

Modelling the Impacts of Grazing and Trampling on Grassland Ecosystems in the Semi-arid Environments

Sam Canpwoyi*

Department of Mathematics, Makerere University, Kampala, Uganda

Department of Mathematics and Biology, Gulu University, Uganda

Amos Ssematimba

Department of Mathematics and Biology, Gulu University, Uganda

Geoffrey M. Malinga

Department of Mathematics and Biology, Gulu University, Uganda

Betty K. Nannyonga

Department of Mathematics, Makerere University, Kampala, Uganda

Linus Carlsson

Department of Mathematics and Applied Mathematics, Malardalens University,

Sweden

*Corresponding Author: s.canpwoyi@gu.ac.ug

Abstract

In semi-arid regions, rainfall is limited and unreliable, and pastoralism is the only viable economic activity and a major source of livelihood. Small-holder farmers mainly practice it with households having livestock ranging from one to 10 head of cattle. Coupled with the low cattle off-take rates in this small-holder sector, there is an ever-growing livestock population, causing over-utilization of the grassland ecosystem. This over-utilization of the grasslands directly affects the structure and functions of the grassland ecosystem, leading to environmental degradation.

In this study, we modelled the effects of grazing and trampling on the grassland

ecosystem using the delay differential equations in which weaning is the time delay/lag. The control strategy used in the study is pulsed harvesting, which aims to reduce the livestock population.

Numerical simulations were applied on a 10-hectare piece of land with five variables: Juveniles, Adults, Gestation, Forage and Intrinsic growth rate.

Numerical results showed that without harvesting, there is over-utilization of forage resources, and thus pulsed harvesting was adapted as an off-take strategy to reduce the livestock population.

This harvesting enabled us to obtain a range of 45-79 animals for sustainable grazing and productivity of the enterprise. The first is realized by keeping 35 juveniles and 15 adult livestock and harvesting a cumulative biomass of 109730 kg, and the second is attained when 12 juveniles and 67 adults are maintained with a cumulative harvested biomass of 107916 kg. Furthermore, the study revealed a need to harvest more adult livestock in the first harvesting scenario and more juveniles in the second to address the pastoral community's ecological, economic and social needs. Besides, there is a need to allow the before animals are taken back to graze again.

We conclude that strategic harvesting coupled with close monitoring of the grassland ecosystem and fallowing of grazed areas should be practiced if we are to sustainably use the grazing resources to minimise overgrazing, hard trampling and, consequently, rangeland degradation.

Keywords: *Land degradation, Trampling, Gestation, Rangelands, Sustainability, Ecosystems*

1 Introduction

Rangelands are native terrestrial ecosystems comprising grasses, forbs, shrubs and dispersed trees (Uniyal et al., 2005) and are used for recreation, wildlife habitats and livestock production. These native rangelands comprise the world's largest land-use system and are also habitats for over 180 million people in developing countries (Seré et

al.,2020). The most suitable economic activity carried out in these areas is livestock farming. In semi-arid regions, there are unfavourable climatic conditions for crop production due to short growing seasons and periodic droughts (Davies & Hatfield, 2007).

This has caused a dramatic increase in the livestock population as it is the only source of livelihood (Egeru et al., 2014) as well as the undue communities' value-attachment to large livestock numbers for prestige and social status resulting in little or no off-takes (Cossins, 1985; Feldt, Neudert, Fust, & Schlecht, 2016). Because of this, we often realize an unproductive livestock system anchored on these self-propagating and communally-owned rangelands. This ever-growing livestock population, if not checked, can exceed the rangeland's carrying capacity with the net effect of causing a declining net primary biomass productivity (Dodd, 1994; Abril & Bucher, 1999; Addison et al., 2012; Hao & He, 2019)). Thus, overgrazing can arise due to too many animals repeatedly grazing on the same piece of land without giving it sufficient time for the grasses/vegetation to recover after a grazing episode. This is detrimental to the environment since it can cause land degradation, consequently affecting the livelihoods of the present and future generations (Hallanaro & Usher, 2005).

With this dilemma, the pastoral communities need to harvest their livestock to bring the number close to the rangeland's carrying capacity, as this will promote efficient use and enhance the provision of ecological goods and services (Havstad et al., 2007). Knowing the quantity of forage biomass available on land, we can plan how much livestock can be maintained for sustainable productivity. Thus, sustainable production and consumption of this natural capital are vital to sustainable development goals (SDGs), which the study seeks to find. This is in line with Goal 15 of "The UN 2030 Agenda on Sustainable Development, which aims at:

" protecting, restoring and promoting sustainable use of terrestrial ecosystems, proper and efficient management of forests, combating desertification, and halting and reversing land degradation and biodiversity loss".

In view of promoting sustainable use of grassland ecosystems, we considered discrete harvesting for juvenile and adult livestock taking place at two different periods of the year, i.e. March-April and October-December. The former is meant to meet breeding purposes, and the latter is for meeting the high demands for animal products during the festive seasons and other social needs/obligations.

In this study, we also considered trampling, the hoof action of grazing animals on the grasses. The trampling effect is dependent on the stride frequency, foraging time per day, and the number of livestock feeding on the rangelands (Hobbs & Searle, 2005; Cumming & Cumming, 2003). It reduces plant cover, promotes run-off and erosion, and facilitates soil compaction

which impedes grass/vegetative regrowth in the ensuing wet/growing season (Dunne et al., 2011; Mwendera & Saleem, 1997).

Understanding the mechanisms of livestock grazing on the dynamics of arid rangelands is therefore critical in monitoring, maintaining productivity and enhancing the ecosystem's goods and services (Brown et al., 2007). The starting point is to regulate the ever-growing livestock population, seeking a stocking level for the livestock industry with long-term and persistent utilization of the grassland ecosystems (forage availability).

With this stocking level, we can maintain and improve productivity while conserving species biodiversity and composition (Gómez-Baggethun et al., 2010) as well as enhancing the socio-economic well-being of the pastoral communities (McPeak et al., 2011; Kariuki et al., 2018; Wilson & Howarth, 2002; Alexander et al., 2016; Costanza, 2020).

Grazing pressure has historically been difficult to quantify due to variable plant responses to grazing and movements within pastures/grasslands, except for, (Kawamura et al., 2005), who used Global Positioning System (GPS), Geographical Information Systems (GIS) and remote sensing data for measuring the impact of hoof-action on plant biomass. This makes the study very expensive and time-consuming.

Therefore, this study aimed to develop mathematical models that rangeland managers can use to determine the optimal number and composition of livestock that promote sustainable livestock grazing systems in Uganda's arid and semi-arid regions.

2 Materials and Methods

2.1 Study area

Karamoja Sub-region is located in northeastern Uganda, encompassing 28,000 km² between 1° and 4° North and 33° - 35° East. The Sub-region comprises nine districts: Abim, Amudat, Kaabong, Karenga, Kotido, Nabilatuk, Nakapiripirit, Napak and Moroto. Karamoja is classified as one of the world's poorest areas, with high rates of malnutrition and sparsely populated with 1.3 million people, and 82% living in absolute poverty (UBOS,2013).

The major economic activity in this semi-arid zone is Pastoralism, and their livelihoods revolve around livestock production with limited crop cultivation in years of adequate rainfall (Kameri-Mbote, 2013). Average annual rainfall is less than 300–500 mm, and the soils are predominantly sandy, having low fertility and water-holding capacity (Filipová & Johanišova, 2017). These areas are usually overgrazed, and shortage of pasture causes nomadic movements in search of pastures and water for the animals during the prolonged dry season (September to April), sometimes causing social conflicts (Ocan & can, 1994; Kagan et al., 2009). With a broad range of climate variability, the region experiences both dry events (drought) and wet events (flooding) occurring frequently. Also, the high environmental variability (vegetation, soils and

terrain) across the region and rainfall significantly impacts livestock production and crop yields, making predictions impossible.

Several studies have employed ordinary and partial differential equations (ODEs & PDEs) to model physical, biological and ecological systems because of their long history (Roos, 1997; Persson et al., 1998; De Roos & Persson, 2001; Cao et al., 2008; Barraquand, 2014). Such models are generally approximations of real systems that can be solved analytically or numerically with high precision (Shampine & Thompson, 2009). Recent works in these fields have shown that some of these phenomena have time delays in the differential equations (e.g see (Kuang, 1993; S Antman, 2009; Gopalsamy, 2013).

Models incorporating history data generally occur in almost all natural and man-made phenomena in biological and control systems (Mahmoud & Ismail, 2005)). For instance, (Bodnar & Forsys, 2000, 2007) applied time delays to describe immune reactions, biochemical reactions and tumor growth. Our study considered the weaning period as the delay, where the calves and the dams do not feed on the away forage but rather on milk and a reserved forage near the homestead. This is a relief for using the away forage since the dams and calves are taken home. The forage-livestock interaction can be modelled using the delay differential equations (DDE) since we are leaving out the dynamics of dams and the calves and, therefore, reducing the number of variables and parameters in the model.

A typical DDE model with constant time delay (lag) τ takes the form:

$$\begin{cases} \dot{y}(t) = G_1(y(t)) + G_2(y(t - \tau)), & \text{for } t \in [0, T], \\ y(t) = \phi(t), & \text{for } t \in [-\tau, 0]. \end{cases} \quad (1)$$

where $t \in [0; T]$, $y: \mathbb{R} \rightarrow \mathbb{R}^n$; $G_1; G_2: \mathbb{R}^n \rightarrow \mathbb{R}^n$ and $\phi: [-\tau; 0] \rightarrow \mathbb{R}^n$ are continuous functions with G_2 having a time-lag $\tau > 0$. The history function, $\phi(t)$, describes the system's past state, which is assumed to be continuous.

2.2 Formulating the Dynamics of the Home Cohort

Once a cow gives birth to a calf, both are taken and kept at home for safe custody as the dam feeds the newborn on milk and the dam grazing on the home forage. This continues until the calf reaches a stage when it can feed on forage and other feeds. At this stage, the calf can be induced to stop suckling and, later, weaned and taken back to the field together with the dam. It should be noted that the calves and the dams have not been feeding on the away-forage over this weaning period τ_H .

Consider a mature livestock of size x_m that gives birth to a calf of size x_b at a reproduction rate of $\beta(t)$. According to de Roos (2008), which was applied to the Daphnia population (marine creatures), it is assumed that all consumed after maturity is used for reproduction. This reproduction is called the rate of biomass production and is given by:

$$\beta(t) = v_A(F) \frac{x_m}{x_b} = \begin{cases} (\epsilon_A q I_{\max A} \frac{F(t)}{F(t)+F_h} - E_A) \frac{x_m}{x_b} & \text{if } F(t) > \frac{F_h}{\epsilon_A \frac{I_{\max A}}{E_A} - 1} \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

with $q = 1$, and the rest of the parameters are defined in Table 1.

In our model, we adapted this as the rate of biomass production:

$$\beta_r(t) = \begin{cases} (\epsilon_A I_{\max A} \frac{F(t)}{F(t)+F_h} - E_A) \frac{x_m}{x_b} & \text{if } F(t) > \frac{F_h}{\epsilon_A \frac{I_{\max A}}{E_A} - 1} \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

Therefore, $\beta_r(t)$ in Eq (3) can be related to the total biomass of all adult livestock $A(t)$ producing a calf of size x_b ,

$$\beta_r(t) A(t) = x_b, \quad (4)$$

From which we have an equivalent expression:

$$\frac{1}{x_b} \beta_r(t) A(t) = 1. \quad (5)$$

This measures the rate of change in the number of newborn calves $N'_G(t)$ per day from the total adult population. The left-hand side of Equation (5) represents the rate of change in the number of adult livestock moving from adult to gestation stage (Figure 1) and thus we have

$$N'_G(t) = \frac{1}{x_b} \beta_r(t) A(t). \quad (6)$$

However, this rate of change in the number of newborn calves depends entirely on the number of adults that have survived the gestation period τ_G at time t . With this gestation period, the rate of change of the number of newborn calves that are moved home will be given by

$$N'_G(t - \tau_G) = \frac{1}{x_b} \beta_r(t - \tau_G) G(t - \tau_G) \exp(-\mu_C \tau_G) \quad (7)$$

where μ_C is the mortality rate of calves and $G(t - \tau_G)$ is the adult population that has survived gestation period.

Multiplying the right-hand side of Equation (7) by the sum of the sizes of the newborn and the dam gives the total biomass $N'_{Total}(t)$ moved home and is given by

$$\begin{aligned} |N'_{Total}(t) &= \frac{(x_b + x_m)}{x_b} \beta_r(t - \tau_G) G(t - \tau_G) \exp(-\mu_C \tau_G) \\ &= \left(1 + \frac{x_m}{x_b}\right) \beta_r(t - \tau_G) G(t - \tau_G) \exp(-\mu_C \tau_G) \end{aligned}$$

for $G(t - \tau_G) > 0$ and 0 if $G(t - \tau_G) = 0$.

Next, we present two critical stages used in the model:

At the time of giving birth

Here, the calf and the dam are separated and are moved home with biomass rates, denoted by $C'_H(t)$ and $D'_H(t)$, respectively. Thus, the associated differential equations are:

$$C'_H(t) = \beta_r(t - \tau_G)G(t - \tau_G) \quad (8)$$

and

$$D'_H(t) = \frac{x_m}{x_b} \beta_r(t - \tau_G)G(t - \tau_G). \quad (9)$$

At the time of weaning

After this weaning period, τ_H the dams are moved back to the field at the rate deduced from Equation (6), given by

$$N'_G(t - \tau_G - \tau_H) = \frac{1}{x_b} \beta_r(t - \tau_G - \tau_H)A(t - \tau_G - \tau_H) \quad (10)$$

However, Equation (10) depends on the probability of surviving dams during the gestation period τ_G , the rate of change of the number of dams, $D'_F(t)$, taken back to the field is given by:

$$D'_F(t) = x_m N'_G(t - \tau_G - \tau_H) \exp(-\mu_D \tau_G) \exp(-\mu_D \tau_H) \quad (11)$$

where μ_D is the mortality rate of the dams.

Substituting Equation (10) in Equation (11) and letting $\tau_{GH} = \tau_G + \tau_H$, we have

$$D'_F(t) = \frac{x_m}{x_b} \beta_r(t - \tau_{GH})A(t - \tau_{GH}) \exp(-\mu_D \tau_G) \exp(-\mu_D \tau_H) \quad (12)$$

Similarly, the rate of change of the number of newborn calves moved to the field after surviving the both the gestation and weaning periods becomes

$$J'_F(t) = \frac{x_w}{x_b} \beta_r(t - \tau_{GH})A(t - \tau_{GH}) \exp(-\mu_D \tau_G) \exp(-\mu_C \tau_H) \quad (13)$$

Compartmental Diagram for a Grazing System

The compartmental diagram consists of four variables: Forage, Juveniles Adults and the Dams livestock populations interacting with away and home forage/environment. The lower rectangle represents the home cohort consisting of the calves and the dams

feeding on the home forage for a weaning period τ_H . After this period, the calves and the dams are taken back to the field to graze with the away livestock population. The returned dams and juveniles will continue to graze and interact freely with the possibility of entering the gestation period, and the process continues with the associated Equations (15-19) and Figure 1.

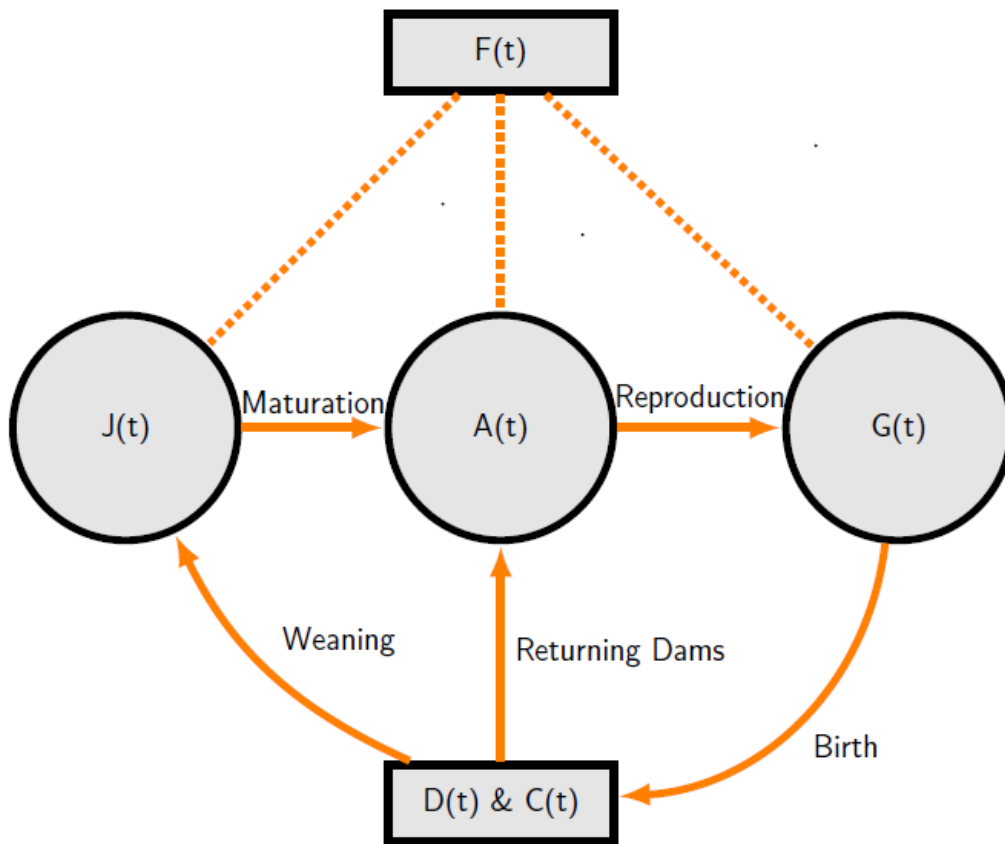


Figure 1: *The Compartmental Diagram for the grazing livestock system.*

2.3 Modelling Livestock Trampling

Trampling (soil compaction by grazing animals) is caused by intensive and continuous feeding on the same area of land for a long period of time. Trampling can become more pronounced when stocking rates are high for small grazing land, causing mechanical injury or loss of vegetation/standing crops/grasses and surface soil compaction (Abdel-

Magid et al., 1987). Therefore, overgrazing and trampling can affect the water infiltration rate (Evans, 1998), impacting the intrinsic growth rate of forage.

For simplicity's sake, we assume that the intrinsic growth rate follows a semi-chemostat growth model (De Roos et al., 2008), which varies directly with the stocking rate (livestock population or biomass).

Thus, the dynamic of the intrinsic growth rate is given by:

$$R'(t) = \phi(t)(R_{max} - R(t)) - \theta (J(t) + A(t) + G(t)) \quad (14)$$

where $\phi(t)$ is the forage recovery potential based on a scale of 5 to 10 rotational days between grazing episodes (Woodward, 2018, R_{max} is the forage intrinsic growth rate in a semi-arid zone, θ is the depletion constant for trampling, and $J(t)$, $A(t)$, $G(t)$ are the biomasses of juveniles, adults and the dams. The recovery potential was estimated because animals are taken back to the same area after a period of at least 5 - 10 days from a previous grazing episode. The default values of 9×10^{-6} and 9×10^{-7} were considered for hard trampling and soft trampling respectively.

Putting Equations (12), (13) and (14) together, we obtain a set of differential equations and DDEs for the grazing system:

$$J'(t) = \frac{x_w}{x_b} \beta_r(t - \tau_{GH}) A(t - \tau_{GH}) \exp(-\mu_D \tau_G) \exp(-\mu_C \tau_H) + (v_J - \gamma(v_J) - \mu_J) J(t) \quad (15)$$

$$A'(t) = \gamma(v_J) J(t) + \frac{x_m}{x_b} \beta_r(t - \tau_{GH}) A(t - \tau_{GH}) \exp(-\mu_D \tau_G) \exp(-\mu_D \tau_H) + \left(v_A - \beta_r(t) - \frac{x_m}{x_b} \beta_r(t) - \mu_A \right) A(t) \quad (16)$$

$$G'(t) = \frac{x_m}{x_b} \beta_r(t) A(t) - \left(1 + \frac{x_m}{x_b} \right) \beta_r(t - \tau_G) G(t - \tau_G) - \mu_G G(t) \quad (17)$$

$$F'(t) = R(t) F(t) \left(1 - \frac{F(t)}{F_{max}} \right) - \frac{F(t)}{F(t) + F_h} (I_{max_J} J(t) + I_{max_A} A(t) + I_{max_G} G(t)) \quad (18)$$

$$R'(t) = \phi(t) (R_{max} - R(t)) - \theta (J(t) + A(t) + G(t)) \quad (19)$$

2.4 Description of the DDE Model

Equation (15) describes the dynamics of the large juveniles, with the first term being the rate of biomass production recruited from the young juveniles in time lag τ_H , the rate of biomass production generated by feeding large juveniles, maturation of the large juveniles into adult livestock together with their mortality and harvesting rates. Whereas Equation (16) is the dynamics of the biomass of adult livestock with recruitment term from the large juveniles, their feeding rate on forage, and the term $\beta_r A(t)$ is the biomass of the newborn calves that are moved home after birth, together with their mortality rates. Equation (17) describes the dynamics of the returning dams as they feed, join the gestation period, reproduce to join the home cohort and die naturally. The fourth Equation (18) represents the dynamics of the forage biomass, which follows a logistic growth model and is consumed (following Holling's type II functional response) by the large juveniles, adult livestock and returning dams. Finally, Equation (19) describes the intrinsic growth rate dynamics which is affected presumably by livestock population (biomasses).

2.5 Seasonal/Pulsed Harvesting

In this study, we carried out a pulsed harvesting strategy at two different times of the year: one at breeding season for the juveniles (size x_w) and the other during festive season for the adult livestock (size x_m). Thus, these harvesting scenarios can be derived as follow:

Let $t_J(n) = 120 + (n - 1) * 365$ denotes the times for juvenile harvesting and n the number of such harvest occurring. Let $H_J(n)$ be the harvested juvenile biomass and thus, we get the recurrence system:

$$\begin{cases} H_J(0) = 0, \\ H_J(n) = H_J(n - 1) + \max(0, J(t_J(n)_-) - C_J), \quad n = 1, 2, 3, \dots \\ J(t_J(n)_+) = J(t_J(n)_-) - \max(0, J(t_J(n)_-) - C_J) \end{cases}$$

where C_J is the threshold biomass for the juveniles and

$$t_J(n)_- = \lim_{h \nearrow 0} t_J(n) + h$$

Similarly, the recursive system for adult livestock harvesting, with $t_A(n) = 280 + (n - 1) * 365$, is given by:

$$\begin{cases} H_A(0) = 0, \\ H_A(n) = H_A(n - 1) + \max(0, J(t_A(n)_-) - C_A), \quad n = 1, 2, 3, \dots \\ A(t_A(n)_+) = A(t_A(n)_-) - \max(0, A(t_A(n)_-) - C_A) \end{cases}$$

where C_A is the threshold biomass for the adult livestock.

Therefore, these harvesting strategies were applied for the juveniles and adult livestock in the production system over the planning horizon of 25 years.

Table 1: Summary of the parameter values used in the delay differential equations model with their sources from literature. (.)^{*} are parameter values applied to juveniles, adults and gestation respectively.

| Parameters | Description | Value/Units | Source |
|--------------|--------------------------|-------------------------|---|
| R_{max} | Intrinsic rate | 0.11 md ⁻¹ | (Mefti, Bouzerzour, Abdelguerfi, & Nouar, 2008) |
| F_{max} | Carrying capacity | 0.5 kgm ⁻² | (Huffaker & Cooper, 1995) |
| I_{maxJ}^* | Max. Ingestion rate | 5.5 kgDMd ⁻¹ | (Huffaker & Cooper, 1995) |
| I_{max}^* | Max. Ingestion rate | 6.5 kgDMd ⁻¹ | (Huffaker & Cooper, 1995) |
| F_h | Half saturation constant | 0.1 kgm ⁻² | (Huffaker & Cooper, 1995) |

| | | | |
|--------------|------------------------------------|---|--|
| * | Conversion efficiency | 0.65 | (Yodzis & Innes, 1992) |
| E^* | Maintenance Energy | $0.45 * I_{max}$ | (Susenbeth, Mayer, Koehler, & Neumann, 1998) |
| μ^* | Mortality rates | 0.05 (year)^{-1} | (Fasae, Sowande, & Adewumi, 2010) |
| x_b | Birth weight | 35 kg | (Manzi, Junga, Ebong, & Mosi, 2012) |
| x_w | Weaning weight | 150 kg | (Manzi et al., 2012) |
| x_m | Maturation weight | 350 kg | (Sawadogo, Tiveau, & Nygård, 2005) |
| τ_H | Weaning period | 300 d | (Lynch, McGee, & Earley, 2019) |
| τ_G | Gestation period | 270 d | (Voh Jr & Otchere, 1989) |
| θ | Trampling proportionality constant | 9×10^{-7} $/9 \times 10^{-6}$ | Test values |
| $\varphi(t)$ | Recovery potential | $\varphi \in [0.5-1.0]$ | (Woodward, 2018) |

3 Numerical Implementation

In order to test our model, we considered a 10-hectare piece of land on which the forage is growing at an intrinsic rate of 0.11 md^{-1} during a growing season of 90 days. We also assumed that the carrying capacity of this piece of land is 50000 kg of dry matter (DM)

per year with a half-saturation biomass level of 10000 kg of DM. Then we introduced 5 adult livestock and 10 juveniles feeding 6.5 and 5.5 kg of DM per day, respectively.

We then simulated the model for a period of 25 years with additional parameters given in Table 1.

3.1 Numerical Results

The model was first simulated without harvesting to observe the effects of over-grazing and trampling on the rangeland. It was observed that juvenile and adult biomasses first increased to 7249 kg and 2836 kg, respectively, as the livestock graze on the available forage biomass and consequently reduced to 4000 and 547 kg, see Figure 2.

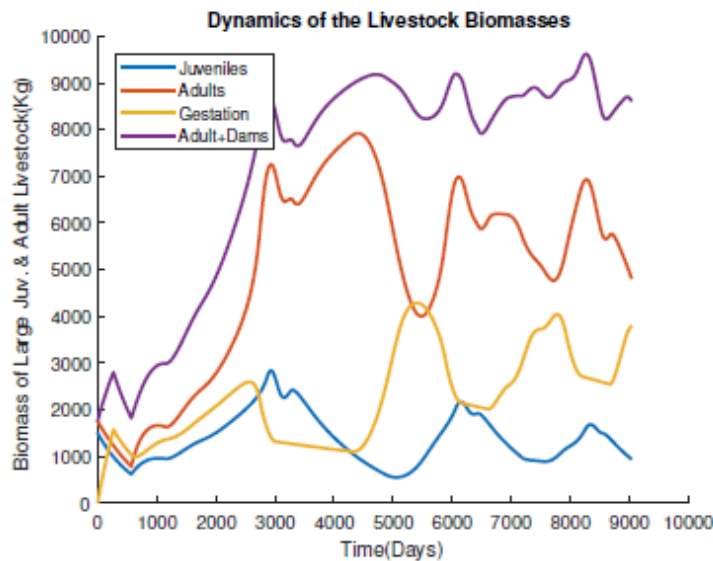


Figure 2: *The dynamics of the livestock population affected by over-grazing and trampling on the grassland ecosystem under no-harvesting scenario.*

The biomasses of the adults and juveniles first increased from 1750 kg and 1500 kg to 7249 kg and 2836 kg in 2948 days, respectively and later dropped to the minimum of 4018 and 548 in 5468 and 5079 days. This shows an unstable solution with drastic fluctuations in livestock biomasses due to starvation and is seen as over-utilization/over-grazing of the forage biomass, see Figure 3. Therefore, for sustainable utilisation of this resource, the number of livestock grazing on this land must be

checked using pulsed harvesting to avoid over-grazing and hard trampling on the forage biomass. This reduction in biomasses (body weight) is due to starvation and mortality caused by lack of food resource as the livestock population increases beyond the environmental carrying capacity. The ever-growing livestock population has caused the forage biomass to reduce to 16550 kg DM from 50000 kg DM due to over-grazing and hard trampling in a period of 3046 days. This is a situation where the livestock would starve, causing their biomasses to reduce and eventually die of starvation.

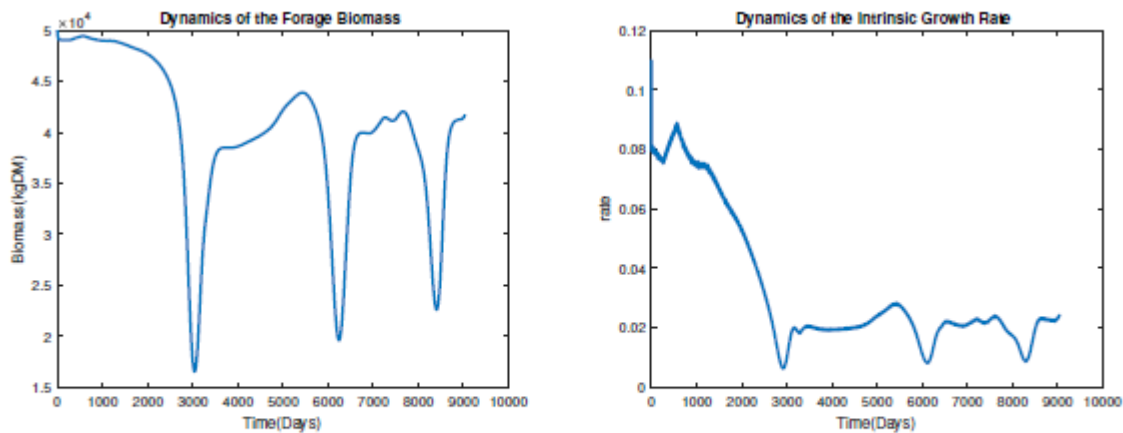


Figure 3: *The effects of over-grazing and hard trampling on the forage biomass under no-harvesting scenario.*

The dynamics of the intrinsic rate shows the value reduced from 0.11 md^{-1} to the least value of 0.000168 md^{-1} in 3046 days with the least value of forage biomass of 16550 kg DM, see Figure 3. This is a bad situation since the forage resource will fail to recover from grazing episodes, thus leading to environmental degradation. This condition of over-grazing/over-utilization of the forage resource is what the study seeks to control.

In the subsequent simulations, we considered the cases of: *no trampling, harvesting and no starvation, and trampling, harvesting and starvation.*

3.1.1 No trampling, Harvesting, No starvation

In this case, we ran the simulation without Equation (19) where no starvation is factored in the mortality rate. This is done by practising rotational grazing within the 10-hectare piece of land.

To implement the model, we introduced 5 adults and 10 juveniles to study the dynamics of the livestock biomasses as they grow to reach the threshold of 15 adults and 35 juveniles respectively, see Figure 4.

As the biomasses of livestock increase, any mass in excess of these thresholds, will be harvested, as depicted by the fluctuating movements in their dynamics. The first adult harvesting of 615 kg took place on day 1375 when the biomass was 5791 kg while that for the juveniles of 485 kg happened at biomass 4957 kg on day 2290 thereby reducing them to their threshold biomasses of 5250 kg and 4526 kg respectively. Meanwhile, the dynamics of the animals on gestation fluctuate due to their movements to and from the field, taking an average of about 242 days.

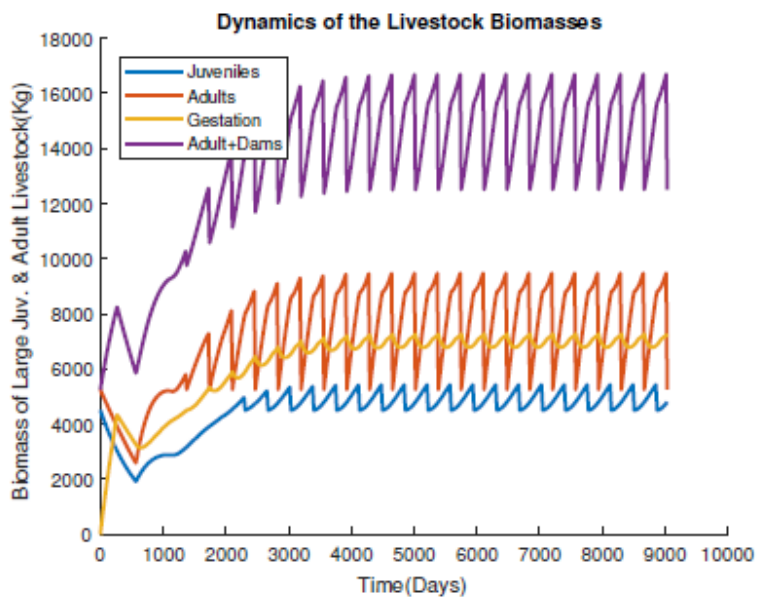


Figure 4: *The dynamics of the livestock population subjected to harvesting over and above the threshold biomasses of 5250 and 4526 kg respectively.*

We also observed that, as the adult livestock graze and interact, they join the gestation period after mating, and their biomass reduces while those in gestation will increase from zero to 4210 kg in 300 days while juvenile biomass drops as some will join the adult stage. This period of about 610 days combines both the gestation and weaning

periods. After this, the juvenile biomass will increase from 1918 kg to 2856 kg due to the weaning of calves, which are taken to the field, causing an increase of 938 kg on day 978. This process continues as livestock on gestation are moved back and forth between field and home. At the same time, the adults and juveniles are being harvested by maintaining the thresholds of 15 adults and 35 juveniles.

For the forage dynamics, its biomass was first reduced due to defoliation by the initial livestock population in the first 242 days and later rose to 48850 kg DM because the dams and calves were moved home. Later on, when these animals are taken back to the field, the forage biomass continues to reduce until it stabilises asymptotically at 46050 kg DM with the application of pulsed harvesting of the livestock population (Figure 5).

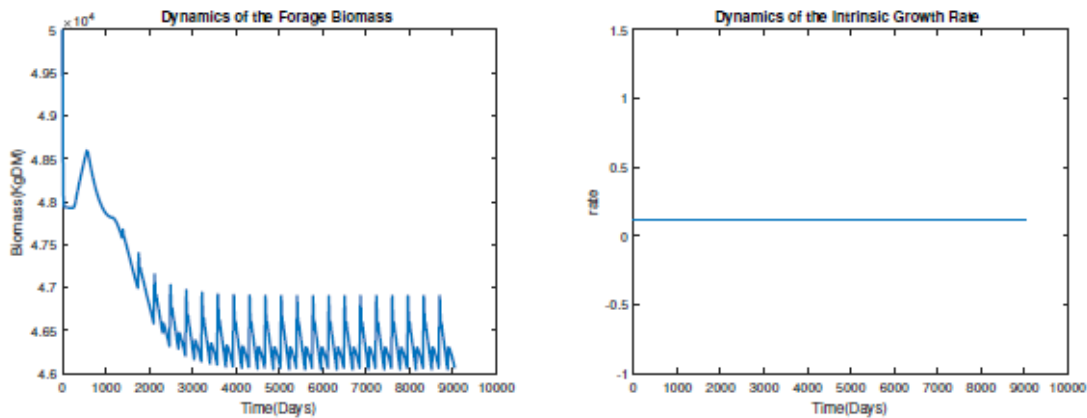


Figure 5: *The dynamics of forage and its intrinsic growth rate which remained constant at R_{max} .*

The graph below (Figure 6) shows that the first adult harvesting of 616 kg occurred on day 1375, and the second one of 619 kg occurred on day 1580, which later increased and became asymptotically stable at mean biomass of 4339 kg.

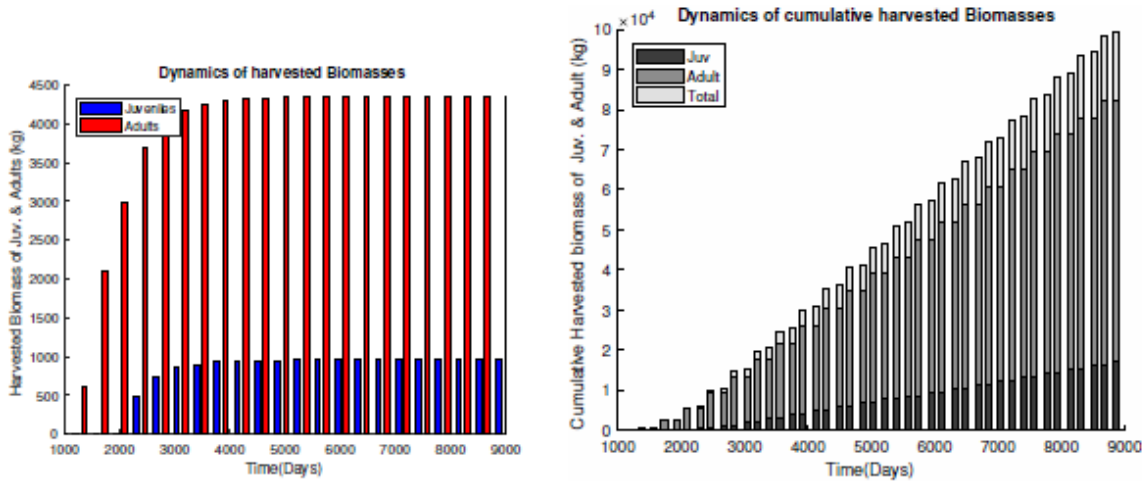


Figure 6: *Harvested biomasses for juveniles and adult livestock.*

Meanwhile, the first juvenile harvesting of 485 kg took place on day 2310, and the second one of 723 kg occurred on day 2675 and later increased and stabilised asymptotically at an average value of 950 kg. The cumulative harvested biomasses for the adult and juvenile livestock was 99570 kg, with respective biomasses of 82400 kg and 17170 kg on day 8880 to the right (Figure 6).

In the case of no trampling, the intrinsic growth rate of forage remained constant at $R_{max} = 0.11 \text{ md}^{-1}$. This means the reduction in the forage biomass from 50000 kg to 47930 kg is caused by the 50 livestock grazing on the land and later rose to about 48590 kg due to the movement of the dams home after reproduction (about 300 days). After 565 days, the juvenile biomass will increase when the dams and the calves are taken back to the field, and the forage biomass continues to reduce and eventually stabilizing asymptotically at a mean value of about 46050 kg DM (Figures 4 and 5).

To determine whether the system reaches a steady state, we ran the simulation for 100 years.

The results show asymptotically cyclic solutions for both the livestock and forage biomasses.

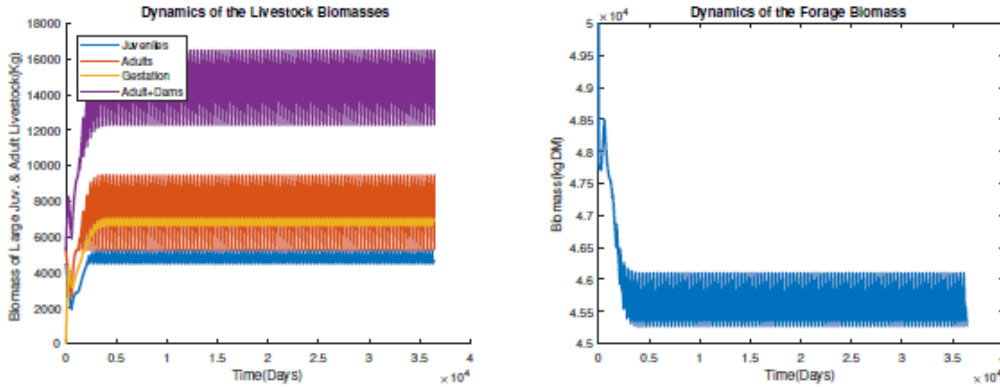


Figure 7: *The dynamics of the livestock and forage over 100-year planning horizon showing that the solutions becomes cyclically and asymptotically stable.*

3.1.2 Trampling, Harvesting, Starvation

Now, we bring in the trampling scenario of Equation (19) in the simulations with some form of starvation. We observed that this affects the intrinsic growth rate of forage, which subsequently directly impacts the quality and quantity of forage biomass available for animal consumption (Figure 8). The intrinsic growth rate dropped from 0.11 md^{-1} to 0.09866 md^{-1} in 163 days and rose again to 0.1041 md^{-1} in 565 days and later dropped and stabilizes at 0.09009 md^{-1} . This has the net effect on the forage dynamics causing it to drop from 50000 kg following the same pattern as above but with the least value at 45270 kg DM, see Figure 8.

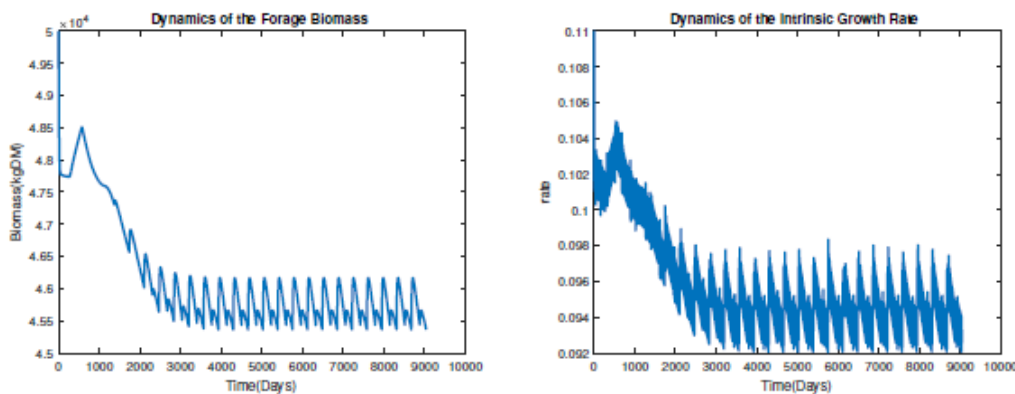


Figure 8: *The dynamics of forage biomass and intrinsic growth rate for 20 Adults and 30 Juveniles on the grazing land. These results were obtained with depletion constant, $\theta = 9 \times 10^{-7}$.*

However, if the depletion constant is increased to a factor of order of 9×10^{-6} , we observed a collapsing dynamics of both forage and intrinsic growth rate (Figure 9).

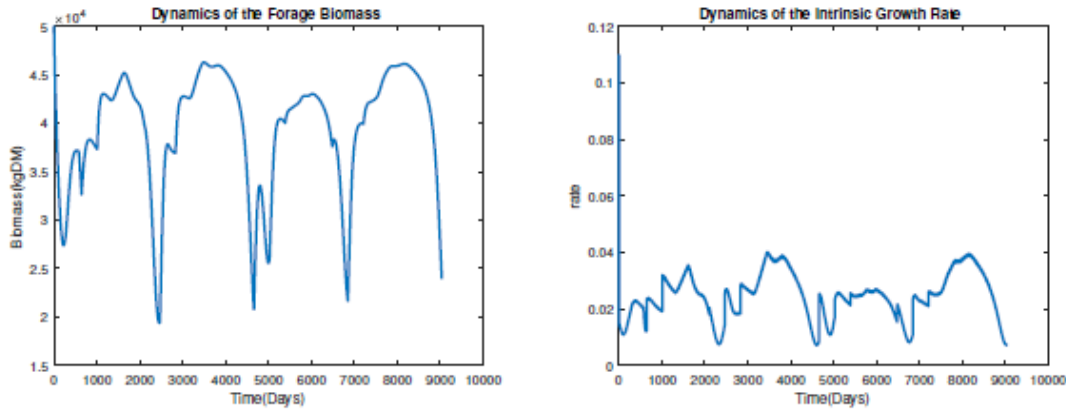


Figure 9: *The dynamics of forage biomass and intrinsic growth rate with 20 Adults and 30 Juveniles on the farm with trampling depletion constant of $\theta=9 \times 10^{-6}$*

Dynamics of the livestock population becomes unstable because of starvation with only adults being harvested when 20 adults and 35 juveniles are on the farm, thereby resulting into hard trampling.

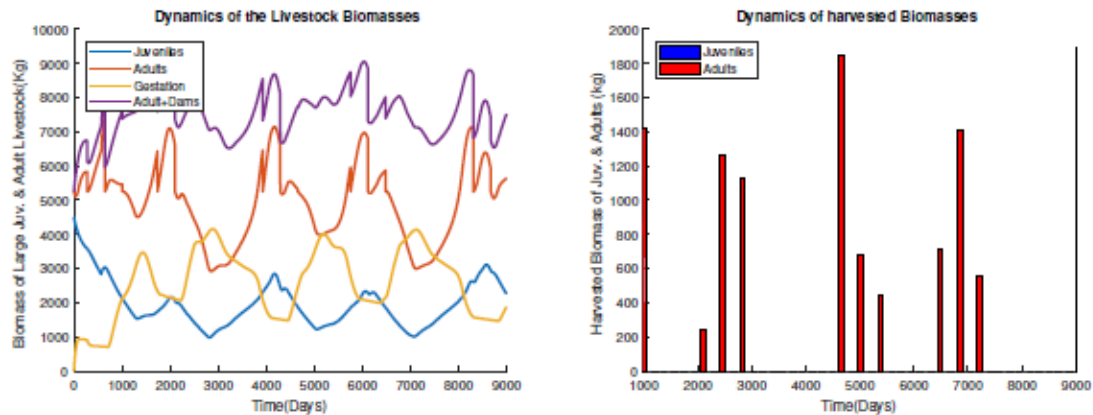


Figure 10: *Unstable population dynamics with depletion constant of 9×10^{-6} , causing an irreversible and expansive land degradation affecting its biodiversity and productivity.*

This trampling affects the intrinsic growth rate by reducing the forage biomass causing dynamics of the livestock population to be unstable (Figure 10). This limited amount of food resource available for the livestock causes starvation which increases the mortality rates causing mostly juveniles to die. This causes a collapse of the production system by having irregular harvesting patterns of only adult livestock, a situation which should be avoided.

Since we are seeking to have a sustainable livelihood through pastoralism, the number of grazing animals on these rangelands need to be controlled by harvesting and regular traditional practice of rotational grazing aimed at avoiding hard trampling on these grasses. In so doing, we are reducing the trampling depletion constant from 9×10^{-6} to 9×10^{-7} and vary the number of juveniles and adult livestock in the grazing system having a maximum of 50 animals.

| Number of Livestock | | Forage Biomass ('000) | | Intrinsic Growth rate | |
|---------------------|--------|-----------------------|---------------|-----------------------|---------------|
| Juveniles | Adults | Minimum Value | Maximum Value | Minimum Value | Maximum Value |
| 30 | 15 | 44.21 | 45.37 | 0.07246 | 0.08037 |
| 30 | 16 | 43.97 | 45.20 | 0.07144 | 0.07936 |
| 30 | 17 | 43.74 | 44.93 | 0.07048 | 0.07899 |
| 30 | 18 | 43.50 | 44.71 | 0.06935 | 0.07795 |
| 30 | 19 | 43.26 | 44.49 | 0.06864 | 0.07694 |
| 30 | 20 | 43.01 | 44.27 | 0.06775 | 0.07595 |
| Number of Livestock | | Forage Biomass ('000) | | Intrinsic Growth rate | |

| Juveniles | Adults | Minimum Value | Maximum Value | Minimum Value | Maximum Value |
|-----------|--------|---------------|---------------|---------------|---------------|
| 30 | 15 | 44.21 | 45.37 | 0.07246 | 0.08137 |
| 31 | 15 | 44.08 | 45.35 | 0.07200 | 0.08127 |
| 32 | 15 | 43.98 | 45.26 | 0.07181 | 0.08086 |
| 33 | 15 | 43.82 | 45.18 | 0.07130 | 0.08041 |
| 34 | 15 | 43.69 | 45.13 | 0.07096 | 0.07931 |
| 35 | 15 | 43.55 | 44.04 | 0.07068 | 0.07924 |

Table 2: Variation of the livestock composition showing the effects of trampling on forage and intrinsic growth rate with minimum and maximum forage biomasses and intrinsic growth rates measured at time $t=7580$, $t=7636$ days and $t=9035$ and $t=8679$ days respectively.

In this section, we assess the effects of trampling on the intrinsic growth rate and forage biomass. In doing this, we vary the number of juveniles from 30 - 35 and that of adults from 15 - 20 (Table 2). The results showed that a better intrinsic growth rate of 0.07068 md^{-1} when we keep 15 adults and 35 juveniles than the 0.06775 md^{-1} when we have 20 adults and 30 juveniles. The corresponding forage biomass of 43550 kg DM which is of better quality than that presented with the composition of 20 adults and 30 juveniles with 43010 kg DM.

On the economic perspective, we also considered varying the livestock composition that gives the maximum harvested biomass from the production system. Variation of the livestock composition in terms of the number of adults and juveniles was simulated from

1 - 20 and 1 - 45 respectively with $\theta = 9 \times 10^{-7}$. It was observed that this maximum occurs with 45 juveniles and 18 adult livestock harvested from the farm (Figure 11), with the maximum cumulative harvested biomass of 109730kg. This gives us the maximum yield representing the economic objective, as one of the pillars of sustainable

development goal. However, this affects the total forage biomass by reducing it to 41910 kg DM with the intrinsic growth rate reduced to $0.06537md^{-1}$, a situation which is detrimental to the environment and may cause rangeland degradation.

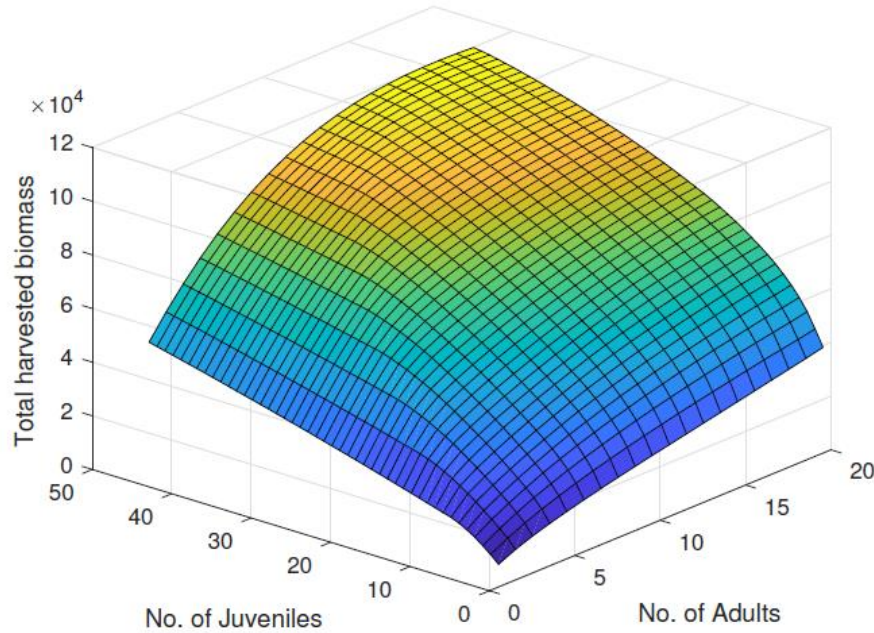


Figure 11: *The surface plot for the harvested biomass with maximum harvest obtained for 18 adults and 45 juveniles and $\theta = 9 \times 10^{-7}$.*

So for a better livestock productivity, we need to keep and maintain animals in the range of 45 - 55 to get a more balanced sustainability benefits: economically, ecologically and socially.

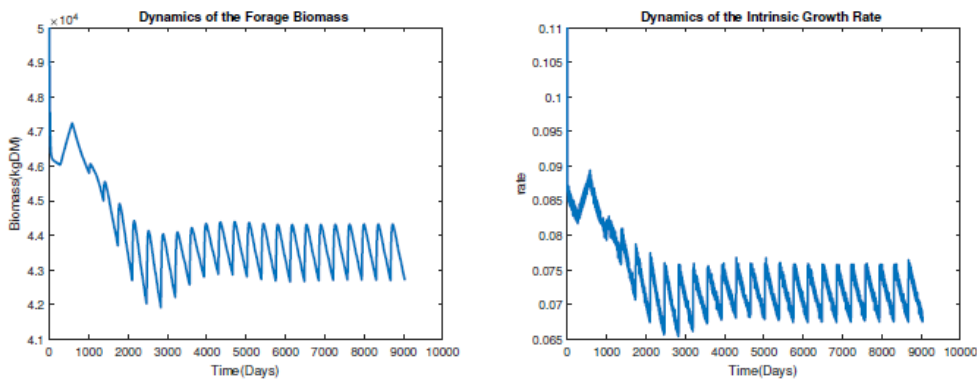


Figure 12: *The dynamics of forage biomass and intrinsic growth rate for 18 adults and 45 juveniles affecting the intrinsic growth rate of forage biomass by reducing them to 41910 kg DM and $0.06537md^{-1}$ respectively.*

To further assess the dynamics of the livestock to ascertain maximum harvest, simulations were run for 1 – 120 juveniles and 1 – 90 adult livestock, and the results are presented in (Figure 1.1) below:

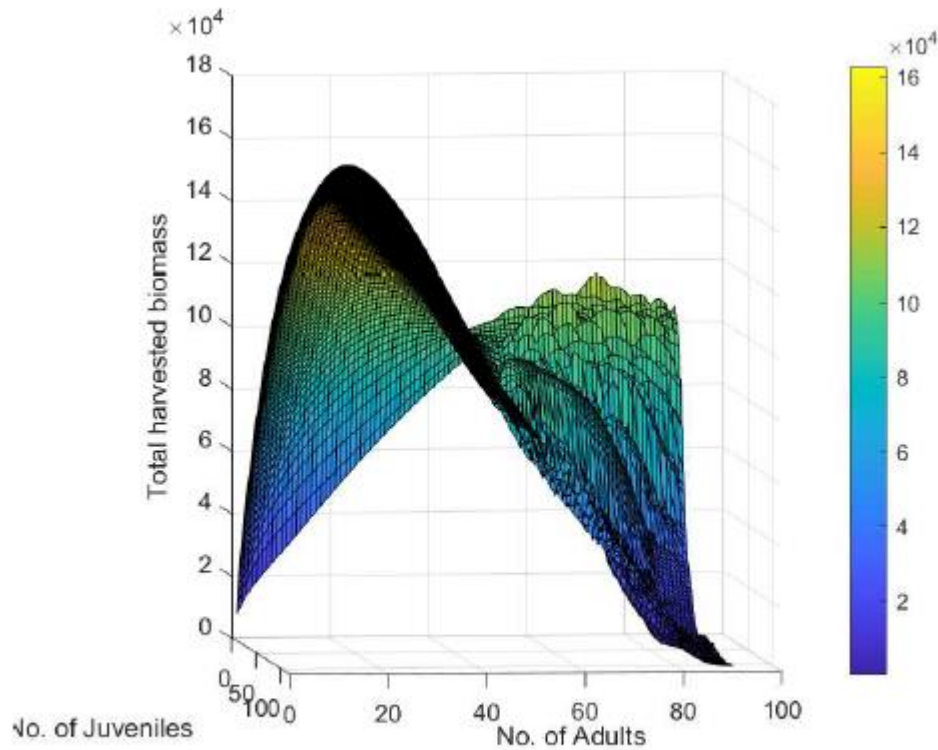


Figure 1.1: Variation of the livestock's composition of adults (1 – 90) and juveniles (1 – 120) simulated with $\theta = 9 \times 10^{-7}$ for economic aspect of sustainability.

We observed that we have maximum harvested biomass of 162842 kg when we maintain 120 juveniles and 12 adults, causing forage biomass to reduce to 41350 kg DM in 276 days. This causes a reduction in the intrinsic growth rate from 0.11 to 0.0845176 md^{-1} in 270 days. This number of animals on the farm affects the intrinsic growth rate due to brutal trampling on the forage.

Besides, there are other maximum harvested biomasses of 115773 kg when we have 1 juvenile and 74 adults, and 12 juveniles and 67 adults with the total maximum harvest of 107916 kg. Of the three compositions, we chose one which caters for all the pillars of sustainability, that is, 12 juveniles and 67 adult livestock. This is because livestock production, the primary source of the community livelihood, needs a fairly balanced

composition of the livestock population, where harvesting occurs in both breeding and festive seasons.

The results obtained here are in conformity with the rangeland ecological theory of equilibrium and non-equilibrium persistent models (Briske et al., 2017); (Briske et al., 2005), (Sasaki, 2010), where there are multiple equilibria, especially in regions with episodic rainfall. Equilibrium grazing systems are usually planned according to stages of range succession and condition of single-species grassland and grazed by one type of animal (cattle, sheep goats etc) (Gufu, 2000). Therefore, grazing programs based on assumptions from equilibrium systems have failed in arid zones because of unpredictable rainfall and highly fluctuating forage distribution (Ellis and Swift 1988; Dodd 1994). This is further exacerbated by livestock mobility, which allows herds to exploit grazing resources that are unevenly distributed in both time and space. Besides, these pastoral communities manage multiple livestock species with different foraging traits and styles (Gufu, 2000), and optimal use of these highly variable grazing resources is hard to attain.

Thus, in our model, we accept that multiple equilibrium points are used to depict the range of values of livestock composition that give maximum cumulative harvested biomasses over the 25-year planning period and beyond.

4 Conclusions and Recommendations

The ever-growing animal population in the semi-arid regions have caused the forage biomass to be over-utilized due to over-grazing. This situation can lead to the collapse of the grazing system, thereby affecting the community's livelihood (see Figures 2 and 3). To avoid such a scenario, there is a need to carry out harvesting on the livestock population. On performing this mix-harvesting, we obtained the total cumulative harvested biomass of 103904 kg when we maintained, on average, a total of 55 animals feeding on this 10-hectare piece of land (Figure 11). Also, when we maintained 12 juveniles and 67 adults on the farm, we obtained the cumulative harvested biomass of

107916 kg at the end of the planning period of 25 years. This gives us a better option because it tries to address most of the livelihood objectives of the pastoral communities in the semi-arid region.

This harvested biomass can be expressed in monetary terms and used to cater for subsistence needs and other social obligations such as marriage(dowries) and breeding purposes.

Varying the composition of these animals aims at studying the effects of hoof-sizes on the forage biomass. The results showed that with 35 juveniles and 15 adults we have a better intrinsic growth rate of 0.07068 md^{-1} for as compared to 0.06775 md^{-1} when we have 30 juveniles and 20 adults. For the 35 juveniles and 15 adults, a forage biomass of 43550 kg DM (Table 2) will be available, while with 20 adults and 30 juveniles, we have forage biomass of 43010 kg DM available for the grazing animals. Thus, maintaining 35 juveniles and 15 adults on the farm would give a better alternative. Therefore, to avoid such a detrimental effect on forage, we need more juveniles than adults on the farm; moreover, these animals will have more forage available for them to feed on.

However, for the case of 12 juveniles and 67 adults, we realized the cumulative harvested biomass of 107916 kg. This caused the biomass to reduce to 34837 kg DM growing at the intrinsic growth rate of $0.0673946 \text{ md}^{-1}$, showing the effects of number of animals as a factor of trampling. Here, we maintained more adults than juveniles on the farm because of the economic benefits of sustainability.

Thus, on this 10-hectare piece of land, we need a stocking level ranging from 45 to 78 animals. For a sustainable livestock production system, receiving a total cumulative harvested biomass of 107916 kg containing more juveniles than adults.

To achieve this, we apply harvesting as the most suitable strategy for regulating the livestock population on the farm by allowing a rest period of at least five days of no grazing on a particular section of the land. Furthermore, we recommend regularly

checking and monitoring the grazing land to avoid the adverse effects of brutal trampling on the grass's intrinsic growth rate.

We intend to mathematically analyse this grazing system modelled by delay differential equations and validate it given site-specific data and parameter values.

Acknowledgements

This research work was supported by the Swedish International Development Cooperation Agency (Sida) and the International Science Programme (ISP) in collaboration with the Sida-Makerere Bilateral Research Cooperation.

Declaration of interest

No conflict of interest registered.

References

- Abdel-Magid, A. H., Trlica, M., & Hart, R. H. (1987). Soil and vegetation responses to simulated trampling.
- Abril, A., & Bucher, E. (1999). The effects of overgrazing on soil microbial community and fertility in the chaco dry savannas of Argentina. *Applied Soil Ecology*, 12 (2), 159–167.
- Addison, J., Friedel, M., Brown, C., Davies, J., & Waldron, S. (2012). A critical review of degradation assumptions applied to Mongolia's gobi desert. *The Rangeland Journal*, 4 (2), 125–137.
- Alexander, S., Aronson, J., Whaley, O., & Lamb, D. (2016). The relationship between ecological restoration and the ecosystem services concept. *Ecology and society*, 21 (1).
- Barraquand, F. (2014). Functional responses and predator–prey models: a critique of ratio dependence. *Theoretical Ecology*, 7 (1), 3–20.
- Bodnar, M., & Forys, U. (2000). Periodic dynamics in a model of immune system. *Applicationes mathematicae*, 27, 113–126.

- Bodnar, M., & Forys, U. (2007). Three types of simple dde's describing tumor growth. *Journal of Biological Systems* , 15 (04), 453–471.
- Briske, D. D., Fuhlendorf, S. D., & Smeins, F. (2005). State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management* , 58 (1), 1–10.
- Briske, D. D., Illius, A. W., & Anderies, J. M. (2017). Nonequilibrium ecology and resilience theory. *Rangeland systems: Processes, management and challenges*, 197–227.
- Brown, T. C., Bergstrom, J. C., & Loomis, J. B. (2007). Defining, valuing, and providing Ecosystem goods and services. *Natural Resources Journal* , 329–376.
- Cao, J., Fussmann, G. F., & Ramsay, J. O. (2008). Estimating a predator-prey dynamical model with the parameter cascades method. *Biometrics* , 64 (3), 959–7.
- Cossins, N. (1985). The productivity and potential of pastoral systems. *ILCA bulletin* .
- Costanza, R. (2020). Valuing natural capital and ecosystem services towards the goals of efficiency, fairness, and sustainability. *Ecosystem Services*, 43 , 101096.
- Cumming, D. H., & Cumming, G. S. (2003). Ungulate community structure and ecological processes: body size, hoof area and trampling in african savannas. *Oecologia*, 134 (4), 560–568.
- Davies, J., & Hatfield, R. (2007). The economics of mobile pastoralism: a global summary. *Nomadic Peoples*, 11 (1), 91–116.
- De Roos, A. M., & Persson, L. (2001). Physiologically structured models from versatile technique to ecological theory. *Oikos*, 94 (1), 51–71.
- De Roos, A. M., Schellekens, T., Van Kooten, T., Van De Wolfshaar, K., Claessen, D., & Persson, L. (2008). Simplifying a physiologically structured population model to a stage-structured biomass model. *Theoretical population Biology*, 73 (1),47–62.
- Dodd, J. L. (1994). Desertification and degradation of Africa's rangelands. *Rangelands*

- Archives, 16 (5), 180–183.
- Dunne, T., Western, D., & Dietrich, W. (2011). Effects of cattle trampling on vegetation, infiltration, and erosion in a tropical rangeland. *Journal of arid environments*, 75 (1), 58–69.
- Egeru, A., Wasonga, O., Kyagulanyi, J., Majaliwa, G., MacOpiyo, L., & Mburu, J. (2014). Spatio-temporal dynamics of forage and land cover changes in Karamoja sub-region, Uganda. *Pastoralism*, 4 (1), 1–21.
- Evans, R. (1998). The erosional impacts of grazing animals. *Progress in Physical Geography*, 22 (2), 251–268.
- Fasae, O., Sowande, O., & Adewumi, O. (2010). Department of animal production and health. Lecture notes prepared by, Department of Animal Production and Health, University of Agriculture, Abeokuta, Nigeria.
- Feldt, T., Neudert, R., Fust, P., & Schlecht, E. (2016). Reproductive and economic performance of local livestock in southwestern Madagascar: Potentials and constraints of a highly extensive system. *Agricultural Systems*, 149, 54–64.
- Filipová, Z., & Johannisova, N. (2017). Changes in pastoralist commons management and their implications in Karamoja (Uganda). *Journal of Political Ecology*, 24 (1), 881–900.
- Gómez-Baggethun, E., De Groot, R., Lomas, P. L., & Montes, C. (2010). The history of ecosystem services in economic theory and practice: From early notions to markets and payment schemes. *Ecological economics*, 69 (6), 1209–1218.
- Gopalsamy, K. (2013). *Stability and oscillations in delay differential equations of population dynamics* (Vol. 74). Springer Science & Business Media.
- Hallanaro, E.-L., & Usher, M. B. (2005). 30 natural heritage trends. *Mountains of Northern Europe: Conservation, Management, People and Nature*, 13, 307.
- Hao, Y., & He, Z. (2019). Effects of grazing patterns on grassland biomass and soil environments in China: A meta-analysis. *PloS one*, 14 (4), e0215223.

- Havstad, K. M., Peters, D. P., Skaggs, R., Brown, J., Bestelmeyer, B., Fredrickson, E., et al. (2007). Ecological services to and from rangelands of the United States. *Ecological Economics*, 64 (2), 261–268.
- Hobbs, N. T., & Searle, K. R. (2005). A reanalysis of the body mass scaling of trampling by large herbivores. *Oecologia*, 145 (3), 462–464.
- Huffaker, R., & Cooper, K. (1995). Plant succession as a natural range restoration factor in private livestock enterprises. *American Journal of Agricultural Economics*, 77 (4), 901–13.
- Kagan, S., Pedersen, L., Ollech, S., & Knaute, D. (2009). The Karamoja syndrome: Transdisciplinary systems research informing policy and advocacy. In 1st world conference of humanitarian studies, Groningen.
- Kameri-Mbote, P. (2013). Preface: Securing the land and resource rights of pastoral peoples In East Africa. *Nomadic Peoples*, 1–4.
- Kariuki, R., Willcock, S., & Marchant, R. (2018). Rangeland livelihood strategies under varying climate regimes: Model insights from Southern Kenya. *Land*, 7 (2), 47.
- Kawamura, K., Akiyama, T., Yokota, H.-o., Tsutsumi, M., Yasuda, T., Watanabe, O., et al. (2005). Quantifying grazing intensities using geographic information systems and satellite remote sensing in the xilingol steppe region, inner mongolia, china. *Agriculture, ecosystems & environment*, 107 (1), 83–93.
- Kuang, Y. (1993). *Delay differential equations: with applications in population dynamics*. Academic press.
- Lynch, E., McGee, M., & Earley, B. (2019). Weaning management of beef calves with implications for animal health and welfare. *Journal of Applied Animal Research*.
- Mahmoud, S., & Ismail, A. (2005). New results on delay-dependent control of time-delay systems. *IEEE Transactions on Automatic Control*, 50 (1), 95–100.

- Manzi, M., Junga, J. O., Ebong, C., & Mosi, R. O. (2012). Factors affecting pre and post-weaning growth of six cattle breed groups at Songa research station in Rwanda.
- McPeak, J. G., Little, P. D., & Doss, C. R. (2011). Risk and social change in an African rural economy: livelihoods in pastoralist communities (Vol. 7). Routledge.
- Mefti, M., Bouzerzour, H., Abdelguerfi, A., & Nouar, H. (2008). Dry matter production and agronomical characteristics of perennial grass genotypes grown under drought conditions in the semi-arid climate of the Algerian high plateaus¹. *Pakistan Journal of agronomy*, 7, 138–147.
- Mwendera, E., & Saleem, M. M. (1997). Infiltration rates, surface runoff, and soil loss as influenced by grazing pressure in the Ethiopian highlands. *Soil use and management*, 13 (1), 29–35.
- Ocan, C. E., & Ocan, C. (1994). Pastoral resources and conflicts in northeastern Uganda: The Karimojong case. *Nomadic peoples*, 123–135.
- Persson, L., Leonardsson, K., De Roos, A. M., Gyllenberg, M., & Christensen, B. (1998). Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical population biology*, 54 (3), 270–293.
- Roos, A. M. de. (1997). A gentle introduction to physiologically structured population models. In *Structured-population models in marine, terrestrial, and freshwater systems* (pp. 119–204). Springer.
- S Antman, S. (2009). *Surveys and tutorials in the applied mathematical sciences*. Springer-Verlag Berlin Heidelberg.
- Sasaki, T. (2010). Paradigm integration between equilibrium and non-equilibrium concepts for evaluating vegetation dynamics in rangeland ecosystems. *Global Environmental Research*, 14 (1), 17–22.
- Sawadogo, L., Tiveau, D., & Nygård, R. (2005). Influence of selective tree cutting, livestock and prescribed fire on herbaceous biomass in the savannah

- woodlands of Burkina faso, West Africa. *Agriculture, Ecosystems & Environment*, 105 (1-2), 335–345.
- Séré, C., Ayantunde, A., Duncan, A., Freeman, A., Herrero, M., Tarawali, S. A., et al. (2020). Livestock production and poverty alleviation challenges and opportunities in arid and semi-arid tropical rangeland based systems.
- Shampine, L. F., & Thompson, S. (2009). Numerical solution of delay differential equations. In *Delay differential equations* (pp. 1–27). Springer.
- Susenbeth, A., Mayer, R., Koehler, B., & Neumann, O. (1998). Energy requirement for eating in cattle. *Journal of Animal Science*, 76 (10), 2701–2705.
- Uniyal, S. K., Awasthi, A., & Rawat, G. S. (2005). Biomass availability and forage quality of *urotia ceratoides* meyer in the rangelands of changthang, eastern Ladakh. *Current Science*, 201–205.
- Voh Jr, A., & Otchere, E. (1989). Reproductive performance of zebu cattle under traditional agropastoral management in northern Nigeria. *Animal Reproduction Science*, 19 (3-4), 191–203.
- Wilson, M. A., & Howarth, R. B. (2002). Discourse-based valuation of ecosystem services: establishing fair outcomes through group deliberation. *Ecological economics*, 41 (3), 431–443.
- Woodward, S. J. (2018). Dynamical systems models and their application to optimizing razing management. In *Agricultural systems modelling and simulation* (pp. 419–473). CRC Press.
- Yodzis, P., & Innes, S. (1992). Body size and consumer-resource dynamics. *The American Naturalist*, 139 (6), 1151–1175.