Technical Report No. 158

AFCØNS: A DYNAMIC SIMULATION MODEL OF AN INTERACTIVE HERBIVORE COMMUNITY

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August 1972

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ABSTRACT

AFCØNS, an acronym for African Consumers, is a nonlinear, differential equation model of an interactive consumer community. Age classes of several herbivore, carnivore, and scavenger species are represented by 38 principal system variables as well as abiotic and vegetation driving variables. Over 800 FORTRAN coded statements constitute the program deck.

Three concurrently operative routines solve sets of equations for energy, balance, change in weight, and change in numbers. Feedback between the routines allows food quality and quantity control of birth, death, and predation rates as well as competitive shifts in diet.

INTRODUCTION

Although the purposes of modelling vary between projects and investigators, it is our judgment that models should attempt to accurately portray real-world phenomena. Therefore, if emphasis is placed on model structure, each model component should be homologous to natural structures; if process or function is the predominant purpose, then model processes should be analogs of those in nature. It is quite feasible to choose either of the major purposes and disregard the other. Rarely, however, have ecological modellers attempted to pursue both.

AFCØNS is an acronym for a nonlinear differential equation model of the consumer dynamics of an East African savanna ecosystem. It is formulated from a background of vertebrate ecology and domestic animal science, although it may be suitably general to represent other classes of consumers. If applied to invertebrates, most likely only the parameter values would change appreciably.

The reasons for development of this model are threefold. First, we aspire to mathematically represent certain consumer population dynamics in a savanna ecosystem. Although we have only included six primary consumer "species" to date, the addition of new species would be simple. Secondly, we attempt to represent realistic feedback mechanisms between habitat conditions and population dynamics. The third major goal is that of representing the interactions that occur between animal energetics and animal population dynamics. We perceive a need for such a model insofar as one of the greatest inadequacies of consumer population models to date is their failure to reflect the compensatory changes manifest in natural communities (Fig. 1).

Whereas further rationale will be given for each of these points as the various sections are developed, the general procedural background is

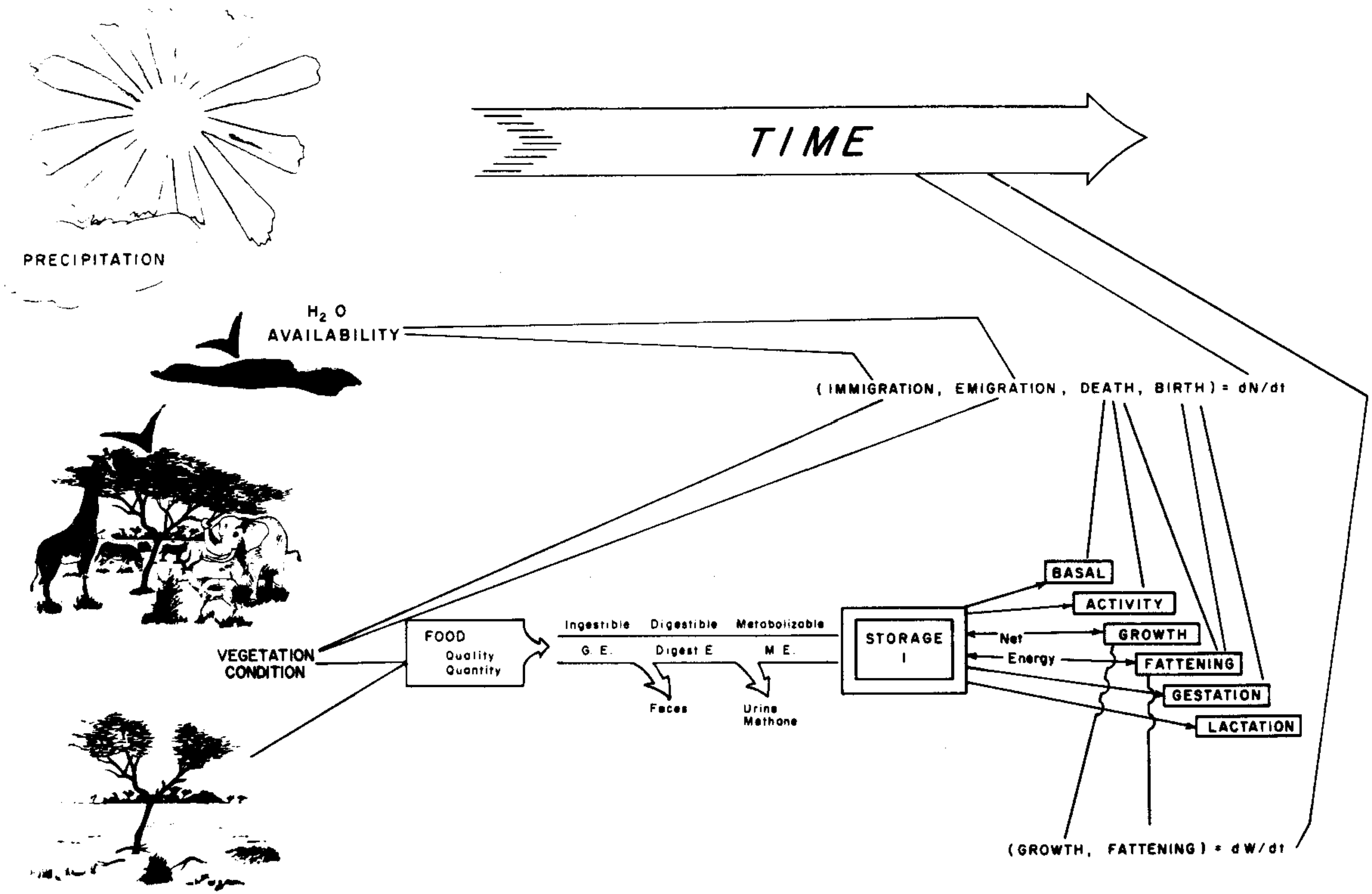


Fig. 1. The conceptual interaction of three component submodels incorporated into AFCØNS.

clarified here. Each of the state variables in the model represents a natural entity, and each equation represents a natural process. We have consciously made some errors of omission. We hope we have made few of commission. The bulk of our background information is derived from basic population dynamics and vertebrate nutrition literature. By induction we have drawn upon specific research results to formulate the necessary system of parameters, variables, and equations. Specifically, AFCØNS refers to African consumers, and the implicit setting is that of an African savanna ecosystem. It is readily acknowledged that parameter values are not known for all the "species" utilized, but neither are they for any species known to man. There is, on the other hand, reason to believe that some of the parameter values applicable to wild animals are not substantially different from the inter-species means developed by animal scientists.

GENERAL DESCRIPTION OF THE MODEL

Functional Groups

AFCØNS presently consists of 38 variables of major interest, 37 of which are biotic and 1 of which is abiotic (Table 1). The principal system variables and driving variables are conveniently divided into five major groups: (i) herbivores, (ii) predators, scavengers, and animal dead, (iii) primary producers, (iv) milk, and (v) precipitation.

Herbivores (variables 1-18). Presently there are six herbivore "species" in the model, each of which is divided into three physiological age classes: immature, mature, and old-aged. The number of age classes utilized is arbitrary, but from the energetics and population dynamics point of view at least three are felt to be necessary. For example, it seems

Table 1. The 38 principal system variables and driving variables are categorized into five major groups consisting of herbivores; predators, scavengers, and animal dead; primary producers; milk; and precipitation. From a notational and analytical standpoint, the variable numbers take on increasing importance, and reference to variable numbers only will be common throughout the text.

Variables	Functional Description	Biological Homolog
1	Leaf browser, immature	Giraffe
2	Leaf browser, mature	Giraffe
3	Leaf browser, old-aged	Giraffe
4	Forb browser, immature	Gazelle
5	Forb browser, mature	Gazelle
6	Forb browser, old-aged	Gazelle
7	Stem grazer, immature	Zebra
8	Stem grazer, mature	Zebra
9	Stem grazer, old-aged	Zebra
10	Leaf grazer, immature	Hartebeest
11	Leaf grazer, mature	Hartebeest
12	Leaf grazer, old-aged	Hartebeest
13	Tree stem browser, immature	Elephant
14	Tree stem browser, mature	Elephant
15	Tree stem browser, old-aged	Elephant
16	Browser-grazer, immature	Impala
17	Browser-grazer, mature	Impala
18	Browser-grazer, old-aged	Impala
19	Predator	Lion
20	Predator-scavenger	Hyaena
21	Predator	Hunting Dog
22	Scavenger	Vulture
23	Animal dead	
24	Tree, bush, and shrub leaves	
25	Tree, bush, and shrub stems	
26	Perennial grass leaves	
27	Perennial grass stems	
28	Annual grasses	
29	Forbs	
30	Standing dead	
31	Litter	
32	Giraffe milk	
33	Gazelle milk	
34	Zebra milk	
35	Hartebeest milk	
36	Elephant milk	
37	Impala milk	
38	Precipitation	

clear that the major food items of immature and adult animals are substantially different insofar as immature mammals require milk production for livelihood. Thus, their growth and mortality rates are greatly affected by the milk production of the adults. Also, there is substantial evidence that the basic energetic requirements of the three age classes are different [Agricultural Research Council (ARC), 1965]. Whereas the daily adult herbivore basal energy requirement is approximately 70 times its metabolic weight (i.e., 70 $kg^{.75}$), it appears that the requirement for young animals is around 100 times their metabolic weights (i.e., 100 $kg^{.75}$) and basal energy requirements of older-aged herbivores drops to about 55 (i.e., 55 $kg^{.75}$) (Brody, 1945; Kleiber, 1947, 1961; Nagy, Knox, and Wesley, 1971; ARC, 1965). Further justification for these classes is derived from population dynamics criteria where reproductive and mortality rates are highly age-specific.

The specific ages (in years) at which animals graduate from one class to another are based largely upon reproductive criteria. That is, pre-reproductive animals are considered immature while all reproductive animals are considered mature. The criteria for when animals graduate to the post-mature class are more arbitrary but are based upon a perusal of the age-structure patterns of the species involved (Estes, 1972). The average time spans in the various age classes are tabulated below.

Species	Immature	Mature	Old-Aged
Giraffe	2	8	15
Gazelle	1	5	4
Zebra	2.5	12.5	7.0
Hartebeest	1	6	5
Elephant	11	44	20
Impala	1	7	4

The diets of these 18 herbivores are derived from the time-dependent standing crop values of variables 24-31 (herbage classes) plus the species-specific milk variables 32-37. Only young animals, of course, have the option of consuming milk. Although considerable flexibility in the diet exists by use of a switching function, to be described later, the initial conditions (i.e., the diet) are specified in tabular format (Table 2). These values are presumed to approximate the mean annual diet over a considerable area; and therefore, they may not accurately portray the localized diet of any group over a short period of time.

Predators, scavengers, and animal dead (variables 19-23). To provide a semblance of an interactive natural community, three predator "species" and one scavenger "species" were incorporated into the model formulation. Each has substantially different food habits such that all herbivorous food resources are drawn upon, yet there is sufficient dietary overlap to allow for compensation if one population wanes (Table 2). This is an attempt to simulate a balanced predator-prey community. The predator and scavenger populations have not been divided into age classes at this time; and therefore, species-specific milk production is not provided for these groups.

Several large species rarely succumb to predation during their mature life stage and only die of disease and accidental death. Therefore, it was necessary to include an animal dead compartment (variable 23). All animal biomass that dies of natural causes and the portions of those animals preyed upon but not immediately eaten [approximately 50% (Wright, 1960)] are transferred to the animal dead compartment. All predators normally utilize some dead while the scavengers (group 22) utilize this resource exclusively (Table 2).

Table 2. Proportions of the various food resource categories contained in the diets of all consumers under ideal conditions. Although these values may seem rigid, a continuous variable switching function allows any consumer to switch diets under certain conditions. Whereas it is known that very young animals consume their parent's milk exclusively for some time, the proportions included here represent a time-weighted approximation over the entire immature period. All variable numbers represent the categories described in Table 1.

Food Resource Categories	Consumer Group																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1																			.02			
2																			.02			
3																			.02			
4																			.04	.03	.05	
5																			.08	.03	.10	
6																			.08	.04	.15	
7																			.04		.04	
8																			.10		.08	
9																			.15		.08	
10																			.04	.04	.04	
11																			.10	.03	.08	
12																			.14	.03	.08	
13																			.02			
14																						
15																						
16																			.02	.02	.05	
17																			.03	.03	.10	
18																			.05	.05	.10	
19																						
20																						
21																						
22																						
23																			.05	.70	.05	1.00
24	.70	.60	.60	.20	.20	.20							.50	.40	.40	.20	.30	.30				
25	.10	.40	.40										.40	.40	.30							
26				.10	.05	.05	.20	.25	.15	.60	.70	.70		.10	.15	.20	.30	.30				
27					.05	.05	.40	.50	.50	.05	.10	.10		.10	.15							
28							.15	.25	.20	.05	.10	.10										
29				.40	.70	.70			.10		.10	.10				.30	.40	.40				
30									.05													
31																						
32	.20																					
33				.30																		
34							.25															
35										.30												
36													.10									
37																.30						

Primary producers (variables 24-31). All vegetation in the savanna system has been arbitrarily divided into six classes: (24) tree, bush, and shrub leaves, (25) tree, bush, and shrub stems, (26) perennial grass leaves, (27) perennial grass stems, (28) annual grasses, (29) forbs, (30) standing dead, and (31) litter. The biomass dynamics of these variables are currently treated as driving variables insofar as they are simulated solely as a function of time.

Milk (variables 32-37). All herbivorous mature and old-aged groups produce milk for suckling immatures. Since we are dealing with populations and not individuals, the amount produced at any time is a function of (i) the lactation period, (ii) the milk demands of the immature segment of the population, and (iii) the nutritional condition of the lactating groups.

Precipitation (variable 38). Another of the driving variables is the time dependent rainfall distribution which was derived from personal research reported by Harris (1970). Its major influence is on available surface water and indirectly upon forage quality.

Types of Variables

Driving variables. Presently there are six different types of variables which appear in AFCØNS (see Table 3). The driving variables are those which are dependent on time only and are therefore exogenous to the system. These are typically necessary for the elaboration of other variables of the system, but their mechanistic description is not of immediate concern. As mentioned above, the herbage standing crop variables and precipitation fall into this class.

Table 3. Examples of variable notation and nomenclature used in AFCØNS.

Type of Variable	Example: Name of Variable	Example: Symbol for Variable
Driving Variable	Precipitation rate (cm/day)	ZPR
Principal System Variable (PSV)	Biomass density of consumer group I (g/m^2)	XC(I)
Intermediate System Variable (ISV)	Harvest rate of consumer group I (g/day)	HA(I)
Independent Variable	Time in days from 1 January, modulo 365	TDMOD
Dummy Function Argument	$\sum_{I=1}^{n} Y(I)$	SUM(Y,N)
Parameter	Maximum allowable food intake rate for consumer group I (g/g/day)	PAFMX(I)

Principal system variables. Principal system variables (PSV's) are the primary variables of concern. A list of values for these variables at any point in time should provide sufficient information to fully describe the state of the system at that time. Examples of PSV's used here are the biomass densities of the 22 animal groups. The values of most PSV's are determined by the solution of differential equations.

Intermediate system variables. Intermediate system variables (ISV's) are those variables necessary for the calculation of the PSV's. The distinction between PSV's and ISV's, then, is that PSV's are determined a priori as desired output variables of the model, whereas ISV's arise a posteriori in the process of writing the PSV equations.

Independent variable. The only independent variable in AFCØNS is time (TDMOD).

Dummy function arguments. Dummy function arguments are functions used solely for their mathematical, as opposed to biological, properties. Examples of these include functions which sum a series of variables and functions which compute maxima and minima of the series of variables.

Parameters. Parameters are utilized herein as variables whose derivatives, with respect to all other variables in the system, are zero. These are frequently termed coefficients or constants in the modelling literature. This categorization of variables is consistent with that described by Bledsoe et al. (1971).

A uniform system of physical units is also used in AFCØNS, and the basic units are as follows.

Measure	Unit
Length	meter
Weight	gram dry weight
Time	day
Energy	kcal

GENERAL MODEL STRUCTURE

Although it does not reflect the overall complexity, the structural conceptualization of the model is represented in Fig. 1. The first major objective of the model is to represent the rate of change of animal biomass with respect to time. Because of great differences in the weight of individuals and a felt need for greater precision, it was necessary to monitor the number and mean weight of individuals in the 22 animal groups. For this, let:

XN(I) = density of individuals in consumer group I (PSV).

W(I) = average dry weight of an individual in consumer group I (PSV).

XC(I) = biomass density of consumer group I (PSV).

In order to compute the biomass density of consumer group I at any given time (I = 1, ..., 22), differential equations are solved for XN and W. Then the algebraic formulation

$$XC(I) = XN(I) \cdot W(I)$$

gives the total biomass density of consumer group I. Note that dry weights are always used in the model unless otherwise specified.

The rate of change of animal density with respect to time ($\frac{d(XN)}{dt}$) is a function of immigration, emigration, death, and birth. Death and birth are affected by the energy budget of the animal at any particular time while immigration and emigration are affected by vegetation abundance and quality and by surface water availability. The mathematical and biological mechanisms which control the ISV's will be discussed later.

The rate of change of the mean weight of animals in a particular consumer group ($\frac{dW}{dt}$) is a function of the rates of growth and fattening of the animals in that group. These rates are controlled by the energy budget of the animals. Thus, if the basic energy demands (e.g., basal; activity; and gestation and lactation, if needed) are not met by the daily ingestion, growth and fattening cannot occur. In fact energy can be removed from the fat storage compartment (a loss of weight to the animal) in order to meet these basic energy demands.

Differential equations are also solved for the rate of production of animal dead material and for the rates of production of milk by the six herbivore species.

All of these equations are first order, and the solutions are obtained by an Euler method.

Driving Variables

The nine driving variables in AFCØNS are given below.

Variable	Symbol	Units
Tree, bush, and shrub leaves	XC(24)	g/m^2
Tree, bush, and shrub stems	XC(25)	g/m^2
Perennial grass leaves	XC(26)	g/m^2
Perennial grass stems	XC(27)	g/m^2
Annual grasses	XC(28)	g/m^2
Forbs	XC(29)	g/m^2
Standing Dead	XC(30)	g/m^2
Litter	XC(31)	g/m^2
Precipitation	ZPR	cm/day

For convenience, precipitation is given in centimeters rather than meters (Fig. 2). Since driving variables are functions of time only, their graphs and the consequent functions are explicit (Fig. 2 through 5). All of these driving variable functions have been generated from stepwise linear approximations to the original curves.

Although "standing dead" is listed as an explicit driving variable, it is not presently utilized. That is, its inclusion gives the potential of drawing upon more sophisticated herbage dynamics models. But for the purposes of this model, the phenomenon of "dead herbage" is incorporated into the digestible and metabolizable energy formulations.

Consumer Variables

The biomass densities of the 22 consumer groups (Table 1) are computed in this part of the model. As described earlier, letting:

XN(I) = density of individuals in group I
($no./m^2$) (PSV).

W(I) = average dry weight of an individual in group I
(g/individual) (PSV).

Then:

XC(I) = biomass density of group I (g/m^2) (PSV).
= XN(I) · W(I).

Thus, first-order differential equations are solved for XN and W in order to derive the biomass density of the 22 consumer groups at any given time.

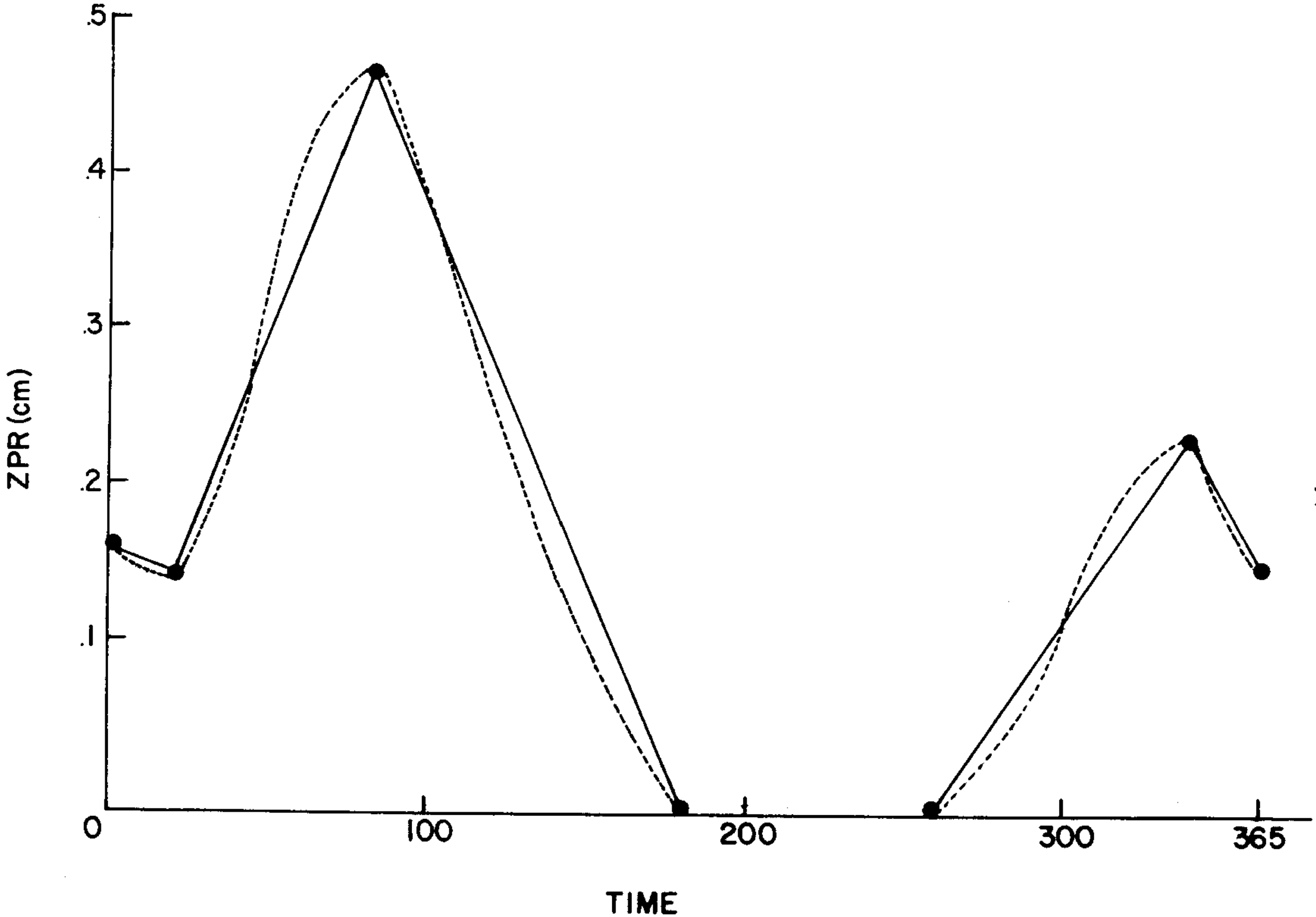


Fig. 2. A stepwise linear approximation to the empirical precipitation driving variable (ZPR). The dashed line represents the average daily precipitation of the Mkomazi Reserve, Tanzania, while the solid line represents the function ZPR.

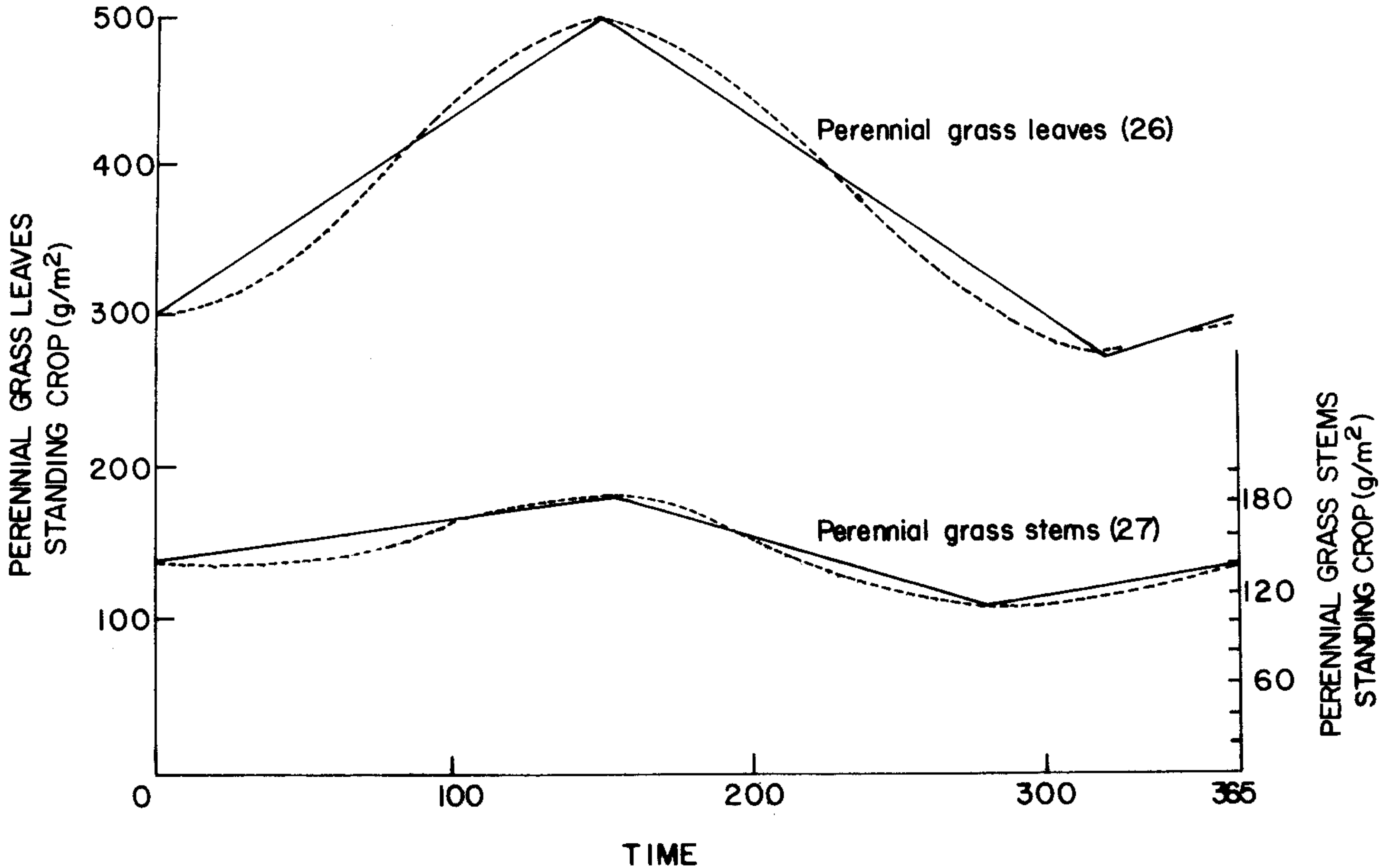


Fig. 3. The dashed lines represent empirical standing crop values for perennial grass leaves and perennial grass stems. The solid lines represent the stepwise linear approximations which are used as driving variables 26 and 27, respectively.

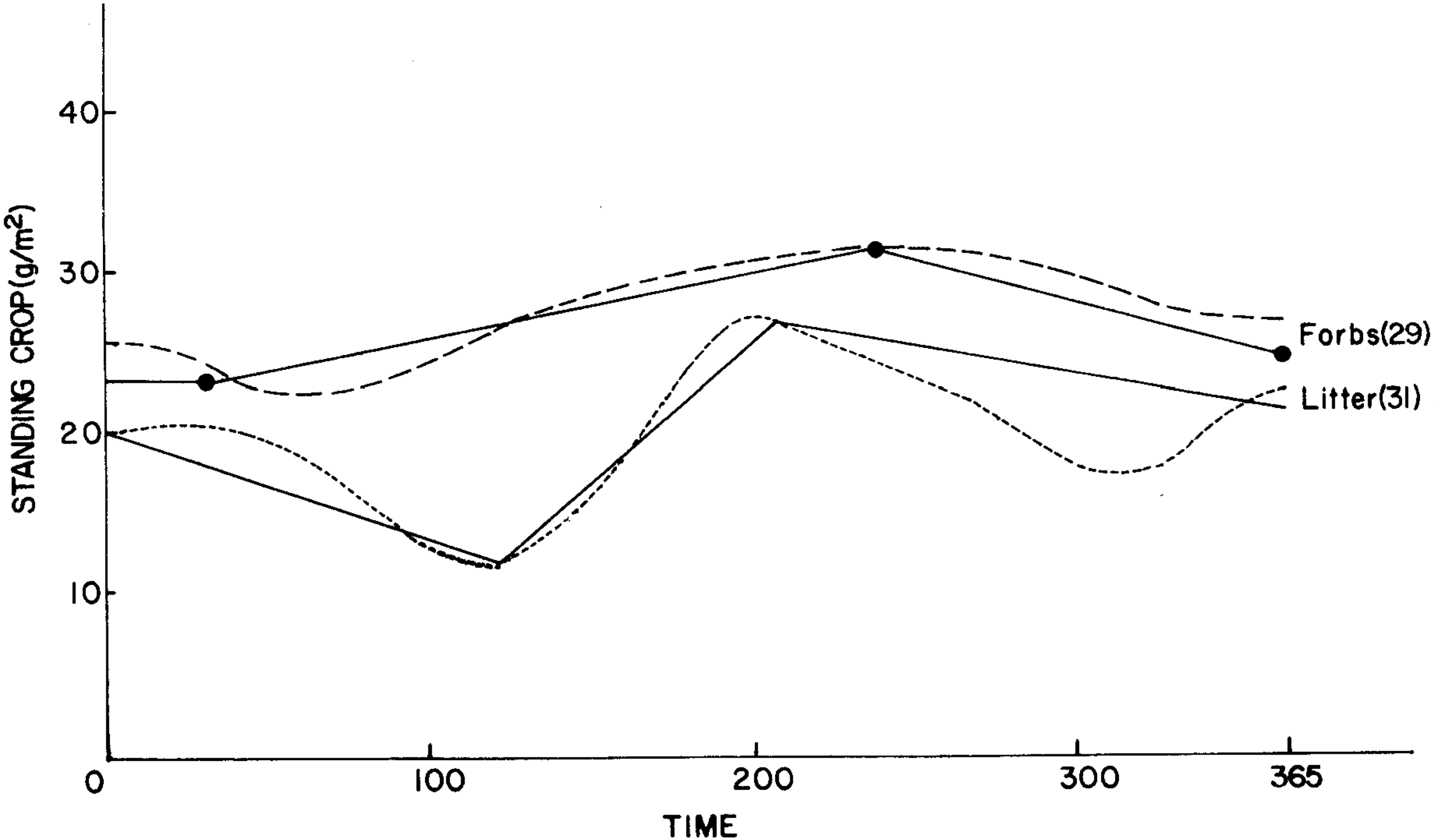


Fig. 4. Standing crop values of forbs and litter in the Mkomazi Reserve, Tanzania, are given as the long-dashed and short-dashed lines, respectively. Their stepwise linear approximations, used as driving variables 29 and 31, are superimposed as solid lines. The curve for annual grasses is assumed to be the same as for forbs.

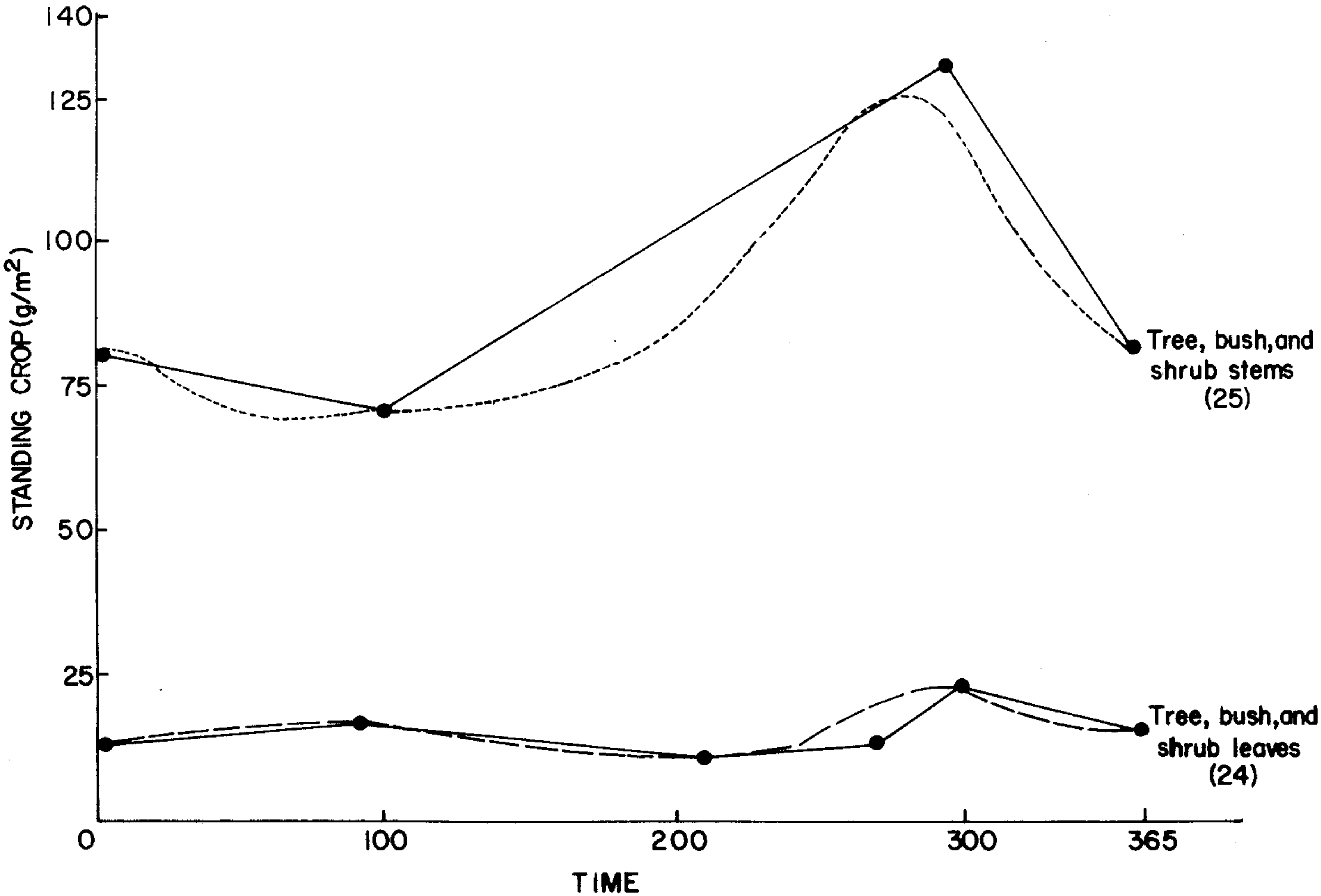


Fig. 5. Empirically derived standing crop values of tree, bush, and shrub leaves and stems from the Mkomazi Game Reserve, Tanzania, along with their stepwise linear approximations used as driving variables 24 and 25, respectively.

Average weight of an individual. In this formulation, the change in average (dry) weight of individuals in any group I is controlled by two intermediate variables: (i) the amount of mass in the "growth" compartment [BG(I)] and (ii) the mass of the "adipose" or "fat storage" compartment [BS2(I)]. In other words, the rate of change of the mean individual weight is simply a function of the rates of change of these two compartments. But there are numerous constraints upon this also. First, the sum of the fat storage and growth compartments does not equal the weight of the animal. The rationale for this is that much of an animal's weight is immobilizable and, in fact, largely static. Therefore, we have arbitrarily assigned a maximum amount of 20% of the live body weight to the growth compartment and a fat storage compartment maximum of 10% of the body weight, yielding a total mobilizable or dynamic portion of 30% of the total body weight.

Mathematically, the equation for the average weight of individuals at any particular time TDMOD is:

$$\frac{d[W(I)]}{dt} = DW(I)$$
$$= DBG(I) + DBS2(I)$$

where

DBG(I) = rate of change of biomass in the growth compartment of an animal in consumer group I (g/day).

DBS2(I) = rate of change of biomass in the storage 2 (fat storage) compartment of an animal in consumer group I (g/day).

Energy use compartments. It is clear that growth and fattening are two relatively minor allocations in the total energy budget of homeothermic animals (Petrusewicz, 1967). Other expenditures, such as the basal energy requirement, are not only greater but also seem to occupy a higher priority in the allocation sequence. Thus, unless a homeotherm maintains its temperature within bounds, none of the other expenditures are significant.

Presently, although there are seven compartments in the energy formulation, only six of these constitute avenues of expenditure. Two (i.e., growth and fattening) have been mentioned; the remaining ones are: (i) temporary storage 1 (homolog of the liver), (ii) the basal energy requirement, (iii) activity requirement, (iv) gestation, and (v) lactation. The requirement for thermal regulation has been consciously omitted from the computer code to date, although we are cognizant of its importance. The rationale for, and function of, the various compartments are briefly described below.

Storage 1. Storage 1 is conceptualized as a homolog of a "liver" through which all energy must flow (Fig. 1). The essential rationale is that metabolizable energy is used with greatly different efficiencies depending upon the allocation. For example, it is generally accepted that the net energy conversion efficiency for basal and activity requirements is about 70%, whereas the conversion efficiency for fattening may be as low as 35% (ARC, 1965). Drawing upon the copious domestic animal literature and limited studies of wild animals (e.g., Crawford, Patterson, and Yardley, 1968; Taylor and Lyman, 1967; Rogerson, 1968; Szaniawski, 1960; Siedler and Schweigert, 1954), we have formulated a set of conversion efficiencies for all required uses (Fig. 6). In spite of the notation, storage 1 only functions as a transfer box insofar as the amount of energy contained in it at any one time is miniscule compared to the amount which passes through it per unit time. The energy demands imposed upon this box are, however, greater than the total

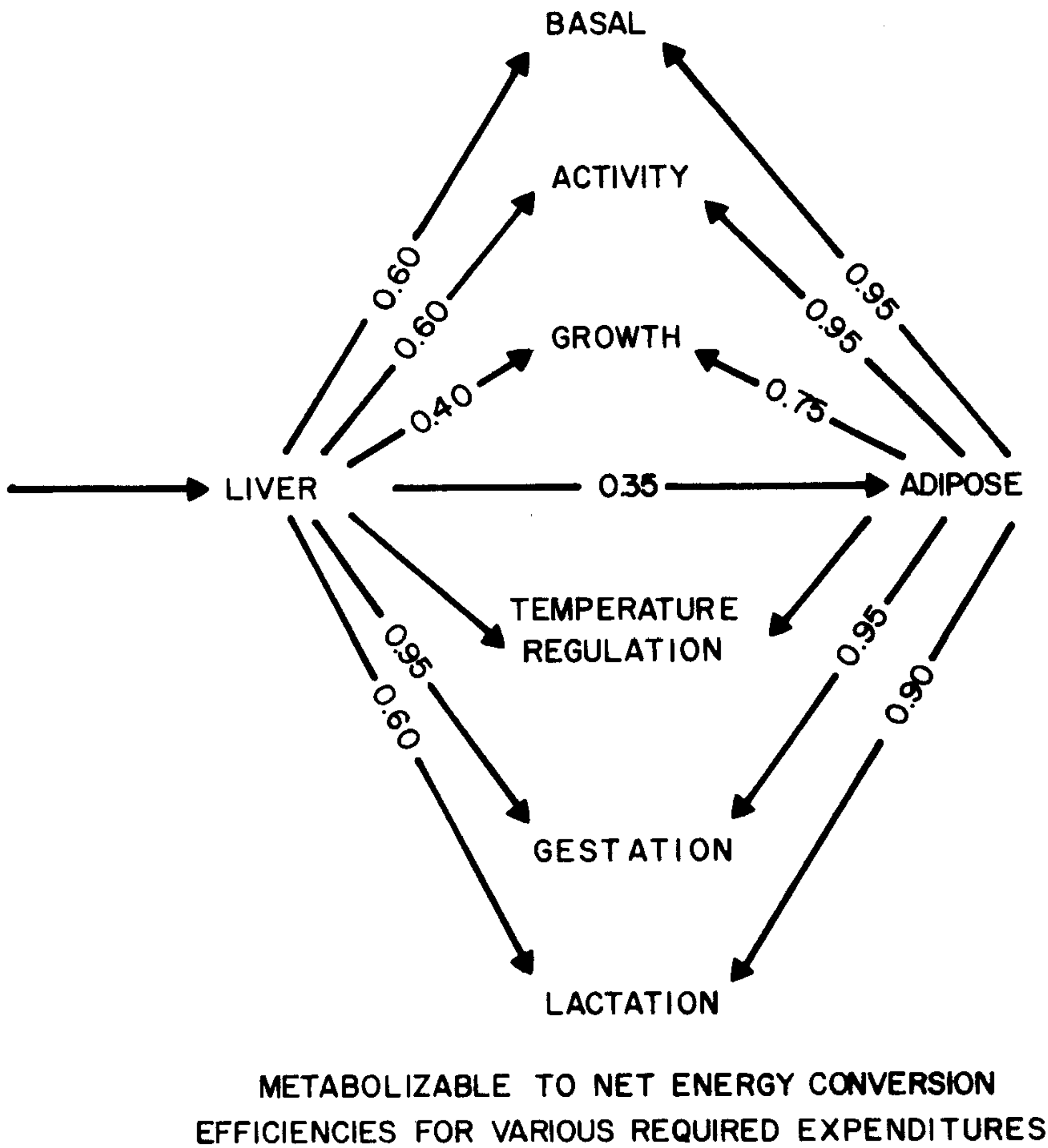


Fig. 6. Schematic representation of energy conversion pathways along with the individual efficiency parameters utilized in AFCØNS.

requirements of the others because of the metabolizable to net energy conversion efficiencies (Fig. 6).

Basal metabolism. The basal or fasting catabolism requirement is that associated with the intrinsic heat production of living organisms. Homeothermic animals require a rather constant and predictable amount of energy as a function of their metabolic weight. There is rather general agreement that the inter-species mean value of 70 kcal/kg of metabolic weight ($kg^{.75}$) is a fair appraisal of the daily requirements of mature homeotherms (Brody, 1945; Kleiber, 1961; Hemmingson, 1950, 1960). Since this rate is dependent upon the ratios of weight to surface and metabolically "active" (brain, heart, liver, and spleen) to metabolically "inactive" tissue, it appears that young animals have higher requirements and older animals have lower requirements (Kleiber, 1947; ARC, 1965). Studies of elephants (Benedict, 1936), wildebeests and elands (Rogerson, 1968), and antelope (Nagy et al., 1971), and white-tailed deer (Silver, Colovos, and Hayes, 1959) suggest that these generalizations are not inappropriate. We have further generalized that the daily basal requirement for immature animals approximates 100 kcal/kg of metabolic weight and that of old-aged animals is 55 kcal/kg of metabolic weight (ARC, 1965; Nagy et al., 1971).

In meeting this demand, the use-specific conversion efficiency from metabolic to net energy must be imposed. We have utilized a 60% efficiency for respiration expenditure (Fig. 6). Therefore, each calorie expended in this manner imposes a 1.67 cal demand upon the storage 1 compartment. There is some evidence (Flatt et al., 1969) that remobilized fat can be utilized with greater efficiency than unstructured compounds. Therefore, if demands cannot be met via ingestion, the mobilization of stored energy (from storage 2) takes place with a 90% efficiency.

Activity. Activity demands obviously vary with the degree of exertion, but it is not uncommon that an expenditure equal to the basal requirement is reported. Thus, twice the basal requirement is reported for livestock maintenance under normal conditions (Brody, 1945; Crampton and Lloyd, 1959). Laboratory experiments seem to corroborate this insofar as animals actively trying to escape had twice the requirement of quiescent animals (Hart, 1952). The considered judgment that wild animals do not "work" under normal conditions is also invoked here, but this is strongly corroborated by an analysis of expenditures associated with small mammals under field conditions (Harris, 1971).

Energy is normally drawn from storage 1 (i.e., ingestion) to meet this demand, but if that source is insufficient, fat can again be mobilized from the adipose compartment (storage 2). The conversion efficiency of metabolizable energy from storage 1 is 60%; and therefore, the demand upon this compartment is again 1.67 times the activity requirement. The mobilization of energy from fat storage is again presumed to occur at about 90% efficiency.

Now, if the activity requirements of any group cannot be met (even with the addition of storage reserves), the first response of the group is to increase the food ingestion rate to the maximum value (Table 4). A second response is that the instantaneous predation rate upon this group is increased.

The aforementioned requirements are hierarchically arranged such that the basal requirements must be met before the activity demands are considered.

Depending upon the class of animal, other functions may now take precedence. For example, the immature classes expend most of their net energy in excess of the maintenance requirement for growth while adults spend it for fattening, lactation, or gestation.

Table 4. Parameter values controlling the mass of the storage compartments and the maximum rates of change for the various consumer groups. The mass values are expressed as percents of the animal's live weight, while the different rates of change are based upon the metabolic weight of the groups and are given as g/g/day.

Physiological Class	Metabolic Weight	>150 $kg^{.75}$ = Elephant		100 to 150 $kg^{.75}$ = Giraffe		<100 $kg^{.75}$ All Others	
		Mass	Rate	Mass	Rate	Mass	Rate
Physiological Class I (Immature)	Growth	.20	.003	.20	.004	.20	.005
	Fat	.10	.0003	.10	.0004	.10	.0005
Physiological Class II (Mature)	Growth	.20	.0003	.20	.0004	.20	.0005
	Fat	.10	.003	.10	.004	.10	.005
Physiological Class III (Old-Aged)	Growth	.20	.000	.20	.000	.20	.000
	Fat	.10	.000	.10	.000	.10	.000

Growth and fattening. Growth, or protoplasmic accretion, is a function of age, energy balance, and other factors. For the purposes of this model, we have generalized to the extent that, within a single age group, only the energy balance affects growth.

In this formulation, young animals expend 90% of the energy in excess of basal and activity requirements for growth (Fig. 7). The remaining 10% is expended for fattening since the gestation and lactation costs for young animals is nil. The only constraint upon this growth function is that it cannot exceed a maximum rate determined by the animals' metabolic weight (e.g., 0.5% of the body weight/day for small animals).

Mature animals, on the other hand, expend a much smaller proportion of their energy on growth. First, the proportionate allocation for each unit of weight-change in this group is 10% proteinaceous loss or gain and 90% adipose loss or gain. Secondly, there are the added requirements of gestation and lactation. These will be discussed below; but suffice it to say for now that the growth allocation is hierarchically ordered below them, and thus only if energy is available will growth occur.

Contrary to the previously mentioned allocations, it appears that the utilization of metabolizable energy for growth is only about 40% efficient among these herbivores (ARC, 1965); and therefore, each calorie of demand imposes a 2.5 cal flow through storage 1.

Gestation. The gestation energy requirement for a population of animals is dependent upon sex ratio, age structure, and fecundity. Although the stage of pregnancy is highly important, it appears that when integrated over the full term, the cost approximates 20% of the daily maintenance (basal + activity) requirement (ARC, 1965). Therefore, were a population to have a

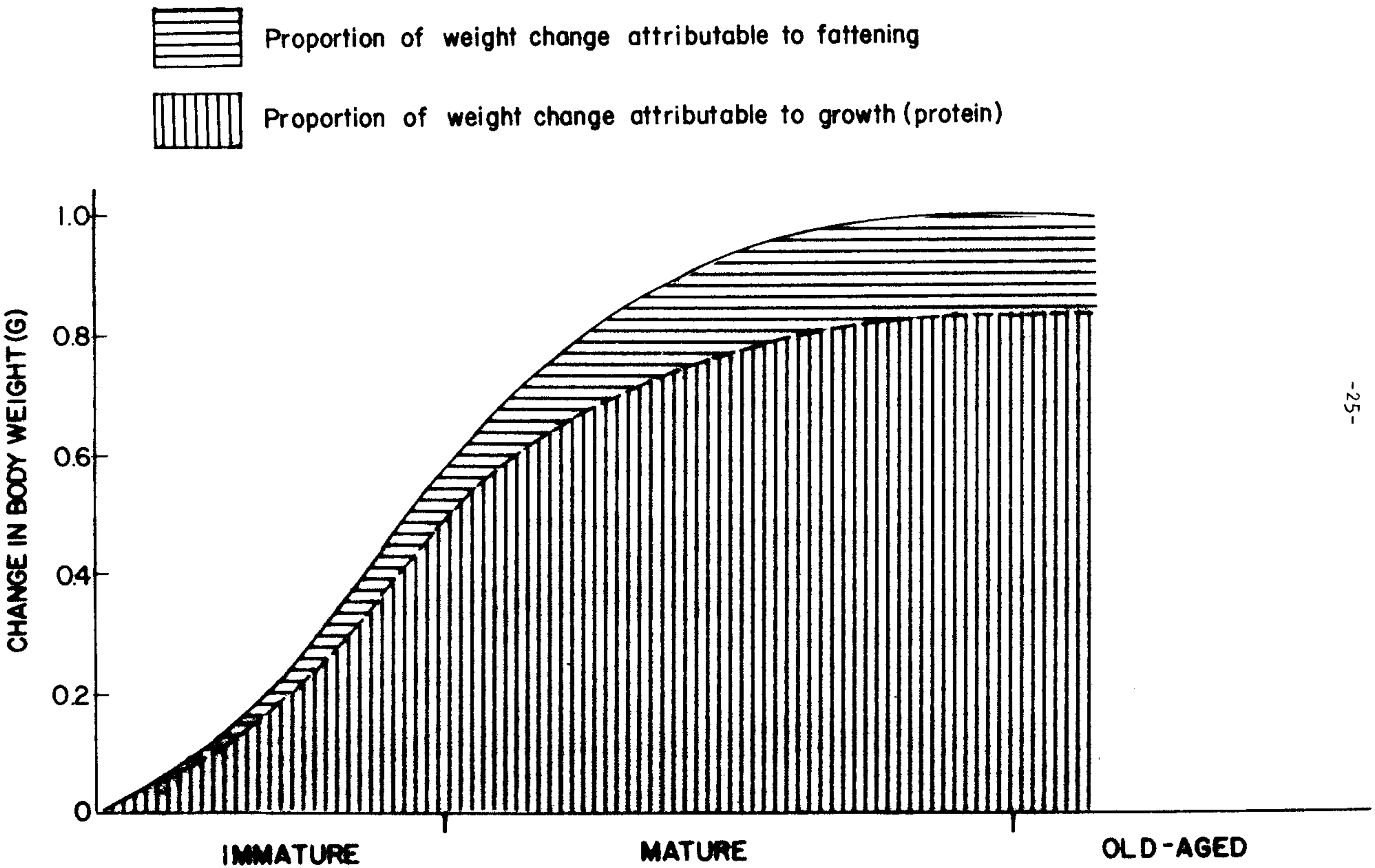


Fig. 7. A generalized change of weight function with the two component categories (protein and fat) separated out. In early stages of growth nearly all weight change is attributable to protein dynamics nearly all weight change of mature animals is affected by adipose dynamics.

1:1 sex ratio and an annual fecundity of 0.8 young per adult female, the total population cost for pregnancy would be 8% of the daily maintenance (20% · 50% · 80%). Yet since the conception and parturition dates are stochastic in nature, so too must be the total gestation cost. In this formulation, the cost distribution is the same as the parturition curve, but preceeds it by the mean gestation period.

It seems that the efficiency of energy conversion for gestation is about 95%; and therefore, the demand imposed upon storage 1 is only 1.05 times the expenditure. When this demand cannot be met by ingestion, adipose can be mobilized. If gestation demands are still not met, the birth rate computed in the concurrent population dynamics model is reduced.

Lactation. The lactation compartment provides a communal drinking pool for the first age class of the same species and thus provides another feedback between adult nutrition and infant mortality. Currently, lactation demands are a simple function of time and population fecundity. The production distribution is the same as that of parturition, but lags it by a mean lactation period. Maximum demand is based upon a milk yield of 1% of the dam's live body weight per day with an energy equivalent of 6 kcal/g dry weight (1.2 kcal/g wet weight). The production efficiency of milk appears to be quite high and approximates 60%.

Food consumption rate. Essential to the weight change and energy expenditure formulations is a food consumption routine. Basically, this routine consists of a set of initial consumption rates based upon empirical information (Table 5). In the event that the energy budget cannot be met with this ingestion rate, daily consumption is immediately increased to a maximum value. On the other hand, there are also maxima placed upon the

Table 5. Normal [XF(I)] and maximum [PAFMX(I)] food intake rates for each of the consumer groups expressed as dry weight intake per unit dry weight (wet weight · .30).

Consumer Group I	XF(I) (g/g/day)	PAFMX(I) (g/g/day)
1	.006	.0105
2	.006	.0105
3	.006	.0105
4	.0075	.0120
5	.0075	.0120
6	.0075	.0120
7	.0075	.0120
8	.0075	.0120
9	.0075	.0120
10	.0075	.0120
11	.0075	.0120
12	.0075	.0120
13	.003	.0075
14	.003	.0075
15	.003	.0075
16	.0075	.0120
17	.0075	.0120
18	.0075	.0120
19	.0009	.0030
20	.0009	.0030
21	.0009	.0030
22	.050	.0500

growth and fattening rates as well as the total mass of these compartments (Table 4).

Dietary composition. Aside from the actual ingestion rates described above, consideration must also be given to food group selection. The concept of an interactive community of primary and higher-order consumers has dominated the objectives of the entire exercise. The way these consumer groups presently interact is through their food resource. Different groups switch onto and away from dietary components as a function of abundance and well-being of the consumed items. To implement this, a series of abundance thresholds has been established such that the dietary composition is highly density-dependent (Fig. 8). An example of the well-being component of selection is incorporated by predators switching onto animal groups which have not met their activity energy requirement during the previous interval.

Dietary quality. The third major component of the dietary subsection deals with the digestibility and metabolizability of the consumed items. Presently, the animal groups are time invariant in their energy value; and since animal groups reflect little species difference, predators are subjected to a rather constant food quality. This is not the case with the herbivores. The fraction of gross energy ingested which is actually digested is termed the DE/GE ratio. The second energetic consideration involves the proportion of digestible energy which is actually metabolizable. This is termed the ME/DE ratio. Both of these are highly species specific as well as time variant (Table 6). Therefore, even though an herbivore has the flexibility of switching off its "normal" diet, it will likely do so at the risk of lower utilizability because of rumen flora and other considerations (Streeter, Clanton, and Hoehne, 1968). Furthermore, since these ratios are highly

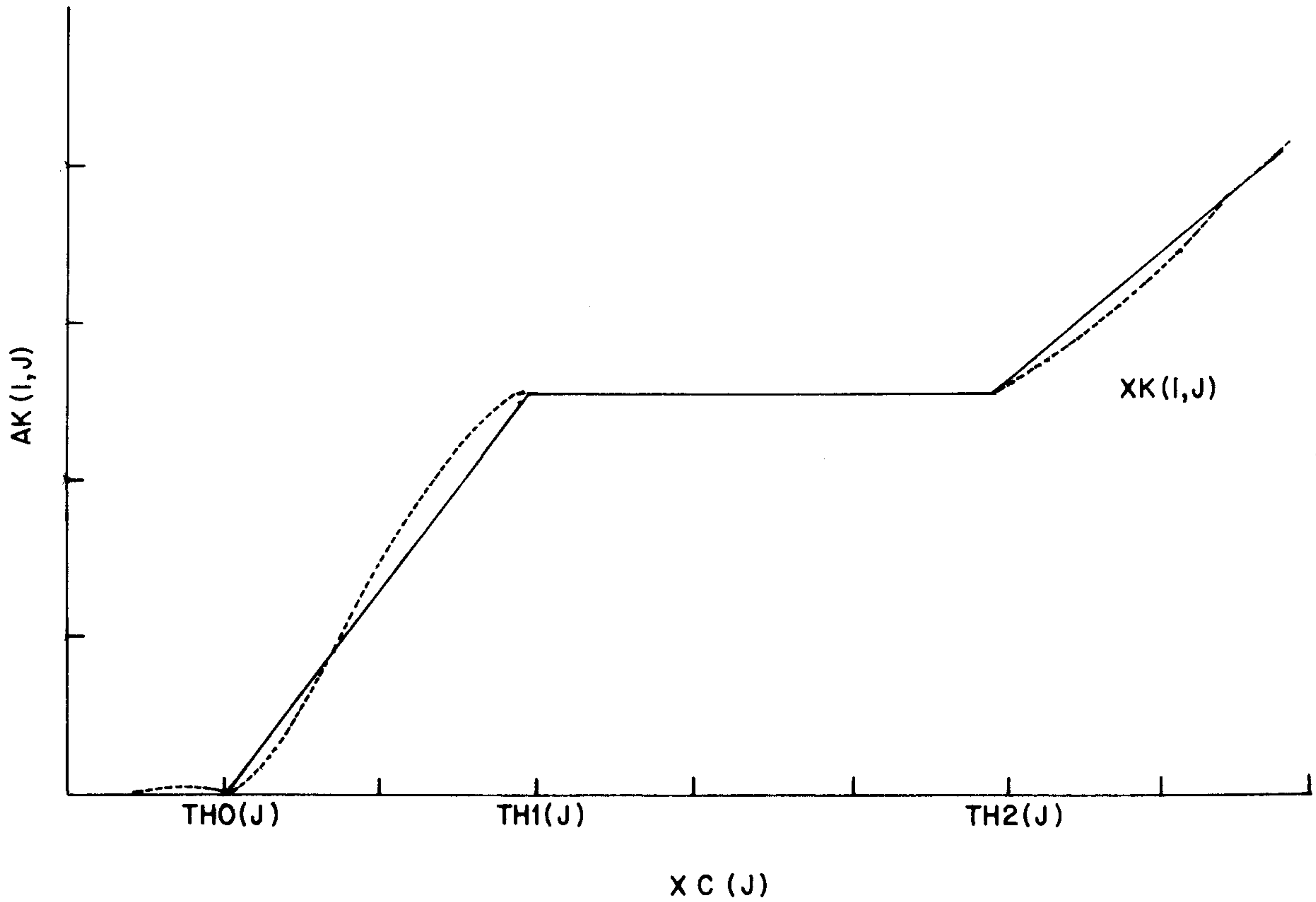


Fig. 8. Proportion of group J in the diet of consumer I [AK(I,J)] as a function of the density of consumed items [XC(J)]. Within the density range TH1 - TH2 items are consumed in the proportions scheduled in the dietary matrix of Table 2.

Table 6. Species-specific parameter values for the digestible-gross energy (first number) and the metabolizable-digestible energy ratios (numbers in parentheses) for the 18 herbivore groups. The predator and scavenger ratios are each taken to be .85 across all animal food sources.[a/]

Consumer Variable	Tree Leaves	Tree Stems	Perennial Grass Leaves	Perennial Grass Stems	Annual Grasses	Forbs	Litter
1	70 (80)	50 (60)	60 (75)	65 (75)	60 (80)	65 (80)	30 (30)
2	70 (80)	50 (60)	60 (75)	65 (75)	60 (80)	65 (80)	30 (30)
3	70 (80)	50 (60)	60 (75)	65 (75)	60 (80)	65 (80)	30 (30)
4	60 (80)	40 (50)	70 (80)	70 (75)	70 (80)	70 (80)	30 (30)
5	60 (80)	40 (50)	70 (80)	70 (75)	70 (80)	70 (80)	30 (30)
6	60 (80)	40 (50)	70 (80)	70 (75)	70 (80)	70 (80)	30 (30)
7	50 (75)	40 (50)	70 (80)	70 (75)	65 (80)	70 (75)	30 (30)
8	50 (75)	40 (50)	70 (80)	70 (75)	65 (80)	70 (75)	30 (30)
9	50 (75)	40 (50)	70 (80)	70 (75)	65 (80)	70 (75)	30 (30)
10	50 (75)	40 (50)	70 (80)	70 (75)	70 (80)	70 (80)	30 (30)
11	50 (75)	40 (50)	70 (80)	70 (75)	70 (80)	70 (80)	30 (30)
12	50 (75)	40 (50)	70 (80)	70 (75)	70 (80)	70 (80)	30 (30)
13	60 (70)	60 (70)	65 (70)	65 (70)	60 (70)	65 (70)	30 (30)
14	60 (70)	60 (70)	65 (70)	65 (70)	60 (70)	65 (70)	30 (30)
15	60 (70)	60 (70)	65 (70)	65 (70)	60 (70)	65 (70)	30 (30)
16	70 (80)	50 (55)	70 (80)	65 (75)	70 (80)	70 (80)	30 (30)
17	70 (80)	50 (55)	70 (80)	65 (75)	70 (80)	70 (80)	30 (30)
18	70 (80)	50 (55)	70 (80)	65 (75)	70 (80)	70 (80)	30 (30)

a/ 85 (85).

time and precipitation dependent, the difficult concept of standing dead vegetation has been eliminated.

After evaluating the rainfall distribution data, indices of vegetation maturity and dryness, and certain literature regarding the nutritive relations of tropical forages (e.g., French, 1957), precipitation-dependent DE/GE and ME/DE curves were formulated (Fig. 9 and 10).

Population numbers. The structure of the population dynamics model revolves around the classical population equation factors; i.e., birth, death, immigration, and emigration rates (Fig. 1). However, since age classes are considered, it is necessary to distinguish between birth and recruitment rates, while graduation, harvest, and natural death all detract from any class's numbers.

As should be clear from the foregoing sections, the birth and death rate junctions are highly dependent upon the energy states of the groups involved. This interaction between concurrent subsections of AFCØNS is highly significant in the mechanistic determination of the overall state variable dynamics.

Conceptually, there is a high degree of feedback to each of these rate functions, and the population density reflects a highly dynamic equilibrium. Presently, however, the emigration and immigration functions are not programmed into the code. The effects of this are twofold. First, it reduces the controls on density by half and, in terms of temporal response, leaves only the two longer-term or slower response factors (birth and death). Possibly of greater importance is the fact that it reduces the model from a spatially dynamic one to a point model and makes all populations dependent only upon food quantity and quality and not upon surface water. Population

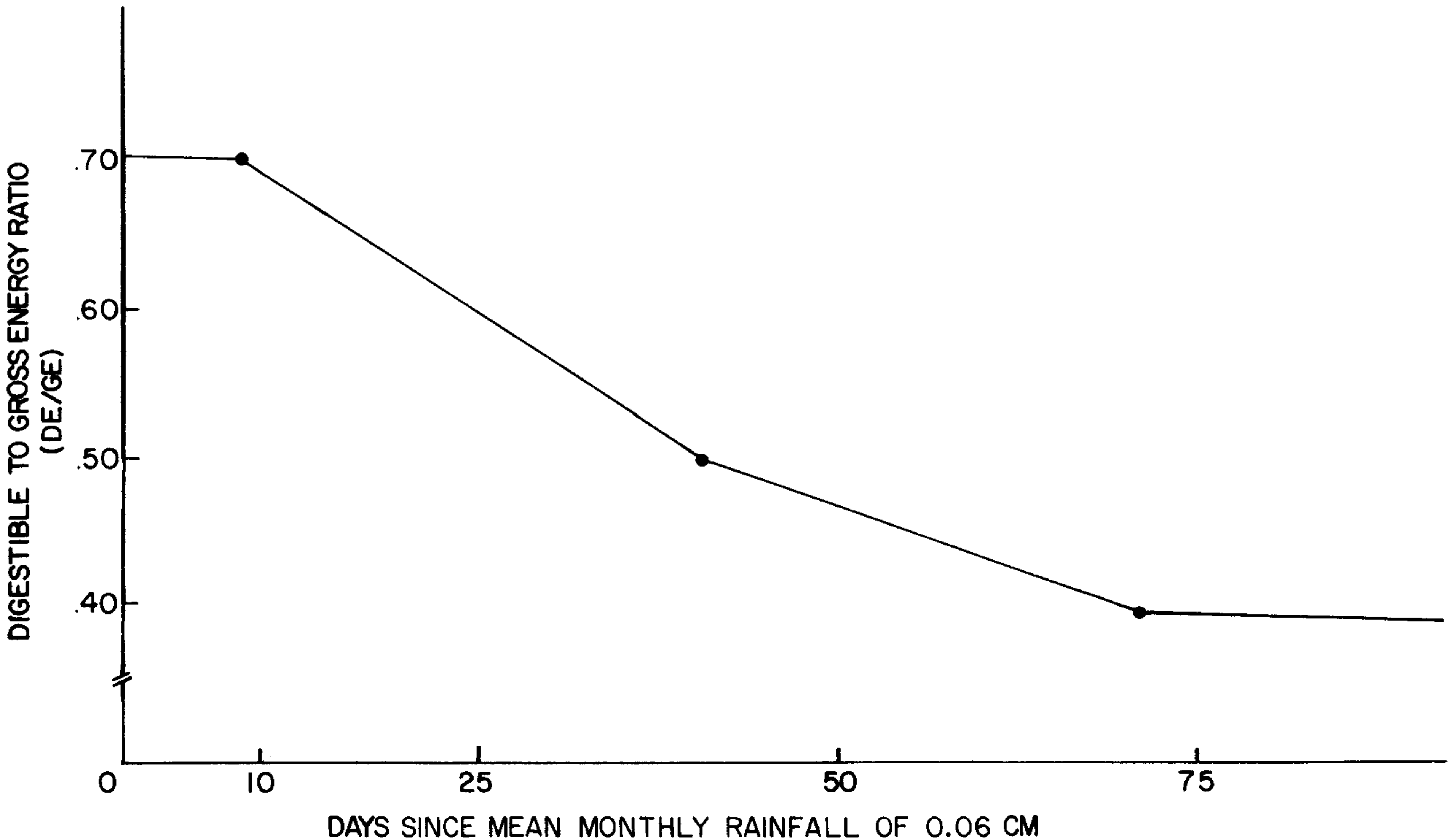


Fig. 9. The relation between the digestible energy and gross energy content of perennial grasses as a function of time since a daily average rainfall of 0.06 cm.

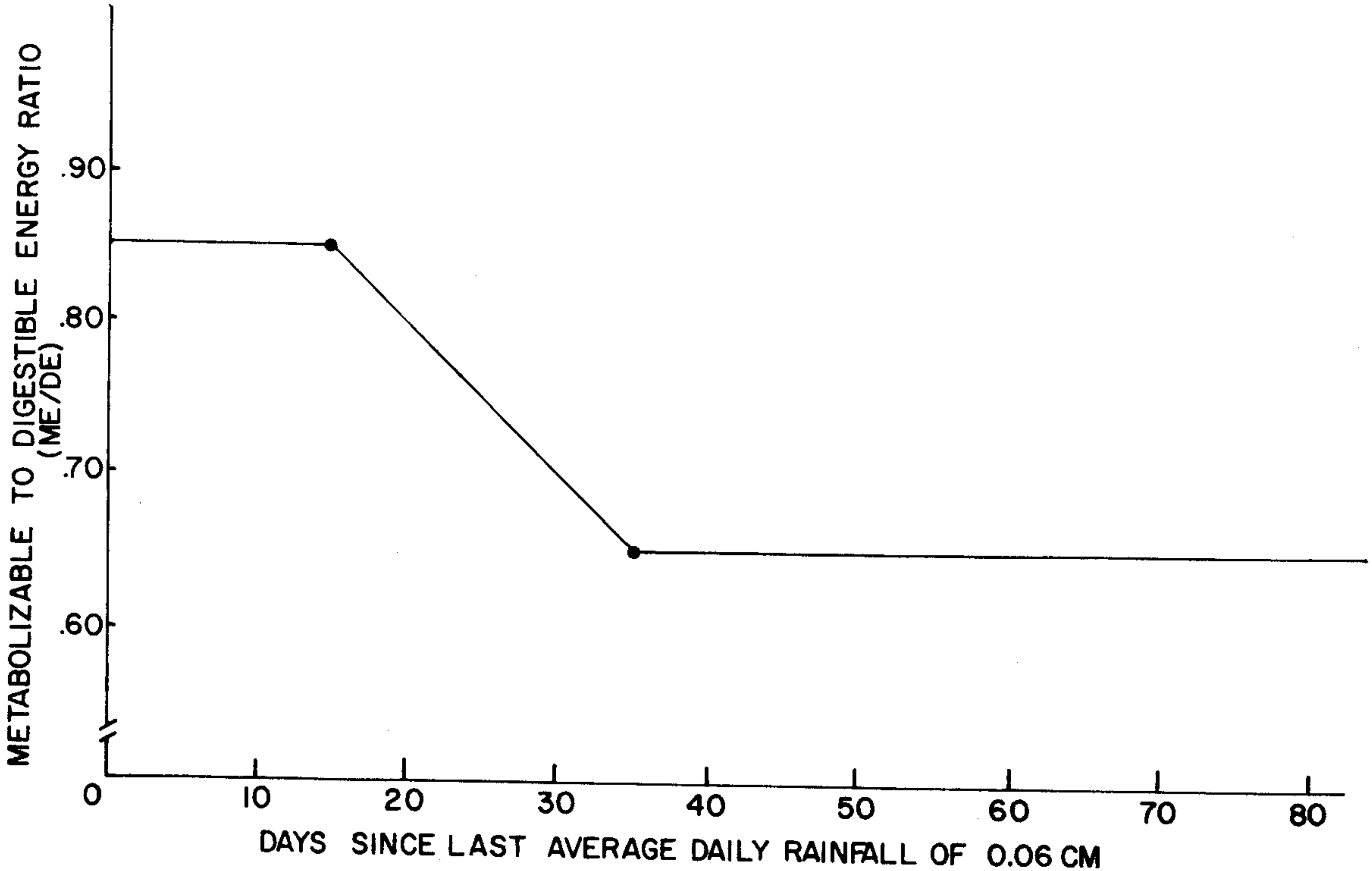


Fig. 10. The relation between the metabolizable and digestible energy content of perennial grasses as a function of time since a daily average rainfall of 0.06 cm.

parameters are based upon literature values as well as studies reported by Harris (1970).

MATHEMATICAL FORMULATION

The simple equations for the average weight of individuals and the biomass density of any consumer group have been given above. We will now present the mathematical formulations commensurate with the various biological functions mentioned in the previous sections.

Food Consumption

Essential to the weight change and energy expenditure formulations is a food consumption routine. The parameters and variables used in this formulation are:

XF(I) = food consumption rate for consumer group I under ideal conditions (g/g/day) (Parameter).

AF(I) = actual food consumption rate for consumer group I (g/g/day) (ISV).

PAFMX(I) = maximum allowable food consumption rate for consumer group I (g/g/day) (Parameter).

PS2MX(I) = maximum allowable fraction of the live body weight of an animal in consumer group I that can be made up of fat (Parameter).

ACTS2(I) = rate of flow of energy from storage 2 to activity during previous integration interval (DT) (kcal/individual/day) (ISV).

XINS2(I) = rate of flow of energy from storage 1 to storage 2 during the previous DT (kcal/individual/day) (ISV).

PMXIN(I) = maximum allowable fraction of total weight that can be transferred from storage 1 to storage 2 per day; maximum fattening rate (g/g/day) (Parameter).

BS2(I) = mass of the fat storage compartment (g/individual) (PSV).

PBS2(I) = conversion factor of energy to biomass in storage 2 (.111 g/kcal) (Parameter).

XING(I) = rate of flow of energy from storage 1 to growth during previous DT (kcal/individual/day) (ISV).

PMXG(I) = maximum allowable fraction of total weight that can be transferred from storage 1 to growth per day; maximum growth rate (g/g/day) (Parameter).

BG(I) = mass of the growth compartment (g/individual) (PSV).

PBG(I) = conversion factor of energy to biomass in growth (.250 g/kcal) (Parameter).

The actual food consumption rate [AF(I)] is determined by one of five alternative equations.

1. If ACTS2(I) > 0, then AF(I) = PAFMX(I).

   That is, if energy was drawn from fat storage to meet activity demands during the previous interval, consumption is increased to the maximum allowable rate.

2. If BS2(I) > PS2MX(I) · W(I), then

   $$AF(I) = XF(I) \left[\frac{PS2MX(I) \cdot W(I)}{PBS2(I)}\right].$$

   That is, if the mass of the fat storage compartment was greater than the maximum allowable percentage of total body weight, consumption is reduced.

3. If $XINS2(I) \cdot PBS2(I) > PMXIN(I) \cdot W(I)$, then

$$AF(I) = XF(I) \cdot \left[\frac{PMXIN(I) \cdot W(I)}{XINS2(I) \cdot PBS2(I)}\right].$$

That is, if the rate of fattening exceeded the maximum fattening rate during the previous interval, food consumption is reduced.

4. If $XING(I) \cdot PBG(I) > PMXG(I) \cdot W(I)$, then

$$AF(I) = XF(I) \cdot \left[\frac{PMXG(I) \cdot W(I)}{XING(I) \cdot PBG(I)}\right].$$

That is, if the rate of growth during the previous interval exceeded the maximum, consumption is reduced.

5. If none of the above cases pertain, then food should be consumed at the "normal" rate [$AF(I) = XF(I)$].

It will quickly be noted from the above that a number of parameter values have had to be supplied. Food consumption rates under ideal conditions have been estimated from general knowledge and literature values. For example, domestic stock is commonly maintained at a dry weight forage of 2.5% of the live body weight per day (Stoddart and Smith, 1955). Using a 30% dry matter constituency for vertebrates (Davis and Golley, 1963), the maintenance consumption rate becomes 0.0075 g/g/day (.025 · .30). Wild ungulates of the same general size are believed to consume about 3% of their body weight per day. This consumption rate is clearly a function of metabolic weight. Although there is no substantive field data regarding the consumption rates of giraffe-sized animals, the ingestion rates of elephants approximate 1% of their body weight per day (Benedict, 1936; Buss, 1961).

The food requirements of domestic carnivores are quite well-known [National Research Council (NRC), 1953], and the consumption rates of wild carnivores have also been measured (Wright, 1960; Kruuk and Turner, 1969). Lions, for instance, seem to consume about 4% of their body weight per day; and, since both predator and prey convert to dry weight equally, this rate is also obtained on a dry weight basis. Hunting dogs seem to manifest their greater activity by consuming about 5% of their body weight per day. Drawing upon the work summarized in Craighead and Craighead (1956), it is estimated that vultures' diets consist of about 10% of their body weight per day.

The maximum allowable consumptions are considerably more arbitrary (Table 5). It is estimated with some confidence that the cattle-sized herbivores could not handle more than 5% of their body weight per day. Ontko and Phillips (1958) estimated that appetite demands of dogs on much more concentrated diets than herbivores "reached the physiological limits of food intake as it approached 3.5 times the maintenance level."

The maximum allowable percentage of fat is based on carcass analysis of both domestic and wild herbivores. It is commonly known that wild herbivores generally have a much higher lean/fat ratio, and it has been stated that East African herbivores carry as little as 1 to 2% of their body weight as fat. Yet this figure is based only upon carcass analysis although it is known that wild herbivores carry substantial fat deposits mesenterically. We have, therefore, let the maximum fat storage of our apocryphal animals reach 10% of the body weight.

Maximum growth and fattening rates are probably related to metabolic weight and not body weight per se. We do know, however, that for domestic-sized stock, a growth rate of 0.5% of the body weight per day is quite rapid. We have adopted this as the maximum rate insofar as elands are known to gain about as fast as domestic stock (Posselt, 1963; Skinner, 1966).

The gram to calorie conversion factors are based upon standard ecological assessments (Slobodkin and Richman, 1961; Golley, 1961). To be conservative, we have converted these factors interchangeably by means of the following schedule.

Material	kcal/g dry wt
All forage and diets	4.0
Animal bodies (in toto)	4.0
Protein in growth compartment	4.0
Mass of fat compartment	9.0
Milk	6.0

Dietary Composition

Aside from the ingestion rate functions discussed above, consideration must also be given to the qualitative selection of food. Throughout the following discussion the subscript I will refer to the consumer while the subscript J will denote the consumed item (subscripts are denoted by parentheses). From this, it is understood that X(1,5) refers to consumer 1 and consumee number 5. Let:

XK(I,J) = fraction of the diet of consumer group I made up of consumed group J under ideal food availability conditions (Parameter).

AK(I,J) = fraction of the diet of consumer group I made up of consumed group J under the existing conditions (ISV).

THO(J) = threshold biomass density for consumed group J below which it ceases to be consumed (g/m^2) (Parameter).

TH1(J) = threshold biomass density for consumed group J below which it decreases in relative importance to its consumers (g/m^2) (Parameter).

TH2(J) = threshold biomass density for consumed group J above which it increases in relative importance to its consumers (g/m^2) (Parameter).

TACT(J) = threshold energy level for activity for consumed group J which, if not exceeding the previous DT, causes the predation on consumed group J to increase (kcal/individual/day) (ISV).

$YK_i(J)$ = a dummy food preference factor i for consumed group J; i = 1, 2.

From this the equations determining the amount of each food item to be consumed are:

1. If $TH1(J) \leq XC(J) < TH2(J)$, then $YK_1(J) = XK(I,J)$. That is, at density levels between a lower threshold TH1(J) and a higher level TH2(J), group I consumes group J with a frequency determined by its "normal" dietary vector.

2. If $THO(J) \leq XC(J) < TH1(J)$, then $YK_1(J) = XK(I,J) \cdot [\frac{XC(J) - THO(J)}{TH1(J) - THO(J)}]$. That is, if a food item J falls below the threshold TH1(J), then the consumer I begins to switch from this dietary constituent. The amount now consumed is density dependent until which time as consumed group J reaches a lower limit.

3. If $XC(J) < THO(J)$, then $YK_1(J) = 0$.

   That is, when consumed group J reaches a lower "threshold of security," it ceases to be a constituent of consumer group I's diet.

4. If $XC(J) > TH2(J)$, then $YK_1(J) = \frac{XK(I,J) \cdot XC(J)}{TH2(J)}$.

   That is, at density levels above a threshold, TH2(J), there will be a switch onto dietary item J, and the frequency with which it is consumed by consumer I will again be a linear function of density.

These four alternatives are depicted in Fig. 8 for futher clarification. Of course, the parameter values (threshold levels and dietary frequencies) may be very different for different consumer-consumee combinations, but complete flexibility for the density-dependent component of dietary constituency exists.

Mention has previously been made of feedback circuits between various energetic, dietary, and population dynamics sections of this model. The feedback between energy balance and predation comes into play here. Let:

TACT(J) = 0.8 · [activity demands during previous DT] (kcal/individual/day) (ISV).

ACT(J) = activity rate for consumed group J (kcal/day) (ISV).

If $ACT(J) \geq TACT(J)$, then $YK_2(J) = YK_1(J)$; and

if $ACT(J) < TACT(J)$, then $YK_2(J) = YK_1(J) \cdot [\frac{TACT(J)}{ACT(J)}]$.

This statement implements the energy-deficit predation switch. If the energy demand for activity during the previous interval could not be met, consumption of (i.e., predation upon) that group increases linearly.

Finally, for any given consumer I, the diet selection vector is normalized such that

$$AK(I,J) = \frac{YK_2(J)}{\sum_{J=1}^{37} YK_2(J)}$$

and

$$\sum_{J=1}^{37} AK(I,J) = 1.0.$$

From the above, the total harvest of any group J [HA(J) (g/day) (ISV)] is obtained by summing the products of consumer density [XC(I)], the actual ingestion rate of the consumer [AF(I)], and the proportion of consumed group J in the diet of consumer I [AK(I,J)] over all consumers such that:

$$HA(J) = \sum_{I=1}^{22} AF(I) \cdot AK(I,J) \cdot XC(I).$$

Energy Partitioning

Once the food intake rate and dietary composition have been determined for any particular consumer group (I), the food starts its energy dissipation process. To formulate the mechanisms, let:

GE(J) = gross energy content of consumed group J (kcal/g) (Parameter).

PDE(I,J) = ratio of digestible energy to gross energy of consumed group J in consumer group I under optimal conditions (Parameter).

PXME(I,J) = ratio of metabolizable energy to digestible energy of consumed group J in consumer group I under optimal conditions (Parameter).

TPP = time since the last day of precipitation over 0.06 cm/day (ISV).

DEMLT(J) = normalized precipitation-dependent coefficient reflecting the digestibility of the forage (Fig. 11) (ISV).

XMEMT(J) = normalized precipitation-dependent coefficient reflecting the metabolizability of the forage (Fig. 11) (ISV).

Then:

DE(I,J) = the actual ratio of digestible energy to gross energy of consumed group J by consumer group I (ISV).

= PDE(I,J) · DEMLT(J).

XME(I,J) = actual ratio of metabolizable energy to digestible energy of consumed group J in consumer group I (ISV).

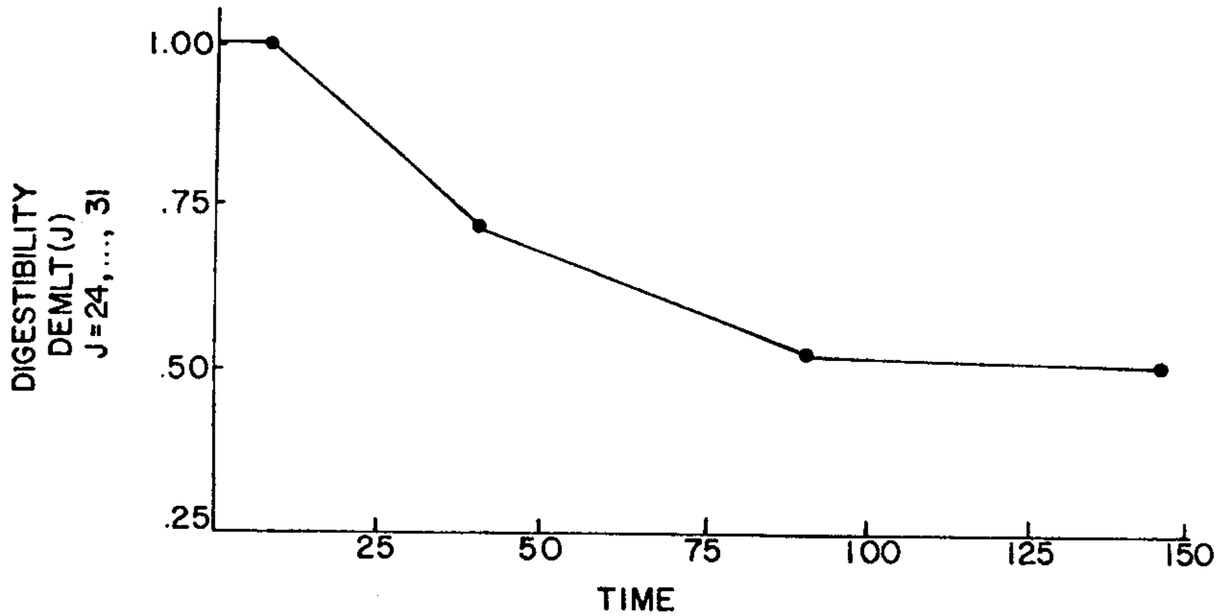
= PXME(I,J) · XMEMT(J).

Storage 1. Now, as time since the last precipitation passes, the digestibility [DEMLT(J)] and metabolizability [XMEMT(J)] coefficients both decrease (Fig. 9 through 11). Therefore, to maintain a positive energy balance, the animal would have to compensate by ingesting greater amounts of forage. Yet it is known that this does not happen beyond a point; and therefore, the animal may be forced into a negative energy balance during the long dry seasons. From all of this, then, the rate of metabolized energy in storage 1 [the liver (kcal/individual/day) (ISV)] is given by:

$$DS1(I) = W(I) \cdot AF(I) \cdot \left\{ \sum_{J=1}^{37} AK(I,J) \cdot GE(J) \cdot DE(I,J) \cdot XME(I,J) \right\}.$$

Basal metabolism. In computing the basal metabolic demand upon storage 1 (and storage 2 if need be) let:

RE(I) = basal demand of consumer group I in kcal/individual/day (ISV).



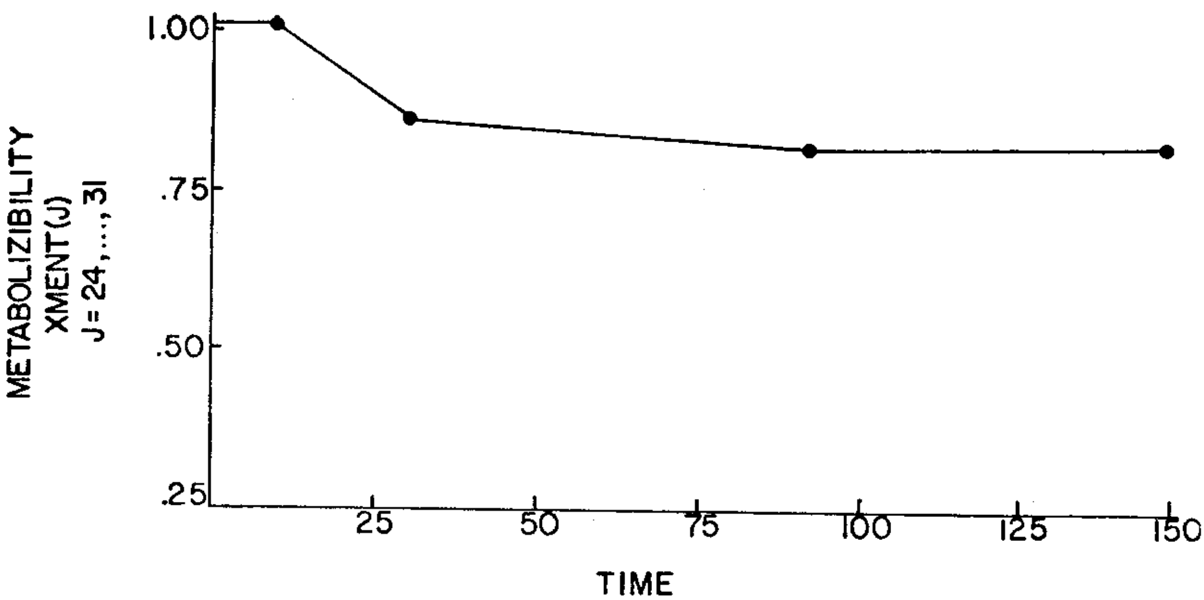


Fig. 11. Normalized curves representing the effects of precipitation on the DE/GE [DEMLT(J)] and the ME/DE [XMENT(J)] ratios.

RES2(I) = rate of utilization of energy drawn from adipose (storage 2) to supplement ingested energy (kcal/individual/day) (ISV).

S2(I) = amount of energy in adipose (kcal/individual) (PSV).

Then initially:

$$RE(I) = 1.667 \cdot PRE1(I) \cdot \left(\frac{3.33 \cdot W(I)}{1000}\right)^{PRE2(I)} .$$

where W(I) is the dry weight of the animal in grams; 3.33 converts the dry weight values to wet weight, and division by 1000 converts to kilograms. PRE2(I) (Parameter) is the exponent converting liveweight in kilograms to metabolic weight, and PRE1(I) (Parameter) is the coefficient for the basal requirement. The constant 1.667 is the reciprocal of 60% efficiency (Fig. 6) and transforms the expenditure into a requirement upon storage 1.

A stepwise procedure now ensues to determine the magnitude and derivation of the energy utilized.

1. If $RE(I) \leq DS1(I)$,

   then all energy for the basal requirement is drawn from storage 1, and DS1(I) is reset to the balance [DS1(I) => DS1(I) - RE(I)].[1/]

2. If $DS1(I) < RE(I) \leq DS1(I) + S2(I)$,

   then all available energy in storage 1 plus the deficit of RE(I) - DS1(I) drawn from storage 2 will be utilized to meet the basal demand. Thus:

   RES2(I) = RE(I) - DS1(I)

   DS1(I) => 0.

3. If $RE(I) > DS1(I) + S2(I)$,

   then all available energy in storage 1 plus the total mobilizable

[1/] A => B means that the value of the variable A is replaced by the value B.

pool of storage 2 will be expended in meeting the basal demand.

Thus:

RE(I) => DS1(I) + S2(I).

DS1(I) => 0.

RES2(I) = S2(I).

Activity. Energy demands for activity are computed in the same manner as the basal metabolic demands. In this case, let:

ACT(I) = activity rate for an individual in consumer group I (kcal/individual/day) (ISV).

ACTS2(I) = rate of utilization of energy from storage 2 in order to meet activity demands in consumer group I (kcal/individual/day) (ISV).

Then initially:

$$ACT(I) = 1.667 \cdot PACT1(I) \cdot \left(\frac{3.33 \cdot W(I)}{1000}\right)^{PACT2(I)}.$$

X2(I) = amount of available energy in storage 2 (after basal metabolism) (ISV).

= S2(I) - RES2(I).

PACT1 = multiplicative parameter for activity equation for group I.

PACT2 = power parameter for activity equation for group I.

A stepwise procedure now ensues in order to determine the derivation, composition, and actual amount of energy for activity.

1. If ACT(I) $\leq$ DS1(I), all energy for activity is taken from storage 1 and DS1(I) is reset to

   DS1(I) => DS1(I) - ACT(I).

2. If DS1(I) < ACT(I) ≤ DS1(I) + X2(I), all available energy in storage 1 plus ACT(I) - DS1(I) from storage 2 are used to meet the activity demands. Thus:

   ACTS2(I) = ACT(I) - DS1(I)

   DS1(I) => 0.

3. If ACT(I) > DS1(I) + X2(I), all of the available energy in both storage 1 and storage 2 is used in order to partially satisfy the activity demand. Thus:

   ACT(I) => DS1(I) + X2(I)

   DS1(I) => 0

   ACTS2(I) = X2(I).

It will be quickly noted that this formulation leads to an equal expenditure to basal under normal conditions. This is derived from the argument that maintenance under normal conditions equals two times the fasting catabolic requirement which has been described in a previous section.

Gestation. Let:

GEST(I) = energy used for gestation for an individual in consumer group I (kcal/individual/day) (ISV).

= GMULT(I) · .10 · [RE(I) + ACT(I)].

where

GMULT(I) = fraction of consumer group I which is pregnant at time TDMOD (ISV).

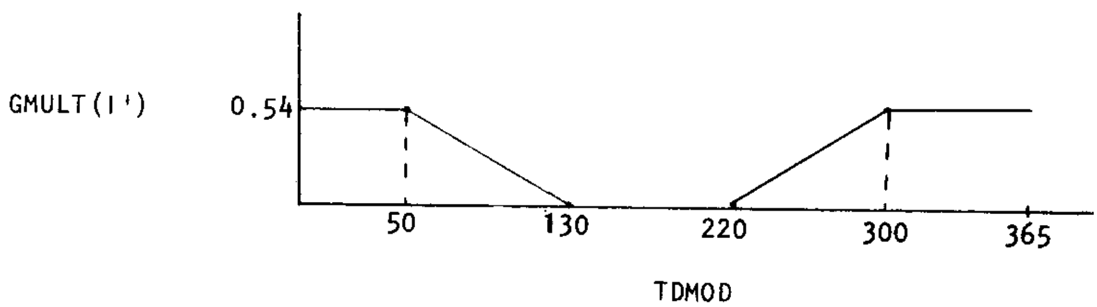
Thus, an animal which is pregnant requires an additional 10% of the energy it uses for basal metabolism and activity in order to meet its gestation demands.

Suppose that a consumer group I has a pregnancy period of 443 days (1.21 year) and produces 0.372 offspring/individual/year (corrected for sex ratio). Then:

$$\text{GMULT}(I) = 1.21 \cdot 0.372$$
$$= 0.450,\ 0 \leq \text{TDMOD} \leq 365.$$

Thus, at any given time of the year, 45% of the population is demanding energy for gestation.

Suppose that another consumer group (I') has a pregnancy period of 195 days with 99% of the births occurring between days 50 and 130 and that the population produces 0.54 offspring/individual/year; then 99% of the gestation periods occur between day 220 of the previous year and day 130 of the given year. Thus, GMULT(I') has the following form as a function of time (TDMOD).



A complete listing of the gestation parameters for each of the 22 consumer groups is given in Table 7.

Once GEST(I) has been computed, the amount of available energy in storage 2 must be updated. Thus

$$X2(I) \Rightarrow X2(I) - \text{ACTS2}(I).$$

In addition:

$$\text{GEST}(I) \Rightarrow 1.053 \cdot \text{GEST}(I).$$

Table 7. Fecundity, gestation, and lactation parameters for each age group of consumers. Fecundity values are given as the number of offspring per individual per year. The gestation period is given by length in days; the birth period as the calendar days between which 99% of the parturition occurs; and the lactation period as the mean length of the lactation period.

Consumer Group	Fecundity	Gestation Period	Birth Period	Lactation Period
1	0	0	0	0
2	.372	443	50-130	180
3	.186	443	50-130	180
4	0	0	0	0
5	.540	195	50-130	60
6	.400	0	50-130	60
7	0	0	0	0
8	.413	350	20-140	80
9	.220	350	20-140	80
10	0	0	0	0
11	.560	280	0-365	70
12	.350	280	0-365	70
13	0	0	0	0
14	.120	650	0-365	365
15	.100	650	0-365	365
16	0	0	0	0
17	.585	195	10-150	65
18	.350	195	10-150	65
19	1.30	64	20-140	120
20	1.65	60	20-140	120
21	2.20	60	20-140	120
22	1.00	30	20-140	30

This reflects the demand for energy for gestation on storage 1 and storage 2 due to a 95% efficiency of transfer of energy from either storage 1 or storage 2 to gestation.

Let:

GSTS2(I) = rate of utilization of energy from storage 2 in order to meet gestation demands in consumer group I (kcal/individual/day) (ISV).

A stepwise procedure now ensues in order to determine the composition and actual amount of energy utilized for gestation.

1. If GEST(I) ≤ DS1(I), all energy for gestation is taken from storage 1 and DS1(I) is reset to

   DS1(I) => DS1(I) - GEST(I).

2. If DS1(I) < GEST(I) ≤ DS1(I) + X2(I), all available energy in storage 1 plus GEST(I) - DS1(I) from storage 2 are used to meet the gestation demand. Thus:

   GSTS2(I) = GEST(I) - DS1(I)

   DS1(I) => 0.

3. If GEST(I) > DS1(I) + X2(I), all of the available energy in both storage 1 and storage 2 is used in order to partially satisfy the gestation demand. Thus

   GEST(I) => DS1(I) + X2(I)

   DS1(I) => 0

   GSTS2(I) = X2(I).

Lactation. Let:

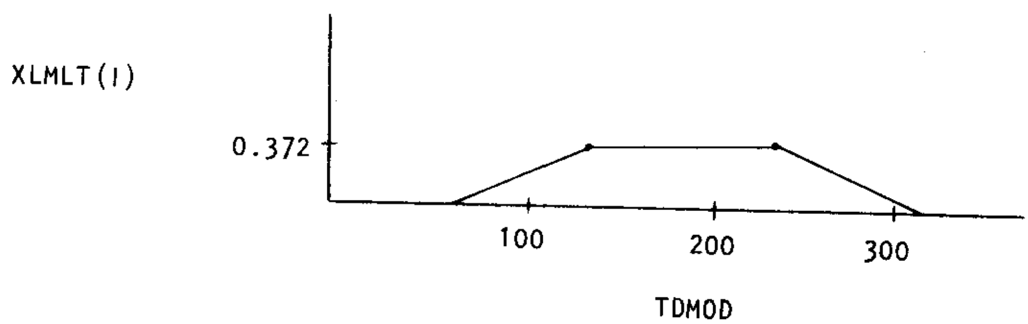
PLACT(I) = maximum milk production rate for consumer group I (g/g female/day) (Parameter).

XLACT(I) = milk production rate for consumer group I (g/g female/day) (ISV)
= XLMLT(I) · PLACT(I) (ISV).

where

XLMLT(I) = fraction of consumer group I lactating at time TDMOD (ISV).

Suppose that a consumer group (I) has a lactation period of 180 days, that 99% of its births occur on the interval (50, 130), and that it produces 0.372 offspring/individual/year; then 99% of the lactation occurs on the time interval (50, 130) and XLMLT(I) has the following form as a function of TDMOD.



The lactation parameters for each of the 22 consumer groups are given along with the gestation parameters of Table 7.

Once XLACT(I) has been computed, we must

1. Update the amount of available energy in storage 2

   X2(I) => X2(I) - GSTS2(I).

2. Convert lactation demands to g/individual/day and then to energy demands (6 kcal/g) on storage 1 and storage 2 (efficiency of transfer of energy from storage 1 and storage 2 to milk = 0.6). Thus:

   ELACT(I) = energy needed for lactation for an individual in consumer group I (kcal/individual/day) (ISV)
   = (6.0) · (1.667) · XLACT(I) · W(I).

A stepwise procedure now ensues in order to determine the derivation and actual amount of energy utilized for lactation.

1. If ELACT(I) $\leq$ DS1(I), all energy for lactation is taken from storage 1, and DS1 is reset to

   DS1(I) => DS1(I) - ELACT(I).

2. If DS1(I) < ELACT(I) $\leq$ DS1(I) + X2(I), all available energy in storage 1 plus ELACT(I) - DS1(I) from storage 2 are used to meet the lactation demands. Thus

   XLTS2(I) = ELACT(I) - DS1(I)

   DS1(I) => 0.

where

XLTS2(I) = rate of utilization of energy from storage 2 in order to meet lactation demands in consumer group I (kcal/individual/day) (ISV).

3. If ELACT(I) > DS1(I) + X2(I), all of the available energy in both storage 1 and storage 2 is used in order to partially satisfy the lactation demand. Thus:

   ELACT(I) => DS1(I) + X2(I)

   DS1(I) => 0

   XLTS2(I) = X2(I).

Finally the energy used for lactation (kcal/individual/day) must be converted into milk production (g/g female/day).

$$\text{XLACT(I)} \Rightarrow 0.6 \cdot \left[\frac{\text{ELACT(I)}}{8}\right].$$

Again, note that the efficiency of transfer of energy (or biomass) from storage 1 (or storage 2) to lactation is 0.60.

Growth and storage 2 (fat). Once the energy requirements for basal metabolism, activity, gestation, and lactation have been satisfied, the balance of the energy in storage 1 is budgeted to growth and storage 2 in the following way.

1. If the animal is a juvenile herbivore (I = 1, 4, 7, 10, 13, 16), energy is partitioned to the growth component before the storage 2 compartment. Let:

   PMXG(I) = maximum allowable rate of flow of biomass into growth for consumer group I (g/g/day) (Parameter).

   Then

   XMXG(I) = maximum allowable rate of flow of energy into growth (kcal/g/day) (ISV).

   $$= \frac{PMXG(I) \cdot W(I)}{PBG(I)} .$$

   where:

   PBG(I) = conversion factor of biomass to energy in growth (g/kcal) (Parameter).

   XING(I) = actual rate of flow of energy from storage 1 to growth (kcal/individual/day) (ISV).

   $= \min \{0.4 \cdot DS1(I), XMXG(I)\}.$

   Then:

   DS1(I) => DS1(I) - XING(I)/0.4.

   Note the following efficiency of transfer of energy from storage 1 to growth of 0.4.

   The balance of energy in storage 1 is now transferred (with efficiency of transfer of 0.35) to storage 2.

XINS2(1) = actual rate of flow of energy from storage 1 to storage 2 (kcal/individual/day) (ISV).

$$= 0.35 \cdot DS1(I).$$

2. If the animal is a breeder or senile herbivore (I = 2, 3, 5, 6, 8, 9, 11, 12, 14, 15, 17, 18) or a predator-carion eater (I = 19, ..., 22), energy is partitioned to the storage 2 compartment before the growth compartment.

Let:

PMXIN(I) = maximum rate of flow of biomass into storage 2 for consumer group I (g/g/day) (Parameter).

PBS2(I) = conversion factor of biomass to energy in storage 2 (g/kcal) (Parameter).

Then:

XMXIN(I) = maximum allowable rate of flow of energy into storage 2 (kcal/day) (Parameter).

$$= \frac{PMXIN(I) \cdot W(I)}{PBS2(I)}.$$

XINS2(I) = actual rate of flow of energy from storage 1 to storage 2 for consumer group I (kcal/individual/day) (ISV).

$$= \min \{0.35 \cdot DS1(I), XMXIN(I)\}.$$

Then:

$$DS1(I) \Rightarrow DS1(I) - \frac{XINS2(I)}{0.35}.$$

The balance of the energy in storage 1 is now transferred (with efficiency of transfer of 0.40) into growth.

$$XING(I) = 0.40 \cdot DS1(I).$$

Change in weight equation. Now that the energy budget for an animal in consumer group I has been completely enumerated, the terms of the differential equation for change in average weight (see section on average weight of an individual) can be computed.

$$DBG(I) = PBG(I) \cdot XING(I)$$

$$DBS2(I) = PBS2(I) \cdot [XINS2(I) - RES2(I) - ACTS2(I) - GSTS2(I) - XLTS2(I)].$$

Population Numbers

The differential equation for the population number in consumer group I, at a particular time TDMOD, is written as:

$$\frac{d[N(I)]}{dt} = DN(I)$$
$$= B(I) + G(I) - XD(I) - \frac{2 \cdot HA(I)}{W(I)} .$$

where

B(I) = recruitment rate into consumer group I (individuals/day) (ISV).

G(I) = graduation rate from consumer I to consumer group I+1 (individuals/day) (ISV).

XD(I) = instantaneous natural mortality rate in consumer group I (1/day) (ISV).

HA(I) = havest rate of consumer group I (g/day) (ISV).

Note that in order to compute the loss to consumer group I due to predation, the harvest rate (i.e., that amount of biomass of consumer group I actually consumed by predators) is multiplied by 2. (It is taken that predators consume 1/2 of the biomass that they kill.) The harvest rate is then converted from biomass to numbers by dividing by the average weight W(I).

Recruitment. Although population recruitment rates can be derived empirically with no breakdown by sex or age class, greater flexibility can be gained by knowing more specific parameters. That is, if the annual number of young per mature female in each age class and the sex ratio of the population are known, more accurate and realistic changes can be simulated. For the purposes of this model we have used age-specific fecundity and sex ratio information (Table 8) along with time-dependent probability distributions for the parturition (and consequently gestation and lactation) period.

From these parameters the population's instantaneous birth rates are derivable. For example, suppose we wish to compute the recruitment (birth) rate for juvenile giraffe (consumer group 1). Giraffes produce .60 offspring/female breeder/year and .30 offspring/female senile/year (Table 8). Transferring these to annual instantaneous rates:

$$e^{0.428} = 1.6$$

=> XB(2) = instantaneous yearly birth rate from consumer group 2 females (1/year) (ISV).

= 0.428.

$$e^{0.248} = 1.3$$

=> XB(3) = instantaneous yearly birth rate from consumer group 3 females (1/year) (ISV).

= 0.248.

The above instantaneous rates are now transformed into daily rates in the following manner:

Table 8. Age-specific population parameters for the consumer groups considered herein.

Consumer Group	Offspring/ Female/Year	Proportion of Females in Population	99% Birth Distribution (days of year)	99% Graduation Distribution (days of year)	Proportionate Graduation per Year
Giraffe			(50,130)		
Immature	.0	.0		(30,150)	.500
Mature	.60	.62		(10,170)	.125
Senile	.30	.62			
Gazelle			(50,130)		
Immature	.0	.0		(30,150)	.990
Mature	.90	.66		(10,170)	.167
Senile	.40	.66			
Zebra			(20,140)		
Immature	.0	.0		(355,170)	.400
Mature	.75	.45		(325,200)	.080
Senile	.40	.45			
Hartebeest			(0,365)		
Immature	.0	.0		(0,365)	.990
Mature	.80	.70		(0,365)	.167
Senile	.50	.70			
Elephant			(0,365)		
Immature	.0	.0		(0,365)	.091
Mature	.20	.60		(0,365)	.023
Senile	.10	.60			
Impala			(10,150)		
Immature	.0	.0		(340,185)	.990
Mature	.90	.65		(305,220)	.143
Senile	.50	.70			
Lion	2.0	.65	(20,140)		
Hyaena	3.0	.55	(20,140)		
Hunting Dog	4.0	.55	(20,140)		
Vulture	2.0	.50	(20,140)		

$$B(1) = [0.62 \cdot XN(2) \cdot XB(2) + 0.62 \cdot XN(3) \cdot XB(3)] \cdot \frac{1}{\sigma\sqrt{2\pi}} \exp\left[\frac{-(TDMOD - 90)^2}{2\sigma^2}\right]$$

where

$$\sigma = \frac{40}{2.576} = 15.528$$

Note that:

1. The sex ratio (fraction female) in both the breeder and senile populations is 0.62. These must be multiplied by the population size in order, in turn, to multiply that by the instantaneous birth rate per female.
2. Births are assumed to be normally distributed over the 99% birth period. Thus, the distribution N $(90, 15.528^2)$ has mean 90 and 99% of its probability lying on the interval (50, 130). Multiplying the instantaneous yearly rates by the N $(90, 15.528^2)$ probability density function yields the desired daily recruitment (birth) rate into consumer group 1.

These recruitment (birth) rates can now be modified if the biomass in the storage 2 compartment falls below a predefined fraction of the total biomass. By letting:

PS2(I) = biomass threshold in storage 2 below which fecundity of consumer group I decreases (g/g/individual) (Parameter).

and

PB(I) = fecundity rate for consumer group I under ideal conditions (individuals/day) (Parameter).

Then:

$$XB(I) \begin{cases} = PB(I) & \text{if } BS2(I) \geq PS2(I) \cdot W(I) \\ = PB(I) \cdot \left[\frac{BS2(I)}{PS2(I) \cdot W(I)}\right] & \text{if } BS2(I) < PS2(I) \cdot W(I). \end{cases}$$

Finally, for all breeder and senile herbivore consumer groups (I = 2, 3, 5, 6, 8, 9, 11, 12, 14, 15, 17, 18)

$$B(I) = -G(I-1).$$

Graduation. Graduation rates are computed in a fashion similar to birth rates. The following parameters are used to compute the graduation rates for the juvenile and breeder herbivore groups (note that G(I) = 0 for all senile and predator-scavenger consumer groups): (i) 99% graduation period (that period of time during the year within which 99% of the graduation occurs) and (ii) the fraction of the population graduating per year (reciprocal of mean amount of time spent in that group) (Table 8).

Again, using giraffe we will exemplify the computation. Giraffes spend, on the average, two years as juveniles. Thus, 50% of the population is expected to graduate to the breeder giraffe population per year. Transforming this to an instantaneous yearly rate:

$$e^{-0.693} = 0.50$$

=> XG(1) = instantaneous yearly graduation rate from consumer group 1 (1/year) (ISV).

= -0.693.

The above instantaneous yearly rate is now transformed into a daily rate in the following manner.

$$G(1) = -0.693 \cdot XN(1) \cdot \frac{1}{\sigma\sqrt{2\pi}} \exp\left[\frac{-(TDMOD - 90)^2}{2\sigma^2}\right]$$

where

$$\sigma = \frac{60}{2.576} = 23.292$$

Note that graduation is assumed to be normally distributed over the 99% graduation period. Thus, the distribution N $(90, 23.292^2)$ has mean 90 and 99% of its probability lying on the interval (30, 150). Multiplying the instantaneous yearly rate by the N $(90, 23.292^2)$ probability density function and then in turn by the population size, gives the desired daily graduation rate in numbers of individuals.

Note again that:

$$G(I) = 0; \; I = 3, 6, 9, 12, 15, 18, \ldots, 22.$$

Natural mortality. Let:

D(I) = instantaneous daily natural mortality rate under normal conditions for consumer group I (1/day) (Parameter).

ACTD(I) = activity demands for consumer group I during last DT (kcal/individual/day) (ISV).

Then:

$$XD(I) \begin{cases} = D(I) & \text{if } ACT(I) \geq ACTD(I) \\ = D(I) \cdot \left[\frac{ACTD(I)}{ACT(I)}\right] & \text{if } ACT(I) < ACTD(I) \end{cases}$$

Thus, natural mortality is increased during a given DT if the activity demands of the animal were not met during the previous DT.

Animal dead. The differential equation for the animal dead compartment, at a particular time TDMOD, is written as:

$$DXC(23) = \sum_{I=1}^{22} [HA(I) + XD(I) \cdot XC(I)] - HA(23).$$

Thus, along with all biomass which dies of natural causes, it is taken that predators consume only about 50% of their kills and that the balance of each kill is transferred to animal dead.

Milk production. The differential equations for the milk compartments for the herbivore consumer groups at a particular time TDMOD are written as:

$$DXC(32) = XLACT(2) \cdot XC(2) + XLACT(3) \cdot XC(3)$$

$$DXC(33) = XLACT(3) \cdot XC(5) + XLACT(6) \cdot XC(6)$$

$$\vdots$$

$$DXC(37) = XLACT(17) \cdot XC(17) + XLACT(18) \cdot XC(18)$$

A listing of all variables and parameters used in AFCØNS is given in Appendix I. The computer code is given in Appendix II.

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APPENDIX I

VARIABLES AND PARAMETERS

A. A list of variables, their code designation, and units.

Code	Variable	Unit
	Principal System Variables and Driving Variables	
ZPR	Daily precipitation	cm/day
XC(I); I=1,...,37	Biomass density of group I	g/m^2
XN(I); I=1,...,22	Population size of group I	$no./m^2$
W(I); I=1,...,22	Average dry weight of an individual in group I	g/individual
S2(I); I=1,...,22	Energy in storage 2 in group I	kcal/individual
BS2(I); I=1,...,22	Biomass in storage 2 in group I	g/individual
BG(I); I=1,...,22	Biomass in growth in group I	g/individual
	Intermediate System Variables	
AF(I); I=1,...,22	Actual food intake rate for group I	g/g/day
AK(I,J); J=1,...,37, I=1,...,22	Amount of diet of consumer group I made up of consumed group J	
YK_i(J); J=1,...,37	Dummy food preference variable, i=1,2	
SY(J); J=1,...,37	Dummy food preference variable	
HC(I,J); J=1,...,37, I=1,...,22	Rate of consumption of consumed group J by consumer group I	g/day
HA(J); J=1,...,37	Total harvest rate of consumed group J	g/day
HD(I); I=1,...,22	Dummy harvest variable	
XA(J); J=1,...,37	Dummy food preference variable	
D(J); J=1,...,37	Dummy digestible energy variable	
XE(J); J=1,...,37	Dummy assimilation variable	
EFF(I); I=1,...,22	Metabolizable efficiency of food consumed by an individual in group I	kcal/g

Code	Variable	Unit
DS1(I); I=1,...,22	Rate of accumulation of metabolizable energy in storage 1 (liver) compartment in consumer group I	kcal/individual/day
RE(I); I=1,...,22	Respiration rate for consumer group I	kcal/individual/day
RES2(I); I=1,...,22	Rate of utilization of energy from storage 2 in order to meet respiration needs in consumer group I	kcal/individual/day
ACT(I); I=1,...,22	Activity rate for consumer group I	kcal/individual/day
ACTS2(I); I=1,...,22	Rate of utilization of energy from storage 2 in order to meet activity needs in consumer group I	kcal/individual/day
XING(I); I=1,...,22	Rate of flow of energy into growth compartment of consumer group I	kcal/individual/day
XINS2(I); I=1,...,22	Rate of flow of energy into storage 2 compartment of consumer group I	kcal/individual/day
G(I); I=1,...,22	Graduation rate from consumer group I to consumer group I+1	individuals/day
B(I); I=1,...,22	Recruitment rate into consumer group I	individuals/day
XB(I); I=1,...,22	Fecundity rate for consumer group I	individuals/day
TACT(J); J=1,...,37	Threshold energy level for activity below which consumption of consumed group J increases	kcal/individual/day
XMXG(I); I=1,...,22	Maximum rate of flow into growth compartment for group I	kcal/g/day
TPP	Time since last precipitation over 0.06 cm/day	cm/day
HH(J); J=1,...,37	Harvest (total) of consumed group J over an entire print interval	g/time
GEST(I); I=1,...,22	Energy used for gestation for consumer group I	kcal/individual/day
XLACT(I); I=1,...,18	Milk production rate for consumer group I	g/g female/day

Code	Variable	Unit
DE(I,J); J=1,...,37, I=1,...,22	Actual ratio of digestible energy to gross energy for consumed group J being consumed by consumer group I	
XME(I,J); J=1,...,37 I=1,...,22	Ratio of metabolizable energy to digestible energy for consumed group J being consumed by consumer group I	
GMULT(I); I=1,...,22	Multiplicative value of consumer group I pregnant at time TDMOD needed to get gestation rates	
XLMLT(I); I=1,...,18	Multiplicative value of consumer group I lactating at time TDMOD needed to get lactation rates	
ELACT(I); I=1,...,18	Energy used for lactation	kcal/individual/day
XLTS2(I); I=1,...,18	Energy from storage 2 necessary to meet lactation demands	kcal/individual/day
GSTS2(I); I=1,...,22	Energy from storage 2 necessary to meet gestation demands	kcal/individual/day
DEMLT(J); J=1,...,37	Multiplicative value which reduces DE/GE ratio as function of precipitation	
XMEMT(J); J=1,...,37	Multiplicative value which reduces ME/DE ratio as function of precipitation	
XS2(I); I=1,...,22	Biomass threshold in storage 2 below which fecundity is reduced	g/individual
A(I); I=1,...,22	Dummy activity variable used for computation of food intake rates	
DDS1(I); I=1,...,22	Amount of energy ingested to storage 1 by animal I	kcal/day
DEMLX	Dummy digestible energy multiplier	
XMEMX	Dummy metabolizable energy multiplier	
XD(I); I=1,...,22	Actual instantaneous daily natural mortality rate	1/day
X2(I); I=1,...,22	Dummy variable to keep track of amount of energy remaining in storage 2 as energy budget solved	

APPENDIX I (continued)

B. A list of parameters, their code designation, and units.

Code	Parameter	Units
D(I); I=1,...,22	Instantaneous daily natural mortality rate for consumer group I	1/day
XF(I); I=1,...,22	Ideal food consumption rate for consumer group I	g/g/day
XK(I,J); J=1,...,37, I=1,...,22	Amount of diet of consumer group I made up of consumed group J under ideal food availability	
TH0(J); J=1,...,37	Threshold biomass density below which consumed group J ceases to be consumed	g/m^2
TH1(J); J=1,...,37	Threshold biomass density below which consumed group J decreases in importance to its consumers	g/m^2
TH2(J); J=1,...,37	Threshold biomass density above which consumption of consumed group J increases due to its overabundance	g/m^2
GE(J); J=1,...,37	Gross energy of consumed group J	kcal/g
PDE(I,J); J=1,...,37, I=1,...,22	Ratio of digestible energy to gross energy for consumed group J being consumed by consumer group I under ideal moisture conditions	
PXME(I,J); J=1,...,37, I=1,...,22	Ratio of metabolizable energy to digestible energy for consumed group J being consumed by consumer group I under ideal moisture conditions	
PRE1(I); I=1,...,22	Multiplicative parameter for respiration equation for consumer group I	
PRE2(I); I=1,...,22	Power parameter for respiration equation for consumer group I	
PS2(I); I=1,...,22	Biomass threshold in storage 2 below which fecundity for consumer group I decreases	g/g/individual
PB(I); I=1,...,22	Fecundity rate for consumer group I under ideal conditions	individuals/day

Code	Parameter	Units
PMXG(I); I=1,...,22	Maximum rate of flow of energy to growth compartment for consumer group I	g/g/day
PBG(I); I=1,...,22	Conversion factor of biomass to energy for material flowing from storage I to growth	g/kcal
PACT1(I); I=1,...,22	Multiplicative parameter for activity equation for group I	
PACT2(I); I=1,...,22	Power parameter for activity equation for group I	
PAFMX(I); I=1,...,22	Maximum allowable food intake rate for group I	g/g/day
PLACT(I); I=1,...,18	Maximum milk production rate for group I	g/g female/day
PBS2(I); I=1,...,22	Conversion factor of biomass to energy for material in storage 2	g/kcal
PS2MX(I); I=1,...,22	Maximum fraction of total weight of animal of group I that can be made up by storage 2	
PMXIN(I); I=1,...,22	Maximum fraction of total weight of animal of group I that can be taken into storage 2 per day	g/g/day
XMXIN(I); I=1,...,22	Conversion of weight change to energy weight change	kcal/day

APPENDIX II

COMPUTER PRINTOUT FOR AFCØNS

```
      PROGRAM AFOE(TAPE7,INPUT,OUTPUT,TAPE5=INPUT,TAPE6)
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),FLACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     READ IN INITIAL PSV
      READ(5,1)XC(23),(XC(I),I=32,37),(XN(I),I=1,22),(W(I),I=1,22),
     1(BS2(I),I=1,22)  ,(BG(I),I=1,22)
1     FORMAT(7G10.0,4(/8G10.0/8G10.0/6G10.0)     )
C     INITIAL CONDITIONS
      XC(30)=0.
      TPP=0.
C     READ IN PARAMETER VALUES.
      READ (5,2)(D(I),I=1,22)
    2 FORMAT(8G10.0/8G10.0/6G10.0)
      READ(5,2)(XF(I),I=1,22)
      READ(5,3)((XK(I,J),J=1,37),I=1,22)
    3 FORMAT(37F2.2)
      READ(5,4)(TH0(J),J=1,37)
      READ(5,4)(TH1(J),J=1,37)
      READ(5,4)(TH2(J),J=1,37)
    4 FORMAT(8G10.0/8G10.0/8G10.0/8G10.0/5G10.0)
      READ(5,4)(GE(J), J=1,37)
      READ(5,3)((PDE(I,J),J=1,37),I=1,22)
      READ(5,3)((PXME(I,J),J=1,37),I=1,22)
      READ(5,6)(PRE1(I),I=1,22)
      READ(5,6)(PRE2(I),I=1,22)
      READ(5,6)(PS2(I),I=1,22)
      READ(5,6)(PB(I),I=1,22)
    6 FORMAT(8G10.0/8G10.0/6G10.0)
      READ(5,6)  (PMXG(I),I=1,22)
      READ(5,6)  (PBG(I),I=1,22)
      READ(5,6)  (PACT1(I),I=1,22)
      READ(5,6)  (PACT2(I),I=1,22)
      READ(5,6)  (PAFMX(I),I=1,22)
      READ(5,7)(PLACT(I),I=1,18)
      READ(5,6)(PBS2(I),I=1,22)
      READ(5,6)(PS2MX(I),I=1,22)
      READ(5,6)(PMXIN(I),I=1,22)
```

```
7     FORMAT(8G10.0/8G10.0/2G10.0)
      DO 402 I=1,22
      G(I)=0.
      ACT(I)=1.667*PACT1(I)*(W(I)*.00333)**PACT2(I)
      ACTS2(I)=0.
      XINS2(I)=0.
      S2(I)=BS2(I)/PBS2(I)
  402 XC(I)=XN(I)*W(I)
      DO403J=1,37
      DEMLT(J)=1.
403   XMEMT(J)=1.
      DXC(23)=0.
      WRITE(6,50)
   50 FORMAT(1H1,26H CONSTANT PARAMETER VALUES)
      WRITE(6,51)(D(I),I=1,22)
   51 FORMAT(1H0//,10H D         ,11G10.4/11G10.4)
      WRITE(6,52)(XF(I),I=1,22)
   52 FORMAT(1H0//,10H XF        ,11G10.4/11G10.4)
      WRITE(6,53)
   53 FORMAT(1H//,3H XK)
      WRITE(6,54)((XK(I,J),J=1,37),I=1,22)
   54 FORMAT(10X,20F5.3/15X,17F5.3)
      WRITE(6,55)(TH0(J),J=1,37)
   55 FORMAT(1H0//,10H TH0       ,12G10.4/13G10.4/12G10.4)
      WRITE(6,56)(TH1(J),J=1,37)
   56 FORMAT(1H0//,10H TH1       ,12G10.4/13G10.4/12G10.4)
      WRITE(6,57) (TH2(J),J=1,37)
   57 FORMAT(1H0//,10H TH2       ,12G10.4/13G10.4/12G10.4)
      WRITE(6,58)(GE(J),J=1,37)
   58 FORMAT(1H0//,10H GE        ,12G10.4/13G10.4/12G10.4)
      WRITE(6,59)
   59 FORMAT(//,4H PDE)
      WRITE(6,60)((PDE(I,J),J=1,37),I=1,22)
   60 FORMAT(10X,20F5.3/15X,17F5.3)
      WRITE(6,90)
   90 FORMAT(//,5H PXME)
      WRITE(6,60)((PXME(I,J),J=1,37),I=1,22)
      WRITE(6,61)(PRE1(I),I=1,22)
   61 FORMAT(1H0//,10H PRE1      ,11G10.4/11G10.4)
      WRITE(6,62)(PRE2(I),I=1,22)
   62 FORMAT(1H0//,10H PRE2      ,11G10.4/11G10.4)
      WRITE(6,63)(PS2(I),I=1,22)
   63 FORMAT(1H0//,10H PS2       ,11G10.4/11G10.4)
      WRITE(6,64)(PB(I),I=1,22)
   64 FORMAT(1H0//,10H PB        ,11G10.4/11G10.4)
      WRITE(6,65)(PMXG(I),I=1,22)
   65 FORMAT(1H0//,10H PXMG      ,11G10.4/11G10.4)
      WRITE(6,66)(PBG(I),I=1,22)
   66 FORMAT(1H0//,10H PBG       ,11G10.4/11G10.4)
      WRITE(6,67)(PACT1(I),I=1,22)
   67 FORMAT(1H0//,10H PACT1     ,11G10.4/11G10.4)
      WRITE(6,68)(PACT2(I),I=1,22)
68    FORMAT(1H0//,10H PACT2     ,11G10.4/11G10.4)
      WRITE(6,69)(PAFMX(I),I=1,22)
```

```
   69 FORMAT(1H0//,10H PAFMX     ,11G10.4/11G10.4)
      WRITE(6,70)(PLACT(I),I=1,18)
70    FORMAT(1H0//,10H PLACT     ,11G10.4/7G10.4)
      WRITE(6,71)(PBS2(I),I=1,22)
71    FORMAT(1H0//,10H PBS2      ,11G10.4/11G10.4)
      WRITE(6,72)(PS2MX(I),I=1,22)
72    FORMAT(1H0//,10H PS2MX     ,11G10.4/11G10.4)
      WRITE(6,73)(PMXIN(I),I=1,22)
73    FORMAT(1H0//,10H PMXIN     ,11G10.4/11G10.4)
      READ(5,200)DT,TSTART,TEND,ND
C     ND=NO. OF DTS BETWEEN PRINTOUTS.
  200 FORMAT(3F10.0,I10)
      TDMOD=TSTART
      NT=TEND-TSTART
      XNT=NT
      XND=ND
      XNT=XNT/(XND*DT)
      NT=XNT
      CALL PROD
      WRITE(6,300)TDMOD
      WRITE(6,301)(XC(I),I=1,37)
      WRITE(6,302)(XN(I),I=1,22)
      WRITE(6,303)(W(I),I=1,22)
      WRITE(6,304)(S2(I),I=1,22)
      WRITE(6,305)(BS2(I),I=1,22)
      WRITE(6,306)(BG(I),I=1,22)
      DO 201J=1,NT
      DO 75 K=1,37
75    HH(K)=0.
      DO 202 I=1,ND
      TDMOD=TDMOD+DT
      CALL CONS(DT)
      DO 76 K=1,37
   76 HH(K)=HH(K)+HA(K)*DT
      DO 203 K=1,22
      XN(K)=XN(K)+DT*DXN(K)
      W(K)=W(K)+DT*DW(K)
      XC(K)=XN(K)*W(K)
      S2(K)=S2(K)+DT*DS2(K)
      BS2(K)=BS2(K)+DT*DBS2(K)
  203 BG(K)=BG(K)+DT*DBG(K)
      XC(23)=XC(23)+DT*DXC(23)
  202 CONTINUE
      WRITE(7) TDMOD,XC,XN,W,S2,BS2,BG
      WRITE(6,300)TDMOD
      WRITE(6,301)(XC(K),K=1,37)
      WRITE(6,302)(XN(I),I=1,22)
      WRITE(6,303)(W(I),I=1,22)
      WRITE(6,304)(S2(I),I=1,22)
      WRITE(6,305)(BS2(I),I=1,22)
      WRITE(6,306)(BG(I),I=1,22)
      WRITE(6,307)(HH(K),K=1,37)
      WRITE(6,308)(RE(I),I=1,22)
      WRITE(6,309)(ACT(I),I=1,22)
```

```
      WRITE(6,310)(GEST(I),I=1,22)
      WRITE(6,311)(ELACT(I),I=1,18)
      WRITE(6,312)(XING(I),I=1,22)
      WRITE(6,313)(XINS2(I),I=1,22)
      WRITE(6,314)(RES2(I),I=1,22)
      WRITE(6,315)(ACTS2(I),I=1,22)
      WRITE(6,316)(XLTS2(I),I=1,18)
      WRITE(6,317)(GSTS2(I),I=1,22)
      WRITE(6,318)(AF(I),I=1,22)
      WRITE(6,319)(DDS1(I),I=1,22)
      WRITE(6,320)(EFF(I),I=1,22)
      WRITE(6,321)(XD(I),I=1,22)
  201 CONTINUE
  300 FORMAT(1H0//,6H TIME=,F10.3)
301   FORMAT(1H0,10H XC        ,12G10.4/13G10.4/12G10.4)
  302 FORMAT(1H0,10H XN        ,11G10.4/11G10.4)
  303 FORMAT(1H0,10H W         ,11G10.4/11G10.4)
  304 FORMAT(1H0,10H S2        ,11G10.4/11G10.4)
  305 FORMAT(1H0,10H BS2       ,11G10.4/11G10.4)
  306 FORMAT(1H0,10H BG        ,11G10.4/11G10.4)
  307 FORMAT(1H0,10H HH        ,12G10.4/13G10.4/12G10.4)
  308 FORMAT(1H0,10H RF        ,11G10.4/11G10.4)
  309 FORMAT(1H0,10H ACT       ,11G10.4/11G10.4)
  310 FORMAT(1H0,10H GEST      ,11G10.4/11G10.4)
311   FORMAT(1H0,10H ELACT     ,11G10.4/7G10.4)
312   FORMAT(1H0,10H XING      ,11G10.4/11G10.4)
313   FORMAT(1H0,10H XINS2     ,11G10.4/11G10.4)
314   FORMAT(1H0,10H RES2      ,11G10.4/11G10.4)
315   FORMAT(1H0,10H ACTS2     ,11G10.4/11G10.4)
316   FORMAT(1H0,10H XLTS2     ,11G10.4/7G10.4)
317   FORMAT(1H0,10H GSTS2     ,11G10.4/11G10.4)
318   FORMAT(1H0,10H AF        ,11G10.4/11G10.4)
319   FORMAT(1H0,10H DDS1      ,11G10.4/11G10.4)
320   FORMAT(1H0,10H EFF       ,11G10.4/11G10.4)
321   FORMAT(1H0,10H XD        ,11G10.4/11G10.4)
      STOP
      END
      SUBROUTINE CONS(DT)
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),PE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XH(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XMF(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DFMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDF(22,37),PXMF(22,37),PRF1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     FUNC. GROUP                        REP. SPECIES
C
C     1 - LEAF STEM BROWSER-JUV.         GIRAFFE
```

```
C       2 -                   -BREED
C       3 -                   -SENILE
C       4 - FORB BROWSER-JUV.              GAZELLE
C       5 -              -BREED
C       6 -              -SENILE
C       7 - STEM GRAZER-JUV.               ZEBRA
C       8 -             -BREED
C       . -             -SENILE
C       10 - LEAF GRAZER-JUV               HARTEBEAST
C       11 -             -BREED
C       12 -             -SENILE
C       13 - BROWSER-GRAZER 1-JUV          ELEPHANT
C       14 -                  -BREED
C       15 -                  -SENILE
C       16 - BROWSER-GRAZER 2-JUV          IMPALA
C       17 -                  -BREED
C       18 -                  -SENILE
C       19 - PREDATOR 1                    LION
C       20 - PREDATOR 2                    HYAENA
C       21 - PREDATOR 3                    HUNTING-DOG
C       22 - SCAVENGER                     VULTURE
C       23 - ANIMAL DEAD
C       24 - TREES,BUSHES,SHRUBS-LEAVES
C       25 -                    -STEMS
C       26 - PERENNIAL GRASSES-LEAVES
C       27 -                  -STEMS
C       28 - ANNUAL GRASSES
C       29 - FORBS
C       30 - STANDING DEAD
C       31 - LITTER
C       32 - MILK-GIRAFFE
C       33 -     -GAZELLE
C       34 -     -ZEBRA
C       35 -     -HARTEBEAST
C       36 -     -ELEPHANT
C       37 -     -IMPALA
C       XC(I)=BIOMASS OF GROUP 2, I=1,37
C       XN(I)=POP. SIZE OF GROUP I, I=1,22
C       W(I)=AVG. WT. OF GROUP I, I=U,22
C       BS2(I)=BIOMASS OF SOTRAGE 2 COMPARTMENT OF GROUP I, I=1,22
C       S2(I)=NET ENERGY OF STORAGE 2 COMPARTMENT OF GROUP I, I=1,22
        CALL PRECIP(DT)
        CALL EMULT
        CALL PROD
        CALL DIET
        CALL HARVC
        CALL STOR1
        CALL RESP
        CALL ACTIV(DT)
        CALL GST(DT)
        CALL LACT(DT)
        CALL GRWS2
        CALL RECRUT
        CALL DEATH
```

```
      DO 2 I=1,22
      DBG(I)=PBG(I)*XING(I)
C     YY AND ZZ KEEP S2 AND W FROM GOING NEGATIVE
      DS2(I)=XINS2(I)-RES2(I)-ACTS2(I)-XLTS2(I)-GSTS2(I)
      YY=-S2(I)/DT
      DS2(I)=AMAX1(YY,DS2(I))
      DBS2(I)=PBS2(I)*DS2(I)
      DW(I)=DBG(I)+DBS2(I)
      ZZ=-W(I)/DT
      DW(I)=AMAX1(ZZ,DW(I))
C     ANY ANIMAL KILLED IS ASSUMED TO BE HALF-EATEN BY ITS PREDATOR
2     DXN(I)=B(I)+G(I)-XN(I)*XD(I)-2.*HA(I)/W(I)
C     BG(I)=BIOMASS OF GROWTH COMPARTMENT
C     MUST GET DEAD ANIMALL BIOMASS FOR ALL 22 GROUPS COMBINED
      DO 3 I=1,22
3     DXC(23)=DXC(23)+HA(I)+XN(I)*D(I)*W(I)
      DXC(23)=DXC(23)-HA(23)
C     MILK PRODUCTION
      DXC(32)=XLACT(2)*XC(2)+XLACT(3)*XC(3)
      DXC(33)=XLACT(5)*XC(5)+XLACT(6)*XC(6)
      DXC(34)=XLACT(8)*XC(8)+XLACT(9)*XC(9)
      DXC(35)=XLACT(11)*XC(11)+XLACT(12)*XC(12)
      DXC(36)=XLACT(14)*XC(14)+XLACT(15)*XC(15)
      DXC(37)=XLACT(17)*XC(17)+XLACT(18)*XC(18)
      RETURN
      END
      SUBROUTINE PRECIP(DT)
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DEP/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES DAILY PRECIP(CM/DAY) FOR THE MODEL
C     AND THE TIME SINCE THE LAST DAILY PRECIP OF .06 CM OR GREATER
      IF(TDMOD.GT.20.)GO TO 2
      ZPR=0.16-0.001*TDMOD
      GO TO 1
2     IF(TDMOD.GT.80.)GO TO 3
      ZPR=0.0333+0.0053*TDMOD
      GO TO 1
3     IF(TDMOD.GT.180.)GO TO 4
      ZPR=0.828-0.0046*TDMOD
      GO TO 1
4     IF(TDMOD.GT.250.)GO TO 5
      ZPR=0.
      GO TO 1
```

```
5       IF(TDMOD.GT.340.)GO TO 6
        ZPR=-0.78+0.003*TDMOD
        GO TO 1
6       ZPR=1.348-0.0032*TDMOD
1       CONTINUE
        IF(ZPR.GT.0.06)GO TO 10
        TPP=TPP+DT
        GO TO 11
10      TPP=0.
11      CONTINUE
        RETURN
        END
        SUBROUTINE PROD
        COMMON/TIME/TDMOD
        COMMON/DRV/ZPR
        COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
        COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
        COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
       1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
       2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
       3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
       4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
        COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
       1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
       2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
       3,PS2MX(22),PMXIN(22)
C       THIS SUBROUTINE COMPUTES VALUES OF THE PRIMARY PRODUCTION
C       DRIVING VARIABLES
        IF(TDMOD.LT.30.)GO TO 1
        IF(TDMOD.GE.30..AND.TDMOD.LT.90.)GO TO 2
        IF(TDMOD.GE.90..AND.TDMOD.LT.100.)GO TO 3
        IF(TDMOD.GE.100..AND.TDMOD.LT.120.)GO TO 4
        IF(TDMOD.GE.120..AND.TDMOD.LT.150.)GO TO 5
        IF(TDMOD.GE.150..AND.TDMOD.LT.210.)GO TO 6
        IF(TDMOD.GE.210..AND.TDMOD.LT.240.)GO TO 7
        IF(TDMOD.GE.240..AND.TDMOD.LT.270.)GO TO 8
        IF(TDMOD.GE.270..AND.TDMOD.LT.300.)GO TO 9
        XC(24)=52.3077-.1077*TDMOD
        XC(25)=332.6923-0.6923*TDMOD
        XC(26)=639.5349-.9302*TDMOD
        XC(27)=103.9535-.093*TDMOD
        XC(28)=44.4-.06*TDMOD
        XC(31)=34.129-.0387*TDMOD
        GO TO 99
1       XC(24)=13.+.0444*TDMOD
        XC(25)=80.-.1*TDMOD
        XC(26)=300.+1.3333*TDMOD
        XC(27)=70.+.1333*TDMOD
        XC(28)=23.-.0167*TDMOD
        XC(31)=20.-.0667*TDMOD
        GO TO 99
2       XC(24)=13.+.0444*TDMOD
        XC(25)=80.-.1*TDMOD
        XC(26)=300.+1.3333*TDMOD
```

```
      XC(27)=70.+.1333*TDMOD
      XC(28)=21.432+.0357*TDMOD
      XC(31)=20.-.0667*TDMOD
      GO TO 99
3     XC(24)=23.-.0667*TDMOD
      XC(25)=80.-.1*TDMOD
      XC(26)=300.+1.333*TDMOD
      XC(27)=70.+.1333*TDMOD
      XC(28)=21.432+.0357*TDMOD
      XC(31)=20.-.0667*TDMOD
      GO TO 99
4     XC(24)=23.-.0667*TDMOD
      XC(25)=42.5+.275*TDMOD
      XC(26)=300.+1.3333*TDMOD
      XC(27)=70.+.1333*TDMOD
      XC(28)=21.432+.0357*TDMOD
      XC(31)=20.-.0667*TDMOD
      GO TO 99
5     XC(24)=23.-.0667*TDMOD
      XC(25)=42.5+.275*TDMOD
      XC(26)=300.+1.3333*TDMOD
      XC(27)=70.+.1333*TDMOD
      XC(28)=21.432+.0357*TDMOD
      XC(31)=-3.2727+.1273*TDMOD
      GO TO 99
6     XC(24)=23.-.0667*TDMOD
      XC(25)=42.5+.275*TDMOD
      XC(26)=639.5349-.9302*TDMOD
      XC(27)=103.9535-.093*TDMOD
      XC(28)=21.432+.0357*TDMOD
      XC(31)=-3.2727+.1273*TDMOD
      GO TO 99
7     XC(24)=-1.5+.05*TDMOD
      XC(25)=42.5+.275*TDMOD
      XC(26)=639.5349-.9302*TDMOD
      XC(27)=103.9535-.093*TDMOD
      XC(28)=21.432+.0357*TDMOD
      XC(31)=34.129-.0387*TDMOD
      GO TO 99
8     XC(24)=-1.5+.05*TDMOD
      XC(25)=42.5+.275*TDMOD
      XC(26)=639.5349-.9302*TDMOD
      XC(27)=103.9535-.093*TDMOD
      XC(28)=44.4-.06*TDMOD
      XC(31)=34.129-.0387*TDMOD
      GO TO 99
9     XC(24)=-60.+.2667*TDMOD
      XC(25)=42.5+.275*TDMOD
      XC(26)=639.5349-.9302*TDMOD
      XC(27)=109.9535-.093*TDMOD
      XC(28)=44.4-.06*TDMOD
      XC(31)=34.129-.0387*TDMOD
99    CONTINUE
      XC(29)=XC(28)
```

```
      RETURN
      END
      SUBROUTINE DIET
      COMMON/TIME/TOMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DEP/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     SUBROUTINE DIET COMPUTES ACTUAL FOOD CONSUMPTION RATE AND ACTUAL
C     DIETARY COMPOSITION FOR GROUP I: I=1,22
C     XF(I)=FOOD CONS. RATE FOR GROUP I UNDER IDEAL CONDITIONS (G/G/DAY)
C     AF(I)=ACTUAL FOOD CONS. RATE FOR GROUP I (G/G/DAY).
C     XK(I,J)=AMOUNT OF DIET OF CONSUMER GROUP I MADE UP OF CONSUMED
C     GROUP J UNDER IDEAL FOOD AVAILABILITY CONDITIONS.
C     AK(I,J)=ACTUAL AMOUNT OF DIET OF CONSUMER GROUP I MADE UP OF
C     CONSUMED GROUP J.
C     TH0(J)=THRESHOLD DENSITY BELOW WHICH CONSUMED GROUP J CEASES TO BE
C     CONSUMED.
C     TH1(J)=THRESHOLD DENSITY BELOW WHICH CONSUMED GROUP J DECREASES IN
C     IMPORTANCE TO ITS CONSUMERS
C     TH2(J)=THRESHOLD DENSITY ABOVE WHICH CONSUMPTION OF CONSUMED GROUP
C     J INCREASES DUE TO ITS OVER-ABUNDANCE.
      DO 2 I=1,22
C     DO NOT WANT TO ERASE XK FROM STORAGE SO DEFINE DUMMY VARIABLE YK
C     TO WORK WITH IN SUBROUTINE
      DO 1 J=1,37
1     YK(J)=XK(I,J)
C     ACTUAL FOOD CONSUMPTION RATE INITIALLY SET EQUAL TO IDEAL FOOD
C     CONSUMPTION RATE.
      AF(I)=XF(I)
C     IF ACTIVITY DEMMAND NOT MET FROM STORAGE 1 LAST DT, FOOD CONS
C     INCREASES TO MAX
      IF(ACTS2(I).LE.0.)GO TO 502
      AF(I)=PAFMX(I)
      GO TO 501
C     IF STORAGE 2 BIOMASS IS GREATER THAN PS2MX OF TOTAL BIOMASS,
C     FOOD CONS DECREASES
502   IF(BS2(I).LE.PS2MX(I)*W(I))GO TO 503
      AF(I)=AF(I)*PS2MX(I)*W(I)/BS2(I)
      GO TO 501
C     IF THE RATE OF FLOW OF ENERGY(XINS2) INTO STORAGE 2,CONVERTED TO
C     BIOMASS, IS GREATER THAN PMXIN OF TOTAL WT, FOOD CONS DECREASES
503   IF(XINS2(I)*PBS2(I).LE.PMXIN(I)*W(I))GO TO 504
      AF(I)=AF(I)*PMXIN(I)*W(I)/(XINS2(I)*PBS2(I))
      GO TO 501
C     IF THE RATE OF FLOW OF ENERGY(XING) INTO GROWTH, CONVERTED TO
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C     BIOMASS(PBG G/KCAL). IS GREATER THAN PMXG OF TOTAL WT. FOOD
C     CONSUMPTION DECREASES
504   IF(XING(I)*PBG(I).GT.PMXG(I)*W(I))AF(I)=AF(I)*PMXG(I)*W(I)/
     1(XING(I)*PBG(I))
501   CONTINUE
C     ELIMINATE ANY CONSUMED GROUP J FROM DIET OF CONSUMER GROUP I IF
C     ITS BIOMASS IS BELOW THRESHOLD TH0(J)
      DO41J=1,37
      IF(XC(J).GE.TH0(J)) GO TO 20
      YK(J) =0.
      GO TO 40
C     IF THE ABUNDANCE OF ANY CONSUMED GROUP J IS LESS THAN TH1(J), THEN
C     THE AMOUNT OF THAT GROUP IN THE DIET OF CONSUMER GROUP I WILL
C     DECREASE LINEARLY.
20    IF(XC(J).GE.TH1(J)) GO TO 30
      YK(J)=(XK(I,J)/(TH1(J)-TH0(J)))*(XC(J)-TH0(J))
      GO TO 40
C     IF THE ABUNDANCE OF CONSUMED GROUP J IS GREATER THAN TH2(J) THEN
C     THE AMOUNT OF THAT GROUP IN THE DIET OF CONSUMER GROUP I WILL
C     INCREASE LINEARLY.
30    IF(XC(J).LT.TH2(J)) GO TO 40
      YK(J)=XK(I,J)*XC(J)/TH2(J)
40    CONTINUE
C     IF THE AMOUNT OF ENERGY NEEDED FOR ACTIVITY OF CONSUMED GROUP J
C     (J=1,18) IS BELOW TACT(J), THEN CONSUMPTION OF THAT GROUP
C     INCREASES LINEARLY.
      IF(J.GT.18) GO TO 41
      TACT(J)=0.8*PACT1(J)*(.00333*W(J))**PACT2(J)
      IF(ACT(J).GE.TACT(J)) GO TO 41
      YK(J)=YK(J)*TACT(J)/(ACT(J)+1.0)
41    CONTINUE
C     THE ACTUAL FOOD PREFERENCE FACTORS FOR GROUP I ARE NOW COMPUTED.
      SY=SUM(YK,37)
      IF(SY.LE.0.) GO TO 3
      DO 50 J=1,37
50    AK(I,J)=YK(J)/SY
      GO TO 2
3     DO 51 J=1,37
51    AK(I,J)=0.
C     MUST CONVERT AF TO WET WT BASIS
2     AF(I)=3.33*AF(I)
      RETURN
      END
      SUBROUTINE HARVC
C     THIS SUBROUTINE COMPUTES THE RATE OF CONSUMPTION (G/DAY) OF
C     CONSUMED GROUP J BY CONSUMER GROUP I, AND THE TOTAL HARVEST RATE
C     (G/DAY) OF CO
C
C     HC(I,J)=RATE OF CONSUMPTION(G/DAY) OF CONSUMED GROUP J BY CONSUMER
C     GROUP I.
C     HA(J)=TOTAL HARVEST RATE OF CONSUMED GROUP J (G/DAY)
      DIMENSION HD(22)
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
```

```
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
      DO 1 J=1,37
      DO 2 I=1,22
      HC(I,J)=AK(I,J)*AF(I)*XC(I)
    2 HD(I)=HC(I,J)
    1 HA(J)=SUM(HD,22)
      RETURN
      END
      SUBROUTINE STOR1
      DIMENSION XA(37),XM(37),XE(37),DD(37)
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES THE AMOUNT OF MATERIAL (KCAL/DAY) ENTERIN
C     ENTERING THE STORAGE 1 COMPARTMENT-DS1(I),I=1,22
C     GE(J)=GROSS ENERGY (KCAL/G) OF CONSUMED GROUP J.
C     DE(I,J)=DIGESTIBLE ENERGY(KCAL/KCAL) OF CONSUMER GROUP I FOR
C     XME(I,J)=METABOLIZABLE ENERGY (KCAL/KCAL) OF CONSUMER GROUP I FOR
C     CONSUMED GROUP J.
      DO 1 I=1,22
      DO 2 J=1,37
      XA(J)=AK(I,J)
      DE(I,J)=PDE(I,J)*DEMLT(J)
      DD(J)=DE(I,J)
      XME(I,J)=PXME(I,J)*XMEMT(J)
      XM(J)=XME(I,J)
    2 XE(J)=XA(J)*GE(J)*DD(J)*XM(J)
      EFF(I)=SUM(XE,37)
      DS1(I)=W(I)*AF(I)*EFF(I)
    1 DDS1(I)=DS1(I)
      RETURN
      END
      SUBROUTINE RESP
      COMMON/TIME/TDMOD
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      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES THE RESPIRATION RATE (KCAL/IND/DAY) FOR
C     THE CONSUMER GROUPS
C     MUST CONVERT TO WET WT(3.33*DRY WT=WET WT) AND THEN TO KG TO APPLY
C     EQUATION
C     ENERGY HAS EFFICIENCY OF .6 GOING FROM STOR1 TO RESP
C     ENERGY HAS EFFICIENCY OF 0.6 GOING FROM STOR2 TO RESP
      DO 1 I=1,22
      RE(I)=1.667*PRE1(I)*(.00333*W(I))**PRE2(I)
      IF(RE(I).LE.DS1(I)) GO TO 2
      RES2(I)=RE(I)-DS1(I)
      IF(S2(I).LT.RES2(I)) GO TO 3
      DS1(I)=0.
      GO TO 1
 3    RES2(I)=S2(I)
      RE(I)=DS1(I)+RES2(I)
      DS1(I)=0.
      GO TO 1
 2    RES2(I)=0.
      DS1(I)=DS1(I)-RE(I)
 1    CONTINUE
      RETURN
      END
      SUBROUTINE ACTIV(DT)
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES THE ACTIVITY RATE (KCAL/IND/DAY) FOR THE
C     CONSUMER GROUPS
C     MUST CONVERT TO WET WT(3.33*DRY WT=WET WT) AND THEN TO KG TO APPLY
C     EQUATION
      DO 1 I=1,22
C     ENERGY HAS EFFICIENCY OF 0.6 GOING FROM STOR1 TO ACT
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C     ENERGY HAS EFFICIENCY OF 0.6 GOING FROM STOR2 TO ACT
      X2(I)=S2(I)-RES2(I)
      ACT(I)=1.667*PACT1(I)*(W(I)*.00333)**PACT2(I)
      IF(ACT(I).LE.DS1(I)) GO TO 2
      ACTS2(I)=ACT(I)-DS1(I)
      IF(X2(I).LT.ACTS2(I)) GO TO 3
      DS1(I)=0.
      GO TO 1
3     ACTS2(I)=X2(I)
      ACT(I)=DS1(I)+ACTS2(I)
      DS1(I)=0.
      GO TO 1
2     ACTS2(I)=0.
      DS1(I)=DS1(I)-ACT(I)
1     CONTINUE
      RETURN
      END
      SUBROUTINE GST(DT)
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES THE LOSS OF ENERGY (KCAL/DAY) FROM THE
C     STORAGE 1 AND STORAGE 2 COMPARTMENTS NECESSARY TO MAINTAIN
C     GESTATION.
C     FIRST COMPUTE IDEAL GESTATION RATES.
      DO 100 I=1,22
      GEST(I)=0.
  100 GMULT(I)=0.
      GEST(2)=0.045*(RE(2)+ACT(2))
      GEST(3)=0.0225*(RE(3)+ACT(3))
      IF(TDMOD.GE.220..AND.TDMOD.LT.300.) GO TO 1
      IF(TDMOD.GE.300..OR.TDMOD.LT.50.) GO TO 2
      IF(TDMOD.GE.50..AND.TDMOD.LT.130.) GO TO 3
      GO TO 4
    1 GMULT(5)=-1.485+0.00675*TDMOD
      GMULT(6)=-1.5+0.005*TDMOD
      GO TO 4
    2 GMULT(5)=0.54
      GMULT(6)=0.40
    3 GMULT(5)=0.8775-0.00675*TDMOD
      GMULT(6)=0.65-0.005*TDMOD
    4 CONTINUE
      GEST(5)=GMULT(4)*0.10*(RE(4)+ACT(4))
      GEST(6)=GMULT(5)*0.10*(RE(5)+ACT(5))
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      GEST(8)=0.0396*(RE(8)+ACT(8))
      GEST(9)=0.0211*(RE(9)+ACT(9))
      GEST(11)=0.431*(RE(11)+ACT(11))
      GEST(12)=0.027*(RE(12)+ACT(12))
      GEST(14)=0.0214*(RE(14)+ACT(14))
      GEST(15)=0.0178*(RE(15)+ACT(15))
      IF(TDMOD.GE.180..AND.TDMOD.LT.320.) GO TO 5
      IF(TDMOD.GE.320..OR.TDMOD.LT.10.) GO TO 6
      IF(TDMOD.GE.10..AND.TDMOD.LT.150.) GO TO 7
      GO TO 8
    5 GMULT(17)=-0.7522+0.0042*TDMOD
      GMULT(18)=-0.45+0.0025*TDMOD
      GO TO 8
    6 GMULT(17)=0.585
      GMULT(18)=0.35
      GO TO 8
    7 GMULT(17)=0.6269-0.0042*TDMOD
      GMULT(18)=0.375-0.0025*TDMOD
    8 CONTINUE
      GEST(17)=GMULT(17)+0.10*(RE(17)+ACT(17))
      GEST(18)=GMULT(18)+0.10*(RE(18)+ACT(18))
      IF(TDMOD.GE.355.) GO TO 9
      IF(TDMOD.LT.20.) GO TO 10
      IF(TDMOD.GE.20..AND.TDMOD.LT.110.) GO TO 11
      IF(TDMOD.GE.120..AND.TDMOD.LT.140.) GO TO 12
      GO TO 13
    9 GMULT(19)=-15.383+0.43*TDMOD
      GMULT(20)=-19.525+0.055*TDMOD
      GMULT(21)=-26.033+0.073*TDMOD
      GMULT(22)=-11.833+0.033*TDMOD
      GO TO 13
   10 GMULT(19)=0.43+0.043*TDMOD
      GMULT(20)=0.55+0.055*TDMOD
      GMULT(21)=0.73+0.073*TDMOD
      GMULT(22)=0.33+0.033*TDMOD
      GO TO 13
   11 GMULT(19)=1.3
      GMULT(20)=1.65
      GMULT(21)=2.2
      GMULT(22)=1.0
      GO TO 13
   12 GMULT(19)=6.02-0.043*TDMOD
      GMULT(20)=7.7-0.055*TDMOD
      GMULT(21)=10.22-0.073*TDMOD
      GMULT(22)=4.62-0.033*TDMOD
   13 CONTINUE
      DO14I=19,22
   14 GEST(I)=GMULT(I)*0.10*(RE(I)+ACT(I))
      DO 15I=1,22
C     ENERGY HAS EFFICIENCY OF .95 GOING FROM STOR1 TO GEST
C     ENERGY HAS EFFICIENCY OF 0.95 GOING FROM STOR2 TO GEST
      X2(I)=X2(I)-ACTS2(I)
      GEST(I)=1.053*GEST(I)
      IF(GEST(I).LE.DSI(I)) GO TO 16
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      GSTS2(I)=(GEST(I)-DS1(I))
      IF(X2(I).LT.GSTS2(I)) GO TO 17
      DS1(I)=0.
      GO TO 15
   17 GSTS2(I)=X2(I)
      GEST(I)=DS1(I)+GSTS2(I)
      DS1(I)=0.
      GO TO 15
   16 DS1(I)=DS1(I)-GEST(I)
      GSTS2(I)=0.
   15 CONTINUE
      RETURN
      END
      SUBROUTINE LACT(DT)
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES MILK PRODUCTION (G/G BODY WT/DAY) FOR
C     EACH CONSUMER GROUP
      DO 1I=1,18
    1 XLMLT(I)=0.
      IF(TDMOD.GE.50..AND.TDMOD.LT.130.) GO TO 2
      IF(TDMOD.GE.130..AND.TDMOD.LT.230.) GO TO 3
      IF(TDMOD.GE.230..AND.TDMOD.LT.310.) GO TO 4
      GO TO 5
    2 XLMLT(2)=-0.625+0.0125*TDMOD
      XLMLT(3)=XLMLT(2)
      GO TO 5
    3 XLMLT(2)=1.
      XLMLT(3)=1.
      GO TO 5
    4 XLMLT(2)=3.875-0.0125*TDMOD
      XLMLT(3)=XLMLT(2)
    5 CONTINUE
C     PLACT(I)=MAXIMUM MILK PRODUCTION (G/G BODY WT/DAY) FOR CONSUMER
C     GROUP I.
      XLACT(2)=XLMLT(2)*0.372*PLACT(2)
      XLACT(3)=XLMLT(3)*0.186*PLACT(3)
      IF(TDMOD.GE.50..AND.TDMOD.LT.120.) GO TO 6
      IF(TDMOD.GE.120..AND.TDMOD.LT.190.) GO TO 7
      GO TO 8
    6 XLMLT(5)=-0.7143+0.0143*TDMOD
      XLMLT(6)=XLMLT(5)
      GO TO 8
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    7 XLMLT(5)=2.717-0.0143*TDMOD
      XLMLT(6)=XLMLT(5)
    8 CONTINUE
      XLACT(5)=XLMLT(5)*0.54*PLACT(5)
      XLACT(6)=XLMLT(6)*0.40*PLACT(6)
      IF(TDMOD.GE.20..AND.TDMOD.LT.120.) GO TO 9
      IF(TDMOD.GE.120..AND.TDMOD.LT.220.) GO TO 10
      GO TO 11
    9 XLMLT(8)=-0.2+0.01*TDMOD
      XLMLT(9)=XLMLT(8)
      GO TO 11
   10 XLMLT(8)=2.2-0.01*TDMOD
      XLMLT(9)=XLMLT(8)
   11 CONTINUE
      XLACT(8)=XLMLT(8)*0.413*PLACT(8)
      XLACT(9)=XLMLT(9)*0.22*PLACT(9)
      XLACT(11)=0.106*PLACT(11)
      XLACT(12)=0.097*PLACT(12)
      XLACT(14)=0.12*PLACT(14)
      XLACT(15)=0.1*PLACT(15)
      IF(TDMOD.GE.10..AND.TDMOD.LT.102.5) GO TO 12
      IF(TDMOD.GE.102.5.AND.TDMOD.LT.215.) GO TO 13
      GO TO 14
   12 XLMLT(17)=-0.1081+0.0108*TDMOD
      XLMLT(18)=XLMLT(17)
      GO TO 14
   13 XLMLT(17)=2.2-0.01*TDMOD
      XLMLT(18)=XLMLT(17)
   14 CONTINUE
      XLACT(17)=XLMLT(17)*0.585*PLACT(17)
      XLACT(18)=XLMLT(18)*0.35*PLACT(18)
      DO 15 I=1,18
C     CONVERT LACTATION DEMMANDS (G/IND/DAY) INTO ENERGY DEMMANDS
C     (KCAL/IND/DAY) ON STORAGE 1 AND STORAGE 2. INCLUDED IN THIS IS
C     LOSS OF ENERGY DUE TO TRANSFER FROM STORGE TO LACTATION
C     CONVERSION FACTOR IN MILK OF 6 KCAL/G
C     ENERGY HAS EFFICIENCY OF 0.6 GOING FROM STOR1 TO LACT
C     ENERGY HAS EFFICIENCY OF 0.6 GOING FROM STOR2 TO LACT
      X2(I)=X2(I)-GSTS2(I)
      ELACT(I)=6.*1.667*XLACT(I)
      IF(ELACT(I).LE.DS1(I)) GO TO 16
      XLTS2(I)=ELACT(I)-DS1(I)
      IF(X2(I).LT.XLTS2(I)) GO TO 17
      DS1(I)=0.
      GO TO 18
   17 XLTS2(I)=X2(I)
      ELACT(I)=DS1(I)+XLTS2(I)
      DS1(I)=0.
      GO TO 18
   16 XLTS2(I)=0.
      DS1(I)=DS1(I)-ELACT(I)
   18 CONTINUE
C     MUST NOW CONVERT ENERGY USED FOR LACTATION (KCAL/IND/DAY) INTO
C     MILK PRODUCTION (G/IND/DAY).
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15 XLACT(I)=0.6*ELACT(I)/8.
   RETURN
   END
   SUBROUTINE GRWS2
   COMMON/TIME/TDMOD
   COMMON/DRV/ZPR
   COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
   COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
   COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
  1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
  2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
  3XMF(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
  4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
   COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
  1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
  2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
  3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES THE AMOUNT OF ENERGY (KCAL/DAY) FLOWING
C     INTO THE GROWTH AND STORAGE 2 COMPARTMENTS. IF THE ANIMAL IS A
C     JUVENILE,GROWTH IS INCREMENTED BEFORE STORAGE 2. IF THE ANIMAL IS
C     A BREEDER,SENILE, OR PREDATOR, STORAGE 2 IS INCREMENTED BEFORE
C     GROWTH
      DO1I=1,18,3
C     PMXG=MAX RATE OF FLOW OF ENERGY INTO GRWTH ( G/GBODY WT/DAY)
C     XMXG=MAX RATE OF FLOW  OF ENERGY INTO GROWTH (KCAL/DAY)
C     ENERGY HAS EFFICIENCY OF 0.4 GOING  FROM STOR1 TO GROWTH
      XMXG(I)=PMXG(I)*W(I)/PBG(I)
      XING(I)=AMIN1(0.4*DS1(I),XMXG(I))
      DS1(I)=DS1(I)-XING(I)/0.4
C     THE BALANCE OF THE ENERGY IN STORAGE 1 GOES TO STORAGE 2
C     ENERGY HAS EFFICIENCY OF 0.35 GOING FROM STORAGE 1 TO STORAGE 2
      XINS2(I)=DS1(I)*0.35
1     DS1(I)=0.
      DO2I=2,22
      IF(I.GT.18)GO TO 3
      IF(MOD(I,3).EQ.1)GO TO 2
C     PMXIN=MAX RATE OF FLOW INTO STORAGE 2(G/G BODY WT/DAY)
C     XMXIN=MAX RATE OF FLOW OF ENERGY INTO STORAGE 2(KCAL/DAY)
3     XMXIN(I)=PMXIN(I)*W(I)/PBS2(I)
      XINS2(I)=AMIN1(0.35*DS1(I),XMXIN(I))
      DS1(I)=DS1(I)-XINS2(I)/0.35
C     THE BALANCE OF ENERGY IN STORAGE 1 GOES INTO GROWTH
      XING(I)=DS1(I)*0.4
      DS1(I)=0.
2     CONTINUE
      RETURN
      END
      SUBROUTINE RECRUT
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RF(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
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      2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
      3XMF(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
      4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
       COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
      1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
      2PRG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
      3,PS2MX(22),PMXIN(22)
C      THIS SUBROUTINE COMPUTES DAILY INSTANTANEOUS RECRUITMENT RATES
C      (BIRTH AND GRADUATION) FOR THE CONSUMER GROUPS
       G(1)=(-0.69314718*XN(1)*EXP(-(TDMOD-90.)**2/1085.0276))/58.384174
       G(2)=(-0.13353139*XN(2)*EXP(-(TDMOD-90.)**2/1929.4472))/77.855886
       G(4)=(-4.60517019*XN(4)*EXP(-(TDMOD-90.)**2/1085.0276))/58.384174
       G(5)=(-0.22314355*XN(5)*EXP(-(TDMOD-90.)**2/1929.4472))/77.855886
       G(7)=-0.51082562*XN(7)*(EXP(-(TDMOD-80.)**2/2441.3121)+EXP(-(TDMOD
      1-445.)**2/2441.3121))/87.576593
       G(8)= -0.08338161*XN(8)*(EXP(-(TDMOD-80.)**2/4340.1103)+EXP(-(TDMO
      1D-445.)**2/4340.1103))/116.76841
       G(10)=-0.01261690*XN(10)
       G(11)=-4.9951E-4*XN(11)
       G(13)=-2.6112E-4*XN(13)
       G(14)=-6.298E-5*XN(14)
       G(16)= -4.60517019*XN(16)*(EXP(-(TDMOD-80.)**2/3322.8970)+EXP(-(TD
      1MOD-445.)**2/3322.8970))/102.17237
       G(17)=-0.15415068*XN(17)*(EXP(-(TDMOD-80.)**2/5907.3724)+EXP(-(TDM
      1OD-445.)**2/5907.3724))/136.22982
       DO50I=1,22
50     XB(I)=PB(I)
C
C      IF THE STORAGE2 COMPARTMENT FALLS BELOW A CERTAIN THRESHOLD VALUE
C      IN EITHER THE BREEDER OR SENILE COMPARTMENT THE NO. OF OFFSPRING
C      PER FEMALE PRODUCED BY THST COMPARTMENT (CONTROLED BY THE ISV
C      XB(I)) WILL DECREASE LINEARLY
C
       DO1I=1,16,3
       K=I+1
       L=I+2
       XS2(K)=PS2(K)*W(K)
       XS2(L)=PS2(L)*W(L)
       IF(BS2(K).LT.XS2(K))XB(K)=PB(K)*BS2(K)/XS2(K)
1      IF(BS2(L).LT.XS2(L))XB(L)=PB(L)*BS2(L)/XS2(L)
       B(1)=(0.62*XN(2)*XB(2)+0.62*XN(3)*XB(3))*EXP(-(TDMOD-90.)**2/482.2
      13448)/38.922930
       B(2)=-G(1)
       B(3)=-G(2)
       B(4)=(0.66*XN(5)*XB(5)+0.66*XN(6)*XB(6))*EXP(-(TDMOD-90.)**2/482.2
      13448)/38.922930
       B(5)=-G(4)
       B(6)=-G(5)
       B(7)=(0.55*XN(8)*XB(8)+0.55*XN(9)*XB(9))*EXP(-(TDMOD-80.)**2/1085.
      10345)/58.384396
       B(8)=-G(7)
       B(9)=-G(8)
       B(10)=(0.70*XN(11)*XB(11)+0.70*XN(12)*XB(12))
       B(11)=-G(10)
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      B(12)=-G(11)
      B(13)=(0.60*XN(14)*XB(14)+0.60*XN(15)*XB(15))
      B(14)=-G(13)
      B(15)=-G(14)
      B(16)=(0.65*XN(17)*XB(17)+0.70*XN(18)*XB(18))*EXP(-(TDMOD-80.)**2/
     11476.8526)/68.115128
      B(17)=-G(16)
      B(18)=-G(17)
      DO2I=19,22
2     IF(S2(I).LT.PS2(I))XB(I)=PB(I)*S2(I)/PS2(I)
      B(19)= 0.26*XN(19)*XB(19)*EXP(-(TDMOD-80.)**2/1085.0345)/58.384379
      B(20)=0.22*XN(20)*XB(20)*EXP(-(TDMOD-80.)**2/1085.0345)/58.384379
      B(21)=0.22*XN(21)*XB(21)*EXP(-(TDMOD-80.)**2/1085.0345)/58.384379
      B(22)=0.125*XN(22)*XB(22)*EXP(-(TDMOD-80.)**2/1085.0345)/58.384371
      RETURN
      END
      SUBROUTINE DEATH
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES THE ACTUAL INST. NAT. MORT. RATES
      DO1I=1,22
C     IF ACTIVITY DEMMANDS NOT MET, NAT. MORT+ INCREASES
      ACTDUM=1.667*PACT1(I)*(.00333*W(I))**PACT2(I)
      IF(ACT(I).GE.ACTDUM)GO TO 2
      XD(I)=D(I)*ACTDUM/(ACT(I)+1.0)
      GO TO 1
2     XD(I)=D(I)
1     CONTINUE
      RETURN
      END
      FUNCTION SUM(Y,N)
      DIMENSION Y(37)
      SUM=0.
      DO1J=1,N
1     SUM=SUM+Y(J)
      RETURN
      END
      SUBROUTINE EMULT
      COMMON/TIME/TDMOD
      COMMON/DRV/ZPR
      COMMON/PSV/XC(37),XN(22),W(22),S2(22),BS2(22),BG(22)
      COMMON/DER/DXC(37),DXN(22),DW(22),DS2(22),DBS2(22),DBG(22)
      COMMON/ISV/AF(22),AK(22,37),YK(37),HC(22,37),HA(37),EFF(22),DS1(22
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     1),RE(22),RES2(22),ACT(22),ACTS2(22),XING(22),XINS2(22),G(22),B(22)
     2,XB(22),TACT(22),XMXG(22),TPP,HH(37),GEST(22),XLACT(22),DE(22,37),
     3XME(22,37),GMULT(22),XLMLT(18),ELACT(18),XLTS2(18),GSTS2(22)
     4,DEMLT(37),XMEMT(37),XS2(22),DDS1(22),XMXIN(22),X2(22),XD(22)
      COMMON/PARAM/D(22),XF(22),XK(22,37),TH0(37),TH1(37),TH2(37),GE(37)
     1,PDE(22,37),PXME(22,37),PRE1(22),PRE2(22),PS2(22),PB(22),PMXG(22),
     2PBG(22),PACT1(22),PACT2(22),PAFMX(22),PLACT(18),PBS2(22)
     3,PS2MX(22),PMXIN(22)
C     THIS SUBROUTINE COMPUTES THE PRECIPITATION DEPENDENT MULTIPLICATIV
C     FACTORS FOR DIGESTIBLE ENERGY AND METABOLIZABLE ENERGY
      IF(TPP.LT.8.)GO TO 1
      IF(TPP.GE.8..AND.TPP.LT.10.)GO TO 2
      IF(TPP.GE.10..AND.TPP.LT.30.)GO TO 3
      IF(TPP.GE.30..AND.TPP.LT.40.)GO TO 4
      IF(TPP.GE.40..AND.TPP.LT.90.)GO TO 5
      DEMLX=0.5714
      XMEMX=0.8125
      GO TO 99
1     DEMLX=1.0
      XMEMX=1.0
      GO TO 99
2     DEMLX=1.1784-0.0223*TPP
      XMEMX=1.0
      GO TO 99
3     DEMLX=1.1784-0.0223*TPP
      XMEMX=1.075-0.0075*TPP
      GO TO 99
4     DEMLX=1.1784-0.0223*TPP
      XMEMX=0.8680-0.0006*TPP
      GO TO 99
5     DEMLX=0.8286-0.0029*TPP
      XMEMX=0.8680-0.0006*TPP
99    CONTINUE
      DO10I=24,31
      DEMLT(I)=DEMLX
10    XMEMT(I)=XMEMX
      RETURN
      END
```