = S(KK) + YY
119 CONTINUE
120 TF (IP, EQ, 1) GO TO 37
121 CLIT00(LITANI, K) = CLIT00(LITANI, K) + Y
122 GO TO 30
123 37 TAL(K) = TAL(K) + Y
124 IF (K, EQ, NELEM2) FRAFAT = FRAFAT + Y
125 30 CONTINUE
126 DO 36 K = 1, NELEMS
127 TF (CBIOH(N, K) - SWOOL(N, K) - SHILKP(N, K), LE, 0.) GO TO 36
128 Y = AMORT * (CBIOH(N, K) - SWOOL(N, K) - SHILKP(N, K))
129 CBIOH(N, K) = CBIOH(N, K) - Y
130 TF (IP, EQ, 1) TAL(K) = TAL(K) + AMINI(S(K), Y)
131 TF (IP, NE, 1) CLIT00(LITANI, K) = CLIT00(LITANI, K) + AMINI(S(K), Y)
132 CLIT00(LITAN2, K) = CLIT00(LITAN2, K) + AMAX(0., Y - S(K))
133 36 CONTINUE
134 RETURN
135 END

```

Subroutine POSITN

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1 SUBROUTINE POSITN (PP, NOTR)
2 COMMON /SPEC/ NCHAM, INSTUR(20), NSPECV, NSPECA, NORGAN, NFRACT, NRAY,
3 INELEM, NOLIT, NCHECK, IDAY, IYDAY, NREFP(120), NDRUG, NHORIZ, NCOM(10),
4 2LTSCH(30), NCHOCU(10), NCOHOR, NFRELMI, NFRACL, NSPCOH, MONTH, HORDEP(6),
5 3LITRUM(5), NREP(20), IYR, DRYFV(3, 6), LITCAT(15), NVFCOH, LISVCO(15),
6 4NVCCH(10), NVCOCU(10), NSECS, TRUN, NUNLIT, TS TO, JST D, ILIT, JLT, ILH,
7 5JLH, SEEDPE(6), NSEEDH, NELEMS, JSTATE, JDAY
8 COMMON /CHANGE/ CVE00(15, 10, 6), SEED00(10, 6, 6), POP(10),
9 1CBIOH(30, 6), CLIT00(15, 6), CORG00(15, 6), CHN00(5, 6), SNOCOV, WATARQ(5)
10 2, ANNCOV, PERCOV, TC0V00, COVFRQ(10), FREVAT, DUMHY(30)
11 COMMON /POSIT/ TRANS(16, 2, 12), NSTSED, NSTLIT, NSTORG, NSTPRY
12 DIMENSION PPS(5)
13 IF (NOTR, LE, NSTSED, OR, NOTR, GT, NSTPRY) GO TO 1
14 IF (NOTR, GT, NSTORG) GO TO 4
15 IF (NOTR, LE, NSTLIT) GO TO 3
16 L = NOTR - NSTLIT
17 DO 7 K=1, NFRELMI
18 CLIT00(L, K) = CLIT00(L, K) + PPK(K)
19 PPK(K) = 0.
20 RETURN
21 3 J = MOD(NOTR - NSTSED, NSPECV)
22 JH = NOTR - J * NSPECV
23 DO 5 K=1, NFRELMI
24 SEED00(I, JH, K) = SEED00(I, JH, K) + PPK(K)
25 PPK(K) = 0.
26 RETURN
27 4 JH = NOTR - NSTORG
28 DO 6 K=1, NFRELMI
29 CORG00(JH, 5) = CORG00(JH, 5) + PPK(K)
30 PPK(K) = 0.
31 RETURN
32 1 WRITE (6, 2)
33 2 FORMAT (' MISTAKE - ADDRESS OF LOCATION TO WHICH EFFECT OF POSITION*
34 3 ITION IS TRANSFERRED')
35 STOP
36 END

```



### SIMULATION: ANIMAL III

The grazing of cattle on the Curlew southern grass site was simulated over one grazing season, December 1 to January 22. The number of cattle brought into the system on December 1 was 0.49/ha, each cow weighing 345 kg and each pregnant.

At the end of the simulation, the adults had each lost 6 kg (net), while the fetuses had put on 3 kg each. The adults were on a protein-deficient diet (80% *Agropyron* and 20% *Atriplex*), and their body composition reflected this deficiency. Energy was not a limiting factor during the grazing period.

The parameters used for this simulation were first determined from the literature and run with the model. The results of this first simulation indicated that the consumption parameter was too high, and upon checking with the value given in the 1973 Curlew Validation Site report,<sup>1</sup> this was confirmed. Once this parameter had been adjusted, the results of the model run were in fairly close accordance with those reported for cattle on the Curlew grass site.

A copy of the data set (with sources) and of the simulation output may be obtained from the author.

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<sup>1</sup>Balph, D. F. (Coordinator), et al. 1973. Curlew Valley validation site report. US/IBP Desert Biome Res. Memo. 73-1. 336 pp.