Sensitivity analysis of a simple linear model of a savanna ecosystem at Nylsvley

W M Getz and A M Starfield

A Report of the Savanna Ecosystem Project
National Programme for Environmental Sciences

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PREFACE

This is the first of a series of technical reports of the Savanna Ecosystem Project of the the National Programme for Environmental Sciences, one of several national scientific programmes administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of non-governmental international scientific effort in the environmental field.

The savanna ecosystem project being carried out at Nylsvley is a joint undertaking of more than thirty scientists from the Department of Agricultural Technical Services, the Transvaal Provincial Administration, the National Parks Board, the CSIR, the Transvaal Museum, and eight universities. As far as this is possible, participating laboratories finance their own research within the project. The shared facilities at the study area and the research of participating universities and museums is also financed from a central fund administered by the National Committee for Environmental Sciences and contributed largely by the Department of Planning and the Environment.

As a first step in the savanna ecosystem project, a simple linear model of the system was developed as an aid to the planning of the research programme. This report describes the first model and its sensitivity analysis.

CURRENT TITLES IN THIS SERIES

1. A description of the Savanna Ecosystem Project, Nylsvley, South Africa. December 1975. 24 pp.
2. Sensitivity analysis of a simple linear model of a savanna ecosystem at Nylsvley. W M Getz and A M Starfield. December 1975. 18 pp.
3. Savanna Ecosystem Project - Progress Report 1974/1975. S M Hirst. December 1975. 27 pp.

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ABSTRACT

The construction of a linear compartmental model of the savanna ecosystem at Nylsvley is discussed. Using crude estimates for the standing crop of the compartments and intercompartmental flow rates the sensitivity of the model to changes in its parameters is analysed. The results obtained from this analysis are discussed and some general statements on important structures in the Nylsvley ecosystem that emerge from the analysis of the model are made. In particular certain conclusions are drawn and some recommendations are made concerning future research of the savanna ecosystem project.

SAMEVATTING

Die opstel van 'n lineêre kompartementele model van die savanne ekosisteem te Nylsvley word bespreek. 'n Analise van die sensitiwiteit van die model vir veranderings in sy parameters word gemaak deur growwe skattings te gebruik vir die staande oes van die kompartemente en interkompartemente vloeitempo's. Die resultate verkry uit hierdie analise word bespreek en sekere algemene stellings word gemaak oor belangrike strukture in Nylsvley ekosisteem wat ontstaan uit die analise van die model. In die besonder word sekere gevolgtrekkings gemaak en sekere aanbevelings word gemaak betreffende toekomstige navorsing in die savanne ekosisteem-projek.

INTRODUCTION

At the time when the work described in this report was undertaken the Savanna Ecosystem Project was only six months into an initial research phase which was scheduled to occupy about two years. The amount of information then available on the system was insufficient to build a biologically realistic model of the system and even by the time that the two-year pilot study phase has been completed it is not expected that anything more than a low-resolution model of the system will have been developed. It was nevertheless considered worthwhile to build a simple linear model on the basis of the available information, recognising that such a model would be biologically naive and incomplete, but regarding it as the first step towards a more realistic model.

This report describes the first linear model of the Nylsvley savanna-ecosystem. It was decided that the most useful approach would be to build a linear compartmental model of the ecosystem, averaged over all the seasons in a climatically typical year. This simply means that our objectives were to develop a model of the system by choosing the major components (compartments) of the system and estimating the flow of material between the compartments as an average flow rate over all seasons of the year.

Any attempt to build a more sophisticated model of the system by including estimates of seasonal flow-rate values between compartments, or by taking non-linearities in the behaviour of the ecosystem into account would have been thwarted by the lack of data. In fact it is possible that an attempt to build too sophisticated a model at this stage might have obscured certain broad principles governing the behaviour of the ecosystem which principles, it was hoped, would emerge from the study.

The objectives of the first model were therefore defined as follows:

(a) to identify the intercompartmental flows and hence various trophic groups into which the compartments may fall (in system terminology this is known as identifying the essential topological structure of the system);

(b) to use sensitivity analysis to identify those flows most influential in their effect on the system and the compartments most sensitive to changes in the system;

(c) to familiarize the various research teams with the findings under (a) and (b) above, and thus to some extent assist in the organization and coordination of the project;

(d) to use results from (b) as a guide in determining research priorities in future project planning;

(e) to introduce the non-mathematically orientated life scientist to the methodology and discipline of the modelling approach to studies of ecosystems.

In view of objective (c) it was decided to separate the qualitative analysis from the mathematical analysis in this report. Section A of the report contains a description of the biological structure of the model and the interpretative conclusions drawn from the mathematical analysis, while section B contains the mathematical analysis upon which the discussion in section A is based.

SECTION A

THE MODELLING STRATEGY

At the time when the preliminary model was designed, the only accurate data available on the Nylsvley ecosystem were the results of vegetation surveys. The rest of the data required for this particular model were estimated at a general workshop meeting attended by the leaders and some participants of the various component research teams involved in the project.

The following points should be noted about the data proposed by this workshop.

(a) yearly average flows between compartments of the model were estimated (as previously discussed) and these values then converted to flow rates by dividing by 50 as the time unit of the model was taken to be 1/50th of a year

(b) the values indicating the average standing crop of the compartments of the model were felt, on the whole, to be more accurate than the values estimated for the intercompartmental flow rates

(c) the volume of data available on the reducer and decomposer components of the system and losses due to respiration, carcasses and dung was so scant that it was decided to lump these elements of the system into a single, all-embracing, unstructured sink.

In view of point (b) above, it was decided to take the unusual approach of building the ecosystem model in reverse. The primary motivation for this approach was the following. The average yearly standing crop of the system, when estimated, was assumed to be typical of a year during which the weather was normal. Since little information was available about the structure or behaviour of the Nylsvley savanna ecosystem and any data on the flows within the system were not as reliable as the estimated standing crop values, it was considered that the best model that could be produced under the circumstances would be one which would in fact predict these estimated average standing crop values as a steady-state solution to the behaviour of the ecosystem. Thus instead of building a model of the system and running the model to obtain a solution giving the biomass levels of each compartment over a period of time, the solution to the model was assumed to be the estimated standing crop values, and those parameters of the model associated with flow rates were adjusted until a model that gave the desired solution was obtained. The parameters in the model associated with the flow rates from a particular compartment to the sink were chosen so as to balance the inputs to the compartment concerned and yield the desired average standing crop value. Certain of the intercompartmental flow rates were adjusted, always giving consideration to whether such a change seemed biologically realistic, to improve the performance of the model in giving the desired solution.

Clearly this technique of building a model of the ecosystem excludes the possibility that certain phenomena, such as woody succession in the system after devastation by fire, can be detected by the model. The detection of such phenomena becomes feasible only if a model has been soundly based on accurate data.

Once the parameters of the model had been adjusted to give the required solution, a sensitivity analysis of the model was undertaken.

COMPARTMENTS AND FLOWS

As a first step in the construction of a linear compartmental model the ecosystem was broken down into 15 component parts (variables). These could be divided into four major trophic groups. An unstructured sink, including the decomposer and reducer components of the system, was included to take care of the material outlows from the 15 components selected to represent the system. These four trophic groups and fifteen variables are listed in Table 1 below, together with the average standing crop of each variable given in biomass per unit area.

The major structural links, i.e. material flow connections, were then decided upon. This structure is illustrated in Figure 1. The symbols F_{ij} represent material flow connections between the various trophic levels, including the sink. The arrows in Figure 1 indicate the direction of flow of materials, e.g. F23b represents the flow from trophic group 2 to trophic group 3b as indicated by the direction of the arrow associated with F23b in Figure 1.

Flow connections between the actual variables in the system were represented in the mathematical model by rate parameters a_{ij}. Thus a_{19}, for example, is the rate parameter for the flow of biomass from the grass compartment (x_1) to the impala compartment (x_9). In fact a_{19} forms part of the larger flow connection F13a in Figure 1.

A topological diagram on the individual flow connection scale has not been included, as it would be unnecessarily complicated. Mathematically this refined topological structure is expressed in the interaction matrix of the system given in Figure 4 at the end of Section B. A list of all the system parameters is given in Table 3. Parameters whose first and second subscripts are the same (e.g. $a_{10\ 10}$), represent the rate for the loss of biomass from the particular compartment concerned (in this case x_{10}) to the sink.

Table 1. Model components of the Nylsvley savanna ecosystem.

Trophic group	System component	Symbol	Average yearly standing crop
	Grass	x_1	240 g/m^2 dry weight
1	Forbs	x_2	16 "
Primary	Small shrubs	x_3	300 "
producers	Large shrubs	x_4	160 "
	Trees	x_5	300 "
2	Moribund grass	x_6	60 "
Dead	Standing dead trees and shrubs	x_7	23 "
vegetation	Litter	x_8	30 "
3a	Impala	x_9	0,9 g/m^2 wet weight
Herbivores	Kudu	x_{10}	0,5 "
	Small herbivores	x_{11}	0,5 "
3b			
Herbivorous	Grass-eating insects	x_{12}	0,75 "
insects	Browsing insects	x_{13}	0,4 "
4			
Secondary	Carnivores	x_{14}	0,4 "
consumers	Insectivores	x_{15}	0,01 "

SENSITIVITY ANALYSIS

Sensitivity analysis is an enlightening and instructive method of analysing dynamic systems, especially with respect to understanding the degree of interdependence of the various system variables. In this particular study we have primarily been concerned with the sensitivity of the system components with respect to changes in the various flow rates between the individual system components. In Table 2 and 3, the results of the sensitivity analysis have been listed in a form that can be easily evaluated.

In non-mathematical terms these results were derived as follows. The effect of a 10 percent increase of a particular parameter in the model on the biomass level of all the components of the system was measured and compared with the biomass levels of the compartments as given by the original model, i.e. the average yearly standing crop values. The measurements were taken after the model had simulated the behaviour of the perturbed system for one and then five years, and were expressed as a percentage change with respect to the average yearly standing crop in Tables 6 and 7. This percentage change may be either positive or negative, depending on whether the biomass levels of the perturbed compartments increased or decreased.

It was found that a 10 percent increase in the flow rate of material from the grass compartment of the model to its small herbivore compartment caused the biomass level of the moribund grass compartment of the model after one year to decrease by 1,6 percent over the average yearly standing crop value, whereas it caused the biomass level of the small herbivore compartment of the model to increase by 84,1 percent over the same period.

Table 2 gives the gross percentage change for each compartment in the model after one year and also after five years with respect to a 10 percent increase in all parameters of the system. The definition of gross percentage change with respect to a 10 percent increase in all parameters of the system is "the sum of the changes caused by a 10 percent increase in all the parameters of the system without taking the sign of the change into account". If the sign of the changes is taken into account when summing, a net percentage change figure is obtained which will give, as a percentage of the average yearly standing crop, the actual biomass level of a system whose flow rates are all 10 percent larger than the system being modelled.

The gross percentage change in a particular compartment is a measure of the sensitivity of that compartment to arbitrary changes in the flow rates of the system, whereas the net percentage change is not. For example, the gross percentage change in the small herbivore compartment after one year is 378 percent, while the net percentage change is zero. The figure 378 percent can be used to compare the sensitivity of the small herbivore compartment with similar figures for other compartments with respect to arbitrary changes in the parameters of the model, while the zero figure conveys nothing beyond the fact that a uniform change in all parameters of the system will not change the biomass level of the herbivore compartment at all after one year.

It is also desirable to have a measure of the sensitivity of the system as a whole to changes in individual parameters. Table 3 lists such a set of values, which was obtained by adding the absolute value of the percentage change in biomass, with respect to standing crop, of each compartment of the model for a 10 percent change in one of the parameters.

Table 2. Change due to a 10 percent increase in all parameters of the model.

Variables	Average yearly standing crop	Gross % change after 1 year	Rank	Gross % change after 5 years	Rank
x_1	240 g/m^2	219	6	14 600	5
x_2	16 "	103	11	4 300	12
x_3	300 "	93	14	6 100	11
x_4	160 "	99	12	11 600	7
x_5	300 "	94	13	9 900	8
x_6	60 "	725	4	47 700	3
x_7	23 "	110	10	14 600	6
x_8	30 "	203	7	19 100	4
x_9	0,9 "	194	9	1 100	14
x_{10}	0,5 "	200	8	1 200	13
x_{11}	0,5 "	378	5	6 500	10
x_{12}	0,75 "	3 157	2	86 800	2
x_{13}	0,4 "	3 688	1	154 100	1
x_{14}	0,4 "	14	15	70	15
x_{15}	0,01 "	1 400	3	7 000	9

Table 3. Percentage change in model due to a 10% increase in a particular parameter value.

Parameters		% change in system after 1 year	Rank	% change in system after 5 years	Rank	Increase factor	Group
a_{16}	0,0072	10,2	26	14,4	32	1,4 times	
a_{26}	0,030	9,2	28	9,9	36	1,1 "	
a_{66}	0,001	0,5	42	1,2	43	2,4 "	
a_{37}	0,003	7,3	32	8,4	37	1,2 "	
a_{47}	0,0019	2,9	40	4,4	41	1,5 "	
a_{57}	0,0038	9,3	27	13,8	33	1,5 "	
a_{77}	0,042	11,7	25	13,2	34	1,1 "	
a_{28}	0,0146	0,5	43	0,5	42	1,0 "	1
a_{38}	0,0032	4,3	36	7,9	38	1,8 "	
a_{48}	0,0046	3,9	38	7,6	39	1,9 "	
a_{58}	0,0031	4,6	34	16,0	30	3,5 "	
a_{68}	0,015	8,1	31	14,6	31	1,8 "	
a_{78}	0,018	5,9	33	6,4	40	1,1 "	
a_{88}	0,122	12,0	24	12,9	35	1,1 "	
a_{19}	0,172	90,7	15	625	18	6,9 times	
a_{39}	0,008	4,5	35	25,9	28	5,8 "	
a_{49}	0,006	3,2	39	19,5	29	6,1 "	
a_{99}	0,185	97,2	14	597	19	6,1 "	
$a_{3\ 10}$	0,079	44,3	17	332	20	7,5 "	2
$a_{4\ 10}$	0,077	43,2	18	316	21	7,3 "	
$a_{5\ 10}$	0,025	13,8	22	105	26	7,6 "	
$a_{10\ 10}$	0,179	100	12	750	17	7,5 "	
$a_{1\ 11}$	0,200	97,2	13	1 686	12	17,3 times	
$a_{2\ 11}$	0,160	79,1	16	1 351	13	17,1 "	
$a_{3\ 11}$	0,025	12,2	23	211	22	17,3 "	3
$a_{4\ 11}$	0,0175	8,5	30	148	24	17,4	
$a_{5\ 11}$	0,018	8,7	29	156	23	17,9 "	
$a_{11\ 11}$	0,4115	200	11	3 466	11	17,3	

Contd....../

Table Continued..../

Parameters			% change in system after 1 year	Rank	% change in system after 5 years	Rank	Increase factor	Group
a_1	12	1,100	989	4	28 150	6	28,5 times	
a_6	12	0,900	812	6	23 030	9	28,4 "	4
a_{12}	12	1,9888	1 784	1	50 868	3	28,5 "	
a_2	13	0,041	33,8	19	1 331	14	39,4 times	
a_3	13	0,810	662	8	26 241	7	39,7 "	
a_4	13	0,452	370	10	14 640	10	39,6 "	
a_5	13	0,810	662	7	26 260	8	39,6 "	5
a_{13}	15	2,099	1 713	2	67 970	2	39,7 "	
a_9	14	0,021	4,0	37	146	25	36,5 times	
a_{10}	14	0,007	1,45	41	50	27	34,5 "	6
a_{11}	14	0,112	23,0	21	834	16	36,2 "	
a_{14}	14	0,140	23,3	20	961	15	40,9 "	
a_{12}	15	0,840	812	5	42 380	4	52,2 "	
a_{13}	15	0,560	546	9	28 520	5	52,2 "	7
a_{15}	15	0,400	1 336	3	70 161	1	52,5 "	

For the evaluation of the comparative sensitivities of the system components and flows, more stress will be placed upon the sensitivity values obtained after one year than upon those obtained after five years, since by assumption the system model is linear and thus becomes more unreliable as a model of the system the further the solution deviates from the equilibrium solution (the average standing crop values).

From Table 2 the insect compartments (x_{12} and x_{13}) appear significantly more sensitive - at least ten times - to changes in the system parameters than the rest of the compartments, except for the insectivore (x_{15}) and moribund grass (x_6) compartments where it is twice and four times as sensitive respectively after one year. The carnivore compartment (x_{14}) is least sensitive to changes in the system flow rates; this suggests that the carnivores may play a relatively minor role in the dynamic behaviour of the system.

In the primary production trophic group (1) the grass compartment (x_1) is the most sensitive. The small herbivores are the most sensitive compartment of the herbivore trophic group (3a). From tables 6 and 7 (discussed in section B) the insect and herbivore compartments appear to be more sensitive to changes in the flow rates from their food source (trophic levels 1 and 2) than to changes in the flow rate to their predators (x_{15}). The difference in sensitivity of the herbivores to these two sets of flow rates is a factor of 315 for the kudu compartment (x_{10}), 130 for the impala compartment and only 13 for the small herbivores. This reflects the much closer link that the small herbivores, as compared with the large herbivores, have with the carnivores.

The parameters to which the system is most sensitive are those between trophic groups 1 and 2 (primary producers and dead vegetation) and the insect compartments, and those between the insect compartments and the insectivores and the sink, i.e. groups 4, 5 and 7 in Table 3.

Within each group the sensitivity value corresponding to the flow rate from a compartment to the sink is larger than any other parameter in that group with the exception of a_{66}. For example a_{77} is larger than either a_{37}, a_{47} or a_{57}, while $a_{15\ 15}$ is larger than either $a_{12\ 15}$ or $a_{13\ 15}$. The reason for this is that the parameters a_{ii} $i=7,\ldots, 15$ represent a number of rates associated with the outflow of biomass to the sink and thus the single parameters a_{ii} are comparatively large. In the case of dead vegetation, for example, the sink represents the reducer and decomposer components of the system, while for the herbivores and carnivores it deals with losses due to respiration and the flow of dung, urine and carcasses from these compartments of the model.

In principle Table 3 can be used to estimate the relative accuracies to which the flow rates of the system should be measured in order to be compatible with the accuracy desired in the solution of the system model. For example a 10 percent change in the parameter $a_{10\ 10}$ produces a change in the system as a whole of 100 percent after one year while a change of only 5 percent in the parameter $a_{11\ 11}$ produces a change in the system as a whole of 100 percent after one year (since a 10 percent change in $a_{11\ 11}$ produces a 200 percent change in the system after one year). Hence the parameter $a_{11\ 11}$ must be known twice as accurately as the parameter $a_{10\ 10}$ in order that the error limits obtained in estimating the real values of these parameters have the same effect on the accuracy of the system solution. The compatibility of the effect of error in the data, on the accuracy of the solution to the model, is desirable since a model of a system is only as reliable as the least accurate data upon which it is based.

The set of parameters associated with the living and dead vegetation in the system (i.e. group 1) have relatively speaking the lowest increase factors compared with the other parameters in the system (Table 3). The increase factors themselves increase as the group number gets higher, although remaining relatively constant within a particular group. For flows to the large herbivores (group 2) the increase factor is about one third that of flows to the small herbivores (group 3), the factor for which, in turn, is about two-thirds and one half that of the flows to the grass-eating insects (group 4) and browsing insects (group 5) respectively. The increase factors for the flows to the carnivores (group 6) are similar to those for group 5 while the increase factor for the flows to the insectivores is the largest of all.

The interpretation of the large differences in increase factors for the various compartments of the system is discussed mathematically in Section B. A possible biological interpretation is that a stable ecosystem is one which can absorb changes in its structure and flow rates without altering its behaviour radically, provided these changes are not too large. Such an ecosystem can, for instance, tolerate variations in climate from year to year provided those variations are not severe and not prolonged over a number of years. Thus, a good model of such an ecosystem should be able to adapt to small changes in the system parameters and still remain stable. This, however, is not true of the model considered in this report, especially since it is linear.

The model behaves well when the parameters in group 1 are increased by 10 percent, as the compartments in the model adjust to the change, as indicated by the one-year sensitivity values in Table 3, and they do not greatly deviate from this value after five years. When, however, any of the parameters in group 7 is increased by 10 percent the changes in the compartments of the model deviate largely after five years with respect to the changes in the compartment of the model after one year, indicating a highly unstable situation.

When a model of a system is built, certain assumptions must be made about the factors governing the flow rates. If the assumptions for the flow rates in one group are a better approximation to the real situation than those in another, the compartments influenced by the first group of flow rates will behave in a more stable fashion than those influenced by the second. This could possibly explain the large difference in the increase factors over the various compartments of this system.

The following is a list of the assumptions that were made in building the model discussed in this paper and the evaluation of these assumptions according to the magnitude of the corresponding increase factors.

(a) It was assumed that the flow rates of the flows between the primary producers and dead vegetation are donor-controlled, i.e. the rate at which live vegetation dies in a particular compartment is proportional to the amount of live material present in that compartment. These parameters comprise group 1 in Table 3. For the most part, the increase factors lie between 1 and 2. The above assumption is thus evaluated as very good.

(b) It was assumed that the flow rates of the flows between the primary producers and large herbivores (impala, kudu) are recipient-controlled. This is equivalent to assuming that the food source of the large herbivores is non-limiting, i.e. the large herbivores always have sufficient food for their needs. These parameters comprise group 2. The increase factors have values around 6 and 7 and this assumption is evaluated as poor. This assumption may turn out to be sufficiently good for part of the year, probably spring and summer, to be used in a seasonal model, but should be modified when it is necessary to model the behaviour of the system during winter.

(c) As in (b) it was assumed that the rates of the flows between the primary producers and small herbivores are recipient-controlled. This assumption is, however, less valid here than in (b) since the values of the increase factors for these parameters (group 3) are about 17. A possible reason for this is that the percentage food intake of the small herbivores, with respect to their body weight, is on average two to three times as large as that of the large herbivores, and thus the small herbivores may find it more difficult than the large herbivores to sustain their summer biomass levels in winter when their food source becomes limiting.

(d) It was assumed that the rates of the flows between the primary producers and the insect compartments of the model are recipient-controlled. This assumption is less valid than in (b) and (c) and the difference could be accounted for by the higher percentage food intake with respect to body weight required by the insects as compared with the small herbivores. The grass-eating insects (group 4) have, however, a smaller increase factor (28,5) than the browsing insects (group 5, increase factor 39,5). The reason for this is not clear, although the fact that there is a flow between the moribund grass compartment and the grass-eating insects which is the only flow from the moribund grass compartment to any other compartment in the model except for the sink, may account for the greater stability of the grass-eating insects compared with the browsing insects.

(e) It was assumed that the rates of the flows from the primary consumers to the secondary consumers are recipient-controlled. The increase factors for the herbivore-carnivore flow rates were between 35 and 41, hence the assumption was evaluated to be very poor. In the case of the insect-insectivore flow rates the increase factors were even larger (about 52) and hence the assumption in this case is even poorer. It is always more accurate to model the flow rates between primary and secondary consumers on the basis of predator-prey type interactions, but of course this makes the model non-linear. Since no linear model can accurately simulate the dynamic behaviour of interating populations of predator and prey species, any realistic model of the Nylsvley savanna ecosystem will have to be non-linear.

CONCLUSIONS AND RECOMMENDATIONS

The main points emerging from the sensitivity analysis, outlined in the previous section, are listed below. It is important, however, to recognize that at this stage in the project, these points are a function of the assumptions built into the mathematical model and do not necessarily reflect the structure and dynamics of the ecosystem itself. All of these points are, however worthy of further consideration: either they do reflect key processes in the ecosystem, or else they pinpoint those areas of the model which are biologically incorrect.

(a) It is important that the standing crop of the insect compartments and the rates of flow to and from these compartments in the system be carefully investigated and accurately estimated.

(b) The dynamics of the moribund grass compartment and its relation to the grass and grass-eating insect compartments should be thoroughly studied.

(c) Care should be taken that the values of the flow rates affecting the grass compartment are at least as accurately estimated as those affecting any other compartment in the primary production section of the system.

(d) A thorough investigation of the small herbivore compartment of the model must be included in the herbivore research programme if the primary producer-herbivore dynamics are to be properly accounted for.

(e) Although the herbivore-carnivore interaction seems to play a minor role in the overall dynamics of the system the small herbivore-carnivore interaction must be emphasized in any general study of the ecosystem.

(f) The flows to the sink have been lumped together in this model. This part of the model needs to be refined and the flows to the sink should be investigated and, where possible, separated. In this respect the following areas should be researched:

    (i) The role of reducers and decomposers in breaking down dead vegetable material.

    (ii) The loss of the consumer compartments of the model due to respiration, dung, urine and carcasses.

(g) Each research project should endeavour to extract as much information as is feasible about the seasonal behaviour of the particular component of the system being studied. This information will be essential if future models are to simulate the seasonal dynamics of the Nylsvley savanna ecosystem.

SECTION B

CONSTRUCTION OF A LINEAR COMPARTMENTAL MODEL OF THE SYSTEM

A linear compartmental model of the Nylsvley savanna ecosystem can be expressed mathematically in the linear system of differential equations

$$\dot{X} = AX + f \qquad (1)$$

when $X^T = (x_1,\ldots,x_{15})$ is a vector of variables representing the biomass concentration levels (measured in g/m^2) of the 15 compartments of the model listed in Table 1; A is the interaction matrix of the system whose construction is discussed below; and f represents a vector of inputs into the system. In this model $f^T = (f_{01},f_{02},\ldots,0)$ since the only inputs to the model considered in this paper are the weekly average net* primary production of grass (x_1) and forbs (x_2) over the year. The average weekly net primary production of the other primary producer compartments was assumed to be proportional to the biomass level of these compartments (x_3, x_4 and x_5) and hence the parameters representing the primary production rates (f_{03}, f_{04} and f_{05}, respectively) of these variables appear in the diagonal entries of the interaction matrix A of the system.

The construction of the matrix A follows standard linear compartment model techniques (Mulholland and Kerner 1974, Patten 1971, Getz 1974 and Walker 1974) for building a system of differential equations to simulate the behaviour of a dynamic system.

The basic topology of the model discussed in this paper is summarized in Figure 1. For the purpose of building an interaction matrix A the following assumptions were made. The flow rates of the flows making up connection F12 in Figure 1 were assumed to be donor-controlled, i.e. the rate of a flow between any two variables in trophic groups 1 and 2 respectively was assumed to be proportional to the source variable, i.e. the variable in group 1. All other inter-trophic flow rates were assumed to be recipient-controlled, i.e. controlled by the terminal variable involved with a particular flow. The accuracy of these assumptions has already been discussed in Section A of this paper.

Using these assumptions, an interaction matrix was constructed as described graphically in Figure 2. The individual entries of the shaded areas in Figure 2 are given in detail in Figure 3. The values in these boxes are the values used in the simulation studies, and their units are appropriately defined biomass flows per 1/50th of a year. (This time interval was chosen as it satisfactorily approximates the natural time interval of 1 week). The off-diagonal terms are the estimated flow rates a_{ij} between the i-th and j-th variables, while the diagonal terms are made up of the appropriate a_{ij}'s, $i \neq j$ and a_{ii}'s which represent the flow rates to the sink. The actual parameters used to estimate a particular entry in Figure 3 are displayed in Figure 4.

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* This net value takes into account the amount of grass removed by cattle during the year.

(1) could be reduced to a 13-variable system

$$\dot{X} = \hat{A}X + \hat{f} \qquad (2)$$

where $\hat{A}$ is the upper left 13 x 13 submatrix of A and

$$\hat{f}^T = \begin{bmatrix} f_{01} \\ f_{02} \\ 0 \\ \cdot \\ \cdot \\ \cdot \\ 0 \\ -(a_{9\ 14} + a_{10\ 14} + a_{11\ 14})\ x_{14}(0) \\ -(a_{12\ 15} + a_{13\ 15})\ x_{15}(0) \end{bmatrix} \begin{matrix} \\ \\ \\ \\ \\ \\ \\ \leftarrow \text{12th element} \\ \leftarrow \text{13th element} \end{matrix}$$

Such a reduction was, however, not implemented as it was decided to include x_{14} and x_{15} in the sensitivity analysis.

The system modelled by equation (1) was run using as initial conditions the yearly average standing crop values given in Table 1. Using C.S.M.P. (Patten 1971) to solve the system, with 1/50th of a year representing a unit time interval, a solution was generated over a 5-year period. Over this period of time the solution for the biomass concentration levels of each variable remained within a fraction of 1 percent of the yearly average standing crop value, which in terms of the discussion in Section A was the type of performance expected from the model.

Equation (1) was now ready to be used in a sensitivity analysis.

SENSITIVITY ANALYSIS

In this particular study we are primarily concerned with the sensitivity of the system components with respect to changes in the various flow rates between the individual system components. In mathematical terms we are interested in the responses of the state variables to changes in the parameters of the system. To carry out this type of analysis it is necessary to generate the sensitivity functions of the state, which are defined to be the set of partial derivatives of all state variables with respect to all parameters of the system,

i.e. the set of sensitivity function = $\left\{\frac{\partial x_i}{\partial a_{jk}} \quad i,j,k=1,2,\ldots,15\right\}$

In general, the generation of these sensitivity functions for fairly large systems is a formidable task (Wilkie and Perkins 1969a, 1969b). For this particular model, however, since it is linear and the matrix A rather sparse, the functions were generated without too much difficulty with respect to all parameters listed in Figure 4, except for f_{03}, f_{04} and f_{05}. Owing to an oversight these parameters were unfortunately omitted as they were not initially included in the matrix A. (Initially the parameters f_{03}, f_{04} and f_{05} were calculated as 1/50th of the estimated net yearly average production of compartments x_3, x_4 and x_5. Later, however, they were converted to intrinsic growth rates for these compartments and incorporated in the matrix A, since this modification of the model was deemed to give a better simulation of the dynamics of the system.) As later indicated these omissions do not seriously affect the sensitivity analysis of the model.

The mathematical analysis and computer programmes used to generate the sensitivity functions for the model are to be found in Ingrams (1975). Tables 4 and 5 list the values of the sensitivity functions after 1 and 5 years respectively. For example the entry in row a_{99} and column x_3 in Table 5 is the numetrical value of

$$\frac{\partial x_3}{\partial a_{39}} \; (250)$$

since after 5 years t = 250 (we recall that one time unit = 1/50th of a year). The values in Tables 4 and 5 give the actual changes in the solution to equation 1 due to a unit increase in the parameters of the matrix A. It is, however, more meaningful to transform the values in Tables 4 and 5 to give the relative change in the solution of the perturbed model with respect to the solution of the unperturbed model, for a fixed percentage change in the parameters of the system. Tables 6 and 7 give the values corresponding to transformations of Tables 4 and 5 respectively, for a 10 percent change in the system parameters and a change relative to the standing crop values (denoted $x_i(0)$ i=1,...,n) of the system, i.e. the values in Tables 6 and 7 are derived from the "normalized" functions

$$\frac{\partial x_i}{\partial a_{jk}} \; \frac{(0.1)a_{jk}}{x_i(0)} \quad i,j,k=1,2,\dots,15.$$

A simple method of analysing the values given in Tables 6 and 7 is to sum the moduli of the entries column-wise and row-wise. This was the method used to derive the figures in Tables 2 and 3. To compensate for the fact that the sensitivity functions for f_{03}, f_{04} and f_{05} were not calculated, the column sums of the variables x_3, x_4, x_5, x_7 and x_8 in Tables 6 and 7 have been slightly adjusted. The effect of these adjustments on the sensitivity of the system has been estimated by relating them to other parameters of the system (in particular a_{37}, a_{47}, a_{57}, a_{38}, a_{48} and a_{58}) and it was found that they altered the column sums in Table 6 by 3 to 4 percent and those in Table 7 by a fraction of 1 percent.

Interestingly enough the eigenvalues of the matrix A turn out to be its diagonal elements (see appendix A) so that a 10 percent increase in all parameters of the system will alter the eigenvalue of the matrix A by 10 percent and hence not alter the basic stability properties of the matrix A (Willems 1970). Owing to this phenomenon, if the column sums of Tables 6 and 7 are evaluated taking the sign of the entries into account, the actual value of these sums will be rather small, as the overall behaviour of the model has not altered radically.

However, a 10 percent change in only selected parameters of the system can change the basic stability properties of the matrix A. For example increasing the parameter $a_{13\ 15}$ only in A by 10 percent changes the last diagonal element of A and hence one of the eigenvalues of A from 0,0000 to -0,0840. It now becomes more difficult to discuss the behaviour of the model over any reasonable interval of time.

If Tables 6 and 7 are evaluated at sufficient points in time to be able to examine the dynamic behaviour of the perturbed system, it will be possible to determine many aspects of the response of the system to these perturbations. For example, it will be possible to evaluate more convincingly the assumptions discussed in section A, and to study the time which stable compartments take to settle to new steady values. A knowledge of these settling times could provide valuable information on the behaviour of the system.

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APPENDIX A

From Figure 3 we see that the matrix A has the following structure:

$$A = \begin{bmatrix} L & A_1 \\ & \\ 0 & U \end{bmatrix} \qquad (1)$$

where L is 8 x 8 and lower triangular and U is 7 x 7 and upper triangular.

Now

$$\det(A-\lambda I_{15}) = \det \begin{bmatrix} L-\lambda I_8 & A_1 \\ & \\ 0 & U-\lambda I_7 \end{bmatrix} \qquad (2)$$

Using Laplace's expansion (schaum 1962) to evaluate (2) we see that the only non-zero 7- square minor of the last 7 rows is $\det(U-\lambda I_7)$ whose algebraic complement is $\det(L-\lambda I_8)$. Hence

$$\det(A-\lambda I_{15}) = \det(L-\lambda I_8)\det(U-\lambda I_7)$$

and the eigenvalues of A are equal to the eigenvalues of L and the eigenvalues of U, and vice versa. However, L and U are triangular, so that their diagonal elements are their eigenvalues. But their diagonal elements are also the diagonal elements of A. Hence the diagonal elements of A are its eigenvalues.

	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8	x_9	x_{10}	x_{11}	x_{12}	x_{13}	x_{14}	x_{15}
a_{16}	-1008	0	0	0	0	6779	0	753	0	0	0	0	0	0	0
a_{26}	0	-403	0	0	0	264	0	27,3	0	0	0	0	0	0	0
a_{66}	0	0	0	0	0	-2487	0	-263	0	0	0	0	0	0	0
a_{37}	0	0	-12889	0	0	0	4293	325	0	0	0	0	0	0	0
a_{47}	0	0	0	-6822	0	0	2378	118	0	0	0	0	0	0	0
a_{57}	0	0	0	0	-15415	0	4082	266	0	0	0	0	0	0	0
a_{77}	0	0	0	0	0	0	- 581	- 79,2	0	0	0	0	0	0	0
a_{28}	0	-403	0	0	0	- 286	0	98,8	0	0	0	0	0	0	0
a_{38}	0	0	-12889	0	0	0	- 45,7	2111	0	0	0	0	0	0	0
a_{48}	0	0	0	-6822	0	0	- 156	1070	0	0	0	0	0	0	0
a_{58}	0	0	0	0	-15415	0	- 663	2050	0	0	0	0	0	0	0
a_{68}	0	0	0	0	0	-2487	0	368	0	0	0	0	0	0	0
a_{78}	0	0	0	0	0	0	- 581	230	0	0	0	0	0	0	0
a_{88}	0	0	0	0	0	0	0	-296	0	0	0	0	0	0	0
a_{19}	- 213	0	- 9,36	- 7,04	0	- 23,3	- ,378	- 2,36	46,2	0	0	0	0	0	0
a_{39}	- 175,5	0	- 55,9	- 7,04	0	- 17,7	- 1,97	- 3,05	46,2	0	0	0	0	0	0
a_{49}	- 175,5	0	- 9,36	- 53,8	0	- 17,7	- 1,40	- 3,43	46,2	0	0	0	0	0	0
a_{99}	175,5	0	9,36	7,04	0	17,7	,378	1,85	-46,2	0	0	0	0	0	0
$a_{3\,10}$	0	0	- 80,2	- 52,2	- 16,87	0	- 3,84	- 3,71	0	27,3	0	0	0	0	0
$a_{4\,10}$	0	0	- 53,4	- 79,1	- 16,87	0	- 3,51	- 3,93	0	27,3	0	0	0	0	0
$a_{5\,10}$	0	0	- 53,4	- 52,2	- 43,5	0	- 4,07	- 3,71	0	27,3	0	0	0	0	0
$a_{10\,10}$	0	0	53,4	52,2	16,87	0	2,93	3,02	0	-27,3	0	0	0	0	0
$a_{1\,11}$	- 151,6	- 75,0	- 18,6	- 13,1	- 13,4	- 48,6	- 1,17	- 5,72	0	0	31,5	0	0	0	0
$a_{2\,11}$	- 130,6	- 87,6	- 18,6	- 13,1	- 13,4	- 54,5	- 1,17	- 6,44	0	0	31,5	0	0	0	0
$a_{3\,11}$	- 130,6	- 75,0	- 44,4	- 13,1	- 13,4	- 45,5	- 2,05	- 6,10	0	0	31,5	0	0	0	0
$a_{4\,11}$	- 130,6	- 75,0	- 18,6	- 39,0	- 13,4	- 45,5	- 1,74	- 6,32	0	0	31,5	0	0	0	0
$a_{5\,11}$	- 130,6	- 75,0	- 18,6	- 13,1	- 39,1	- 45,5	- 2,27	- 6,11	0	0	31,5	0	0	0	0
$a_{11\,11}$	130,6	75,0	18,6	13,1	13,4	45,5	1,17	5,44	0	0	-31,5	0	0	0	0
$a_{1\,12}$	-1155	0	0	0	0	- 923	0	- 81,4	0	0	0	50,3	0	0	0
$a_{6\,12}$	-1123	0	0	0	0	- 944	0	- 83,7	0	0	0	50,3	0	0	0
$a_{12\,12}$	1123	0	0	0	0	918	0	81,0	0	0	0	-50,3	0	0	0
$a_{2\,13}$	0	- 27,2	-529	-296	-528	- 7,27	- 36,3	- 32,1	0	0	0	0	29,0	0	0
$a_{3\,13}$	0	- 17,1	-550	-296	-528	- 7,27	- 37,0	- 31,8	0	0	0	0	29,0	0	0
$a_{4\,13}$	0	- 17,1	-529	-317	-528	- 7,27	- 36,7	- 32,0	0	0	0	0	29,0	0	0
$a_{5\,13}$	0	- 17,1	-529	-296	-548	- 7,27	- 37,2	- 31,8	0	0	0	0	29,0	0	0
$a_{13\,13}$	0	17,1	529	296	528	7,27	36,3	31,3	0	0	0	0	- 29,0	0	0
$a_{9\,14}$	29,8	11,90	3,70	2,76	2,06	6,45	,185	,747	- 3,12	- ,362	- 6,54	0	0	2,00	0
$a_{10\,14}$	22,0	11,90	7,46	6,52	3,38	5,66	,398	,903	- 1,07	- 2,47	- 6,54	0	0	2,00	0
$a_{11\,14}$	32,5	17,90	4,78	3,49	3,13	9,30	,262	1,102	- 1,07	- ,362	- 9,06	0	0	2,00	0
$a_{14\,14}$	- 22,0	- 11,90	- 3,29	- 2,44	- 2,06	- 5,66	- ,168	- ,667	1,07	,362	6,54	0	0	- 2,00	0
$a_{12\,15}$	220	4,11	115	64,5	115	181	6,73	20,2	0	0	0	- 13,4	- 8,96	0	,50
$a_{13\,15}$	205	4,54	129	80,0	128	169	7,64	19,9	0	0	0	- 12,8	- 9,69	0	,50
$a_{15\,15}$	-205	- 4,11	-115	- 64,5	-115	-169	- 6,73	- 19,1	0	0	0	12,8	8,96	0	- ,50

T A B L E 4. Sensitivity function values after 1 year

	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8	x_9	x_{10}	x_{11}	x_{12}	x_{13}	x_{14}	x_{15}
a_{16}	-27892	0	0	0	0	4026	0	520	0	0	0	0	0	0	0
a_{26}	0	- 509	0	0	0	63,3	0	2,0	0	0	0	0	0	0	0
a_{66}	0	0	0	0	0	-5686	0	- 695	0	0	0	0	0	0	0
a_{37}	0	0	-37903	0	0	0	3115	- 516	0	0	0	0	0	0	0
a_{47}	0	0	0	-19566	0	0	2018	- 429	0	0	0	0	0	0	0
a_{57}	0	0	0	0	-86130	0	- 100	-2079	0	0	0	0	0	0	0
a_{77}	0	0	0	0	0	0	- 649	- 95,9	0	0	0	0	0	0	0
a_{28}	0	- 509	0	0	0	- 919	0	12,8	0	0	0	0	0	0	0
a_{38}	0	0	-37903	0	0	0	-1851	1192	0	0	0	0	0	0	0
a_{48}	0	0	0	-19566	0	0	- 615	476	0	0	0	0	0	0	0
a_{58}	0	0	0	0	-86130	0	-5047	377	0	0	0	0	0	0	0
a_{68}	0	0	0	0	0	-5686	0	80,0	0	0	0	0	0	0	0
a_{78}	0	0	0	0	0	0	- 649	223	0	0	0	0	0	0	0
a_{88}	0	0	0	0	0	0	0	- 318	0	0	0	0	0	0	0
a_{19}	-3306	0	- 274	- 209	0	- 980	- 17,8	- 129	258	0	0	0	0	0	0
a_{39}	-3200	0	- 542	- 209	0	- 940	- 30,2	- 133	258	0	0	0	0	0	0
a_{49}	-3200	0	- 274	- 483	0	- 980	- 26,0	- 135	258	0	0	0	0	0	0
a_{99}	3200	0	274	209	0	940	17,8	124	- 258	0	0	0	0	0	0
$a_{3\ 10}$	0	0	-2014	-1818	- 574	0	- 169	- 149	0	194	0	0	0	0	0
$a_{4\ 10}$	0	0	-1837	-1999	- 574	0	- 166	- 150	0	194	0	0	0	0	0
$a_{5\ 10}$	0	0	-1837	-1818	- 748	0	- 171	- 149	0	194	0	0	0	0	0
$a_{10\ 10}$	0	0	1837	1818	574	0	161	143	0	- 194	0	0	0	0	0
$a_{1\ 11}$	-5145	-1791	-1045	- 741	- 744	-3273	- 102	- 467	0	0	468	0	0	0	0
$a_{2\ 11}$	-5087	-1807	-1045	- 741	- 744	-3280	- 102	- 468	0	0	468	0	0	0	0
$a_{3\ 11}$	-5087	-1791	-1192	- 741	- 744	-3251	- 108	- 469	0	0	468	0	0	0	0
$a_{4\ 11}$	-5087	-1791	-1045	- 892	- 744	-3251	- 106	- 470	0	0	468	0	0	0	0
$a_{5\ 11}$	-5087	-1791	-1045	- 741	- 888	-3751	- 110	- 469	0	0	468	0	0	0	0
$a_{11\ 11}$	5087	1791	1045	741	744	3251	- 102	464	0	0	- 468	0	0	0	0
$a_{1\ 12}$	-56791	0	0	0	0	-46316	0	-5145	0	0	0	1034	0	0	0
$a_{6\ 12}$	-56704	0	0	0	0	-46328	0	-5146	0	0	0	1034	0	0	0
$a_{12\ 12}$	56704	0	0	0	0	46282	0	5141	0	0	0	-1034	0	0	0
$a_{2\ 13}$	0	-831	-50907	-28716	-50436	-786	-5267	-4045	0	0	0	0	917	0	0
$a_{3\ 13}$	0	-818	-51024	-28716	-50436	-786	-5272	-4046	0	0	0	0	917	0	0
$a_{4\ 13}$	0	-818	-50909	-28836	-50436	-786	-5270	-4047	0	0	0	0	917	0	0
$a_{5\ 13}$	0	-818	-50907	-28716	-50552	-786	-5273	-4046	0	0	0	0	917	0	0
$a_{13\ 13}$	0	818	50907	28716	50436	786	5267	4042	0	0	0	0	-917	0	0
$a_{9\ 14}$	3635	1236	713	525	457	2049	64,9	290	- 39,9	- 10,4	-343	0	0	10,0	0
$a_{10\ 14}$	3493	1236	831	645	498	2008	75,6	295	- 28,6	- 23,4	-343	0	0	10,0	0
$a_{11\ 14}$	3900	1380	783	576	516	2268	72,3	322	- 28,6	- 10,4	-381	0	0	10,0	0
$a_{14\ 14}$	-3493	-1236	- 700	- 516	- 457	-2008	- 64,1	- 285	28,6	10,4	343	0	0	- 10,0	0
$a_{12\ 15}$	42070	704	39615	22313	39299	34977	3978	6825	0	0	0	-860	-817	0	2,50
$a_{13\ 15}$	41314	724	40887	23030	40560	34380	4109	6858	0	0	0	-847	-840	0	2,50
$a_{15\ 15}$	-41314	- 704	-39615	-22313	-39299	-34360	-3978	6757	0	0	0	847	817	0	-2,50

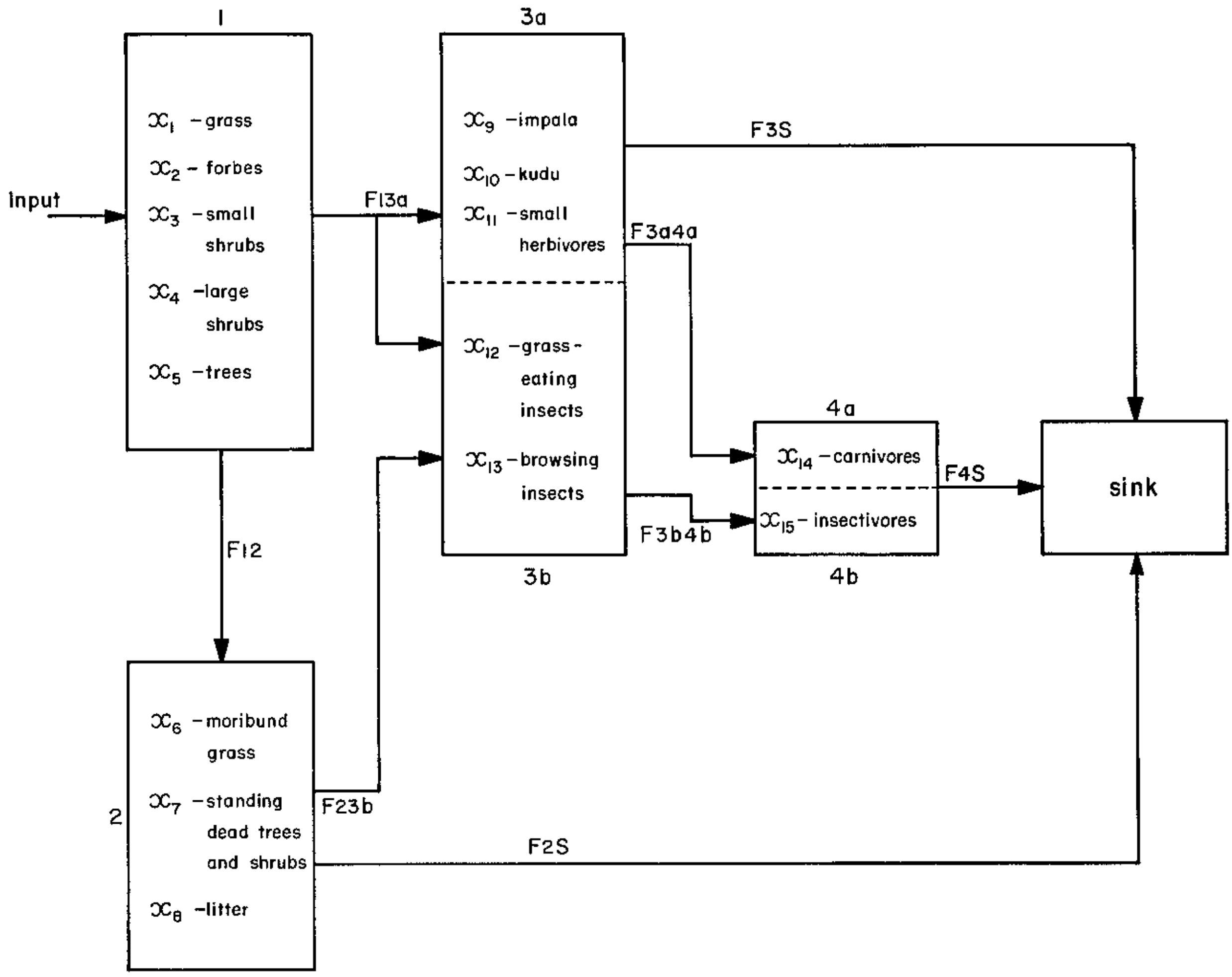
T A B L E 5. Sensitivity function values after 5 years

	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8	x_9	x_{10}	x_{11}	x_{12}	x_{13}	x_{14}	x_{15}
a_{16}	- 0,30	0	0	0	0	8,10	0	1,80	0	0	0	0	0	0	0
a_{26}	0	- 7.56	0	0	0	1,32	0	0,28	0	0	0	0	0	0	0
a_{56}	0	0	0	0	0	- 0,41	0	- 0,09	0	0	0	0	0	0	0
a_{37}	0	0	- 1,30	0	0	0	5,64	0,33	0	0	0	0	0	0	0
a_{47}	0	0	0	- 0,83	0	0	2,01	0,07	0	0	0	0	0	0	0
a_{57}	0	0	0	0	- 1,95	0	6,74	0,34	0	0	0	0	0	0	0
a_{77}	0	0	0	0	0	0	- 10,63	- 1,11	0	0	0	0	0	0	0
a_{28}	0	- 0,37	0	0	0	- 0,07	0	0,05	0	0	0	0	0	0	0
a_{38}	0	0	- 1,37	0	0	0	- 0,64	2,25	0	0	0	0	0	0	0
a_{48}	0	0	0	- 1,96	0	0	- 0,31	1,64	0	0	0	0	0	0	0
a_{58}	0	0	0	0	- 1,58	0	- 0,89	2,10	0	0	0	0	0	0	0
a_{68}	0	0	0	0	0	- 6,22	0	1,84	0	0	0	0	0	0	0
a_{78}	0	0	0	0	0	0	- 4,55	1,38	0	0	0	0	0	0	0
a_{88}	0	0	0	0	0	0	0	12,03	0	0	0	0	0	0	0
a_{19}	- 0,15	0	- 0,05	- 0,08	0	- 0,67	- 0,03	- 1,38	88,33	0	0	0	0	0	0
a_{39}	- 0,06	0	- 0,02	- 0,00	0	- 0,24	- 0,07	- 0,01	4,11	0	0	0	0	0	0
a_{49}	- 0,04	0	- 0,00	- 0,02	0	- 0,02	- 0,00	- 0,01	3,08	0	0	0	0	0	0
a_{99}	1,35	0	0,06	0,08	0	0,55	0,03	0,11	- 95,01	0	0	0	0	0	0
$a_{3\ 10}$	0	0	- 0,21	- 0,26	- 0,04	0	- 0,13	- 0,10	0	43,53	0	0	0	0	0
$a_{4\ 10}$	0	0	- 0,14	- 0,38	- 0,04	0	- 0,12	- 0,10	0	42,43	0	0	0	0	0
$a_{5\ 10}$	0	0	- 0,05	- 0,08	- 0,04	0	- 0,04	- 0,03	0	13,78	0	0	0	0	0
$a_{10\ 10}$	0	0	0,32	0,58	0,10	0	0,23	0,18	0	- 98,63	0	0	0	0	0
$a_{1\ 11}$	- 1,26	- 9,37	- 0,12	- 0,16	- 0,09	- 1,62	- -0,10	- 0,38	0	0	84,10	0	0	0	0
$a_{2\ 11}$	- 0,87	- 8,76	- 0,10	- 0,13	- 0,07	- 1,45	- 0,08	- 0,34	0	0	67,28	0	0	0	0
$a_{3\ 11}$	- 0,14	- 1,17	- 0,04	- 0,02	- 0,01	- 0,19	- 0,02	- 0,05	0	0	10,51	0	0	0	0
$a_{4\ 11}$	- 0,10	- 0,82	- 0,01	- 0,04	- 0,01	- 0,13	- 0,01	- 0,04	0	0	7,36	0	0	0	0
$a_{5\ 11}$	- 0,10	- 0,84	- 0,01	- 0,01	- 0,02	- 0,14	- 0,02	- 0,04	0	0	7,57	0	0	0	0
$a_{11\ 11}$	2,24	19,29	0,26	0,34	0,18	3,12	0,21	0,75	0	0	-173,06	0	0	0	0
$a_{1\ 12}$	- 52,91	0	0	0	0	-169,13	0	- 29,86	0	0	0	737,22	0	0	0
$a_{6\ 12}$	- 42,11	0	0	0	0	-141,45	0	- 25,12	0	0	0	603,18	0	0	0
$a_{12\ 12}$	93,06	0	0	0	0	304,26	0	53,70	0	0	0	-1332,89	0	0	0
$a_{2\ 13}$	0	- 0,70	- 0,72	- 0,76	- 0,72	- 0,05	- 0,65	- 0,44	0	0	0	0	29,76	0	0
$a_{3\ 13}$	0	- 8,64	- 14,84	- 14,99	- 14,25	- 0,98	- 13,03	- 8,59	0	0	0	0	586,50	0	0
$a_{4\ 13}$	0	- 4,82	- 7,97	- 8,95	- 7,95	- 0,55	- 7,22	- 4,82	0	0	0	0	327,28	0	0
$a_{5\ 13}$	0	- 8,64	- 14,29	- 14,99	- 14,81	- 0,98	- 13,09	- 8,59	0	0	0	0	586,50	0	0
$a_{13\ 13}$	0	22,40	37,03	38,85	36,93	2,54	33,12	21,88	0	0	0	0	-1519,91	0	0
$a_{9\ 14}$	0,03	0,16	0,00	0,00	0,00	0,02	0,00	0,01	- 0,73	- 0,15	- 1,83	0	0	1,05	0
$a_{10\ 14}$	0,01	0,05	0,00	0,00	0,00	0,01	0,00	0,00	- 0,08	- 0,35	- 0,61	0	0	0,35	0
$a_{11\ 14}$	0,15	1,25	0,02	0,00	0,01	0,17	0,01	0,04	- 1,33	- 0,81	- 13,53	0	0	5,60	0
$a_{14\ 14}$	- 0,13	- 1,04	- 0,02	- 0,02	- 0,01	- 0,13	- 0,01	- 0,03	1,66	1,01	12,21	0	0	- 7,00	0
$a_{12\ 15}$	7,69	2,16	3,23	3,39	3,23	25,22	2,46	5,66	0	0	0	-150,51	-188,24	0	419,97
$a_{13\ 15}$	4,78	1,59	2,40	2,52	2,46	15,76	1,86	3,72	0	0	0	- 95,33	-135,63	0	279,98
$a_{15\ 15}$	- 11,94	- 3,60	- 5,39	- 5,65	- 5,38	- 39,36	- 4,10	- 8,93	0	0	0	238,32	313,73	0	-699,96

TABLE 6. Sensitivity function values after 1 year as a percentage of the initial standing crop for a 10% increase in parameter values

	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8	x_9	x_{10}	x_{11}	x_{12}	x_{13}	x_{14}	x_{15}
a_{16}	- 8,33	0	0	0	0	4,81	0	1,24	0	0	0	0	0	0	0
a_{26}	0	- 9,54	0	0	0	0,32	0	0,01	0	0	0	0	0	0	0
a_{66}	0	0	0	0	0	- 0,95	0	- 0,23	0	0	0	0	0	0	0
a_{37}	0	0	- 3,82	0	0	0	4,09	- 0,52	0	0	0	0	0	0	0
a_{47}	0	0	0	- 2,37	0	0	1,70	- 0,28	0	0	0	0	0	0	0
a_{57}	0	0	0	0	- 10,91	0	- 0,17	- 2,63	0	0	0	0	0	0	0
a_{77}	0	0	0	0	0	0	- 11,86	- 1,34	0	0	0	0	0	0	0
a_{28}	0	- 0,46	0	0	0	- 0,22	0	0,01	0	0	0	0	0	0	0
a_{38}	0	0	- 4,04	0	0	0	- 2,58	1,27	0	0	0	0	0	0	0
a_{48}	0	0	0	- 5,63	0	0	- 1,23	0,73	0	0	0	0	0	0	0
a_{58}	0	0	0	0	- 8,84	0	- 6,76	- 0,39	0	0	0	0	0	0	0
a_{68}	0	0	0	0	0	- 14,21	0	0,40	0	0	0	0	0	0	0
a_{78}	0	0	0	0	0	0	- 5,08	1,34	0	0	0	0	0	0	0
a_{88}	0	0	0	0	0	0	0	- 12,94	0	0	0	0	0	0	0
a_{19}	- 23,70	0	- 1,58	- 2,25	0	- 28,10	- 1,33	- 75,59	492,80	0	0	0	0	0	0
a_{39}	- 1,07	0	- 0,14	- 0,10	0	- 1,25	- 0,11	- 0,35	22,92	0	0	0	0	0	0
a_{49}	- 0,80	0	- 0,05	- 0,18	0	- 0,94	- 0,07	- 0,27	17,19	0	0	0	0	0	0
a_{99}	24,66	0	1,69	2,41	0	28,97	1,43	7,67	-530,00	0	0	0	0	0	0
$a_{3\ 10}$	0	0	- 5,30	- 8,98	- 1,51	0	- 5,75	- 3,92	0	306,2	0	0	0	0	0
$a_{4\ 10}$	0	0	- 4,72	- 9,62	- 1,47	0	- 5,56	- 3,86	0	290,8	0	0	0	0	0
$a_{5\ 10}$	0	0	- 1,53	- 2,92	- 0,62	0	- 1,85	- 1,24	0	96,9	0	0	0	0	0
$a_{10\ 10}$	0	0	10,96	20,33	3,43	0	12,50	8,55	0	-693,8	0	0	0	0	0
$a_{1\ 11}$	- 42,9	-223,8	- 7,0	- 9,3	- 5,0	-109,1	- 8,9	- 31,1	0	0	1249	0	0 0	0	0
$a_{2\ 11}$	- 33,9	-180,6	- 5,6	- 7,4	- 4,0	- 87,5	- 7,1	- 25,0	0	0	999	0	0	0	0
$a_{3\ 11}$	- 5,3	- 30,0	- 1,0	- 1,2	- 0,6	- 13,5	- 1,2	- 3,9	0	0	156	0	0	0	0
$a_{4\ 11}$	- 3,7	- 19,6	- 0,6	- 1,0	- 0,4	- 9,5	- 0,8	- 2,7	0	0	109	0	0	0	0
$a_{5\ 11}$	- 3,8	- 20,1	- 0,6	- 0,8	- 0,5	- 9,6	- 0,9	- 2,8	0	0	112	0	0 0	0	0
$a_{11\ 11}$	87,3	460,5	14,3	19,1	10,2	223,0	18,2	63,7	0	0	-2570	0	0	0	0
$a_{1\ 12}$	-2603	0	0	0	0	-8491	0	-1886	0	0	0	15170	0	0	0
$a_{6\ 12}$	-2127	0	0	0	0	6949	0	-1543	0	0	0	12410	0	0	0
$a_{12\ 12}$	4700	0	0	0	0	-15340	0	3409	0	0	0	-27419	0	0	0
$a_{2\ 13}$	0	- 21	- 70	- 74	- 69	- 5,5	- 94	- 55	0	0	0	0	942	0	0
$a_{3\ 13}$	0	- 414	-1378	-1454	-1362	- 106	-1857	-1093	0	0	0	0	18570	0	0
$a_{4\ 13}$	0	- 231	- 767	- 815	- 760	- 59	-1036	- 610	0	0	0	0	10360	0	0
$a_{5\ 13}$	0	- 414	-1375	-1454	-1365	- 106	-1857	-1093	0	0	0	0	18570	0	0
$a_{13\ 13}$	0	1073	3562	3768	3529	275	4807	2827	0	0	0	0	-48130	0	0
$a_{9\ 14}$	3,18	16,22	0,50	0,69	0,32	7,17	0,59	2,03	- 9,32	- 4,38	- 96,14	0	0	5,15	0
$a_{10\ 14}$	1,02	5,41	0,19	0,28	0,12	2,34	0,23	0,69	- 2,22	- 3,27	- 32,05	0	0	1,75	0
$a_{11\ 14}$	18,20	96,57	2,93	0,40	1,93	42,32	3,52	12,02	- 35,57	- 23,32	- 568,71	0	0	28,00	0
$a_{14\ 14}$	- 20,38	- 108,20	- 3,27	- 4,52	- 2,13	- 46,84	- 3,96	- 13,29	44,46	29,15	640,96	0	0	- 35,00	0
$a_{12\ 15}$	1473	370	1109	1172	1100	4896	1452	1911	0	0	0	-9635	-17160	0	2099
$a_{13\ 15}$	964	254	763	806	757	3209	1001	1280	0	0	0	-6322	-11770	0	1399
$a_{15\ 15}$	-2409	- 616	-1848	-1953	-1834	-8018	-2421	-3153	0	0	0	15810	28600	0	-3499

TABLE 7. Sensitivity function values after 5 years as a percentage of the initial standing crop for a 10% increase in parameter values



1 Primary producers (net values)

2 Dead vegetation

3a Primary consumers – herbivores

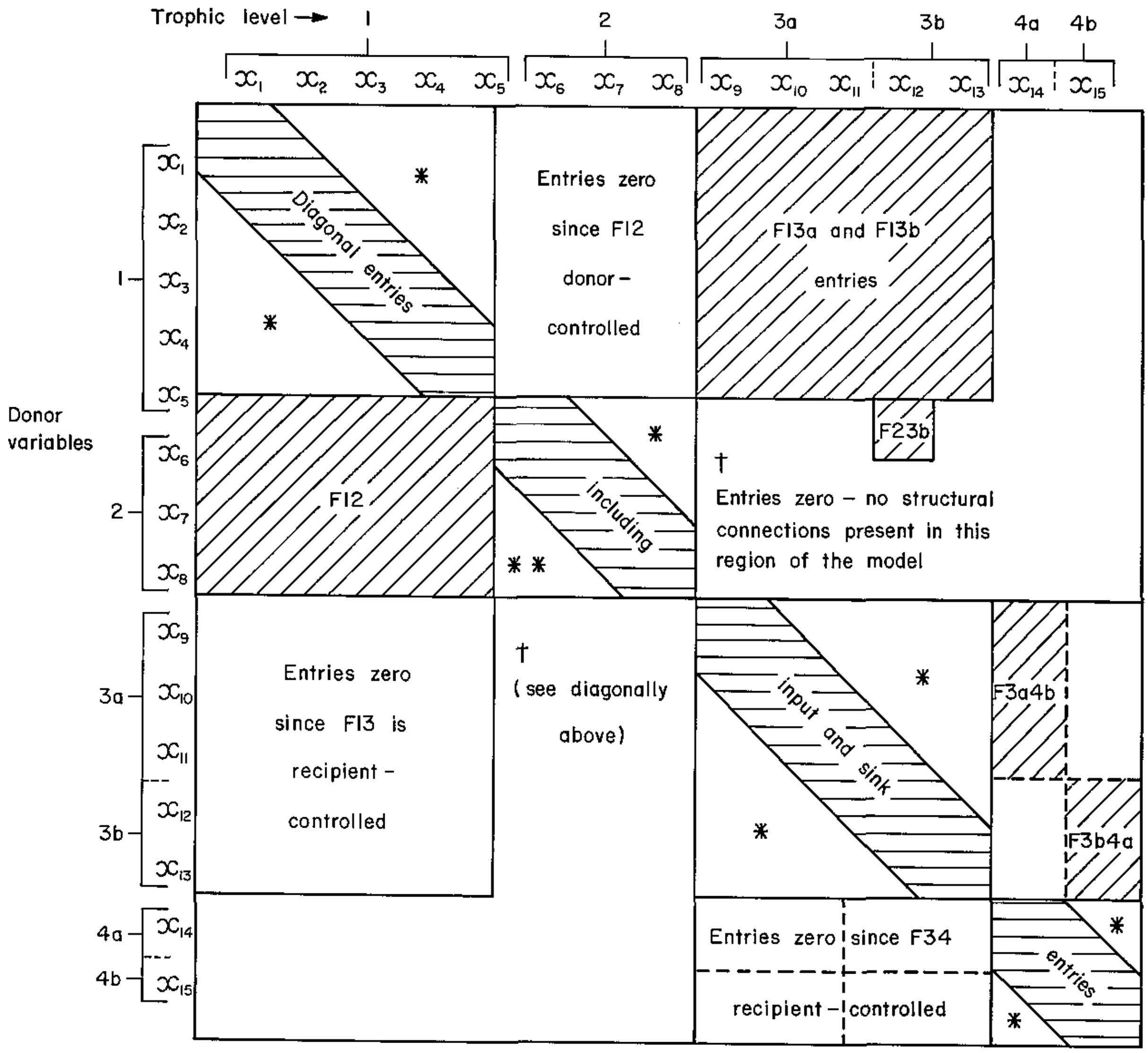
3b Primary consumers – insects

4a Secondary consumers – carnivores

4b Secondary consumers – insectivores

FIGURE 1

Topology of the model



* Entries zero since no intra-trophic variable connections present.

** Some non-zero entries present due to intra-trophic variable connections

FIGURE 2

Recipient variables

	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8	x_9	x_{10}	x_{11}	x_{12}	x_{13}	x_{14}	x_{15}
x_1	-,0072								-,172		-,2	-1,1			
x_2		-,03146									-,16		-,041		
x_3			,0013						-,008	-,079	-,025		-,81		
x_4		0		,00146					-,006	-,077	-,0175	0	-,452		
x_5					,0011					-,025	-,018		-,81		
x_6	,007	,03				-,016				0		-,9			
x_7			,003	,00194	,0038	0	-,06								
x_8		,00146	,0032	,0046	,0031	,015	,018	-,122							
x_9									,001					-,021	
x_{10}										,002				-,007	
x_{11}											,009			-,112	
x_{12}				0								,0112			-,84
x_{13}													,014		-,56
x_{14}														,0000	0
x_{15}															,0000

FIGURE 3

The values used matrix A

	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8	x_9	x_{10}	x_{11}	x_{12}	x_{13}	x_{14}	x_{15}
x_1	$-a_{1\,6}$								$-a_{1\,9}$		$-a_{1\,11}$	$-a_{1\,12}$			
x_2		$-a_{2\,6}$ $-a_{2\,8}$									$-a_{2\,11}$		$-a_{2\,13}$		
x_3			$f_{0\,3}$ $-a_{3\,7}$ $-a_{3\,8}$						$-a_{3\,9}$	$-a_{3\,10}$	$-a_{3\,11}$	0	$-a_{3\,13}$		
x_4		0		$f_{0\,4}$ $-a_{4\,7}$ $-a_{4\,8}$					$-a_{4\,9}$	$-a_{4\,10}$	$-a_{4\,11}$		$-a_{4\,13}$		
x_5					$f_{0\,5}$ $-a_{5\,7}$ $-a_{5\,8}$					$-a_{5\,10}$	$-a_{5\,11}$		$-a_{5\,13}$		
x_6	$a_{1\,6}$	$a_{2\,6}$				$-a_{6\,6}$ $-a_{6\,8}$				0		$-a_{6\,12}$			
x_7			$a_{3\,7}$	$a_{4\,7}$	$a_{5\,7}$	0	$-a_{7\,7}$ $-a_{7\,8}$								
x_8		$a_{2\,8}$	$a_{3\,8}$	$a_{4\,8}$	$a_{5\,8}$	$a_{6\,8}$	$a_{7\,8}$	$-a_{8\,8}$							
x_9									$a_{1\,9}+a_{3\,9}+a_{5\,9}-a_{9\,9}$					$-a_{9\,14}$	
x_{10}										$a_{3\,10}+a_{4\,10}+a_{5\,10}-a_{10\,10}$				$-a_{10\,14}$	
x_{11}											$a_{1\,11}+a_{2\,11}+a_{3\,11}+a_{4\,11}+a_{5\,11}-a_{11\,11}$			$-a_{11\,14}$	
x_{12}				0								$a_{1\,12}+a_{6\,12}-a_{12\,12}$			$-a_{12\,15}$
x_{13}													$a_{2\,13}+a_{3\,13}+a_{4\,13}+a_{5\,13}-a_{13\,13}$		$-a_{13\,15}$
x_{14}														$a_{9\,14}+a_{10\,14}+a_{11\,14}-a_{14\,14}$	0
x_{15}															$a_{12\,15}+a_{13\,16}-a_{15\,15}$

FIGURE 4

The structure of matrix A