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Global dynamics and parameter identifiability in a predator-prey interaction model

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Abstract: This paper discusses a predator-prey model with prey refuge. We investigate the role of prey refuge on the existence and stability of the positive equilibrium. The global asymptotic stability of positive interior equilibrium solution is established using suitable Lyapunov functional, which shows that the prey refuge has no influence on the permanence property of the system. Mathematically, we analyze the effect of increase or decrease of prey reserve on the equilibrium states of prey and predator species. To assess the usability of proposed predator-prey model in practical scenarios, we also suggest, the use of Levenberg-Marquardt (LM) method for associated parameter estimation problem. Numerical results demonstrate faithful reconstruction of system dynamics by estimated parameter by LM method. The analytical results found in this paper are illustrated with the help of suitable numerical examples.

Keywords: Levenberg-Marquardt; Prey refuge; Parameter estimation; Fluctuation Lemma; Lyapunov functional; Permanence

1 Introduction

In ecology, over predation and unregulated harvesting are commonly practiced, which in turn threatens global biodiversity by eliminating several species. One approach to prevent over predation and harvesting is the creation of protected areas (refuge) [1]–[14]. Protected areas can be crucial baseline to judge ecological change. An exhaustive study for bifurcation and stability analysis of a temperature-dependent mite predator-prey interaction model incorporating a prey refuge has been carried out by Collings [6]. Kar [8] considered a predator-prey model with Holling type II response function incorporating prey refuge. He proved the existence of exactly one stable limit cycle when the positive equilibrium is unstable. Ko and Ryu [11] studied a predator-prey model with Holling type II functional response incorporating prey refuge under homogeneous Neumann boundary conditions. Ji and Wu [12] proposed and analyzed a predator-prey system with constant-rate prey harvesting incorporating a constant prey refuge. Ma et al. [13] proposed a patchy predator-prey system with one patch as refuge and other as open habitat and studied the effect of prey refuge. The global stability of unique positive equilibrium by constructing a suitable Lyapunov functional has been presented in [14]. Alaoui and Okiye [21] proposed and analyzed a predator-prey model with modified Leslie-Gower and Holling-type II schemes. The stability analysis of limit cycle in a delayed predator-prey model with Holling-type second schemes has been discussed in Yafia et al. [22]. Recently Gupta and Chandra [24] discussed Leslie-Gower predator-prey model with nonlinear prey harvesting.

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In this work, we consider the following predator-prey model with modified Leslie-Gower and Holling-type II schemes incorporating a refuge protecting mx of the prey, where $m \in [0, 1)$ is constant:

$$\begin{aligned}\frac{dx}{dt} &= x\left(r_1 - b_1x - \frac{a_1(1-m)y}{(1-m)x + k_1}\right), \\ \frac{dy}{dt} &= y\left(r_2 - \frac{a_2y}{(1-m)x + k_2}\right),\end{aligned}\tag{1}$$

with the initial conditions

$$x(0) > 0 \quad y(0) > 0,\tag{2}$$

where $x(t)$ and $y(t)$ are the prey and predator population densities respectively. Here all the parameters $r_1, r_2, a_1, a_2, b_1, k_1$ and k_2 are positive and we refer to Alaoui and Okiye [21] for their biological meanings. The first equation of system (1) is standard. However, the second equation is absolutely not standard. It contains a modified Leslie-Gower term [21]. System (1) is defined on the set: $\mathbb{R}_+^2 = \mathbb{R}^+ \times \mathbb{R}^+ = \{(x, y) \in \mathbb{R}^2 | x \geq 0, y \geq 0\}$.

System (1) is characterized by two dynamic variables ($x(t), y(t)$) which evolves over time and a set of constant parameters (eg. m, r_1, r_2 etc). Given the experimental data of prey and predator population, it is essential to identify the hidden parameters from the data for analyzing the system dynamics in future times. Even if the bounds of the parameters are known, employing parameter sweeping procedure in higher dimensions is impractical and unreliable. This parameter estimation [25, 26] problem can be formulated as constrained non-linear optimization problem. Choice of solution algorithm to solve associated optimization problem depends upon underlying system dynamics. Several algorithms like conjugate gradient [36], trust region method [27] and heuristic algorithms [37]–[41] are proposed in literature for parameter estimation. Particularly for system (1), we suggest the use of Levenberg-Marquardt (LM) method. Reconstructed system dynamics from estimated parameter value by LM method, manifests faithful recovery.

The aim of this paper is to analyze the effect of prey refuge on the dynamics of the two dimensional autonomous differential equations model (1). More precisely, we give an application of Levenberg-Marquardt (LM) method to estimate the parameter prey refuge (m).

The rest of the paper is structured as follows. In the next section, we present mathematical results related to the model system (1). In particular, we show a useful application of Fluctuation lemma to establish existence, uniqueness and global stability of interior equilibrium solution. Section 3 is devoted for effect of prey reserve on the predator and prey equilibrium densities. In the section 4, we present numerical simulations to illustrate the established results. To mimic the real world scenario, in section 5, parameter estimation with identifiability is discussed. More precisely, we also solve the inverse problem of estimation of model parameter (m) using the sampled data of the system. Concluding remarks are presented in the last section.

2 Mathematical analysis of the system (1)

2.1 Positivity, Boundedness and Permanence

To prove boundedness and permanence, we need to recall the following Lemmas and definition:

Lemma 2.1. [18, 20] *If $p > 0, q > 0$ and $\frac{du}{dt} \leq (\geq) u(t)(q - pu(t))$ with $u(0) > 0$, then we have*

$$\limsup_{t \rightarrow +\infty} u(t) \leq \frac{q}{p} \quad \left(\liminf_{t \rightarrow +\infty} u(t) \geq \frac{q}{p} \right).$$

In fact, the above lemma is quantitatively equivalent to the following lemma:

Lemma 2.2. *If $p > 0, q > 0$ and $\frac{du}{dt} \leq u(t)(q - pu(t))$ with $u(0) > 0$, then for all $t \geq 0$*

$$u(t) \leq \frac{q}{p - Ce^{-at}} \text{ with } C = p - \frac{q}{u(0)}.$$
In particular, $u(t) \leq \max \{u(0), \frac{q}{b}\}$ for all $t \geq 0$.

Definition 2.3. *The system (1) is said to be permanent if \exists positive constants η_1 and η_2 with $0 < \eta_1 \leq \eta_2$ such that*

$$\min \left\{ \liminf_{t \rightarrow +\infty} x(t), \liminf_{t \rightarrow +\infty} y(t) \right\} \geq \eta_1, \max \left\{ \limsup_{t \rightarrow +\infty} x(t), \limsup_{t \rightarrow +\infty} y(t) \right\} \leq \eta_2,$$
for all solutions $(x(t), y(t))$ of model system (1) with positive initial values.

Proposition 2.4. (i) *The positive quadrant $(Int(\mathbb{R}_+^2))$ is invariant for the model system (1).*
 (ii) *All solutions of the model system (1) are bounded, for all $t \geq 0$.*
 (iii) *The model system (1) with the initial conditions (2) is permanent (refer the Definition 2.3) if*

$$\frac{a_1 r_2 (1 - m)(r_1 (1 - m) + b_1 k_2)}{a_2 b_1 k_1} < r_1.$$

Proof. (i) To show that the positive quadrant $(Int(\mathbb{R}_+^2))$ is invariant, we only need to prove that for all $t \in [0, P]$, $x(t) > 0, y(t) > 0$, where P is any positive real number. This can easily be proved by following similar steps as in the proof of the Lemma 2.1 in [9].

(ii) Now using the positivity of variables x, y from (1), we obtain

$$\frac{dx}{dt} \leq x(r_1 - b_1 x). \tag{3}$$

Using Lemma 2.2, we get

$$x(t) \leq \max \left\{ x(0), \frac{r_1}{b_1} \right\} \equiv S_1 \text{ for all } t \geq 0.$$

Further, from the predator equation of (1), we have

$$\frac{dy}{dt} \leq y \left(r_2 - \frac{a_2 y}{(1 - m)S_1 + k_2} \right). \tag{4}$$

Again from the Lemma 2.2, we have

$$y(t) \leq \max \left\{ y(0), \frac{r_2((1 - m)r_1 + b_1 k_2)}{b_1 a_2} \right\} \equiv S_2 \text{ for all } t \geq 0.$$

In other words, we can say that all trajectories of the model system (1) initiating from any point in \mathbb{R}_+^2 ultimately lies in some fixed bounded region. This completes the proof of boundedness of solutions and hence the flow/dynamical system associated with model system (1) is dissipative.

(iii) From (3) and Lemma 2.1, it is obvious that $0 < x(t) < \frac{r_1}{b_1}$. Furthermore, from (4) and Lemma 2.1, we

obtain $y(t) \leq \frac{r_2(r_1(1 - m) + b_1 k_2)}{b_1 a_2}$ for sufficiently large t .

Thus, from the first equation of (1), we have

$$\frac{dx}{dt} \geq x \left(r_1 - b_1 x - \frac{a_1(1 - m)r_2((1 - m) + k_2)}{a_2 k_2} \right) = x(\xi_1 - b_1 x) \text{ for sufficiently large } t, \text{ where } \xi_1 = r_1 - \frac{a_1 r_2 (1 - m)(r_1 (1 - m) + b_1 k_2)}{a_2 b_1 k_1}.$$

If $\xi_1 > 0$ $\left(\frac{a_1 r_2 (1 - m)(r_1 (1 - m) + b_1 k_2)}{a_2 b_1 k_1} < r_1 \right)$ then from Lemma 2.1, we obtain

$$\liminf_{t \rightarrow +\infty} x(t) \geq \frac{\xi_1}{b_1} \equiv \omega_1. \tag{5}$$

Further, from the predator equation of (1), we have

$$\frac{dy}{dt} \geq y \left(r_2 - \frac{a_2 y}{k_2} \right),$$

which on using Lemma 2.1 gives

$$\liminf_{t \rightarrow +\infty} y(t) \geq \frac{r_2 k_2}{a_2} \equiv \omega_2. \tag{6}$$

From the equations (3) and (4) together with Lemma 2.1, we have

$$\limsup_{t \rightarrow +\infty} x(t) \leq \frac{r_1}{b_1} \equiv \sigma_1, \quad \limsup_{t \rightarrow +\infty} y(t) \leq \frac{r_2(S_1(1-m) + k_2)}{a_2} \equiv \sigma_2. \tag{7}$$

Now choosing $\zeta_1 = \min(\omega_1, \omega_2)$ and $\zeta = \max(\sigma_1, \sigma_2)$, permanence (refer the Definition 2.3) of the system (1) is established. \square

2.2 Existence and stability of biomass equilibria

It is easy to verify that system (1) has the following three trivial equilibria (belonging to the boundary of \mathbb{R}_+^2 , i.e., at which one or more of the populations has zero density): (i) The trivial equilibrium $E_0 = (0, 0)$, (ii) The predator free axial equilibrium $E_1 = \left(\frac{r_1}{b_1}, 0\right)$, i.e., in the absence of predator population, prey population reaches its carrying capacity. (iii) The prey extinction equilibrium point $E_2 = \left(0, \frac{r_1 k_2}{a_2}\right)$.

Theorem 2.5.

For the model system (1):

- (a) The origin $E_0 = (0, 0)$ is always unstable.
- (b) The axial equilibrium $E_1 = \left(\frac{r_1}{b_1}, 0\right)$ is always a saddle point.
- (c) The axial equilibrium $E_2 = \left(0, \frac{r_1 k_2}{a_2}\right)$ is a saddle point if $\frac{r_2 k_2(1-m)}{a_2} < \frac{r_1 k_1}{a_1}$ and a stable point if $\frac{r_2 k_2(1-m)}{a_2} > \frac{r_1 k_1}{a_1}$.

Proof. One can easily prove (a) and (b) just by computing the jacobian matrix at E_0 and E_1 respectively. It should be noticed that the stabilities of E_0 and E_1 are independent of the prey reserve m . Here we prove the part (c).

(c) The Jacobian matrix of the system (1) evaluated at the $\left(0, \frac{r_1 k_2}{a_2}\right)$ is given by

$$J_2 = \begin{pmatrix} r_1 - \frac{a_1(1-m)r_2 k_2}{a_2 k_1} & 0 \\ \frac{(1-m)r_2}{a_2} & -r_2 \end{pmatrix},$$

The eigenvalues of J_2 at E_2 are $\lambda_1 = a_{11} = r_1 - \frac{a_1(1-m)r_2 k_2}{a_2 k_1} > 0$ and $\lambda_2 = a_{22} = -r_2$. Hence from the coexistence condition (9) of E_* , we have $\lambda_1 > 0$. Thus the result follows. \square

Now we discuss existence and uniqueness of the interior (positive) equilibrium solution.

Theorem 2.6. *There exist a unique interior $E_* = (x^*, y^*)$ equilibrium solution if*

$$\frac{r_2 k_2(1-m)}{a_2} < \frac{r_1 k_1}{a_1}. \tag{8}$$

Proof. The interior equilibrium solution E_* satisfies the following equilibrium equations

$$(r_1 - b_1 x^*)((1-m)x^* + k_1) = (1-m)a_1 y^*, \tag{9}$$

$$y^* = \frac{r_2(x^*(1-m) + k_2)}{a_2}. \tag{10}$$

Obviously, the equilibrium solution E_* is one of the roots of the following quadratic equation

$$a_2 b_1(1-m)x^2 + (a_1 r_2(1-m)^2 - a_2 r_1(1-m) + a_2 b_1 k_1)x + a_1 r_2 k_2(1-m) - a_2 r_1 k_1 = 0,$$

and thus,

$$x_{\pm} = \frac{1}{2a_2b_1(1-m)} \left(-(a_1r_2(1-m)^2 - a_2r_1(1-m) + a_2b_1k_1) \pm \sigma^{\frac{1}{2}} \right), \tag{11}$$

where $\sigma = (a_1r_2(1-m)^2 - a_2r_1(1-m) + a_2b_1k_1)^2 - 4a_2b_1(1-m)(a_1r_2k_2(1-m) - a_2r_1k_1)$. Thus one can easily see after some algebraic computations that under the condition (8), σ is positive and system (1) possesses unique interior equilibrium E_* given by

$$x^* = \frac{1}{2a_2b_1(1-m)} \left(-(a_1r_2(1-m)^2 - a_2r_1(1-m) + a_2b_1k_1) + \sigma^{\frac{1}{2}} \right), \tag{12}$$

$$y^* = \frac{r_2(x^*(1-m) + k_2)}{a_2}. \tag{13}$$

Remark 2.7. Under the assumption that the extent to which the environment provides protection to both the predator and prey is same (i.e. $k_1 = k_2 = k$), the interior equilibrium solution is given by (x^*, y^*) , where $x^* = \frac{1}{a_2b_1} (a_2r_1 - a_1r_2(1-m))$ and $y^* = \frac{r_2}{a_2^2b_1} (a_2b_1k + (1-m)(a_2r_1 - a_1r_2(1-m)))$ provided $a_2r_1 > a_1r_2$. □

In the Figure 1, one can see all the possible configurations of both the isoclines with respect to the prey reserve m . In Figures 1(a)-1(d), dashed straight line is prey nullcline and solid straight line is predator nullcline.

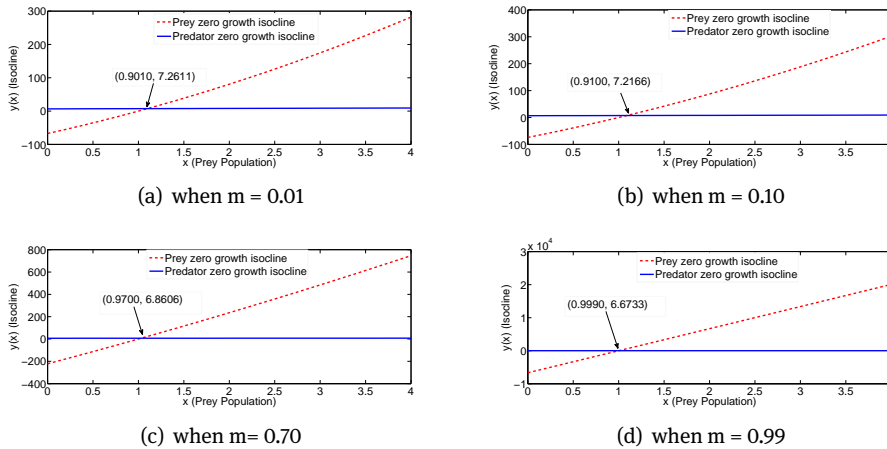


Figure 1: Figure showing existence of interior equilibrium solution and the prey zero growth rate isocline and predator zero growth rate isocline for different values of m mentioned under the graphs.

Remark 2.8. Let J_{E^*} denotes jacobian matrix of system (1) at E^* . If $b_1 - \frac{a_1(1-m)^2y^*}{(x^* + k_1)^2} > 0$, then determinant of J_{E^*} is positive and trace of J_{E^*} remains negative. Hence the interior equilibrium point E_* is locally asymptotically stable if $b_1 - \frac{a_1(1-m)^2y^*}{(x^* + k_1)^2} > 0$. Since if $b_1 - \frac{a_1(1-m)^2y^*}{(x^* + k_1)^2} > 0$ holds for $m = m_1$, then $b_1 - \frac{a_1(1-m)^2y^*}{(x^* + k_1)^2} > 0$ always holds for all $m = m_2 > m_1$. Hence the prey reserve m leaves positive effect on the local stability of E_* .

To prove the global asymptotic stability of interior equilibrium, we need the following lemma [15].

Lemma 2.9. Fluctuation Lemma. [10, 16, 19] Let, $f : [b, \infty) \rightarrow \mathbb{R}$, be a bounded and differentiable function. Let f', f^∞ and f_∞ denote the derivative of f , limit superior and limit inferior of f as $t \rightarrow \infty$ respectively. Then \exists sequences s_k and t_k such that

- (i.) $f(s_k) \rightarrow f^\infty, f'(s_k) \rightarrow 0,$
- (ii.) $f(t_k) \rightarrow f_\infty, f'(t_k) \rightarrow 0.$

Theorem 2.10. *In addition to the condition obtained in the result (iii) of Proposition 2.4, the system (1) has unique interior equilibrium solution (x^*, y^*) which is globally asymptotically stable under the condition*

$$2a_2b_1\omega_1 + (a_2b_1k_1 - a_2r_1(1 - m) - a_1r_2(1 - m)^2) > 0, \tag{14}$$

where ω_1 is defined in the proof of Proposition 2.4.

Proof. Note that the result (iii) of Proposition 2.4 implies $a_1k_2r_1(1 - m) < a_2k_1r_1$, that is, condition (8) of the Theorem 2.6 holds. Thus, the model system (1) has a unique positive equilibrium. Let $(x(t), y(t))$ be any positive solution of the model system (1). Hence from the previous discussion, $\bar{x} \equiv \limsup_{t \rightarrow \infty} x(t) \geq \hat{x} \equiv \liminf_{t \rightarrow \infty} x(t) \geq \omega_1$, $\bar{y} \equiv \limsup_{t \rightarrow \infty} y(t) \geq \hat{y} \equiv \liminf_{t \rightarrow \infty} y(t) \geq \omega_2$, where ω_1 and ω_2 are defined in the proof of Proposition 2.4.

Now, we claim that $\bar{x} = \hat{x}$. To prove this, on the contrary, let us suppose that $\bar{x} > \hat{x}$. Fluctuation Lemma 2.9 says that there exist four sequences $\xi_n \rightarrow \infty, \eta_n \rightarrow \infty, \tau_n \rightarrow \infty$ and $\sigma_n \rightarrow \infty$ such that $\dot{x}(\xi_n) \rightarrow 0, \dot{x}(\eta_n) \rightarrow 0, x(\xi_n) \rightarrow \bar{x}, x(\eta_n) \rightarrow \hat{x}, \dot{y}(\tau_n) \rightarrow 0, \dot{y}(\sigma_n) \rightarrow 0, y(\tau_n) \rightarrow \bar{y}, y(\sigma_n) \rightarrow \hat{y}$ as $n \rightarrow \infty$.

From the second equation of (1), we have the following inequalities:

$$\dot{y}(\tau_n) \leq \left(r_2 - \frac{a_2y(\tau_n)}{(1 - m)\sup_{t \geq \tau_n} x(t) + k_2} \right) y(\tau_n), \dot{y}(\tau_n) \geq \left(r_2 - \frac{a_2y(\tau_n)}{(1 - m)\inf_{t \geq \tau_n} x(t) + k_2} \right) y(\tau_n).$$

Taking $n \rightarrow \infty$, we obtain $0 \leq \left(r_2 - \frac{a_2\bar{y}}{(1 - m)\bar{x} + k_2} \right) \bar{y}, 0 \geq \left(r_2 - \frac{a_2\bar{y}}{(1 - m)\hat{x} + k_2} \right) \bar{y}$. Those in turn imply

$$\frac{r_2((1 - m)\hat{x} + k_2)}{a_2} \leq \bar{y} \leq \frac{r_2((1 - m)\bar{x} + k_2)}{a_2}. \tag{15}$$

In the similar fashion, one can also obtain the following inequality

$$\frac{r_2((1 - m)\hat{x} + k_2)}{a_2} \leq \hat{y} \leq \frac{r_2((1 - m)\bar{x} + k_2)}{a_2}. \tag{16}$$

Furthermore, from the first equation of (1), we have

$$\dot{x}(\xi_n) = x(\xi_n) \left(r_1 - b_1x(\xi_n) - \frac{a_1(1 - m)y(\xi_n)}{(1 - m)x(\xi_n) + k_1} \right),$$

which in turn gives

$$\dot{x}(\xi_n) \leq x(\xi_n) \left(r_1 - b_1x(\xi_n) - \frac{a_1(1 - m)\inf_{t \geq \xi_n} y(t)}{(1 - m)x(\xi_n) + k_1} \right). \tag{17}$$

Equation (17) together with $n \rightarrow \infty$ implies that

$$0 \leq \bar{x} \left(r_1 - b_1\bar{x} - \frac{a_1(1 - m)\hat{y}}{(1 - m)\bar{x} + k_1} \right). \tag{18}$$

With the help of Eq. (16), Eq. (18) gives

$$(a_2r_1(1 - m) - a_2b_1k_1)\bar{x} - a_2b_1(1 - m)\bar{x}^2 + a_2r_1k_1 \geq a_1r_2(1 - m)((1 - m)\hat{x} + k_2). \tag{19}$$

Similarly, we have

$$(a_2r_1(1 - m) - a_2b_1k_1)\hat{x} - a_2b_1(1 - m)\hat{x}^2 + a_2r_1k_1 \leq a_1r_2(1 - m)((1 - m)\bar{x} + k_2). \tag{20}$$

Applying (-1)(19)+(20), we obtain

$a_2b_1(1 - m)(\bar{x} + \hat{x}) + (a_2b_1k_1 - a_2r_1(1 - m) - a_1r_2(1 - m)^2) \leq 0$, which contradicts (14). So, $\bar{x} = \hat{x}$, and our claim is true. Hence, $\lim_{t \rightarrow \infty} x(t)$ exists and is denoted by x^* . From (15) and (16), we observe that $\lim_{t \rightarrow \infty} y(t)$ exists and we denote it by y^* . One can also observe that (x^*, y^*) satisfies (1), that is, (x^*, y^*) is a positive equilibrium of the model system (1). This completes the proof as the positive equilibrium is unique. \square

Now, we establish the global asymptotic stability of the interior equilibrium solution $E^* = (x^*, y^*)$ of model system (1).

Theorem 2.11. Let $S_1 = \max \{x(0), \frac{r_1}{b_1}\}$ and $\limsup_{t \rightarrow +\infty} \sigma_2 \equiv \sigma_2 = \frac{r_2(S_1(1-m) + k_2)}{a_2}$. If (i) $\sigma_2 < \frac{r_1 k_1}{a_1(1+k_1)}$, (ii) $k_1 < 2k_2$ and (iii) $4(r_1 + b_1 k_1) < a_1(1-m)^2$ hold, then interior equilibrium solution $E^* = (x^*, y^*)$ of model system (1) is globally asymptotically stable.

Proof. With the help of the equilibrium equations (9) and (10), the model system (1) takes the following form

$$\frac{dx}{dt} = x \left(-b_1(x - x^*) + \frac{(1-m)a_1 y^*}{(1-m)x^* + k_1} - \frac{(1-m)a_1 y}{(1-m) + k_1} \right), \quad (21)$$

$$\frac{dy}{dt} = y a_2 \left(\frac{y^*}{(1-m)x^* + k_2} - \frac{y}{(1-m)x + k_2} \right).$$

Now, consider the function $V(x, y) : \mathbb{R}_+^2 \rightarrow \mathbb{R}$, such that

$$V(x, y) = V_1(x, y) + V_2(x, y), \quad (22)$$

where $V_1(x, y) = ((1-m)x^* + k_1) \left(x - x^* - x^* \ln(x/x^*) \right)$, $V_2(x, y) = \frac{a_1(1-m)((1-m)x^* + k_2)}{a_2} \left(y - y^* - y^* \ln(y/y^*) \right)$. This particular kind of Lyapunov function has been considered widely (see, e.g., [17, 21, 23]). Obviously this function is well defined and continuous on $\text{Int}(\mathbb{R}_+^2)$. $V(x, y)$ is positive in the interior of \mathbb{R}_+^2 except at $E^*(x^*, y^*)$ and $V(x, y)$ vanishes at $E^*(x^*, y^*)$. Further, $\frac{\partial V_1(x)}{\partial x} > 0$ when $x > x^*$, $\frac{\partial V_1(x)}{\partial x} < 0$ when $x < x^*$ and $\frac{\partial V_2(y)}{\partial y} > 0$ when $y > y^*$, $\frac{\partial V_2(y)}{\partial y} < 0$ when $y < y^*$. Hence, $V(x, y)$ takes minimum value at (x^*, y^*) . Now, we evaluate the time derivative of this scalar valued function along the solutions of the model system (1).

The time derivatives of V_1 and V_2 along the solution of (21) are

$$\begin{aligned} \frac{dV_1}{dt} &= ((1-m)x^* + k_1) \frac{(x-x^*)}{x} \frac{dx}{dt} = ((1-m)x^* + k_1)(x-x^*) \left(-b_1(x-x^*) \right. \\ &\quad \left. + \frac{-a_1(1-m)k_1(y-y^*) + a_1(1-m)^2(y(x-x^*) - x(y-y^*))}{(x(1-m) + k_1)((1-m)x^* + k_1)} \right), \\ \frac{dV_2}{dt} &= \frac{a_1(1-m)((1-m)x^* + k_2)}{a_2} \frac{(y-y^*)}{y} \frac{dy}{dt} = a_1(1-m)((1-m)x^* \\ &\quad + k_2)(y-y^*) \frac{-k_2(y-y^*) + (1-m)(-x(y-y^*) + y(x-x^*))}{(x(1-m) + k_2)((1-m)x^* + k_2)}. \end{aligned}$$

Differentiating (22) and putting the values of $\frac{dV_1}{dt}$ and $\frac{dV_2}{dt}$ and after some algebraic manipulations, we obtain

$$\begin{aligned} \frac{dV}{dt} &= \left(-b_1((1-m)x^* + k_1) + \frac{a_1(1-m)^2 y}{(1-m)x + k_1} \right) (x-x^*)^2 \\ &\quad + \left(-a_1(1-m) + \frac{a_1(1-m)^2 y}{(1-m)x + k_2} \right) (x-x^*)(y-y^*) - a_1(1-m)(y-y^*)^2. \end{aligned}$$

The right hand side of the above expression should be considered as a quadratic form in the variables $(x-x^*)$ and $(y-y^*)$ which is negative definite (i.e. $\frac{dV}{dt} < 0$) if the following matrix

$$A = \begin{pmatrix} -g(x, y) & -h(x, y) \\ -h(x, y) & a_1 \end{pmatrix},$$

where $g(x, y) = -b_1((1 - m)x^* + k_1) + \frac{a_1(1 - m)^2 y}{(1 - m)x + k_1}$ and $h(x, y) = \frac{1}{2} \left(-a_1(1 - m) + \frac{a_1(1 - m)^2 y}{(1 - m)x + k_2} \right)$ is positive definite. This is positive definite if and only if

(i) $g(x, y) < 0$ and

(ii) $\Phi(x, y) = -a_1 g(x, y) - h^2(x, y) < 0$.

From (9), we have $g(x, y) = \frac{1}{x^*} [-r_1((1 - m)x^* + k_1) + (1 - m)a_1 y^*] + \frac{a_1(1 - m)^2 y}{(1 - m)x + k_1}$. From (7), we have $g(x, y) \leq -r_1(1 - m) + a_1(1 - m)[1 + \frac{1}{k_1}] \sigma_2$. As $0 \leq m < 1$, hence if the hypothesis of the Theorem 2.11 holds, we have $g(x, y) < 0$ for all $t \geq 0$.

Furthermore, since (for fixed x) $\frac{\partial \Phi(x, y)}{\partial y} = -\frac{a_1^2(1 - m)^2}{x(1 - m) + k_1} - \frac{1}{2} \left(\frac{-a_1^2(1 - m)^2}{x(1 - m) + k_2} + \frac{-a_1^2(1 - m)^2 y}{(x(1 - m) + k_2)^2} \right)$

< 0 , then $\frac{\partial^2 \Phi}{\partial y^2} = -\frac{a_1^2(1 - m)^2}{2((1 - m)x + k_2)^2} < 0$. Hence, $\frac{\partial \Phi(x, y)}{\partial y}$ is strictly decreasing in \mathbb{R}^+ with respect to y .

One can easily observe that $\frac{\partial \Phi(x, y)}{\partial y} \Big|_{y=0} = (1 - m)^2 a_1^2 \frac{-x(1 - m) - 2k_2 + k_1}{2((1 - m)x + k_1)((1 - m)x + k_2)}$. Thus if $k_1 < 2k_2$

then $\frac{\partial \Phi(x, y)}{\partial y} \Big|_{y=0} < 0$ in \mathbb{R}^+ and hence $\Phi(x, y)$ is strictly decreasing in \mathbb{R}^+ . This gives $\Phi(x, y) < \Phi(x, 0)$ i.e.

$\Phi(x, y) < a_1 b_1 (x^* + k_1) - \frac{1}{4} a_1^2 (1 - m)^2$.

Using (7), we have $\Phi(x, y) < a_1 \left(r_1 + b_1 k_1 - \frac{1}{4} a_1 (1 - m)^2 \right)$. Hence if $4(r_1 + b_1 k_1) < a_1 (1 - m)^2$ then $\Phi(x, y) < 0$.

Thus, we conclude that if the hypotheses of Theorem 2.11 are satisfied, then $\frac{dV}{dt} < 0$ along all the trajectories in \mathbb{R}_+^2 except $E^* = (x^*, y^*)$. Therefore $E^* = (x^*, y^*)$ is globally asymptotically stable. \square

3 Prey reserve and steady states of predator and prey densities

From the Theorem 2.11, we have

$$\lim_{t \rightarrow \infty} x(t) = x^* > 0, \quad \lim_{t \rightarrow \infty} y(t) = y^* > 0. \tag{23}$$

We have seen in the subsection 2.2 that x^* and y^* depend on the coefficients of system (1) but independent of the solutions of the system (1). Hence, (23) clearly shows that the prey refuge has no influence on the permanence of the system, as for all $m \in [0, 1)$, system (1) is always permanent. Kar [8] and Ma [13] showed that when the effect of prey refuge are strong enough, predator will extinct (i.e., predator reach at the level of sufficiently low abundance) and prey population reach their carrying capacity eventually. The result of this study are consistent with those of [14] and contrast with that of Kar [8]. They assumed that predator species have no other option for food except prey while in our model the assumption of $r_2 > 0$ being a positive constant determines that predator species not only take x (prey) as food, but also has other food sources.

Let $k_1 = k_2 = k$. We notice that (x_1^*, y_1^*) , where $x_1^* = \frac{a_2 r_1 - a_1 r_2}{a_2 b_1}$, $y_1^* = \frac{r_2}{a_2^2 b_1} (a_2 b_1 k + a_2 r_1 - a_1 r_2)$ is the interior equilibrium solution of (1) without prey refuge. Clearly for all $m \in [0, 1)$, $a_2 r_1 - a_1 (1 - m) r_2 > a_2 r_1 - a_1 r_2$. Thus for any fixed value of prey refuge $m \in [0, 1)$, the prey refuge increases the prey density. Moreover we also have $\frac{dx^*}{dm} = \frac{a_1 r_2}{a_2 b_1} > 0$, for all $m \in [0, 1)$. Hence x^* is strictly increasing function of m .

Now we determine the effect of prey refuge on the steady state of predator species. The derivative of y^* with respect to m gives

$$\frac{dy^*}{dm} = \frac{r_2}{a_2^2 b_1} \left(-a_2 r_1 + 2a_1 r_2 (1 - m) \right).$$

We discuss this in the following two cases:

(i) If $2a_1 r_2 \leq a_2 r_1$ then $\frac{dy^*}{dm} < 0 \forall m \in [0, 1)$. Hence y^* is a strictly decreasing function of m . Here $y^*(m)$ takes its maximum value at $m = 0$, that is, $(y^*(m))_{\max} = \frac{r_2}{a_2^2 b_1} (a_2 b_1 k + a_2 r_1 - a_1 r_2)$.

(ii) If $2a_1r_2 > a_2r_1$ then $\frac{dy^*}{dm} > 0$ for all $m < m_1$ and $\frac{dy^*}{dm} < 0$ for all $m > m_1$, where $m_1 = 1 - \frac{a_2r_1}{2a_1r_2}$. Thus y^* is a strictly increasing function of m on $(0, m_1)$ while y^* is a strictly decreasing function of m on $(m_1, 1)$. Moreover, y^* obtains its maximum value at $m = m_1$ which is given by $y^*(m_1) = \frac{r_2}{a_2^2b_1} \left(a_2b_1k + (1 - m_1)(a_2r_1 - a_1r_2(1 - m_1)) \right)$.

4 Numerical simulations

Consider the model system (1) with the following set of parametric values:

$$r_1 = 10, r_2 = 1, b_1 = 10, a_1 = a_2 = 1.5, k_1 = 10, k_2 = 10, m = 0.01. \tag{24}$$

One can compute that $b_1 - \frac{a_1(1 - m)^2y^*}{(x^* + k_1)^2} = 10 - \frac{1.47 \times 7.26}{10.90} = 9.0209 > 0$ and $a_1r_2(1 - m)(r_1(1 - m) + b_1k_2) = 1.485 \times 109 = 161.865 < 1500 = a_2b_1k_1r_1$. Hence the set of parametric values given in (24) satisfy the local stability condition given in Remark 2.8 and the permanence condition obtained in Proposition 2.4. We observe that the parametric values given in (24) also satisfy the global stability condition (14) of the Theorem 2.10 as $2a_2b_1\omega_1 + (a_2b_1k_1 - a_2r_1(1 - m) - a_1r_2(1 - m)^2) = 26.7 + (150 - 15 \times 0.99 - 1.5 \times 0.98) = 176.7 - 16.32 = 150.38 > 0$. Thus, for the set of parametric values (24), the unique interior equilibrium solution ($E^* = (0.9010, 7.2610)$) is globally asymptotically stable (see Figures 2(a) and 2(b)).

We vary the parameter m (the prey reserve) while keeping other parameters fixed as mentioned in (24). For the set of parametric values (24), we have, $a_2r_1 - a_1(1 - m)r_2 = 15.52 > a_2r_1 - a_1r_2 = 13.50$ and $2a_1r_2 = 3 \leq a_2r_1 = 15$. Hence the prey density increases with prey reserve m while predator density decreases (see Table 1 and Figures 3(a)-3(d)). Table 1 shows that the equilibrium value of predator population decreases with m whereas the interior equilibrium value of prey population increases with m . This indicates that prey refuge could influence the densities of both the prey and predator species. The Table 1 along with Figure 3 show that the model system (1) remains stable for all the values of prey reserve $m > 0.01$. This supports our conclusion obtained in the Remark 2.8.

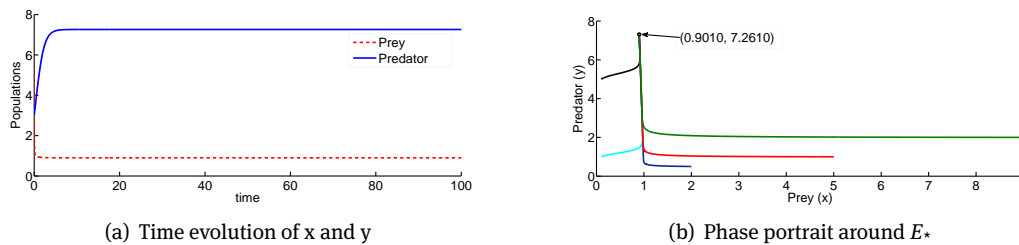


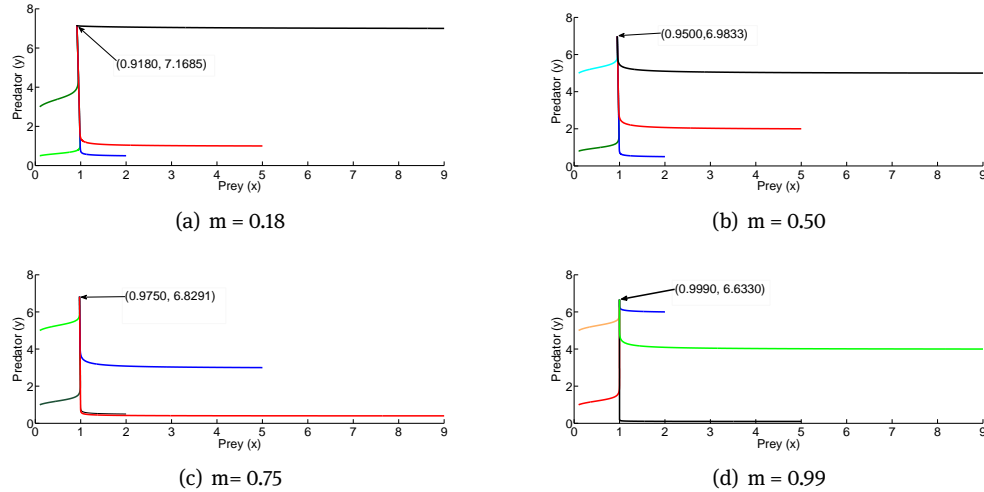
Figure 2: Solutions $x(t)$ and $y(t)$ in (x, y, t) and (x, y) of (1) with the initial conditions near E^* . The solid circle represents the corresponding equilibrium point.

5 Parameter estimation:

Model calibration is an indispensable part of the modelling process. Models, particularly involving system of differential equations, are characterized by dynamic variables and several unknown or poorly known constant parameters which is to be estimated from the given experimental data. Trial and error procedure employed for parameter estimation is unreliable and often impracticable when there are large number of con-

Table 1: Equilibrium values of x^* and y^* of the system (1) for different values of m

m (other parameters are same as defined in (24))	Equilibrium prey (x^*)	Equilibrium predator (y^*)
$m = 0.01$	0.9010	7.2610
$m = 0.18$	0.9180	7.1685
$m = 0.50$	0.9500	6.9833
$m = 0.75$	0.9750	6.8291
$m = 0.99$	0.9990	6.6630

**Figure 3:** The phase portrait of system (1) with different values of prey refuge m .

stant parameters in the model for estimation. On the other hand, numerical optimization procedures have shown as promising alternative for parameter estimation for non-linear dynamic models.

In our system (1), since model data is unknown therefore a twin experiment technique [28] is used to study the system behaviour. In this experiment, first the system (1) is solved for known parameter(s) and then the system response is randomly sampled at different time instant. We have sampled (50%) of the data from the generated response of the system. Further, since experimental data is always inherited with unwanted random noise, we introduce independent identically normally distributed homoscedastic noise in each of the observation of the constructed data. In the second step, the parameter(s) are estimated by optimization procedure which minimizes the residual sum of squares (RSS) from sampled experimental data with a constraint on permissible parameter values (for e.g., in system (1) $m \in [0, 1)$). For clarity, we present our analysis for the estimation of the single parameter i.e prey refuge (m) but similar analysis can be done for all constant parameters used in the model.

Let $y(t) = (y(t_1), y(t_2), \dots, y(t_N))$ denotes the response of the system (1) sampled at N different time instants (t_1, t_2, \dots, t_N) with random noise. $\hat{y}(t, \hat{m})$ is a function of unknown parameter m (prey refuge).

Then related optimization problem for estimating \hat{m} can be formulated as

$$\begin{aligned} & \text{Minimize} && \text{RSS}(\hat{m}) \equiv \text{RSS}(y(t), \hat{y}(t, \hat{m})) \\ & \text{subject to :} && 0 \leq \hat{m} < 1 \end{aligned} \quad (24)$$

where, $\text{RSS}(y(t), \hat{y}(t, m)) = \sum_{i=1}^N (y(t_i) - y(t_i, m))^2$. Above problem is a non-linear least square problem. We propose the use of Levenberg-Marquardt (LM) method [29, 32] as solution algorithm for solving parameter estimation problem arising from system (1). Among plethora of optimization algorithms, LM method is an

efficient and robust method for solving non-linear least square problem [33–35]. The noteworthy feature of the algorithm is its less sensitivity to initial guess of the solution. This fact increases its applicability over wide range of fields.

LM method is an iterative procedure which is known to be inherits the properties of two optimization algorithms – Gradient decent methods and Gauss-Newton method [30, 31]. A LM step update can be interpreted as interpolation of step update of these two algorithms. LM method is provided with initial guess for parameter value and further updates are adaptively behaves like gradient decent step update or Gauss-Newton step update. The algorithm behaves more like gradient decent method if the current approximation is far from the optimal and otherwise it acts more like Gauss-Newton method. In this way, LM methods combines the power of both gradient decent methods and Gauss-Newton method.

Table 2: Parameter estimation and residual sum of squares by LM method

Reference Value (m)	Estimated value (\hat{m})	Minimum RSS
0.18	0.181903	0.246074
0.50	0.510249	0.176209
0.75	0.746447	0.208821
0.99	0.999998	0.267325

We employ LM method for solving the optimization problem in equation (5). Table 2 shows the estimated value by LM method for different values of reference parameter value (m). It is clearly depicted from the table that difference between reference values and that of estimated values by LM method is negligible. We computed the system response and phase portrait for these estimated values and compared with the system response with reference values shown in Figure 4 and Figure 5 respectively. Both the figures clearly show the faithful reconstruction of system responses for different values of m . It should be noted that the minimum sum of residual squares is not exactly zero (refer Table 2), therefore, it is not an exact recovery, however this discrepancy cannot be easily seen in figures 4 and 5. This is due differences in system response is at very higher precision.

6 Discussion

Most of the theories in the area of predator-prey system deal with predator response to prey (e.g., functional, developmental switching) or predator responses to other predators (e.g., mutual interference). Comparatively little empirical or theoretical work have been carried about the effect of prey responses to predators (e.g., prey refuge) on the dynamics of the predator-prey interaction. Incorporating prey refuge into a modified Leslie-Gower predator-prey system (1) provides more realistic model, since many prey mite populations do have some form of spatial refuge available. This spatial refugia afford to prey some degree of protection from predation and reduce the chance of extinction due to predation. Motivated by this, in this paper, we have proposed and analyzed a mathematical eco-system (1) which addresses the combined effects of predator response to prey and prey response to predators (prey refuge) on the dynamics of the predator-prey interaction.

We have discussed the boundedness, persistence and permanence behaviour of the model system (1) under certain conditions on the parameters involved in the model system (1). The local stability of all the trivial equilibrium solutions along with uniqueness, existence and global stability of the non-trivial equilibrium E_* have also been investigated. The theoretical findings and parametric conditions obtained during the analytical study of uniqueness, existence, local stability, global stability of interior equilibrium E_* and the effect of prey reserve on the dynamics of the system have been validated by numerical examples (see the parametric values mentioned in (24)). It is proved that the E_2 is a saddle point under the co-existence condition of E_* and in this case the stability of E_2 is independent of prey reserve m . We have also given an interesting appli-

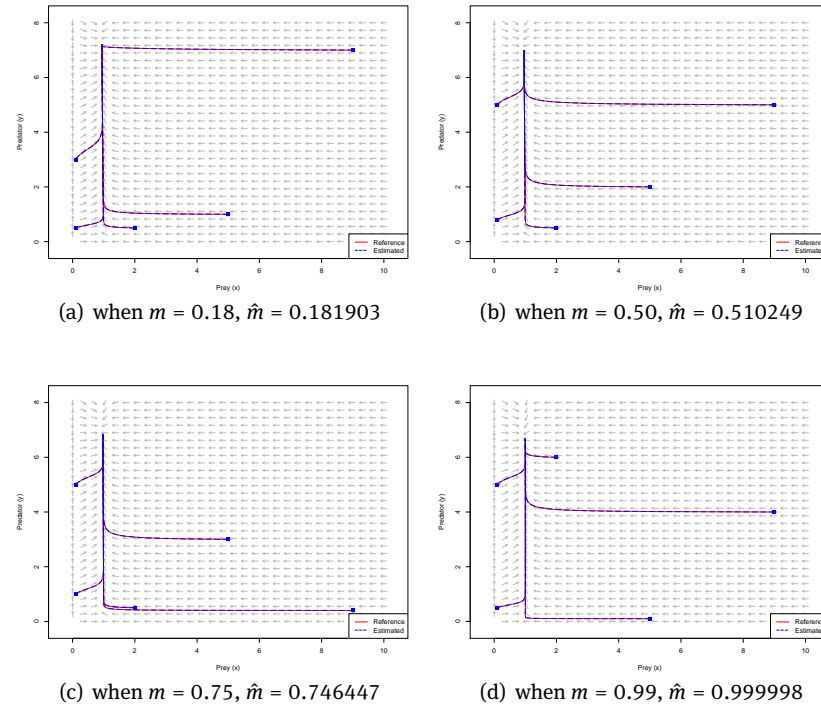


Figure 4: Figure showing differences in phase plot of system (1) for the phase portrait of true value m and estimated parameter value (\hat{m}) by LM method.

cation of Fluctuation lemma to prove existence and global stability of E_* followed by numerical simulation (Theorem 2.10 and simulations for the system (1)).

The existence of refuges can have important effect on the coexistence and stability of predator-prey system. The effect of prey reserve is discussed thoroughly in section 3. It is shown numerically as well as theoretically (see Remark 2.8) that the prey reserve leaves positive effect on the stability of E_* . The analysis of the stability and permanence of the considered systems reveal the following conclusions:

(i) It is shown that the prey refuge has no influence on the persistence property of the system. The predator species depend not only on the prey species but also on other food sources (as $r_2 > 0$). Thus our result is in contrast with Kar [8] who showed that when the effect of prey refuge is strong enough, the predator will extinct and prey population reach their carrying capacity.

(ii) The equilibrium prey density increases with prey reserve m while equilibrium predator density decreases with increase in prey reserve. Our results are in contrast with those of Ma et al. [13].

(iii) Our results also show that the effect of prey refuge plays an important role in determining the stability of the interior equilibrium solution (E_*). The refuge used by prey can stabilize the interior equilibrium point (stabilizing effect).

Parameter identifiability: Finally, recognizing the importance of parameter identification for system (1), our numerical study suggests the use of LM method for the estimation. It can be clearly seen from Table 2, negligible difference between the reference and estimated parameter value. By comparing system responses from the reference with that of estimated parameter values, we can conclude the reliability of LM method for parameter estimation in system (1). To establish the robustness of suggested algorithm, we have used sampled data corrupted with random noise. The result obtained in this study are very promising and encouraging.

In this study, we have focused on the identifiability of the parameters for the proposed modified Leslie-Gower predator-prey interaction model. A natural extension for the future work is to consider the real predator-prey populations data for identifiability of parameters. Though current study establishes that a sim-

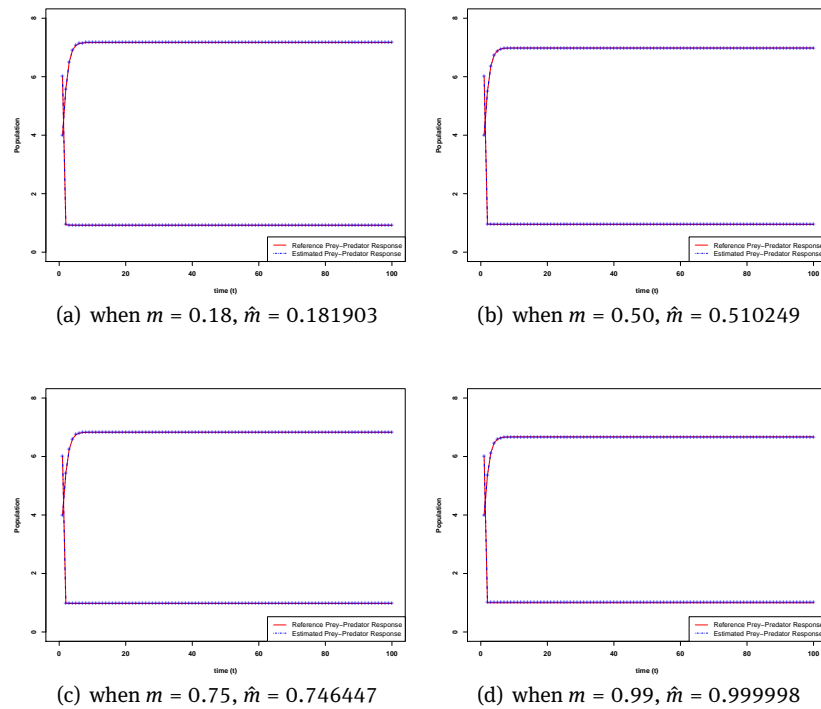


Figure 5: Figures showing differences in solutions $x(t)$ and $y(t)$ of system (1) for different value of true parameter value m and estimated parameter value (\hat{m}) by LM method.

ple population-based algorithm is effective in estimation of unknown parameters, it will be interesting to compare estimating capabilities of more advanced population-based algorithms specifically over predator-prey interaction models.

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