Sensitivity of an Ecological System Dynamics Model to Combination Parameter Changes

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ABSTRACT

The question as to how sensitive a System Dynamics Model is to combination parameter changes in general is a complex one. A recent technique due to J.W.Hearne enables one to find the combination of parameter changes to which the system is most sensitive. The technique is applied here to an ecological model and a perturbation of the system along the most sensitive direction in parameter space is compared with single parameter perturbations of the same magnitude. The method may be useful in population control.

1.INTRODUCTION

A system dynamics mathematical model can be described by a system of n non-linear differential equations of the form

$$\dot{x}_j = f_j(\mathbf{x},\mathbf{p},t)$$

where

$$\mathbf{x}=(x_1,x_2, \ldots\ldots ,x_n)^T \quad \text{and} \quad \mathbf{p}=(p_1,p_2, \ldots\ldots ,p_m)^T$$

are the state variables at time t and the parameters of the system respectively. The solution trajectory of the above system of equations is called the standard trajectory and describes the path in n-dimensional state space.

System Dynamics Models are solved by numerical methods and only particular solutions are usually obtained by simulation. Such solutions can only be considered representative of system behaviour if small changes in parameter values leave unaltered the main qualitative characteristics. The sensitivity of such a model to parameter changes is often investigated by varying one parameter at a time and comparing the simulated behaviour in each case with that of the standard run. Combination parameter changes, if investigated at all, are usually done on a fairly ad hoc basis. It is however of importance to find combination parameter changes to which the system will be most sensitive. One such technique, due to J.W. Hearne (Hearne) is outlined below and then applied to an ecological model in the sequel.

2.THE MOST SENSITIVE DIRECTION IN PARAMETER SPACE.

If the parameter vector $\mathbf{p}$ is perturbed by an amount $\Delta\mathbf{p}$ each component of the state vector will change:

$$x_j(\mathbf{p}+\Delta\mathbf{p},t)=x_j(\mathbf{p},t)+\Delta x_j(\mathbf{p},\Delta\mathbf{p},t)$$

If for each parameter p_j the perturbation Δp_j is small then

$$\Delta x_i \approx \sum_{j=1}^{m} (\partial x_i/\partial p_j).\Delta p_j$$

$$=\sum_{j=1}^{m} N_{ij}(\Delta p_j/p_j)x_i$$

where

$$N_{ij} = \frac{\partial x_i}{\partial p_j}.\frac{p_j}{x_i}$$ is a normalized sensitivity coefficient.

Thus

$$(\Delta x_i/x_i)=\sum_{j=1}^{m} N_{ij}.(\Delta p_j/p_j)=\sum_{j=1}^{m} N_{ij}a_j$$

where $a_j=\Delta p_j/p_j$.

A reasonable measure of the difference between the nominal trajectory $\mathbf{x}(\mathbf{p},t)$ and the perturbed one $\mathbf{x}(\mathbf{p}+\Delta\mathbf{p},t)$ is defined by

$$\int_{t_o}^{t_f} \sum_{i=1}^{n}(\Delta x_i/x_i)^2 dt$$

where t_o,t_f are the initial and final times for which a solution to the system is required. This measure may be expressed as

$$a^T\left(\int_{t_o}^{t_f} N^T N dt\right)a$$

where $a=(a_1,a_2,\ldots,a_m)^T$ and N is the nxm matrix with entries N_{ij}. Placing a constraint on the magnitude of the parameter changes such that

$$\sum_{j=1}^{m} a_j^2 = a^T a = c>0$$

it can then be shown that the value of a which will maximize the above measure (subject to the constraint) is given by the solution to the eigenvalue problem

$$\left(\int_{t_o}^{t_f} N^T N dt\right)a = ka$$

If f is an eigenvector corresponding to the largest eigenvalue chosen such that $f^T f=c$ then a =f gives the most sensitive direction in parameter space relative to the measure introduced above.

We now describe the model to which the method above is applied in the sequel.

3.AN ECOLOCICAL MODEL

A.Model Description: A system dynamics model of the caracal lynx and hyrax populations in the Mountain Zebra National Park in the north-eastern Cape region of South Africa is formulated below. Detailed data concerning the hyrax population can be found in a thesis by Fourie (Fourie 1983).

In order to conform to Fourie's data the hyrax population is divided into 11 male and 11 female groups, denoted by HM_j and HF_j (j=1,11) respectively. Relatively little is known about fecundity and mortality rates of caracal lynxes (Fourie 1983, Stuart 1982) and the lynx population is simply divided into two groups: juveniles (LJ) and adults (LA).

In order to formulate the model, certain other concepts are required. As a prey item, grazer or predator, a juvenile does not have the same effect on the system as an adult. We therefore define Hyrax Units Total (HUT) and Lynx Units Total (LUT) as follows:

$$HUT=HJF.(HF_1 + HM_1) + \sum_{i=2}^{11}(HF_i + HM_i)$$

$$LUT=LJF.LJ + LA$$

where the Hyrax Juvenile Factor (HJF) and Lynx Juvenile Factor (LJF) convert juveniles to the equivalent adult units.

Hyrax Units Normal (HUN) is defined as the highest value of HUT that can be supported in the given region before overcrowding adversely affects fecundity and mortality. HUN can therefore be equated with carrying capacity. When HUT is greater than HUN the excess hyraxes spill over to neighbouring farming territory and consume pasture at the expense of sheep. Hyrax Density (HD) is defined by the ratio

$$HD=HUT/HUN$$

Hyraxes constitute the preferred natural diet of the caracal lynx. Lynx Units Normal (LUN) is defined as the greatest value of LUT that can be attained for which HUN is sufficient for normal predation rates to be sustained. When the ratio HUT/LUT is less than HUN/LUN the lynxes experience a shortage in their natural food. This leads to Prey Abundance (PA) being defined as follows:

$$PA=(HUT/LUT)/(HUN/LUN)$$

PA thus serves as an index of the availability of hyrax as prey for the caracal lynx population. When PA is less than one, the lynx population will find alternate prey such as sheep.

The full effect of a change in variable such as HD or PA is not always felt immediately and exponential smoothing is employed, where appropriate, to give an averaged value of the variable. Thus Hyrax Density Average (HDA) is calculated by integrating the following differential equation:

$$\dot{HDA} = (HD-HDA)/DAT$$

where DAT is the Density Averaging Time.
Prey Abundance Average (PAA) is defined similarly.

B.Hyrax Sector. The structure of the female and male subsectors are similar and only the formulation of the female subsector is given below. The rates determining the levels of the eleven groups in this sector are births, deaths, aging and predation.

Births: The annual rate of female births $R_{1,o}$ is given by

$$R_{1,o} = \sum_{i=1}^{11} HF_i.FN_i.FM_i.HSM$$

The Fecundity Normal (FN_i) is the number of females born per year to an individual in group i when FM_i and HSM are unity. The Fecundity Multiplier (FM_i) modifies the fecundity rate according to changes in the hyrax density and is a decreasing function of HDA. The Hyrax Seasonal Multiplier (HSM) is an exogenous variable imposing seasonal fluctuations upon fecundity rates in accordance with observations. The ratio of female births to male births is 1:1.

Aging: The annual aging rate of individuals from group i to i+1 (i=1,10) is given by

$$R_{1,i} = HF_i.AN_i.HSM$$

where the Aging Normal (AN_i) is the fraction of individuals in group i that age to group i+1 in any given year.

Deaths: The annual rate of deaths in group i at any time is calculated as follows:

$$R_{2,i} = HF_i.FDN_i.DM_i$$

where the Female Death Normal (FDN_i) is the fraction of group i that die per year if the Death Multiplier (DM_i) is unity. DM_i reflects the effect of density on the juvenile death rate and is calculated as follows:

$$FDM_1 = DMF(HD)$$

$$FDM_i = 1 \quad (i=2,11)$$

The function DMF is an increasing function of HD.

Predation: The Predation Normal (PN) is defined as the number of adult hyraxes required per adult lynx per year. The predation rate is modified according to the relative abundance of hyraxes as measured by PA. We have

Hyrax adult units consumed per year = LUT.PN.PM

where the Prey Multiplier (PM) is an increasing function of PA.
Assuming that predation is spread uniformly throughout the different hyrax groups, the loss per year through lynx predation to group i is given by

$$R_{3,i} = (HF_i / HUT).LUT.PN.PM$$

In the absence of culling, a model for the female sub-sector is described by the system of differential equations

$$\dot{HF}_i = R_{1,i-1} - \sum_{j=1}^{3} R_{j,i} \qquad (i=1,11)$$

C.Lynx Sector. The flows determining the levels of Lynx Juveniles and Lynx Adults are given by

$$\dot{LJ} = \text{Births} - \text{Aging} - \text{Deaths}$$

$$\dot{LA} = \text{Aging} - \text{Deaths}$$

where the rates on the right are calculated in a similar way to the corresponding rates in the hyrax sector. In this case the Lynx Fecundity Multiplier and Lynx Juvenile Death Multiplier are functions of PAA (the delayed version of PA).

A FORTRAN program was written to solve the system of equations on a SPERRY 1100/70 computer.

4.SENSITIVITY ANALYSIS

A good idea of the dynamics of the hyrax sector is provided by analizing the variable HUT. In addition, population control decisions may well be based on fluctuations of this variable. A parameter sensitivity analysis of this variable was therefore carried out. In table 1, the parameter nominal values are listed together with the maximum normalized sensitivity coefficients of HUT attained during a 36 month simulation period once the system had reached equilibrium (apart from seasonal fluctuations). The normalized sensitivity coefficients are defined by

$$N_j = (\partial HUT / \partial p_j)/(HUT/p_j) \qquad (j=1,39)$$

and are given approximately by the % change in HUT corresponding to a 1% increase in the parameter p_j.

TABLE 1

Parameter	Symbol	Value	Max N_j
Hyrax Female Death Normal (group 1)	FDN_1	.50	-0.8879
Hyrax Male Death normal (group 1)	MDN_1	.50	-0.0318
Hyrax Female Death Normal (group 2)	FDN_2	.23	-0.4255
Hyrax Male Death Normal (group 2)	MDN_2	.18	-0.0114
Hyrax Female Death Normal (group 3)	FDN_3	.14	-0.2209
Hyrax Male Death Normal (group 3)	MDN_3	.26	-0.0121
Hyrax Female Death Normal (group 4)	FDN_4	.18	-0.2023
Hyrax Male Death Normal (group 4)	MDN_4	.26	-0.0102
Hyrax Female Death Normal (group 5)	FDN_5	.19	-0.1443
Hyrax Male Death Normal (group 5)	MDN_5	.27	-0.0084
Hyrax Female Death Normal (group 6)	FDN_6	.34	-0.1569
Hyrax Male Death Normal (group 6)	MDN_6	.37	-0.0080
Hyrax Female Death Normal (group 7)	FDN_7	.44	-0.1108
Hyrax Male Death Normal (group 7)	MDN_7	.26	-0.0048
Hyrax Female Death Normal (group 8)	FDN_8	.33	-0.0577
Hyrax Male Death Normal (group 8)	MDN_8	.30	-0.0039
Hyrax Female Death Normal (group 9)	FDN_9	.24	-0.0255
Hyrax Male Death Normal (group 9)	MDN_9	.25	-0.0023
Hyrax Female Death Normal (group 10)	FDN_{10}	.32	-0.0162
Hyrax Male Death Normal (group 10)	MDN_{10}	.20	-0.0013
Hyrax Female Death Normal (group 11)	FDN_{11}	1.00	-0.0286
Hyrax Male Death Normal (group 11)	MDN_{11}	1.00	-0.0033
Hyrax Fecundity Normal (group 1)	FN_1	.03	0.0082
Hyrax Fecundity Normal (group 2)	FN_2	1.04	0.4619
Hyrax Fecuntity Normal (group 3)	FN_3	1.23	0.5088
Hyrax Fecundity Normal (group 4)	FN_4	1.50	0.4758
Hyrax Fecundity Normal (group 5)	FN_5	1.28	0.3079
Hyrax Fecundity Normal (group 6)	FN_6	1.68	0.2738
Hyrax Fecundity Normal (group 7)	FN_7	1.38	0.1423
Hyrax Fecundity Normal (group 8)	FN_8	1.50	0.1056
Hyrax Fecundity Normal (group 9	FN_9	1.33	0.0679
Hyrax Fecundity Normal (group 10)	FN_{10}	1.00	0.0347
Hyrax Fecundity Normal (group 11)	FN_{11}	1.08	0.0321
Hyrax Juvenile Factor	HJF	0.50	-0.0430
Predation Normal	PN	84.11	-0.6273
Lynx Juvenile Factor	LJF	.50	0.0022
Lynx Fecundity Normal	LFN	.70	-0.1145
Lynx Juvenile Death Normal	LJDN	.50	0.0582
Lynx Death Normal	LDN	.13	0.0957

We next applied the theory outlined in section 1 to calculate the direction in parameter space to which HUT is most sensitive. The ten largest components of the eigenvector f corresponding to the largest eigenvalue are listed in table 2. In column 2 the largest component of f was arbitrarily assigned the value 100, the other components being scaled accordingly. The remaining components, not shown, are all less than 15% the value of the largest component.

TABLE 2

Component	Value	Perturbation Value
FDN_1	100.00	0.050
PN	69.32	0.035
FN_3	-58.79	-0.029
FN_4	-54.83	-0.027
FN_2	-53.80	-0.026
FDN_2	47.81	0.023
FN_5	-35.38	-0.017
FN_6	-31.37	-0.015
FDN_3	24.82	0.012
FDN_4	22.72	0.011

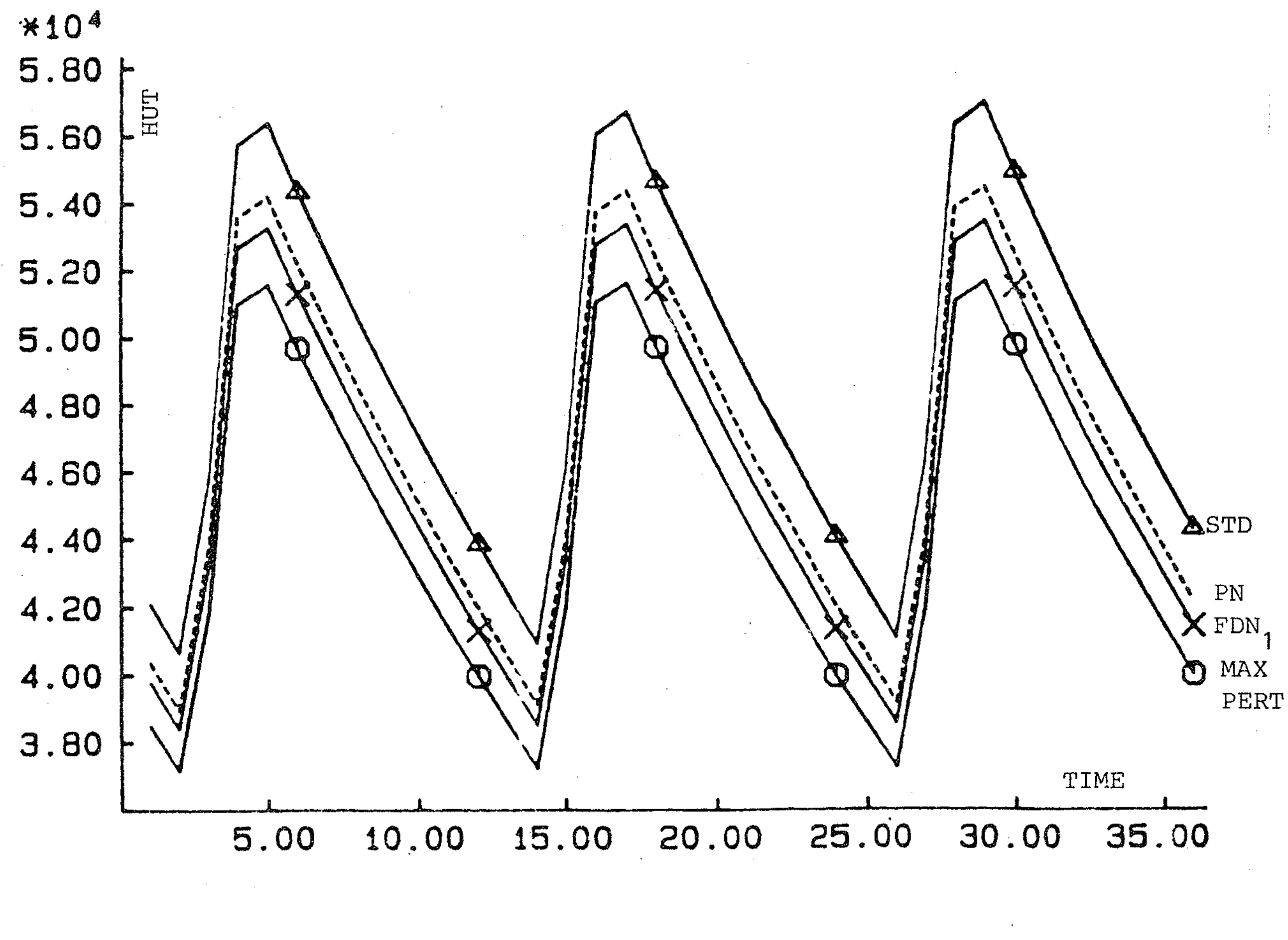
In table 3 we show the average absolute value of the appropriate normalized sensitivity coefficients with respect to the parameters listed in table 2 over the same simulation period. In column 3 these were scaled in such a way that the largest one has value 100. In comparing these values with the absolute values of the components of the eigenvector in table 2, a remarkable correspondence is noted. This confirms that the measure used by Hearne is a natural one.

TABLE 3

Parameter	Average Absolute Value of N_j	Percentage Scale
FDN_1	.8076	100.00
PN	.5601	69.36
FN_3	.4749	58.81
FN_4	.4428	54.83
FN_2	.4347	53.83
FDN_2	.3862	47.82
FN_5	.2857	35.38
FN_6	.2533	31.36
FDN_3	.2005	24.82
FDN_4	.1835	22.72

In order to compare the trajectory of HUT when perturbed in the direction of the eigenvector above with the standard trajectory, the components of the ten parameters shown in table 2 were perturbed by the proportionate amounts shown in column 3 of table 2. Thus, for example, FDN_1 was increased by 0.050 of its value and FN_2 was decreased by 0.026 of its nominal value. In this way the most sensitive parameter was only perturbed by 5%.In figure 1 the standard trajectory is shown as the curve marked with triangles and the simulated behaviour of HUT, when perturbed along the most sensitive direction described above, is represented by the curve marked with circles. The curve marked with crosses as well as the dotted curve represent simulations under single parameter perturbations. In the first instance the single most sensitive parameter FDN_1 was perturbed by 8.5% and in the second case PN was perturbed by the same amount, thus having the same value of the constraint constant c(see section 2) in every case. The simulations were all carried out over the same 36 month period (after equilibrium had been attained) described earlier on. Using the magnitudes of the ten most sensitive parameters and perturbing them in a direction orthogonal to the 'most sensitive direction' yielded a plot indistinguishable from the standard trajectory.

FIGURE 1



CONCLUSION

The method of Hearne outlined above provides the most sensitive direction in parameter space relative to the perturbation measure introduced by him. Simulations illustrate the importance of finding the correct linear combination of parameter perturbations for maximum effect on the system. The correspondence of the results in tables 2 and 3 indicate that the perturbation measure introduced is a natural one. In the event that control can be exercised over the parameters, the method may be useful in population control situations.

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