A MATHEMATICAL MODEL
OF
A GRAZING SYSTEM INCLUDING BEETLES

by

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CHAPTER ONE

INTRODUCTION

A number of mathematical studies of herbivore (predator)- grass (prey) models (e.g. Noy-Meir 1975, 1976,1978; Wielgolaski 1973; Christian et al. 1978) have been developed. With the exception of a few (Jackson 1980), in all these models the accumulation of dung in pastures is regarded as being negligible. In reality herbivore dung may cover a non-negligible area of pasture and thus sensibly reduce the carrying capacity of the grazing land. Waterhouse (1974) found that an average of 12 dung pads are dropped by a single bovine every day. According to MacLusky (1960) cattle dung blankets an area of approximately 6600sq.cm per cow per day. If the pads are not disposed of, and taking into account the ensuing unpalatable rank growth, the effective area of pasture is thereby reduced by each animal by about 20% of an acre per year (Waterhouse, 1974). Hence one can give a conservative estimation that one million cattle may be putting out of service as much as 100000 acres of grazing land per annum, an area which can feed about 30000 cattle.

In this thesis a mathematical model of a grassland-herbivore system with a CHANGING AREA of grazing due to the accumulation of dung will be developed. The effect of the activity of dung beetles (Coleoptera: Scarabaeidae) towards the removal of fresh dung will be studied. A case similar to this phenomenon occurs in pastures of Australia where the accumulation of dried dung of introduced cattle has now reached an extent where up to 15% of the available grazing lands has been covered. When Australia imported cattle and sheep 2 centuries ago the seriousness of the omission of their fellow travelers, i.e. dung beetles, went unnoticed. As the number of bovines increased it became evident that the native beetles were failing to cope with the large, moist dung pads and that they were nearly wholly attracted to the small fibrous droppings of the indigenous marsupials. In an effort to restore its pastures Australia has been importing dung-beetles from South Africa for a number of years. These insects, by using fresh dung for nutrition and reproduction, are proving to be effective in reducing the area of lost pasture.

Another example of a series of pests to have been brought under biological control in Australia is Salvinia. This water weed can double its weight within 3 days if the conditions are optimal. In June 1981, the researchers released a batch of adult black weevil (called Cyrtobagous singularis) into enclosures among Australia's worst infestation - on Lake Moondarra, in Northern Queensland (New Scientist, vol-93, pg 500). A yield of Salvinia biomass less than 1 tonne was recorded in August 1981, contrary to the expected biomass of about 40000 tonnes.

1.1. A BRIEF DESCRIPTION OF THE MODEL

In PART 1 of the thesis a model is formulated to describe biomass dynamics in pastures that are grazed by a herbivore population, e.g. cattle, sheep. Herbivores are assumed to be kept at a constant density and that they are grazing on green vegetation. The growing season of green biomass is taken to be unlimited and the environmental factors affecting plant growth are constant. The arrival of herbivore-dung reduces the area available for plant growth and thus resulting in the varying area of grazing land.

The fresh dung, deposited on the surface, changes rapidly into dry dung in a semi-arid climate, and thus the model includes "components" for fresh and dry dung.

Dung-beetles are introduced into the herbivore-grazing system as specialists in the removal of fresh dung. A short discussion of the model with a single life stage of beetles (Jackson, 1980) is given. Then the system is modified firstly to include 4 beetle life stages viz. eggs, larvae, pupae, and adults, and later to include 2 life stages, viz. pre-adult and adult beetles. The pre-adult stage consists of eggs, larvae and pupae combined into one compartment. In view of the importance of nitrogen in plant growth an equation describing the rate of change of soil-nitrogen is introduced into the model. At this stage it becomes important to add a third component of dung, viz. buried dung. The burial of dung by beetles improves the soil decreasing nitrogen losses through volatilization, and by speeding up mineral recycling. To make the model more realistic time delays are introduced into the system of equations.

Throughout the development of the model steady state conditions are given. In each case 'local' stability analysis is performed. In this context local stability refers to the stability of a system in response to small perturbations or disturbances away from a steady state. If the perturbation is sufficiently small or localized about the point of equilibrium, then the stability of a nonlinear system will be identical to that of its linearized equivalent. Therefore the analysis of local stability reduces to the analysis for a linear system. Concerning the relevance of this method of analysis Cushing(1977) writes, "Although such local stability results are sometimes criticized as being too restrictive and inappropriate in general for the study of what should be a broader concept of 'ecological stability,' we will justify this approach by saying that such a study surely contributes at least a first step towards understanding the qualitative nature of models considered here."

PART 2 contains computed results. The numerical methods employed are also discussed in this section. Although some values of parameters used in the model were approximated from published data, a large number of the parameter values resulted from "guesstimates" made by the writer. In order to collect more data about beetles the Australian CSIRO has started a Dung-Beetle Research Station near Pretoria.

PART ONE

Formulation of the Model

and

Stability Analysis

CHAPTER TWO

DESCRIPTION OF THE BASIC MODEL

Basic assumptions for a grass-herbivore system will be given in this chapter. A constant herbivore population will be assumed to be grazing on a constant area of pastureland. The area will be "allowed" to vary due to the accumulation of herbivore-dung in the pasture. This highly simplified model of a grazing system will consist of 3 differential equations in all. These equations describe the net growth rate of green vegetation, and rates of change of areas covered by both fresh dung and dried dung.

2.1. ASSUMPTIONS AND FORMULATION OF THE MODEL

In Noy-Meier(1975) a simple grassland-grazing model is formulated and analysed in considerable detail. Jackson(1980) used this model in the formulation of a grassland-herbivore model with a changing area for grazing. The model that is derived in the present study is based on both these models on the grounds of simplicity and because they include only the minimum of grazing systems features that must be included in a basic model. Other grassland models could be used if it is desired to model particular grazing situations in greater and more realistic detail. The model is wholly deterministic and ignores a number of stochastic elements common to all grazing systems. Such factors might be introduced into a model using, say, a random number generator, e.g. in determining pasture growth patterns so as to simulate the unpredictability of weather changes, see Christian et al (1978).

2.1.1. BASIC ASSUMPTIONS

Grassland, as in Moore (1964), is considered here as a plant community in which the bulk of herbage consists of perennial grasses, there are very few or no shrubs, and trees are absent. V will denote the quantity of vegetation (per unit area) which is available both for producing plant growth and for consumption by animals.

Consider a situation where a herbivore population is grazing on pastureland of fixed area. The net growth rate of green vegetation(V) will be of the form :

$$\frac{\partial V}{\partial t} = \text{growth rate of green biomass} - \text{consumption rate of green vegetation by herbivores}$$

i.e.

$$\frac{dV}{dt} = G(V) - R(V,H) \qquad (1)$$

where V=quantity of green vegetation per unit area (g)
G=growth rate of green vegetation in the absence of herbivores (g/sec),
R=removal rate (by consumption) of green vegetation by herbivores (g/sec),
d/dt=differentiation w.r.t. time t .

Equation (1) holds for a case where the area covered by herbivore dung is taken as being negligible. It may be assumed that in the absence of a predation factor (herbivores) the growth of green vegetation will only be limited by the availability of space. All other factors like the abundancy of nitrates, environmental and seasonal changes are assumed to be constant. Green vegetation may be assumed to have exponential growth at low values of V, and that V will level off to a maximum value due to steadily increasing self-competition. Thus we obtain the logistic term

$$G(V) = g\,[1-V/V_{max}]\,V \qquad (2)$$

where g = maximum relative growth rate (per sec)

V_{max} = maximum value of green biomass per unit area (g)

Noy-Meier describes $V=V_{max}$ as the point at which 'maintenance' losses equals photosynthesis and then $G=0$. Using this definition of V_{max} the carrying capacity of a given pasture may be varied by, say, improving the fertility of the soil. An equation describing changes due to the variatiation of nitrates will be added in chapter 5.

The consumption rate of green vegetation by the herbivores is assumed to be dependent upon both the animal density and the available green vegetation. As in the model of Noy-Meier a function $R(V,H)$ that "...increases at low V and reaching a plateau at high V ..." will be chosen. Suggested possibilities :

$$R(V,H)=e_1 H\,(1-\exp[-kV])$$

and

$$R(V,H)=e_1 H\,V/(V+V_S) \qquad (3)$$

where e_1, V_S, and k are constants,

e_1 = maximum consumption rate per animal (g/sec/animal)

V_S = Michaelis constant (g),

H = animal density (number of animals per unit area)

The animal density (H) will be kept constant - as is the case in Noy-Meier. H is sometimes called a stocking rate. The qualitative behaviour of the system will be shown at different levels of the stocking rate. Assume that the herbivore population is not necessarily homogeneous. The stock may consist of, say, cattle and sheep. Then depending upon the amount of food taken up per day one sheep is assumed to be a certain fraction of a steer. As an example, if a sheep is consuming an average of 10kg/day of grass and a steer an average of 25kg/day then each sheep will be counted as 2/5 grazing units.

Only the Menton-Michaelis eqtn (3) will be used. The term $e_1HV/(V+V_s)$ is used to model the uptake (consumption) of vegetation by the herbivores. Noy-Meier(1975) describe the Michaelis constant V as a level of green vegetation at which the consumption rate is one half the maximum uptake rate. Combining equations (2) and (3) with eqtn (1) we obtain :

$$\frac{dV}{dt} = g\ V(t)\ [1-V(t)/V_{max}] - e_1\ HV(t)/[V(t)+V_s\ ] \qquad (4)$$

The first term on the right hand side is an 'upside down' parabola with zeros at V=0 and at $V=V_{max}$, while the second term is a right hyperbola with an asymptote at $V=-V_s$ and which approaches e_1H as V--$+\infty$. It is useful to plot these two terms on the same graph, and the most important possibilities are sketched in Fig. 2.1. Points $V=V_e$ in figure 2.1 (a) and (b) are points of stability whereas points $V=V_u$ in (b) and (c) are unstable equilibrium points representing cases of overgrazing to extinction.

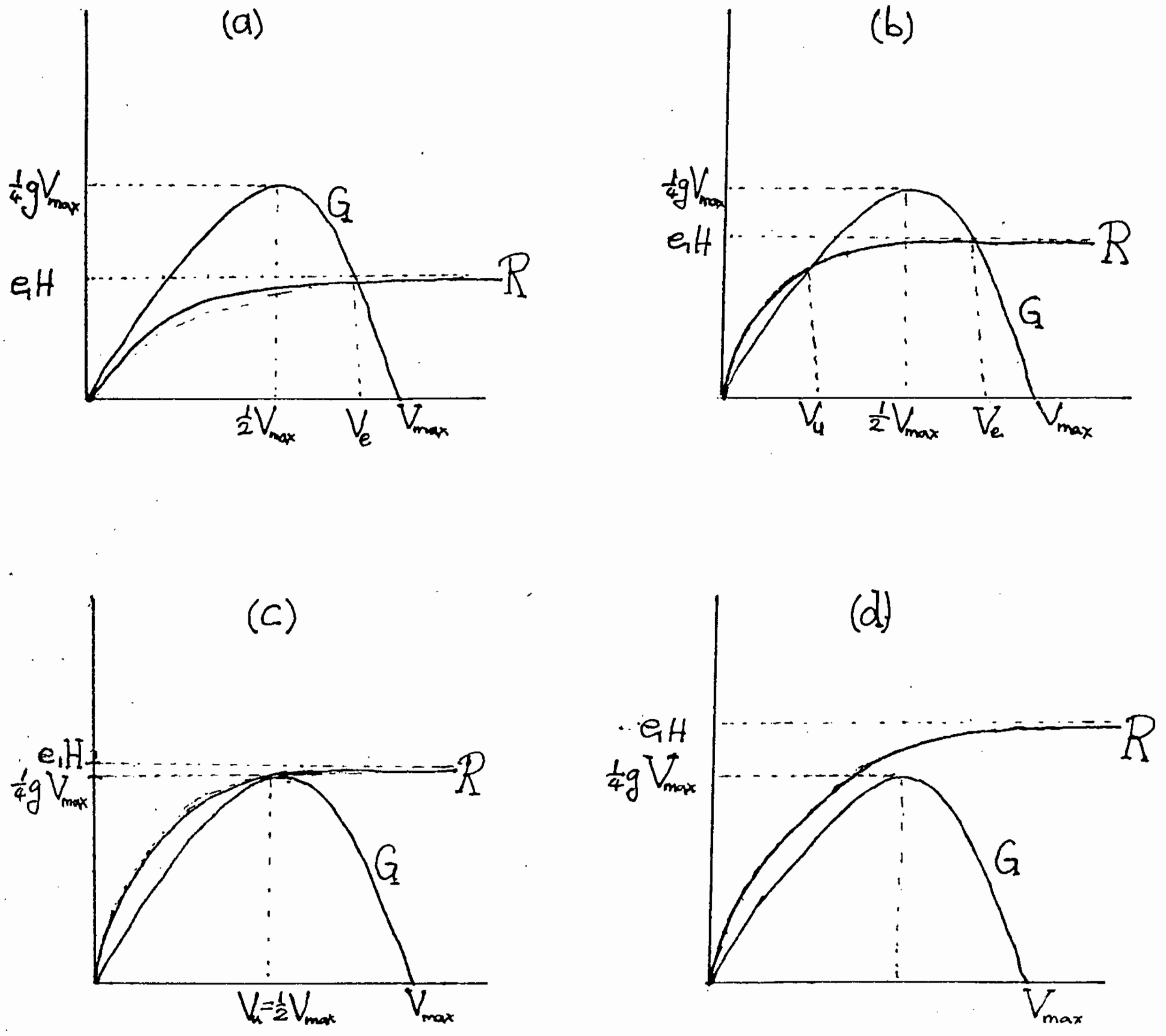
Figure 2-1. GRAPHS RESULTING FROM VARYING ANIMAL DENSITY, H

(a) Represents undergrazing for all values of V ;

(b) Steady-state and unstable turning point (V_u) leading to extinction of V;

(c) and (d) overgrazing to extinction for all values of V_u;

and $V_u=V_{max}/2$ in (c) represents an unstable point leading to extinction of V .



2.1.2. THE ACCUMULATION OF DUNG IN PASTURES.

The presence of herbivores may result in the accumulation of dung in pastures and thus reducing the area of grazing land. This may sensibly reduce the carrying capacity of a pasture. Assume that the total area of our grazing land is $\bar{A}_T$(hectare), the area covered by fresh dung is $\bar{F}$ (hectare), area covered by dried dung is $\bar{D}$ (hectare), and $\bar{A}$ (hectare) to be the area not covered by dung, i.e. the area available for plant growth. Thus it is clear that $\bar{A}=\bar{A}_T-\bar{F}-\bar{D}$. For convenience we shall redefine the above areas to be dimensionless as follows:

$F(t)=\bar{F}/\bar{A}_T$=area covered by fresh dung at any time t (dimensionless)

$D(t)=\bar{D}/\bar{A}_T$=area covered by dry dung at time t (dimensionless)

$A(t)=\bar{A}/\bar{A}_T$=area not covered by dung, i.e. area available for plant growth (dimensionless).

$$\therefore \quad A(t) = 1-F(t)-D(t) \tag{5}$$

When the grazing area A(t) changes the transformation of equation (4) is done in the following manner:

Let $\rho(t) = V(t)/A(t)$ = vegetative density (g)

so that $V(t)=\rho(t)A(t)$, then

$$\frac{dV}{dt} = A(t)\, d\rho/dt + \rho(t)\, dA/dt$$

Note that when $A(t)=1$ for all t then $V=\rho=G(V)$, (leaving aside removal rate by herbivores). This suggests that equation (4) can be modified to

$$\frac{dV}{dt} = gV_{(t)}\,[1 - V_{(t)}/V_{max}]\,A_{(t)} + \frac{V_{(t)}}{A_{(t)}}\frac{dA}{dt} - \frac{e_1 H V_{(t)}}{V_{(t)}+V_s} \tag{6}$$

Note that equation (5) implies

$$\frac{dA}{dt} = -\frac{dF}{dt} - \frac{dD}{dt} \qquad (7)$$

The consideration of the definition of V_{max} becomes important in examining the validity of equation (6). Again leaving aside consumption by animals, the present form of eqtn (6) (with the previous definition of V_{max} as being the maximum biomass per unit area) means that green vegetation can still grow to V_{max} no matter by how much A(t) is being reduced. For homogeneously distributed green vegetation in a grazing area $A \leqslant 1$ the maximum possible biomass is expected to be an A-th fraction of V_{max}, i.e. AV_{max}. Thus equation (6) can be improved to take the form:

$$\frac{dV}{dt} = g V_{(t)} \left[1 - \frac{V_{(t)}}{A_{(t)} V_{max}}\right] A_{(t)} + \frac{V_{(t)}}{A_{(t)}} \frac{dA}{dt} - \frac{e_1 H V_{(t)}}{V_{(t)} + V_s} \qquad (8)$$

where V = green vegetation (g)

H = herbivore density (animals / unit area)

A = area available for grazing (dimensionless)

g = maximum relative growth rate (per sec)

V_{max} = max value of green biomass per unit area (g)

e_1 = max consumption rate per animal (g/animal/sec)

V_s = Michaelis constant (g)

2.2. EQUATIONS FOR FRESH AND DRY DUNG

In the mathematical model by Jackson(1980) the following assumptions are made: The rate of deposition of fresh dung is proportional to the consumption rate of vegetation. The rate at which fresh dung changes to dry dung is proportional to the amount of fresh dung instantaneously present, and that dry dung erodes, or is removed by bacterial action, at a rate proportional to the amount of dry dung instantaneously present. Although these assumptions ignore many factors they will also be adopted in the present model.

In this version of the model the quantity of fresh dung is expressed in terms of its dry weight (dry matter) thus eliminating the factor of evaporation. The simple relationship between the quantity of dung and the area it covers is derived from the assumption that fresh dung is moist enough and hence plastic enough to cover an average area proportional to its mass. Fresh dung is assumed to be deposited according to a uniform probability distribution over the unit area under consideration as the herbivores move randomly about. The dung will then fall on uncovered grass with probability A(t), where A(t) is the dimensionless area of uncovered pasture. Thus two additional equations can now be given.

$$\dot{F}=(\alpha/e_1)R(V,H)A-cF \qquad (10)$$

$$\dot{D}=cF-bD \qquad (11)$$

where $F(t)$ = area covered by fresh dung at time t

$D(t)$ = area covered by dry dung at any time t

$R(V,H)= eHV/[V+V]$

α, c, b are all positive constants (sec^{-1})

Equations (8), (10), and (11) describe a simple grazing system model with the area of grassland varying because of the accumulation of dung. The model now consists of the following system of equations:

$$\frac{dV}{dt} = g\,V_{(t)}\left[A_{(t)} - V_{(t)}/V_{max}\right] + \frac{V_{(t)}}{A_{(t)}}\frac{dA}{dt} - \frac{e_1 H V_{(t)}}{V_{(t)} + V_s}$$

$$\frac{dF}{dt} = \frac{\alpha H A_{(t)} V_{(t)}}{V_{(t)} + V_s} - cF_{(t)} \qquad (M)$$

$$\frac{dD}{dt} = cF_{(t)} - b\,D_{(t)}$$

In chapter 3 system (M) will be analysed about an equilibrium point. Steady state conditions are given. Liapunov stability theorem is applied in analysing the stability of the system.

CHAPTER THREE

STABILITY OF THE GRAZING SYSTEM

Questions about the global stability of nonlinear systems are generally quite difficult to answer. Nevertheless, the analysis of local stability can be developed easily and it will be extremely useful for the analysis to be performed both here and in later chapters. Assuming that a sufficiently small perturbation is introduced into a system about an equilibrium point, then the stability of a nonlinear system will be identical to that of its linearized equivalent (Savageau, 1976). For a more detailed discussion of stability see LaSalle (1961), May (1971,1973,1977); Rosen (1970).

A simple model of a grass-herbivore system with a changing area for grazing, due to the accumulation of dung, was presented in Chapter 2. In the present chapter steady state conditions of the system of equations (2.M) are considered. The system (2.M) is linearized in section 3.2 and local stability analysis is carried out. The linear approximation is useful primarily because there are powerful methods of linear mathematical analysis with which the local behavior of the system being approximated can be predicted accurately. A discussion of Liapunov stabilty theorems and Routh-Hurwitz stability criterion is given in Appendices B , and A , respectively.

3.1. STEADY STATE CONDITIONS.

When the point of equilibrium is reached then we have

$$\frac{dV}{dt} = \frac{dF}{dt} = \frac{dD}{dt} = \frac{dA}{dt} = 0 \ .$$

Let V_e , F_e , D_e , and A_e represent steady state values of V , F D and A respectively. Then, at equilibrium, the system of equations (M) implies that :

$$gV_e\left[A_e - V_e/V_{max}\right] = e_1 H V_e/\left[V_e+V_s\right] ,$$

$$\alpha H V_e A_e/\left[V_e+V_s\right] = cF_e ,$$

$$cF_e = bD_e \ .$$

Note that $A_e = 1 - F_e - D_e$.

Eliminating F_e , D_e , and A_e we obtain

$$\frac{g}{e_1 H}\left[V_e+V_s\right] - \frac{gV_e}{e_1 c H V_{max}}\left\{\left[V_e+V_s\right]c + \gamma\alpha H V_e\right\} = 1 + \frac{\gamma\alpha H V_e}{c\left[V_e+V_s\right]} \qquad (1)$$

where $\gamma = (b+c)/b$.

This equation for V_e has the same roots as the cubic equation

$$\frac{g}{e_1 H}\left[V_e+V_s\right]^2 - \frac{g}{e_1 c H V_{max}} V_e\left\{\left[V_e+V_s\right]^2 c + \gamma\alpha H V_e\left[V_e+V_s\right]\right\} = \left[V_e+V_s\right] + \frac{\gamma\alpha H V_e}{c} \qquad (2)$$

and it may be interpreted graphically by letting

$$y_1(V_e) = \frac{g}{e_1 H}\left[V_e+V_s\right] - \frac{gV_e}{e_1 H c V_{max}}\left\{\left[V_e+V_s\right]c + \gamma\alpha H V_e\right\} \qquad (3)$$

which is a parabola,

and $$y_2(V_e) = 1 + \frac{\gamma\alpha H}{c}\,\frac{V_e}{V_e+V_s} \qquad (4)$$

which is a hyperbola .

We note that

$$y_1(0)=\frac{gV_s}{e_1 H}\quad ; \qquad y_2(0)=1 \quad ;$$

$$y_1(-V_s)=-\frac{\gamma\alpha g V_s^2}{c e_1 V_{max}}\quad ; \qquad y_2(-V_s)=-\infty$$

$$y_2 \longrightarrow 1+\frac{\gamma\alpha H}{c} \quad \text{as} \quad V_e \longrightarrow +\infty$$

Let V_2 be a root of $y_2(V)=0$

then $y_2(V_2)=0 \implies V_2=-\frac{cV_s}{c+\gamma\alpha H}$

Denote the roots of $y_1 = 0$ by $V_\pm$;

then . $$V_\pm = \frac{-(c-cV_s/V_{max}) \pm \sqrt{(c-cV_s/V_{max})^2+4c[c+\gamma\alpha H]V_s/V_{max}}}{2[c+\gamma\alpha H]/V_{max}} .$$

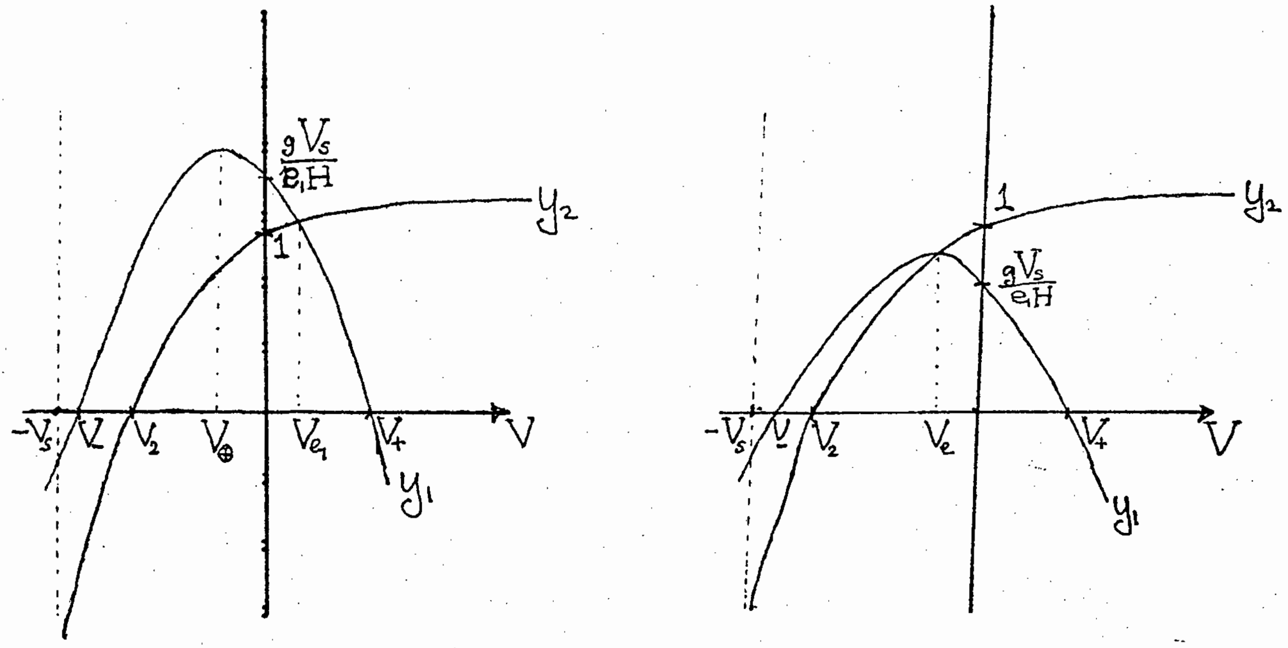
Also note the following

$$y_1(V_2) = \frac{g\gamma\alpha V_s}{e_1[c+\gamma\alpha H]} > 0$$

$$\frac{dy_1}{dV_e}=0 \quad \text{at} \quad V_e = -\frac{[V_{max}-V_s]c}{2[c+\gamma\alpha H]}$$

The possible situations are shown on the graphs in Fig 3.1 below:

Figure 3-1. POSSIBLE STEADY STATE SITUATIONS



(a): Undergrazing at all values of V_{e_1} in the case where $gV_s > e_1H$.

(b): Overgrazing to a low value of V_e with $gV_s < e_1H$.

From fig 3.1 it can be deduced that the cubic eqtn (2) has one real root and two complex conjugate roots. Thus the system of eqtns (1.M) will have only one point of equilibrium. In section 3.2 system (1.M) will be linearized about this equilibrium point, viz. (V_e, E_e, D_e).

3.2. LIAPUNOV STABILITY

Liapunov's stability theorem states that if for a system of differential equations

$$\dot{\underset{\sim}{X}} = \underset{\sim}{f}(\underset{\sim}{X}) \qquad (5)$$

there exists a scalar function $L(\underset{\sim}{X})$ such that $L(\underset{\sim}{X})$ is continuous together with its first partial derivatives in a certain open region about the origin, and such that both $L(\underset{\sim}{X})$

and $-\dot{L}(\underset{\sim}{X}) = -\underset{\sim}{X}\cdot\mathrm{grad}[L(\underset{\sim}{X})]$ are positive definite then the system (5) is asymptotically stable in the region .

In the present study we are only interested in local stability analysis. System (M) must first be linearized before conditions for local stability can be given. Let $x_1(t)=V(t)-V_e$, $x_2(t)=F(t)-F_e$, and $x_3(t)=D(t)-D_e$, where the x_i , $i=1,2,3$, are small pertubations from the equilibrium point. The linearized equivalent of system (M) is given by

$$\begin{aligned}\dot{x}_1 &= -a_{11}x_1 + a_{12}x_2 + a_{13}x_3 \;; \\ \dot{x}_2 &= a_{21}x_1 - a_{22}x_2 - a_{23}x_3 \;; \\ \dot{x}_3 &= c\,x_2 - b\,x_3\end{aligned} \qquad (6)$$

where $a_{11} = e_1 H V_s/[V_e+V_s]^2 + \alpha H V_e V_s/[V_e+V_s]^2 + g[2V_e/V_{max} - A_e]$;

$$a_{12} = \alpha H V_e^2/[A_e\{V_e+V_s\}] \;;$$

$$a_{13} = \{\alpha H V_e/[V_e+V_s] + b\} V_e/A_e \;;$$

$$a_{21} = \alpha H A_e V_s/[V_e+V_s]^2 \;;$$

$$a_{22} = c + \alpha H V_e/[V_e+V_s] \;;$$

$$a_{23} = \alpha H V_e/[V_e+V_s] \,.$$

Let a Liapunov function be

$$L(x_1,x_2,x_3) = \tfrac{1}{2}\cdot\{l_1 x_1^2 + l_2 x_2^2 + l_3 x_3^2\} \,,$$

where the l_i are all non-negative constants to be determined. Now differentiating function L w.r.t time

$$\begin{aligned}\frac{dL}{dt} &= l_1 x_1 \dot{x}_1 + l_2 x_2 \dot{x}_2 + l_3 x_3 \dot{x}_3 \\ &= -\left(\sum_{i=1}^{3} l_i a_{ii} x_i^2\right) + (l_1 a_{12} + l_2 a_{21})\,x_1 x_2 + l_1 a_{13} x_1 x_3 - (l_3 c - l_2 a_{23})\,x_2 x_3\end{aligned}$$

from equations (6).

Choose $\lambda_2 = \frac{c\lambda_3}{a_{23}}$;

so that $\frac{dL}{dt} = -(qx_1 - px_2)^2 - (rx_1 - sx_3)^2$

$$= -(q^2+r^2)x_1^2 - p^2x_2^2 - s^2x_3^2 + 2pq\,x_1x_2 + 2rs\,x_1x_3$$

provided that $p^2 = a_{22}c\lambda_3/a_{23}$ (7a)

$s^2 = b\lambda_3$ (7b)

$r^2 = a_{13}^2\lambda_1^2/(4b\lambda_3)$ (7c)

$q^2 = a_{23}[a_{12}\lambda_1 + a_{21}c\lambda_3/a_{23}]^2/(a_{22}c\lambda_3)$ (7d)

$q^2 + r^2 = \lambda_1 a_{11}$ (7e)

Using these values of r and q in eqtn (7e) we get the following relationship :

$$\left[\frac{a_{12}\lambda_1 + c\,a_{21}\lambda_3/a_{23}}{2\sqrt{a_{22}c\lambda_3/a_{23}}}\right]^2 + \left[\frac{a_{13}\lambda_1}{2\sqrt{b\lambda_3}}\right]^2 = \lambda_1 a_{11}$$

If $\lambda_2 = c/a_{23}$, and $\lambda_3 = 1$ we have

$$\left[\frac{a_{13}^2}{4b} + \frac{a_{23}a_{12}^2}{4a_{22}c}\right]\lambda_1^2 + \left[\frac{a_{12}^2}{2a_{22}} - a_{11}\right]\lambda_1 + \frac{a_{21}^2c}{4a_{22}a_{23}} = 0$$

which is a quadratic equation in λ_1 .

Hence $$\lambda_1 = \frac{\left(a_{11} - \frac{a_{12}^2}{2a_{22}}\right) \pm \sqrt{\left(a_{11} - \frac{a_{12}^2}{2a_{22}}\right) - 4\left(\frac{a_{13}^2}{4b} + \frac{a_{23}a_{12}^2}{4a_{23}c}\right)\left(\frac{a_{21}^2c}{4a_{22}a_{23}}\right)}}{2\left(\frac{a_{13}^2}{4b} + \frac{a_{23}a_{12}^2}{4a_{22}c}\right)}$$

For λ_1 to be real we must have

$$\left(2a_{11} - \frac{a_{12}^2}{a_{22}}\right)^2 \geq \left(\frac{a_{13}^2}{b} + \frac{a_{23}a_{12}^2}{a_{22}c}\right)\left(\frac{a_{21}^2c}{a_{22}a_{23}}\right)$$

and for λ_1 to be positive we require that

$$a_{11} > \frac{a_{12}^2}{2a_{22}}$$

It follows that the model (M) of the grassland-herbivore system is asymptotically stable near an equilibrium point provided that these conditions are satisfied.

CHAPTER FOUR

EXTENSION OF MODEL TO INCLUDE BEETLES

In this chapter compartments for dung-beetle activities will be added to the simple model presented in chapter 2. Seasonal phenomena will still be averaged over the year. A brief discussion of the model by Jackson(1980) will be given in section 4.1. In section 4.2 we discuss in detail the modified model with 4 beetle life stages, viz. egg, larval, pupal and adult stages. Section 4.3 ends the chapter by questioning the necessity of having to include 4 life stages of beetles; and hence an analysis of the version of the model with 2 beetle life stages, viz. pre-adult and adult stages concludes the discussion.

4.1. MODEL WITH ONE ADDITIONAL DIFFERENTIAL EQUATION

Jackson derived a highly simplified model of a dung-beetle population which was added to a simple grazing system. A few of the assumptions that were made are listed below:

(1) A single continuous variable, $B(t)$, is sufficient to describe the adult beetle population, and that all stages of the life cycle can be lumped together without taking into account time delays between generations.

(2) The beetle population grows according to a logistic law, with the amount of fresh dung available acting as the limiting factor.

(3) The beetles constantly redistribute themselves uniformly throughout the fresh dung and use it for

both nutrition and reproduction according to a Michaelis law that allows for satiation.

A system of differential equations of this version of the moodel analysed by Jackson will be given below for easy reference.

$$\begin{aligned}
\frac{dV}{dt} &= g\,V(t)\,[1-V(t)/V_{max}]\,A(t) + \frac{V(t)}{A(t)}\frac{dA}{dt} - \frac{e_1 H V(t)}{V(t)+V_s} \\
\frac{dF}{dt} &= \frac{\alpha H V(t) A(t)}{V(t)+V_s} - cF(t) - \frac{e_2 B(t)\,F(t)}{F(t)+F_5} \qquad\qquad (J) \\
\frac{dD}{dt} &= cF(t) - bD(t) \\
\frac{dB}{dt} &= d_1 B(t)\,[e_3 F(t) - B(t)]
\end{aligned}$$

where B(t) is the number of betlees present at any time t, D(t) and F(t) are respectively areas covered by dry and fresh dung, V is mass of green vegetation . Positive constants g, e_1, V_s, α, e_2, b, d, and area A=1-F-D same as defined in Chapter 2, page 7.

The main handicap of model (J) is the assumption that beetles give birth to young which immediately perform the same duties, as far as the removal of fresh dung is concerned, as the adults. In actual fact the young must still go through egg, larval, and pupal stages and only then become fully developed beetles. Instead of making this gross simplification of a biological reality, these different life stages deserve consideration.

Note that in the model (2.M) for grazing systems developed in chapter 2 the equation for the net change rate of green biomass was assumed to be

$$\frac{dV}{dt} = g\,V(t)\,[1 - V(t)/((A(t)V_{max})]A(t) + \frac{V(t)}{A(t)}\frac{dA}{dt} - \frac{e_1 H V(t)}{V(t)+V_s}$$

Another point to be noted is that rather than just assuming that the birth rate of beetles will be proportional to the abundancy of fresh dung (at high values of F this can lead to explosive increases of beetle populations) a replacement of F, in the equation describing the growth rate of beetles, by a Menton-Michaelis term $[F/(F+F_s)]$, where F_s is a Michaelis constant, may improve the model. This gives:

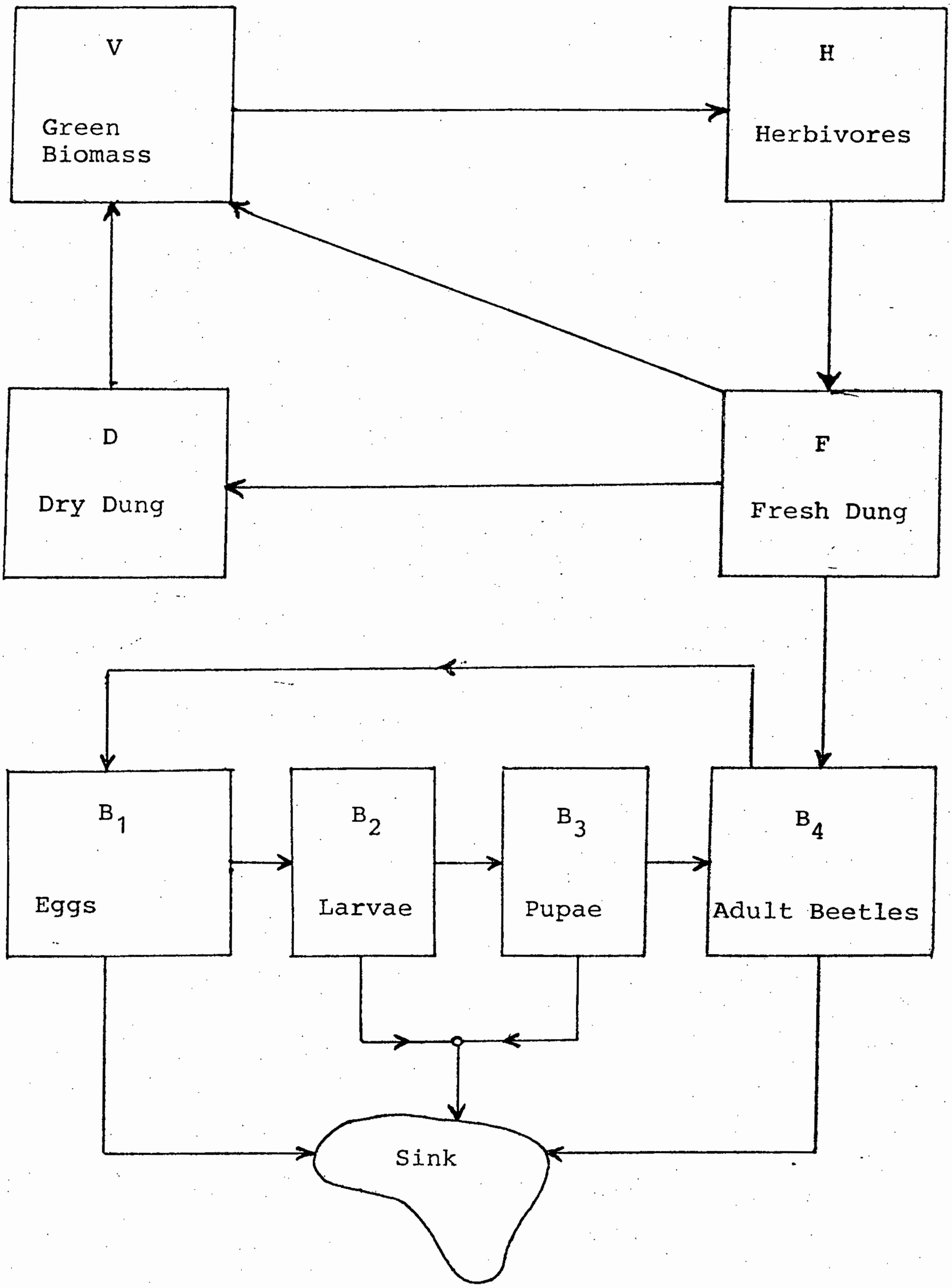
$$\frac{dB}{dt} = d_1 B(t) \left[\frac{e_3 F(t)}{F(t)+F_s} - B(t) \right]$$

In section 4.2 the model will be extended to include all the pre-adult life stages, i.e. eggs, larvae, and pupae.

4.2. MODEL WITH 4-BEETLE LIFE STAGES.

In this section models (2.M) and (4.J) will be modified to include beetles with their pre-adult stages. A flow chart of the model is shown in Fig 4.1. The sink indicates beetle biomass "flowing out" of the system due to deaths at different life stages.

Figure 4.1 : FLOW CHART OF A GRAZING SYSTEM



Sink indicates biomass leaving the system because of the death of beetles.

4.2.1. ASSUMPTIONS

Assume that the rate at which eggs are laid is a product of a function of $h_1(F)$ of fresh dung and a function $f_1(B_4)$ of adult beetles. As seen in section 4.1 the function h_1 will be chosen from the pair of possible forms,

$$h_1(F) = \begin{cases} F \\ \text{or} \\ F/[F+F_s] \end{cases} \qquad (1)$$

for convenience in the analysis of the mathematics of the model. For $f_1(B_4)$ either an open system may be assumed, i.e. where the beetle population increases exponentially with $f_1(B_4)=B_4$, or a case where the birth rate will be inhibited by overcrowding of adult beetles (B_4), i.e. $f_1(B_4)=B_4[1-B_4/B_{max}]$. This assumes that at high values of B_4 the competition will be so high that the rate will drop, reaching zero at $B_4=B_{max}$. This assumption is in line with Bornemissza's (1970) observation that in the field when beetle populations are high, the nests of each pair seldom contain more than 10 or 12 brood balls, one egg per brood ball, owing to intense competition for dung. A single pair of beetles can construct up to 40 brood balls in one nest, depending on the availability of fresh dung (Bornemissza, 1970). Thus

$$f_1(B_4) = \begin{cases} B_4 \\ \text{or} \\ B_4\,[1-B_4\,/B_{max}] \end{cases} \qquad (2)$$

will be appropriate mathematical forms.

Further assume that constant proportions of eggs, larvae, and pupae are subjected to natural mortality and to graduation to the next life stage per unit time. In the case of adult beetles the mortality rate is assumed to be a function of the amount of fresh dung present. The contribution of predation to the mortality rates at different life stages will not be included since very few observations have been done in that area. Assume that the mortality rate of adult beetles, due to starvation, is at a maximum when F=0 and that it decreases as F increases. Taking $f_2(F)$ as a natural mortality factor the expected behaviour of f is shown in Fig 4.2.

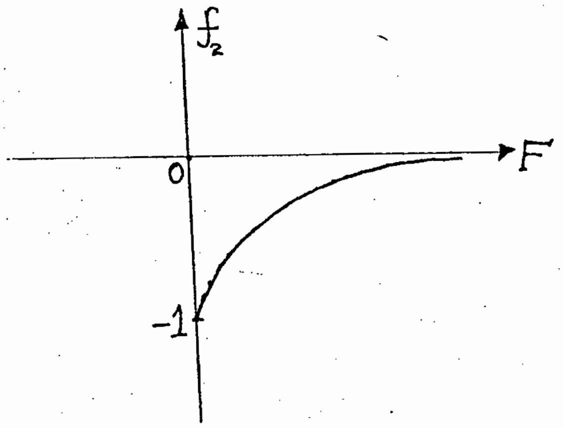


Figure 4-2. DIAGRAM SHOWING RELATIVE MORTALITY RATE.

The shape of figure 4.2 suggests that

$$f(F) = \begin{cases} -\exp(-d_2 F) \\ \text{or} \\ -[F+E_2] \end{cases} \qquad (3)$$

where d_2 and E_2 are positive constants, will be accurate enough mathematical descriptions of the relative mortality rate. In the next sub-section a system of equations of our model with four life stages will be given.

4.2.2. THE EQUATIONS OF THE MODEL WITH 4 LIFE STAGES

From the assumptions given in subsection 4.2.2 the system of differential equations for the modified model may now be written as follows:

$$\frac{dV}{dt} = g\,V(t)\left[1 - \frac{V(t)}{A(t)V_{max}}\right]A(t) + \frac{V(t)}{A(t)}\frac{dA}{dt} - \frac{e_1 H V(t)}{V(t)+V_s} \qquad (4)$$

$$\frac{dF}{dt} = \frac{\alpha H A(t) V(t)}{V(t)+V_s} - cF(t) - e_3 B_4(t)\, h_1(F(t)) \qquad (5)$$

$$\frac{dD}{dt} = cF(t) - bD(t) \qquad (6)$$

$$\frac{dB_1}{dt} = k_1 \cdot h_1(F(t)) \cdot f_1(B_4(t)) - g_1 B_1(t) - m_1 B_1(t) \qquad (7)$$

$$\frac{dB_2}{dt} = g_1 B_1(t) - g_2 B_2(t) - m_2 B_2(t) \qquad (8)$$

$$\frac{dB_3}{dt} = g_2 B_2(t) - g_3 B_3(t) - m_3 B_3(t) \qquad (9)$$

$$\frac{dB_4}{dt} = g_3 B_3(t) + m_4 f_2(F(t)) \cdot B_4(t) \qquad (10)$$

As usual $A(t) = 1 - F(t) - D(t)$ (11)

and B_1, B_2, B_3, and B_4 are, respectively, biomasses of beetle egg, larval, pupal, and adult compartments (g) at any time t. V is the mass of green vegetation (g). D and F are respectively areas covered by dry and fresh dung.

and $h_1(F)$, $f_1(B_4)$, $f_2(F)$ are chosen from functions shown in equations (1), (2),. and (3) respectively,

and the positive constants k_1, g_i, m_i are defined below as:

k_1 = maximum relative production rate of eggs (sec^{-1})

g_i = relative recruitment rates from the i-th population class to the (i+1)-th class, for i=1,2,3; (sec^{-1})

m_i = relative natural mortality rates (sec^{-1}), i=1,2,3,4.

4.2.3. STEADY STATE CONDITIONS.

At a steady state the time derivatives in equations (4) to (10) will be equal to zero. Let the steady state values of B_1, B_2, B_3, B_4, D, F, and V be represented by B_{1e}, B_{2e}, B_{3e}, B_{4e}, D_e, F_e, and V_e respectively. Then for the particular case where $f_1(B_4)=B_4[1-B_4/B_{max}]$, $f_2(F)=-\exp(-d_2F)$ and $h_1(F)=F/[F+F_s]$ eqtns (4) to (11) imply that :

$$B_{1e}=\frac{(g_2+m_2)(g_3+m_3)m_4}{g_1\,g_2\,g_3}\cdot\exp(-d_2F_e)\cdot B_{4e}\quad;$$

$$B_{2e}=\frac{(g_3+m_3)m_4}{g_2\,g_3}\cdot\exp(-d_2F_e)\cdot B_{4e}\quad;$$

$$B_{3e}=\frac{m_4}{g_3}\cdot\exp(-d_2F_e)\cdot B_{4e}\quad;$$

$$B_{4e}=B_{max}\left[1-\left\{\prod_{i=1}^{3}\left(\frac{g_i+m_i}{g_i}\right)\right\}m_4\left\{\frac{F_e+F_s}{k_1F_e}\right\}\cdot\exp(-d_2F_e)\right]$$

Now using $D_e=cF_e/b$ and $A_e=1-F_e-D_e=1-(b+c)F_e/b$ together with equations (4) and (5) we get the following families of graphs:

$$y_1(V,F) = V/[V+V\ ]-\Phi_1(F)$$

$$y_2(V,F) = -V/V-[eH/g]/[V+V\ ] - \Phi(F)$$

where $y_1(V_e, F_e) = y_2(V_e, F_e) = 0$ simultaneously.

y_1 and y_2 dependent upon the parameter F_e via

$$\Phi_1(F_e) = \frac{1}{\alpha H\cdot[1-(\frac{b+c}{b})F_e]}\cdot\left[1-\left\{\prod_{i=1}^{3}\left(\frac{g_i+m_i}{g_i}\right)\right\}m_4\left\{\frac{F_e+F_s}{k_1F_e}\right\}\cdot\exp(-d_2F_e)\right]$$

$$\Phi_2(F_e) = ([b+c]/b)F_e-1.$$

Functions ϕ_1 and ϕ_2 are defined for $0<F_e<b/[b+c]$ and these functions are increasing in this interval. As F_e increases from zero through its allowable range the graphs of y_1 and y_2 are both translated vertically downwards. During this translation the intersection of the two graphs moves downwards and to the right. When $F=F_e$ then $y_1=y_2=0$ and the point of intersection is at $V=V_e$ on the V-axis. The foregoing discussion is shown graphically in Fig 4.3.

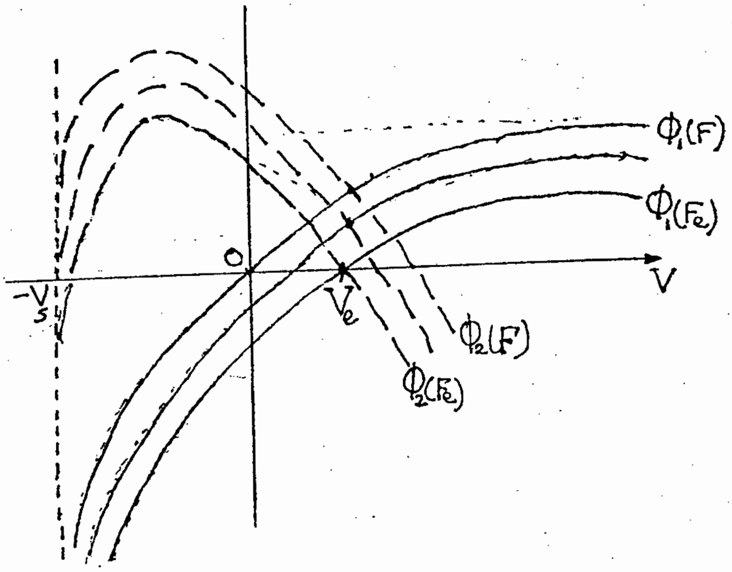


Figure 4-3. DIAGRAM OF INTERSECTIONS OF ϕ_1 AND ϕ_2

If the intersection of the graphs given by eqtns (2.13) and (2.14) yielded a unique positive steady state V_{e_1} (see Fig 2.2a) then Fig 4.3 shows that there will be a unique positive steady state V_e for the model (4) to (11) such that $V_{e_1} < V_e$. Note that the first necessary requirement for this steady state case is that $gV_s>e_1H$.

4.2.4. STABILITY ANALYSIS.

Let $h_1(F)=F/[F+F_S]$ and $f_1(B_4)=B_4[1-B_4/B_{max}]$ in equations (5) and (7) and linearize system (4) to (10) about an equilibrium point (B_{1e}, B_{2e}, B_{3e}, B_{4e}, D_e, F_e, V_e) found in section 4.2.3 for the case $V_e>0$. Let $B_i=B_{ie}+x_i$ for i=1,2,3,4 and let $D=D_e+x_5$, $F=F_e+x_6$, $V=V_e+x_7$. The x_i's, for i=1,2,...,7, are small perturbations from the above equilibrium point of the system. By ignoring small quantities of second order and higher we obtain the linearized system:

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{x}_3 \\ \dot{x}_4 \\ \dot{x}_5 \\ \dot{x}_6 \\ \dot{x}_7 \end{bmatrix} = \begin{bmatrix} -h_1 & 0 & 0 & -w_{14} & 0 & w_{16} & 0 \\ g_1 & -h_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & g_2 & -h_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & g_3 & -h_4 & 0 & w_{46} & 0 \\ 0 & 0 & 0 & 0 & -h_5 & c & 0 \\ 0 & 0 & 0 & -w_{64} & -w_{65} & -h_6 & w_{67} \\ 0 & 0 & 0 & w_{74} & w_{75} & w_{76} & -h_7 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \\ x_6 \\ x_7 \end{bmatrix} \qquad (M_L)$$

where: $h_i = g_i + m_i$ for $i=1,2,3$; $\qquad h_4 = m_4 \exp(-d_2 E_e)$

$h_6 = (c + \alpha HV_e / \{V_e + V_s\} + e_3 B_{4e} F_s / [F_e + F_s]^2)$; $\qquad h_5 = b$

$h_7 = g(2V_e/V_{max} - A_e) + (e_1 H + \alpha HV_e) V_s / (V_s + V_e)^2$

$w_{14} = (k_1 F_e / [F_e + F_s])(2B_{4e} / B_{max} - 1)$;

$w_{16} = \{k_1 F_s / (F_e + F_s)^2\} [1 - B_{4e} / B_{max}]$

$w_{64} = e_3 F_e / (F_e + F_s)$; $\qquad w_{65} = \alpha HV_e / (V_e + V_s)$;

$w_{67} = \alpha H A_e V_s / [V_e + V_s]^2$

$w_{74} = e_3 F_e V_e / [A_e (F_e + F_s)]$; $\quad w_{75} = -gV + \alpha H (V_e)^2 / [A_e (V_e + V_s)]$;

$w_{76} = (V_e / A_e)(-gA_e + e_3 B_{4e} F_e / (F_e + F_s) + \alpha HV_e / [V_e + V_s])$

System (M) is a linear system of the form:

$$\dot{\underset{\sim}{X}} = M \underset{\sim}{X}$$

where $\underset{\sim}{X} = (x_1, x_2, \ldots, x_7)^T$ and $\dot{\underset{\sim}{X}}$ its time derivative, M is a 7 by 7 matrix with constant coefficients.

Let $a_1 = h_1 + h_2 + h_3 + h_4$

$a_2 = h_1 h_2 + h_1 h_3 + h_1 h_4 + h_2 h_3 + h_2 h_4 + h_3 h_4$

$a_3 = h_1 h_2 h_3 + h_1 h_2 h_4 + h_2 h_3 h_4 + h_1 h_3 h_4$

$a_4 = h_1 h_2 h_3 h_4 + w_{14} g_1 g_2 g_3$

We shall use the following convention:

$\overset{\Sigma}{\Pi}_{r,s,\ldots}(h_i h_j \ldots)$ = summation of products $(h_i h_j \ldots)$ where $i, j, \ldots$ are the combinations of $(r, s, \ldots)$.

e.g. $a_1 = \overset{\Sigma}{\Pi}_{1,2,3,4}(h_i)$; $a_2 = \overset{\Sigma}{\Pi}_{1,2,3,4}(h_i h_j)$; $a_3 = \overset{\Sigma}{\Pi}_{1,2,3,4}(h_i h_j h_k)$

The characteristic polynomial of the matrix M is $p(\lambda) = \det(M-\lambda I)$

i.e. $p(\lambda) = -[\lambda^7 + p_1\lambda^6 + p_2\lambda^5 + p_3\lambda^4 + p_4\lambda^3 + p_5\lambda^2 + p_6\lambda + p_7]$

where $p_1 = \sum_{i=1}^{7} h_i$

$p_2 = \overset{\Sigma}{\Pi}_{1,2,\ldots,7}(h_i h_j) + w_{67}w_{76} + c\ w_{65}$

$p_3 = \overset{\Sigma}{\Pi}_{1,2,\ldots,7}(h_i h_j h_k) + h_5 w_{67}w_{76} + c\ w_{67}w_{75} + c h_5 w_{65} + a_1 c\ w_{65} + g_3 w_{64}$

$p_4 = \overset{\Sigma}{\Pi}_{1,2,\ldots,7}(h_i h_j h_k h_l) + w_{14} g_1 g_2 g_3 + a_1 h_5 w_{67}w_{76} + a_2 w_{67}w_{76} + a_1 w_{67}w_{75}$

$+ a_1 c h_7 w_{65} + a_2 c\ w_{65} + g_3 w_{67}w_{74} + g_3 w_{64}[\overset{\Sigma}{\Pi}_{1,2,5,7}(h_i)]$

$p_5 = \overset{\Sigma}{\Pi}_{1,2,\ldots,7}(h_i h_j h_k h_l h_m) + a_2 h_5 w_{67}w_{76} + a_3 w_{62}w_{76} + a_2 c\ w_{67}w_{75} + a_2 c h_7 w_{65}$

$+ a_3 c\ w_{65} + g_3 w_{67}w_{74}(h_1 + h_2 + h_5) + g_3 w_{64}\overset{\Sigma}{\Pi}_{1,2,5,7}(h_i h_j) + g_1 g_2 g_3 w_{14}(h_5 + h_6 + h_7)$

$p_6 = \overset{\Sigma}{\Pi}_{1,2,\ldots,7}(h_i h_j h_k h_l h_m h_n) + a_3 h_5 w_{67}w_{76} + [w_{67}w_{76} + c\ w_{65}]h_1 h_2 h_3 h_4 + a_3 c\ w_{67}w_{75}$

$+ a_3 c h_7 w_{65} - g_3 w_{67}\overset{\Sigma}{\Pi}_{1,2,5}(h_i h_j) + g_3 w_{64}\overset{\Sigma}{\Pi}_{1,2,5,7}(h_i h_j h_k) + g_1 g_2 g_3 w_{16}w_{64}$

$+ g_1 g_2 g_3 [w_{14}w_{67}w_{75} + w_{16} w_{67}w_{74} + c\ w_{14}w_{65} + w_{14}\overset{\Sigma}{\Pi}_{5,6,7}(h_i h_j)]$

$p_7 = h_1 h_2 h_3 h_4 h_5 h_6 h_7 + (h_5 w_{67}w_{76} + c\ w_{67}w_{76} + c\ h_7 w_{65})h_1 h_2 h_3 h_4$

$$-g_3 h_1 h_2 h_5 w_{67} + g_3 h_1 h_2 h_5 h_7 w_{64} + g_1 g_2 g_3 [h_5 h_6 h_7 w_{14}$$

$$+ h_5 w_{14} w_{67} w_{75} + h_5 w_{16} w_{67} w_{74} + h_7 w_{14} w_{65} + c\; w_{14} w_{67} w_{75}].$$

The first Hurwitz stability criterion is that $p_i > 0$ for $i=1,2,\ldots,7$. (The Hurwitz theorem for stability is given in Appendix A). This is satisfied if the terms $g_3 w_{67}$, $\prod^{\neq}_{1,2,5}(h_i h_j)$ and $g_3 h_1 h_2 h_5 w_{67}$ are small enough.

The second condition for stability is that all determinants of the principal matrices of the Hurwitz matrix must be positive, where principal submatrices of H are defined below. Element H_{ij} of the k-th submatrix D_k is defined as

$$H_{ij} = \begin{cases} p & \text{if } \; 0 < 2j-i < k \\ 0 & \text{otherwise} \end{cases}$$

where $k=1,2,\ldots,7$.

Thus provided that these two conditions are satisfied it means that a necessary and sufficient requirement for polynomial $p(\lambda)$ to have zeros with negetive real parts only is satisfied near the equilibrium point $(V_e,\; F_e,\; D_e,\; B_{1e},\; B_{2e},\; B_{3e},\; B_{4e})$.

4.2.5. ISOLATION OF DUNG-BEETLE SUBMODEL.

ASSUMPTION: In this section we assume that a small disturbance introduced to the dung beetle population, when the system is in equilibrium, will cause an infinitesimally small perturbation in fresh dung, i.e. this latter pertubation may be ignored. This assumption may only be expected to hold in situations where equilibrium is reached at a high value of F.

Since the beetles do not directly interact with both the green plants and the dry dung it means that we can consider the local stability of the submodel consisting of only those equations which describe the 4 beetle life stages. Using the notation of the previous section this implies that $x_5=x_6=x_7=0$, i.e. the remaining variables of the model remain at their equilibrium values to within second order perturbations; not first order. The linear system to be considered is thus:

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \\ \dot{x}_3 \\ \dot{x}_4 \end{bmatrix} = \begin{bmatrix} -h_1 & 0 & 0 & -w_1 \\ g_1 & -h_2 & 0 & 0 \\ 0 & g_2 & -h_3 & 0 \\ 0 & 0 & g_3 & -h_4 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \end{bmatrix} \qquad (B_5)$$

where $h_i = g_i + m_i$ for $i=1,2,3$

$h_4 = m_4 \exp(-d_2 F_e)$;

$w_1 = [2B_{4e}/B_{max} - 1]k_1 F_e/(F_e + F_s)$

To test stability of the system (B_5) the Hurwitz stability criterion will again be used. The characteristic equation of the matrix A is given by:

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$$

where a_1, a_2, a_3, a_4 are as defined on page 4-11.

Note that $a_i > 0$ for $i=1,2,3,4$.

Let H be the Hurwitz matrix corresponding to the coefficients of the characteristic equation, i.e.

$$H = \begin{bmatrix} a_1 & a_3 & 0 & 0 \\ 1 & a_2 & a_4 & 0 \\ 0 & a_1 & a_3 & 0 \\ 0 & 1 & a_2 & a_4 \end{bmatrix}$$

The principal determinants of H are:

$D_1 = a_1 > 0$; $D_2 = a_1 a_2 - a_3 > 0$;

and $D_3 = a_1 a_2 a_3 - a_3^2 - a_1^2 a_4 = a_3(a_1 a_2/2 - a_3) + a_1(a_2 a_3/2 - a_4 a_1) > 0$

Hence according to Hurwitz' theorem the fact that $a_i > 0$ and $D_i > 0$ for i=1,2,3,4 implies that the characteristic equation will have roots with negative real parts. This in turn implies that system (B_6) is asymptotically stable. Therefore, under the assumption used, if a disturbance, which is small enough, is introduced into the beetle population the system (B_S) will return to its point of equilibrium.

4.2.6. DUNG-BEETLE SUBMODEL.

Another way of examining the growth rate of dung-beetles is to consider the case of a density independent birth rate, i.e. instead of a logistic growth we take an exponential one in which case the the growth rate of beetles is only limited by the availability of fresh dung. Thus the present assumption implies $f_1(B_4)=B_4$. As in section 4.2.5 the beetle population submodel will be treated in isolation from the main model. Hence all the conclusions to be drawn below will only be valid as long as a disturbance in beetle population results in a negligible perturbation in fresh dung.

The equations for the dung beetle submodel are given below for easy reference:

$$\frac{dB_1}{dt} = k_1 B_4 F / [F+F_S] - g_1 B_1 - m_1 B_1 \qquad (12)$$

$$\frac{dB_2}{dt} = g_1 B_1 - g_2 B_2 - m_2 B_2 \qquad (13)$$

$$\frac{dB_3}{dt} = g_2 B_2 - g_3 B_3 - m_3 B_3 \qquad (14)$$

$$\frac{dB_4}{dt} = g_3 B_3 - m_4 \exp(-d_2 F)\, B_4 \qquad (15)$$

$$\dot{\underset{\sim}{X}} = \begin{bmatrix} -(g_1+m_1) & 0 & 0 & -k_1 F_e/[F_e+F_s] \\ g_1 & -(g_2+m_2) & 0 & 0 \\ 0 & g_2 & -(g_3+m_3) & 0 \\ 0 & 0 & g_3 & -m_4 \exp(-d_2 F_e) \end{bmatrix} \underset{\sim}{X} \qquad \text{(L)}$$

where $\underset{\sim}{X} = (x_1, x_2, x_3, x_4)^T$.

The Liapunov function

$$f(\underset{\sim}{X}) = [1/2]\,[p x_1^2 + q x_2^2 + r x_3^2 + s x_4^2] \qquad (17)$$

will be used to test asymptotic stability of linear system (L). Assume that constants p, q, r, and s are positive. Their values will be determined below.

We have

$$df/dt = p x_1 \dot{x}_1 + q x_2 \dot{x}_2 + r x_3 \dot{x}_3 + s x_4 \dot{x}_4$$

$$= -p(g_1+m_1)x_1^2 - q(g_2+m_2)x_2^2 - r(g_3+m_3)x_3^2 - s m_4 \exp(-d_2 F_e)\, x_4^2$$
$$- p k_1 F_e/(F_e+F_s)\, x_1 x_4 + q g_1 x_1 x_2 + r g_2 x_2 x_3 + s g_3 x_3 x_4 \quad ;$$

using system of eqtns (L).

Now: $$df/dt = -(\eta_1 x_1 - \eta_2 x_2)^2 - (\xi_1 x_1 - \xi_4 x_4)^2 - (\tau_2 x_2 - \tau_3 x_3)^2 - (\rho_4 x_4 - \rho_3 x_3)^2 \qquad (18)$$

provided that

$\eta_1^2 + \xi_1^2 = p\,(g_1 + m_1)$; $\eta_2^2 + \tau_2^2 = q\,(g_2 + m_2)$;

$\tau_3^2 + \rho_3^2 = r\,(g_3 + m_3)$; $\xi_4^2 + \rho_4^2 = s\, m_4 \exp(-d_2 F_e)$

$2\,\xi_1 \xi_4 = -p\, k_1 F_e/[F_e+F_s]$; $2\,\eta_1 \eta_2 = -q\, g_1$;

$2\,\tau_2 \tau_3 = r\, g_2$; $2 \rho_3 \rho_4 = s\, g_3$.

i.e. 8 equations in 8 unknowns. The system can be reduced to a system of 4 eqtns in 4 unknowns as follows :

$$\begin{aligned} \xi_1^2 &= p\,(g_1 + m_1) - q^2 g_1^2/(4\eta_2^2) \\ \eta_2^2 &= q\,(g_2 + m_2) - r^2 g_2^2/(4\tau_3^2) \\ \tau_3^2 &= r\,(g_3 + m_3) - s^2 g_3^2/(4\rho_4^2) \\ \rho_4^2 &= s\, m_4 \exp(-d_2 F_e) - p^2 k_1^2 F_e^2/[4\xi_1^2\{F_e+F_s\}^2] \end{aligned} \qquad (19)$$

Choose $p=(g_1 + m_1)^{-1}$, $q=(g_2 + m_2)^{-1}$,

$r=(g_3 + m_3)^{-1}$, $s= 1/m_4$.

Then system (19) takes the form :

$$\begin{aligned} \xi_1^2 &= 1 - C_1/\eta_2^2 && \text{where} && C_1 = (1/4)\, q^2 g_1^2 \,, \\ \eta_2^2 &= 1 - C_2/\tau_3^2 && \text{"} && C_2 = (1/4)\, r^2 g_2^2 \,, \\ \tau_3^2 &= 1 - C_3/\rho_4^2 && \text{"} && C_3 = (1/4)\, s^2 g_3^2 \,, \\ \rho_4^2 &= 1 - C_4/\xi_1^2 && \text{"} && C_4 = (1/4)\, p k_1^2 F_e^2/[F_e+F_s]^2 \end{aligned} \qquad (20)$$

System (20) gives the following :

$$\xi_1^2 = 1 - [C_1 \xi_1^2 - (C_1 C_3 + C_1 C_4)]/[\xi_1^2 - (C_2 + C_3 + C_4)]$$

which has the form

$$x = T - C/[x-E] \qquad (21)$$

where: $x=\xi_1^2$, $T=1-C_1$, $C=C_1 \cdot C_2$, $E=C_1+C_3+C_4$.

Then, provided that $x \neq E$, the roots of eqtn (21) are given by :

$$x_{\pm} = (1/2)\,[(E+T) \pm \sqrt{(E+T)^2 - 4(ET+C)}\,]$$

Since only real and positive values of x are needed then we require that

$$(E+T)^2 - 4(ET+C) > 0 .$$

This predicts 2 possible values of ξ_1. The remaining parameters in eqtn (20) are found by back substitution. According to eqtn (18) the signs of parameters η, ρ, ξ, and τ do not affect the stability of the system. By the Liapunov stability criterion it can be concluded that the system (12) to (15) is locally asymptotically stable. A point to be emphasized is that the validity of this conclusion is only true if the assumption that perturbation of fresh dung will be negligibly small holds.

4.3. MODEL WITH TWO BEETLE LIFE STAGES.

Is it really necessary to treat eggs, larvae, and pupae separately in the model? It seems to be an unnecessary complication of the system under consideration. These three stages do not interact directly with the incoming dung. The only important function of these compartments is the time delay they introduce in the development of the young. Thus because these first 3 life stages of beetles do not deal directly with the arriving fresh dung they can be combined into one compartment called pre-adult beetles. This reduces the total number of the equations describing the system (M) by two.

The pre-adult stage consists of eggs, larvae, and pupae combined into one component. Let B denote the total biomass of the preadults, and let B denote the biomass of adult beetles. Thus the new model is:

$$\frac{dV}{dt} = g\,V(t)\left[A(t) - V(t)/V_{max}\right] + \frac{V(t)}{A(t)}\frac{dA}{dt} - \frac{e_1 H V(t)}{V(t)+V_s}$$

$$\frac{dF}{dt} = \frac{\alpha H A(t) V(t)}{V(t) + V_s} - cF(t) - e_3 B_2(t) \cdot h_1(F(t))$$

$$\frac{dD}{dt} = cF(t) - bD(t) \qquad (M_2)$$

$$\frac{dB_1}{dt} = k_1 \cdot h_1(F(t)) \cdot f_1(B_2(t)) - g_1 B_1(t) - m_1 B_1(t)$$

$$\frac{dB_2}{dt} = g_1 B_1(t) + m_2 \cdot f_2(F(t)) \cdot B_2(t)$$

where : B_1 = biomass of pre-adult beetles (g).

B_2 = biomass of dult beetles (g).

and the remaining symbols are as defined previously.

At steady state the time derivatives in system (M) vanish. Assume that the values of V, F, D, B_1, B_2 at the equilibrium point are V_e, F_e, D_e, B_{1e}, B_{2e} respectively. Hence, linearizing system (M_2) near an equilibrium point, gives

$$\dot{\underset{\sim}{X}} = M \cdot \underset{\sim}{X} \qquad (24)$$

where $\underset{\sim}{X}=(x_1, x_2, x_3, x_4, x_5)^T$ and $\underset{\sim}{X}=d\underset{\sim}{X}/dt$, with components $x_1=B_1-B_{1e}$, $x_2=B_2-B_{2e}$, $x_3=D-D_e$, $x_4=F-F_e$, $x_5=V-V_e$. M is the 5 by 5 matrix of coefficients:

$$M = \begin{bmatrix} -z_{11} & z_{12} & 0 & z_{14} & 0 \\ z_{21} & -z_{22} & 0 & z_{24} & 0 \\ 0 & 0 & -z_{33} & z_{34} & 0 \\ 0 & -z_{42} & -z_{43} & -z_{44} & z_{45} \\ 0 & z_{52} & -z_{53} & -z_{54} & -z_{55} \end{bmatrix}$$

The entries of M are defined in Appendix 4-1, at the end of the chapter.

Stability conditions for the system (24) are determined from the Hurwitz Stability theorem. The characteristic equation of matrix M is given by:

$$p(\lambda) = \det(\lambda I - M) = 0$$

with $p(\lambda) = \lambda^5 + \Phi_1\lambda^4 + \Phi_2\lambda^3 + \Phi_3\lambda^2 + \Phi_4\lambda + \Phi_5$

where $\Phi_1 = \sum_{i=1}^{5} (z_{ii})$

$$\Phi_2 = \overline{\prod_{1,2,\ldots,5}}(z_{ii}z_{jj}) + z_{24}z_{42} + z_{45}z_{54} - z_{12}z_{21}$$

$$\Phi_3 = \overline{\prod_{1,2,\ldots,5}}(z_{ii}z_{jj}z_{kk}) + (z_{11} + z_{33})z_{24}z_{42} + z_{14}z_{21}z_{42} + [z_{11} + z_{22}]z_{34}z_{43}$$
$$+ z_{34}z_{43}z_{55} + z_{24}z_{42}z_{55} + z_{45}z_{54}[\sum_{i=1}(z_i)] + z_{34}z_{45}z_{53} - z_{24}z_{52}z_{45}$$
$$- z_{12}z_{21}z_{55} - z_{12}z_{21}z_{33} - z_{12}z_{21}z_{44}$$

$$\Phi_4 = \overline{\prod_{1,2,\ldots,5}}(z_{ii}z_{jj}z_{kk}z_{ll}) + z_{11}z_{24}z_{33}z_{42} + z_{14}z_{21}z_{33}z_{42} + z_{11}z_{22}z_{34}z_{43} + z_{14}z_{21}z_{42}z_{55}$$
$$+ [z_{11} + z_{33}]z_{24}z_{42}z_{55} + [z_{11} + z_{22}]z_{34}z_{43}z_{55} + z_{45}z\ [\overline{\prod_{1,2,3}}(z_{ii}z_{jj})]$$
$$- [z_{11} + z_{22}]z_{34}z_{45}z_{53} - z_{12}z_{21}z_{33}z_{44} - z_{12}z_{21}z_{34}z_{43} - z_{12}z_{21}z_{45}z_{54}$$
$$- z_{12}z_{21}[z_{33} + z_{44}]z_{55} - z_{14}z_{21}z_{45}z_{52} - [z_{11} + z_{33}]z_{24}z_{45}z_{52}$$

$$\Phi_5 = z_{11}z_{22}z_{33}z_{44}z_{55} + z_{11}z_{24}z_{33}z_{42}z_{55} + z_{14}z_{21}z_{33}z_{42}z_{55} + z_{11}z_{22}z_{34}z_{43}z_{55}$$
$$+ z_{11}z_{22}z_{33}z_{45}z_{54} + z_{11}z_{22}z_{34}z_{45}z_{53} - z_{12}z_{21}z_{33}z_{44}z_{55} - z_{12}z_{21}z_{34}z_{43}z_{55}$$
$$- z_{11}z_{24}z_{33}z_{45}z_{52} - z_{12}z_{21}z_{33}z_{45}z_{54} - z_{14}z_{21}z_{33}z_{45}z_{52} - z_{12}z_{21}z_{34}z_{45}z_{53}$$

The first requirement for asymptotic stability is that

$\Phi_i > 0$ for i=1 to 5.

Consider the following Hurwitz matrix, H

$$H = \begin{bmatrix} \Phi_1 & \Phi_3 & \Phi_5 & 0 & 0 \\ 1 & \Phi_2 & \Phi_4 & 0 & 0 \\ 0 & \Phi_1 & \Phi_3 & \Phi_5 & 0 \\ 0 & 1 & \Phi_2 & \Phi_4 & 0 \\ 0 & 0 & \Phi & \Phi_3 & \Phi_5 \end{bmatrix}$$

The Hurwitz determinants are:

$$H_1 = \Phi_1$$

$$H_2 = \Phi_1 \Phi_2 - \Phi_3$$

$$H_3 = \Phi_3 H_2 + \Phi_1 (\Phi_5 - \Phi_1 \Phi_4)$$

$$H_4 = \Phi_4 H_3 + \Phi_5 (\Phi_1 \Phi_4 + \Phi_2 \Phi_3 - \Phi_5 - \Phi_1 \Phi_2^2)$$

$$H_5 = \Phi_5 H_4$$

The second requirement for asymptotic stability is that

$$H_i > 0 \qquad \text{for } i=1 \text{ to } 5 .$$

If these two requirements are satisfied it means that the system (M_2) is locally asymptotically stable in the vicinity of equilibrium point $(B_{1e}, B_{2e}, V_e, D_e, F_e)$.

APPENDIX 4-1.

ELEMENTS OF MATRIX M ON PAGE 4-19.

The elements of matrix M given on page 19 are listed below:

$z_{11} = g_1 + m_1$; $z_{12} = k_1 h_1(F_e) f_1'(B_{2e})$

$z_{14} = k_1 h_1'(F_e) f_1(B_{2e})$; $z_{21} = g_1$

$z_{22} = - m_2 f_2(F_e)$; $z_{24} = -m_2 f_2'(F_e) B_{2e}$

$z_{33} = b$; $z_{34} = c$;

$z_{42} = e_3 h_1(F_e)$; $z_{43} = \alpha H V_e / (V_e + V_s)$;

$z_{44} = \alpha H V_e / (V_e + V_s) + c + e_3 B_{2e} h_1'(F_e)$;

$z_{45} = \alpha H A_e V_s / (V_e + V_s)^2$; $z_{52} = e_3 V_e h_1(F_e) / A_e$

$z_{53} = g V_e - [b V_e / A_e] - \alpha H V_e^2 / [(V_e + V_s) A_e]$

$z_{54} = g V_e - \alpha H V_e^2 / [(V_e + V_s) A_e] - e_3 B_{2e} h_1'(F_e) V_e / A_e$;

$z_{55} = g[2 V_e / V_{max} - A_e] + V_s [e_1 H + \alpha H V_e] / (V_e + V_s)^2$

Note that

$$f_1' = \frac{\partial f_1}{\partial B_2}$$

$$f_2' = \frac{\partial f_2}{\partial F}$$

$$h_1' = \frac{\partial h_1}{\partial F} .$$

CHAPTER FIVE

EFFECTIVENESS OF BEETLES IN IMPROVING SOIL

In Chapter 4 the usefulness of dung beetles was only considered as being limited to their removal of cattle droppings from the surface. Bornemissza (1960) mentioned further benefits which can accrue from the activity of beetles, viz.

(1) the rapid incorporation of dung into the soil;
(2) improved retention of volatile nitrogenous, and other constituents of dung in the soil;
(3) accelerated decomposition of the dung as a result of digestion by the beetle and its larvae;

In the present chapter two more equations will be added to the mathematical model - one for dung buried underground by beetles, and the other describing nitrogen changes in the soil.

Dung-beetles bury fresh dung as food for themselves and for their new born larvae. It has been observed that this burial results in the nutrients present in dung being recycled more efficiently and quickly within the pasture ecosystem. Bornemissza and Williams (1970) obtained substantial increases in plant yield when dung was intimately mixed with the soil (treatment 1) or when beetles were present in dung-treated pots (treatment 2); but in the case where dung was applied to the surface in the absence of beetles (treatment 3) much smaller increases in yield resulted. For comparison a table of a few of the results obtained by these authors is given in the next page.

Table 5-1. Yield of Japanese millet and the uptake into the plant tops of nitrogen (Bornemisssza and Williams,1970).

TREATMENT	YIELD (g/pot)		NITROGEN UPTAKE
	Top	Roots	(mg N/pot)
1. Dung mixed	37.0	18.4	255
2. Dung+Beetles	31.3	14.7	206
3. Dung only	17.3	12.7	127

Any plant 'constituent' or 'component' may be important to the well being of a plant, but some have a greater significance than others. Trace elements may be of vital importance in some situations. Nitrogen is a key element in the grassland ecosystem. According to Reuss and Innis (1978) soil nitrate and ammonium levels are normally low because of their rapid utilization by grasses and decomposer organisms. The productivity of grasslands is almost always limited by the supply of plant-available nitrogen. Thus addition of an equation describing the rate of change of soil nitrogen is essential for a complete model.

Henkens (1978) approximates nitrogen lost by volatization from cattle droppings lying on top of the soil as about 20%. Hence with the addition of compatments for dung buried and nitrogen our model's vegetation may be expected to reflect a higher level of growth.

5.1. ASSUMPTIONS.

The rate of arrival of dung buried underground is assumed to be directly proportional to the removal rate of fresh dung by beetles. A constant proportion of buried dung is assumed to be spread over an area proportional to the area from which fresh dung was removed, thus implying that the area occupied by buried dung is proportional to the area previously covered by fresh dung.

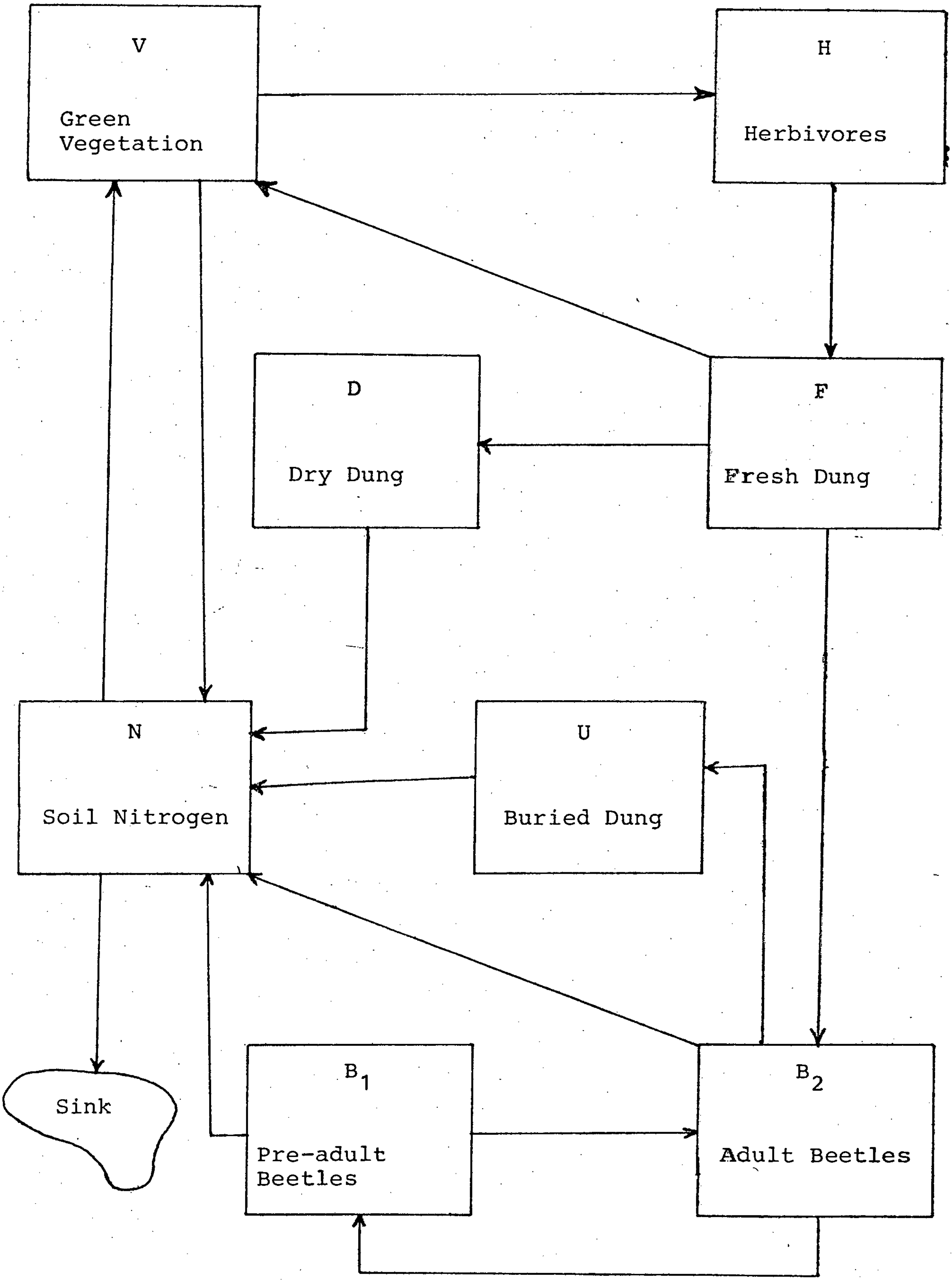
Nitrogen (N) is assumed to be increasing at a rate proportional to the biomass of beetles (both pre-adult and adult stages included) that suffered mortality, to decomposing green vegetation, and to decomposing dung (i.e. dry dung and buried dung). As in the Grassland Nitrogen-flow simulation model (Reuss and Innis, 1978) consumption rate of nitrogen by plants is described by a Menton-Michaelis term. Leaching rate of nitrogen is assumed to be a constant fraction of nitrogen available.

Two more terms are added to the equation describing the net growth rate of vegetation in system (4.M). One is for the natural death rate of vegetation which is assumed proportional to the green biomass. The other term accounts for growth of green vegetation resulting from the availabity of nitrogen.

The final model can, at this stage, be represented by the following flow diagram :

Note that the SINK indicates the loss of soil-nitrogen through leaching.

FIGURE 5.1 : FLOW CHART OF THE MODEL



Sink indicates the loss of soil nitrogen through leaching.

where $U(t)$ = effective area 'containing' buried dung,

$N(t)$ = soil nitrogen (g N)

and the rest of the state variables are as defined in Chapter 2.

d_1 = constant of relative proportion of green biomass dying per unit time (sec^{-1})

e_2 = maximum relative growth rate of green biomass due to the presence of nitrogen (sec^{-1}).

N_5 = concentration of soil nitrogen at which the growth rate of plants is half its maximum (g N).

q_1 = scaling factor for the relationship between area from which dung was removed and the area in which it is buried.

(q_1e_3) = relative incoming rate of buried dung (sec^{-1}).

q_2 = proportion of buried dung decomposing per unit of time (sec^{-1}).

c_5 = relative leaching rate of soil nitrogen (sec^{-1}).

c_6 = relative consumption rate of soil nitrogen by plants (sec^{-1}).

5.3. LINEARIZED FORM.

Introduce small perturbations from the equilibrium state such that

$$B_1(t) = B_{1e} + x_1(t) , \quad B_2(t) = B_{2e} + x_2(t) , \quad D(t) = D_e + x_3(t) ,$$

$$F(t) = F_e + x_4(t) , \quad V(t) = V_e + x_5(t) , \quad N(t) = N_e + x_6(t) ,$$

$$U(t) = U_e + x_7(t) .$$

where $(B_{1e}, B_{2e}, D_e, F_e, V_e, N_e, U_e)$ is the equilibrium point of system (M) discussed in section 5.2. The vector

$$\underset{\sim}{X} = (x_1 , x_2 , x_3 , x_4 , x_5 , x_6 , x_7)^T$$

is the resulting displacement of the system from equilibrium. Now, assuming that the vector $\underset{\sim}{X}(t)$ is near enough to the origin, terms of second order in x_i, for i=1 to 7, may be truncated from the model. This gives the following linear system:

$$
\begin{aligned}
\dot{x}_1 &= -[q+m_1]x_1(t) + [k_1\{1-2B_{2e}/B_{max}\}F_e/(F_e+F_s)]x_2(t) \\
&\quad + [k_1B_{2e}\{1-B_{2e}/B_{max}\}F_s/(F_e+F_s)^2]x_4(t) \\
\dot{x}_2 &= g_1\,x_1(t) - m_2\exp(-d_2F_e)\;x_2(t) + m_2d_2\exp(-d_2F_e)\;x_4(t) \\
\dot{x}_3 &= -\,b\;x_3(t) + c\;x_4(t) \\
\dot{x}_4 &= -\,[e_3F_e/(F_e+F_s)]\;x_2(t) - [\alpha HV_e/(V_e+V_s)]\;x_3(t) \\
&\quad - [\alpha HV_e/(V_e+V_s) + c + e_3B_{2e}F_s/(F_e+F_e)^2]\;x_4(t) && \text{(L)} \\
&\quad + [\alpha HA_eV_s/(V_e+V_s)^2]\;x_5(t) \\
\dot{x}_5 &= [e_3V_eF_e/\{A_e(F_e+F_s)\}]\;x_2(t) - [gV_e-bV_e/A_e-\alpha HV_e^2/\{A_e(V_e+V_s)\}]x_3(t) \\
&\quad - [gV_e - \alpha HV_e^2/\{A_e(V_e+V_s)\} - e_3B_{2e}V_eF_s/\{A_e(F_e+F_s)^2\}]\;x_4(t) \\
&\quad + [e_2V_eN_s/(N_e+N_s)^2]\;x_6(t) - [d_1 + \alpha HV_eV_s/(V_e+V_s)^2 + 2gV_e/V_{max} \\
&\quad - gA_e + e_1HV_e/(V_e+V_s)^2 - e_2N_e/(N_e+N_s)]\;x_5(t) \\
\dot{x}_6 &= c_1\,x_1(t) + c_2\,x_2(t) + c_3\,x_3(t) - [c_6N_e/\{N_e+N_s\}-c_4]\;x_5(t) \\
&\quad - [c_6V_eN_s/(N_e+N_s)^2 + c_5]\;x_6(t) + c_7\,x_7(t) \\
\dot{x}_7 &= [q_1e_3F_e/(F_e+F_s)]\;x_2(t) + [q_1e_3B_{2e}F_s/(F_e+F_s)^2]\;x_4(t) - q_2\,x_7(t)
\end{aligned}
$$

Note that $A(t)=1-F(t)-D(t)$ implies $dA/dt = -\,\dot{x}_3(t) - \dot{x}_4(t)$

System (L) is of the form $\dot{\underset{\sim}{X}}(t)=M\underset{\sim}{X}(t)$, where vector $\dot{\underset{\sim}{X}}(t)$ is the time derivative of column vector $\underset{\sim}{X}(t)$, and M is a 7 by 7 matrix of coefficients. A convenient form of writing M is:

$$M = \begin{bmatrix} -w_{11} & w_{12} & 0 & w_{14} & 0 & 0 & 0 \\ w_{21} & -w_{22} & 0 & w_{24} & 0 & 0 & 0 \\ 0 & 0 & -w_{33} & w_{34} & 0 & 0 & 0 \\ 0 & -w_{42} & -w_{43} & -w_{44} & w_{45} & 0 & 0 \\ 0 & w_{52} & -w_{53} & -w_{54} & -w_{55} & w_{56} & 0 \\ w_{61} & w_{62} & w_{63} & 0 & -w_{65} & -w_{66} & w_{67} \\ 0 & w_{72} & 0 & w_{74} & 0 & 0 & -w_{77} \end{bmatrix}$$

where the elements (w_{ij}) of matrix M are given in detail at the end of the chapter in Appendix 5-1.

5.3.1. Stability Conditions.

The characteristic equation of system (L) is given by

$$\det(\lambda I - M) \equiv \lambda^7 + \delta_1\lambda^6 + \delta_2\lambda^5 + \delta_3\lambda^4 + \quad \lambda^3 + \delta_5\lambda^2 + \delta_6\lambda + \delta_7 = 0$$

where I = 7 by 7 identity matrix;

$$\delta_1 = \sum_{i=1}^{7} w_{ii}$$

$$\delta_2 = \Big(\prod_{1,2,\dots,7}(w_{ii}\, w_{jj})\Big) + \eta_1 + w_{24}w_{42} + w_{34}w_{43} + w_{45}w_{54} - w_{12}w_{21}$$

$$\delta_3 = \Big(\prod_{1,2,\dots,7} w_{ii}\, w_{jj}\Big)w_{77} + w_{77}\eta_1 + w_{24}w_{42}w_{77} + w_{34}w_{43}w_{77} + w_{45}w_{59}w_{77} + w_{66}\Sigma_2$$

$$+ \Sigma_3 + \eta_2 - w_{12}w_{21}w_{77}$$

$$\delta_4 = w_{66}w_{77}\Sigma_2 + w_{77}\Sigma_3 + w_{77}\eta_2 + w_{66}\Sigma_3 + \Sigma_4 + w_{45}w_{56}w_{67}w_{74} + \eta_3$$

$$\delta_5 = w_{66}w_{77}\Sigma_3 + w_{77}\Sigma_4 + w_{77}\eta_3 + w_{66}\Sigma_4 + \Sigma_5 + w_{24}w_{45}w_{56}w_{67}w_{74} + \eta_4$$

$$+ \Big(\sum_{i=1}^{3} w_{ii}\Big)w_{45}w_{56}w_{67}w_{74}$$

$$\delta_6 = W_{66}W_{77}\Sigma_4 + W_{77}\Sigma_5 + W_{77}\eta_4 + W_{66}\Sigma_5 + \eta_5 + W_{14}W_{21}W_{45}W_{56}W_{67}W_{74}$$

$$+ [W_{11} + W_{33}]W_{24}W_{45}W_{56}W_{67}W_{72} + [\sum_{1,2,3}\prod(W_{ii}W_{jj})]W_{45}W_{56}W_{67}W_{74}$$

$$- W_{12}W_{21}W_{45}W_{56}W_{67}W_{74}$$

$$\delta_7 = W_{66}W_{77}\Sigma_5 + W_{77}\eta_5 + W_{11}W_{22}W_{33}W_{45}W_{56}W_{67}W_{74} + W_{11}W_{24}W_{33}W_{45}W_{56}W_{67}W_{72}$$

$$+ W_{14}W_{33}W_{45}W_{56}W_{67}W_{72}W_{21} - W_{12}W_{21}W_{33}W_{45}W_{56}W_{67}W_{74}$$

where $\eta_1 = W_{56}W_{65}$

$$\eta_2 = W_{56}W_{65}\sum_{i=1}^{4}W_{ii}$$

$$\eta_3 = W_{56}W_{65}[\sum_{1,2,3,4}\prod(W_{ii}W_{jj})] + W_{24}W_{42}W_{56}W_{65} + W_{43}W_{34}W_{56}W_{65} - W_{24}W_{45}W_{56}W_{62} -$$

$$- W_{14}W_{45}W_{56}W_{61} - W_{34}W_{45}W_{56}W_{63} - W_{12}W_{21}W_{56}W_{65}$$

$$\eta_4 = [W_{11} + W_{22}]W_{34}W_{43}W_{56}W_{65} + W_{56}W_{65}[\sum_{1,2,3,4}\prod(W_{ii}W_{jj}W_{kk})] + W_{14}W_{21}W_{42}W_{56}W_{65}$$

$$[W_{11} + W_{33}]W_{24}W_{42}W_{56}W_{65} - [W_{11} + W_{33}]W_{24}W_{45}W_{56}W_{62} - W_{12}W_{24}W_{45}W_{56}W_{61}$$

$$- W_{14}W_{21}W_{45}W_{56}W_{62} - W_{14}[W_{22} + W_{33}]W_{45}W_{56}W_{61} - [W_{11} + W_{22}]W_{34}W_{45}W_{56}W_{63}$$

$$- W_{12}W_{21}[W_{33} + W_{44}]W_{56}W_{65}$$

$$\eta_5 = W_{12}W_{21}W_{34}W_{45}W_{56}W_{63} + W_{11}W_{22}W_{34}W_{43}W_{56}W_{65} + W_{11}W_{22}W_{33}W_{44}W_{56}W_{65}$$

$$+ W_{12}W_{24}W_{33}W_{45}W_{56}W_{65} + W_{14}W_{21}W_{42}W_{33}W_{56}W_{65} - W_{11}W_{24}W_{33}W_{45}W_{56}W_{62}$$

$$- W_{12}W_{24}W_{33}W_{45}W_{56}W_{61} - W_{14}W_{21}W_{33}W_{45}W_{56}W_{62} - W_{12}W_{21}W_{33}W_{45}W_{56}W_{61}$$

$$- W_{11}W_{22}W_{34}W_{45}W_{56}W_{63} - W_{12}W_{21}W_{34}W_{43}W_{56}W_{65} - W_{12}W_{21}W_{33}W_{44}W_{56}W_{65}$$

$$\Sigma_2 = [\sum_{1,2,\ldots,5}\prod(W_{ii}W_{jj})] + W_{24}W_{42} + W_{34}W_{43} + W_{45}W_{54} - W_{12}W_{21}$$

$$\Sigma_3 = [\sum_{1,2,\ldots,5}\prod(W_{ii}W_{jj}W_{kk})] + W_{24}W_{42}W_{55} + W_{34}W_{43}W_{55} + [W_{11} + W_{33}]W_{24}W_{42}$$

$$+ W_{14}W_{42}W_{21} + [W_{11} + W_{22}]W_{34}W_{43} + [\sum_{i=1}^{3}(W_{ii})]W_{45}W_{54} + W_{34}W_{45}W_{53}$$

$$- w_{12} w_{21} w_{55} - w_{12} w_{21} [w_{33} + w_{44}] - w_{24} w_{45} w_{52}$$

$$\Sigma_4 = [\overset{\sum}{\prod_{1,2,\ldots,5}} (w_{ii}\, w_{jj}\, w_{kk} w_{ll}] + [w_{11} + w_{33}] w_{24} w_{42} w_{53} + w_{14} w_{21} w_{42} w_{55} + w_{11} w_{24} w_{33} w_{42}$$

$$+ [w_{11} + w_{22}] w_{34} w_{43} w_{55} + w_{14} w_{21} w_{33} w_{42} + w_{11} w_{22} w_{34} w_{43}$$

$$+ [\overset{\sum}{\prod_{1,2,3}} (w_{ii}\, w_{jj}] w_{45} w_{54} + [w_{11} + w_{22}] w_{34} w_{45} w_{53} - w_{14} w_{21} w_{45} w_{52} - w_{12} w_{21} w_{45} w_{54}$$

$$- w_{12} w_{21} w_{33} w_{44} - w_{12} w_{21} [w_{33} + w_{44}] w_{55} - w_{12} w_{21} w_{34} w_{43} - [w_{11} + w_{33}] w_{24} w_{45} w_{52}$$

$$\Sigma_5 = w_{11} w_{22} w_{33} w_{44} w_{55} + w_{11} w_{24} w_{33} w_{42} w_{55} + w_{14} w_{21} w_{33} w_{42} w_{55} + w_{11} w_{22} w_{34} w_{43} w_{55}$$

$$+ w_{11} w_{22} w_{33} w_{45} w_{54} + w_{11} w_{22} w_{34} w_{45} w_{53} - w_{12} w_{21} w_{33} w_{45} w_{54} - w_{12} w_{21} w_{34} w_{45} w_{53}$$

$$- w_{12} w_{21} w_{33} w_{44} w_{55} - w_{12} w_{21} w_{34} w_{43} w_{55} - w_{11} w_{24} w_{33} w_{45} w_{52} - w_{14} w_{21} w_{33} w_{45} w_{52}$$

For system (L) to be asymptotically stable at the origin the Hurwitz stability criterion requires that

$$\delta_i > 0 \qquad \text{for } i=1 \text{ to } 7,$$

$$D_i > 0 \qquad \text{for } i=1 \text{ to } 6;$$

where $D_1 = \delta_1$

$$D_2 = \delta_1 \delta_2 - \delta_3$$

$$D_3 = \delta_3 D_2 + \delta_1 [\delta_5 - \delta_1 \delta_4]$$

$$D_4 = \delta_1 [\delta_2 \delta_3 \delta_4 - \delta_2^2 \delta_5 + \delta_4 \delta_5 - \delta_1 \delta_4^2 + \delta_1 \delta_2 \delta_6 - \delta_3 \delta_6]$$
$$+ \delta_2 \delta_3 \delta_5 + \delta_1 \delta_4 \delta_5 + \delta_3 \delta_7 - \delta_3^2 \delta_4 - \delta_5^2 - \delta_1 \delta_2 \delta_7$$

$$D_5 = \begin{bmatrix} \delta_1 & \delta_3 & \delta_5 & \delta_7 & 0 \\ 1 & \delta_2 & \delta_4 & \delta_6 & 0 \\ 0 & \delta_1 & \delta_3 & \delta_5 & \delta_7 \\ 0 & 1 & \delta_2 & \delta_4 & \delta_6 \\ 0 & 0 & \delta_2 & \delta_3 & \delta_5 \end{bmatrix}$$

$$D_6 = \begin{bmatrix} \delta_1 & \delta_3 & \delta_5 & \delta_7 & 0 & 0 \\ 1 & \delta_2 & \delta_4 & \delta_6 & 0 & 0 \\ 0 & \delta_1 & \delta_3 & \delta_5 & \delta_7 & 0 \\ 0 & 1 & \delta_2 & \delta_4 & \delta_6 & 0 \\ 0 & 0 & \delta_1 & \delta_3 & \delta_5 & \delta_7 \\ 0 & 0 & 1 & \delta_2 & \delta_4 & \delta_6 \end{bmatrix}$$

The satisfaction of these conditions implies that the equilibrium point is asymptotically stable. For a general system of this size it is rather difficult to investigate as to whether these conditions are actually met or not.

APPENDIX 5-1.

ELEMENTS OF MATRIX M

The elements of matrix M given on page 5-1 are listed below:

$w_{11} = g_1 + m_1$; $w_{12} = k_1 [1-2B_{2e}/B_{max}] F_e /(F_e+F_s)$

$w_{14} = k_1 B_{2e}[1-2B_{2e}/B_{max}] F_s /(F_e+F_s)^2$; $w_{21} = g_1$;

$w_{22} = m_2 \exp(-d_2 F_e)$; $w_{33} = b$;

$w_{34} = c$; $w_{42} = e_1 F_e/(F_e+F_s)$;

$w_{43} = \alpha H V_e /(V_e+V_s)$; $w_{45} = \alpha H A_e V_s /(V_e+V_s)^2$;

$w_{44} = \alpha H V_e /(V_e+V_s) + c + e_3 B_{2e} F_s /(F_e+F_s)^2$;

$w_{52} = e_1 V_e F_e /[(F_e+F_s) A_e]$;

$w_{53} = g V_e - b V_e /A_e - \alpha H V_e^2/[(V_e+V_s) A_e]$;

$$w_{55} = d_1 + \alpha H V_e V_s /(V_e+V_s)^2 + g[2V_e/V_{max} - A_e] + e_1 H V_s /(V_e+V_s)^2$$
$$- e_2 N_e /(N_e+N_s) \;;$$

$w_{54} = g V_e - \alpha H V_e^2/[(V_e+V_s) A_e] - e_3 B_{2e} V_e F_s/[(F_e+F_s)^2 A_e]$;

$w_{56} = e_2 V_e N_s /(N_e+N_s)^2$; $w_{67} = c_7$;

$w_{61} = c_1$; $w_{62} = c_2$;

$w_{65} = c_6 N_e /(N_e+N_s) - c_4$; $w_{63} = c_3$;

$w_{66} = c_6 V_e N_s /(N_e+N_s)^2 + c_5$; $w_{72} = q_1 e_3 F_e /(F_e+F_s)$;

$w_{74} = q_1 e_3 B_{2e} F_s /(F_e+F_s)^2$; $w_{77} = q_2$

CHAPTER SIX

MODEL WITH DELAY TERMS

In the real world, the growth rate of a species population will often not respond immediately to changes in its own population or to that of an interacting species, but rather will do so after a time lag (May, 1973). Time delays in growth dynamics of a population or of several interacting species can arise from a variety of causes and are undoubtedly always present in varying degrees. Macdonald (1978) makes a distinction between time delays that are inherent in the system studied, and lags that enter a model because of specific approximations involved in setting up the model.

In the present chapter time delays will be introduced in the final model (5.M) presented in chapter 5 and will, to a limited extent, help improve the model. Possible delay terms that may be added to the model are either discrete lags or distributed (continuous) delays. Delay terms will, however, only be included where they are considered to play a significant role.

6.1. INTRODUCING TIME LAGS

For purposes of easy reference the system of equations (5.M), describing a grazing system with 2 life stages of beetles, presented in chapter 5 will be rewritten below:

$$\dot{B}_1(t)=k_1[F(t)/\{F(t)+F_s\}]B_2(t)[1-B_2(t)/B_{max}]-g_1\, B_1(t)-m_1B_1(t)$$

$$\dot{B}_2(t)=g_1B_1(t)-m_2B_2(t)\ \exp[-d_2F(t)]$$

$$\dot{D}(t)=cF(t)-bD(t)$$

$$\dot{F}(t)=\alpha A(t)V(t)/[V(t)+V_s]-cF(t)-e_3B_2(t)F(t)/[F(t)+F_s] \qquad (M)$$

$$\dot{U}(t)=q_1e_3B_2(t)F(t)/[F(t)+F_s]-q_2U(t)$$

$$\dot{N}(t)=c_1B_1(t)+c_2B_2(t)+c_4V(t)+c_7U(t)-c_5N(t)+c_3D(t)$$

$$-c_6V(t)N(t)/[N(t)+N_8]$$

$$\dot{V}(t)=gV(t)[A(t)-V(t)/V_{max}]+[V(t)/A(t)]\dot{A}(t)-d_1V(t)$$

$$+e_1HV(t)/[V(t)+V_s]+e_2V(t)N(t)/[N(t)+N_s]$$

$$A(t)=1-F(t)-D(t)$$

The equilibrium point of system (M) will still be denoted by $(B_{1e}\ ,\ B_{2e}\ ,\ F_e\ ,\ D_e\ ,\ U_e\ ,\ N_e\ ,\ V_e\ )$ as in Chapter 5.

6.1.1. DELAY TERM IN THE NITROGEN EQUATION.

A careful look at the model (M) reveals that there are only very few terms, if any, where one can say that the change of the biomass is independent of the past history of the system. Consider, say, the nitrogen equation. To assume that the rate of increase of nitrogen is directly proportional to the death rates of pre-adult beetles $B_1(t)$, adult beetles $B_2(t)$, vegetation $V(t)$, and the removal rate of dry dung $D(t)$, and buried dung $U(t)$, is rather too simplistic. In reality the material in these compartments must still undergo decomposition before being converted into nitrates which can be taken up by plant roots. This suggests that one needs to introduce time delays in these variables. If discrete delay terms are included in the nitrogen equation we obtain

$$\dot{N}(t) = c_1B_1(t-T_1) + c_2B_2(t-T_2) + c_3D(t-T_3) + c_4V(t-T_4) + c_7U(t-T_5) - c_5N(t) - c_6V(t)N(t)/[N(t)+N_S] \qquad (1)$$

where T_i $(i=1,2,\ldots,5)$ are measures of time lags.

These delays allow time for decomposition of dead material before being converted into nitrates. An alternative to this would be an addition of one more differential equation describing decomposition of dead material. To keep our model at a 'managable' size the number of equations must be kept at a minimum. One can still simplify equation (1) by reducing the number of delay terms. A way of getting around the complication involved is to assume that when decomposition takes place, the dead material is converted into what Wielgolaski (1973) calls an unavailable pool, i.e. nitrogen not readily consumable by plants. This intermediate state can be considered as being the organic nitrogen which is in fact an immobilized state. Thus assuming a more realistic distributed delay, equation (1) can be rewritten as:

$$\dot{N}(t) = c_1B_1(t) + c_2B_2(t) + c_3D(t) + c_4V(t) + c_7U(t) - c_5N(t) - c_6V(t)\,\bar{N}(t)/[\bar{N}(t)+N_S] \qquad (2)$$

where $$N(t) = \int_{-\infty}^{t} N(\tau)\, k(t-\tau)\, d\tau \qquad (3)$$

$k(s)$ is a delay kernel or a memory function which can be thought of as a distributing (or weighing) function of N. The delay kernel is normalised as:

$$\int_0^{\infty} k(s)\cdot ds = 1. \qquad (4)$$

This normalisation ensures that the equilibrium point of the system with delay terms is the same as that of the instantaneous system (M), i.e. $(B_{1e}, B_{2e}, E_e, D_e, U_e, N_e, V_e)$ remains an equilibrium point. Note that for the case

$$k(s) = \delta(s-T)$$

then $\overline{N}(t) = N(t-T)$,

which is a discrete lag. But for the present case $k(s)$ will be chosen as

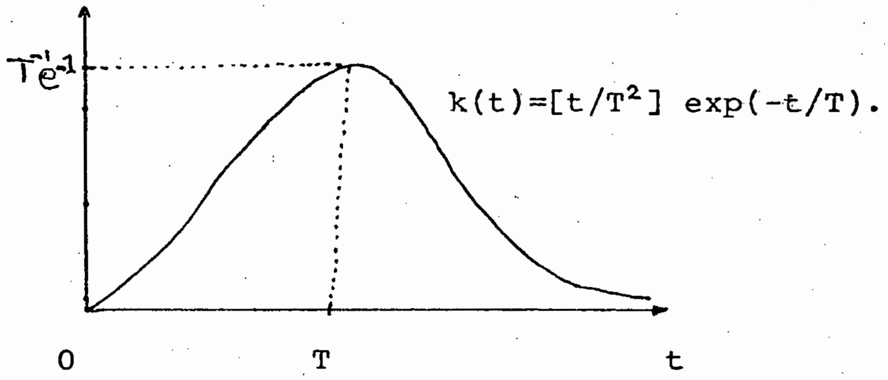
$$k(s) = [s/T^2] \exp(-s/T) \qquad (5)$$

with the average lag $\overline{T}$ of the memory function

$$\overline{T} = \int_0^\infty s \cdot k(s) \cdot ds = T$$

It can be easily verified that equation (5) satisfies the requirement of equation (4). This kernel is shown diagrammatically in Fig 6.1.

Figure 6-1. GENERIC DELAY KERNEL.



The inclusion of the delay term in the nitrogen equation necessitates similar changes in the equation describing the net rate of increase of green vegetation. Instead of assuming that the growth rate of green biomass is dependent on the instantaneous mass of nitrogen we should postulate a distributed lag in the availability of nitrogen. Thus the new equation for the net change of vegetation is:

$$\dot{V}(t) = gV(t)[A(t)-V(t)/V_{max}] + [V(t)/A(t)]\dot{A}(t) - d_1V(t)$$
$$- e_1HV(t)/[V(t)+V_s] + e_2V(t)\bar{N}(t)/[\bar{N}(t)+N_6] \qquad (6)$$

where $\bar{N}(t)$ is as described in equation (3).

The memory function given above can be said qualitavely to represent the case when the maximum influence on growth rate response of green biomass at any time t is due to the soil nitrogen concentration at the previous time t-T.

6.1.2. DELAY TERM IN ADULT-BEETLE EQUATION.

In the equation for the net growth rate of the population of adult beetles the mortality rate is taken to depend on the quantity of fresh dung available at one instant of time. Taking into account the fact that beetles can survive long periods of starvation, a replacement of the instantaneous term of fresh dung, F(t), by a continuous delay term spread over a period of time can help improve the model. Assume that the influence of the availability of fresh dung on the death rate of beetles, at any time t, decays exponentially as one moves backwards in time, i.e. if $\bar{F}(t)$ is the fresh dung with a delay term then

$$\bar{F}(t) = \int_{-\infty}^{t} F(s)\cdot G(t-s)\cdot ds \qquad (7)$$

where $G(s) = a\exp(-as) \qquad (8)$

Thus the equation describing the rate of change of adult beetles may be written as:

$$\dot{B}_2(t) = g_1 B_1(t) - m_2 B_2(t) \exp(-d_2 \overline{F}(t)) \qquad (9)$$

6.1.3. Delay in equation for Pre-Adult Beetles.

In this case the effect of introducing a discrete delay in the term for fresh dung F(t) in the equation for growth rate of pre-adult beetles will be shown from the computed results. Consider the following instantaneous equation for pre-adult beetles,

$$\dot{B}_1(t) = k_1 F(t)/[F(t)+F_8]B_2(t)[1-B_2(t)/B_{max}]-g_1B_1(t)-m_1B_1(t) \qquad (10)$$

Assume that the birth rate of pre-adults, $B_1(t)$, at time t does not only depend on fresh dung , F(t), instantaneously present at time t, but also on fresh dung that had been available the previous day, i.e. at time (t-1). This allows time for mating. Further assume that F(t) will have a greater influence on the birth rate than F(t-1). Then in equation (10) F(t) will be replaced by $\hat{F}(t)$ where

$$\hat{F}(t) = \delta_1 F(t) + \delta_2 F(t-1) \qquad (11)$$

with $$\delta_1 + \delta_2 = 1, \qquad \delta_1 > \delta_2 \geq 0. \qquad (12)$$

The restriction (12) ensures that the the equilibrium point of the system remains unchanged from the one obtained in the instantaneous system of equations (M).

6.1.4. INITIAL CONDITIONS.

Assume, without much loss of generality, that before time t=0 the fresh dung was constant, say $F(t)=F_0$, and that nitrogen was also constant, i.e. $N(t)=N_0$ for $t \leq 0$. The observations were only started at t=0 and there is no way of telling about the behaviour of the system before the instant t=0. The above assumption will only have a great influence at low values of t, but in the long run it will not affect the qualitative behaviour of the model.

Thus the nitrogen N(t) with a delay term can be evaluated using equations (3) and (5) as:

$$\overline{N}(t) = \int_{-\infty}^{t} T^{-2}\cdot(t-s)\cdot\exp(-[t-s]/T)\cdot N(s)\cdot ds$$

$$= \int_{-\infty}^{0} T^{-2}\cdot(t-s)\cdot\exp(-[t-s]/T)\cdot N_0\cdot ds + T^{-2}\int_{0}^{t}(t-s)\cdot\exp(-[t-s]/T)N(s)\,ds$$

$$= N_0\,[1+t/T]\,\exp(-t/T) + T^{-2}\int_{0}^{t}(t-s)\cdot\exp(-[t-s]/T)\cdot N(s)\cdot ds \qquad (13)$$

Using the above assumption, and equations (7) and (8), fresh dung with a distributed time lag can be evaluated as :

$$\overline{F}(t) = \int_{-\infty}^{t} F(s)\cdot a\cdot\exp(-a[t-s])\cdot ds$$

$$= \int_{-\infty}^{0} F_0\cdot a\cdot\exp(-a[t-s])\cdot ds + \int_{0}^{t} F(s)a\,\exp(-a[t-s])\,ds$$

$$= F_0\,\exp(-at) + a\int_{0}^{t} F(s)\cdot\exp(-a[t-s])\cdot ds \qquad (14)$$

The final model with time delays can now be written below.

$$\dot{B}_1 = k_1 \hat{F}(t)/[\hat{F}(t)+F_S]\, B_2(t)[1-B_2(t)/B_{max}] - g_1B_1(t) - m_1B_1(t)$$

$$\dot{B}_2 = g_1 B_1(t) - m_2 B_2(t) \exp(-d_2 \bar{F}(t))$$

$$\dot{F} = \alpha A(t)V(t)/[V(t)+V_S] - cF(t) - e_3 B_2(t)F(t)/[F(t)+F_S]$$

$$\dot{D} = c\, F(t) - b\, D(t) \qquad (M_F)$$

$$\dot{U} = q_1\, e_3 B_2(t)F(t)/[F(t)+F_S] - q_2 U(t)$$

$$\dot{N} = c_1 B_1(t) + c_2 B_2(t) + c_3 D(t) + c_4 V(t) + c_7 U(t)$$

$$- c_6 V(t)\, \bar{N}(t)/[\bar{N}(t)+N_S] - c_5 N(t)$$

$$\dot{V} = g\, V(t)[A(t)-V(t)/V_{max}] + [V(t)/A(t)]\, \dot{A}(t) - d_1 V(t)$$

$$- e_1 HV(t)/[V(t)+V_S] + e_2 V(t)\, \bar{N}(t)/[\bar{N}(t)+N_S]$$

where $A(t) = 1 - F(t) - D(t)$

$$\hat{F}(t) = \delta_1 F(t) + \delta_2 F(t-1), \qquad \delta_1+\delta_2=1, \ \delta_1 > \delta_2 \geq 0.$$

$$\bar{F}(t) = \int_{-\infty}^{t} F(s) \cdot a \cdot \exp[-a(t-s)] \cdot ds$$

$$\bar{N}(t) = \int_{-\infty}^{t} N(s)\, T\, [t-s] \exp[-(t-s)/T]\, ds$$

The equilibrium point of system (M_F) remains the same as the one obtained for the instantaneous system (M) .

Thus $(B_{1e}, B_{2e}, F_e, D_e, U_e, N_e, V_e)$ = EQUILIBRIUM POINT

6.2. LOCAL STABILITY ANALYSIS.

The system (M_F) in a linearized form are listed below. Let

$x_1(t)=B_1(t)-B_{1e}$, $x_2(t)=B_2(t)-B_{2e}$, $x_3(t)=F(t)-F_e$, $x_4(t)=D(t)-D_e$

$x_5(t)=U(t)-U_e$, $x_6(t)=N(t)-N_e$, $x_7(t)=V(t)-V_e$.

$$\dot{x}_1(t) = -(g_1+m_1)x_1(t) + k_1[1-2B_{2e}/B_{max}]\{F_e/[F_e+F_s]\}\, x_2(t)$$

$$+ k_1 B_{2e}\,[1-B_{2e}/B_{max}]\cdot[F_s/(F_e+F_s)^2]\, x_3(t)$$

$$\dot{x}_2(t) = g_1\, x_1(t) - m_2 \exp(-d_2 F_e)x_2(t) + m_2 d_2 \exp(-d_2 F_e)\overline{x}_3(t)$$

$$\dot{x}_3(t) = -e_3 F_e/[F_e+F_s]\, x_2(t) - \{\alpha HV_e/[V_e+V_s]+c+e_3 B_{2e}F_s/[F_e+F_s]^2\}x_3(t)$$

$$- [\alpha HV_e/(V_e+V_s)]x_4(t) + [\alpha HA_e V_s/(V_e+V_s)^2]\, x_7(t)$$

$$\dot{x}_4(t) = c\, x_3(t) - b\, x_4(t) \qquad (M_L)$$

$$\dot{x}_5(t) = q_1 e_3 F_e/[F_e+F_s]\, x_2(t) + [q_1 e_3 B_{2e} F_s/(F_e+F_s)^2]\, x_3(t) - q_2\, x_5(t)$$

$$\dot{x}_6(t) = c_1 x_1(t) + c_2 x_2(t) + c_3 x_4(t) + c_7 x_5(t) - c_5 x_6(t)$$

$$-[c_6 V_e N_s/(N_e+N_s)^2]\overline{x}_6(t) - [c_6 N_e/(N_e+N_s) - c_4]\, x_7(t)$$

$$\dot{x}_7(t) = [e_3 V_e F_e/\{A_e(F_e+F_s)\}]\, x_2(t) - [gV_e - \alpha H\, V_e^2/\{A_e(V_e+V_s)\}$$

$$- e_3 B_{2e} V_e F_s/\{A_e(F_e+F_s)^2\}]\, x_3(t) - [gV_e - bV_e/A_e$$

$$- \alpha H\, V_e^2/\{A_e(V_e+V_s)\}]\, x_4(t) + [e_2 V_e N_s/\{N_e+N_s\}^2]\, \overline{x}_6(t)$$

$$- [d_1 + \alpha H\, V_e V_s/\{V_e+V_s\}^2 + g\{2V_e/V_{max} - A_e\} + e_1 HV_s/(V_e+V_s)^2$$

$$-e_2 N_e/\{N_e+N_s\}]\, x_7(t)$$

where: $A_e = 1 - F_e - D_e$,

$$\overline{x}_3(t) = \int_{-\infty}^{t} x_3(s)\, a \exp[-a(t-s)]\, ds$$

$$\overline{x}_6(t) = \int_{-\infty}^{t} x_6(s)\, T^{-2}\{t-s\} \exp[-(t-s)/T]\, ds$$

To analyse the local stability of the system of equations (M_L) we employ the technique called the 'linear chain trick', (Macdonald, 1978). Given a system of equations

$$d\underset{\sim}{X}/dt = f(\underset{\sim}{X}, z) \qquad (15)$$

where $\underset{\sim}{X}$ is a column vector and z is one of the variables $x_1, \ldots, x_n$, but with a delay term. Then if, say

$$z(t) = \int_{-\infty}^{t} x_i(u) \cdot G(t-u) \cdot du$$

and the delay kernel G(u) is chosen such that it satisfies

$$G(u) = G_a^p(u) = [a^{p+1}u^p/(p!)] \exp(-au) \qquad (16)$$

then equation (15) is supplemented by the equations

$$\begin{aligned} dz/dt &= a\,[y-z] \\ &\;" \\ &\;" \\ &\;" \\ dv/dt &= a\,[x_i - v], \end{aligned} \qquad (17)$$

i.e., with (p+1) extra equations in all. Each of these additional equations is linear, and each links two successive members of a chain of variables starting with z and ending with x_i. For a full discussion of this method see Appendix C.

In the case of our model we have for $\bar{x}_3(t) = \int_{-\infty}^{t} x_3(s) a \exp[-a(t-s)]ds$ that the memory function, using the notation of equation (16), is given by

$$G(u) = G_a^0(u)$$

and this means that we must add one extra equation to the model. Let $x_8(t) = \bar{x}_3(t)$, then the extra equation is

$$\dot{x}_8(t) = a\,[x_8(t) - x_3(t)] \qquad (18)$$

In the case of $\bar{x}_6(t) = \int_{-\infty}^{t} x_6(s) \cdot T^{-2}[t-s] \cdot \exp[-(t-s)/T]\, ds$ the memory function $G(u)$ can be said to be

$$G(u) = G^{1}_{T^{-1}}(u) ,$$

i.e. $p=1$, and $a=1/T$.

Thus in this case we need two extra equations. Let $x_{10} = \bar{x}_6$, $x_9 = \int_{-\infty}^{t} x_6(s) \cdot T^{-1} \cdot \exp[-(t-s)/T] \cdot ds$. Hence the equations

$$\dot{x}_9(t) = T^{-1}[x_{10}(t) - x_9(t)] \tag{19}$$

$$\dot{x}_{10}(t) = T^{-1}[x_6(t) - x_{10}(t)] \tag{20}$$

are two extra equations added into the system (M_L). Combining eqts (M_L), (18), (19), and (20) we get an equivalent linearized form of system (M_F). This new system has 10 variables. Further stability analysis is done using particular values of parameters. For a general system of this size it is impossible to proceed analytically.

PART TWO

Presentation of Computed Results

and

Conclusion.

CHAPTER SEVEN

RESULTS OF THE INSTANTANEOUS MODEL

Because the model was not developed for a particular grazing system and, very few values of the parameters could be obtained or approximated from published data, we were mainly interested in the qualitative behaviour of the model at different levels of grazing. In this chapter the general results of the instantaneous model (5.M) will be given. The values of the constants used are listed in Table 7-1. Section (7.1) discusses briefly the method of solution and the computer program used in solving system (5.M). In section (7.2) we consider the basic model (2.M) consisting only of the three components green vegetation, fresh dung, and dried dung. The results of the accumulation of dung on the pasture at different herbivore densities are given. In section (7.3) we consider the same model but with the addition of a nitrogen equation. Thus in this section we present the results of a grazing system (5.M) but keeping the population of dung beetles at zero. General results of the model with all the seven state variables are given in section (7.4). The chapter is concluded with the sensitivity analysis of parameters.

7.1. METHOD OF SOLUTION

In PART I we developed a model of grazing systems with dung beetles consisting of a set of nonlinear ordinary differential equations which can be written in a general form below as:

$$\dot{\underset{\sim}{Y}} = \underset{\sim}{f}(t,\underset{\sim}{Y}) \qquad (1)$$

where $\underset{\sim}{Y} = (y_1, y_2, \ldots, y_n)^T$ and $\underset{\sim}{f} = (f_1, f_2, \ldots, f_n)^T$

The solution of a system of the form (1) can, if not too "stiff", be computed accurately using Hamming's method. Hamming's predictor-corrector method employs the fourth-order Milne method predictor; the technique of modifying both the predicted and the corrected value of of the solution for the the fourth-order Milne method is usually followed. This method of computation is explained in Carnahan et al. (1969).

The computer program that was used in solving the equations of system (5.M) calls on the fourth-order Runge-Kutta function RUNGE to find the necessary starting values for Hamming's algorithm and, thereafter, calls on Hamming's function HAMING to calculate estimates of $\underset{\sim}{y}$ and $d\underset{\sim}{y}/dt$ on the time interval $[0,t\ ]$. The function RUNGE generates the first 3 values $y(t_1)$, $y(t_2)$, and $y(t_3)$. The multi-step function HAMING cannot be called directly when $t=t_0$. . Since RUNGE implements the fourth-order Runge-Kutta method, the solutions computed using this function should be comparable in accuracy with the solutions generated by the predictor-corrector algorithm, which is also of the fourth-order. A disadvantage of the Runge-Kutta process applied to a set of equations is its possible instability.

The program has two subroutines, DEFINE and PLOTER. The equations of the model are defined in subroutine DEFINE. Subroutine PLOTER calls on the CALCOMP SUBROUTINES for the plotting of graphs. The listing of the program for the instantaneous system (5.M) is given in Appendix D.

7.2. RESULTS OF THE MODEL (2.M)

Model (2.M) contains the variables of green vegetation, fresh dung and dried dung. In this section we compare the results obtained by varying the herbivore density. It was assumed that the maximum biomass of vegetation is 100 units (kg) per unit area (acre), i.e. V =100 kg/acre. Figures 7.2, 7.3, and 7.4 give graphs obtained by varying the stocking rates. These graphs respectively represent undergrazing, overgrazing to a low value of vegetation V, and and overgrazing leading to extinction of V. Corresponding areas blanketed by dung (fresh + dry dung) are also shown in these graphs. Herbivore densities (H) in these cases are respectively 0.3300, 0.6315, and 0.8000 animals per unit area (acre).

As the density of herbivore population, i.e. the grazing level, is increased from zero, the steady state values of the area covered by dung also increased from zero until it reached a maximum at H=0.640 . A further increase in herbivore density resulted in substantial decreases of the area covered with dung. For values of $H \geq 0.698$ we get overgrazing leading to extingtion. Hence the steady state values of the corresponding areas covered with dung will be zero. An interesting fact which can be deduced from this is that it is impossible to have the whole area of pastureland covered with dung. A graph showing the relationship between herbivore density and the resultant steady state percentage area covered with dung is given in figure 7.1 below.

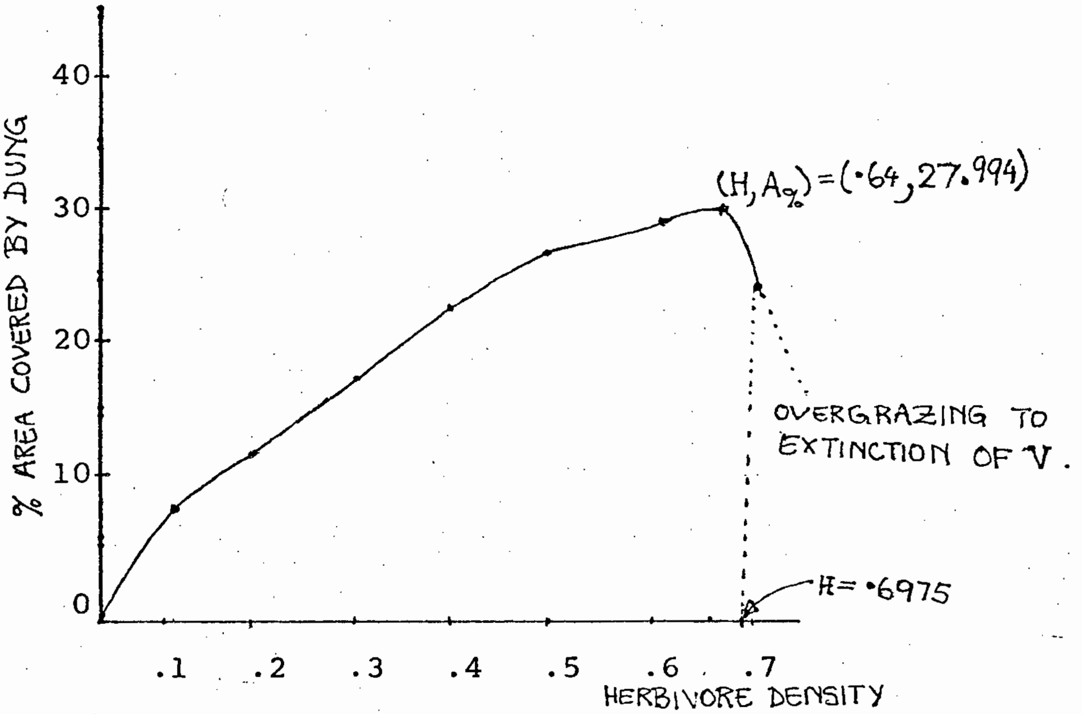


Figure 7-1. AREA COVERED WITH DUNG AS A FUNCTION OF HERBIVORE DENSITY

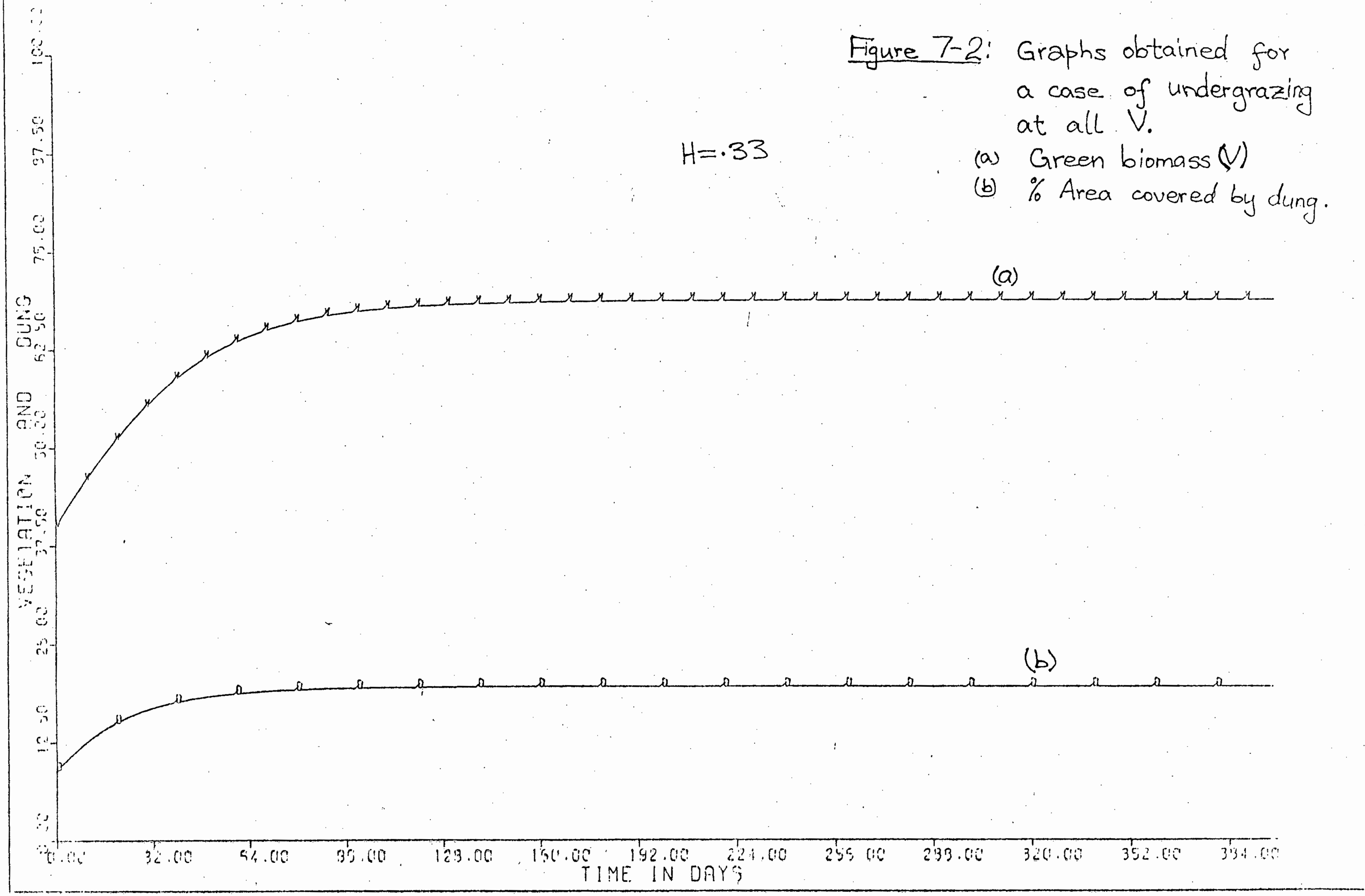


Figure 7-2: Graphs obtained for a case of undergrazing at all V.
(a) Green biomass (V)
(b) % Area covered by dung.

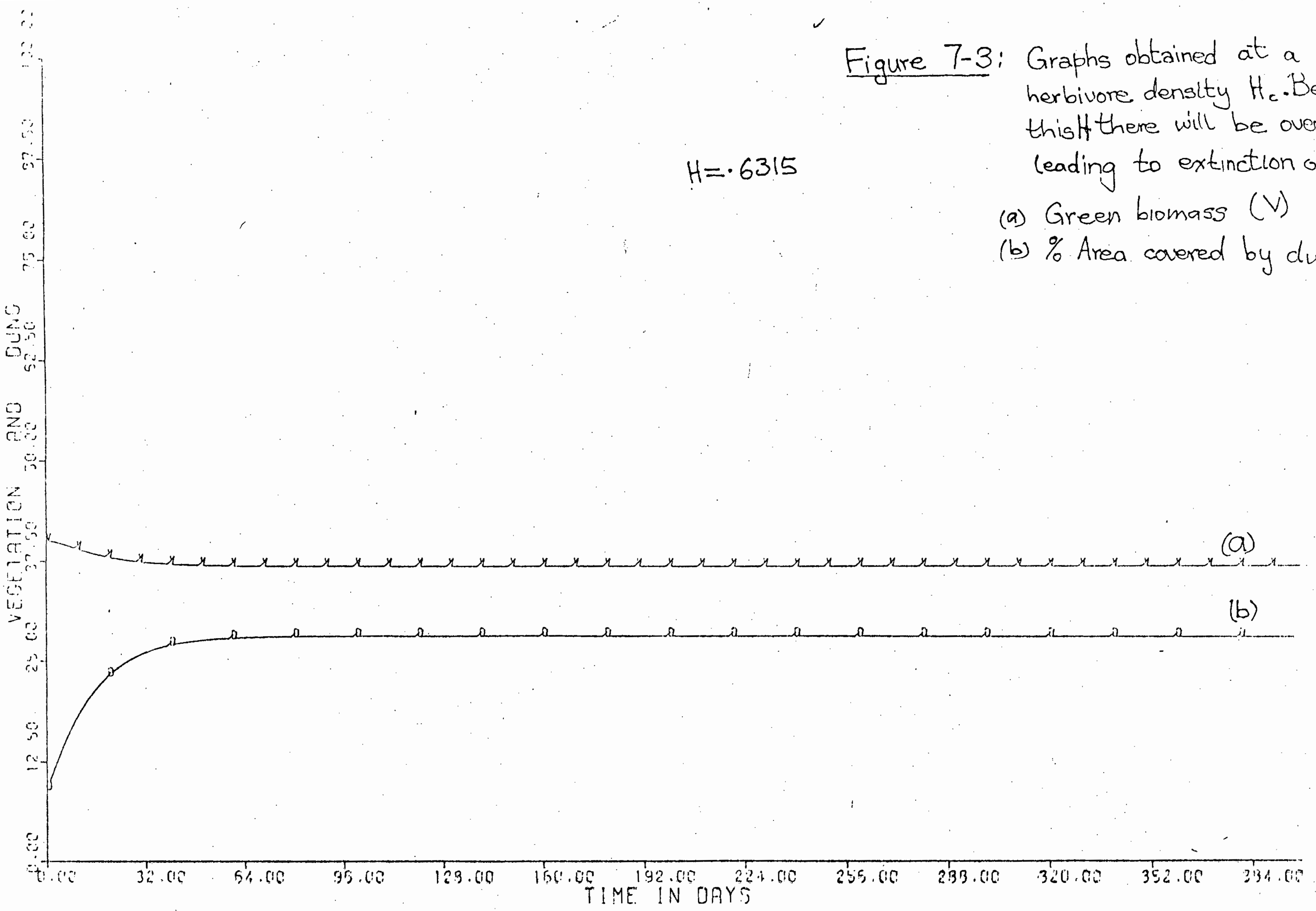


Figure 7-3: Graphs obtained at a herbivore density H_c. Beyond this H there will be overgrazing leading to extinction of V.

(a) Green biomass (V)

(b) % Area covered by dung.

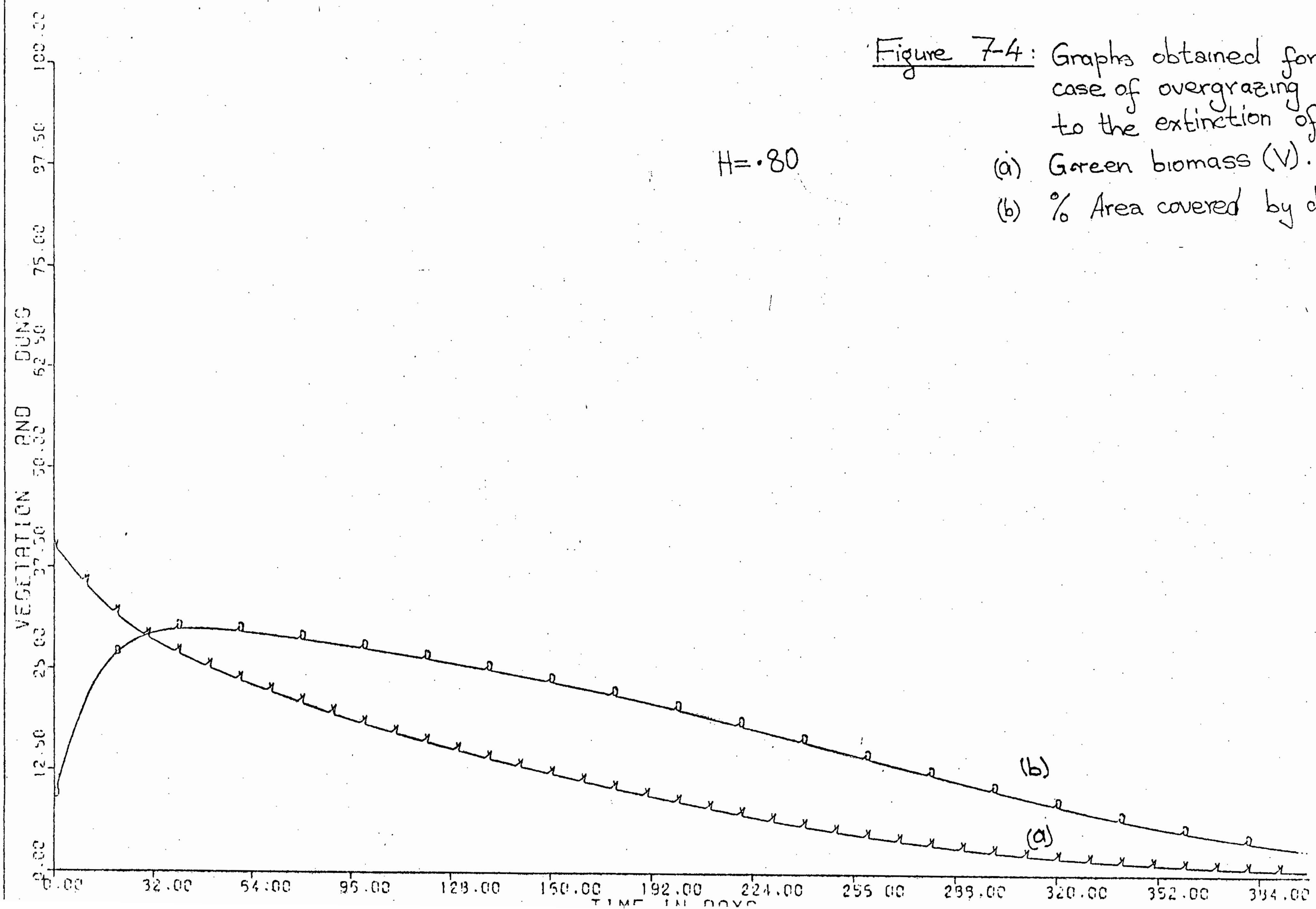


Figure 7-4: Graphs obtained for a case of overgrazing leading to the extinction of V.

(a) Green biomass (V).

(b) % Area covered by dung.

The values of the parameters used in the model are listed in Table 7-1 below:

The value of the herbivore density (H) was varied from time to time.

Table 7-1. VALUES OF THE PARAMETERS USED IN THE MODEL.

k_1	F_S	g_1	m_1	m_2	d_2	α	V_S
.81	.01	.08	.04	.25	6.9	.038	20.

c	e_3	b	q_1	e_1	q_2	g	V_{max}	e_2
.20	.001	.05	1.4	1.9	.26	.06	100.	.013

c_1	c_2	c_3	c_4	c_5	c_6	c_7	N_S	d_1
$1x10^{-5}$	$1x10^{-5}$	.052	$1.2x10^{-4}$	0.	$1x10^{-3}$	.33	1.5	0.

7.3. MODEL (5.M) WITHOUT BEETLES.

The absence of dung beetles from system (5.M) implies that there will be no burial of dung, thus reducing the number of state variables from 7 to 4. The present model differs from the basic model (2.M) of grazing systems in that a nitrogen equation has now been added. In this section we shall only compare the changes resulting from the addition of the nitrogen equation.

The addition of the nitrogen component did not change the qualitative behaviour of the system. The only difference is that green vegetation reflected a higher level of growth. A general increase of dung on the pastureland was also reflected in the results. This increase can be explained in terms of the increased food (i.e. vegetation) for herbivores which in turn means that more fresh dung is being deposited on the on the surface of the grazing land. Figure 7.5A gives graphs showing changes or shifts of both the vegetation biomass and the percentage area the percentage area of the "lost pasture" resulting from the inclusion of nitrogen equation. The graphs drawn with the dotted lines indicate the situation obtained after the addition of the nitrogen equation, while graphs with solid lines give results of the 3 component model (2.M).

7.4. GRAZING SYSTEMS WITH BEETLES.

The inclusion of beetles into the model (5.M) of grazing systems contributed much in the removal of dung and, thus, making large areas of the lost pasture available for plant growth. At low herbivore densities the general shape of graphs of the variable V did not change from that obtained for a case where the beetle

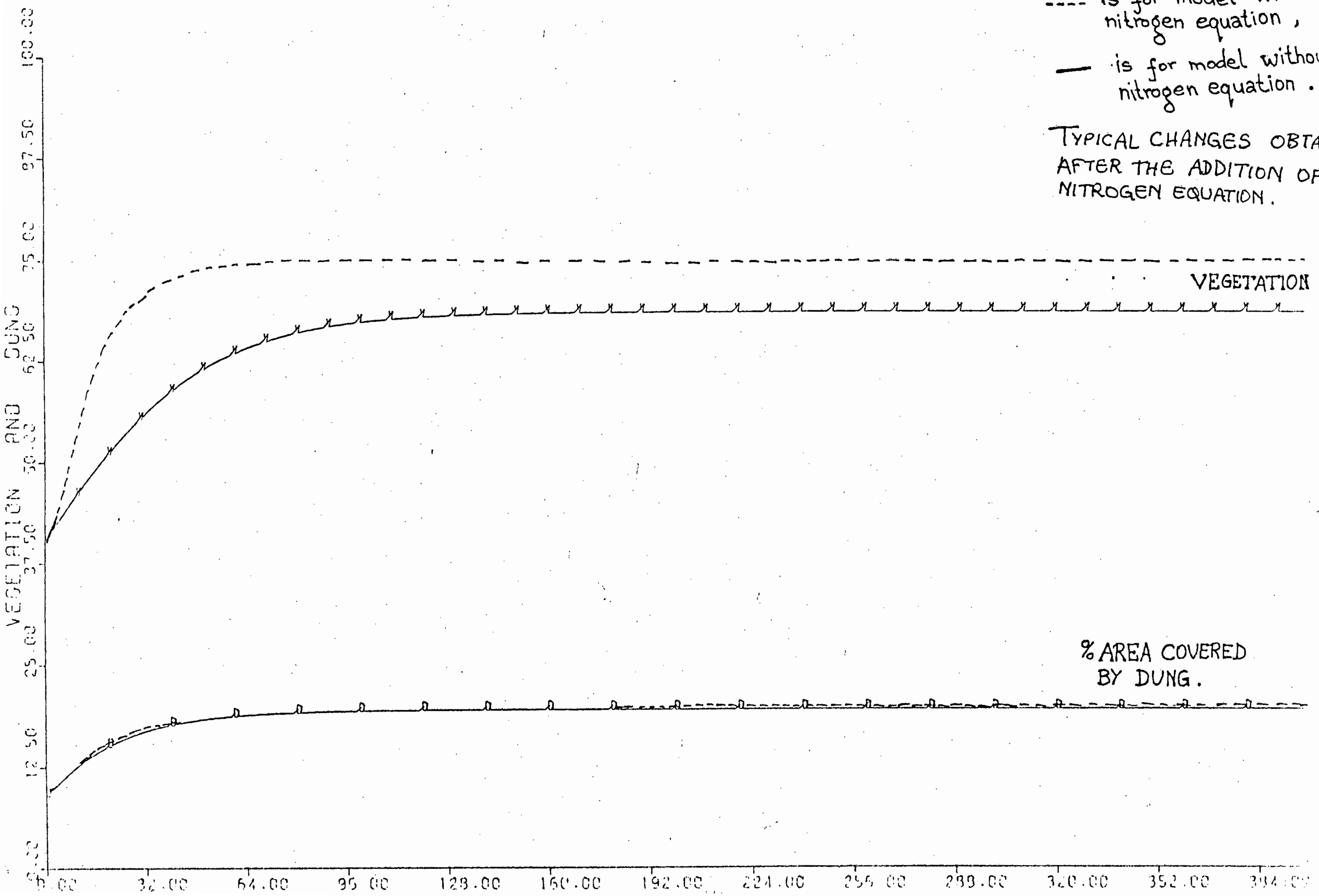


Figure 7-5^A RESULTS FOR H=·33

---- is for model with a nitrogen equation,

— is for model without a nitrogen equation.

TYPICAL CHANGES OBTAINED AFTER THE ADDITION OF A NITROGEN EQUATION.

population was kept at zero. The only difference was that steady state values of V were generally increased.

The effect observed in choosing various initial values of state variables was that the steady state values remained unchanged. Hence from this it can be deduced that the system has a unique point of equilibrium. All the variables, but nitrogen, rapidly approached steady state.

As the herbivore density (H) was steadily increased, steady state values of V decreased and F increased. The steady state values of B_1 and B_2 also increased. Such an increase can be said to have resulted from the increased incoming fresh dung because of the added herbivores. A higher level of fresh dung means that a greater number of beetles can be maintained. Figures (7-6) and (7-7) show the behaviour of V and B_2 at different herbivore densities.

At a high stocking rate the dung beetle population increased to a level where all the incoming fresh dung could be finished. F started oscillating. These oscillations were passed to the rest of state variables. Further increases in H magnified these oscillations. Overgrazing leading to the extinction of V was observed for all H>1.023. This shows an improvement in the carrying capacity of the grazing land. In the absence of beetles the carrying capacity of our grazing system was predicted to be H=0.897. Thus showing an improvement of about 14% in the carrying capacity of the grazing land. Figure (7-8) gives graphs showing the percentage area covered by dung, at different stocking rates (H) in both the absence and the presence of beetles.

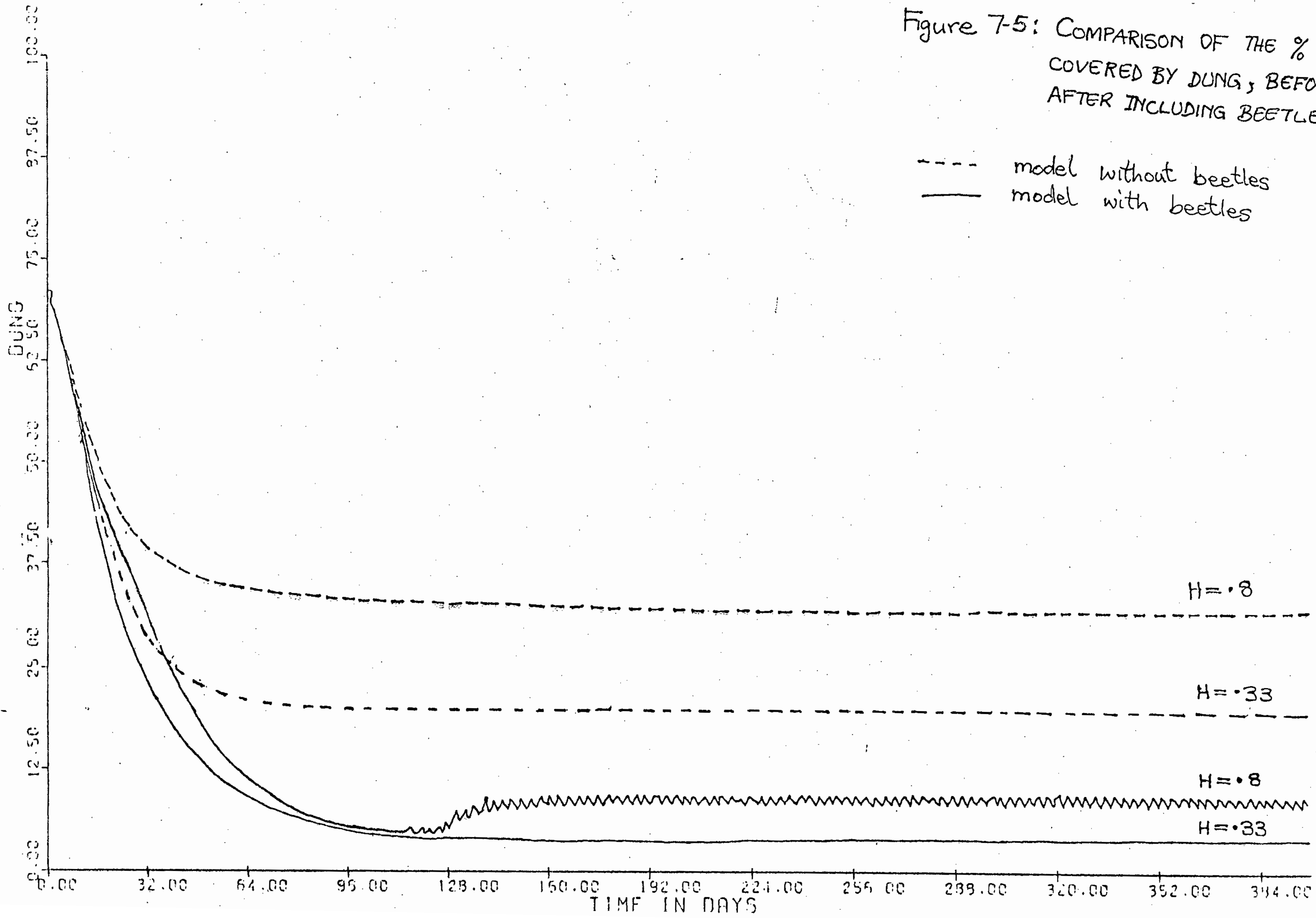
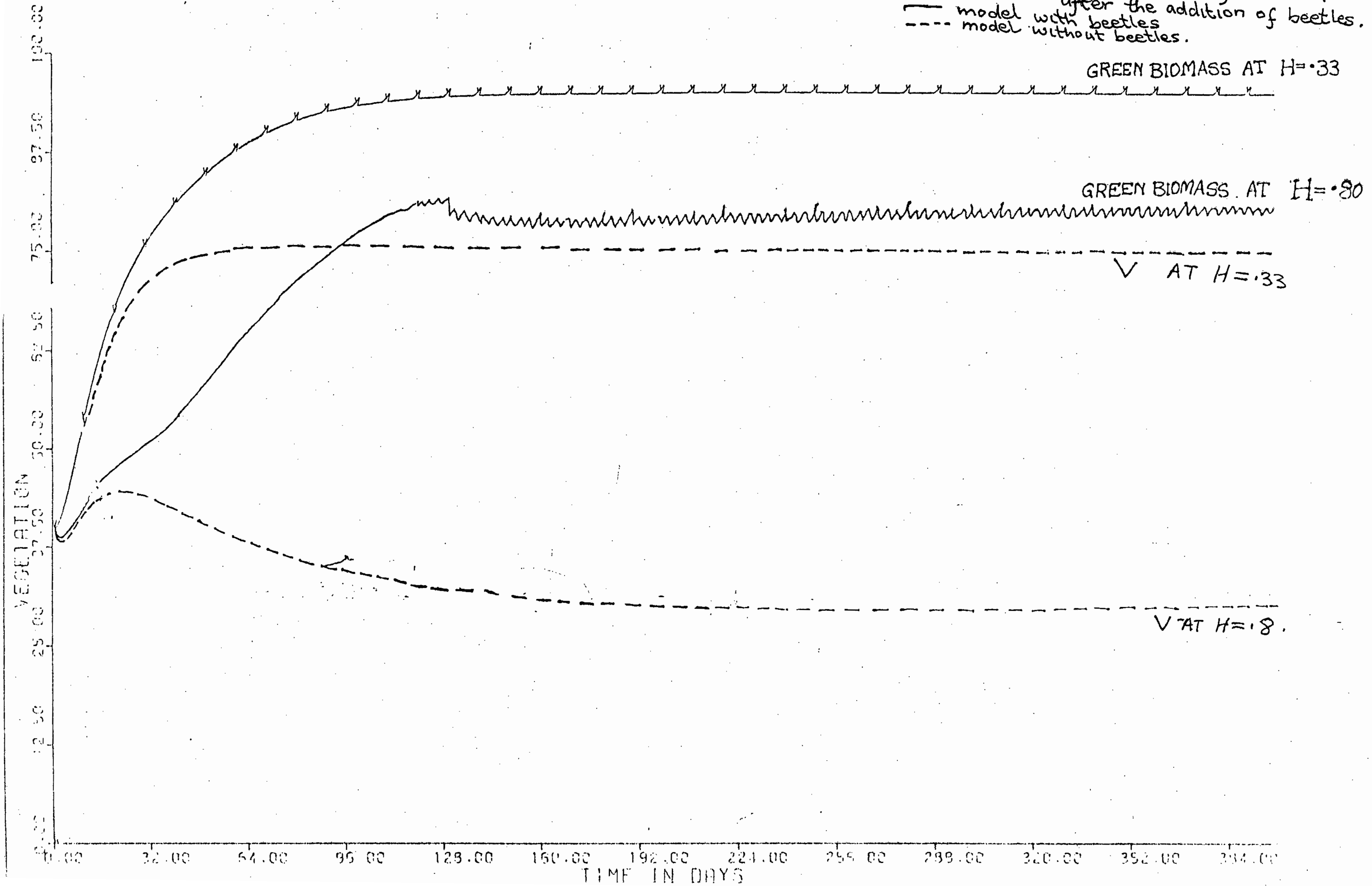


Figure 7-5: COMPARISON OF THE % AREA COVERED BY DUNG, BEFORE AND AFTER INCLUDING BEETLES.

Figure 7-6. Vegetation before and after the addition of beetles.



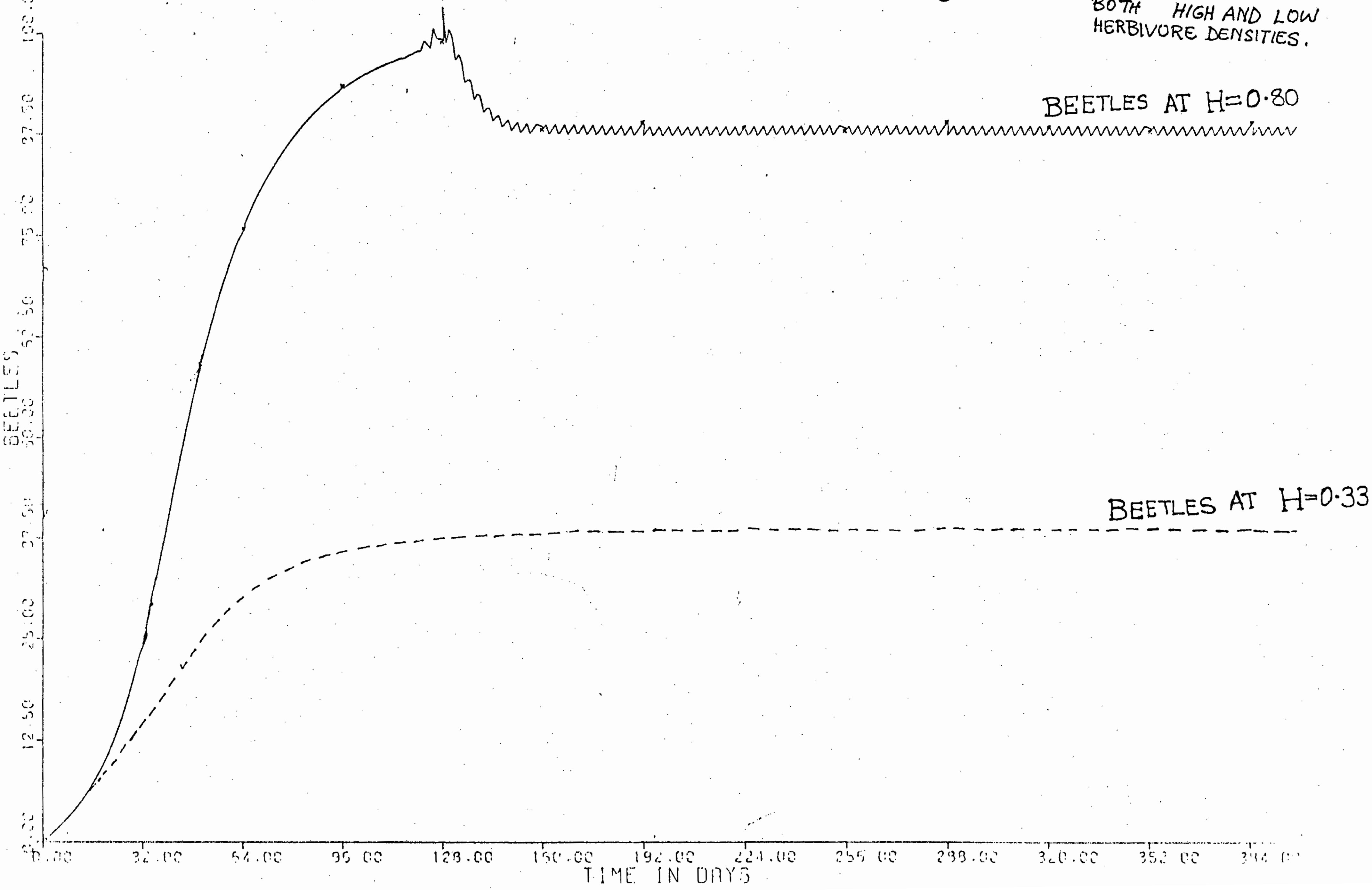


Figure 7-7: BEETLE·POPULATION AT BOTH HIGH AND LOW HERBIVORE DENSITIES.

7.5. SENSITIVITY ANALYSIS.

The method of sensitivity analysis used in this section is the most rudimentary. All that was done was to introduce a 10% change in the parameter values of the model. Because of the size of the model, only a limited number of parameters were chosen for investigation. The reason for doing this analysis was just to get an idea of the relative sensivity of the model output to each of the parameters chosen. In Table (7-2) we give percentage changes that were observed in the steady state values of the state variables when the parameters were either increased or decreased by 10%, one parameter at a time.

Table 7-2. RESULTS OBTAINED BY INTRODUCING A 10% CHANGE.

PARAMETER	ΔV%	ΔB%	ΔF%	ΔU%	ΔN%
k_1+10%	.085	10.201	-9.475	-0.311	.024
k_1-10%	-.966	-13.360	19.334	4.730	-1.671
g_1+10%	.230	4.075	-4.737	1.199	.186
g_1-10%	-.294	-4.704	6.146	-1.487	-.259
m_1+10%	-.278	-4.254	5.634	-1.354	-.493
m_1-10%	.267	4.500	-5.250	1.310	6.584
m_2+10%	-.851	-12.121	17.285	-4.219	-1.260
m_2-10%	.021	11.408	-8.451	2.287	1.035
d_2+10%	.043	.708	-.768	2.220	.064
d_2-10%	-.161	-.708	.896	-1.998	-.065
α+10%	.480	11.980	0.0	11.992	9.242
α-10%	-.483	-11.959	0.0	-11.947	-8.814
c+10%	-.400	-2.334	0.0	-2.331	-.676
c-10%	.400	2.339	0.0	2.373	.675
b+10%	.294	.414	0.0	.422	.676
b-10%	-.360	-.503	0.0	-.488	-.833
e_3+10%	-.018	-9.095	0.0	0.0	-.333
e_3-10%	.021	11.120	0.0	0.0	.410
g+10%	.265	-.068	0.0	0.0	-.140
g-10%	-.327	-.068	0.0	-.066	.233
e_1+10%	-1.043	-.220	0.0	-.222	.745
e_1-10%	1.024	.215	0.0	.222	-.714
e_2+10%	.737	.157	0.0	.115	-.516
e_2-10%	-.743	-.152	0.0	-.155	.528

7.5.1. SUMMARY OF THE RESULTS.

Perturbations of the parameters e_1, e_2, and c induced small changes in the steady state values of the system. Although e_3 induced little changes in most variables, B_1 and B_2 showed large changes. The components of B_1, B_2, F, and D seem to be very sensitive to changes in the parameters k_1, g_1, m_1, and m_2. The greatest changes of the model output were observed when the perturbations were introduced into the parameter k_1. Thus an extra care will be required in determining the value of k_1. Changes in d_2 resulted in very little changes of the model output.

When α was perturbed by 10% the variables B_1, B_2, U, and N underwent changes of about 12% each, while both F and D remained unchanged. This is an interesting result which means that, say, increasing the relative arrival rate fresh dung will not result in dung accumulating to a higher level. Instead, what will happen is that the population of beetles increases and, thus resulting in more dung being buried underground. This in turn increases soil nitrogen.

CHAPTER EIGHT

RESULTS OF THE MODEL WITH TIME LAGS.

In this chapter we present the computed results obtained for the model (6.M) of a grazing system with time delays. As in chapter 7 our main interest will still be in the changes of the qualitative behaviour of the system due to the addition of delay terms.

The listing of a modified program is given in Appendix E. Because changes were only made in the subroutine DEFINE, only this subroutine is listed. In addition a function GAUSS, which performs numerical integration, is also included. The use of this function was necessitated by the fact that the model (6.M) involves integro-differential equations. GAUSS calls on the functions FRESHD and FNITRO to approximate values F and N, respectively using linear interpolation.

8.1. MODEL WITH DELAY TERMS.

At low herbivore densities (H=0.33) the addition of time delays in the system did not change the behaviour of the system. Steady state values remained unchanged. But as the average time lags of the variables N and F, as defined in equations (6.3) and (6.7), were increased some oscillations were observed at the steady state conditions of the system. At high herbivore densities (H=0.80) the inclusion of time delays into the system resulted in changes of steady values of variables. Firstly, the addition of a time lag (as in equation [6.9]), in a function of beetle mortality rate, resulted in the steady state value of adult beetles B_2 attaining a lower value. The oscillations at steady state were magnified in B_2. The steady state values of the other variables showed minimum changes.

When a second delay term was introduced in equation (6.10), in a function F of the birth of pre-adult beetles, again the steady state values of all the variables, except B_1 and B_2, resulted in very small changes. For all δ_1 and δ_2, satisfying $\delta_1>\delta_2\geq 0$, the new steady state levels of B_1 and B_2 increased to higher values than that predicted by the instantaneous model.

When a third delay term was introduced into the soil-nitrogen varible N, as in equations (6.2) and (6.6), the steady state values of the system with 3 delay terms did not show any changes from the the one obtained for a system with 2 delay terms. As the average lag $\bar{T}=T$ was increased it was observed that the level of $\bar{N}$ showed some very small increases.

In figure (8-1) a graph is given showing changes in the steady state values of the adult beetle variable B_2 at a herbivore density H=0.80. For this particular case we chose the average lag for $\bar{N}$ as T=3.0, the average lag for $\bar{F}$ was $\bar{T}=1/a=2.0$. In the case of a discrete lag in $\hat{F}$ we used $\delta_1=0.6$ and $\delta_2=0.4$.

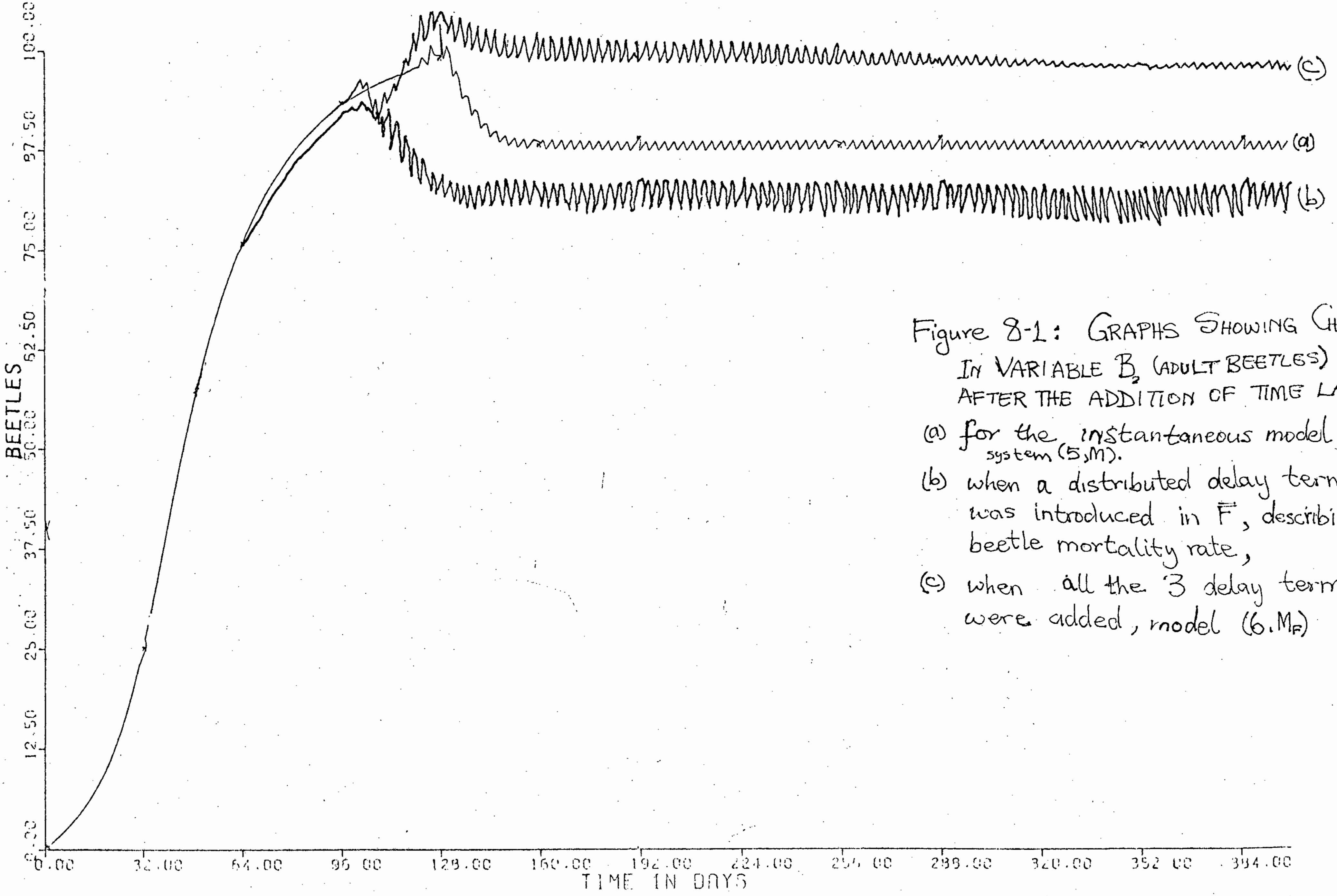


Figure 8-1: GRAPHS SHOWING CHANGES IN VARIABLE B_2 (ADULT BEETLES) AFTER THE ADDITION OF TIME LAGS,

(a) for the instantaneous model, system (5,M).

(b) when a distributed delay term was introduced in $\bar{F}$, describing beetle mortality rate,

(c) when all the 3 delay terms were added, model (6.M_F)

CHAPTER NINE

CONCLUSION.

In this last chapter we shall conclude by giving a summary of the results obtained in the computation of the model.

9.1. SUMMARY OF THE RESULTS.

The model shows a high degree of stability. At all herbivore densities(H) the state variables rapidly approached a steady state. At high grazing, in the absence of beetles, the system approached an oscillatory steady state. With the addition of time delay terms in the system (6.M), the oscillations were decreased. The variables B_1 and B_2, describing both beetle life stages, proved to be very sensitive to the addition of time lags. The other parameters showed very small changes.

An interesting fact deduced from the model results is that it is impossible to have the whole area of pastureland covered with dung - even in the absence of dung beetles. Before such a situation can arise the green vegetation will have been overgrazed to extinction. The addition of beetles also showed an improvement of about 14% in the carrying capacity of the pastureland.

9.2. CONCLUSION

Although most parameter values used resulted from the "guesstimates" made by the writer, useful conclusions can still be drawn from the predictions of the model. The results of the model confirm the benefits of the addition of dung beetles into a herbivore-grazing system. The removal and burial of fresh dung by beetles results in an improvement in the carrying capacity of a grazing land. An increase of the herbivore population also results in the level of beetles increasing. Increasing the rate of the arrival of fresh dung will not necessarilly result in the accumulation of dung on the pastureland, instead the beetle population may increase to balance the increased fresh dung.

The simplifying assumptions and approximations that have been made in the formulation of the model limits the applicability of the predictions of the model to situations where the environmental variables and seasonal weather changes are (almost) constant. By, say, making use of the Noy-Meier's(1978) model of seasonal pastures, the present model can be made to be more realistic. Noy-Meier's model describes biomass dynamics in pastures that are grazed continuously throughout a limited growing season. Further developments which can still be added in the model are predators of beetles, e.g. toads. In the case of the Australian situation the model may be extended to include the effects of beetles on the breeding and abundance of the bushflies.

APPENDIX A

ROUTH-HURWITZ CRITERION

1.1.1. DEFINITION:

The equation $p(s)=0$ is called the characteristic equation. The polynomial $p(s)$ is called the characteristic polynomial. Consider the characteristic polynomial

$$p(s) = p_n s^n + p_{n-1} s^{n-1} + \dots + p_1 s + p_0 \qquad p_i > 0.$$

The choice of $p_n > 0$ minimize a lot of sign arithmetic. If the zeros $z_1, z_2, \dots, z_n$ of $p(s)$ have negative real parts, then all the coefficients $p_0, p_1, p_2, \dots, p_{n-1}$ have the same sign. This follows from the fact that the ratios :

$$\frac{p_{n-1}}{p_n} = - \sum_i z_i$$

$$\frac{p_{n-2}}{p_n} = + \sum_{i \neq j} z_i z_j$$

"

"

$$\frac{p_0}{p_n} = (-1)\, z_1 z_2 \dots z_n$$

are positive and hence $p_i > 0$ for $i=1, 2, \dots, n$. This condition is necessary but not sufficient.

Consider the square matrix of order n :

$$H = \begin{bmatrix} p_{n-1} & p_{n-3} & p_{n-5} & \cdot & \cdot & \cdot & 0 \\ p_n & p_{n-2} & p_{n-4} & \cdot & \cdot & \cdot & 0 \\ 0 & p_{n-1} & p_{n-3} & \cdot & \cdot & \cdot & 0 \\ 0 & p_n & p_{n-2} & \cdot & \cdot & \cdot & 0 \\ \cdot & 0 & p_{n-1} & \cdot & \cdot & \cdot & 0 \\ \cdot & \cdot & p_n & & & & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \cdot & \cdot & \cdot & p_0 \end{bmatrix}$$

H is called the Hurwitz matrix. The index of the coefficients increases by 1 along a column and decreases by 2 along a row.

The element

$$h_{ij} = \begin{cases} p_{n+i-2j} & \text{if} \quad 0 < i-2j < n \\ 0 & \text{if} \quad i < 2j \quad \text{or } i-2j>n \end{cases}$$

The principal minors of the square matrix A

The principal minors of a square matrix A , with a_{ij} an ij^{th} element of A and i,j=1 to n, are the following determinants:

$$D_1 = |a_{11} \, , \quad D_2 = \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix}, \quad \cdot \cdot \cdot \cdot \cdot \, , \quad D_n = \det(A).$$

THEOREM

A necessary and sufficient condition for the polynomial p(s) to have zeros with negative real parts only is that the Hurwitz Determinants (principal minors) $D_k > 0$ for k=1,2,...,n . The proof is given in Willem's (1970)

APPENDIX B

LIAPUNOV STABILITY THEOREMS

2.2. Theorem 1

The null solution of the system $\dot{\underset{\sim}{X}}=\underset{\sim}{f}(\underset{\sim}{X})$ is stable if there is some neighbourhood of the origin where a positive definite function $V(\underset{\sim}{X})$ exists such that its derivative $\dot{V}(\underset{\sim}{X})$ along the solutions of

$\dot{X}=\underset{\sim}{f}(\underset{\sim}{X})$ is negative semi-definite.

2.3. Theorem 2

The null solution of the system $\dot{\underset{\sim}{X}}=\underset{\sim}{f}(\underset{\sim}{X})$ is asymptotically stable if there is some neighbourhood of the origin where a positive definite function $V(\underset{\sim}{X})$ exists such that its derivative $\dot{V}(\underset{\sim}{X})$ along solutions of $\dot{\underset{\sim}{X}}=\underset{\sim}{f}(\underset{\sim}{X})$ is negative definite.

2.4. Theorem 3

If the conditions of theorem 2 are satisfied for every $\underset{\sim}{X}$ and if $V(\underset{\sim}{X})$ is radically unbounded, then the null solution of $\dot{\underset{\sim}{X}}=\underset{\sim}{f}(\underset{\sim}{X})$ is asymptotically stable in the large.

In practice it is very difficult in finding a $V(\underset{\sim}{X})$ satisfying conditions of theorem 2 and theorem 3 and, hence, these conditions may be relaxed slightly. We shall give a theorem 2 below with the above conditions slightly relaxed.

2.5. Theorem 2'

The null solution of the autonomous system

$$\dot{\underset{\sim}{X}} = \underset{\sim}{f}(\underset{\sim}{X}) \qquad (1)$$

is asymptotically stable if in some region R of the origin, there is a positive definite function $V(\underset{\sim}{X})$ such that its derivative $\dot{V}(\underset{\sim}{X})$ along solutions of (1) is negative definite in R and such that $V(\underset{\sim}{X})$ does not vanish identically along any solution of (1) in R other than the null solution.

APPENDIX C.

THE LINEAR CHAIN TRICK (MacDonald, 1978)

The idea of replacing delay by an extension of the set of variables lies behind the policy of setting down conditions under which a set of equations with delays is equivalent to a dynamical system, that is to say to a set of differential equations. With a special choice of memory function this approach gives a convinient method of dealing with delays. Macdonald derives "the linear chain trick" as follows :

Assume we start with an instantaneous equation for a set of variables $x_i(t)$

$$\dot{x}_i = g_i(x_1, \ldots x_n), \quad i=1, \ldots , n, \tag{1}$$

and we introduce a distributed lag in one term of one of these equations, so that the k'th equation becomes

$$\dot{x}_k = \hat{g}_k(x_1, \ldots x_m, \bar{x}_m, \ldots x_n) \tag{2}$$

$$\bar{x}_m = \int_{-\infty}^{t} x_m(\tau)\, G(t-\tau)\, d\tau \tag{3}$$

$$G(u) = G_a^p(u) = a^{p+1} u^p \exp(-au) \tag{4}$$

where a is a positive number and p is a positive integer or zero. Then is clear that

(a) $G_a^p(\infty) = 0$

(b) $G_a^p(0) = 0, \quad p=0$

(c) $G_a^{o}(0) = a.$

Renaiming $\widetilde{x}_m$ as x_{n+p+1}, and defining new variables x_{n+1} to x_{n+p} as

$$x_{n+j} = \int_{-\infty}^{t} x_m(\tau)\ G_g^{j-1}(t-\tau)\ d\tau$$

the results (a,b,c) imply that the new variables satisfy a satisfy a sequence of linear ordinary differential equations

$$\dot{x}_{n+j} = a\ [x_{n+j-1} - x_{n+j}]\ , \quad j=2,\ \ldots\ p+1,$$

$$\dot{x}_{n+1} = a\ [x_m - x_{n+1}] \qquad (5)$$

Supplementing equations (1) and (2) by the set (5) is equivalent to using (3) and (4), provided that the new variables are given appropriate initial values.

APPENDIX D

LISTING OF THE PROGRAM

```
C*********************************************************
C*                                                       *
C*         HAMING'S  PREDICTOR-CORRECTOR  METHOD         *
C*                                                       *
C*********************************************************
C
C  THIS TEST PROGRAM SOLVES A SYSTEM OF N FIRST-ORDER ORDINARY
C  DIFFERENTIAL EQUATIONS USING THE HAMING PREDICTOR-CORRECTOR
C  METHOD. THE PROGRAM READS A STARTING VALUE FOR INDEPENDENT
C  VARIABLE,X,THE INTEGRATION STEP SIZE,H,THE UPPER LIMIT OF
C  INTEGRATION,XMAX,AND N INITIAL CONDITIONS YR(1),...,YR(N)
C  Y AND F ARE MATRICES CONTAINING SOLUTION AND DERIVATIVE
C  VALUES. TE(J) IS THE TRUNCATION ERROR ESTIMATE FOR THEJ'TH
C  CORRECTOR EQUATION. COUNT IS THE STEP COUNTER.
C
C  THE FUNCTION RUNGE IS CALLED TO INTEGRATE ACROSS THE FIRST
C  THREE STEPS AND YIELDS THE STARTING VALUES NEEDED FOR HAMING-
C  METHOD. THEREAFTER,THE EQUATIONS ARE INTEGRATED USING ALTERN-
C  ATLY THE PREDICTOR AND CORRECTOR PORTIONS OF THE FUNCTION
C  HAMING.
C
      REAL K1,M1,M2,NS,NITRO(402),NO
      REAL DAY(402),GREEN(402),DUNG(402),BEETLE(402)
      INTEGER COUNT,RUNGE,HAMING
C
      DIMENSION TE(20),YR(20),FR(20),Y(4,20),F(3,20),FFR(20),
     1          FRR(20),YCOP(20)
C
      COMMON /SET1/ K1,FS,G1,M1,M2,D2,ALPHA,HBV,VS
      COMMON /SET2/ C,E3,B,Q1,E1,Q2,G,VMAX,E2
      COMMON /SET3/ C1,C2,C3,C4,C5,C6,C7,NS,D1
      COMMON /SET4/ FRDUNG(402),F0,AT
      COMMON /SET5/ X,H
      COMMON /SET6/ NITRO,NO,T1
C
C ---      READ IN PARAMETERS AND INITIAL CONDITIONS
C
      READ(3,*)X,H,XMAX,INT,N,(YR(J),J=1,N)
      READ(3,*) K1,FS,G1,M1,M2,D2,ALPHA,HBV,VS
      READ(3,*) C,E3,B,Q1,E1,Q2,G,VMAX,E2
      READ(3,*) C1,C2,C3,C4,C5,C6,C7,NS,D1
      AT=0.5
      T1=3.0
C
```

```
C ---       PRINT PARAMETERS,HEADING AND INITIAL CONDITIONS
C
      WRITE(5,300) K1,FS,G1,M1,M2,D2,ALPHA,HBV,VS
      WRITE(5,300) C,E3,B,Q1,E1,Q2,G,VMAX,E2
      WRITE(5,300) C1,C2,C3,C4,C5,C6,C7,NS,D1
      WRITE(5,200)H,XMAX,INT,N,(J,J=1,N)
      WRITE(5,201)X,(YR(J),J=1,N)
C
      JET=1
      DAY(1)=X
      FRDUNG(1)=YR(3)
      F0=YR(3)
      NITRO(1)=YR(6)
      N0=YR(6)
      DUNG(1)=(YR(3)+YR(4))*100.0
      BEETLE(1)=YR(2)
      GREEN(1)=YR(7)
C
C ---     INITIALIZE STEP COUNTER AND FIRST ROW OF Y MATRIX
C ---     SET TRUNCATION ERRORS EQUAL TO ZERO.
C
      COUNT=0
      DO 2 J=1,N
      TE(J)=0.0
2     Y(4,J)=YR(J)
C
C ---    CALL RUNGE TO INTEGRATE ACROSS FIRST THREE STEPS.
C
3      IF(RUNGE(N,YR,FR,X,H).NE.1)GOTO 4
      CALL DEFINE(YR,FR,N,X)
      GO TO 3
C
C ---    PUT APPROPRIATE INITIAL VALUES IN THE Y AND F MATRICES.
C
4     COUNT=COUNT+1
      ISUB=4-COUNT
      DO 5 J=1,N
5     Y(ISUB,J)=YR(J)
      CALL DEFINE(YR,FFR,N,X)
      DO 55 L=1,N
55    F(ISUB,L)=FFR(L)
C
C ---    PRINT SOLUTION AFTER EVERY INT STEPS.
C
6     IF(COUNT/INT*INT.NE.COUNT) GO TO 7
      JET=JET+1
      IF(COUNT.LE.3) JIL=ISUB
      IF(Y(1,3).LT.0.0) Y(1,3)=0.0
      IF(COUNT.GT.3) JIL=1
      WRITE(5,202)X,(Y(JIL,J),J=1,N)
      DAY(JET)=X
      FRDUNG(JET)=Y(JIL,3)
      NITRO(JET)=Y(JIL,6)
      DUNG(JET)=(Y(JIL,3)+Y(JIL,4))*100.0
      BEETLE(JET)=Y(JIL,2)
      GREEN(JET)=Y(JIL,7)
C
C ---    IF X EXCEEDS XMAX,TERMINATE INTEGRATION.
C
```

```
7    IF(X.GT.XMAX-H/2.)GOTO 1
C
C-------CALL RUNGE OR HAMING TO INTEGRATE ACROSS NEXT STEP.
C
     IF(COUNT.LT.3) GOTO 3
C
C-------CALL HAMING (PREDICTION OR CORRECTION)
C
8    M=HAMING(N,Y,F,X,H,TE)
     DO 88 L=1,N
88   YCOP(L)=Y(1,L)
     CALL DEFINE(YCOP,FRR,N,X)
     DO 93 L=1,N
93   F(1,L)=FRR(L)
     IF(M.EQ.1)GOTO 8
C
C ---    INCREMENT STEP COUNTER AND CONTINUE INTEGRATION.
     COUNT=COUNT+1
     GOTO 6
C
C ****   FORMATS FOR INPUT AND OUTPUT STATEMENTS.
C
100   FORMAT(5X,F10.4,10X,F10.6,12X,F10.4/5X,I5,15X,I2/
    1      (20X,4F12.5))
200   FORMAT(10H1H      =  ,E15.3/10H XMAX   =  ,F12.4/10H  INT   =
,
    1   I7/10H N      = ,I7/1H0/,5X,1HX,10X,7(2HY(,I2,1H),10X))
201   FORMAT(1H0,F10.4,7F14.5/(1H ,10X,4F14.5))
202   FORMAT(1H ,F10.4,7F14.5/(1H,10X,4F14.5))
300   FORMAT(5X,12HPARAMETERS  ,10F10.3)
C
C
  1  CALL PLOTER(DAY,GREEN,DUNG,BEETLE)
     STOP
     END
C
C
C************************************************
C*                                              *
     FUNCTION HAMING(N,Y,F,X,H,TE)
C*                                              *
C************************************************
C
     IMPLICIT REAL(A-H,O-Z)
     REAL Y,F,X,H,TE
     INTEGER HAMING
     LOGICAL PRED
     DIMENSION YPRED(20),TE(20),Y(4,20),F(3,20)
     DATA PRED /.TRUE./
C
C  ---   IS CALL FOR PREDICTOR OR CORRECTOR SECTION
C
     IF(.NOT.PRED) GOTO 44
C
C  ---   PREDICTOR SECTION OF HAMING
C  ---   COMPUTE PREDICTED Y(J) VALUES AT NEXT POINT
C
     DO 11 J=1,N
11   YPRED(J)=Y(4,J)+4.*H*(2.*F(1,J)-F(2,J)+2*F(3,J))/3.
```

```
C
C  ---   UPDATE THE Y AND F TABLES
C
     DO 22 J=1,N
     DO 22 K5=1,3
     K=5-K5
     Y(K,J)=Y(K-1,J)
22   IF(K.LT.4) F(K,J)=F(K-1,J)
C
C  ---    MODIFY PREDICTED Y(J) VALUES USING THE TRUNCATION
C  ---    ERROR ESTIMATES FROM PREVIOUS STEP.
     DO 3 J=1,N
3     Y(1,J)=YPRED(J)+112.*TE(J)/9.
     X=X+H
C
C  ---    SET PRED. AND REQUEST UPDATED DERIVATIVE VALUES
     PRED=.FALSE.
     HAMING=1
     RETURN
C
C  ---   CORRECTOR SECTION OF HAMING
C  ---   COMPUTE CORRECTED AND IMPROVED VALUES OF Y(J) AND
C  ---   SAVE TRUNC. ERROR ESTIMATES FOR CURRENT STEP
44   DO 55 J=1,N
     Y(1,J)=(9.*Y(2,J)-Y(4,J)+3.*H*(F(1,J)+2.*F(2,J)-F(3,J)))/8.
     TE(J)=9.*(Y(1,J)-YPRED(J))/121.
55   Y(1,J)=Y(1,J)-TE(J)
C
C  ---   SET PRED AND RETURN WITH SOLUTIONS FOR CURRENT STEP
     PRED=.TRUE.
     HAMING=2
     RETURN
     END
C
C
C************************************************
C*                                              *
     FUNCTION RUNGE(N,Y,X,H)
C*                                              *
C************************************************
C
C
     IMPLICIT REAL(A-H,O-Z)
     REAL Y,F,X,H
     INTEGER RUNGE
     DIMENSION PHI(50),SAVEY(50),Y(20),F(20)
     DATA M/0/
C
     M=M+1
     GO TO (1,2,3,4,5),M
C
C ................PASS 1....................
C
1     RUNGE=1
     RETURN
C
C .................PASS 2...................
C
2     DO 22 J=1,N
```

```
     SAVEY(J)=Y(J)
     PHI(J)=F(J)
22    Y(J)=SAVEY(J)+.5*H*F(J)
     X=X+.5*H
     RUNGE=1
     RETURN
C
C ....................PASS 3..................
C
3     DO 33 J=1,N
     PHI(J)=PHI(J)+2.*F(J)
33    Y(J)=SAVEY(J)+.5*H*F(J)
     RUNGE=1
     RETURN
C
C ....................PASS 4....................
4     DO 44 J=1,N
     PHI(J)=PHI(J)+2.*F(J)
44    Y(J)=SAVEY(J)+H*F(J)
     X=X+.5*H
     RUNGE=1
     RETURN
C
C ...................PASS 5........................
C
5     DO 55 J=1,N
55    Y(J)=SAVEY(J)+(PHI(J)+F(J))*H/6.
     M=0
     RUNGE=0
     RETURN
     END
C
C
C*********************************************************
C*                                                       *
     SUBROUTINE DEFINE(Y,YRATE,N,TIME)
C*                                                       *
C*********************************************************
C
C  THE SYSTEM OF EQUATIONS (5.M) IS GIVEN IN THIS SUBROUTINE
C
     REAL K1,M1,M2,NS,NDELAY,NO,NITRO(402)
     DIMENSION Y(20),YRATE(20)
     EXTERNAL FUNCTN,GAUSS
     COMMON /SET1/ K1,FS,G1,M1,M2,D2,ALPHA,HBV,VS
     COMMON /SET2/ C,E3,B,Q1,E1,Q2,G,VMAX,E2
     COMMON /SET3/ C1,C2,C3,C4,C5,C6,C7,NS,D1
     COMMON /SET4/ FRDUNG(402),F0,AT
     COMMON /SET6/ NITRO,NO,T1
C
C NOTE THAT:  Y(1)=ADULT BEETLE(B1);  Y(2)=PRE-ADULT BEETLE(B2);
C             Y(3)=FRESH DUNG(F);     Y(4)=DRY DUNG(D);
C             Y(5)=BURIED DUNG(B);    Y(6)=SOIL NITROGEN(N);
C             Y(7)=GREEN VEGETATION(V).
C
     IF(Y(3).LT.0.0) Y(3)=0.0
     FRESH=Y(3)/(Y(3)+FS)
     TRATE=Y(6)/(Y(6)+NS)
     VEG=Y(7)/(Y(7)+VS)
```

```
      AREA=1.0-Y(3)-Y(4)
C
      YRATE(1)=K1*Y(2)*FRESH-(G1+M1)*Y(1)
      YRATE(2)=G1*Y(1)-M2*Y(2)*EXP(-D2*Y(3))
      YRATE(3)=ALPHA*HBV*AREA*VEG-C*Y(3)-E3*Y(2)*FRESH
      YRATE(4)=C*Y(3)-B*Y(4)
      YRATE(5)=Q1*E3*Y(2)*FRESH-Q2*Y(5)
      YRATE(6)=C1*Y(1)+C2*Y(2)+C3*Y(4)+C4*Y(7)-C5*Y(6)
     1        -C6*Y(7)*TRATE+C7*Y(5)
      DADT = -YRATE(3)-YRATE(4)
      YRATE(7)=G*Y(7)*(AREA-Y(7)/VMAX)+DADT*Y(7)/AREA
     1       -E1*HBV*VEG+E2*Y(7)*TRATE+D1*Y(7)
      RETURN
      END
C
C
C*************************************************
C*                                               *
      SUBROUTINE PLOTER(DAY,GREEN,DUNG,BEETLE)
C*                                               *
C*************************************************
C
C          THIS SUBROUTINE CALLS ON THE CALCOMP SUBROUTINES
C          TO PLOT GRAPHS.
C
      DIMENSION DAY(402),GREEN(402),DUNG(402),BEETLE(402)
      CALL NEWPAG
      CALL PAGSIZ(28.0,20.0)
      CALL FACTOR(2.0)
      CALL PLOT(0.5,0.5,-3)
C
      CALL AXIS(0.0,0.0,'TIME IN DAYS',-12,12.5,0.0,
     1          0.0,32.00)
      CALL AXIS(0.0,0.0,'VEGETATION BEETLES DUNG',23,
     1          8.0,90.0,0.0,12.50)
      DAY(401)=0.0
      DAY(402)=32.0
      GREEN(401)=0.0
      GREEN(402)=12.5
      DUNG(401)=0.0
      DUNG(402)=12.5
      BEETLE(401)=0.0
      BEETLE(402)=12.5
      CALL LINE(DAY,GREEN,400,1,10,51)
      CALL LINE(DAY,DUNG,400,1,20,33)
      CALL LINE(DAY,BEETLE,400,1,32,13)
      CALL ENDPLT
      RETURN
      END
```

APPENDIX E

LISTING OF THE PROGRAM WITH TIME LAGS

```
C*******************************************************
C*                                                     *
      SUBROUTINE DEFINE(Y,YRATE,N,TIME)
C*                                                     *
C*******************************************************
C
C   THE SYSTEM OF EQUATIONS (5.M) IS GIVEN IN THIS SUBROUTINE
C
      REAL K1,M1,M2,NS,NDELAY,NO,NITRO(402)
      DIMENSION Y(20),YRATE(20)
      EXTERNAL FRESHD, FNITRO, GAUSS
      COMMON /SET1/ K1,FS,G1,M1,M2,D2,ALPHA,HBV,VS
      COMMON /SET2/ C,E3,B,Q1,E1,Q2,G,VMAX,E2
      COMMON /SET3/ C1,C2,C3,C4,C5,C6,C7,NS,D1
      COMMON /SET4/ FRDUNG(402),F0,AT
      COMMON /SET6/ NITRO,N0,T1
C
C  NOTE THAT:   Y(1)=ADULT BEETLE(B1);   Y(2)=PRE-ADULT BEETLE(B2);
C               Y(3)=FRESH DUNG(F);      Y(4)=DRY DUNG(D);
C               Y(5)=BURIED DUNG(B);     Y(6)=SOIL NITROGEN(N);
C               Y(7)=GREEN VEGETATION(V).
C
      IF(Y(3).LT.0.0) Y(3)=0.0
      FRESH=Y(3)/(Y(3)+FS)
      VEG=Y(7)/(Y(7)+VS)
      AREA=1.0-Y(3)-Y(4)
      FDELAY=F0*EXP(-AT*TIME)+AT*GAUSS(0.0,TIME,15,FRESHD)
      NDELAY=N0*(1.+TIME/T)*EXP(-TIME/T)
      NDELAY=NDELAY+(1./(T*T))*GAUSS(0.0,TIME,15,FNITRO)
      I=IFIX(TIME)
      DELTA=0.6
      FBAR=DELTA*FRDUNG(I)+(1.0-DELTA)*FRDUNG(I-1)
      FD=FBAR/(FBAR+FS)
      TRATE=Y(6)/(Y(6)+NS) C
      YRATE(1)=K1*Y(2)*FD-(G1+M1)*Y(1)
      YRATE(2)=G1*Y(1)-M2*Y(2)*EXP(-D2*FDELAY)
      YRATE(3)=ALPHA*HBV*AREA*VEG- C*Y(3)-E3*Y(2)*FRESH
      YRATE(4)= C*Y(3)-B*Y(4)
      YRATE(5)=Q1*E3*Y(2)*FRESH-Q2*Y(5)
      YRATE(6)=C1*Y(1)+C2*Y(2)+C3*Y(4)+C4*Y(7)-C5*Y(6)
     1         -C6*Y(7)*TRATE+C7*Y(5)
      DADT = -YRATE(3)-YRATE(4)
      YRATE(7)=G*Y(7)*(AREA-Y(7)/VMAX)+DADT*Y(7)/AREA
     1        -E1*HBV*VEG+E2*Y(7)*TRATE+D1*Y(7)
```

```
      RETURN
      END
C****************************************************
C*                                                   *
C             GAUSS-LEGENDRE QUADRATURE
C*                                                     *
C******************************************************
C****************************************************
C*                                                   *
      FUNCTION GAUSS(A,B,M,FUNTCN)
C*                                                     *
C******************************************************
C  THE FUNCTION GAUSS USES THE M-POINT GAUSS-LEGENDRE QUADRT.
C  FORMULA COMPUTE THE INTEGRAL OF FUNCTION(X)*DX BETWEEN
C  INTEGRATION LIMITS A AND B. THE ROOTS OF SEVEN LEGENDRE
C  POLYNOMIALS AND THE WEIGHT FACTORS FOR THE CORRESPONDING
C  QUADRATURES ARE STORED IN THE Z AND WEIGHT ARRAYS RESP..
C  M MAY ASSUME VALUES 2,3,4,5,6,10, AND 15 ONLY. THE APPROPR.
C  VALUES FOR THE M-POINT FORMULA ARE LOCATED IN THE ELEMENTS
C Z(KEY(I)...Z(KEY(I+1)-1) AND WEIGHT(KEY(I))...WEGHT(KEY(I+1)-
C  WHERE THE PROPER VALUE OF I IS DETERMINED BY FINDING THE
C  SUBSCRIPT OF THE ELEMENT OF THE ARRAY NPOINT WHICH HAS THE
C  VALUE M. IF AN INVALID VALUE OF M IS USED, A TRUE ZERO IS
C  RETURNED AS THE VALUE OF GAUSS.
C
      IMPLICIT REAL(A-H,O-Z)
      REAL A,B,FRESHD
      DIMENSION NPOINT(7),KEY(8),Z(24),WEIGHT(24)
C
C/////// PRESENT NPOINT,KEY,Z, AND WEIGHT ARRAYS ///
C
      DATA NPOINT /2,3,4,5,6,10,15/
C
      DATA KEY   /1,2,4,6,9,12,17,25/
C
      DATA Z          / 0.577350269,0.0        ,0.774596669,
     1      0.339981044,0.861136312,0.0        ,0.538469310,
     2      0.906179845,0.238619186,0.661209387,0.932469514,
     3      0.148874339,0.433395394,0.679409568,0.865063367,
     4      0.973906529,0.0        ,0.201194094,0.394151347,
     5      0.570972173,0.724417731,0.848206583,0.937273392,
     6      0.987992518 /
C
      DATA WEIGHT        / 1.0        ,0.888888889,0.555555555,
     1         0.652145155,0.347854845,0.568888889,0.478628671,
     2         0.236926885,0.467913935,0.360761573,0.171324493,
     3         0.295524225,0.269266719,0.219086363,0.149451349,
     4         0.066671344,0.202578242,0.198431485,0.186161000,
     5         0.166269205,0.139570678,0.107159221,0.070366047,
     6         0.030753242 /
C
C///// FIND SUBSCRIPT OF FIRST Z AND WEIGHT VALUE /////
C
      DO 1 I=1,7
      IF(M.EQ.NPOINT(I)) GOTO 2
1      CONTINUE
C
      GAUSS=0.0
      RETURN
```

```
C
C      ......... SET UP INITIAL PARAMETERS ...........
2      JFIRST=KEY(I)
      JLAST=KEY(I+1)-1
      C=(B-A)/2.0
      D=(B+A)/2.0
C
C  ...... ACCUMULATE THE SUM IN THE M-POINT FORMULA ...
      SUM=0.0
      DO 5 J=JFIRST,JLAST
      IF(Z(J).EQ.0.0) SUM=SUM+WEIGHT(J)*FRESHD(D)
5      IF(Z(J).NE.0.0) SUM=SUM+WEIGHT(J)*(FRESHD(Z(J)*C+D)
     1                                   +FRESHD(-Z(J)*C+D))
C
C ...... MAKE INTERVAL CORRECTION AND RETURN........
      GAUSS=C*SUM
      RETURN
      END
C
C
C@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C@                                         @
      FUNCTION FRESHD(S)
C@                                         @
C@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C
C  FUNCTION FOR INTERPOLATING VARIABLE FOR FRESH DUNG, F.
C  SEE EQUATION (6.14)
C
      REAL S,F,H
      COMMON /SET4/ FRDUNG(402),F0,AT
      COMMON /SET5/ X,H
      I=1+IFIX(S/H)
      F=(FRDUNG(I+1)-FRDUNG(I))*(S-(I-1)*H)/H+FRDUNG(I)
      FRESHD=F*EXP(-AT*(X-S))
      RETURN
      END
C
C
C@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C@                                         @
      FUNCTION FNITRO(S)
C@                                         @
C@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@@
C
C  FUNCTION FNITRO FOR DOING LINEAR INTERPOLATION FOR
C  NITROGEN ARIABLE N.   SEE EQUATION (6.13).
C
      REAL N,NITRO(402)
C
      COMMON /SET5/ X,H
      COMMON /SET6/ NITRO,N0,T
C
      I=1+IFIX(S/H)
      N=(NITRO(I+1)-NITRO(I))*(S-(I-1)*H)/H+NITRO(I)
      FNITRO=N*(X-S)*EXP(-(X-S)/T)
      RETURN
      END
```

REFERENCES.

1. Bornemissza, G. F. (1960). Could Dung Eating Insects Improve Our Pastures? J. Aust. Inst. Agric. Sci. 26(1):54-56.
2. Bornemissza, G. F. (1970). Insectary Studies on the control of dung flies by the activity of dung beetle,Onthophagus Gazella F. J. Aust. ent. Soc. 9:31-41.
3. Bornemissza, G. F. and Williams, C.H. (1970). An effect of dung beetle activity on plant yield. Pedobiologia 10:1-7.
4. Carnahan, B. et al. (1969). Applied Numerical Methods. John Wiley & Sons, Inc. New York.
5. Christian, K. R. et al (1978). Simulation of Grazing Systems. Center for Agricultural Publishing and Documentation.
6. Cushing, J. M. (1977). Integrodifferential Equations and Delay Models in Population Dynamics. Lecture Notes in Biomath 20. (Springer-Verlag, Berlin)
7. Henkens, Ch.H. (1978). Agro-ecosystems in the Netherlands. Cycling of Mineral Nutrients in Agricultural Ecosystems. Development in Agricultural & Managed-Forest Ecology 3. (Editor: M.J. Frissel).
8. Jackson, F. (1980). A Mathematical Model of a Grazing System Including Dung Beetles. Notices of S.A. Math. Soc.
9. LaSalle,J. Lefschetz,S. (1961). Stability by Liapunov's Direct Method with Applications. (Academic Press, London)
10. Macdonald, N. (1978). Time Lags in Biological Models. Lecture Notes in Biomath 27. (Spring-Verlag)
11. May, R. (1971). Stabilty of Multispecies Community Models. Math. Biosciences 16: 69-79.

12. May, R. (1973). Stability and Complexity in Model Ecosystems. (Princeton University Press,Princeton, New Jersey.)

13. May, R. (1977). Threshold and Breakpoints in Ecosystem with a Multiplicity of Stable States. Nature. 269: 471-477.

14. Moore, G.R. (1964). Grasses and grasslands. Editor: C. Barnard. (MacMillan, London.)

15. Noy-Meier, I. (1975). Stability of Grazing Systems: An Application Predator-Prey Graphs. J. of Ecology 63: 459-481.

16. Noy-Meier, I. (1976). Rotation grazing in a continuously grazed pasture: a simple model. Agricultural Systems 1: 87-112.

17. Noy-Meier, I. (1978). Grazing and Production in Seasonal Pastures: Analysis of a simple model. J. of Applied Ecology 15: 809-835.

18. Reuss,J.O. Innis,G.S. (1978). A Grassland Nitrogen-Flow Simulation Model. Grassland Simulation Model. Edited: G.S. Innis Ecological Studies 26: 185-203. (Spriner-Verlag)

19. Rosen, R. (1976). Biochemical Systems Analysis. A study of Function and Design in Molecular Biology.

20. Waterhouse, D. F. (1974). The Biological Control of dung. Scientific American - April,1974.

22. Wielgolaskie, F. (1973). A Grazing lands Simulation Model. Mathematical Analysis of Decision Problems in Ecology. Lecture Notes in Biomath. 5: 45-82.

23. Willems, J.L. (1970). Stability Theory of Dynamic Systems. Nelson.