DYNAMICS OF A PLANT-HERBIVORE MODEL WITH STRONG ALLEE EFFECT ON PLANT

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Abstract: In this paper, we analyze a ratio-dependent plant-herbivore model with strong Allee effect on the plant by making a parametric analysis of the stability properties of the dynamics of the system in which the functional response is a function of the ratio of plant to herbivore abundance. In this model, the functional response is undefined at the origin. All the feasible equilibria of the system were obtained and the conditions for the existence of the interior equilibrium were determined.

Keywords: Allee effect, Plant-Herbivore system, Ratio-Dependent, Stability Analysis.

Introduction: Over the past two decades, intensive research in ecology, evolutionary biology and resource management have been focused on plant-herbivore interactions. The dynamical relationship between plant and herbivore has long been and will continue to be one of the dominant themes in ecology due to its universal existence and importance [3], [7]. The dynamical problems involved with mathematical modeling of plant-herbivore systems may appear to be simple at first sight; however, the detailed analysis of these model systems often leads to very complicated as well as challenging problems. The most important part of modeling population ecosystem is to make sure that the concerned mathematical model can exhibit the well known system behaviors for the system. Dynamical modeling of ecological systems is an evolving process frequently, a better understanding of the plausible models and the exposed discrepancies can be done through systematic mathematical approaches which in turn lead to the necessary modifications.

In this paper, our aim is to build a better understanding of how Allee effect affects the dynamic behavior of plant-herbivore interactions. Allee effects occur in small or sparse populations and, although rarely detected, are widely believed to be common in nature [1], [2]. Growth of populations subject to Allee effects is reduced at low density [4]–[11]. The originator was Warder Clyde Allee. It is a positive association between absolute average individual fitness and population size over some finite interval. Such a positive association may (but does not necessarily) give rise to a critical population size below which the population cannot persist. Allee effects that cause critical population sizes are called strong, while Allee effects that do not result in critical sizes are called weak.

Mathematical Model: We consider a plant-herbivore model where the plant growth rate is subject to an Allee effect and the functional response of herbivores consuming the plants is ratio-dependent. The species interactions are described by the following system of ordinary differential equations:

$$\begin{cases} \dfrac{dP}{dT} = Pg(P) - f\left(\dfrac{P}{H}\right)H \\ \dfrac{dH}{dT} = ef\left(\dfrac{P}{H}\right)H - \vartheta H \end{cases} \qquad (1)$$

where $P(T)$ and $H(T)$ represent the populations, at time T, of plant and herbivore respectively; $f\left(\frac{P}{H}\right)$ is the functional response of herbivore which is ratio-dependent; e is the herbivore efficiency rate; ϑ is the herbivore death rate. The function $g(P)$ represents the average plant rate of growth in the absence of herbivore. In this paper, we assume Allee dynamics for the plant population. In case of a strong Allee effect we require that the per capita growth rate should be negative near zero: $g(0) < 0$. The growth function considering Allee effect is expressed by:

$$g(P) = r(P - P_0)\left(1 - \frac{P}{K}\right) \quad (2)$$

where $'r'$ denotes the intrinsic per capita growth rate of the population, K is the carrying capacity. The parameter P_0 has the meaning of the plant survival threshold for the strong Allee effect (in this case $0 < P_0 \leq K$). Thus at small species densities $0 < P < P_0$ the plant growth rate becomes negative since the death rate is larger than the birth rate. In case of a weak Allee effect, the value of $P_0$is negative and it should satisfy the condition $-K < P_0 \leq 0$. If $P_0 = -K$ then the equation for plant growth rate is equivalent to the logistic equation. We consider the functional response of herbivore to be ratio-dependent and given by

$$f(P,H) = \frac{aP}{P + ahH} \quad (3)$$

Where $'a'$ represents the attack-rate of herbivore and h is the handling time of single plant by herbivore. With functions (2) and (3), model (1) becomes

$$\begin{cases} \frac{dP}{dT} = rP(P - P_0)\left(1 - \frac{P}{K}\right) - \frac{aPH}{P + ahH} \\ \frac{dH}{dT} = \frac{eaPH}{P + ahH} - \vartheta H \end{cases} \quad (4)$$

with the initial conditions $P(0), H(0) > 0$.

In order to reduce the number of parameters in the model we shall introduce the dimensionless variables given by

$x = P/K, y = ahH/K$ and $t = rKT$

$$\begin{cases} \frac{dx}{dt} = x(x - \beta)(1 - x) - \frac{\alpha xy}{x + y} \\ \frac{dy}{dt} = \frac{\mu xy}{x + y} - \delta y \end{cases} \quad (5)$$

where $\beta = P_0/K$, $\alpha = 1/rKh$, $\mu = ea/rK$ and $\delta = \vartheta/rK$. Modelling a strong Allee effect implies $0 < \beta \leq 1$, whereas a weak Allee effect requires $-1 < \beta \leq 0$. Model (5) now contains only four parameters (against seven in the original equations). The parameter δ represents the death rate of the re-defined herbivore y; the parameter α is the maximum plant death rate due to predation for an infinite number of herbivores, it is known as the consumption ability; μ is the maximum herbivore growth rate for an infinite number of plant, it is called the herbivore growing ability.

System (5) is analytical at all points in the (x, y) plane except at the axes $x = 0$ and $y = 0$, but the origin is a removable singularity. Extending the domain to the first quadrant $x \geq 0$ and $y \geq 0$ and then applying the time rescaling $dt \to (x + y)dt$ we obtain the system

$$\begin{cases} \frac{dx}{dt} = x(x - \beta)(1 - x)(x + y) - \alpha xy \\ \frac{dy}{dt} = \mu xy - \delta y(x + y) \end{cases} \quad (6)$$

The equilibrium solutions are determined analytically by setting $\frac{dx}{dt} = \frac{dy}{dt} = 0$, it is easy to verify that this system (6) has five equilibrium points which are

$E_0(0,0), E_1(\beta, 0), E_2(1,0), E_3(x_3, y_3)$ and $E_4(x_4, y_4)$ where

$$x_{3,4} = \frac{\left\{\mu(1+\beta) \pm \sqrt{\mu^2(1-\beta)^2 - 4\alpha\mu^2 + 4\alpha\delta\mu}\right\}}{2\mu};$$

$$y_{3,4} = \frac{(\mu-\delta)\left\{\mu(1+\beta) \pm \sqrt{\mu^2(1-\beta)^2 - 4\alpha\mu^2 + 4\alpha\delta\mu}\right\}}{2\mu\delta}$$

Positivity and Boundedness: Positivity and boundedness of a model guarantee that the model is biologically well behaved. It is easy to notice that the functions on the right side of each equation in system (5) are continuously differentiable in R^2. Therefore the solutions of (5) with a positive initial condition exists and is unique. For positivity of the system (5), we have the following theorem.

Theorem: 1: The positive quadrant is invariant for system (5).

Proof: To prove that $R_{+0}^2 = \{(x, y): x \geq 0 \; and \; y \geq 0\}$ is an invariant set.

We can write from equations in (5),

$x(t) = x(0)exp\left[\int_0^t \left((x(s)-\beta)(1-x(s)) - \frac{\alpha y(s)}{x(s)+y(s)}\right) ds\right]$ $y(t) = y(0)exp\left[\int_0^t \left(\frac{\mu x(s)}{x(s)+y(s)} - \delta\right) ds\right]$

This shows that $x(t) \geq 0$ and $y(t) \geq 0$ whenever $x(0) > 0$ and $y(0) > 0$. Hence all solutions remain within the first quadrant of the xoy plane starting from an interior point of it. Further we can easily establish that solution trajectories starting from $(x_0, 0)$ remain within the positive x axis at all future times and similar result holds for trajectories starting from a point on the positive y axis.

Therefore $R_{+0}^2 = \{(x, y): x \geq 0 \; and \; y \geq 0\}$ is an invariant set

Theorem 2: If $x(t) \leq \max\{x(0), 1\} \; for \; all \; t \geq 0$ then $\lim_{t\to\infty} \sup x(t) \leq 1$

Proof: Consider

$x(t) = x(0)exp\left[\int_0^t \left((x(s)-\beta)(1-x(s)) - \frac{\alpha y(s)}{x(s)+y(s)}\right) ds\right]$

Case A: First we consider $0 < x_0 < 1$ and our claim is $x(t) \leq 1$ for all $t \geq 0$.

If possible, assume that our claim is not true. Then it is possible to find two positive real numbers t_1 and t_2 $(t_2 > t_1)$ such that $x(t_1) = 1$ and $x(t) > 1$ for all $t \in (t_1, t_2)$. Then for all $t \epsilon (t_1, t_2)$, we have from the first equation of (5),

$x(t) = x(0)exp\left[\int_0^t F(x(s), y(s)) \, ds\right]$

Where $F(x(s), y(s))$

$$= \left((x(s)-\beta)(1-x(s)) - \frac{\alpha y(s)}{x(s)+y(s)}\right)$$

$$= x(0)exp\left[\int_0^{t_1} F(x(s), y(s)) \, ds\right] \times exp\left[\int_{t_1}^{t} F(x(s), y(s)) \, ds\right]$$

$= x(t_1) \; exp\left[\int_{t_1}^t F(x(s), y(s)) \, ds\right]$, [Since $m < 1$, we have $F(x(s), y(s)) < 0 \; for \; all \;\; t \in (t_1, t_2)$].

Therefore $x(t) < x(t_1), \; where \; x(t_1) = 1$

Which contradicts to the assumption that $x(t) > 1$ for all $t \in (t_1, t_2)$. Hence $x(t) \leq 1$ for all $t \geq 0$.

Case B: Now we consider $x(0) > 1$. we claim that $\lim_{t\to\infty} \sup x(t) \leq 1$. If possible, assume that our claim is not true. Then

$$x(t) = x(0)exp\left[\int_0^t F(x(s), y(s)) \, ds\right]$$

$< x(0)$, Since $F(x(s), y(s)) < 0$ for $x(t) \geq 1$ and there is no equilibrium point in the region $\{(x, y): x > 1, y \geq 0\}$.

Hence combining case A & case B, we can say that any positive solution satisfies $x(t) \leq max\{x(0), 1\}$ for all $t \geq 0$. Hence $\lim_{t\to\infty} \sup x(t) \leq 1$.

The following theorem ensures the boundedness of the system (5).

Theorem 3: All the solutions of the system (5) with the positive initial condition (x_0, y_0) are uniformly bounded within a region Ω, where

$\Omega = \left\{(x, y) \in R_{+0}^2 : x, y \geq 0, 0 \leq x + \left(\frac{\alpha}{\mu}\right) y \leq \frac{\gamma}{\delta}\right\}$ and $\gamma = \max_{t\geq 0}\{x(x-\beta)(1-x) + \delta x\}$

Proof: Let us consider the relation,

$$W(t) = x(t) + \left(\frac{\alpha}{\mu}\right) y(t).$$

Differentiating $W(t)$ with respect to t and using (5) we get

$\frac{dW(t)}{dt} = \frac{dx}{dt} + \frac{\alpha}{\mu}\frac{dy}{dt} = x(x-\beta)(1-x) - \frac{\alpha\delta y}{\mu}$

$= x(x-\beta)(1-x) + \delta x - \delta\left(x + \frac{\alpha}{\mu} y\right)$

Let $\gamma = \max_{t\geq 0}\{x(x-\beta)(1-x) + \delta x\}$ then we have

$\frac{dW(t)}{dt} \leq \gamma - \delta\left(x(t) + \frac{\alpha}{\mu} y(t)\right)$

From the above expression we get the following result,

$$0 \leq x(t) + \left(\frac{\alpha}{\mu}\right) y(t) \leq \left(x(0) + \left(\frac{\alpha}{\mu}\right) y(0)\right) e^{-\delta t} + \frac{\gamma}{\delta}$$

Thus as $t \to \infty$, $0 \leq x(t) + \left(\frac{\alpha}{\mu}\right) y(t) \leq \frac{\gamma}{\delta}$, this ensures that the system (5) is dissipative with the asymptotic bound $\frac{\gamma}{\delta}$ This asymptotic bound for the function $W(t) = x(t) + \left(\frac{\alpha}{\mu}\right) y(t)$ ensures the existence of compact neighbourhood Ω which in turn is a proper subset of R^2_{+0} and consequently for sufficiently large initial conditions (x_0, y_0) the solution of the system of equations (5) will be always within the set Ω.

Stability Analysis: The local stability analysis of the equilibrium points can be done based upon the standard linearization technique and using the Jacobian matrix. The Jacobian matrix for the model system (6) at any point (x, y) takes the following form

$J(x, y) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$, where

$a_{11} = -4x^3 + 3x^2(1 + \beta - y) - y(\alpha + \beta) + 2x(\beta y - \beta + y);$

$a_{12} = -x^3 + x^2(1 + \beta) - x(\alpha + \beta);$

$a_{21} = (\mu - \delta)y;\ a_{22} = (\mu - \delta)x - 2\delta y.$

Proposition 1: The stability of the Allee threshold equilibrium $E_1(\beta, 0)$ for $0 < \beta \leq 1$ is as follows;

a) an unstable node if $\mu > \delta$, or

b) a saddle point if $\mu < \delta$

The Jacobian matrix evaluated at $E_1(\beta, 0)$ is $J(x, y) = \begin{bmatrix} \beta^2(1 - \beta) & -\alpha\beta \\ 0 & (\mu - \delta)\beta \end{bmatrix}$

which gives the eigenvalues

$\lambda_1 = \beta^2(1 - \beta) > 0, (0 < \beta \leq 1)$ and

$\lambda_2 = (\mu - \delta)\beta = \begin{cases} < 0 \ if \ \mu < \delta \\ > 0 \ if \ \mu > \delta \end{cases}$

Therefore, the Allee threshold equilibrium point is a saddle point if $\mu < \delta$ and is an unstable node if $\mu > \delta$

Proposition 2:

The stability of the carrying capacity equilibrium $E_2(1,0)$ for $0 < \beta \leq 1$ is as follows;

c) a saddle point if $\mu > \delta$, or

d) a stable node if $\mu < \delta$

The Jacobian matrix evaluated at $E_2(1,0)$ is given by $J(x, y) = \begin{bmatrix} -1 + \beta & -\alpha \\ 0 & \mu - \delta \end{bmatrix}$ which gives the eigenvalues

$\lambda_3 = -1 + \beta < 0, (0 < \beta \leq 1)$ and $\lambda_4 = \mu - \delta = \begin{cases} < 0 \ if \ \mu < \delta \\ > 0 \ if \ \mu > \delta \end{cases}$

Therefore, the carrying capacity equilibrium point is a saddle point if $\mu > \delta$ and is a stable node if $\mu < \delta$.

Proposition 3:

The Jacobian matrix at the origin is a zero matrix. So the system (6) can be reduced to the following homogeneous system

$$\begin{cases} \frac{dx}{dt} = -x^2\beta - xy\alpha - \beta xy \\ \frac{dy}{dt} = \mu xy - \delta xy - \delta y^2 \end{cases} \quad (7),$$

(Neglecting the terms of order higher than two) Now we have to study the behavior of the system (7) by the following two cases.

Case: (a) Changing the variables $x = x, y = px$ and by rescaling the time variable $dt \to xdt$, we get

$$\begin{cases} \dfrac{dx}{dt} = -x[\beta + p\beta + p\alpha] \\ \dfrac{dp}{dt} = p[\mu + \beta - \delta + p\beta + p\alpha - p\delta] \end{cases} \quad (8)$$

This system has two equilibrium points $(0,0)$ and $\left(0, \frac{\delta-\mu-\beta}{\beta-\delta+\alpha}\right)$. The Jacobian matrix for the model system (8) at the point (x,p) takes the following form $J(x,p) = \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix}$, where

$b_{11} = -\beta - p\alpha - p\beta; b_{12} = -x\beta - x\alpha;$
$b_{21} = 0;\ b_{22} = \beta + \mu - \delta + 2p(\alpha + \beta - \delta)$

For the equilibrium point $(0,0)$ the eigen values of the Jacobian matrix are $-\beta$ and $(\mu + \beta - \delta)$. Therefore, the equilibrium point $(0,0)$ is a saddle point if $(\mu + \beta - \delta) > 0$ and is a stable node if $(\mu + \beta - \delta) < 0$. At $\left(0, \frac{\delta-\mu-\beta}{\beta-\delta+\alpha}\right)$ the eigenvalues of the Jacobian matrix are $\left(\frac{\mu\alpha-\alpha\delta+\mu\beta}{\alpha+\beta-\delta}\right)$ and $(\delta - \mu - \beta)$.
Therefore, the equilibrium point $\left(0, \frac{\delta-\mu-\beta}{\beta-\delta+\alpha}\right)$ is asymptotically stable node if $(\delta - \mu - \beta)$ and $(\beta - \delta + \alpha)$ are negative.

Case: (b) We now changing the variables $y = y$, $x = qy$ and by rescaling the time variable $dt \to ydt$, we get

$$\begin{cases} \dfrac{dq}{dt} = q(\delta - \alpha - \beta) + q^2(\delta - \mu - \beta) \\ \dfrac{dy}{dt} = y[q\mu - \delta(1 + q)] \end{cases} \quad (9)$$

This system has two equilibrium points $(0,0)$ and $\left(\frac{\delta-\alpha-\beta}{\mu+\beta-\delta}, 0\right)$. The Jacobian matrix for the model system (9) at the point (q,y) takes the following form $J(q,y) = \begin{bmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{bmatrix}$, where

$c_{11} = \delta - \alpha - \beta - 2q(\mu + \beta - \delta);$
$c_{12} = 0\ ; c_{21} = y(\mu - \delta)\ ;$
$c_{22} = \mu q - \delta(q + 1).$

At $(0,0)$ the eigenvalues of the Jacobian matrix are $(\delta - \alpha - \beta)$ and $-\delta$.
Therefore, the equilibrium point $(0,0)$ is a saddle point if $(\delta - \alpha - \beta) > 0$ and is a stable node if $(\delta - \alpha - \beta) < 0$.

Proposition 4:
If $\mu > \delta$ and the discriminant $[\mu^2(1-\beta)^2 - 4\alpha\mu^2 + 4\alpha\delta\mu] > 0$ then the system (6) has two interior points $\left(\frac{\mu(1+\beta)+\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}}{2\mu}, \frac{(\mu-\delta)[\mu(1+\beta)+\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}]}{2\mu\delta}\right)$;
$\left(\frac{\mu(1+\beta)-\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}}{2\mu}, \frac{(\mu-\delta)[\mu(1+\beta)-\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}]}{2\mu\delta}\right)$ in the first quadrant.

The stability of the equilibrium point $\left(\frac{\mu(1+\beta)+\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}}{2\mu}, \frac{(\mu-\delta)[\mu(1+\beta)+\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}]}{2\mu\delta}\right)$ for $\mu > \delta$ is as follows;

a) a stable node if
Det of $J(x_3, y_3) > 0$ and
Trace of $J(x_3, y_3) < 0$

b) an unstable node if
Det of $J(x_3, y_3) > 0$ and
Trace of $J(x_3, y_3) > 0$

The Determinant of the Jacobian matrix at (x_3, y_3) is $\left(\frac{(\mu-\delta)\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}}{8\mu\delta}\right) \times$

$$\left(\sqrt{\mu^2(1-\beta)^2 - 4\alpha\mu^2 + 4\alpha\delta\mu} - \sqrt{\mu}(\beta + 1)\right)^3$$

is positive when $\mu > \delta$ and the Trace of the Jacobian matrix evaluated at (x_3, y_3) is equal to

$$\frac{\left(\sqrt{\mu}(1+\beta)-\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}\right)\times\left[\begin{array}{c}\mu\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}\times\\ \left(\sqrt{\mu}(1+\beta)-\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}\right)\\ -2\delta(\mu^2+\alpha\delta-\alpha\mu-\mu\delta)\end{array}\right]}{\sqrt[3]{\mu}(4\delta)}$$

The sign of the trace is defined as follows;

$$\begin{cases} Trace\ of\ J(x_3,y_3) < 0, \quad if \\ \left(\sqrt{\mu}(1+\beta)-\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}\right) \\ \quad < 2\delta(\mu^2+\alpha\delta-\alpha\mu-\mu\delta) \\ Trace\ of\ J(x_3,y_3) > 0, \quad if \\ \left(\sqrt{\mu}(1+\beta)-\sqrt{\mu^2(1-\beta)^2-4\alpha\mu^2+4\alpha\delta\mu}\right) \\ \quad > 2\delta(\mu^2+\alpha\delta-\alpha\mu-\mu\delta) \end{cases}$$

Hence the equilibrium point (x_3, y_3) is

1. a stable node if
   $Det\ of\ J(x_3,y_3) > 0$ and
   $Trace\ of\ J(x_3,y_3) < 0$
2. an unstable node if
   $Det\ of\ J(x_3,y_3) > 0$ and
   $Trace\ of J(x_3,y_3) > 0$
   and also (a) if the discriminant $[\mu^2(1-\beta)^2 - 4\alpha\mu^2 + 4\alpha\delta\mu] = 0$ then the system (6) has unique interior point $\left(\frac{(1+\beta)}{2}, \frac{(\mu-\delta)(1+\beta)}{2\delta}\right)$ in the first quadrant.

(b) if the discriminant $[\mu^2(1-\beta)^2 - 4\alpha\mu^2 + 4\alpha\delta\mu] < 0$ then the system (6) has no interior equilibrium point in the first quadrant.

Conclusion: In this paper, we have considered a plant-herbivore model with ratio-dependent functional response and a strong Allee effect affects the growth of plant. Allee effect provides a contemporary research experience and also gives a better idea and understanding of ecological phenomena of real world. The local stability of various equilibrium points were discussed by analyzing the nature of roots of concerned characteristic equations of the system. Here the behaviour of ratio dependent model at the origin is also discussed. Since this model has difficult dynamics in the neighborhood of the point (0, 0) and system (5) cannot be linearized, thus we introduce an equivalent system (6) which is continuous extension of system (5), it is used to study the analytical behaviour of the system close to the origin and we have also analyzed the system mathematically and described some of its biological applications as well.

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