

# A Holling's predator-prey model with handling and searching predators

SZE-BI HSU<sup>(a)</sup>, ZHIHUA LIU<sup>(b)\*</sup> AND PIERRE MAGAL<sup>(c)†</sup>

<sup>(a)</sup> *Department of Mathematics and The National Center for Theoretical Science,  
National TsingHua University, Hsinchu 300, Taiwan*

<sup>(b)</sup> *School of Mathematical Sciences, Beijing Normal University,  
Beijing 100875, People's Republic of China*

<sup>(c)</sup> *Univ. Bordeaux, IMB, UMR 5251, F-33400 Talence, France.  
CNRS, IMB, UMR 5251, F-33400 Talence, France.*

## Abstract

The goal of this paper is to explain how to derive the classical Rosenzweig-MacArthur's model by using a model with two groups of predators in which we can separate the vital dynamic and consumption of prey to describe the behavior of the predators. This will be especially very convenient if we want to add an age or size structure to the predator population. As mentioned by Holling (without mathematical model), we divide the population of predators into the searching and the handling predators. In this article we study some properties of this model and conclude the paper proving that the model converges to the classical Rosenzweig-MacArthur's model by using an appropriate rescaling. This convergence property is observed by using numerical simulations. We also apply this model to the Canadian snowshoe Hares and the Lynx.

**Key words:** handling and searching predators, dissipative system, uniform persistence, equilibrium, limit cycle, type-K competitive systems.

**Mathematics Subject Classification:** 34C25, 34K20, 34G20, 92D25

## 1 Introduction

The article is devoted to the following predator prey system with handling and searching predators

$$\left\{ \begin{array}{l} N' = \underbrace{\beta_N N - \mu_N N - \delta N^2}_{\text{Logistic growth}} - \underbrace{N \kappa P_S}_{\text{Consumption of prey by predators}} \\ P'_S = \underbrace{-(\mu_P + \eta) P_S}_{\text{Mortality}} - \underbrace{P_S \rho \kappa N}_{\text{Searching becoming handling}} + \gamma P_H \\ P'_H = \underbrace{-\mu_P P_H}_{\text{Mortality}} + \underbrace{P_S \rho \kappa N}_{\text{Handling becoming searching}} - \underbrace{\gamma P_H}_{\text{Handling becoming searching}} + \underbrace{\beta_P (P_S + P_H)}_{\text{New born predator}} \end{array} \right. \quad (1.1)$$

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where  $N(t)$  is the number of prey at time  $t$ ,  $P_S(t)$  is the number of predators searching for prey at time  $t$ , and  $P_H(t)$  is the number of predators handling the prey at time  $t$ .

Here the terminology "handling and searching predators" refers to Holling himself [11]. We should mention that Metz and Diekmann had similar ideas of searching and handling predator in their edited book [17, pages 6-7]. In the model (1.1), the term  $\beta_P(P_S(t) + P_H(t))$  is the flux of new born predators. Here we assume that all the new born predators are handlers. The parameter  $\rho$  should be interpreted as a conversion rate. The term  $P_S(t) \rho \kappa N(t)$  (in the  $P_S$ -equation or the  $P_H$ -equation) is a flux of searching predators becoming handling predators. The term  $\gamma P_H(t)$  (in the  $P_S$ -equation or the  $P_H$ -equation) is the flux of handling predators becoming searching predators. The term  $\mu_P$  is the natural mortality of the predators and  $\eta$  is an extra mortality term for the searching predators only. The term  $N(t) \kappa P_S(t)$  in the  $N$ -equation corresponds to the consumption of the prey by the predators. The part  $\beta_N N(t) - \mu_N N(t) - \delta N(t)^2$  in the  $N$ -equation is the standard logistic equation.

The main idea about this model is to distinguish the vital dynamics (birth and death process) of the predators and their survival due to the consumption of prey. In the model the survival of predators will depend on the status searching or handling. The handling predators are satisfied with their consumption of prey and they don't need to find more prey to survive. At the opposite the searching predators are unsatisfied with their consumption of prey and they need to find some prey to survive. Once a searching predator finds a prey (or enough prey) he becomes a handling and after some time the handling predator becomes a searching predator again.

This process only influences the survival of predators which depends on their ability to find a prey. In our model, a predator can reproduce at time  $t$  because he found enough prey to survive from its birth until the time  $t$ . In section 2 we will first make some basic assumptions in order for the predators to extinct in absence of prey. Then based on these setting we will analyze the dynamical properties of the system (1.1). The main advantage with the model (1.1) is that we can separate the vital dynamic and consumption of prey to describe the behavior of the predators. This will be especially very convenient if we want to add an age or size structure to the predator population. This kind of question is left for future work.

In section 6 we will see that our model is also comparable to the standard predator prey model whenever  $\rho = \frac{\chi}{\varepsilon}$  and  $\gamma = \frac{1}{\varepsilon}$  for  $\varepsilon > 0$  small which means that predators are going back and forth from handling to searching very rapidly. In that case (as a singular limit) we obtain a convergence result to the standard Rosenzweig-MacArthur model [19]

$$\begin{cases} N' = rN \left(1 - \frac{N}{K}\right) - P \frac{mN}{a+N}, \\ P' = P \left(\frac{mN}{a+N} - d\right), \end{cases} \quad (1.2)$$

which is the most popular predator-prey system discussed in the literature.

Let us recall that the derivation of Holling type II functional response  $\frac{mN}{a+N}$  can be found in Holling [10, 11] and Hsu, Hubbell and Waltman [12]. There are two mathematical problems for the system (1.2), namely, the global asymptotic stability of the locally asymptotically stable interior equilibrium (when it exists) and the uniqueness of the limit cycles when the interior equilibrium is unstable. For the global asymptotic stability of this equilibrium we may apply the Dulac's criterion Hsu, Hubbell and Waltman [13], weak negative Bendixson Lemma Cheng, Hsu and Lin [3] or construction Lyapunov function Ardito and Ricciardi [1]. For uniqueness of limit cycle of Rosenzweig-MacArthur model (1.2), Cheng [2] employed the symmetry of the prey isocline to prove the exponential asymptotic stability of each limit cycle. Kuang and Freedman [15] reduced (1.2) to a generalized Lienard equation which has the uniqueness of

limit cycle Zhang [23]. We refer to Murray [18], Hastings [9], Turchin [21] for more results about predator prey models.

The plan of the paper is the following. In section 2 we set some basic assumptions in order for the predators to extinct in absence of prey. In section 3 we prove that the system is dissipative. In section 4 we study the uniform persistence and extinction properties of the predators. We study the system in the interior region which corresponds the region of co-existence of prey and predators in section 5. We should mention that we can obtain a rather complete description of the asymptotic behavior thanks to the fact the system is competitive (for a new partial order). In section 6 we prove the convergence of our model to the Rosenweig-MacArthur model. In section 7 we apply the model to the Canadian snowshoe Hares and the Lynx.

## 2 Basic assumptions

In this section, we set some basic assumptions in order for the predators to extinct in absence of prey. Consider the total number of predators

$$P = P_H + P_S.$$

Then

$$P' = (\beta_P - \mu_P - \eta) P_S + (\beta_P - \mu_P) P_H. \quad (2.1)$$

The following assumptions mean that when  $\frac{P_S}{P_H} > -\frac{\beta_P - \mu_P}{\beta_P - \mu_P - \eta}$ , the total population of predators decreases. The total population of predators increases otherwise.

**Assumption 2.1** *We assume that all the parameters of the model (1.1) are strictly positive and*

$$\beta_N - \mu_N > 0, \beta_P - \mu_P > 0 \text{ and } \beta_P - \mu_P - \eta < 0.$$

In absence of prey the dynamics of predator population is described by

$$\begin{cases} P'_S = -(\mu_P + \eta) P_S + \gamma P_H \\ P'_H = \beta_P P_S + (\beta_P - \mu_P - \gamma) P_H. \end{cases}$$

Define

$$M = \begin{bmatrix} -\mu_P - \eta & \gamma \\ \beta_P & \beta_P - \mu_P - \gamma \end{bmatrix}. \quad (2.2)$$

By using Assumption 2.1 we have

$$\text{tr}(M) = (\beta_P - \mu_P - \gamma) - (\mu_P + \eta) < 0.$$

Therefore in absence of prey the population of predators goes to extinct if and only if

$$\det(M) = -(\mu_P + \eta)(\beta_P - \mu_P - \gamma) - \beta_P \gamma > 0.$$

This last inequality can be equivalently reformulated in the following assumption.

**Assumption 2.2 (Extinction of the predators)** *We assume that*

$$(\beta_P - \mu_P - \gamma) < -\frac{\beta_P \gamma}{\mu_P + \eta} \Leftrightarrow (\beta_P - \mu_P) < -\frac{\gamma}{\mu_P + \eta} (\beta_P - \mu_P - \eta). \quad (2.3)$$

**Remark 2.3** The first inequality in (2.3) implies that  $(\beta_P - \mu_P - \gamma) < 0$ . Moreover the second inequality in (2.3) and  $(\beta_P - \mu_P) > 0$  imply that  $(\beta_P - \mu_P - \eta) < 0$ .

**Lemma 2.4** Let Assumptions 2.1 and 2.1 be satisfied. Then in absence of prey the population of predators goes to extinct.

### 3 Dissipativity

In this section, we will prove that the system (1.1) is dissipative. We look for a positive left eigen-vector  $(\tilde{P}_S, \tilde{P}_H) \in (0, +\infty)^2$  and an eigenvalue  $\lambda > 0$  such that

$$(\tilde{P}_S, \tilde{P}_H) \begin{bmatrix} -\mu_P - \eta & \gamma \\ \beta_P & \beta_P - \mu_P - \gamma \end{bmatrix} = -\lambda(\tilde{P}_S, \tilde{P}_H)$$

that is equivalent to

$$\begin{cases} -(\mu_P + \eta)\tilde{P}_S + \beta_P\tilde{P}_H = -\lambda\tilde{P}_S \\ \gamma\tilde{P}_S + (\beta_P - \mu_P - \gamma)\tilde{P}_H = -\lambda\tilde{P}_H \end{cases} \Leftrightarrow \begin{cases} \beta_P\tilde{P}_H = [(\mu_P + \eta) - \lambda]\tilde{P}_S \\ \gamma\tilde{P}_S = [-(\beta_P - \mu_P - \gamma) - \lambda]\tilde{P}_H. \end{cases}$$

Thus the sign  $\tilde{P}_S$  and  $\tilde{P}_H$  are the same if we impose

$$\lambda \in (0, \min((\mu_P + \eta), -(\beta_P - \mu_P - \gamma)))$$

and  $\lambda$  must satisfy the following equation

$$1 = \frac{[(\mu_P + \eta) - \lambda]}{\beta_P} \frac{[-(\beta_P - \mu_P - \gamma) - \lambda]}{\gamma} =: \Psi(\lambda).$$

The function  $\lambda \rightarrow \Psi(\lambda)$  decreases between 0 and  $\min((\mu_P + \eta), -(\beta_P - \mu_P - \gamma))$  and by using (2.3) we have  $\Psi(0) > 1$ . It follows that there exists a unique  $\lambda^* \in (0, \min((\mu_P + \eta), -(\beta_P - \mu_P - \gamma)))$  such that

$$1 = \frac{[(\mu_P + \eta) - \lambda^*]}{\beta_P} \frac{[-(\beta_P - \mu_P - \gamma) - \lambda^*]}{\gamma}. \quad (3.1)$$

Note that

$$\frac{[-(\beta_P - \mu_P - \gamma) - \lambda^*]}{\gamma} < 1 \Leftrightarrow -(\beta_P - \mu_P) < \lambda^*.$$

By assumption  $(\beta_P - \mu_P) > 0$  it follows from (3.1) that

$$\frac{[(\mu_P + \eta) - \lambda^*]}{\beta_P} > 1.$$

Since

$$\gamma\tilde{P}_S = [-(\beta_P - \mu_P - \gamma) - \lambda^*]\tilde{P}_H,$$

it follows that

$$\tilde{P}_H > \tilde{P}_S > 0. \quad (3.2)$$

By using  $P_S$ -equation and  $P_H$ -equation of system (1.1) we obtain

$$\tilde{P}_S P'_S + \tilde{P}_H P'_H = -\lambda^* [\tilde{P}_S P_S + \tilde{P}_H P_H] - (\tilde{P}_S - \tilde{P}_H) P_S \rho \kappa N. \quad (3.3)$$

By using the  $N$ -equation and comparison principle it is clear that we can find some  $N^* = \max(N(0), (\beta_N - \mu_N) / \delta)$  such that

$$N(t) \leq N^*, \forall t \geq 0,$$

where  $N(0)$  is the initial value. Then it follows that

$$\rho(\tilde{P}_H - \tilde{P}_S) N' + \tilde{P}_S P'_S + \tilde{P}_H P'_H \leq -\rho(\tilde{P}_H - \tilde{P}_S) \mu_N N - \lambda^* [\tilde{P}_S P_S + \tilde{P}_H P_H] + \rho(\tilde{P}_H - \tilde{P}_S) \beta_N N^*$$

and the dissipativity follows.

Set

$$M = \frac{\rho(\tilde{P}_H - \tilde{P}_S) \beta_N N^*}{\min(\mu_N, \lambda^*)} > 0.$$

As a consequence of the last inequality, we obtain the following results.

**Proposition 3.1** *Let Assumptions 2.1 and 2.2 be satisfied. The system (1.1) generates a unique continuous semiflow  $\{U(t)\}_{t \geq 0}$  on  $[0, \infty)^3$ . Moreover the domain*

$$D = \{(N, P_S, P_H) \in [0, \infty)^3 : \rho(\tilde{P}_H - \tilde{P}_S) N + \tilde{P}_S P_S + \tilde{P}_H P_H \leq M\}$$

*is positively invariant by the semiflow generated by  $U$ . That is to say that*

$$U(t)D \subset D, \forall t \geq 0.$$

*Furthermore  $D$  attracts every point of  $[0, \infty)^3$  for  $U$ . That is to say that*

$$\lim_{t \rightarrow \infty} \delta(U(t)x, D) = 0, \forall x \in [0, \infty)^3,$$

*where  $\delta(x, D) := \inf_{y \in D} \|x - y\|$  is the Hausdorff's semi-distance. As a consequence the semiflow of  $U$  has a compact global attractor  $\mathcal{A} \subset [0, \infty)^3$ .*

## 4 Uniform persistence and extinction of predators

In this section, we study the uniform persistence and extinction of the predators. Firstly we consider the existence of the equilibrium. The equilibrium  $(\bar{N}, \bar{P}_S, \bar{P}_H) \in [0, \infty)^3$  satisfies the following system

$$\begin{cases} 0 = \bar{N} [\beta_N - \mu_N - \delta \bar{N} - \kappa \bar{P}_S], \\ 0 = -(\mu_P + \eta) \bar{P}_S - \bar{P}_S \rho \kappa \bar{N} + \gamma \bar{P}_H, \\ 0 = -\mu_P \bar{P}_H + \bar{P}_S \rho \kappa \bar{N} - \gamma \bar{P}_H + \beta_P (\bar{P}_S + \bar{P}_H). \end{cases}$$

By using Assumptions 2.1 and 2.2, we deduce that the only equilibrium satisfying  $\bar{N} = 0$  is  $E_1 = (0, 0, 0)$ . If we assume next that  $\bar{N} > 0$ , we obtain the system

$$\begin{cases} 0 = \beta_N - \mu_N - \delta \bar{N} - \kappa \bar{P}_S, \\ 0 = -(\mu_P + \eta) \bar{P}_S - \bar{P}_S \rho \kappa \bar{N} + \gamma \bar{P}_H, \\ 0 = -\mu_P \bar{P}_H + \bar{P}_S \rho \kappa \bar{N} - \gamma \bar{P}_H + \beta_P (\bar{P}_S + \bar{P}_H). \end{cases}$$

From the first equation we have

$$\bar{N} = \hat{N} - \frac{\kappa}{\delta} \bar{P}_S$$

with

$$\hat{N} = \frac{\beta_N - \mu_N}{\delta}.$$

By adding the last two equations, we have

$$\bar{P}_H = \frac{(\mu_P + \eta - \beta_P)}{(\beta_P - \mu_P)} \bar{P}_S.$$

Combining the above two equations with

$$-(\mu_P + \eta) \bar{P}_S - \bar{P}_S \rho \kappa \bar{N} + \gamma \bar{P}_H = 0,$$

we have

$$\left( -(\mu_P + \eta) - \frac{(\beta_N - \mu_N) \rho \kappa}{\delta} + \gamma \frac{(\mu_P + \eta - \beta_P)}{(\beta_P - \mu_P)} \right) \bar{P}_S + \frac{\kappa^2 \rho}{\delta} \bar{P}_S^2 = 0$$

and then

$$\bar{P}_S = 0 \text{ or } \bar{P}_S = \left( (\mu_P + \eta) - \frac{\gamma(\mu_P + \eta - \beta_P)}{(\beta_P - \mu_P)} \right) \frac{\delta}{\kappa^2 \rho} + \frac{(\beta_N - \mu_N)}{\kappa}.$$

Thus we get the following lemma.

**Lemma 4.1** *Let Assumptions 2.1 and 2.2 be satisfied. System (1.1) always has the following two boundary equilibria*

$$E_1 = (0, 0, 0), \quad E_2 = (\hat{N}, 0, 0).$$

Moreover there exists a unique interior equilibrium  $E^* = (N^*, P_S^*, P_H^*)$  if and only if

$$(\beta_N - \mu_N)(\beta_P - \mu_P) \kappa \rho + \delta (\beta_P - \mu_P)(\mu_P + \eta) > -\delta \gamma (\beta_P - \mu_P - \eta). \quad (4.1)$$

Furthermore, we have

$$\begin{aligned} N^* &= \frac{-(\beta_P - \mu_P)(\mu_P + \eta) - \gamma(\beta_P - \mu_P - \eta)}{(\beta_P - \mu_P) \kappa \rho} > 0, \\ P_S^* &= \frac{\delta (\beta_P - \mu_P)(\mu_P + \eta) + \delta \gamma (\beta_P - \mu_P - \eta) + (\beta_N - \mu_N)(\beta_P - \mu_P) \kappa \rho}{(\beta_P - \mu_P) \kappa^2 \rho} > 0, \\ P_H^* &= -\frac{(\beta_P - \mu_P - \eta)}{\beta_P - \mu_P} P_S^* > 0. \end{aligned}$$

#### 4.1 Stability of the equilibrium $E_1$

The Jacobian matrix at the equilibrium  $E_1$  is

$$\begin{bmatrix} \beta_N - \mu_N & 0 & 0 \\ 0 & -\mu_P - \eta & \gamma \\ 0 & \beta_P & \beta_P - \mu_P - \gamma \end{bmatrix}$$

and the characteristic equation is

$$[(\lambda + \mu_P + \eta)(\lambda - (\beta_P - \mu_P - \gamma)) - \beta_P \gamma] [\lambda - (\beta_N - \mu_N)] = 0.$$

So one of the eigenvalues is  $\lambda_{1,E_1} = \beta_N - \mu_N > 0$ . Thus we can get that the equilibrium  $E_1$  is unstable. The rest of the spectrum coincides with the spectrum of the matrix  $M$  defined in (2.2). Thus we obtain the following lemma.

**Lemma 4.2** *Let Assumptions 2.1 and 2.2 be satisfied. The equilibrium  $E_1$  is hyperbolic and the unstable manifold is one dimensional.*

## 4.2 Stability of the equilibrium $E_2$

The Jacobian matrix at the equilibrium  $E_2$  is

$$\begin{bmatrix} -(\beta_N - \mu_N) & -\kappa \widehat{N} & 0 \\ 0 & -((\mu_P + \eta) + \rho \kappa \widehat{N}) & \gamma \\ 0 & \rho \kappa \widehat{N} + \beta_P & \beta_P - \mu_P - \gamma \end{bmatrix}$$

and the characteristic equation is

$$[(\lambda + \mu_P + \eta + \rho \kappa \widehat{N})(\lambda - (\beta_P - \mu_P - \gamma)) - \gamma(\rho \kappa \widehat{N} + \beta_P)] [\lambda + (\beta_N - \mu_N)] = 0.$$

So one of the eigenvalues is  $\lambda_{1,E_2} = -(\beta_N - \mu_N) < 0$  and the remaining part of the characteristic equation is

$$\lambda^2 + a\lambda + b = 0$$

with

$$a = (\mu_P + \eta + \rho \kappa \widehat{N}) - (\beta_P - \mu_P - \gamma)$$

and

$$b = (\mu_P + \gamma - \beta_P)(\mu_P + \eta + \rho \kappa \widehat{N}) - \gamma(\rho \kappa \widehat{N} + \beta_P).$$

By using Assumptions 2.1 and 2.2 we have  $a > 0$ . Moreover by using the Routh-Hurwitz criterion  $E_2$  is stable if and only if  $b > 0$  which corresponds to

$$\begin{aligned} & (\mu_P + \gamma - \beta_P)(\mu_P + \eta + \rho \kappa \widehat{N}) - \gamma(\rho \kappa \widehat{N} + \beta_P) > 0 \\ \Leftrightarrow & (\beta_N - \mu_N)(\beta_P - \mu_P) \kappa \rho + \delta(\beta_P - \mu_P)(\mu_P + \eta) < -\delta \gamma (\beta_P - \mu_P - \eta) \end{aligned}$$

Now we obtain the following result.

**Lemma 4.3** *Let Assumptions 2.1 and 2.2 be satisfied.  $E_2$  is unstable if the interior equilibrium exists (i.e. the condition 4.1 is satisfied) and the unstable manifold is one dimensional and the stable manifold is two dimensional.*

### 4.3 Extinction of the predators and the global stability of $E_2$

We decompose the positive cone  $M = \mathbb{R}_+^3$  into the interior region

$$\overset{\circ}{M} = \{(N, P_S, P_H) \in M : N > 0 \text{ and } P_S + P_H > 0\},$$

the boundary region with predators only

$$\partial M_P := \{(N, P_S, P_H) \in M : N = 0\}, \quad (4.2)$$

and the boundary region with prey only

$$\partial M_N := \{(N, P_S, P_H) \in M : P_S + P_H = 0\}. \quad (4.3)$$

Each sub domain  $\overset{\circ}{M}$ ,  $\partial M_P$  and  $\partial M_N$  is positively invariant by the semiflow generated by (1.1).

**Theorem 4.4** *Let Assumptions 2.1 and 2.2 be satisfied. Assume that  $E_2$  is locally asymptotically stable (i.e.  $(\mu_P + \eta + \rho\kappa\widehat{N})(\mu_P + \gamma - \beta_P) > \gamma(\beta_P + \rho\kappa\widehat{N})$ ). Then the predator goes to extinction. More precisely for each initial value in  $M = (N(0), P_S(0), P_H(0)) \in [0, \infty)^3$ ,*

$$\lim_{t \rightarrow \infty} P_S(t) + P_H(t) = 0.$$

and

$$\lim_{t \rightarrow \infty} N(t) = \begin{cases} \widehat{N}, & \text{if } N(0) > 0, \\ 0, & \text{if } N(0) = 0. \end{cases}$$

*Proof.* The boundary region with predator only  $\partial M_P$  is positively invariant by the semiflow generated by (1.1) and by Assumption 2.2 any solution starting from  $\partial M_P$  exponentially converges to  $E_1$ .

So it remains to investigate the limit of a solution starting from  $\overset{\circ}{M} \cup \partial M_N \setminus \{E_1\}$ . We consider the Liapunov function

$$V(N, P_S, P_H) = \int_{\widehat{N}}^N \frac{\xi - \widehat{N}}{\xi} d\xi + c_1 P_S + c_2 P_H \quad (4.4)$$

where  $c_1 > 0$  and  $c_2 > 0$  to be determined. We have

$$\begin{aligned} \dot{V} &= (N - \widehat{N})(\beta_N - \mu_N - \delta N - \kappa P_S) \\ &+ c_1(-(\mu_P + \eta)P_S - \rho\kappa P_S N + \gamma P_H) \\ &+ c_2(-\mu_P P_H + \rho\kappa P_S N - \gamma P_H + \beta_P(P_S + P_H)) \\ &= (N - \widehat{N})(-\delta(N - \widehat{N}) - \kappa P_S) \\ &+ c_1(-(\mu_P + \eta)P_S - \rho\kappa P_S(N - \widehat{N}) - \rho\kappa P_S \widehat{N} + \gamma P_H) \\ &+ c_2(-\mu_P P_H + \rho\kappa P_S(N - \widehat{N}) + \rho\kappa P_S \widehat{N} - \gamma P_H + \beta_P(P_S + P_H)). \end{aligned} \quad (4.5)$$

Thus we obtain

$$\begin{aligned} \dot{V} &= -\delta(N - \widehat{N})^2 + \kappa P_S(N - \widehat{N})(-1 - c_1\rho + c_2\rho) \\ &+ P_S(-c_1(\mu_P + \eta) - c_1\rho\kappa\widehat{N} + c_2\rho\kappa\widehat{N} + c_2\beta_P) \\ &+ P_H(-c_2\mu_P + c_1\gamma - c_2\gamma + c_2\beta_P). \end{aligned} \quad (4.6)$$

We claim that we can choose  $c_1 > 0$  and  $c_2 > 0$  such that  $c_2 = c_1 + \frac{1}{\rho}$  and the following inequalities are satisfied

$$-c_1(\mu_P + \eta) - c_1\rho\kappa\widehat{N} + c_2\rho\kappa\widehat{N} + c_2\beta_P < 0 \text{ and } -c_2\mu_P + c_1\gamma - c_2\gamma + c_2\beta_P < 0. \quad (4.7)$$



In fact the inequalities in (4.7) lead to consider the lines

$$c_2 = c_1 \frac{\gamma}{\mu_P + \gamma - \beta_P} \quad (L_1)$$

and

$$c_2 = c_1 \frac{(\mu_P + \eta) + \rho\kappa\widehat{N}}{\beta_P + \rho\kappa\widehat{N}} \quad (L_2).$$

By Assumption 2.2 (see Remark 2.3) we have  $\mu_P + \gamma - \beta_P > 0$  and by Assumption 2.1 we have  $\mu_P + \eta > \beta_P$  and then

$$\frac{(\mu_P + \eta) + \rho\kappa\widehat{N}}{\beta_P + \rho\kappa\widehat{N}} > 1.$$

Note that

$$\begin{aligned} \frac{(\mu_P + \eta) + \rho\kappa\widehat{N}}{\beta_P + \rho\kappa\widehat{N}} &> \frac{\gamma}{\mu_P + \gamma - \beta_P} \\ \Leftrightarrow (\mu_P + \eta + \rho\kappa\widehat{N})(\mu_P + \gamma - \beta_P) &> \gamma(\beta_P + \rho\kappa\widehat{N}) \end{aligned}$$

and thus we obtain that the slope of  $L_2$  is greater than the slope of  $L_1$ . Finally we have

$$\lim_{N \rightarrow 0^+} V(N, P_S, P_N) = (N - \widehat{N}) - \widehat{N} \ln\left(\frac{N}{\widehat{N}}\right) + c_1 P_S + c_2 P_N = +\infty.$$

By LaSalle's invariance principle we obtain that  $E_2$  is globally asymptotically stable for the system restricted to  $\overset{\circ}{M} \cup \partial M_N \setminus \{E_1\}$ . ■

#### 4.4 Uniform persistence of the predators

We decompose the positive cone into

$$\mathbb{R}_+^3 = \partial M \cup \overset{\circ}{M}$$

where the boundary region is defined as

$$\partial M := \partial M_P \cup \partial M_N.$$

It is clear that both regions  $\overset{\circ}{M}$  and  $\partial M$  are positively invariant by the semiflow generated by the system. Moreover we have the following result.

**Theorem 4.5** *Let Assumptions 2.1 and 2.2 be satisfied. If the interior equilibrium exists then the predators uniformly persist with respect to the domain decomposition  $(\partial M, \overset{\circ}{M})$ . That is to say that there exists  $\nu > 0$  such that for each initial value  $N(0) > 0$  and  $P_S(0) + P_H(0) > 0$*

$$\liminf_{t \rightarrow \infty} N(t) > \nu \text{ and } \liminf_{t \rightarrow \infty} P_S(t) + P_H(t) > \nu.$$

*Proof.* The equilibrium  $E_1 = \{(0, 0, 0)\}$  is clearly chained to  $E_2 = \{(\widehat{N}, 0, 0)\}$ . By using Theorem 4.1 in [8], we only need to prove that

$$W^s(E_i) \cap \overset{\circ}{M} = \emptyset,$$

where  $i = 1, 2$  and

$$W^s(E_i) = \{(N, P_S, P_H) \in M : \omega((N, P_S, P_H)) \neq \emptyset \text{ and } \omega((N, P_S, P_H)) \subset E_i\},$$

where  $\omega$  means the  $\omega$ -limit set. Assume that there exists  $E^0 = (N^0, P_S^0, P_H^0) \in \overset{\circ}{M}$  (which means  $N^0 > 0$  and  $P_S^0 + P_H^0 > 0$ ) such that  $\omega(E^0) \subset E_1$ . Then for any  $\varepsilon > 0$ , there exists  $t_0 \geq 0$ , such that

$$N(t) + P_S(t) + P_H(t) \leq \varepsilon, \forall t \geq t_0$$

where  $(N(t), P_S(t), P_H(t)) = U(t)E^0$ . By using the first equation of model (1.1)

$$N' = \beta_N N - \mu_N N - \delta N^2 - N \kappa P_S,$$

we have

$$N' \geq N(\beta_N - \mu_N - \delta \varepsilon - \kappa \varepsilon).$$

Therefore for  $\varepsilon > 0$  small enough, we have  $\beta_N - \mu_N - \delta \varepsilon - \kappa \varepsilon > 0$  and then

$$\lim_{t \rightarrow \infty} N(t) = \infty$$

which is in contradiction to the dissipativity of the model. Assume that there exists  $E^0 = (N^0, P_S^0, P_H^0) \in \overset{\circ}{M}$  such that  $\omega(E^0) \subset E_2$ . Then for any  $\varepsilon > 0$ , there exists  $t_0 \geq 0$ , such that

$$|N(t) - \widehat{N}| + P_S(t) + P_H(t) \leq \varepsilon, \forall t \geq t_0$$

where  $(N(t), P_S(t), P_H(t)) = U(t)E^0$ . By using the two last equation of system (1.1), we obtain

$$\begin{aligned} P_S' &\geq -(\mu_P + \eta)P_S - P_S \rho \kappa (\widehat{N} + \varepsilon) + \gamma P_H \\ P_H' &\geq -\mu_P P_H + P_S \rho \kappa (\widehat{N} - \varepsilon) - \gamma P_H + \beta_P (P_S + P_H) \end{aligned} \quad (4.8)$$

By using the fact that for  $\varepsilon > 0$  small enough the right hand side of (4.8) is a cooperative system together with Lemma 4.3 we deduce that

$$\lim_{t \rightarrow \infty} P_S(t) + P_H(t) = \infty.$$

This gives a contradiction with the dissipativity of the system. Therefore the uniform persistence follows.

■

As a consequence of the dissipativity as well as the uniform persistence (see Magal and Zhao [16]) we deduce the following result.

**Theorem 4.6** *Let Assumptions 2.1 and 2.2 be satisfied. Assume in addition that the interior equilibrium exists. Then the system (1.1) has a global attractor  $A_0$  in the interior region  $\overset{\circ}{M}$ . Namely  $A_0$  is a compact invariant set by the semiflow generated by (1.1) on  $\overset{\circ}{M}$  and  $A_0$  is locally stable and attracts the compact subsets of  $\overset{\circ}{M}$ .*

## 5 Interior region

In this section, we will study the system in the interior region which corresponds to the region of co-existence of prey and predators.

## 5.1 Local stability of $E^*$

The Jacobian matrix at the equilibrium  $E^*$  is

$$\begin{bmatrix} (\beta_N - \mu_N - 2\delta N^* - \kappa P_S^*) & -N^* \kappa & 0 \\ -P_S^* \rho \kappa & -(\mu_P + \eta + \rho \kappa N^*) & \gamma \\ P_S^* \rho \kappa & \rho \kappa N^* + \beta_P & \beta_P - \mu_P - \gamma \end{bmatrix}.$$

and the characteristic equation is

$$\lambda^3 + p_1 \lambda^2 + p_2 \lambda + p_3 = 0$$

with

$$\begin{aligned} p_1 &= -(\beta_N - \mu_N - 2\delta N^* - \kappa P_S^*) + (\mu_P + \eta + \rho \kappa N^*) - (\beta_P - \mu_P - \gamma), \\ p_2 &= -(\mu_P + \eta + \rho \kappa N^*) (\beta_N - \mu_N - 2\delta N^* - \kappa P_S^*) - N^* \kappa P_S^* \rho \kappa \\ &\quad + (\beta_N - \mu_N - 2\delta N^* - \kappa P_S^*) (\beta_P - \mu_P - \gamma) \\ &\quad - (\mu_P + \eta + \rho \kappa N^*) (\beta_P - \mu_P - \gamma) - (\rho \kappa N^* + \beta_P) \gamma, \\ p_3 &= (\beta_N - \mu_N - 2\delta N^* - \kappa P_S^*) (\mu_P + \eta + \rho \kappa N^*) (\beta_P - \mu_P - \gamma) \\ &\quad + N^* \kappa \gamma P_S^* \rho \kappa + \gamma (\beta_N - \mu_N - 2\delta N^* - \kappa P_S^*) (\rho \kappa N^* + \beta_P) + \\ &\quad P_S^* \rho \kappa N^* \kappa (\beta_P - \mu_P - \gamma). \end{aligned}$$

By using Routh-Hurwitz criterion, we get that the equilibrium  $E^*$  is stable if and only if

$$p_1 > 0, p_1 p_2 - p_3 > 0 \text{ and } p_3 > 0.$$

By computing, we have

$$\begin{aligned} p_1 &= \frac{-\kappa \rho (\beta_P - \mu_P - \gamma) (\beta_P - \mu_P) - \gamma (\delta + \kappa \rho) (\beta_P - \mu_P - \eta) - \delta (\beta_P - \mu_P) (\mu_P + \eta)}{\kappa \rho (\beta_P - \mu_P)}, \\ p_2 &= \frac{[(\beta_P - \mu_P - \gamma) (\mu_P + \eta) + \gamma \beta_P] \{(\beta_P - \mu_P) [\delta (\beta_P + \eta + \gamma) + \kappa \rho (\beta_N - \mu_N)] - 2\delta \gamma \eta\}}{\kappa \rho (\beta_P - \mu_P)^2}, \\ p_3 &= \frac{[(\beta_P - \mu_P - \gamma) (\mu_P + \eta) + \gamma \beta_P] \left\{ \begin{array}{l} -\delta (\beta_P - \mu_P - \gamma) (\mu_P + \eta) - \gamma \delta \beta_P - \\ \kappa \rho (\beta_P - \mu_P) (\beta_N - \mu_N) \end{array} \right\}}{\kappa \rho (\beta_P - \mu_P)}. \end{aligned}$$

Thus we have the following result.

**Lemma 5.1** *Let Assumptions 2.1, 2.2 and inequality (4.1) be satisfied. The equilibrium  $E^*$  is stable if and only if  $(\beta_P - \mu_P) [\kappa \rho (\beta_N - \mu_N) + \delta (\eta + \gamma)] < \delta [2\gamma \eta - \beta_P (\beta_P - \mu_P)]$ .*

## 5.2 Three dimensional $\mathbb{K}$ -competitive system

In this section we use a Poincaré-Bendixson theorem for three dimensional  $\mathbb{K}$ -competitive system.

**Theorem 5.2** ([20, Theorem 4.2 p. 43]) *Let the autonomous system of ordinary differential equations  $x' = f(x)$  be a competitive system, where  $f$  is continuously differentiable on an open subset  $D \subset \mathbb{R}^3$  and suppose that  $D$  contains a unique equilibrium point  $p$  which is hyperbolic. Suppose further that  $W^s(p)$  is one-dimensional and tangent at  $p$  to a vector  $v \gg 0$ . If  $q \in D \setminus W^s(p)$  and  $\gamma^+(q)$  has compact closure in  $D$  then  $\omega(q)$  is a nontrivial periodic orbit.*

By applying this theorem to the system (1.1) restricted to the interior global attractor  $A_0$  we obtain the following result.

**Theorem 5.3** *Suppose that  $E^* = (N^*, P_S^*, P_H^*)$  exists and is hyperbolic and unstable for (1.1). Then the stable manifold  $W^s(E^*)$  of  $E^*$  is one dimensional and the omega limit set  $\omega(N(0), P_S(0), P_H(0))$  is a nontrivial periodic orbit in  $\mathbb{R}_+^3$  for every  $(N(0), P_S(0), P_H(0)) \in \mathbb{R}_+^3 \setminus W^s(E^*)$ .*

*Proof.* The Jacobian matrix of the vector field (1.1) at the point  $(N, P_S, P_H) \in (0, \infty)^3$  is given by

$$J = \begin{pmatrix} (\beta_N - \mu_N) - 2\delta N - \kappa P_S & -\kappa N & 0 \\ -\rho\kappa P_S & -(\mu_P + \eta) - \rho\kappa N & \gamma \\ \rho\kappa P_S & \rho\kappa N + \beta_P & -\mu_P + \beta_P - \gamma \end{pmatrix}. \quad (5.1)$$

The off-diagonal entries of  $J$  are sign-stable and sign symmetric in  $\mathbb{R}_+^3$ .

Let

$$\mathbb{K} = \{(N, P_S, P_H) \in \mathbb{R}_+^3 : N \geq 0, P_S \geq 0, P_H \leq 0\}.$$

The system is  $\mathbb{K}$ -competitive, since the matrix of the time-reversed linearized system  $-J$  is cooperative with respect to the cone  $\mathbb{K}$ . ■

## 6 Convergence to the Rosenzweig-MacArthur model

The time scale for the life expectancy (as well as the time scale needed for the reproduction) is the year, while the time needed for the lynx to handle the rabbit is measured by days (no more than one week). Therefore there is a huge difference between the time scales for the vital dynamic and the consumption dynamic.

The consumption of prey by the predator is a fast process compared to the vital dynamic which is slow. In the model  $\gamma^{-1}$  is the average time spent by the predators to handle prey.  $\gamma^{-1}$  should be very small in comparison with the other parameters. Then it makes sense to make the following assumption.

**Assumption 6.1** *Assume that*

$$\rho = \frac{\chi}{\varepsilon} \text{ and } \gamma = \frac{1}{\varepsilon}$$

*with  $\varepsilon \ll 1$  is small.*

Under the above assumption the system (1.1) becomes

$$\begin{cases} \dot{N}^\varepsilon = (\beta_N - \mu_N) N^\varepsilon - \delta (N^\varepsilon)^2 - \kappa N^\varepsilon P_S^\varepsilon \\ \dot{P}_S^\varepsilon = -(\mu_P + \eta) P_S^\varepsilon - \frac{\chi}{\varepsilon} \kappa N^\varepsilon P_S^\varepsilon + \frac{1}{\varepsilon} P_H^\varepsilon \\ \dot{P}_H^\varepsilon = -\mu_P P_H^\varepsilon + \frac{\chi}{\varepsilon} \kappa N^\varepsilon P_S^\varepsilon - \frac{1}{\varepsilon} P_H^\varepsilon + \beta_P (P_S^\varepsilon + P_H^\varepsilon) \end{cases} \quad (6.1)$$

and we fix the initial value

$$N^\varepsilon(0) = N_0 \geq 0, P_S^\varepsilon(0) = P_{S0} \geq 0 \text{ and } P_H^\varepsilon(0) = P_{H0} \geq 0.$$

The first equation of (6.1) is

$$\dot{N}^\varepsilon = (\beta_N - \mu_N) N^\varepsilon - \delta(N^\varepsilon)^2 - \kappa N^\varepsilon P_S^\varepsilon. \quad (6.2)$$

Hence

$$\dot{N}^\varepsilon \leq (\beta_N - \mu_N) N^\varepsilon. \quad (6.3)$$

By summing the two last equations of (6.1) we obtain

$$\dot{P}^\varepsilon = (\beta_P - \mu_P) P^\varepsilon - \eta P_S^\varepsilon \quad (6.4)$$

and  $P_S^\varepsilon \geq 0$  implies that

$$\dot{P}^\varepsilon \leq (\beta_P - \mu_P) P^\varepsilon. \quad (6.5)$$

Therefore by using (6.3) and (6.5) we obtain the following finite time estimation uniform in  $\varepsilon$ .

**Lemma 6.2** *For each  $\tau > 0$  we can find a constant  $M = M(\tau, N_0, P_0) > 0$  (independent of  $\varepsilon > 0$ ) such that*

$$0 \leq N^\varepsilon(t) \leq M \text{ and } 0 \leq P^\varepsilon(t) \leq M, \forall t \in [0, \tau]. \quad (6.6)$$

and

$$\sup_{t \in [0, \tau]} |\dot{N}^\varepsilon(t)| \leq M \text{ and } \sup_{t \in [0, \tau]} |\dot{P}^\varepsilon(t)| \leq M. \quad (6.7)$$

*Proof.* We first deduce (6.6) by using the inequalities (6.3) and (6.5). By using the fact  $P_S \geq 0$  and  $P_H \geq 0$  we have

$$0 \leq P_S^\varepsilon(t) \leq M, \text{ and } 0 \leq P_H^\varepsilon(t) \leq M, \forall t \in [0, \tau]. \quad (6.8)$$

Therefore by injecting these estimations into (6.2) and (6.4) we deduce (6.7).  $\blacksquare$

By using Lemma 4.1, and the Arzela-Ascoli theorem we deduce that we can find a sequence  $\varepsilon_n \rightarrow 0$  such that

$$\lim_{n \rightarrow \infty} N^{\varepsilon_n} = N \text{ and } \lim_{n \rightarrow \infty} P^{\varepsilon_n} = P$$

where the convergence is taking place in  $C([0, \tau], \mathbb{R})$  for the uniform convergence topology.

Moreover by using the fact that  $P_H^\varepsilon = P^\varepsilon - P_S^\varepsilon$ , the  $P_S^\varepsilon$ -equation can be rewritten as

$$\dot{P}_S^\varepsilon = - \left( (\mu_P + \eta) + \frac{\chi}{\varepsilon} \kappa N^\varepsilon \right) P_S^\varepsilon + \frac{1}{\varepsilon} (P^\varepsilon - P_S^\varepsilon). \quad (6.9)$$

By using (6.8), the map  $t \rightarrow P_S^\varepsilon(t)$  is bounded uniformly in  $\varepsilon$ . So the family  $\varepsilon_n \rightarrow P_S^{\varepsilon_n}$  is bounded in  $L^\infty((0, \tau), \mathbb{R})$  which is the dual space of  $L^1((0, \tau), \mathbb{R})$ . Therefore by using the Banach-Alaoglu-Bourbaki's theorem, we can find a sub-sequence (denoted with the same index) such that  $\varepsilon_n \rightarrow P_S^{\varepsilon_n}$  converges to  $P_S \in L^\infty((0, \tau), \mathbb{R})$  for the weak star topology of  $\sigma(L^\infty((0, \tau), \mathbb{R}), L^1((0, \tau), \mathbb{R}))$ . That is to say that for each  $\chi \in L^1((0, \tau), \mathbb{R})$

$$\lim_{n \rightarrow \infty} \int_0^\tau \chi(t) (P_S^{\varepsilon_n}(t) - P_S(t)) dt = 0.$$

By multiplying (6.9) by  $\chi \in C_c^1((0, \tau), \mathbb{R})$  (the space  $C^1$  functions with compact support in  $(0, \tau)$ ) and by integrating over  $[0, \tau]$  we obtain

$$-\int_0^\tau \dot{\chi}(t) P_S^{\varepsilon_n}(t) dt = \int_0^\tau \chi(t) \left[ -\left( (\mu_P + \eta) + \frac{\chi}{\varepsilon_n} \kappa N^{\varepsilon_n}(t) \right) P_S^{\varepsilon_n}(t) + \frac{1}{\varepsilon_n} (P^{\varepsilon_n}(t) - P_S^{\varepsilon_n}(t)) \right] dt.$$

Hence by multiplying both sides by  $\varepsilon_n$  and by taking the limit when  $n$  goes to infinity we obtain

$$0 = \int_0^\tau \chi(t) \left[ -(\chi \kappa N(t)) P_S(t) + (P(t) - P_S(t)) \right] dt$$

and since  $C_c^1((0, \tau), \mathbb{R})$  is dense in  $L^1((0, \tau), \mathbb{R})$  we deduce that

$$P_S^{\varepsilon_n}(t) \xrightarrow{*} \frac{1}{1 + \chi \kappa N(t)} P(t) \text{ as } n \rightarrow \infty.$$

By using the first equation of (6.1) and (6.4), we have

$$\begin{aligned} N^{\varepsilon_n}(t) &= \frac{e^{\int_0^t \beta_N - \mu_N - \kappa P_S^{\varepsilon_n}(\sigma) d\sigma} N_0}{1 + \delta \int_0^t e^{\int_0^l \beta_N - \mu_N - \kappa P_S^{\varepsilon_n}(\sigma) d\sigma} N_0 dl}, \\ P^{\varepsilon_n}(t) &= e^{(\beta_P - \mu_P)t} P_0 - \int_0^t e^{(\beta_P - \mu_P)(t-s)} \eta P_S^{\varepsilon_n}(\sigma) d\sigma. \end{aligned}$$

By taking the limit on both sides we deduce that

$$\begin{cases} \dot{N} = (\beta_N - \mu_N) N(t) - \delta N(t)^2 - \frac{\kappa N(t)}{1 + \chi \kappa N(t)} P(t), \\ \dot{P} = (\beta_P - \mu_P) P - \eta \frac{1}{1 + \chi \kappa N(t)} P. \end{cases}$$

Therefore we obtain the following theorem.

**Theorem 6.3** *Let  $\tau > 0$  be fixed. For each fixed initial values  $N_0 \geq 0$ ,  $P_{S0} \geq 0$  and  $P_{H0} \geq 0$ , we have the following results:*

$$\lim_{\varepsilon \rightarrow 0} N^\varepsilon(t) = N(t) \text{ and } \lim_{\varepsilon \rightarrow 0} P_S^\varepsilon(t) + P_H^\varepsilon(t) = P(t)$$

where the limit is uniform on  $[0, \tau]$ ,  $(N^\varepsilon(t), P_S^\varepsilon(t), P_H^\varepsilon(t))$  is the solution of (6.1) with the initial conditions

$$N^\varepsilon(0) = N_0 \geq 0, P_S^\varepsilon(0) = P_{S0} \geq 0 \text{ and } P_H^\varepsilon(0) = P_{H0} \geq 0$$

and  $(N(t), P(t))$  is the solution of the Rosenzweig-MacArthur model

$$\begin{cases} \dot{N} = (\beta_N - \mu_N) N(t) - \delta N(t)^2 - \frac{\kappa N(t)}{1 + \chi \kappa N(t)} P(t), \\ \dot{P} = (\beta_P - \mu_P - \eta) P + \eta \frac{\chi \kappa N(t)}{1 + \chi \kappa N(t)} P \end{cases} \quad (6.10)$$

with the initial conditions

$$N(0) = N_0 \text{ and } P(0) = P_{S0} + P_{H0}.$$

**Remark 6.4** If instead of the model (1.1) we consider the following model

$$\begin{cases} \dot{N} = (\beta_N - \mu_N)N - \delta N^2 - \kappa N^l P_S \\ \dot{P}_S = -(\mu_P + \eta)P_S - \rho \kappa N^m P_S + \gamma P_H, \\ \dot{P}_H = \beta_P(P_S + P_H) - \mu_P P_H + \rho \kappa N^m P_S - \gamma P_H \end{cases} \quad (6.11)$$

Then by using the same procedure above we obtain a convergence result to the most classical predator prey model

$$\begin{cases} \dot{N} = (\beta_N - \mu_N)N(t) - \delta N(t)^2 - \frac{\kappa N(t)^l}{1 + \chi \kappa N(t)^m} P(t), \\ \dot{P} = (\beta_P - \mu_P - \eta)P + \eta \frac{\chi \kappa N(t)^m}{1 + \chi \kappa N(t)^m} P. \end{cases} \quad (6.12)$$

By choosing  $l = m$  we obtain the classical Holling's type functional response.

## 7 Application to the Snowshoe Hares and the Lynx

In this section we reconsider predator-prey system form by the hares (prey) and lynxes (predator) in the years 1900-1920 recorded by the Hudson Bay Company. The data are available for example in [5].

Year	Hares (in thousands)	Lynx (in thousands)
1900	30	4
1901	47.2	6.1
1902	70.2	9.8
1903	77.4	35.2
1904	36.3	59.4
1905	20.6	41.7
1906	18.1	19
1907	21.4	13
1908	22	8.3
1909	25.4	9.1
1910	27.1	7.4
1911	40.3	8
1912	57	12.3
1913	76.6	19.5
1914	52.3	45.7
1915	19.5	51.1
1916	11.2	29.7
1917	7.6	15.8
1918	14.6	9.7
1919	16.2	10.1
1920	24.7	8.6

Table 1: Numbers of hares (prey) and lynxes (predator) in the years 1900-1920 recorded by the Hudson Bay Company

The limit model obtain for  $\varepsilon$  small enough is given by

$$\begin{cases} \dot{N} = (\beta_N - \mu_N)N \left(1 - \frac{\delta N}{\beta_N - \mu_N}\right) - \frac{\kappa P N}{1 + \chi \kappa N}, \\ \dot{P} = (\beta_P - \mu_P - \eta)P + \eta \frac{\chi \kappa P N}{1 + \chi \kappa N} \end{cases} \quad (7.1)$$

with initial value

$$N(0) = N_0 = 30 \times 10^3 \text{ and } P(0) = P_0 = 4 \times 10^3.$$

Symbol	Interpretation	Value	Unit	Method
$1/\mu_N$	Life expectancy of hares	1	year	fixed
$\beta_N$	Birth rate of hares	1.6567	number of new born/year	fitted
$\delta$	Carrying capacity of hares	303000	year	fitted
$\kappa$		$3.2 \times 10^{-5}$		fitted
$\chi$		0.11		fitted
$1/\mu_P$	Life expectancy of Lynx	7	year	fixed
$\beta_P$	Birth rate of Lynx	8.5127	number of new born/year	fitted
$\eta$	Extra mortality of searching Lynx	9.24	year <sup>-1</sup>	fitted
$\beta_P - \mu_P - \eta$	Growth of searching lynx	-0.8702		fitted
$\eta\chi$	Conversion rate	1.0164		fitted

Table 2: List parameters for the model (7.1), their interpretations, values and symbols. In this table we have fixed  $\mu_N$  and  $\mu_P$  and we have obtain all the remaining parameters by using a least square method between the data in Table 1 the solution of the model (7.1). The life expectancy of Snowshoe Hares is not known [4, 7]. Here we fix the life expectancy of hares to be 1 year (similarly to [22]). In the wild a Canadian Lynx can live up to 14 years. Here we fix the life expectancy to be 7 years (see [6] for more result). A Canadian lynx can have between 1 and 8 new babies [14]. So the estimation obtained for the brith rate of lynx is still reasonable.



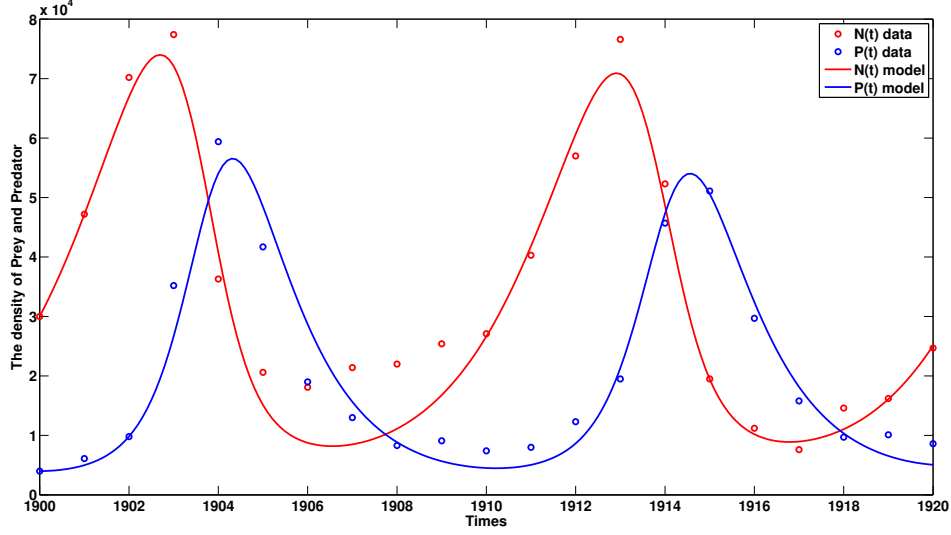


Figure 1: In this figure we run a simulation of the model (7.1) (solide lines) compared with the data (circles).

In section 6, we proved that the model (7.1) can be obtained as singular limit (when  $\varepsilon \rightarrow 0$ ) of the following model

$$\begin{cases} \dot{N}^\varepsilon = (\beta_N - \mu_N) N^\varepsilon \left(1 - \frac{\delta N^\varepsilon}{\beta_N - \mu_N}\right) - \kappa N^\varepsilon P_S^\varepsilon \\ \dot{P}_S^\varepsilon = -(\mu_P + \eta) P_S^\varepsilon - \frac{\chi}{\varepsilon} \kappa N^\varepsilon P_S^\varepsilon + \frac{1}{\varepsilon} P_H^\varepsilon \\ \dot{P}_H^\varepsilon = -\mu_P P_H^\varepsilon + \frac{\chi}{\varepsilon} \kappa N^\varepsilon P_S^\varepsilon - \frac{1}{\varepsilon} P_H^\varepsilon + \beta_P (P_S^\varepsilon + P_H^\varepsilon) \end{cases} \quad (7.2)$$

and we fix the initial value

$$N^\varepsilon(0) = N_0 = 30 \times 10^3 \geq 0, P_S^\varepsilon(0) = P_{S0} \geq 0 \text{ and } P_H^\varepsilon(0) = P_{H0} \geq 0.$$

In Theorem 6.3 we proved that for  $\varepsilon$  small enough

$$P_S^\varepsilon(t) \simeq \frac{1}{1 + \chi \kappa N(t)} P(t) \text{ and } P_H^\varepsilon(t) \simeq \left(1 - \frac{1}{1 + \chi \kappa N(t)}\right) P(t) = \frac{\chi \kappa N(t)}{1 + \chi \kappa N(t)} P(t). \quad (7.3)$$

By using the value for  $\chi \kappa$  estimated in Table 2, we obtain the following initial values for the model (7.2)

$$P_{S0}^\varepsilon = \frac{P_0}{1 + \chi \kappa N_0} = \frac{4 \times 10^3}{1 + 1.0164 \times 30 \times 10^3} \text{ and } P_{R0}^\varepsilon = \frac{\chi \kappa N_0}{1 + \chi \kappa N_0} P_0 = \frac{1.0164 \times 30 \times 10^3}{1 + 1.0164 \times 30 \times 10^3} 4 \times 10^3. \quad (7.4)$$

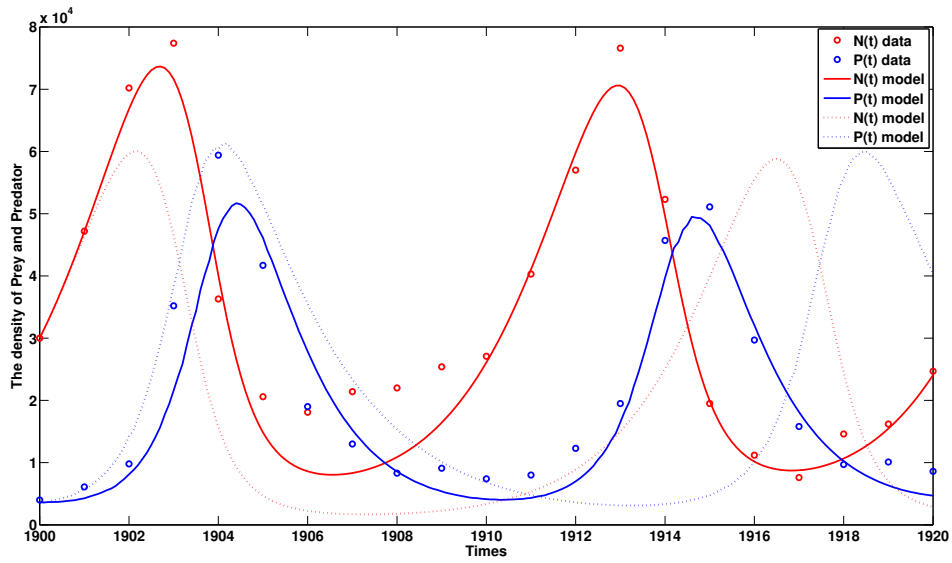


Figure 2: In this figure we run a simulation of the model (7.2) (solide and dotted lines) compared with the data (circles). The solide lines correspond to  $\varepsilon = 10^{-4}$  and the dotted lines correspond to  $\varepsilon = 5.10^{-3}$ .

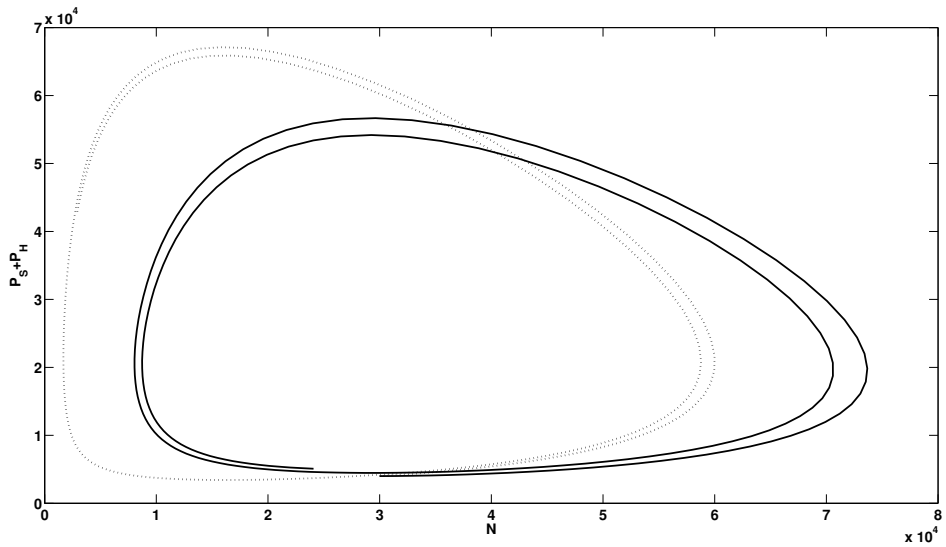


Figure 3: In this figure we run a simulation of the model (7.2) with  $\varepsilon = 10^{-4}$  for solide line and with  $\varepsilon = 5.10^{-3}$  for dotted line.

From Figures 1 and 2, we can see that  $\varepsilon$  does not need to be very small ( $\varepsilon = 10^{-4}$ ) to get an almost perfect match of our model (7.2) with the Rosenzweig-MacArthur model (7.1). Our simulations for hares and lynxes fit the data reported by the Hudson Bay Company. As we mentioned the main advantage with the model (7.2) is that we can separate the vital dynamic and consumption of prey (hares) to describe the behavior of the predators (lynxes). From our model (7.2), people can study the interaction between predator and prey in detail and get more information.

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