Notes on resource-consumptions (predator-prey) models

1 Introduction

2 Definitions

Let

$$\begin{aligned} n &= \text{prey density} \\ p &= \text{predator density} \end{aligned} \tag{2.1}$$

a predator-prey model takes the general form

$$\begin{aligned} \dot{n} &= f(n) - g(n)\,p \\ \dot{p} &= \gamma\,g(n)\,p - \delta\,p \end{aligned} \tag{2.2}$$

How do we model f and g?

1. If no predators are present, we have

$$\dot{n} = f\,(n) \tag{2.3}$$

   In such a case we can model the prey dynamics independently of that of predators.

2. We interpret

$$g(n) = \text{number of prey captured per predator per unit of time}$$

   This quantity will be also referred to as *functional response of the predator*.

$$\gamma = \text{conversion constant: prey} \;\rightarrow\; \text{predator} \qquad \& \qquad \frac{1}{\gamma} = \text{yield}$$

3 Holling's functional response theory

3.1 First model of functional response

1. individual states N, P
2. individual level processes

$$\begin{aligned} &P + N \xrightarrow{\beta} P + \gamma\,P \\ &P \xrightarrow{\delta} \emptyset \end{aligned} \tag{3.1}$$

The p-level equations are

$$\begin{aligned} \dot{n} &= f(n) - \beta\, n\, p \\ \dot{p} &= \gamma\, \beta\, n\, p - \delta\, p \end{aligned} \tag{3.2}$$

The functional response is

$$g(n) = \beta\, n \tag{3.3}$$

Remark 3.1. The reaction

$$P + N \xrightarrow{\beta} P + \gamma\, P \tag{3.4}$$

is biologically meaningful for $\gamma \in \mathbb{N}$. Alternatively one can adopt a *probabilistic interpretation* of the individual level reaction

$$P + N \begin{cases} \xrightarrow{(1-\gamma)\,\beta} P + N \\ \xrightarrow{\gamma\,\beta} P \end{cases} \tag{3.5}$$

3.2 Second model of functional response

Individual states:

1. N prey.
2. X hunting predator.
3. Y resting predator.

Individual processes

$$\begin{array}{ll} X \xrightarrow{\delta} \emptyset & \text{death of a hunting predator} \\ Y \xrightarrow{\delta} \emptyset & \text{death of a resting predator} \\ N + X \xrightarrow{\beta} Y & \text{prey capture} \\ Y \begin{array}{l} \xrightarrow{\mu} X \\ \xrightarrow{\lambda} 2\,X \end{array} & \begin{array}{l} \text{resume hunting} \\ \text{reproduction and resume hunting} \end{array} \end{array} \tag{3.6}$$

Population dynamics equations

$$\begin{aligned} \dot{n} &= f(n) - \beta\, n\, x \\ \dot{x} &= -\delta\, x - \beta\, n\, x + \mu\, y + 2\,\lambda\, y \\ \dot{y} &= -\delta\, y + \beta\, n\, x - \mu\, y - \lambda\, y \end{aligned} \tag{3.7}$$

The total number of predator states is

$$p = x + y \tag{3.8}$$

In terms of the predator states (3.7) becomes

$$\begin{aligned} \dot{n} &= f(n) - \beta\, n\, x \\ \dot{x} &= -\delta\, x - \beta\, n\, x + (\mu + 2\,\lambda)\,(p - x) \\ \dot{p} &= \lambda\,(p - x) - \delta\, p \end{aligned} \tag{3.9}$$

The above system describes the demographic dynamics, when the rates of each of the involved processes are comparable. The number of degrees of freedom can be systematically reduced if we assume a *time scale separation* among the processes. Let us assume that prey capturing $N + X \to Y$ and hunting resuming $Y \to X$ are fast processes. The hypothesis can be rephrased by setting

$$\beta := \frac{\beta_\star}{\varepsilon} \qquad \& \qquad \mu := \frac{\mu_\star}{\varepsilon} \tag{3.10}$$

with $\mu_\star$ and $\beta_\star$ two constant decay rates and ε a pure number determining the relative weight of the interactions. As ε tends to zero, prey capturing and hunting resuming become faster and faster processes. In such a limit the population dynamics equations

$$\begin{aligned}
\dot{n} &= f(n) - \frac{\beta_\star}{\varepsilon}\, n\, x \\
\dot{x} &= -\delta\, x - \frac{\beta_\star}{\varepsilon}\, n\, x + \left(\frac{\mu_\star}{\varepsilon} + 2\,\lambda\right)\, (p - x) \\
\dot{p} &= \lambda\, (p - x) - \delta\, p
\end{aligned} \tag{3.11}$$

admit nevertheless a non-trivial solution when we assume that the hunting and the resting predator densities vanish linearly with $O(\varepsilon)$. In order to validate this claim in what follows we will present two methods different methods:

1. the scaling limit method,

2. the multiple scale perturbation theory method.

3.2.1 Scaling limit method

The idea underlying the method is to take the limit of vanishing ε whilst simultaneously rescaling population densities and the time unit. To this scope we define the *fast time*

$$s := \frac{t}{\varepsilon} \tag{3.12}$$

and introduce the rescaled predator densities

$$x^\star := \frac{x}{\varepsilon} \quad \& \quad p^\star := \frac{p}{\varepsilon} \tag{3.13}$$

In terms of these new quantities the system (3.11) become

$$\begin{aligned}
\frac{dn}{ds} &= \varepsilon\, [f(n) - \beta_\star\, n\, x^\star] \\
\frac{dx^\star}{ds} &= -\varepsilon\, \delta\, x^\star - \beta_\star\, n\, x^\star + \left(\frac{\mu_\star}{\varepsilon} + 2\,\lambda\right)\, \varepsilon\, (p^\star - x^\star) \\
\frac{dp^\star}{ds} &= \varepsilon\, \lambda\, (p^\star - x^\star) - \varepsilon\, \delta\, p^\star
\end{aligned} \tag{3.14}$$

and yields for $\varepsilon \downarrow 0$:

$$\begin{aligned}
\frac{dn}{ds} &= 0 \\
\frac{dx^\star}{ds} &= -\beta_\star\, n\, x^\star + \mu_\star\, (p^\star - x^\star) \\
\frac{dp^\star}{ds} &= 0
\end{aligned} \tag{3.15}$$

The conclusion is that n (prey density) and p (the total predator density) are *independent* of the fast time s. On the contrary, the fraction of hunting predators varies on faster time scales. The dynamics of this latter quantity is one-dimensional, and relaxes with an *effective rate* $\beta_\star\, n + \mu_*$ to a *quasi-steady state*

$$x^\star = \frac{\mu_\star\, p^\star}{\mu_\star + \beta_\star\, n} \tag{3.16}$$

Once the faster time scale has driven the x into the quasi-steady state the evolution of the remaining degrees of freedom in system occurs with slower time scale t. In order to identify the slow dynamics it is sufficient to insert the quasi-steady state equation into (3.14) and look at the variation with t

$$\frac{dn}{dt} = f(n) - \frac{\beta_\star\, \mu_\star\, n\, p^\star}{\mu_\star + \beta_\star\, n} \tag{3.17}$$

and

$$\frac{dp^\star}{dt} = \left(\lambda - \delta - \frac{\mu_\star\, \lambda}{\mu_\star + \beta_\star\, n}\right) p^\star = \left(\frac{\lambda\, \beta_\star\, n}{\mu_\star + \beta_\star\, n} - \delta\right) p^\star \tag{3.18}$$

We identify Holling Type II functional response:

$$g(n) = \frac{\lambda\, \mu_\star\, \beta_\star\, n}{\mu_\star + \beta_\star\, n} \quad \& \quad \gamma = \frac{\lambda}{\mu_\star} \tag{3.19}$$

The scaling limit method provides a fast and intuitive way to derive the fast dynamics from the slow. The shortcoming is, however, is that it is not immediately evident how to derive systematic corrections to the limit slow-fast dynamics for small but finite ε. This goal can be instead achieved by using *multiple scale* perturbation theory as it will be shown below.

3.2.2 Multiple scale method

The idea is to expand the solution of (3.11) in a power series in ε:

$$\begin{bmatrix} n_\star \\ x_\star \\ p_\star \end{bmatrix} := \sum_{k=0}^{\infty} \varepsilon^k \begin{bmatrix} n_k \\ x_k \\ p_k \end{bmatrix} \tag{3.20}$$

In analogy with what done in the previous section, we will suppose that the functional dependence of the dynamics on the time variable occurs with a hierarchy of time scales which is treated as independent:

$$\frac{t}{\varepsilon}\,, t\,, \varepsilon\, t\,, \varepsilon^2\, t\,, \dots = s\,, t\,, s_1\,, s_2\, \dots \tag{3.21}$$

The value of the corresponding partial derivatives can be then determined, order by order in the expansion, by requiring the perturbative expansion to remain well defined as t grows to infinity (see e.g. chapter 6 of [1] for further details). In practice, for (3.11) we write

$$\begin{bmatrix} n \\ x \\ p \end{bmatrix} = \begin{bmatrix} n_0\left(\frac{t}{\varepsilon}\,, t\right) \\ x_0\left(\frac{t}{\varepsilon}\,, t\right) \\ p_0\left(\frac{t}{\varepsilon}\,, t\right) \end{bmatrix} + \varepsilon \begin{bmatrix} n_1\left(\frac{t}{\varepsilon}\,, t\right) \\ x_1\left(\frac{t}{\varepsilon}\,, t\right) \\ p_1\left(\frac{t}{\varepsilon}\,, t\right) \end{bmatrix} + \varepsilon^2 \begin{bmatrix} n_2\left(\frac{t}{\varepsilon}\,, t\right) \\ x_2\left(\frac{t}{\varepsilon}\,, t\right) \\ p_2\left(\frac{t}{\varepsilon}\,, t\right) \end{bmatrix} + O(\varepsilon^3\, \varepsilon\, t) \tag{3.22}$$

Correspondingly, the total time derivative acts of the densities as

$$\frac{d}{dt} = \frac{1}{\varepsilon}\frac{\partial}{\partial s} + \frac{\partial}{\partial t} + O(\varepsilon) \tag{3.23}$$

Inserting (3.22) and (3.23) into (3.11) the system foliates in a hierarchy of equations weighted by different powers of ε.

1. $O\left(\varepsilon^{-1}\right)$ equations:

$$
\begin{aligned}
\partial_s n_0 &= -\beta_\star\, n_0\, x_0 \\
\partial_s x_0 &= -\beta_\star\, n_0\, x_0 + \mu_\star\, (p_0 - x_0) \\
\partial_s p_0 &= 0
\end{aligned}
\tag{3.24}
$$

   The system admits the solution

$$
x_0^\star = p_0^\star = \partial_s n_0^\star = 0 \tag{3.25}
$$

   which is the only compatible with the assumption that of a slow prey dynamics.

2. $O(\varepsilon^0)$ equations:

$$
\begin{aligned}
&\partial_t n_0 = f(n_0) - \beta_\star\, (n_0\, x_1 + n_1\, x_0) \\
&\partial_s x_1 + \partial_t x_0 = -\delta\, x_0 - \beta_\star\, (n_0\, x_1 + n_1\, x_0) + \mu_\star\, (p_1 - x_1) + 2\,\lambda\, (p_0 - x_0) \\
&\partial_s p_1 + \partial_t p_0 = \lambda\, (p_0 - x_0) - \delta\, p_0
\end{aligned}
\tag{3.26}
$$

   Upon inserting (3.25) reduce to

$$
\begin{aligned}
&\partial_t n_0 = f(n_0) - \beta_\star\, n_0\, x_1 \\
&\partial_s x_1 = -\beta_\star\, n_0\, x_1 + \mu_\star\, (p_1 - x_1) \\
&\partial_s p_1 = 0
\end{aligned}
\tag{3.27}
$$

   The fraction of hunting predators has a fixed point *with respect to the fast time scale* for

$$
x_1^\star = \frac{\mu_\star\, p_1^\star}{\mu_\star + \beta_\star\, n_0^\star} \qquad \& \qquad \partial_s x_1^\star = \partial_s p_1^\star = 0 \tag{3.28}
$$

   The fixed point brings about a non-trivial dynamics in the slow time scale for the prey density:

$$
\partial_t n_0^\star = f\,(n_0^\star) - \frac{\beta_\star\, \mu_\star\, p_1^\star\, n_0^\star}{\mu_\star + \beta_\star\, n_0^\star} \tag{3.29}
$$

   The dynamics is, however, not yet fully specified as we cannot rule out a dependence upon the slow time-scale of $p_1\,, n_1$. In order to address this issue we need to inquire one order more in our perturbative expansion.

3. $O(\varepsilon)$ equations:

$$
\begin{aligned}
&\partial_t n_1 = n_1 (\partial_n f)(n_0) - \beta_\star (n_0\, x_2 + 2\, n_1\, x_1 + n_2\, x_0) \\
&\partial_s x_2 + \partial_t x_1 = -\delta\, x_1 - \beta_\star (n_0\, x_2 + 2\, n_1\, x_1 + n_2\, x_0) + \mu_\star\, (p_2 - x_2) + 2\,\lambda\, (p_1 - x_1) \\
&\partial_s p_2 + \partial_t p_1 = \lambda\, (p_1 - x_1) - \delta\, p_1
\end{aligned}
\tag{3.30}
$$

   Using (3.25) and (3.29) we obtain

$$
\begin{aligned}
&\partial_t n_1^\star = n_1 (\partial_n f)(n_0^\star) - \beta_\star (n_0^\star\, x_2 + 2\, n_1^\star\, x_1^\star) \\
&\partial_s x_2 + \partial_t \left(\frac{\mu_\star\, p_1^\star}{\mu_\star + \beta_\star\, n_0^\star} \right) = -\frac{\delta\, \mu_\star\, p_1^\star}{\mu_\star + \beta_\star n_0^\star} - \beta_\star \left(n_0^\star\, x_2 + \frac{2\, \mu_\star\, n_1^\star\, p_1^\star}{\mu_\star + \beta_\star n_0^\star} \right) + \mu_\star\, (p_2 - x_2) + 2\, \frac{\lambda\, \beta_\star\, n_0^\star\, p_1^\star}{\mu_\star + \beta_\star\, n_0^\star} \\
&\partial_s p_2 + \partial_t p_1^\star = \frac{\lambda\, \beta_\star\, n_0^\star\, p_1^\star}{\mu_\star + \beta_\star\, n_0^\star} - \delta\, p_1^\star
\end{aligned}
\tag{3.31}
$$

By (3.28) the resting predator density $p_1^\star$ is independent from the fast time scale s. This means that the third of the above equations has the general solution

$$p_2^\star = \bar{p}_2^\star + \left(\frac{\lambda\,\beta_\star\,n_0^\star\,p_1^\star}{\mu_\star + \beta_\star\,n_0^\star} - \delta\,p_1^\star - \partial_t p_1^\star \right)\,s \tag{3.32}$$

where $p_2^\star$ is an arbitrary initial condition. The solution implies a *marginal instability* (linear in time) of the perturbative expansion. As s grows the quantity $\varepsilon^2\,s = \varepsilon\,t$ becomes of the order of the unity and the perturbative expansion in ε meaningless. The circumstance can be prevented by requiring

$$\partial_t p_1^\star = \left(\frac{\lambda\,\beta_\star\,n_0^\star}{\mu_\star + \beta_\star\,n_0^\star} - \delta \right)\,p_1^\star \tag{3.33}$$

This latter condition fully specifies the solution of (3.11) at leading order in each of the densities.

To summarize, the reduced dynamical system associated to (3.11) is

$$\begin{aligned} &\partial_t n_0^\star = f\,(n_0^\star) - \frac{\beta_\star\,\mu_\star\,p_1^\star\,n_0^\star}{\mu_\star + \beta_\star\,n_0^\star} \\ &\partial_t p_1^\star = \left(\frac{\lambda\,\beta_\star\,n_0^\star}{\mu_\star + \beta_\star\,n_0^\star} - \delta \right)\,p_1^\star \\ &x_1^\star = \frac{\mu_\star\,p_1^\star}{\mu_\star + \beta_\star\,n_0^\star} \\ &x_0^\star = p_0^\star = \partial_s x_1^\star = \partial_s p_1^\star = \partial_s p_2^\star = 0 \end{aligned} \tag{3.34}$$

We can use this result for a individual process interpretation of the functional responses in the predator prey model (2.2). Dropping for simplicity sake sub and superscripts we find that the functional response is

$$g(n) = \frac{\beta\,n}{1 + \frac{\beta}{\mu}\,n} \qquad \& \qquad \gamma = \frac{\lambda}{\mu} \tag{3.35}$$

where all parameters have a individual level interpretation

$$\begin{aligned} &\beta = \text{attack rate} \\ &\frac{1}{\mu} = \text{average handling time} \end{aligned} \tag{3.36}$$

Holling's first model of functional response is recovered from the second model by taking the limit of *vanishing handling time*:

$$\lim_{\mu \uparrow \infty} \frac{\beta}{1 + \frac{\beta}{\mu}\,n} = \beta \tag{3.37}$$

3.3 Holling's empirical interpretation

Based on an experiment that he did with the help of his secretary, Holling proposed the following interpretation for the terms appearing in the functional response. He defined:

1. dt time unit.
2. n_c number of preys captured by a predator during the time unit.
3. $h\,n_c$ prey handling time by the predator.

4. $dt - h\,n_c$ hunting time during the time unit

and supposed that the total number of prey captured is proportional to the total prey density and the time spent hunting by the predator:

$$n_c = \beta\, n\; (dt - h\, n_c) \qquad \Rightarrow \qquad n_c = \frac{\beta\, n\, dt}{1 + \beta\, n\, h} \tag{3.38}$$

According to the above reasoning, the capture rate per predator is

$$\frac{n_c}{dt} = \frac{\beta\, n}{1 + \beta\, h\, n} = g(n) \tag{3.39}$$

4 Prey escape model

A prey may escape its predator. This event can be taken into account by introducing a state C corresponding to the pair of a prey and a predator stalking it. The individual processes are described by the diagram

$$\begin{aligned} & N + X \underset{\alpha}{\overset{\beta}{\rightleftarrows}} C \overset{\nu}{\rightarrow} Y \begin{array}{l} \overset{\mu}{\rightarrow} X \\ \overset{\lambda}{\rightarrow} 2\,X \end{array} \\ & X \overset{\delta}{\rightarrow} \emptyset \\ & Y \overset{\delta}{\rightarrow} \emptyset \\ & C \overset{\delta}{\rightarrow} \emptyset \end{aligned} \tag{4.1}$$

The corresponding population dynamics equation are

$$\begin{aligned} \dot{n} &= f(n) - \beta\, n\, x + \alpha\, c \\ \dot{x} &= -\beta\, n\, x + \alpha\, c + \mu\, y + 2\,\lambda\, y - \delta\, x \\ \dot{y} &= \nu\, c - \mu\, y - \lambda\, y - \delta\, y \\ \dot{c} &= \beta\, n\, x - \alpha\, c - \nu\, c - \delta\, c \end{aligned} \tag{4.2}$$

The total predator density is now

$$p = x + y + c \tag{4.3}$$

Eliminating c in favor of p the equations become

$$\begin{aligned} \dot{n} &= f(n) - \beta\, n\, x + \alpha\, (p - x - y) \\ \dot{x} &= -\beta\, n\, x + \alpha\, (p - x - y) + (\mu + 2\,\lambda)\, y - \delta\, x \\ \dot{y} &= \nu\, (p - x - y) - (\mu + \lambda + \delta)\, y \\ \dot{p} &= \lambda\, y - \delta\, p \end{aligned} \tag{4.4}$$

As in the previous section we introduce a separation of time scales by assuming

$$\begin{aligned} & \lambda\,, \delta \sim O(1) \\ & \alpha\,, \beta\,, \mu\,, \nu \sim O(\varepsilon^{-1}) \\ & x\,, y\,, p \sim O(\varepsilon) \end{aligned} \tag{4.5}$$

Proceeding as in the previous section, we write

$$\begin{aligned} \dot{n} &= f(n) - \frac{\beta_\star}{\varepsilon}\, n\, x + \frac{\alpha_\star}{\varepsilon}\, (p - x - y) \\ \dot{x} &= -\frac{\beta_\star}{\varepsilon}\; n\, x + \frac{\alpha_\star}{\varepsilon}\; (p - x - y) + \left(\frac{\mu_\star}{\varepsilon} + 2\,\lambda\right)\; y - \delta\, x \\ \dot{y} &= \frac{\nu_\star}{\varepsilon}\, (p - x - y) - \left(\frac{\mu_\star}{\varepsilon} + \lambda + \delta\right)\; y \\ \dot{p} &= \lambda\, y - \delta\, p \end{aligned} \tag{4.6}$$

We can use the scaling limit method to decouple fast and slow degrees of freedom. We define as before

$$x_\star = \frac{x}{\varepsilon} \quad \& \quad y_\star = \frac{y}{\varepsilon} \quad \& \quad p_\star = \frac{p}{\varepsilon} \tag{4.7}$$

and write (4.6) in terms of the fast time

$$\begin{aligned}
\frac{1}{\varepsilon}\frac{dn}{ds} &= f(n) - \beta_\star\, n\, x^\star + \alpha_\star\, (p^\star - x^\star - y^\star) \\
\frac{dx^\star}{ds} &= -\beta_\star\, n\, x^\star + \alpha_\star\, (p^\star - x^\star - y^\star) + \left(\frac{\mu_\star}{\varepsilon} + 2\,\lambda\right)\, \varepsilon\, y^\star - \varepsilon\, \delta\, x^\star \\
\frac{dy^\star}{ds} &= \nu_\star\, (p^\star - x^\star - y^\star) - \left(\frac{\mu_\star}{\varepsilon} + \lambda + \delta\right)\, \varepsilon\, y^\star \\
\frac{dp^\star}{ds} &= \varepsilon\, (\lambda\, y^\star - \delta\, p^\star)
\end{aligned} \tag{4.8}$$

The limit ε tending to zero then yields

$$\begin{aligned}
\frac{dn}{ds} &= 0 \\
\frac{dx_\star}{ds} &= -\beta_\star\, n\, x_\star + \alpha_\star (p_\star - x_\star - y_\star) + \mu_\star\, y_\star \\
\frac{dy_\star}{ds} &= \nu_\star\, (p_\star - x_\star - y_\star) - \mu_\star\, y_\star \\
\frac{dp_\star}{ds} &= 0
\end{aligned} \tag{4.9}$$

Again, the prey and the total predator densities appear under our working hypotheses as slow quantities. The fraction of predators hunting or resting vary instead on a faster time scale. The fast dynamics is now governed by the two-dimensional system

$$\begin{aligned}
\frac{dx_\star}{ds} &= -\beta_\star\, n\, x_\star + \alpha_\star (p_\star - x_\star - y_\star) + \mu_\star\, y_\star \\
\frac{dy_\star}{ds} &= \nu_\star\, (p_\star - x_\star - y_\star) - \mu_\star\, y_\star
\end{aligned} \tag{4.10}$$

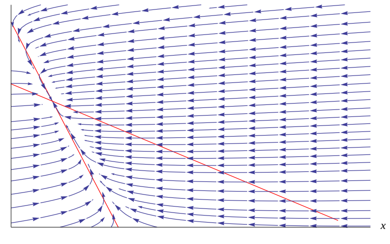
The phase plane diagram of the fast dynamics is obtained from the study of the *isoclines*

1. $\partial_s x_\star = 0$

$$y = \frac{\alpha_\star\, p_\star}{\alpha_\star - \mu_\star} - \frac{\alpha_\star + \beta_\star\, n}{\alpha_\star - \mu_\star}\, x \tag{4.11}$$

2. $\partial_s y_\star = 0$

$$y = \frac{\nu_\star\, p_\star}{\mu_\star + \nu_\star} - \frac{\nu_\star}{\mu_\star + \nu_\star}\, x \tag{4.12}$$



(4.13)

The quasi-steady state is the intercept between the isoclines

$$\begin{aligned} x^\star &= \frac{\mu_\star\,(\alpha_\star+\nu_\star)\,p_\star}{\mu_\star\,(\alpha_\star+\nu_\star)+\beta_\star\,(\mu_\star+\nu_\star)} \\ y^\star &= \frac{\beta_\nu\,\nu_\star\,p_\star\,n}{\mu_\star\,(\alpha_\star+\nu_\star)+\beta_\star\,(\mu_\star+\nu_\star)} \end{aligned} \tag{4.14}$$

References

[1] A.H. Nayfeh, *Perturbation Methods*, Wiley-VHC (2004).