Optimal Harvesting of Wildebeest-Lion Interactions in Serengeti Ecosystem with Prey Refuge

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Abstract
This paper describes an optimal harvesting policy for a wildebeest-lion prey-predator system in the Serengeti ecosystem with prey refuge. A Holling Type II prey-predator model with a nonlinear harvesting aspect was developed. Theoretical and numerical analyses were performed, and the dynamic behaviour of the system was found to be mathematically well-posed. Data on lion population density from the Serengeti ecosystem were used to fit the model using the maximum-likelihood method. The optimal harvesting policy was numerically determined using Pontryagin's maximum principle. Furthermore, the impact of prey refuge on the predator population was numerically evaluated. The results of this study highlight the importance of managing the lion population in the ecosystem, specifically in terms of harvesting criteria, to ensure that the threshold for wildebeest-lion coexistence is not exceeded. Based on the findings, this paper argues that the lion population should be given special attention in terms of managerial harvesting criteria so that the threshold for the wildebeest-lion coexistence in the ecosystem is not exceeded.

Keywords: Prey-predator System, Wildebeest-Lion Harvesting, Serengeti Ecosystem, Prey Refuge.

Introduction
Human harvesting of species has been a topic of considerable interest in population ecology and community dynamics, and numerous theoretical studies have been conducted to investigate its effects on various populations. Given that human harvesting is often considered a significant cause of mortality and population variability, it is crucial to present and consider these studies in detail, particularly for the exploited populations (Costa and Anjos 2021). As a result, harvesting procedures must be carefully monitored to avoid resource over-utilization.

Species harvesting practices among other areas are also found in the Serengeti ecosystem, which is one of the most important and famous cross-border conservation regions worldwide (Sinclair 1979). The ecosystem which is located in the northern part of Tanzania is well known for the annual migration of the wildebeests and a healthy stock of other resident wildlife particularly the big five namely; lion, African leopard, African elephant, black rhinoceros,

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and African buffalo (Boone et al. 2006, Sagamiko et al. 2015). Furthermore, harvesting of species in the Serengeti ecosystem is permitted only in game reserves such as Maswa, Kirejeshi, Gurunnet, Loliondo, and Ikorongo, whereas it is prohibited in the national park.

This study considers the optimal harvesting of wildebeests and lions in a prey-predator relationship. According to the theory, predator populations rely on prey species for survival, lowering prey population survival and fecundity rates (Sagamiko et al. 2015). The study also incorporates the concept of prey refuge because migratory wildebeests seek refuge in the western part of the ecosystem, where there is human habitation, tending to reduce their risks of predation. Furthermore, their gregarious behaviour reduces the likelihood of being detected and preyed upon by predators (Riipi et al. 2001, Sagamiko 2015).

A set of mathematical models of population dynamics has been provided to explore the relationships between prey and predator populations (Han et al. 2021), indicating that the mathematical modelling of exploited biological resources is an interesting field of research (Kar et al. 2010). Clark (1979, 1990), for example, interpreted the effects of harvesting on fisheries control, whereas Hoekstra and Van den Bergh (2005) reviewed a prey-predator model with predator conservation and harvesting and demonstrated a model of optimal harvesting solutions controlled by ecological and economic parameters. Ji and Wu (2010) investigated a prey-predator model with a constant rate of harvesting and constant prey refuge. Likewise, Krishna et al. (1998), Gupta and Chandra (2013) investigated a two-species prey-predator model with a Michalis-Menten harvesting function, with the main goal of maximizing economic benefits while maintaining ecological balance and preventing predator annihilation. Abdulghafour and Naji (2018) investigated the role of refuge in the prey-predator model and the effects of critical parameters on system dynamics.

Purohit and Chaudhuri (2004) developed a two-species bio-economic fishery model that employed nonlinear harvesting for both species similarly, Haque and Sarwardi (2018) investigated a two-species harvesting model for both species that used the Holling type-II functional response and included prey refuge. Hu and Cao (2017) considered a prey-predator model in which only the predators are harvested using Michaelis-Menten function. Raw et al. (2020) focused solely on the improvement of the nonlinear harvesting of fish species in the plankton fish model.

Biological resources in the prey-predator system are most likely to be harvested and sold for monetary gain. Many studies have shown that harvesting has a significant impact on population dynamics. Moreover, various types of harvesting functions were presented. Das et al. (2009) discussed a prey-predator fishery bioeconomic model with constant harvesting, while Chakraborty et al. (2012) investigated the global dynamics and bifurcation of the prey-predator relationships with continuous harvesting. In analysing the economic benefits of harvesting, three types of harvesting functions, namely constant harvesting, constant-effort harvesting, and nonlinear harvesting, have been extensively studied by many researchers, such as Tapasi et al. (2009), Srinivasu (2001), Gupta and Peeyush (2013). These types of harvesting are expressed mathematically as follows: constant harvesting $H(x,E) = c$, where $H(x,E)$ is harvesting function, x harvested species and c is constant harvesting while constant-effort harvesting $H(x,E) = qEx$ where the catch is proportional to the stock and effort applied, q which stands for coefficient of catchability, E is the effort applied to harvesting and nonlinear harvesting $H(x,E) = \dfrac{qEx}{l_1 E + l_2 x}$, where l_1 and l_2 are suitable positive constants that ensure the harvested species does not become extinct. In a comparison of the harvesting results, it was observed that the nonlinear harvesting function produces more realistic

outcomes when compared to other types of functions and it satisfied the condition

$$\lim_{E \to \infty} H(x, E) = \frac{qx}{l_1} \text{ and}$$

$$\lim_{x \to \infty} H(x, E) = \frac{qE}{l_2}.$$

However, the nonlinear function demonstrates saturation effects regarding both the level of harvesting effort and stock abundance. This has been observed in several studies, including those by Das et al. (2009) and Tapasi et al. (2009), Srinivasu (2001), Gupta et al. (2012), Gupta and Chandra (2013), Meng et al. (2017). Therefore, this study focuses on the nonlinear harvesting function when analysing the economic profits of harvesting.

Illegal hunting is a significant off-farm activity for rural communities living in the Serengeti ecosystem (Kideghesho 2010). This activity has long posed a major management challenge for conservation officials, as it results in the overharvesting of wildlife populations (Ndibalema and Songorwa 2008). The present study offers optimal harvesting criteria for wildebeests and lions found in the Serengeti ecosystem, which can assist conservation authorities in implementing necessary control measures to ensure that only the allowable numbers of these species are harvested. By doing so, the study findings will not only promote the conservation needs of the species considered in the study but also aid in mitigating the impact of illegal hunting on the ecosystem.

Materials and Methods
Mathematical model formulation

An ecological system of two species containing the wildebeest populations as prey (X) and the lion populations as the predator (Y) is formulated for the Serengeti ecosystem. The model includes a prey refuge with a functional response Holling Type II and a Michalis-Menten harvest function. The prey population is assumed to increase logistically in the absence of a predator. Meanwhile, in the model, the predators are expected to die exponentially in the absence of prey. It is assumed also that a fixed number of prey refugees have entered the preserved area to avoid being attacked by predators. A predator can, however, attack non-refuge prey $(1 - mX)$, where m is the proportion of the prey population not exposed to predation. The concept of harvesting was incorporated into the model to determine the biological impact. Mathematically, the model is described as follows:

$$\frac{dX}{dt} = rX\left[1 - \frac{X}{k}\right] - \frac{w_1(1-m)XY}{1+a(1-m)X} - \frac{c_1 E_1 X}{l_1 E_1 + l_2 X},$$

$$\frac{dY}{dt} = -\alpha Y + \frac{w_2(1-m)XY}{1+a(1-m)X} - \frac{c_2 E_2 Y}{l_3 E_2 + l_4 Y},$$

$$(1)$$

where $l_i, i = 1, 2, 3, 4$ are positive constants are arbitrarily chosen to ensure the harvested population does not extinct, E_1 and E_2 represent harvesting efforts for wildebeests and lions, respectively, r is the prey intrinsic growth rate, k is the prey carrying capacity, w_1 is the per capita predation rate, w_2 is the predator biomass gain, a is the predator half-saturation, c_1 and c_2 are the coefficients of harvesting for prey and predator, respectively, and α is the lion mortality rate. To reduce the complexity analysis of the model (1), the model is rescaled by assuming the following:

$$X = kx, \quad Y = \frac{ky}{w_1}, \quad b_1 = \frac{c_1 E_1}{kl_2}, \quad b_2 = \frac{l_1 E_1}{kl_2}, \quad b_3 = \frac{1}{ka(1-m)}, \quad b_4 = \frac{w_1}{a}, \quad b_5 = \frac{l_3 E_2 w_1}{kl_4},$$

$$b_6 = \frac{c_2 E_2 w_1}{kl_4}, \quad b_7 = \frac{w_2}{a}$$

Thus, the rescaled model (1) becomes;

$$\frac{dx}{dt} = \left[r(1-x) - \frac{b_4 y}{b_3 + x} - \frac{b_1}{b_2 + x} \right] x,$$

$$\frac{dy}{dt} = \left[-\alpha + \frac{b_7 y}{b_3 + x} - \frac{b_6}{b_5 + y} \right] y.$$

(2)

To ensure a comprehensive understanding of the animal population represented by model (2), it is imperative to conduct a theoretical evaluation of its biological behaviour and the probability of a positive solution occurring at time t. Consequently, the following lemma is imposed:

Lemma 1 *The solution of the model system (2) exists under the interval* $[0, \infty)$ *and* $x(t) > 0, \quad y(t) > 0$ *for the time* $t \geq 0$.

Proof: Given that $f(x, y)$ and $g(x, y)$ are continuous functions and satisfy the local Lipschitz $C^1(\mathbf{R}_+^2)$ then the solution of model system (2) exists and is unique in $(0, \varpi)$ such that $0 < \varpi \leq +\infty$.

The solution of the model system (2) for the x and y is obtained by using the Hale (1977) approach, which was also applied by Lakshmi and Sattwika (2017) and Lakshmi et al. (2020). Thus, the solution is given as:

$$x(t) = x(0) \exp \left[\int_0^t \left(r(1-x(s)) - \frac{b_4 y(s)}{b_3 + x(s)} - \frac{b_1}{b_2 + x(s)} \right) ds \right] \geq 0$$

and

$$y(t) = y(0) \exp \left[\int_0^t \left(-\alpha + \frac{b_7 y(s)}{b_3 + x(s)} - \frac{b_6}{b_5 + x(s)} \right) ds \right] \geq 0.$$

This brings the proof to an end.

Lemma 2 *The model system (2) has uniformly bounded solutions in* $\mathbf{R}_+^2$.

Proof: The function $\psi(t) = x(t) + \frac{\omega}{\lambda} y(t)$ is used to demonstrate the lemma, where ω and λ are any positive constant number.

Thus differentiating $\psi(t)$ with respect to *t gives*

$$\frac{d\psi}{dt} = \frac{dx}{dt} + \frac{\omega}{\lambda} \frac{dy}{dt}.$$

(3)

Substituting the equations of system (2) into (3) and simplifying gives

$$\frac{d\psi}{dt} = r(1-x)x - \frac{\omega}{\lambda} \alpha y.$$

Thus, for any constant number $\tau > 0$ the results give

$$\frac{d\psi}{dt} + \tau \psi = r(1-x)x - \frac{\omega}{\lambda} \alpha y + \tau \left(x + \frac{\omega}{\lambda} y \right).$$

Then

$$\psi(t) = [r + \tau - rx]x + \frac{\omega}{\lambda}[\tau - \alpha]y.$$

Using the concept of completing the square and simplifying $\psi(t)$, results into

$$\psi(t) \leq \frac{1}{4r}(r + \tau)^2 + \frac{\omega}{4\lambda}(\tau - \alpha)^2.$$

Assume any number say $\theta > 0$ then $\frac{d\psi}{dt} + \tau\psi \leq \theta$, this leads to

$$\psi(t) \leq e^{-\tau t}\psi(0) + \frac{\theta}{\tau}(1 - e^{-\tau t}) \leq \max\left[\psi(0), \frac{\theta}{\tau}\right].$$

From $x(0) > 0$, $y(0) > 0$; $\psi(0) = x(0) + \frac{\varpi}{\lambda}y(0)$, as $t \to \infty$ leads to

$\limsup \psi(t) \leq \frac{\theta}{\tau}$ which is unaffected by the initial conditions. Furthermore, it is observed

that, all of the system's solutions that begin in R_+^2 end up in the

region $\Omega = \left[(x, y) \in R_+^2 : \psi = \frac{\theta}{\tau} + Q\right]$, for some $Q > 0$, which concludes the proof.

Steady states of the model

Equilibrium points, in the context of ecology, refer to stable states or conditions within an ecosystem where the various ecological factors and populations reach a balance. These points represent a state of equilibrium where the rates of change for different ecological variables, such as population sizes, nutrient cycling, and energy flow, are relatively constant over time.

Equilibrium points are essential in ecology because they provide insights into the dynamics and stability of ecosystems.

To calculate the equilibrium points of the model (2), its right-hand side is equated to zero. That is, $\frac{dx}{dt} = 0$ and $\frac{dy}{dt} = 0$.

Model (2) has three equilibrium points;

(i) Trivial equilibrium points $P^0 = (0, 0)$ always exist

(ii) Boundary equilibrium point $P^1 = (x^*, 0)$ where

$$x^* = \frac{1}{2}\left(1 - b_2 + \sqrt{\frac{r(b_2 + 1)^2 - 4b_1}{r}}\right) \text{ and exists if}$$

$$1 + \sqrt{\frac{r(b_2 + 1)^2 - 4b_1}{r}} > b_2.$$

(iii) Co-existence equilibrium point $P^2 = (x^*, y^*)$ where

$$y^* = \frac{\left(\left(x^* + b_2\right)\left(1 - x^*\right)r - b_1\right)\left(b_3 + x^*\right)}{\left(b_2 + x^*\right)b_4}$$ and x^* is the positive solution of

$$A_1 x^4 + A_2 x^3 + A_3 x^2 + A_4 x + A_5 = 0 \tag{4}$$

where

$A_1 = r\left(b_4 w_2 - \alpha\right)$, $A_2 = r\left(b_4 w_2 - \alpha\right)\left(1 - b_2 - b_3\right)$,

$A_3 = rb_3\left(1 - b_2\right)\left(2\alpha - b_4 w_2\right) + b_4\left(b_1 w_2 - \alpha b_5 - b_6\right)r\alpha b_3^2 - rb_2\left(b_4 w_2 - \alpha\right) - \alpha b_1$,

$A_4 = r\alpha b_3^2\left(1 - b_2\right) + rb_2 b_3\left(2\alpha - b_4 w_2\right)b_3 b_4\left(b_1 w_2 - \alpha b_5\right) - b_3\left(2\alpha b_1 + b_4 b_6\right) + b_2 b_4\left(\alpha b_5 - b_6\right) + b_4 b_5 w_2$,

$A_5 = b_2 b_4^2 w_2 - b_2 b_3 b_4\left(\alpha b_5 + b_6\right) + \alpha b_3^2\left(rb_2 - b_1\right)$.

Therefore, $P^2 = \left(x^*, y^*\right)$ uniquely exists in xy plane provided the following conditions are satisfied:

(i) $r\left(x^* + b_2\right)\left(1 - x^*\right) > b_1$.

(ii) For positive roots of the polynomial (3), the coefficients A_i, $i = 1, \dots, 5$ must meet the following criteria:

$$\begin{cases}
A_i > 0; & i = 1, \dots, 5 \\
A_i < 0; & i = 1, \dots, 4 \quad \text{and} \quad A_5 > 0 \\
A_1 < 0 \quad \text{and} \quad A_i > 0; & i = 2, \dots, 5 \\
A_1 > 0, A_2 > 0, A_3 > 0, A_4 < 0, A_5 < 0 \\
A_i > 0; & i = 1, \dots 4, A_5 < 0 \\
A_1 > 0 \quad \text{and} \quad A_i < 0; & i = 2, 3, 4, 5.
\end{cases}$$

Stability analysis of the model

The model stability is assessed using the Jacobian matrix around the equilibrium points, where the model system (2) is expressed in the form of $f_{ij}\left(x, y\right)$, giving

$$J\left(x, y\right) = \begin{pmatrix} f_{11} & f_{12} \\ f_{21} & f_{22} \end{pmatrix}, \tag{5}$$

where

$$f_{11} = r\left(1 - 2x\right) - \frac{b_3 b_4 y}{\left(b_3 + x\right)^2} - \frac{b_1 b_2}{\left(b_2 + x\right)^2}, \quad f_{12} = \frac{-b_4 x}{\left(b_3 + x\right)},$$

$$f_{21} = \frac{w_2 b_3 b_4}{\left(b_3 + x\right)^2} \quad \text{and} \quad f_{22} = \frac{w_2 b_4 x}{b_3 + x} - \frac{b_5 b_6}{\left(b_5 + y\right)^2} - \alpha.$$

The behaviour of the system at $P^0 = \left(0, 0\right)$

The variational matrix at the trivial equilibrium point is

$$J\left(P^0\right) = \begin{pmatrix} r - \dfrac{b_1}{b_2} & 0 \\ 0 & -\alpha - \dfrac{b_6}{b_5} \end{pmatrix}, \tag{6}$$

With the eigenvalues of $\lambda_1 = \dfrac{rb_2 - b_1}{b_2}$ and $\lambda_2 = -\dfrac{\alpha b_5 + b_6}{b_5}$.

From the nature of the given eigenvalues, it is concluded that P^0 is locally asymptotically stable if $rb_2 < b_1$ otherwise, it's unstable under the condition $rb_2 > b_1$.

The behaviour of the system at $P^1 = \left(x^*, 0\right)$

The eigenvalues of the resultant Jacobian matrix for $P^1 = \left(x^*, 0\right)$ are given as

$$\lambda_1 = -\dfrac{2rx^{*3} + \left(4b_2 - 1\right)rx^{*2} + 2rb_2\left(b_2 + 1\right)x^* + b_2\left(rb_2 - b_1\right)}{x^{*2} + 2x^* b_2 + b_2^{\;2}},$$

$$\lambda_2 = -\dfrac{\left(\alpha b_5 + b_6\right)}{b_5}. \tag{7}$$

Thus, if the following conditions are met, the equilibrium point $P^1 = \left(x^*, 0\right)$ will be locally asymptotically stable;

(i) $b_2 > \dfrac{1}{4}$,

(ii) $rb_2 > b_1$, implies that $r > \dfrac{c_1}{l_1}$ whereby r is the prey intrinsic growth rate, c_1 is the prey harvesting coefficient, and l_1 is the positive coefficient for prey harvesting effort.

The behaviour of the system at $P^2 = \left(x^*, y^*\right)$

The variational matrix $P^2 = \left(x^*, y^*\right)$ for model (2) leads to the following quadratic equation;

$$C_1 \lambda^2 + C_2 \lambda + C_3 = 0. \tag{8}$$

where

$$C_1 = \left(2x^* - 1\right)r + \alpha - \dfrac{w_2 b_4 x^*}{b_3 + x^*} + \dfrac{b_3 b_4 y}{\left(b_3 + x^*\right)^2} + \dfrac{b_1 b_2}{\left(b_2 + x^*\right)^2} + \dfrac{b_5 b_6}{\left(b_5 + y^*\right)^2},$$

$$C_2 = \left(\left(\frac{b_4 y}{\left(b_3 + x^*\right)^2} + \frac{b_1}{\left(b_2 + x^*\right)^2} - r\right)x^* + r\left(1 - x^*\right) - \frac{b_4 y^*}{b_3 + x^*} - \frac{b_1}{b_2 + x^*}\right)\left(\frac{b_6 y^*}{\left(b_5 + y^*\right)^2} - \alpha + \frac{w_2 b_4 x^*}{b_3 + x^*} - \frac{b_6}{b_5 + y^*}\right),$$

$$C_3 = \frac{b_4^2 w_2 b_3 x^* y^*}{\left(b_3 + x^*\right)}.$$

Both roots of Equation (8) are in the open left half-plane, and the characteristic equation is stable if the following conditions are met:

    (i)   the coefficients $C_i > 0$ for $i = 1, 2, 3$.

    (ii) $C_1 C_3 > 0$ and

    (iii) $C_2^2 - 4 C_1 C_3 > 0$.

Global stability behaviour of the system

    The Lyapunov method is applied to analyse the global stability of the interior equilibrium point of the model (2).

Thus, the Lyapunov function is defined as;

$$V\left(x, y\right) = x - x^* ln\left(\frac{x}{x^*}\right) + y - y^* ln\left(\frac{y}{y^*}\right) \tag{9}$$

The time derivative of (9) is given by:

$$\frac{dV}{dt} = \frac{x - x^*}{x}\frac{dx}{dt} + \frac{y - y^*}{y}\frac{dy}{dt}. \tag{10}$$

Substituting (2) in (10) and simplifying, results to

$$\frac{dV}{dt} = -\left(x - x^*\right)^2\left(\frac{b_4\left(y - y^*\right)}{b_3 + \left(x - x^*\right)} + \frac{b_1}{b_2 + \left(x - x^*\right)} - r - r\left(x - x^*\right)\right)$$

$$-\left(y - y^*\right)^2\left(\alpha + \frac{b_6}{b_5 + \left(y - y^*\right)} - \frac{w_2 b_4\left(x - x^*\right)}{b_3 + \left(x - x^*\right)}\right).$$

Therefore, the Lyapunov function is globally asymptotically stable for $\frac{dV}{dt} < 0$ if the following conditions are satisfied:

    (a) $\dfrac{b_4\left(y - y^*\right)}{b_3 + \left(x - x^*\right)} + \dfrac{b_1}{b_2 + \left(x - x^*\right)} > r + r\left(x - x^*\right)$ and

    (b) $\alpha + \dfrac{b_6}{b_5 + \left(y - y^*\right)} > \dfrac{w_2 b_4\left(x - x^*\right)}{b_3 + \left(x - x^*\right)}.$

    This concludes the proof.

Bionomic equilibria

    The previous section outlined the biological equilibrium points for the model system (2). This section focuses on the economic equilibrium point, which is determined when the net income of the biomass trade is equal to the inclusive collection effort, as outlined by Krishna et al.

(1998) and Kar et al. (2006) referred to as bionomic equilibrium. In a broader perspective, a bionomic equilibrium refers to a state of balance or stability in the natural environment, specifically within ecosystems. It describes the intricate interactions and interdependencies among living organisms and their surrounding environment, including both biotic (living) and abiotic (non-living) components. Bionomic equilibria encompass the dynamic processes that regulate populations, energy flow, nutrient cycling, and other ecological factors. Assuming that q_1 and q_2 are the cost per unit effort for the wildebeests and the lions, respectively and the price per unit biomass of wildebeests is p_1 while the price per unit biomass of lion is p_2, it implies that

$$\Pi_1 = \left(\frac{p_1 c_1 x}{l_1 E_1 + k l_2 x} - q_1 \right) E_1 \text{ and } \Pi_2 = \left(\frac{p_2 c_2 y}{l_3 E_2 + k l_4 y} - q_2 \right) E_2 ,$$

where Π_1 and Π_2 are the economic rent or net revenue of wildebeests and lions, respectively. At any time, the total revenue is given by $\Pi = \Pi_1 + \Pi_2$.

Thus

$$\Pi = \left(\frac{p_1 c_1 x}{l_1 E_1 + k l_2 x} - q_1 \right) E_1 + \left(\frac{p_2 c_2 y}{l_3 E_2 + k l_4 y} - q_2 \right) E_2 . \tag{11}$$

The economic equilibrium of (2) and (11) with the impact of harvesting is evaluated as

$$r(1-x) - \frac{b_4 y}{b_3 + x} - \frac{c_1 E_1}{l_1 E_1 + k l_2 x} = 0 , \tag{12}$$

$$-\alpha y + \frac{b_7 x}{b_3 + x} - \frac{c_2 E_2}{l_3 E_2 + k l_4 y} = 0 , \tag{13}$$

$$\left(\frac{p_1 c_1 x}{l_1 E_1 + k l_2 x} - q_1 \right) E_1 + \left(\frac{p_2 c_2 y}{l_3 E_2 + k l_4 y} - q_2 \right) E_2 = 0 , \tag{14}$$

The following cases are examined to determine the bioeconomic equilibrium:

Case I: if $\dfrac{p_1 c_1 x}{l_1 E_1 + k l_2 x} < q_1$,

That is to say, the cost per unit effort for the wildebeests is higher than income; so, the harvest loss would then begin as $E_1 = 0$. Only the lion option is available for harvesting, that is;

$$\frac{p_2 c_2 y}{l_3 E_2 + k l_4 y} > q_2 .$$

From Equation (12) when $E_1 = 0$ we have

$$r(1-x) - \frac{b_4 y}{b_3 + x} = 0 . \tag{15}$$

Thus we have

$$x^2 - (1 - b_3) x - b_3 + \frac{b_4}{r} y = 0 . \tag{16}$$

Equation (16) gives the biological curve which meets the y-axis at $\left(0, y^*\right)$ where $y^* = \dfrac{rb_3}{b_4}$.

Similarly, the curve meets the x-axis at $\left(x^*, 0\right)$, where $x^* = 1$, and $x^* = -b_3$. However, the value of $x^* > 0$.

Therefore, the bionomic equilibrium $\left(x_\infty, y_\infty\right)$ is determined using Equation (16) together with the condition

$$\left(\frac{p_1 c_1 x}{l_1 E_1 + k l_2 x} - q_1\right) E_1 + \left(\frac{p_2 c_2 y}{l_3 E_2 + k l_4 y} - q_2\right) E_2 = 0. \tag{17}$$

Equation (17) is referred to as the zero profit line. From Equation (17), we have

$$y = \frac{x\left(E_1 c_1 p_1 - E_1 l_2 q_1 - E_2 l_2 q_2\right) k l_3 E_2 - l_3 E_2 \left(E_1^2 l_1 q_1 + E_1 E_2 l_1 q_2\right)}{x\left(k^2 E_2 l_2 l_4 q_2 + k^2 E_1 l_2 l_4 q_1 - k E_2 c_2 l_2 p_2 - k E_1 c_1 l_4 p_1\right) + k E_1 E_2 l_1 l_4 q_2 + k E_1^2 l_1 l_4 q_1 - E_1 E_2 c_2 l_1 p_2}. \tag{18}$$

Then Equation (16) becomes

$$\left(rx^2 - r\left(1 - b_3\right) x - r b_3\right)\left(b_8 x + b_9\right) - b_{10} x + b_{11} = 0. \tag{19}$$

where

$b_8 = k^2 E_2 l_2 l_4 q_2 + k^2 E_1 l_2 l_4 q_1 - k E_2 c_2 l_2 p_2 - k E_1 c_1 l_4 p_1$,

$b_9 = E_1^2 l_1 l_4 q_1 + E_1 E_2 l_1 l_4 q_2 - k E_1 E_2 c_2 l_1 p_2$,

$b_{10} = k b_4 l_3 E_2 \left(E_1 c_1 p_1 - E_1 l_2 q_1 - E_2 l_2 q_2\right)$, $b_{11} = k b_4 l_3 E_2 E_1 \left(E_1 l_1 q_1 + E_2 l_1 q_2\right)$.

Equation (19) can be simplified as

$$Ax^3 + Bx^2 + Cx + D = 0, \tag{20}$$

where

$A = r b_8, B = r b_9 - r b_8 \left(1 - b_3\right), C = r b_3 b_9 - r b_3 b_8 - r b_9 - b_4 l_3 E_2 \left(E_1 c_1 p_1 - E_1 l_2 q_1 - E_2 l_2 q_2\right)$,

$D = b_4 l_3 E_3 E_1 \left(E_1 l_1 q_1 + E_2 l_1 q_2\right) - r b_3 b_9$.

Therefore, for case I; the bio-economic equilibrium will exist if the following conditions are satisfied:

$$\begin{cases} A > 0,\ B > 0,\ C > 0,\ D > 0 \\ A > 0,\ B > 0,\ C > 0,\ \text{and } D < 0 \\ A > 0,\ B < 0,\ C < 0,\ D < 0 \\ A < 0,\ B < 0,\ C < 0,\ \text{and } D > 0 \end{cases} \tag{21}$$

Case II: if $\dfrac{p_2 c_2 y}{l_3 E_2 + k l_4 y} < q_2$,

That is to say, the cost per unit effort for the lions is higher than the income. So the harvest loss would then begin to close $E_2 = 0$. Only the wildebeest option is available for harvesting, that

implies $x_\infty = \dfrac{q_1 l_1 E_1}{p_1 c_1 - k l_2 q_1}$.

As $E_2 = 0$ from Equation (13) we have

$$-\alpha y\left(b_3 + x_\infty\right) + b_7 x_\infty = 0.$$

Thus,

$$y_\infty = \frac{b_7 q_1 l_1 E_1}{\alpha b_3\left(p_1 c_1 - k q_1 l_2\right) + \alpha q_1 l_1 E_1} \quad \text{and is positive if } \frac{p_1}{c_1} > \frac{k l_2}{c_1}.$$

Therefore, bionomic equilibrium exists for any of the above cases.

Optimal harvesting

Determining an optimal commercial wildlife harvest policy, this section presents a fundamental problem for identifying the optimal compromise between current and future harvests. This challenge has been highlighted in numerous studies, including those by Clark (1990), Jerry and Raissi (2001), Song and Chen (2001), Kar and Pahari (2007), Das et al. (2008), Chakraborty et al. (2011), and Belkhodja and Alli (2014).

As pointed out by Clark (1990), this type of resource conservation problem is extremely difficult, not only mathematically, but also politically and philosophically. Time plays a crucial role in temporal profit issues and is essential for the survival of a program or business. Although the social legitimacy of this concept is highly debatable, time reductions constitute a standard practice in corporate management, as presented by Clark (1979).

Mathematically, the biological equilibrium is evaluated by setting $\frac{dx}{dt} = 0, \frac{dy}{dt} = 0$ and solving the resultant model equations simultaneously whereby the economic equilibrium is obtained as the total revenue equals the total cost. The profit function for the exploited predator and prey populations is further expressed as;

$$\Pi = \left(\frac{p_1 c_1 x}{l_1 E_1 + k l_2 x} - q_1\right) E_1 + \left(\frac{p_2 c_2 y}{l_3 E_2 + k l_4 y} - q_2\right) E_2. \tag{22}$$

The main objective is to maximize the present value J of the net income function as

$$J = \int_0^\infty e^{-\delta t}\left[\left(\frac{p_1 c_1 x}{l_1 E_1 + k l_2 x} - q_1\right) E_1 + \left(\frac{p_2 c_2 y}{l_3 E_2 + k l_4 y} - q_2\right) E_2\right] dt. \tag{23}$$

The symbol δ states the discount rate of the net revenue. The goal is to maximize the present value J subject to Equation (2) by following Pontryagin's maximum principle (Grass et al. 2003). The variables E_1 and E_2 are subject to the condition $0 \le E_i \le E_{i\max}$ for $i = 1, 2$ which results from the following Hamiltonian function:

$$H = e^{-\delta t}\left[\left(\frac{p_1 c_1 x}{l_1 E_1 + k l_2 x} - q_1\right) E_1 + \left(\frac{p_2 c_2 y}{l_3 E_2 + k l_4 y} - q_2\right) E_2\right] +$$

$$\lambda_1\left[r(1-x) - \frac{b_4 y}{b_2 + x} - \frac{c_1 E_1}{l_1 E_1 + k l_2 x}\right] x + \lambda_2\left[-\alpha + \frac{b_7 x}{b_5 + y} - \frac{c_2 E_2}{l_3 E_2 + k l_4 y}\right] y, \tag{24}$$

where the variables λ_1, and λ_2 are the adjoints of the problem.

Thus, $\dfrac{\partial H}{\partial E_1} = 0$ and $\dfrac{\partial H}{\partial E_2} = 0$ are the necessary conditions for the control variables E_1 and E_2 to be optimal.

Thus,

$$\frac{\partial H}{\partial E_1} = -\frac{p_1 c_1 x l_1 E_1 e^{(-\delta t)}}{\left(kl_2 x + l_1 E_1\right)^2} + \left(\frac{p_1 c_1 x}{kl_2 x + l_1 E_1} - q_1\right)e^{(-\delta t)} - \frac{\lambda_1 c_1 x}{kl_2 x + l_1 E_1} + \frac{\lambda_1 c_1 E_1 x l_1}{\left(kl_2 x + l_1 E_1\right)^2}. \quad (25)$$

and

$$\frac{\partial H}{\partial E_2} = -\frac{p_2 c_2 x l_3 E_2 e^{(-\delta t)}}{\left(kl_4 x + l_3 E_2\right)^2} + \left(\frac{p_2 c_2 x}{kl_4 x + l_3 E_2} - q_2\right)e^{(-\delta t)} + \lambda_2 y\left(-\frac{c_2}{kyl_4 + l_3 E_2} + \frac{c_2 E_2 l_3}{\left(kyl_4 + l_3 E_2\right)^2}\right) \quad (26)$$

Thus

$$\lambda_1 = -\frac{e^{(-\delta t)}\left(k^2 x^2 l_2^2 q_1 - kx^2 c_1 l_2 p_1 + 2kxE_1 l_1 l_2 q_1 + E_1^2 l_1^2 q_1\right)}{c_1 x^2 kl_2}$$

and

$$\lambda_2 = -\frac{e^{(-\delta t)}\left(k^2 x^2 l_4^2 q_2 - kx^2 c_2 l_4 p_2 + 2kxE_2 l_3 l_4 q_2 + E_2^2 l_3^2 q_2\right)\left(kyl_4 + l_3 E_2\right)^2}{\left(kl_4 x + l_3 E_2\right)^2 y^2 c_2 kl_4}$$

From the Hamiltonian Equation (24), we also have

$$\frac{d\lambda_1}{\partial t} = -\frac{\partial H}{\partial x} = -\left(\frac{p_1 c_1}{kl_2 x + l_1 E_1} - \frac{p_1 c_1 x kl_2}{\left(kl_2 x + l_1 E_1\right)^2}\right)E_1 e^{(-\delta t)} + \lambda_1 rx - \lambda_1 r\left(1 - x\right)$$

$$+ \frac{\lambda_1 b_4 y}{b_2 + x} - \frac{\lambda_1 b_4 yx}{\left(b_2 + x\right)^2} + \frac{\lambda_1 c_1 E_1}{kl_2 x + l_1 E_1} - \frac{\lambda_1 c_1 E_1 x kl_2}{\left(kl_2 x + l_1 E_1\right)^2} - \frac{\lambda_2 yb_7}{b_5 + y} \quad (27)$$

$$\frac{d\lambda_2}{\partial t} = -\frac{\partial H}{\partial y} = -\left(\frac{p_2 c_2}{kyl_4 + E_2 l_3} - \frac{p_2 c_2 y kl_4}{\left(kyl_4 + E_2 l_3\right)^2}\right)E_2 e^{(-\delta t)} + \frac{\lambda_1 b_4 x}{b_2 + x} - $$

$$\lambda_2\left(-\alpha + \frac{b_7 x}{b_5 + y} - \frac{c_2 E_2}{kyl_4 + E_2 l_3}\right) - \lambda_2 y\left(-\frac{b_7 x}{\left(b_5 + y\right)^2} + \frac{c_2 E_2 kl_4}{\left(kyl_4 + E_2 l_3\right)^2}\right). \quad (28)$$

Hence, from the solution of λ_1 and λ_2 in connection with the adjoint equations (27) and (28), we obtain the solution of the optimal harvesting parameters E_1 and E_2 which optimizes the objective function. Due to the complexity of the model, the analysis will be carried out numerically.

Numerical Results and Discussions
Model fitting and parameter estimation

The model was first solved using literature parameters $r = 0.98$ (Mduma 1996), $w_1 = 0.674$ (Fryxell et al. 2007), $w_2 = 0.25$ (Schaller 1972), $\alpha = 0.01$ (Sinclair et al. 2008), $a = 0.21$ (Sinclair et al. 2008), while other parameters were chosen based on their ecological importance as $k = 300$, $m = 0.4$, $c_1 = 0.4$, $c_2 = 0.02$, $E_1 = 0.1$, $E_2 = 0.001$, $l_1 = 0.2$, $l_2 = 0.4$, $l_3 = 0.01$, and $l_4 = 0.001$. To validate the accuracy of the model, the solution with these parameter

values was compared to real data, as shown in Figure 1. The data used for the lion population were obtained from the Tanzania Wildlife Research Institute (TAWIRI) from 1965 to 2014, and the model was fitted through parameter estimation. The parameters were estimated using the maximum likelihood (ML) method, which aims to maximize the likelihood function. In this study, the goodness of fit was evaluated using the sum of squares of residuals (SSR), defined as

$$L(\theta) = \sum_{i=1}^{N} \left(f_i - f_i^{est} \right)^2 \qquad (29)$$

The optimal parameters that minimize $L(\theta)$ are obtained through equation (29), where $\{f_i\}_{i=1}^{N}$ is the set of real data and $\{f_i^{est}\}_{i=1}^{N}$ is the solution of the ODE at a given parameter value. With the $L(\theta)$, a built-in MATLAB optimizer called fminsearch was used to obtain the optimal parameters. Finally, the estimated parameters were generated, as shown in Table 1, and used to fit the model, as shown in Figure 2.
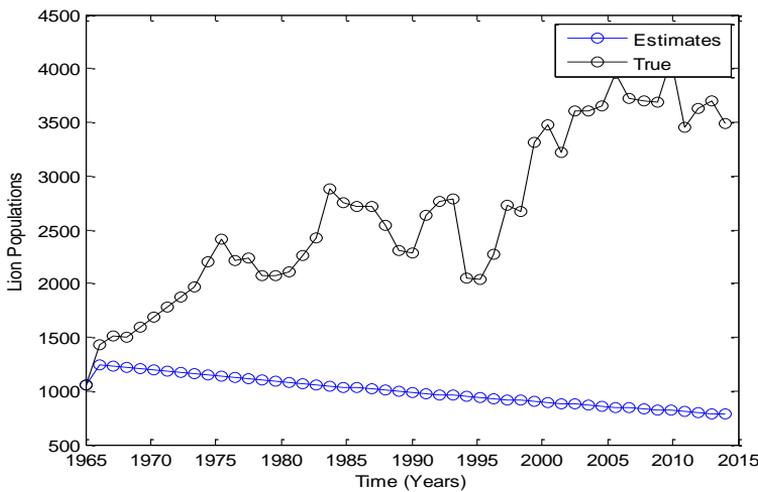

Figure 1: Comparison of model literature solutions with real data from 1964 to 2014 for the lion population in the Serengeti ecosystem. The model solution deviates completely from the real data.
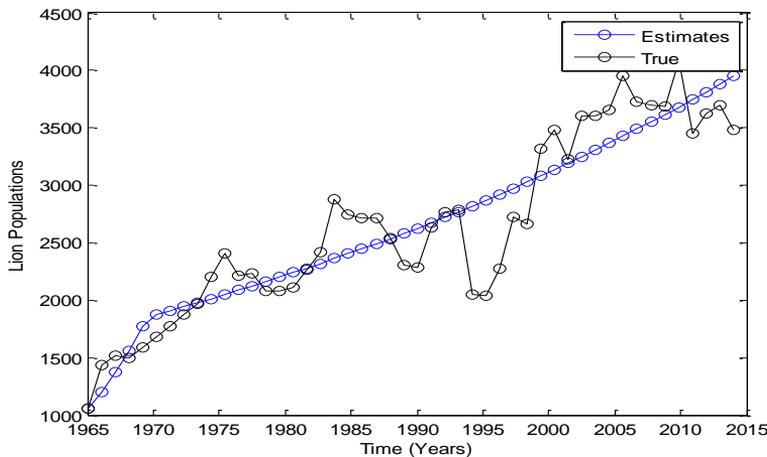

Figure 2: Model fitting using the maximum likelihood method for real data from 1964 to 2014 of the lion population in the Serengeti ecosystem. The model solution follows the trend of real data**.**

Table 1: Parameter value estimated using MLE for the data from 1964 to 2014

Parameters	Literature values	Estimated values
r	0.9	0.9989
k	300	302.4379
w_1	0.674	0.354755208
a	0.21	0.266733431
m	0.4	0.4875
c_1	0.4	0.129886245
E_1	0.1	0.221583676
l_2	0.4	0.274548758
l_1	0.2	0.2866
α	0.01	0.0006876
w_2	0.25	0.541796018
l_3	0.01	0.0076
E_2	0.001	0.0005098
l_4	0.001	0.000756646
c_2	0.02	0.00869071

Numerical analysis

The model was numerically fitted using data on the lion population in Tanzania gathered by the Tanzania Wildlife Research Institute (TAWIRI) from 1965 to 2014. The ecological impact of harvesting lions has become a subject of scrutiny in the Serengeti ecosystem. Although the activity is not straightforward, its effects are evaluated next.

Figure 3 shows the effect of harvesting efforts on the lion population. The first column shows the balance of the ecosystem when the harvesting effort for the wildebeest population is less than 50% and the harvesting effort for the lion population is 0.01%. However, increasing the harvesting effort for wildebeests to 80% while keeping the harvesting effort for lions at 0.01%, will help to keep the ecosystem balanced. The balance of the ecosystem in these two cases is due to the size of the wildebeest population in the Serengeti ecosystem, which outnumbers all other herbivores, out of the 29 large herbivorous species found in the ecosystem (Hopcraft 2010).

The second column indicates a decline in the predator population, which does not lead to extinction as the prey harvesting effort is increased from 0.01% to 80% while maintaining a predator harvesting effort of 50%. The lion population would become extinct when its harvesting effort rises to 80%, even if the wildebeest harvesting effort increases at the same rate as described in the third column. Moreover, harvesting prey and predator populations can be used as controls to determine a dynamic framework for investigating the optimal utilization of these resources. These results concur with those reported by Chakraborty et al. (2012). The increase or decrease in the populations may be attributed to either harvesting or refuge aspects; therefore, the effect of prey refuge on predators is presented next.
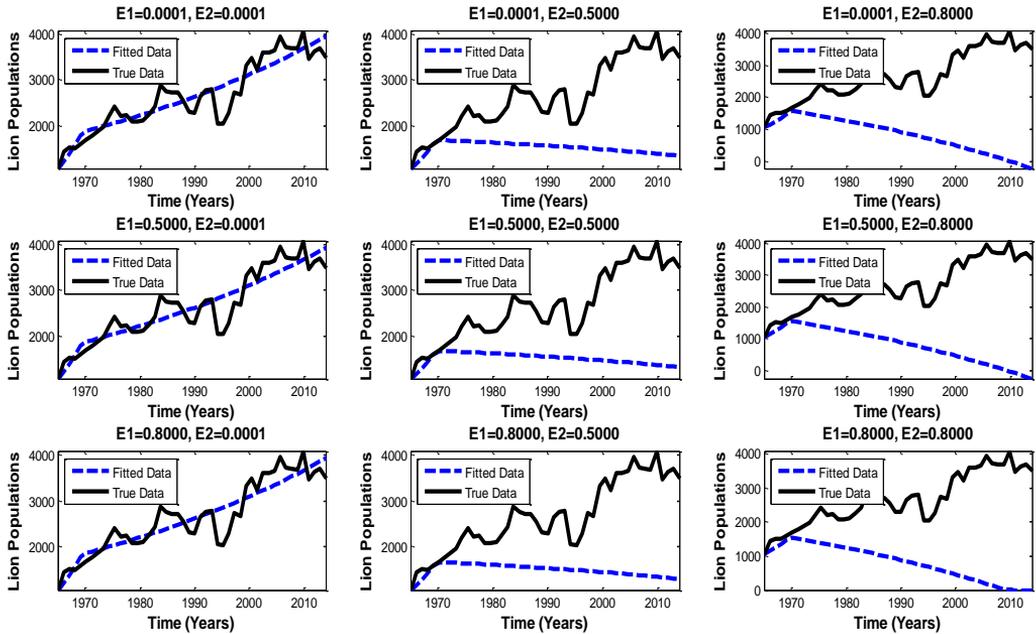
Figure 3: Effects of harvesting on wildebeest and lion populations in the Serengeti ecosystem. To keep the ecosystem balance, the harvesting effort for lions should be kept at the effort of 0.01%.
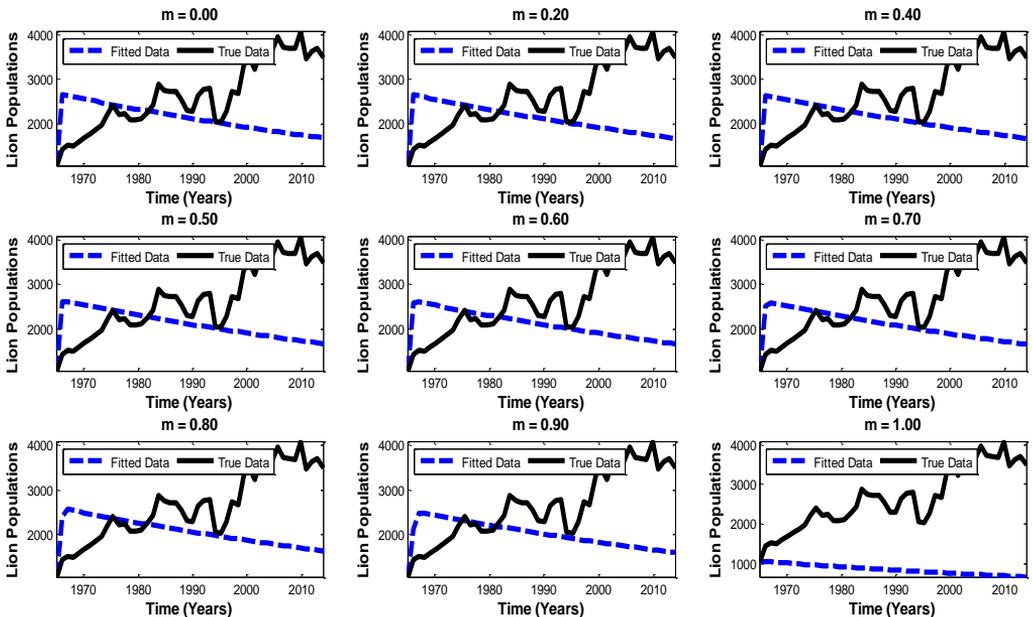

Figure 4: Effects of wildebeests population refuge from lion predation in Serengeti ecosystem. To maintain ecological balance, the rate of prey refuge should not exceed 90%.

Wildebeest migration is the world's largest animal migration. Every year, over two million animals (wildebeests, zebras, and gazelles) migrate clockwise across the Serengeti (Tanzania) and Masai Mara (Kenya) ecosystems (UNESCO 2020). Figure 4 depicts the impact of prey refuge, which shows that, as the rate of prey refuge increases, the density of predator populations decreases slightly, which is consistent with the findings of Kar (2005), Ma et al. (2013), and Tang (2014). As a result, an increase in the prey refuge rate by up to 0.90% is beneficial for the coexistence of prey and predator populations. From an ecological standpoint, if the rate of prey refuge decreases, the predator can capture more prey populations, increasing the predator population density. In a particular study, the predator population was thought to be dependent on the prey population; thus, the predator population density decreased at a rate above 0.90% of prey refuge. As the rate of prey refuge increases, predator populations tend to decline, as illustrated in Figure 4.

Conclusion

This study introduces a Holling Type II model of the wildebeest-lion prey-predator system in the Serengeti ecosystem. The model includes prey refuge and a Michalis-Menten harvest function that determines the optimal harvesting criteria for wildebeests and lions in the ecosystem. A theoretical analysis of the model shows that all solutions are bounded within a certain range, and the interior point is stable under the specified conditions. Furthermore, the bionic equilibrium was evaluated. To fit the lion population data from 1965 to 2014 in Serengeti National Park, the model was validated using the maximum likelihood method, and the results demonstrated a good fit.

This study examined the impact of harvesting on the wildebeest and lion populations in the Serengeti Ecosystem. The lion population was found to have a harvesting effort threshold of 0.01%, which means that the harvest should not exceed this limit to avoid harming the population. By increasing the wildebeest harvesting effort to 80%, while maintaining the lion-harvesting effort threshold, the ecosystem could remain balanced. The wildebeest population is the largest of the 29 large herbivorous species in the Serengeti ecosystem, making it a vital food source for predators. The effect of prey refuge on the predator population was also assessed, and it was discovered that a high rate of prey refuge tends to reduce the predator population, as it is a source of food.

Therefore, to maintain the sustainable coexistence of wildebeests and lions in the ecosystem, the harvesting threshold of lion populations must be carefully monitored. The findings of this study argue that the lion population should be given special attention in terms of managerial harvesting criteria so that the threshold for the wildebeest-lion coexistence in the ecosystem is not exceeded. A general recommendation for future work is to incorporate stochasticity into the model to capture more information about conditions with high uncertainty in natural systems.

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