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The logistic model-generated optimal stocking levels, optimal species mix and carrying capacity of wild herbivores in southern rangelands game ranches in Kenya

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This paper derives logistic models for Grant's gazelle (*Gazella granti*), Thompson's gazelle (*Gazella thomsonii*) and plains Zebra (*Equus burchellii*), in a game ranching system. The study was conducted on an 8100 hectares savannah ecosystem in Machakos district, with an average annual rainfall of 514 ± 159.3 mm. Modelled as discrete-time logistic equations with fixed carrying capacities, it captures the wildlife herbivore population dynamics. Time series data, covering a period of 16 years, is used to generate the fixed carrying capacities and the interaction parameters endogenously. The estimation of the logistic models involves estimation of econometric models for each herbivore species, followed by the recovery of the carrying capacities, mathematically. The model-generated carrying capacities are 144.30 AU, 75.53 AU and 54.65 AU; the equivalent number of animals is 986, 929 and 144; for Grant's gazelle, Thompson's gazelle and Zebra, respectively. The derived "maximum sustainable yield" (MSY) stocking levels is 44 AU, 24 AU and 29 AU; the equivalent animal number is 297, 393 and 76; for Grant's gazelle, Thompson's gazelle and Zebra, respectively. Similarly, the MSY off-take level is 10.42 AU, 8.39 AU and 6.37 AU for these species respectively. These results show that the discrete-time logistic models are applicable to sustainable management of game ranching enterprise.

Key words: Carrying capacity, animal units, game ranching, species mix, logistic models, MSY.

INTRODUCTION

Proper game management requires good grazing management strategies that provide effective means of manipulating the grazing game animals, so as to achieve the highest level of animal production sustainably (Pratt and Gwynne, 1977). The key issues in grazing management are the determination of optimal stocking level, optimal species mix and carrying capacity; the latter is the upper bound stocking level. The current method of estimating these parameters involves trial and error approximations, based on the availability of forage on the

one hand, and the animal forage requirements on the other (Pratt and Gwynne, 1977; Stoddart et al., 1975). This method is clearly subjective. An alternative method of determining herbivore optimal stocking levels, optimal species mix and carrying capacities is based on systems analysis procedures (Njoka and Kinyua, 2006; Kinyua, 1998).

This method involves deriving a set of logistic equations for each species in a given ranch (Equations 1) (Njoka and Kinyua, 2001), coupled with recovery of

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carrying capacities from these equations mathematically. This approach is completely objective, and it is the underlying the objective of this study.

Under this formulation, both carrying capacity and exchange ratios are endogenously determined (Kinyua and Njoka, 2001), making it possible to empirically estimate the population growth models for Grant's gazelle, Thompson's gazelle and Zebra.

$$H_{it+1} - H_{it} = \Delta H_{it} = \beta_i H_{it} \left(1 - \frac{(H_{it} + \sum_{j=1}^{n-1} \lambda_{ij} H_{jt})}{K_i} \right) - Y_{it} \quad (1)$$

for $i = 1, \dots, n-1$ $j = 1, \dots, 2$ and $i \neq j$.

Here H_{it+1} , measured in animal units, is the standing herbivore population at period $t+1$ where time step is measured in periods of six months. Y_{it+1} is a control variable, representing the off-take level of Herbivore species i at period $t+1$ and is measured in animal units; H_{it} represents the standing biomass of game herbivore species i at period t and is measured in animal units; and K_i , also measured in animal units, represents the carrying capacity for game herbivore species i . The parameter β_i represents the exponential growth rate for the game herbivore species i . The parameter σ_{ij} represents the interaction effect of game herbivore species j on species i , and this interaction parameter is negative, zero or positive depending on whether the interactive relationship is complementary, supplementary or competitive, respectively. This parameter also gives an estimate of exchange ratios or grazing pressure equivalence among species, that is, it plays the role of converting H_{jt} animal units into the equivalent H_{it} animal units. For this particular study, "n" is equal to three animal species.

Conceptual view

The formulation of wild herbivores' discrete-time logistic equations with fixed carrying capacity is captured in Equations 1 which are difference equations (Starfield and Bleloch, 1986; Anderson, 1991; Caughley and Sinclair, 1994; Njoka and Kinyua, 2006). Conceptually, the term K_i represents the maximum number of animal units of game herbivore species i that can be supported through period t . There are three cases as shown in (Equations 2, 3 and 4).

Case 1 (stocking level below carrying capacity):

$$K_i > (H_{it} + \sum_{j=1}^{n-1} \sigma_{ij} H_{jt}), \quad (2)$$

for $i = 1, \dots, n$, $j = 1, \dots, n-1$ and $i \neq j$.

This implies that the animal unit months (AUMs) of available

forage exceeds the AUMs of forage demand by the standing population of game herbivores species i . The standing game herbivore population increases since there is enough forage to meet their maintenance requirements and leave a balance for growth and reproduction.

Case 2 (stocking level equal to carrying capacity):

$$K_i = (H_{it} + \sum_{j=1}^{n-1} \sigma_{ij} H_{jt}), \quad (3)$$

for $i = 1, \dots, n-1$, $j = 1, \dots, n-1$ and $i \neq j$.

This implies that the AUMs of available forage exactly matches the AUMs of forage demand by the standing population of game animal species i . The standing herbivore population barely meets its maintenance requirements, leaving no balance for growth and reproduction. As a result, the population change is zero, implying that H_{it} is at the maximum stocking level.

Case 3 (stocking level above carrying capacity):

$$K_i < (H_{it} + \sum_{j=1}^{n-1} \sigma_{ij} H_{jt}), \quad (4)$$

for $i = 1, \dots, n$, $j = 1, \dots, n-1$ and $i \neq j$.

In this case the forage demand by wild herbivore species i is greater than the AUMs of available forage, or the standing herbivore population is greater than the carrying capacity. The excess number of animals will die out, resulting in the decline of the standing population of herbivore species i .

The discrete-time game herbivore logistic models, (Equations 1) is a quadratic equations without an intercept (Beattie and Taylor, 1985) and are derived from the discrete time compounding equations (Equations 5a).

$$H_{it} = H_{i0} (1 + r_i)^t - Y_{it}, \quad (5a)$$

for $i = 1, \dots, n$.

Where, H_{it} represents the population of herbivore species i at period t ; H_{i0} represents the initial population (at $t = 0$) of herbivore species i ; r_i represents the rate of herbivore population growth per period; Y_{it} represents the off-take level for herbivore species i at period t ; t represents discrete time-steps of periods of six months. The term $H_{i0} (1 + r_i)^t$ is the discrete-time compounding formula, capturing the population growth of herbivore species i . When $t = 1$, Equations (5a) become Equations (5b).

$$H_{i1} = H_{i0} (1 + r_i)^1 - Y_{i1}, \quad (5b)$$

for $i = 1, \dots, n$.

When $t = 2$, Equations (5b) become Equations (5c).

$$H_{i2} = H_{i0}(1+r_i)(1+r_i) - Y_{i2} = H_{i1}(1+r) - Y_{i2} \quad (5c)$$

for $i = 1, \dots, n$.

The general form of Equations (5c) is shown in Equations (5d); these equations are independent of time

$$H_{it+1} = H_{it}(1+r_i) - Y_{it+1}, \quad (5d)$$

for $i = 1, \dots, n$.

From an ecological point of view, the rate of herbivore population growth per period (r_i), is hypothesized to be determined by intra- and inter-species competition thus it is more realistically modelled as shown in Equations (5e).

$$r_i = \{\beta_i - (\delta_i H_{it} + \sum_{j=1}^{n-1} \lambda_{ij} H_{jt})\}.$$

for $i = 1, \dots, n, j = 1, \dots, n-1$ and $i \neq j$. (5e)

Here parameter β_i represents the fixed rate of population change for species i while parameter δ_i represents intra species competition. Parameter λ_{ij} represents inter species interaction between species i and species j ; this parameter is negative, zero or positive depending on whether the interactive relationship is competitive, supplementary or complementary, respectively. Substituting (r_i) in Equations (5d) with (r_i) in Equations (5e) yields Equation (5f)

$$H_{it+1} = H_{it} \{1 + [\beta_i - (\delta_i H_{it} + \sum_{j=1}^{n-1} \lambda_{ij} H_{jt})]\} - Y_{it+1}$$

for $i = 1, \dots, n, j = 1, \dots, n-1$ and $i \neq j$. (5f)

Multiplying out Equations (5f) and rearranging terms yields Equations (6a), and like Equations (1), they are different equations. Shifting Y_{it+1} from the right to the left hand side of Equations (6a) yields Equations (6b). Equations (6b) are the econometric (statistical) models, and although they are nonlinear in variables, they are linear in parameters.

$$H_{it+1} - H_{it} = \Delta H_{it} = \beta_i H_{it} - \delta_i H_{it}^2 + \sum_{j=1}^{n-1} \lambda_{ij} H_{it} H_{jt} - Y_{it+1}, \quad (6a)$$

for $i = 1, \dots, n, j = 1, \dots, n-1$ and $i \neq j$.

$$H_{it+1} - H_{it} + Y_{it+1} = \Delta H_{it} + Y_{it+1} = \beta_i H_{it} - \delta_i H_{it}^2 + \sum_{j=1}^{n-1} \lambda_{ij} H_{it} H_{jt}, \quad (6b)$$

for $i = 1, \dots, n$,
 $j = 1, \dots, n-1$ and
 $i \neq j$.

MATERIALS AND METHODS

Study area

The study area is located on the David Hopcraft Ranch, 40km south-east of Nairobi, on the Athi-Kapiti Plains along the Nairobi-Mombasa road in Machakos District, Eastern Province of the Republic of Kenya. The ranch area is 8100 ha and its altitude is 1600 m to 1700 m above sea level. The ranch vegetation is typical of eco-climatic zone 4 (Pratt and Gwynne, 1977). The ranch vegetation comprises of *Themeda triandra* grassland, a mixture of *Balanites glabra-Themeda triandra* tree grassland, *Acacia drepanolobium* and *Balanites glabra* bush grassland, and *Acacia seyal* and *Acacia xanthophloea* riverine woodland. Its average annual rainfall is 514±159.3 mm. The median rainfall for the study site for the same period was 599.4 mm between 2001 and 1978 with an annual range from 177.4 to 924.5 mm.

Methods

This study focused on analysis of sustainable management and sustainable conservation of Grant's gazelle, Thompson's gazelle and Zebra, coupled with game cropping. The Zebra is a large non-ruminant grazer (267 - 318 kg) capable of consuming bulk forage especially grasses. The Thompson's gazelle (20 to 25 kg) and is a selective feeder consuming highly nutritious grasses and while the Grant's gazelle (32 to 42 Kg) is slightly stockier than the Grant's gazelle, and is a mixed feeder utilizing both high quality grass and browse (Hofmann and Stewart, 1972). The feeding habits of the Grant's gazelle would therefore overlap with that of the Thompson's gazelle and the Zebra depending on forage availability and level of interspecies and intraspecies competition. Grazing requirement is also based on the metabolic weight of the animal which is calculated from the Animal Unit Coefficient (AUC) Table 1.

Through on-the site visits to the David Hopcraft ranch, during 1995 and 1996, time series data covering the period 1981 through 1996 on Grant's gazelle Thompson's gazelle and Zebra populations and off-take levels were collected from ranch records. Animal numbers and off-take levels were then converted to animal units (AUs), effectively converting discrete data to continuous data, where one animal unit (AU) is equivalent to the metabolic body weight of 454 kg. Based on this data, the econometric population growth models, Equations (6b), were estimated for each of the three herbivore species, namely, Grant's gazelle, Thompson's gazelle and Zebra, using SPSS software (Kleinbaum and Kupper, 1978). This procedure was used to estimate livestock growth models (Njoka and Kinyua, 2006); these models can also be estimated using cross-sectional data.

After the estimation of the econometric models (Equation 6b), the logistic models (Equations 1) is recovered (Figure 1) from the former as follows:

The derived logistic models, that is,

$$\Delta H_{it} = \beta_i H_{it} \left(1 - \frac{H_{it} + \sum_{j=1}^2 \sigma_{ij} H_{jt}}{K_i}\right) - Y_{it+1}$$

for $i = 1, \dots, 3, j = 1, \dots, 2$ and $i \neq j$; portray three scenarios as follows:

(a) When $Y_{it+1} \succ \Delta H_{it}$,
 for $i = 1, \dots, 3$

Table 1. Approximate exchange ratios for animals based on metabolic body weight.

Species	Approximate weight (Kg)	Animal unit coefficient
Grant's gazelle	35	0.1463
Thompson's gazelle	23	0.0813
Zebra	272	0.38

Source: (Kinyua, 1998)

$$\Delta H_{it} = \beta_i H_{it} \left(1 - \frac{H_{it} + \sum_{j=1}^2 \sigma_{ij} H_{jt}}{K_i}\right) - Y_{it+1}$$

the game harvests are higher than the populations growth per period; as a result, the populations decline.

(b) When $Y_{it+1} = \Delta H_{it}$,

for $i = 1, \dots, 3$, game harvests are equal to the t growth of the populations per period; as a result, the populations are constant or at a steady state.

This also means that

$$\Delta H_{it} = 0$$

and that,

$$Y_{it+1} = \beta_i H_{it} \left(1 - \frac{H_{it} + \sum_{j=1}^2 \sigma_{ij} H_{jt}}{K_i}\right)$$

for $i=1, \dots, 3$;

These equations are quadratic production functions without intercept. Multiplying out these equations yield their equivalent counterpart, also production functions without intercept (equations 6c), as follows:

$$Y_{it+1} = \beta_i H_{it} - \delta_i H_{it}^2 + \sum_{j=1}^{n-1} \lambda_{ij} H_{it} H_{jt}$$

for $i = 1, \dots, 3, j = 1, \dots, 2$ and $i \neq j$.

These equations are then solved for the first order conditions which, in turn, are solved simultaneously because the animal species share resources. The solutions are the "maximum sustained yield" stocking levels; by substituting the values of "maximum sustained yield" stocking levels into equations 6c, the outcomes are "maximum sustained yield" off-take levels.

(c) When

$$Y_{it+1} < \Delta H_{it}$$

for $i = 1, \dots, 3$, the game harvests are less than the growth of the populations per period; as a result, the populations increase.

RESULTS AND DISCUSSION

The estimation results of Grant's gazelle, Thompson's gazelle and Zebra econometric models (equations 6b) are presented in Table 2. The F-test for the econometric models for the Grant's gazelle, Thompson's gazelle and Zebra were significant ($P < 0.05$). This shows that the econometric model is suitable for capturing the population change for all three species. The exponential growth rate parameters for the three models were positive, as expected, and significant ($P < 0.05$) for all species. The intra-species competition parameters were negative, as expected, and significant ($P < 0.05$) for the three models.

The interaction parameter of Grant's gazelle and Thompson's gazelle were negative ($P < 0.05$), suggesting that Thompson's gazelle is competitive with Grant's gazelle. In retrospect, this negative interaction of Thompson's gazelle with Grant's gazelle could emanate from overlap of their feeding habits. Grant's gazelle is a mixed feeder, eating both grass and browse, while Thompson's gazelle is a grazer. Both species prefer open grassland plains. By virtue of Grant's gazelle being a grazer, its feeding habit overlaps with that of Thompson's gazelle and consequently they tend to compete for the available resources.

The interactive parameter of Grant's gazelle with Zebra is negative ($P < 0.1$), suggesting that the two species are competitive on the grounds that the former is a mixed feeder while the latter is a grazer. The R^2 for the model is 0.413. Thompson's gazelle's interaction parameter with Zebra is negative ($P < 0.05$) depicting a competitive relationship which may explain why Zebra competes with Thompson's gazelle. Grant's gazelle interaction parameter is positive suggesting complementary relationship. However the parameter was not significant ($P > 0.1$) The R^2 for Thompson's gazelle model is 0.45 which is good.

For the Zebra model, the Thompson's gazelle's interaction parameter is negative and significant ($P < 0.05$), suggesting competitive relationships between the two species. Both Zebra and Thompson's gazelle are grazers preferring open grasslands plains. By virtue of their dietary requirement, Thompson's gazelle likely competes with Zebra for available feed resources. In contrast

Table 2. Parameter estimates for the econometric models. Equation (6b) (n = 3)^a

Species	Gr	Th	Zb
Gr	0.722 (3.842)**	0.001 (0.001)	0.007 (1.193)
Gr ²	-0.005 (-2.121)**		
	-0.006 (-2.356)**	1.027 (4.335)**	-0.017 (-4.249)**
Th ²		-0.014 (-4.031)**	
Gi ²			
Zb	-0.005 (-1.851)	-0.014 (-3.836)**	1.258 (5.235)**
Zb ²			-0.023 (-4.577)**
R ²	0.413	0.45	0.560
F	(4.755)**	(5.522)**	(8.579)**

Gr=Grants gazelle; Th=Thompson's gazelle; Zb=Zebra; ^aResults are for equations identified in top row of the table, with parameters indicated in the left-hand column; F and t-statistics are in parenthesis: ** indicates significant at the 0.05 level and * at the 0.1 level.

Table 3. Parameter values for the logistic population models, Equation (1), after derivation from the econometric models in.

Species	Gr	Th	Zb
Gr	0.722	-0.074	0.006
Th	1.198	1.027	-0.328
Zb	1.0	1.0	1.258
K ^b	144.3 (986)	75.529 (929)	54.645 (144)

Gr, Grant's gazelle; Th, Thompson's gazelle and Zb, Zebra ^aResults are for equations identified in top row of table, with parameters indicated in the left-hand column; t-statistics are in parenthesis: ** indicates significant at the 0.05 level and * at the 0.1 level.

^bCarrying capacity in AUs; figures in bracket represent carrying capacities in animal numbers.

the intra-species parameter between Zebra and grant's gazelle is slightly but not significantly positive ($P > 0.1$), suggesting complementary relationship. This may be explained by the likelihood that Grant's gazelle does not compete for the grass favoured by Zebra.

The other components of the results are the recovery of the logistic models to estimate the species carrying capacity, the derivation of the "maximum sustained yield" stocking level and the "maximum sustained yield" off-take level.

The derivation of the logistic models, as discussed earlier, is shown in Table 3 for Grant's gazelle, Thompson's gazelle and Zebra. The carrying capacities in animal units (AUs) are 144.3, 75.529 and 54.645 for Grant's gazelle, Thompson's gazelle and Zebra, respectively. This converts to 986 Grant's gazelle, 929

Thompson's gazelle and 144 Zebra. The Carrying Capacity is the upper boundary stocking rate for the ranch.

The "maximum sustainable yield" (MSY) stocking levels are 43.504AUs, 23.840AUs and 28.785AUs, or 279, 293 and 76 animals for Grant's gazelle, Thompson's gazelle and Zebra, respectively. The "maximum sustained yield off-take" levels are 10.42AUs, 8.39AUs and 6.37AUs or 71, 103 and 17 animals for these species, respectively.

Conclusion

The key issues in the sustainable management of wild and domestic herbivores are the optimal stocking levels, the carrying capacities, the "maximum sustained yield off-

take" levels and the optimal species mix. This systems analysis approach, based on the logistic model, has been applied here to solve the range manager dilemma. This is a novel ground breaking approach, which provides an alternative to showing how the key parameters can be determined in a ranching enterprise. The results obtained in this study confirmed that it is possible to derive the "fixed carrying capacity" logistic model for three wildlife species. These models have in turn been used to estimate the carrying capacity for each of the species and provide solutions for the MSY. Observations at the David Hopcraft ranch showed stocking level numbers of between 138 and 552 Grant's gazelle, 155 and 971 Thompson's gazelle and 122 and 154 Zebra over the period covered by the study, while the carrying capacity models predicted 986, 929 and 144 animal numbers respectively. In comparison the Grant's gazelle remained consistently understocked over the years; the Thompson's gazelle on average was understocked while the Zebra fluctuated within the range predicted by the model. In particular, this procedure has direct application in determining the number of animals to be harvested in a wildlife cropping policy and in wildlife culling as a management tool. It is also usable in determining the animal numbers that should be translocated for management purposes. Finally, this procedure can be used to analyse the dynamics of wild herbivores, including issues like the population doubling time.

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