Some Recent Results on Certain Stochastic Predator-Prey Models

N.H. Du, N.H. Dang, and G. Yin

Hanoi National University and Wayne State University

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Outline

1. Introduction
2. Threshold between Extinction and Permanence
3. Degenerate Case
4. Numerical Examples
5. Concluding Remarks

Introduction

- As the building blocks of the bio- & ecosystems, the basic premise of the predator-prey models is: species compete, evolve, and disperse for the purpose of seeking resources to sustain their struggle and existence.
- Denote two population sizes at time t by $x(t)$ and $y(t)$.
- A general deterministic model called Kolmogorov system is

$$\begin{cases} \dot{x}(t) = xf(x,y), \\ \dot{y}(t) = yg(x,y). \end{cases}$$

- When $f(x,y) = b - py$ and $g(x,y) = cx - d$: Lotka-Volterra model.
  x: prey (example, rabbit) y: predator (fox)

Work from the PDE community: Ni and co-authors.

Some references for stochastic models: Hofbauer & Sigmund (1998), Mao, Sabais, & Renshaw (2003), Bao, Mao, Y, Yuan (2011), Zhang, Sun, & Jin (2012)

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- Holling initiated the study of functional response, where he introduced several types of such responses.
- Holling type II functional response is characterized by a decelerating intake rate following from the assumption that the consumer is limited by its capacity to process food.
- Similar to Holling-type functional response with an extra term describing mutual interference by predators, Beddington and DeAngelis and colleagues introduced the Beddington-DeAngelis functional response

Introduction (cont.)

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- A typical stochastic predator prey model with Beddington-DeAngelsis functional response is

$$\begin{cases} dx(t) = x(t)\big(a_1 - b_1 x(t) - \dfrac{c_1 y(t)}{m_1 + m_2 x(t) + m_3 y(t)}\big)dt + \alpha x(t) dB_1(t), \\ dy(t) = y(t)\big(-a_2 - b_2 y(t) + \dfrac{c_2 x(t)}{m_1 + m_2 x(t) + m_3 y(t)}\big)dt + \beta y(t) dB_2(t), \end{cases} \tag{1.1}$$

where $a_i, b_i, c_i, m_i > 0$, $\alpha \neq 0, \beta \neq 0$, and $B_1(\cdot), B_2(\cdot)$ are two mutually independent Brownian motions.

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- Much effort has been devoted to finding conditions needed for stochastic permanence. Using suitable Lyapunov-type functions, some conditions for extinction or permanence were also provided and ergodicity was investigated.

Stochastic Permanence

Definition 1.1

The population system is said to be stochastically permanent if for any $\varepsilon \in (0,1)$, there exist positive constants $H = H(\varepsilon), K = K(\varepsilon)$ such that

$$\liminf_{t\to\infty} P\{|x(t)| \geq H\} \geq 1-\varepsilon,$$
$$\liminf_{t\to\infty} P\{|x(t)| \leq K\} \geq 1-\varepsilon,$$

where $x(t)$ is the solution of the population system with any initial condition $x(0)$.

It will reach extinction if $\lim_{t\to\infty} |x(t)| = 0$ a.s.

A Result of Ji and Jiang (2011)

Theorem 1.2

- *Assume*

$$(c_2 - a_2 m_2)a_1/b_1 > a_2 m_1,\ b_1 > a_1 m_2/(m_1 + m_2 x^*)$$

and $\alpha > 0, \beta > 0$ *such that*

$$\delta < \min\{c_2(b_1 - m_2(a_1 - b_1 x^*)/m_1)(m_1 + m_3 y^*)(x^*)^2, \\ b_2 c_1 (m_1 + m_2 x^*)(y^*)^2\},$$

where

$$\delta = c_2 x^* \alpha^2/2 + c_1 y^* \beta^2/2$$

and (x^*, y^*) *is the positive equilibrium of the corresponding deterministic system. Then there is a stationary distribution* $\pi(\cdot)$ *for the system.*

- $\lim_{t\to\infty} y(t) = 0$ *a.s. if* $a_2 + \dfrac{\beta^2}{2} \geq \dfrac{c_2}{m_2}$.

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- We also consider the degenerate case when $B_1(\cdot) = B_2(\cdot)$.
- In lieu of finding a suitable Lyapunov function, we analyze the asymptotic properties of solutions on the boundary to give the threshold λ. Hence, our method can be applied to other stochastic predator-prey models with various types of functional response.

Threshold value separating extinction and permanence

- If $a_1 \leq \dfrac{\alpha^2}{2}$, then $\lim_{t\to\infty} x(t) = \lim_{t\to\infty} y(t) = 0$ a.s. Therefore, we always assume that $a_1 > \dfrac{\alpha^2}{2}$.

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- In the absence of the prey, the predator is eventually die out, that is, on the y-axis the solution converges to the origin a.s. On the x-axis we have the following equation

$$d\varphi(t) = \varphi(t)(a_1 - b_1\varphi(t))dt + \alpha\varphi(t)dB_1(t). \tag{2.1}$$

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- Putting $\theta(t) = \ln\varphi(t)$, it becomes

$$d\theta(t) = \left(a_1 - \frac{\alpha^2}{2} - b_1\exp\big(\theta(t)\big)\right)dt + \alpha dB_1(t). \tag{2.2}$$

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- (2.2) has a unique invariant probability measure with density

$$f^*(x) = C\exp\left(\frac{2a_1 - \alpha^2}{\alpha^2}x - \frac{2b_1}{\alpha^2}\exp(x)\right).$$

Let $\psi(t)$ be the solution to

$$d\psi(t) = \psi(t)\big(-a_1 + \frac{c_2}{m_2} - b_2\psi(t)\big)dt + \beta\psi(t)dB_2(t). \qquad (2.3)$$

Then $y(t) \leq \psi(t) \forall t \geq 0$ a.s. provided $y(0) = \psi(0) > 0$, Hence, w.p.1,

$$\limsup_{t\to\infty} \frac{1}{t} \ln y(t) \leq 0, \text{ and} \qquad (2.4)$$

$$\limsup_{t\to\infty} \frac{1}{t} \int_0^t y^p(s)ds \leq \widehat{K}_p \text{ for some } \widehat{K}_p > 0. \qquad (2.5)$$

Define the threshold

$$\lambda := -a_2 - \frac{\beta^2}{2} + \int_{-\infty}^{\infty} \frac{c_2 \exp(x)}{m_1 + m_2 \exp(x)} f^*(x)dx.$$

Threshold value between extinction and permanence

- In view of ergodicity, we have

$$\lim_{t\to\infty}\frac{1}{t}\int_0^t\Big[-a_2-\frac{\beta^2}{2}+\frac{c_2\varphi(s)}{m_1+m_2\varphi(s)}\Big]ds=\lambda \text{ a.s.}$$

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- Let $(x(t),y(t))$ be a solution to (1.1) with $(x(0),y(0))\in\mathbb{R}_+^{2,\circ}$. By comparison theorem, $x(t)\le\varphi(t)$ a.s. given that $x(0)=\varphi(0)$.

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- Let $(x(t),y(t))$ be a solution to (1.1) with $(x(0),y(0))\in\mathbb{R}_+^{2,\circ}$. By comparison theorem, $x(t)\le\varphi(t)$ a.s. given that $x(0)=\varphi(0)$.
- By comparing $y(t)$ and $\varphi(t)-x(t)$ and making use of the ergodicity of $\varphi(t)$ we can prove the following result.

Threshold value between extinction and permanence

Theorem 2.1

If $\lambda < 0$, then the predator is eventually extinct, that is, $\lim_{t\to\infty} y(t) = 0$ a.s. Moreover the distribution of $x(t)$ converges weakly to $\mu_-(\cdot)$, which is the unique invariant probability measure of $\varphi(t)$ on $\mathbb{R}_+$. Note that $\mu_-(\cdot)$ is the distribution of e^θ provided that θ is a random variable with density function f^*.

Ergodicity for the nondegenerate case

- If $\lambda > 0$, we can obtain $\liminf \frac{1}{t}\int_0^t y(s)ds > \overline{m}$ a.s. where $\overline{m}$ is some positive constant. This property enables us to prove the following result.

Theorem 2.2

If $\lambda > 0$, the process $(x(t), y(t))$ has an invariant probability measure concentrated on $\mathbb{R}_+^{2,\circ}$. Moreover, since (1.1) is non-degenerate, μ^* has support $\mathbb{R}_+^{2,\circ}$ and $\forall (x(0), y(0)) \in \mathbb{R}_+^{2,\circ}$,

(a) *For any μ^*-integrable $f(x,y) : \mathbb{R}_+^{2,\circ} \to \mathbb{R}$, we have*

$$\lim_{t\to\infty} \frac{1}{t}\int_0^t f(x(s), y(s))ds = \int f(x,y)\mu^*(dx, dy) a.s.$$

(b) $\lim_{t\to\infty} \|P(t,(x,y),\cdot) - \mu^*(\cdot)\| = 0 \, \forall (x,y) \in \mathbb{R}_+^{2,\circ}$ *where $\|\cdot\|$ is the total variation norm.*

Permanence and average values in time

Corollary 2.3

If $\lambda > 0$, the system (1.1) *is stochastically permanent in the sense that for any $\varepsilon > 0$, there is some $\delta \in [0,1]$ such that* $\liminf_{t\to\infty} P(t,x,y,[\delta,\delta^{-1}]^2) > 1-\varepsilon$. *Moreover, we have the following limits almost surely.*

$$0 < \lim_{t\to\infty} \frac{1}{t}\int_0^t x^p(s)ds = \int x^p \mu^*(dx,dy) < \infty\, \forall (x(0),y(0)) \in \mathbb{R}_+^{2,\circ},\ p > 0,$$
$$0 < \lim_{t\to\infty} \frac{1}{t}\int_0^t y^p(s)ds = \int y^p \mu^*(dx,dy) < \infty\, \forall (x(0),y(0)) \in \mathbb{R}_+^{2,\circ},\ p > 0.$$

Degenerate case

- Suppose that $B_1(\cdot) = B_2(\cdot) = W(\cdot)$. We consider the equation

$$\begin{cases} dx(t) = x(t)\big(a_1 - b_1 x(t) - \dfrac{c_1 y(t)}{m_1 + m_2 x(t) + m_3 y(t)}\big)dt + \alpha x(t) dW(t), \\ dy(t) = y(t)\big(-a_2 - b_2 y(t) + \dfrac{c_2 x(t)}{m_1 + m_2 x(t) + m_3 y(t)}\big)dt + \beta y(t) dW(t). \end{cases} \tag{3.1}$$

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- By the symmetry of Brownian motion, we can suppose $\alpha > 0$.
- Since estimates in the previous section still hold for this case, we have $\lim_{t\to\infty} y(t) = 0$ when $\lambda < 0$ while $x(t)$ converges weakly to the stationary distribution of μ_- of $\varphi(t)$. In what follows, we suppose $\lambda > 0$ for which the process has an invariant probability measure μ^* on $\mathbb{R}_+^{2,\circ}$.

Degenerate case

- Put $\xi(t) = \ln x(t)$ and $\eta(t) = \ln y(t)$, Equation (3.1) becomes
- $$\begin{cases} d\xi(t) = \Big(a_1 - \dfrac{\alpha^2}{2} - b_1 e^{\xi(t)} - \dfrac{c_1 e^{\eta(t)}}{m_1 + m_2 e^{\xi(t)} + m_3 e^{\eta(t)}}\Big)dt + \alpha dW(t), \\ d\eta(t) = \Big(-a_2 - \dfrac{\beta^2}{2} - b_2 e^{\eta(t)} + \dfrac{c_2 e^{\xi(t)}}{m_1 + m_2 e^{\xi(t)} + m_3 e^{\eta(t)}}\Big)dt + \beta dW(t). \end{cases} \tag{3.2}$$
- Denote by $(\xi^{u,v}(t), \eta^{u,v}(t))$ the solution with initial value (u,v) to (3.2) and let $\widehat{P}(t,(u,v),\cdot)$ be its transition probabilities.

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  where ϕ is taken from the set of piecewise continuous real valued functions defined on $\mathbb{R}_+$.

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- Let $(u_\phi(t,u,v),\ v_\phi(t,u,v))$ be the solution to Equation (3.3) with control ϕ and initial value (u,v).
- Denote by $\mathscr{O}_1^+(u,v)$ the reachable set from (u,v), that is the set of $(u',v') \in \mathbb{R}^2$ such that there exists a $t \geq 0$ and a control $\phi(\cdot)$ satisfying $u_\phi(t,u,v) = u', v_\phi(t,u,v) = v'$.

Degenerate case

- The following assumption guarantees the accessibility of (3.3), i.e., $\mathscr{O}_1^+(u,v)$ has non-empty interior for every $(u,v) \in \mathbb{R}^2$ (see V. Jurdjevic (1997)).

Assumption 3.1

The Lie algebra $L(u,v)$ *generated by* $A(u,v)$ *and* B *satisfies* $\dim L(u,v) = 2$ *at every* $(u,v) \in \mathbb{R}^2$. *In other words, the set of vectors* $A, B, [A,B], [A,[A,B]], [B,[A,B]], \ldots$ *spans* $\mathbb{R}^2$, *where*

$$A(u,v) = \begin{pmatrix} a_1 - \dfrac{\alpha^2}{2} - b_1 e^u - \dfrac{c_1 e^v}{m_1 + m_2 e^u + m_3 e^v} \\ -a_2 - \dfrac{\beta^2}{2} - b_2 e^v + \dfrac{c_2 e^u}{m_1 + m_2 e^u + m_3 e^v} \end{pmatrix}, B = \begin{pmatrix} \alpha \\ \beta \end{pmatrix},$$

and $[\cdot,\cdot]$ *denotes Lie bracket.*

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- Although verifying this assumption for our model in general involves cumbersome calculations, it seems that this assumption and even the stronger one given below are satisfied for any $a_i, b_i, c_i, m_1, m_2, m_3, \alpha > 0, i = 1, 2, \beta \neq 0$.

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The ideal L_0 in L generated by B satisfies $\dim L(u, v) = 2$ at every $(u, v) \in C$. In other words, the set of vectors $B, [A, B], [B, [A, B]], [B, [B, A, B]], \ldots$ spans $\mathbb{R}^2$.

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- Assumption 3.2, called Hörmander condition, guarantees that $\widehat{P}(t,u,v,\cdot)$ has density function.

Support of the invariant measure for degenerate case

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- Let A be a subset of $\mathbb{R}^2$ satisfying the property that for any $w_1,w_2\in A$, we have $w_2\in\overline{\mathscr{O}_1^+(w_1)}$. Then there is a unique maximal set $B\subset A$ such that this property still holds for B. Such B is called a control set. A control set C is said to be invariant if $\overline{\mathscr{O}_1^+(w)}\subset\overline{C}$ for all $w\in C$.

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- We use a result of Kliemann (1987) that the support of an ergodic i.p.m is an invariant control set provided Assumption 3.1 holds.

Support of the i.p.m for degenerate case

- Analyzing the control system (3.3), we claim that

Proposition 3.1

If $\lambda > 0$, there is $c^* > -\infty$ such that $C = \{(u', v') : v' - \frac{\beta}{\alpha} u' \leq c^*\}$ is contained in $\mathscr{O}_1^+(u, v)$ for any $(u, v) \in \mathbb{R}^2$. Consequently, C is the only invariant control set of the control system (3.3)*. In case $0 < \beta < \alpha$, we have $c^* = \infty$, hence $C = \mathbb{R}^2$.*

Support of the i.p.m for degenerate case

- Analyzing the control system (3.3), we claim that

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- It is proved in the previous section that $\lambda > 0$, there is an i.p.m π^* of (3.2). It follows from Proposition 3.1 that π^* is unique.

Properties in the invariant control set

- Applying results in W. Kliemann (1987) and K. Ichihara, K. Kunita (1974) we have for any $(u, v) \in C$ that if Assumption 3.1 holds then.

$$\mathbb{P}\Big\{ \lim_{t\to\infty} \frac{1}{t}\int_0^t f\big(\xi^{u,v}(s), \eta^{u,v}(s)\big)\,ds = \int_{\mathbb{R}^2} f(u', v')\pi^*(du', dv') \Big\} = 1. \tag{3.4}$$

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- Moreover, if Assumption 3.2 is satisfied,

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- We aim to prove that (3.4) (under Assumption 3.1) and (3.5) (under Assumption 3.2) hold for all $(u,v)\in\mathbb{R}^2$. We need only consider the case $\beta<0$ or $\beta\geq\alpha$ since $C=\mathbb{R}^2$ if $0<\beta<\alpha$.

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- We aim to prove that (3.4) (under Assumption 3.1) and (3.5) (under Assumption 3.2) hold for all $(u, v) \in \mathbb{R}^2$. We need only consider the case $\beta < 0$ or $\beta \geq \alpha$ since $C = \mathbb{R}^2$ if $0 < \beta < \alpha$.
- We will prove that $\xi^{u,v}(\cdot), \eta^{u,v}(\cdot)$ eventually enters C almost surely.

Case $\beta \geq \alpha$

- In the proof of the existence of an i.p.m given that $\lambda > 0$, we have already shown that the process $(\xi^{u,v}(\cdot), \eta^{u,v}(\cdot))$ is recurrent relative to $A = \{(u,v) : u \leq d_1, d_2 \leq v \leq d_1\}$ for some $d_1, d_2 \in \mathbb{R}$.

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- We construct $D = \{(u,v) \in \mathbb{R}^2 : u < \frac{\alpha}{\beta}(d_3 - c^*), v < d_3\}$ and $E = \{(u,v) \in \mathbb{R}^2, u, v \leq d_4\}$ where d_3, d_4 are negative large number chosen to satisfy our purpose. Let $d_5 \ll d_4$ and devide A into $A_1 = \{(u,v) : u < d_5, d_2 \leq v \leq d_1\}$ and $A_2 = A \setminus A_1$.

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- A_2 is compact, using the support theorem and the Feller property, we can estimate a positive lower bound for the probability of entering C from A_2.

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- A_2 is compact, using the support theorem and the Feller property, we can estimate a positive lower bound for the probability of entering C from A_2.
- Using the property of the drift, we can also estimate a positive lower bound for the probability of entering E from A_1. Moreover, when the solution exits D after entering E, the solution will go through the right side of D with a large probability.

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- A_2 is compact, using the support theorem and the Feller property, we can estimate a positive lower bound for the probability of entering C from A_2.
- Using the property of the drift, we can also estimate a positive lower bound for the probability of entering E from A_1. Moreover, when the solution exits D after entering E, the solution will go through the right side of D with a large probability.
- We can find a positive lower bound for the probability of entering C from A. Since the process is recurrent relative to A, it must enter C almost surely due to the strong Markov property.

Case $\beta < 0$

- In this case, set $A_1 = C^\circ \cap A$, $A_2 = A \setminus A_1$. We can give a positive lower bound for the probability of entering C from A_2 while A_1 is already in C. Hence, using similar argument as in the previous case, the solution eventually go into C with probability 1.

Ergodicity and convergence in total variation for degenerate case

In conclusion, we have $\forall (u, v) \in \mathbb{R}^2$,

Theorem 3.2

Suppose $\alpha, \beta \neq 0$, $\lambda > 0$ and Assumption 3.1 holds. Then, (3.2) *has a unique invariant probability measure π^* satisfying that for any π^*-integrable function f,*

$$\mathbb{P}\left\{ \lim_{t\to\infty} \frac{1}{t} \int_0^t f(\xi^{u,v}(s), \eta^{u,v}(s))\, ds = \int_{\mathbb{R}^2} f(u', v') \pi^*(du', dv') \right\} = 1. \quad (3.6)$$

Moreover, if Assumption 3.2 is satisfied, the transition probability $\widehat{P}(t, (u, v), \cdot)$ converges to $\pi^*(\cdot)$ in total variation.

Example 1

- Consider (3.1) with parameters $a_1 = 10$, $a_2 = 1$, $b_1 = 1$, $b_2 = 2$, $c_1 = 1$, $c_2 = 10$, $m_1 = 1$, $m_2 = 1$, $m_3 = 1$, $\alpha = 1$, and $\beta = 2$. Direct calculation shows that $\lambda = 6.005$ and Assumption 3.2 holds. As a result, the conclusion of Theorem 3.2 holds.

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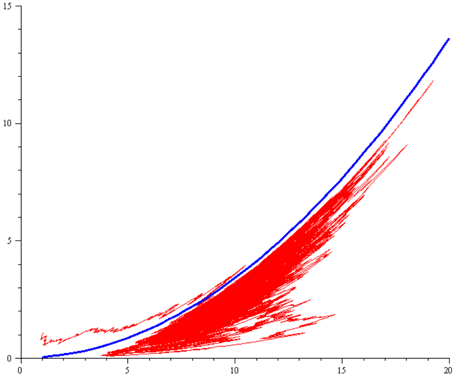

Figure: Phase portrait of (3.1) and the curve $y = \widehat{c}x^2$.

Example 2

- Consider (3.1) with the same parameters as in Example 1, except that $\beta = -2$. The conclusion of Theorem 3.2 also holds for this example.

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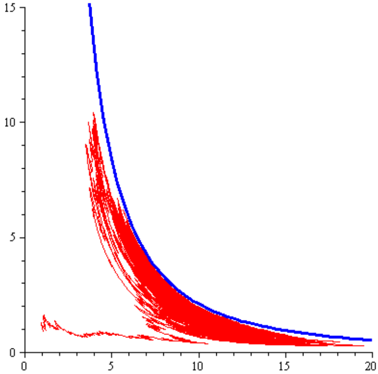
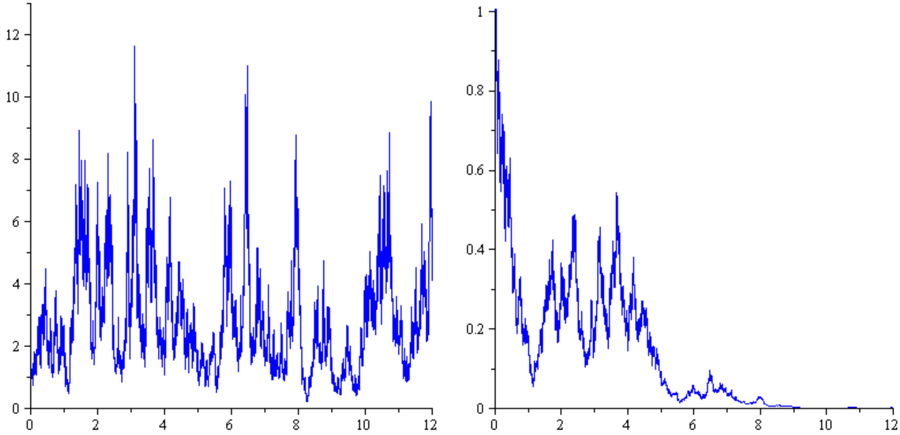
- 

Figure: Phase portrait of (3.1) and the curve $y = \widehat{c}x^{-2}$.

Example 3

- Consider (1.1) with $a_1 = 8$, $a_2 = 1$, $b_1 = 2$, $b_2 = 2$, $c_1 = 3$, $c_2 = 2$, $m_1 = 2$, $m_2 = 1$, $m_3 = 1.5$, $\alpha = 2$, and $\beta = 1$. We obtain $\lambda = -0.096 < 0$. As a result of Theorem 2.1 that $y(t) \to 0$ a.s. as $t \to \infty$. This claim is justified in Figures 3 and 4.



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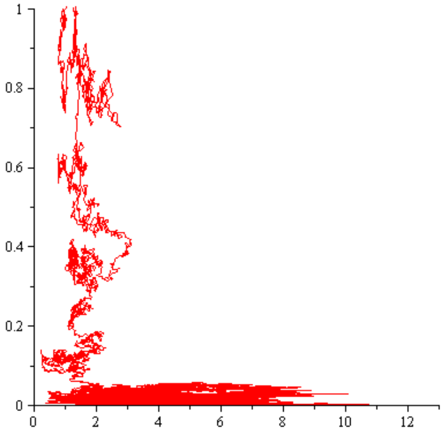

Figure: Phase portrait of (3.1) in Example 3.

Concluding Remarks

- While using Lyapunov function requires restrictive conditions, our method of analyzing the properties of solutions on the boundary provide a much sharper result. We have given a sufficient and almost necessary condition for permanence and ergodicity of the stochastic predator-prey model with Beddington-DeAnglesis functional response.

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- In case $m_1 = 1, m_2 = 1, m_3 = 0$, the functional response is called Holling type II. Our result is also better than that in J. Lv, K. Wang (2011).

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- In case $m_1 = 1, m_2 = 1, m_3 = 0$, the functional response is called Holling type II. Our result is also better than that in J. Lv, K. Wang (2011).
- Our method can be used to obtain similar results for more general stochastic predator-prey models.

Thank you

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