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SENSITIVITY OF A MATHEMATICAL MODEL USED TO OPTIMIZE REVENUE IN A PREDATION-COMPETITION FARMING ENVIRONMENT

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ABSTRACT

Sheep farmers in the Cape Midlands region of South Africa frequently sustain stock losses through predation by caracal lynx. Further losses are incurred when hyrax compete with sheep for available pasture. Hyrax constitute the natural prey for lynx with the result that culling either hyrax or lynx has complicated feedback effects. In order to investigate the spill-over problems from the natural predator-prey system on farming revenue, a differential equations model was previously formulated, comprising the sectors Hyrax, Lynx, Sheep, Pasture and Revenue and an optimization procedure was used to determine the optimal culling rate policy for farmers. The purpose of this paper is to investigate the numerical, behavioural and policy sensitivity of this model to parameter uncertainty.

1. INTRODUCTION

The sheep farming region of the Cape Midlands, South Africa, includes many areas too rugged for agricultural exploitation. The hyrax *Procavia capensis* and lynx *Felis caracal* that abound in most of these wilderness areas pose a problem to the farmer. When the hyrax population exceeds the carrying capacity of the wilderness areas, the hyrax encroach upon farming land and consume pasture in competition with sheep. Although hyrax constitute the principal food of lynx [Fairall 1980, Grobler 1981] farmers sustain further losses to their flocks through lynx predation.

A mathematical model comprising Sheep, Hyrax, Lynx, Pasture and Revenue was previously formulated to investigate the general consequences of different culling strategies aimed at curbing lynx predation of sheep and hyrax competition with sheep [Swart & Hearne 1989]. To keep the model simple, the populations were divided into a limited number of age classes. The different groups, their initial values and the rates determining their levels are shown in table 1. A region of 200 000 ha was chosen as the model boundary.

Group	Initial Value	Age (yrs)	Recruitment	Losses
HJ	350 000	0–1	Births	Maturation, Death, Predation
HF	262 500	1+	Maturation	Death, Culling, Predation
HM	262 500	1+	Maturation	Death, Culling, Predation
LJ	200	0–1	Births	Maturation, Death
LF	300	1+	Maturation	Death, Culling
LM	300	1+	Maturation	Death, Culling
SJ	80 670	0–2	Births	Maturation, Death, Predation, Culling
SF	75 567	2+	Maturation	Death, Culling
SM	50 379	2+	Maturation	Death, Culling

Table 1.

Population Groups. Symbols beginning with H, L and S indicate Hyrax, Lynx and Sheep, respectively. The last letter of each symbol refers to Juveniles, Females and Males.

It is assumed that emigration from this region is approximately equal to immigration. The numbers involved in migration are in any case likely to be insignificantly small compared with the population of this large region. Due to practical difficulties hyrax and lynx juveniles are not subjected to culling [Fourie 1983]. Although lynx do sometimes kill adult sheep, predation of sheep is confined to the juvenile group (lambs) in the model.

As a grazer, prey item or predator a juvenile does not have the same effect on the system as an adult. The juveniles were converted to equivalent adult units and added to the corrresponding adults to yield the quantities [initial values in brackets]:

HUT	=	Hyrax Units Total	[700 000]
LUT	=	Lynx Units Total	[700]
SSU	=	Small Stock Units (sheep)	[180 000]

When there is insufficient hyrax for the lynx to sustain their natural diet, lynx fecundity and juvenile mortality are adversely affected. Furthermore when the Prey Abundance (PA) is low, lynx will supplement their diet by killing lambs. When the hyrax density (HD) exceeds the carrying capacity of the wilderness area, hyrax spill over onto farming land and affect the rate at which pasture is grazed.

Revenue is obtained from mutton sales (directly proportional to sheep culling), wool sales (proportional to the number of sheep in each cohort) and interest on revenue. Loss of revenue is incurred through lynx culling, hyrax culling and veterinary and other costs (directly proportional to the number of sheep). Certain other fixed costs were not included as they do not reveal anything about the relative merits of a culling strategy. Culling of hyrax and lynx is by means of shooting; trapping and poisoning are not practised. It is likely that culling costs of hyrax and lynx per head will rise at lower population densities, resulting from higher culling rates, and this has been taken into account in the model.

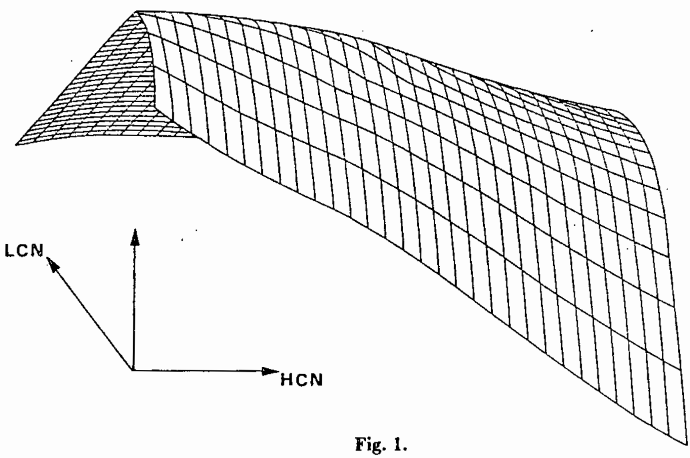

Fig. 1.

The Total Revenue surface

The appendix to this article includes the model equations and a symbol name listing, but for a detailed formulation of the model, the reader is referred to Swart & Hearne [1989]. In the above article it was established that simultaneous culling of hyrax and lynx was necessary for reasonable profitability. A simple objective function, incorporating the revenue generated over the simulation period as well as the stock position at the end of this period, was set up to measure the relative merits of various strategies. An optimization procedure was used to obtain optimal culling rates to maximize the "Total Revenue" so obtained.

In figure 1 the graph of Total Revenue is plotted against Hyrax Culling Normal (*HCN*) and Lynx Culling Normal (*LCN*) to illustrate the nature of the surface to be maximized. The optimal annual culling rates for hyrax and lynx were found to be 0.31 and 0.33 respectively.

The differential equations describing the model were solved numerically and simulations were carried out on a Sperry 1100/71 computer using FORTRAN 77.

2. PARAMETER SENSITIVITY ANALYSIS

The model is described by a system of non-linear first order differential equations of the form

$$dx_i / dt = f_i (x, p)$$

where $x = (x_1, \ldots, x_n)$ and $p = (p_1, \ldots, p_m)$ are the state variables at time t and the parameters of the system respectively, and we now investigate the sensitivity of the model to parameter uncertainty. Several relationships in the model are described non-linearly and it is highly desirable to include the sensitivity of the model to changes in functional relationships [Swart 1990]. For this reason, table functions were specified using the three parameter analytical form [Uys 1984]:

$$\text{for } A > 1, \ 0 < B < 1 \quad \text{and} \quad t,s > 0 \quad \text{we define}$$

$$f(\mathrm{A,B,s,t}) = \mathrm{A}/[1 + \mathrm{E.exp}(-\mathrm{C}.\, \mathrm{t}^{\mathrm{s}})]$$

where

$$E = (A/B) - 1$$

$$C = \ln\,[E/(A - 1)].$$

The table functions used in certain rate equations in the model were defined as follows:

$$HJDM = f(1.7,\ 0.5,\ 1.5,\ HDA)$$

$$LPM = f(2.0,\ 0.1,\ 0.6,\ PA)$$

$$LFM = f(1.5,\ 0.7,\ 1.5,\ PAA)$$

$$GM = f(2.0,\ 0.1,\ 1.0,\ PAI)$$

$$SFM = f(2.0, 0.01, 0.5, GMA)$$
$$HFM = 1/f(2.5, 0.625, 2.5, HDA)$$
$$LJDM = 1/f(1.43, 0.71, 2.0, PAA)$$
$$SJDM = 1/f(1.66, 0.335, 3.5, GMA).$$

The functions above refer respectively to Hyrax Juvenile Death Multiplier, Lynx Predation Multiplier, Lynx Fecundity Multiplier, Grazing Multiplier, Sheep Fecundity Multiplier, Hyrax Fecundity Multiplier, Lynx Juvenile Death Multiplier and Sheep Juvenile Death Multiplier. As the full impact of a change in variables such as HD and PA are not always felt immediately, exponentially smoothed versions of these variables (HDA and PAA) occur as function arguments above. The Pasture Availability Index (PAI) measures the relative abundance of pasture and GMA is a smoothed version of the Grazing Multiplier (GM). The graphs of two typical functions $HJDM$ and $SJDM$ are shown in figure 2 below.

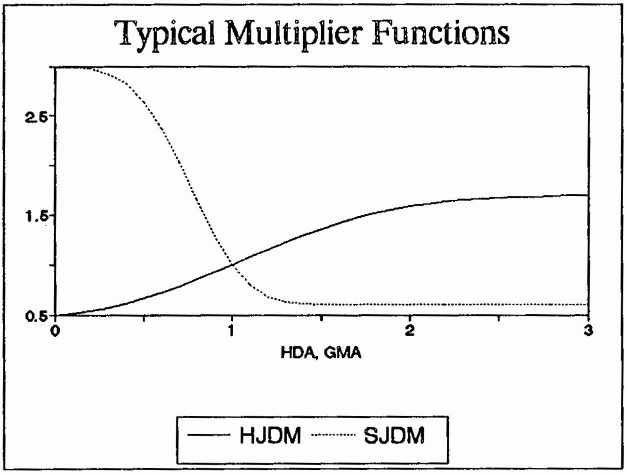

Fig 2.

Hyrax Juvenile Death Multiplier as a function of HDA and Sheep Juvenile Death Multiplier as a function of GMA.

By using the analytic specification above, each table function is completely determined by three parameters A, B and s. Uncertainty in the model can therefore be tested by analyzing parameter uncertainty only. In the parameter sensitivity analysis below, the three parameters specifying the *n th* of the eight functions listed above, are denoted *An*, *Bn* and *Sn* respectively. Thus *A*3, *B*3 and *S*3 are the parameters associated with the function *LFM* with nominal values 1.5, 0.7 and 1.5 respectively.

Numerical sensitivity

The normalized sensitivity functions

$$N_{ij}(t) = (\partial x_i/\partial p_j)/(x_i/p_j)$$

give the approximate percentage change in the variable x_i at time t corresponding to a one percent change in the parameter p_j and provide a useful indication of small parameter uncertainty. The nine state variables listed in table 1 as well as *Total Revenue* were used in this analysis. As the model displays seasonal dynamics, the time during a simulation run at which output is measured will affect the results of a sensitivity analysis. The sensitivity functions were evaluated at monthly intervals during a three year period once the system, operating under the above determined optimal culling rates (kept fixed during the sensitivity analysis), had reached seasonal equilibrium.

Parameter	Nominal Value	Maximum N_{ij}	State Variable
Lynx Fecundity Normal	0.7	2.5341	*LJ*
Ewe Culling Normal	0.3	1.6244	*SM*
A3	1.5	1.6125	*LJ*
Sheep Fecundity Normal	0.75	−1.3916	*SM*
Hyrax Juvenile Maturation Normal	1.0	−1.1673	*HJ*
Hyrax Units Normal	700 000	1.1550	*HF*,*HM*
Hyrax Fecundity Normal	1.5	0.8718	*HJ*
Lynx Female Death Normal	1.13	−0.8258	*LF*
Sheep Male Culling Normal	0.3	−0.8083	*SM*
Lynx Juvenile Death Normal	0.5	−0.7313	*SJ*

Table 2.

Maximum normalized sensitivity function values.

In table 2 the parameter normal values are listed together with the maximum normalized sensitivity value obtained during the simulation period. The table includes only the ten largest normalized sensitivity function values so obtained. The last column lists the state variable which showed the largest response elasticity. The most sensitive parameter identified in this way is the Lynx Fecundity Normal in which a 1% increase would lead to a maximum increase of 2.5% in the state variable Lynx Juvenile at a certain time during the simulation period.

It is interesting to compare the behaviour of normalized sensitivity functions with that of the state variable in which the largest variation occurs for a given parameter.The behaviour of the normalized sensitivity function N_{ij} corresponding to the state variable *SM* (wethers) and the parameter *SFCN* (ewe culling normal) over the three year simulation period is illustrated in fig.3.

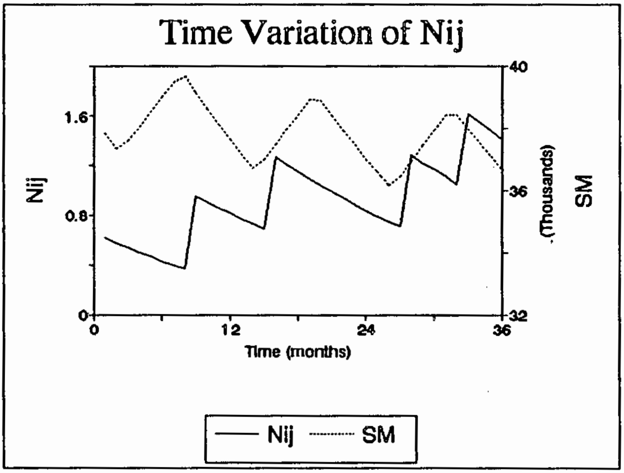

Fig. 3

Behaviour of N_{ij} corresponding to state variable SM and parameter SFCN.

The importance of investigating combinations of parameter changes is well known [Vermeulen and De Jongh 1976, Hearne 1985]. The latter derived a method for determining the combination of parameter changes to which the system is most sensitive, subject to a suitable constraint on perturbation magnitude. The 10 largest components of the eigenvector specifying the most sensitive direction in parameter space are listed in table 3. The largest component was assigned the value 100 and the other components scaled accordingly.

Component	Relative Value	Perturbation Value
Lynx Fecundity Normal	100.00	0.1000
A3	50.80	0.0508
Lynx Units Normal	32.67	0.0327
Lynx Female Death Normal	−31.30	−0.0313
Lynx Juvenile Death Normal	−29.03	−0.0290
Hyrax Fecundity Normal	24.83	0.0248
B3	−24.60	−0.0246
A7	19.37	0.0194
S3	17.53	0.0175
Lynx Juvenile Maturation Normal	9.70	0.0097

Table 3.

The eigenvector giving the most sensitive direction in parameter space.

Behavioural sensitivity

In order to observe the effects of a perturbation along the most sensitive direction on model output, the most sensitive component was perturbed by 10%, other components being perturbed by the appropriate proportional amounts shown in column 3 of table 3. Thus, for example, the Lynx Juvenile Death Normal (*LJDN*) was decreased by 0.0290 of its nominal value and the parameter *A*3 associated with the Lynx Fecundity Multiplier function *LFM*, increased by 0.0508 of its nominal value.

The effect of the perturbations on parameters *A*3, *B*3 and *S*3 on the function *LFM* is illustrated in fig. 4. Model output as measured, for example by *HUT*, *LUT* and *SSU* remained behaviourally the same as in the standard run as may be seen in figures 5 and 6. The graph of *HUT* , like that of *SSU*, remains almost identical in the two runs and is not shown. The graph of *LUT* shows an appreciable upwards shift, but the pattern over time remains the same. The shift is readily understood as virtually every component of the direction eigenvector favours a higher lynx population. The Total Revenue generated over the simulation period changed by only 0.1%.

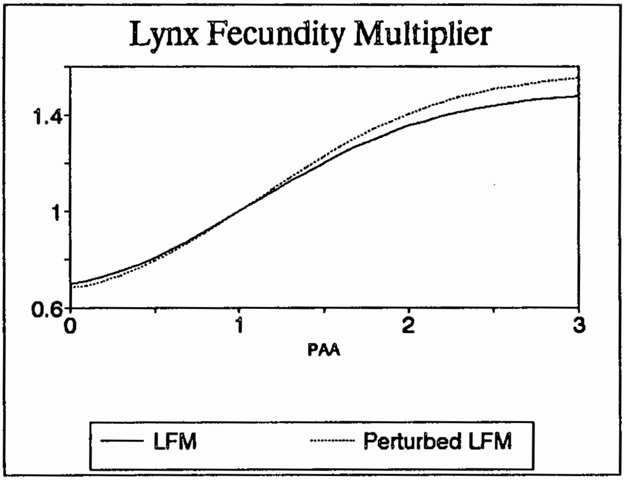

Fig. 4

The standard and perturbed Lynx Fecundity Multipliers.

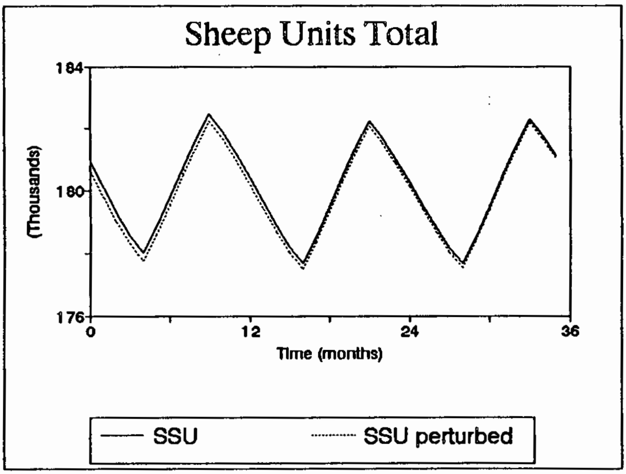

Fig. 5

The effect of parameter variation on sheep.

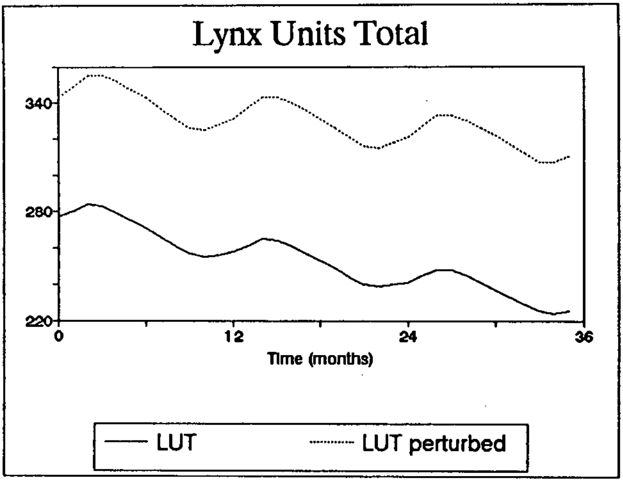

Fig. 6

The effect of parameter variation on lynx.

Policy sensitivity

In order to implement the optimal culling policy, population numbers are required on a continuing basis and because of the difficulty involved in estimating hyrax and lynx populations [Fourie 1983], it is likely that population counts may be in error by a substantial amount. A policy recommendation for the farmers could be to aim for culling rates of 30% in both hyrax and lynx, and assuming a worst case error in population counts of 40%, this would mean that actual culling rates may vary between 0.18 and 0.42. By applying an optimization procedure, the lowest *Total Revenue* determined by $0.18 \leq HCN,LCN \leq 0.42$ was found to differ from that obtained in the optimal solution by approximately 3%, thus suggesting that the model is quite robust from a policy point of view. By comparing the worst possible outcome of the policy recommendation with the best possible outcome of the farmers' present policy of culling lynx only, the superiority of the simultaneous culling policy is also clearly demonstrated (see table 4).

Policy	Revenue generated over 10 years (millions)
Optimal	9.3
Worst case: $.18 \leq \text{HCN}, \text{LCN} \leq .42$	9.0
Farmer's best	8.6
No culling	7.8

Table 4.

Comparison of culling strategies.

3. CONCLUSION

The combination of parameter changes to which the system is most sensitive has been identified and a perturbation along this direction yields similar model behaviour and a new optimal solution not substantially different from the standard one. The model is policy insensitive and in addition seems to be quite robust, at least for small parameter variation, both numerically and behaviourally.

Hyrax fecundity and death normals were derived from data collected in a comprehensive demographic study [Fourie 1983], but the corresponding values for lynx are not as accurately known [Grobler 1981, Fourie 1983]. The Lynx Fecundity Normal has been identified as the most sensitive system parameter. Furthermore, all three parameter values $A3$, $B3$, $S3$ specifying the function LFM (Lynx Fecundity Multiplier) appear amongst the top 10 components of the direction eigenvector. More effort by zoologists in determining the lynx parameters more accurately would be well worthwhile.

4. APPENDIX: Model Equations Listing

Symbols not defined in the test appear in the symbol list below.

Hyrax sector

$$\frac{d}{dt} HJ = HJB - HJD - HJM - HJP$$

$$\frac{d}{dt}HF = 0.5(HJM) - HFD - HFC - HFP$$

$$\frac{d}{dt}HM = 0.5(HJM) - HMD - HMC - HMP$$

$HJB = HF.\ HFN.\ HFM.\ HSFM$
$HJD = HJ.\ HJDN.\ HJDM$
$HJM = HJ.\ HJMN$
$HJP = LUT.\ LPN.\ LPM.\frac{HJ}{HT}$, where $HT = HJ + HF + HM$
$HFD = HF.\ HFDN$
$HFC = HF.\ HCN$
$HFP = LUT.\ LPN.\ LPM.\ \frac{HF}{HT}$
$HMD = HM.\ HMDN$
$HMC = HM.\ HCN$
$HMP = LUT.\ LPN.\ LPM.\ \frac{HM}{HT}$

Lynx sector

$$\frac{d}{dt}LJ = LJB - LJD - LJM$$

$$\frac{d}{dt}LF = 0.5(LJM) - LFD - LFC$$

$$\frac{d}{dt}LM = 0.5(LJM) - LMD - LMC$$

$LJB = LF.\ LFN.\ LFM.\ LSFM$
$LJD = LJ.\ LJDN.\ LJDM$
$LJM = LJ.\ LJMN$
$LFD = LF.\ LFDN$
$LFC = LF.\ LCN$
$LMD = LM.\ LMDN$
$LMC = LM.LCN$

Sheep sector

$$\frac{d}{dt}SJ = SJB - SJD - SJM - SJP - SJC$$

$$\frac{d}{dt}SF = 0.6(SJM) - SFD - SFC$$

$$\frac{d}{dt}SM = 0.4(SJM) - SMD - SMC$$

$SJB = SF.\ SFN.\ SFM$
$SJD = SJ.\ SJDN.\ SJDM$
$SJM = SJ.\ SJMN$
$SJP = max\{0, (1 - LPM)\}.\ LUT.\ SJPN$
$SJC = SJ.\ SJCN$
$SFD = SF.\ SFDN$
$SFC = SF.\ SFCN$
$SMD = SM.\ SMDN$
$SMC = SM.\ SMCN$

Pasture sector

$$\frac{dP}{dt} = PP - PG$$

$$PP = PPN.\ AREA.\ PPM$$

$$PG = TSSU.\ GN.\ GM$$

$$TSSU = SSU + max\left\{0, \frac{HUT-HUN}{HS}\right\}$$

where HS = number of hyrax consuming same amount of pasture as one SSU.

Revenue sector

$$\frac{d}{dt} REV = MSLS + WSLS + CAPINT - SCST - CCST$$

$$MSLS = SJC.\ SJMV + SFC.\ SFMV + SMC.\ SMMV$$

$$WSLS = SJ.\ SJWV + SF.\ SFWV + SM.\ SMWV$$

$$CAPINT = REV.\ INT$$

$$SCST = SJ.\ SJC + (SF + SM).\ SC$$

$$CCST = (LFC + LMC).LCC.\ LCCM + (HFC + HMC).\ HCC.\ HCCM$$

Name	Symbol	Units/(function argument)
Hyrax Juvenile Birth rate	HJB	hyrax/yr
Hyrax Juvenile Death rate	HJD	hyrax/yr
Hyrax Juvenile Maturation rate	HJM	hyrax/yr
Hyrax Juvenile Predation rate	HJP	hyrax/yr
Hyrax Female Death rate	HFD	hyrax/yr
Hyrax Female Culling rate	HFC	hyrax/yr
Hyrax Female Predation rate	HFP	hyrax/yr
Hyrax Male Death rate	HMD	hyrax/yr
Hyrax Male Culling rate	HMC	hyrax/yr
Hyrax Male Predation rate	HMP	hyrax/yr
Hyrax Fecundity Normal	HFN	fraction/yr
Hyrax Fecundity Multiplier	HFM	(HDA)
Hyrax Seasonal Fecundity Multiplier	HSFM	(Time-periodic)
Hyrax Juvenile Death Normal	HJDN	fraction/yr
Hyrax Juvenile Death Multiplier	HJDM	(HDA)
Hyrax Juvenile Maturation Normal	HJMN	fraction/yr
Hyrax Female Death Normal	HFDN	fraction/yr
Hyrax Male Death Normal	HMDN	fraction/yr
Hyrax Culling Normal	HCN	fraction/yr
Hyrax Units Normal	HUN	hyrax
Hyrax Culling Cost	HCC	Rand/hyrax/yr
Hyrax Culling Cost Multiplier	HCCM	(HD)

Name	Symbol	Units/(function argument)
Lynx Predation Normal	LPN	hyrax/lynx/yr
Lynx Predation Multiplier	LPM	(PA)
Lynx Juvenile Birth rate	LJB	lynx/yr
Lynx Juvenile Death rate	LJD	lynx/yr
Lynx Juvenile Maturation rate	LJM	lynx/yr
Lynx Female Death rate	LFD	lynx/yr
Lynx Female Culling rate	LFC	lynx/yr
Lynx Male Death rate	LMD	lynx/yr
Lynx Male Culling rate	LMC	lynx/yr
Lynx Fecundity Normal	LFN	fraction/yr
Lynx Fecundity Multiplier	LFM	(PAA)
Lynx Seasonal Fecundity Multiplier	LSFM	(Time–periodic)
Lynx Juvenile Death Normal	LJDN	fraction/yr
Lynx Juvenile Death Multiplier	LJDM	(PAA)
Lynx Juvenile Maturation Normal	LJMN	fraction/yr
Lynx Female Death Normal	LFDN	fraction/yr
Lynx Culling Normal	LCN	fraction/yr
Lynx Male Death Normal	LMDN	fraction/yr
Lynx Culling Cost	LCC	Rand/lynx/yr
Lynx Culling Cost Multiplier	LCCM	(Lynx Density)
Sheep Juvenile Birth rate	SJB	sheep/yr
Sheep Juvenile Death rate	SJD	sheep/yr
Sheep Juvenile Maturation rate	SJM	sheep/yr
Sheep Juvenile Predation rate	SJP	sheep/yr
Sheep Juvenile Culling rate	SJC	sheep/yr
Sheep Female Death rate	SFD	sheep/yr
Sheep Female Culling rate	SFC	sheep/yr
Sheep Male Death Rate	SMD	sheep/yr
Sheep Male Culling rate	SMC	sheep/yr
Sheep Fecundity Normal	SFN	fraction/yr
Sheep Fecundity Multiplier	SFM	(GMA)
Sheep Juvenile Death Normal	SJDN	fraction/yr
Sheep Juvenile Death Multiplier	SJDM	(GMA)
Sheep Juvenile Maturation Normal	SJMN	fraction/yr
Sheep Juvenile Predation Normal	SJPN	lambs/lynx/yr
Sheep Juvenile Culling Normal	SJCN	fraction/yr
Sheep Female Death Normal	SFDN	fraction/yr
Sheep Female Culling Normal	SFCN	fraction/yr
Sheep Male Death Normal	SMDN	fraction/yr
Sheep Male Culling Normal	SMCN	fraction/yr
Sheep Juvenile Meat Value	SJMV	Rand/lamb/yr
Sheep Female Meat Value	SFMV	Rand/sheep/yr
Sheep Male Meat Value	SMMV	Rand/sheep/yr
Sheep Juvenile Wool Value	SJWV	Rand/lamb/yr
Sheep Female Wool Value	SFWV	Rand/sheep/yr
Sheep Male Wool Value	SMWV	Rand/sheep/yr
Sheep Juvenile Cost	SJC	Rand/lamb/yr
Sheep Cost	SC	Rand/sheep/yr

Name	Symbol	Units/((function argument)
Pasture	P	grazing days
Pasture Production	PP	grazing days/yr
Pasture Grazed	PG	grazing days/yr
Pasture Production Normal	PPN	grazing days /yr/ha
Area	AREA	ha
Pasture Production Multiplier	PPM	(Time-periodic)
Total Small Stock Units	TSSU	small stock units
Grazing Normal	GN	grazing days /yr/SSU
Grazing Multiplier	GM	(PAI)
Revenue	REV	Rand
Meat Sales	MSLS	Rand/yr
Wool Sales	WSLS	Rand/yr
Interest on Capital	CAPINT	Rand/yr
Sheep Cost	SCST	Rand/yr
Culling Cost	CCST	Rand/yr
Interest rate	INT	fraction /yr

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