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Permanence and Optimization of Harvesting Return: A Stage-Structured Prey-Predator Fishery

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Abstract: In this research we study the dynamics of a prey-predator system, where predator has two stages, a juvenile stage and a mature stage and are harvested by two different groups of fishermen. The existence of possible steady states along with their local and global stability is discussed. We obtained the condition for permanence of the system. We analyzed optimum management of these fisheries and determined optimal levels of stock, effort and catch using a hypothetical set of parameter values.

Key words: Stage structure, multi-fleet, global stability, permanence, bio-economic

INTRODUCTION

Many consumer species go through two or more life stages as they proceed from birth to death. However, the majority of the models in the literature always assumed that during the whole life histories, each individual admits the same density-dependent rate as well as the identical ability to bear and compete with other species, which clearly unrealistic. In many species, only the mature predator food on the prey and its immature are too weak to food on the prey. Therefore, it is practical to introduce the stage-structure into the competitive or prey-predator models. Some of the stage structure models can be found in Aiello and Freedman (1990), Aiello *et al*. (1992), Freedman and Wu (1991), Gambell (1985), Landahl and Hanson (1975), Wood *et al*. (1989) and the references therein. A good overview on stage-structured models can be found in the recent book by Murdoch *et al*. (2003). Recently, papers like Bosch and Gabriel (1997), Kar (2003), Kar and Matsuda (2006), Zhang *et al*. (2000) and Wikan (2004) study the stage structure of species with or without time delays.

Harvesting has also a strong impact on a dynamic property of a population. Depending on the nature of applied harvesting strategy, the long-run stationary density of the population may be significantly smaller than the long run stationary density of a population in the absence of harvesting. In the absence of harvesting, a population can be free from extinction risk; however, harvesting can lead to the incorporation of a positive extinction probability and therefore, to potential extinction in a finite time. If a population is subject to a positive extinction rate then harvesting can drive the population density to a dangerously low level at which extinction becomes sure no matter how the harvester affects the population afterwards.

A fundamental issue in population biology is what are the minimal conditions to ensure the long term survivorship for all of the interacting components. When these conditions are meet the interacting populations are said to persist or coexist. Permanence corresponds to the existence of a positive attractor that attracts all positive population trajectories. Permanence implies positive population trajectories can recover from large perturbations of the state variables. This question is of particular interest to fishing managers. If it is known that the system exhibits such a permanent behaviour, then ecological planning based on a fixed eventual population can be carried out. Realizing the problem we have obtained the conditions for permanence of the solutions of our system considered.

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Though the application of bioeconomics has usually limited to the determination of Total Allowable Catch (TAC), the sharing of the TAC between heterogeneous fisher groups is an important issue to be considered. The fact that different fisher groups harvest different cohorts within fish stocks and thereby have different effects upon both stocks growth and the economics of the fishery, is not taken into account. Political determination of harvest shares has bioeconomic effects, for instance, in the shape of reduced payoffs from the fishery or even extinction. This study is focused on the optimal steady state fish stock level and hence on the steady state Total Allowable Catch (TAC). This is done using a cooperative game theoretic approach to the issue of sharing the harvest. We assume that the harvest strategies of the two vessel groups are determined by their existing technologies and their respective fishing grounds. Thus, the overall optimal sharing of the resource can be determined, after deciding the weights that should be given to the two parties preferences.

THE MODEL

The ecosystem in our model consists of a prey-predator system. We assume that the prey population (denoted by N_1) is subjected to a logistic growth condition. The predator population is divided into two stage groups: juvenile predators (denoted by N_2) and adult predators (denoted by N_3). Here we also assume that only adult predators are capable of preying on the prey species and that the juvenile predators live on their parents. For example, the Chinese Alligator can be regarded as a stage-structured species since the mature is more than 10 years old and can also be regarded as a predator because almost all aquatic animals are the chief food of the Chinese Alligator. Another key and somewhat novel feature of our model is to account for the universally prevalent intra-specific competition in the consumer growth dynamic (Kuang *et al*., 2003). This intra-specific competition is assumed to induce additional instantaneous deaths only to the adult population and the increased death rate is proportional to the square of the adult population. Holling type II functional response probably a better description of the actual predation seen in nature but for simplicity, we assume the simplest description.

With this assumptions, we have the following plausible two stage prey-predator interaction model:

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1-\frac{N_1}{k}\right) - \alpha N_1 N_3, \\ \frac{dN_2}{dt} &= \beta N_3 - r_2 N_2, \\ \frac{dN_3}{dt} &= -r_3 N_3 + m\alpha N_1 N_3 + \gamma N_2 - \delta N_3^2. \end{aligned} \tag{1}$$

Here r_1 is the specific growth rate of the prey and k is its carrying capacity. α is the predation parameter; m is the conversion factor; r_3 is the death rate of mature predator species; γ is the proportionality constant of transformation of immature to mature predators; $r_2 = \mu + \gamma$, where μ is the death rate; β is the birth rate of the immature populations.

We can reduce the number of parameters by making the following transformation of variables:

$$N_1 = \frac{k r_2}{r_1} x_1,\; N_2 = \frac{\beta x_2}{m\alpha},\; N_3 = \frac{r_2 x_3}{m\alpha},\; t = \frac{\tau}{r_2}.$$

Making these changes, system (1) assume the much simpler form

$$\frac{dx_1}{d\tau} = a x_1 - x_1^2 - b x_1 x_3$$

$$\frac{dx_2}{d\tau} = x_3 - x_2 \qquad (2)$$

$$\frac{dx_3}{d\tau} = -cx_3 + dx_1 x_3 + ex_2 - fx_3^2$$

where

$$a = \frac{r_1}{r_2},\ b = \frac{1}{m},\ c = \frac{r_3}{r_2},\ d = \frac{m\alpha k}{r_1},\ e = \frac{\gamma\beta}{r_2^2},\ f = \frac{\delta}{m\alpha}$$

Now we assume that two groups of fishermen targeting two sub-stocks consist of different stage groups of predators, with mature fish in one sub-stock and immature fish in the other. Under this assumption system (2) becomes

$$\frac{dx_1}{d\tau} = ax_1 - x_1^2 - bx_1 x_3$$

$$\frac{dx_2}{d\tau} = x_3 - x_2 - q_1E_1x_2 \qquad (3)$$

$$\frac{dx_3}{d\tau} = -cx_3 + dx_1 x_3 + ex_2 - fx_3^2 - q_2E_2x_3$$

Here $q_1E_1x_2$ and $q_2E_2x_3$ are based on the catch-per-unit-effort hypothesis (Clark, 1990), where $q_1$and q_2 are catchability co-efficients, E_1 and E_2 are harvesting efforts.

We are not making any case study but the North-East Atlantic cod fishery is a good example for it. The technology that the trawlers and coastal vessels utilize is different, as are the areas of fishing activity and therefore size of harvested fish. The trawlers catch fish of a smaller size than the coastal vessels, as the older fish tend to migrate in to the coast to spawn.

The Iberoatlantic Hake fishery is another example of multifleet fisheries. In this fishery, the species is caught using several fishing methods, particularly trawling, longlining and fixed gillnetting. Specially, trawling acts intensely on younger individuals, whereas the other fishing methods mainly affect more mature specimens.

EQUILIBRIA AND STABILITY ANALYSIS

System (3) has to be analyzed with the following initial conditions : $x_1(0) > 0$, $x_2(0) > 0$ and $x_3(0) > 0$. We observe that the right-hand side of the system (3) is smooth function of the variables (x_1, x_2, x_3) and the parameters, as long as these quantities are non-negative, so local existence and uniqueness properties hold in the positive octant. The state space for system (3) is in the positive octant, $\{(x_1, x_2, x_3): x_1 > 0, x_2 > 0 \text{ and } x_3 > 0\}$, which is clearly an invariant set, since the vector field on the boundary does not point to the exterior. Our next result concerns the existence of equilibrium points.

We find the steady states of system (3) by equating the derivatives on the left hand sides to zero and solving the resulting algebraic equations. This gives three possible steady states, namely, $P_0(0, 0, 0)$, $P_1(a, 0, 0)$ and $P_2(x_1^*, x_2^*, x_3^*)$ where

$$x_1^* = \frac{af + bc + bq_2E_2 - \dfrac{be}{1+q_1E_1}}{db + f},$$

$$x_2^* = \frac{da + \dfrac{e}{1+q_1E_1} - c - q_2E_2}{(1+q_1E_1)(db + f)},$$

$$x_3^* = \frac{da + \dfrac{e}{1+q_1E_1} - c - q_2E_2}{db + f}.$$

Here we want to remark that there exists another equilibrium in the absence of prey if $e>c$. But it is not realistic since prey is the only source of food for the predator. So throughout the paper we assume that

Therefore, P_2 is feasible if

$$c + q_2E_2 < da + \frac{e}{1+q_1E_1} \text{ hold.}$$

Particularly we are interested on the interior equilibrium point $P_2(x^*_1, x^*_2, x^*_3)$ for its usual importance.

Next we consider first the local stability of the equilibria. The variational matrix of the system (3) is given by

$$M(x_1, x_2, x_3) = \begin{bmatrix} a - 2x_1 - bx_3 & 0 & -bx_1 \\ 0 & -1 - q_1E_1 & 1 \\ dx_3 & e & -c + dx_1 - 2fx_3 - q_2E_2 \end{bmatrix}$$

Now,

$$M(0, 0, 0) = \begin{bmatrix} a & 0 & 0 \\ 0 & -1 - q_1E_1 & 1 \\ 0 & e & -c - q_2E_2 \end{bmatrix}$$

The diagonalization of the Jacobian matrix M (0, 0, 0), yields the following characteristic equation:

$$(a - \lambda)\,\{\lambda^2 + (1 + c + q_1E_1 + q_2E_2)\,\lambda + (1 + q_1E_1)(c + q_2E_2) - e\} = 0.$$

Which shows that $P_0(0, 0, 0)$ is unstable.

$$M(a, 0, 0) = \begin{bmatrix} -a & 0 & -ba \\ 0 & -1 - q_1E_1 & 1 \\ 0 & e & -c + ad - q_2E_2 \end{bmatrix}$$

Characteristic equation of M(a, 0, 0) is

$$(a+\lambda)\,\{\lambda^2-\lambda(ad-c-1-q_1E_1-q_2E_2)+\{(1+q_1E_1)(c+q_2E_2-ad)-e\}=0$$

$\therefore P_1(a, 0, 0)$ is locally asymptotically stable for c>e + ad.

Now.

$$M(x^*_1, x^*_2, x^*_3) = \begin{bmatrix} -x^*_1 & 0 & -bx^*_1 \\ 0 & -1-q_1E_1 & 1 \\ dx^*_3 & e & -c-2fx^*_3+dx^*_1-q_2E_2 \end{bmatrix}$$

The characteristic equation of $M(x^*_1, x^*_2, x^*_3)$ is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$, where

$$A = 1+\frac{e}{1+q_1E_1}+x^*_1+fx^*_3 > 0,$$

$$B = fx^*_3+x^*_1+x^*_1(fx^*_3+\frac{e}{1+q_1E_1})+bdx^*_1x^*_3,$$

$$C = (f+bd)\,x^*_1\,x^*_3 > 0.$$

Obviously, AB-C>0. According to Routh-Hurwitz criteria, $P_2(x^*_1, x^*_2, x^*_3)$ is locally asymptotically stable if

$$c+q_2E_2 < da+\frac{e}{1+q_1E_1} \text{ hold.}$$

Now we shall discuss the condition of global stability, permanence and extinction of system (3). At first, we give the following notations and definitions

$$R_3^+ = \{x=(x_1, x_2, x_3)\in R_3 : x_i \ge 0\},\ \text{Int } R_3^+ = \{x=(x_1, x_2, x_3)\in R_3 : x_i > 0\}.$$

Definition 1

An equilibrium point $P_2(x_1, x_2, x_3)$ is said to be globally asymptotically stable in R_3^+ if it is locally asymptotically stable and all trajectories in R_3^+ converges to $P(x_1, x_2, x_3)$.

Lemma 1

- If, $c+q_2E_2 \ge da+e$ then the equilibrium $P_1(a, 0, 0)$ is globally asymptotically stable in R_3^+.
- If, $c+q_2E_2 < da+\frac{e}{1+q_1E_1}$ then the only interior equilibrium point $P_2(x^*_1, x^*_2, x^*_3)$ is globally asymptotically stable in $\text{Int } R_3^+$.

Proof

- We construct the following Lyapunov function

$$V_1 = \alpha_1(x_1-a-a\ln\frac{x_1}{a})+\alpha_2x_2+\alpha_3x_3$$

where α_i, i = 1, 2, 3 are positive constants to be determined in the subsequent steps.

Calculating the derivative of V_1 along each solution of (3), we have

$$\frac{dV_1}{d\tau} = \alpha_1 \left(\frac{x_1 - a}{x_1}\right) \frac{dx_1}{d\tau} + \alpha_2 \frac{dx_2}{d\tau} + \alpha_3 \frac{dx_3}{d\tau}$$

$$= -\alpha_1 (x_1 - a)^2 - \alpha_1 b(x_1 - a)x_3 + (\alpha_2 x_3 - c\alpha_3 x_3)$$
$$- \alpha_2 x_2 - \alpha_2 q_1 E_1 x_2 + \alpha_3 e x_2 + \alpha_3 d x_1 x_3 - \alpha_3 f x_3^2 - \alpha_3 q_2 E_2 x_3$$

Let $\alpha_1 = d/b$, $\alpha_2 = e$ and $\alpha_3 = 1$.
Then,

$$\frac{dV_1}{d\tau} = -(d/b)(x_1 - a)^2 - eq_1 E_1 x_2 - (c - e - ad + q_2 E_2)\, x_3 - f x_3^2 < 0$$

in Int. R_3^+, for $c \geq e+ad$.

Therefore, by Lyapunov-LaSalle (Hale, 1969), it follows that P_1 is locally asymptotically stable and all trajectories starting in Int. R_3^+ approaches to P_1 as t goes to infinity. This establishes the global asymptotic stability (Fig. 1).

- Let us take the Lyapunov function

$$V_2(x_1, x_2, x_3) = \Sigma \alpha_i \left(x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*}\right)$$

where α_i, i = 1, 2, 3 are positive constants to be determined in the subsequent steps.

Calculating the derivative along each solution of (3), we have

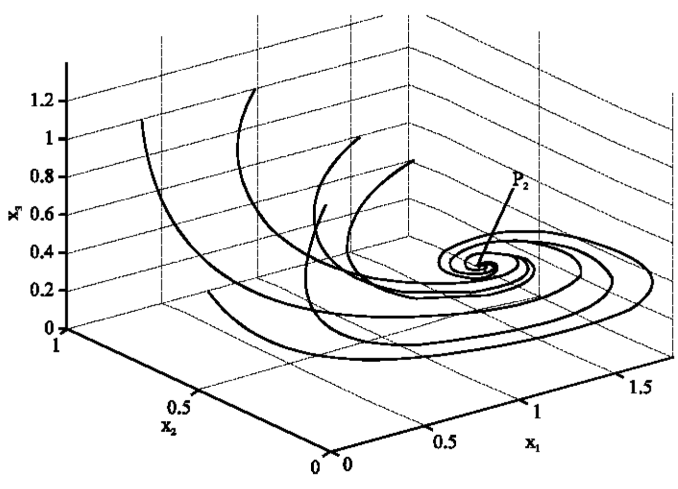

Fig. 1: Phase space trajectories of system (3) beginning with different initial states. It is seen that P_2 (1.22, 0.31, 0.45) is a global attractor, where a = 3, b = 4, c = 2.5, d = 3.0, e = 0.2, f = 0.7, q_1 = 0.3, q_2 = 0.5, E_1 = 1.5, E_2 = 2

$$\frac{dV_2}{d\tau} = \Sigma\alpha_i\left(\frac{x_i - x_i^*}{x_i}\right)\frac{dx_i}{d\tau}$$

$$= -\alpha_1(x_1 - x_1^*)^2 - b\alpha_1(x_1 - x_1^*)(x_3 - x_3^*) + \alpha_2(x_2 - x_2^*)\left(\frac{x_3}{x_2} - \frac{x_3^*}{x_2^*}\right)$$

$$+\alpha_3 d(x_3 - x_3^*)(x_1 - x_1^*) + e\alpha_3(x_3 - x_3^*)\left(\frac{x_2}{x_3} - \frac{x_2^*}{x_3^*}\right) - f\alpha_3(x_3 - x_3^*)^2$$

Let $\alpha_1 = d/b$, $\alpha_2 = e$ and $\alpha_3 = 1$.

$$\therefore \frac{dV_1}{d\tau} = -(d/b)(x_1 - x_i^*)^2 - f(x_3 - x_3^*)^2 - e\left(\frac{x_3}{x_2 x_2^*}\right)(x_2 - x_2^*)^2$$

$$-e\left(\frac{x_2}{x_3 x_3^*}\right)(x_3 - x_3^*)^2 + \frac{2e}{x_2^*}(x_2 - x_2^*)(x_3 - x_3^*)$$

$$= -(d/b)(x_1 - x_i^*)^2 - f(x_3 - x_3^*)^2 - e x_2^*\left[\sqrt{\frac{x_3}{x_2}}(x_2 - x_2^*)^2 - \sqrt{\frac{x_2}{x_3}}(x_3 - x_3^*)\right]^2 < 0$$

By similar arguments as we have used for P_1, we may state that $P_2(x_1^*, x_2^*, x_3^*)$ is globally asymptotically stable if $c + q_2E_2 < da + \frac{e}{1 + q_1E_1}$ hold.

Definition 2

System (3) is said to be permanent if there are positive constants m and M such that each positive solution $x(t, x_0)$ of (3) with initial condition $x_0 \in \mathrm{Int}\, R_3^+$ satisfies

$$m \le \lim_{t\to\infty}\inf x_i(t, x_0) \le \lim_{t\to\infty}\sup x_i(t, x_0) \le M,\ i = 1,2,3.$$

Definition 3

The ith species of system (3) is said to be extinctive if each positive solution $x(t, x_0)$ of (3) with initial condition $x_0 \in \mathrm{Int}\ R_3^+$ satisfies

$$\lim_{t\to\infty} x_i(t, x_0) = 0,\ i = 1, 2, 3.$$

Combining all these results we get the following theorem.

Theorem 1

- The predator species of system (3) is extinctive and the prey species is not extinctive if and only if $c+q_2E_2 \ge e+ad$ hold.
- Both prey and predator species are permanent if and only if

$$c + q_2E_2 < da + \frac{e}{1 + q_1E_1}\ \text{hold.}$$

Proof

By Definitions 1 and 2 and the Lemma 1, we can easily prove the Theorem.

THE BIOECONOMIC ENVIRONMENT

Once the process of harvesting the resource is started, the problem of management of the fisheries can be viewed in terms of rent maximization, as is the case of several theories of fisheries economics. In this section, the goal is to find the efforts E_1 and E_2 to maximize a weighted average of the objective functionals obtain from immature and mature predator fish, respectively.

$$\text{Let } \Pi_1 = (p_1 q_1 x_2 - c_1)E_1 \text{ and } \Pi_2 = (p_2 q_2 x_3 - c_2)E_2$$

represent the net revenues for the immature and mature species, respectively.

Thereby the present values of the two sub-stocks are, respectively

$$PV_1 = \int_0^\infty e^{-\delta t}(p_1 q_1 x_2 - c_1)E_1\, dt$$

$$PV_2 = \int_0^\infty e^{-\delta t}(p_2 q_2 x_3 - c_2)E_2\, dt$$

where δ is the discount rate, p_i is the unit price of the resource, c_i is the unit cost of harvesting the resource substock 1 and 2.

The aim of the social manager would be to select the efforts E_i and stock level to maximize a weighted average of their objective functional, PV. The weights β and $(1-\beta)$ indicate how much weight is given to the objective functionals. For a given $\beta \in [0, 1]$, the management objective functional translates into maximize

$$PV = \beta PV_1 + (1-\beta) PV_2,$$

subject to the stock dynamics given by Eq. 3 and to the control constraints $0 \le E_i \le E_{imax}$. Given the structure of our problem, we arrive at two equations that implicitly define the optimal (steady state) equilibrium for the doubly singular solution (Appendix):

$$\beta\left(p_1 - \frac{c_1}{q_1 x_2}\right)(-\delta - 1 - q_1 E_1) + e(1-\beta)\left(p_2 - \frac{c_2}{q_2 x_3}\right) + \beta p_1 q_1 E_1 = 0 \tag{4}$$

$$\left[(1-\beta)p_2 q_2 E_2 + \beta\left(p_1 - \frac{c_1}{q_1 x_2}\right) + (1-\beta)\left(p_2 - \frac{c_2}{q_2 x_3}\right)(-c - \delta + dx_1 - 2fx_3 - q_2 E_2)\right] \left(\frac{\delta}{x_1} + 1\right) - bdx_3(1-\beta)\left(p_2 - \frac{c_2}{q_2 x_3}\right) = 0 \tag{5}$$

The solutions to Eq. 4 and 5 are pursued numerically. From these solutions, we can determine the optimal equilibrium harvest of the two sub-stocks and efforts.

Remark

$$\frac{\partial H}{\partial E_1} = 0 \Rightarrow \lambda_1 q_1 x_2 = \frac{\partial \Pi_1}{\partial E_1},$$

and

$$\frac{\partial H}{\partial E_2} = 0 \Rightarrow \lambda_2 q_2 x_3 = \frac{\partial \Pi_2}{\partial E_2}.$$

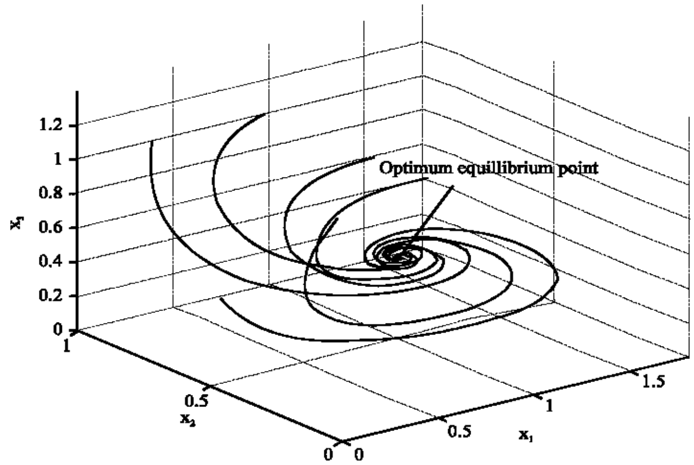

Fig. 2: Phase space trajectories of system (3) corresponding to the optimal harvesting efforts. It is seen that the optimal equilibrium point (0.18, 4.59, 1.62) is also a global attractor

This implies that, for each species, the user cost of harvest per unit effort must equal the discounted value of the future marginal profit of effort at the steady state effort level.

For simulation let us take a = 3, b = 4, c = 2.5, d = 3.0, e = 0.2, f = 0.7, q_1 = 0.3, q_2 = 0.5, c_1 = 7, c_2 = 8, p_1 = 90, p_2 = 100, δ = 0.05 in appropriate units.

For the above values of the parameters, optimum harvest is attained for β=0.4. This implies that the highest discounted total profit is achieved when about 40% of the harvest is taken from juvenile fish and 60% taken from the mature fish. The optimum harvesting efforts are $E_{1\delta} = 0.33$ and $E_{2\delta} = 0.34$. Optimum equilibrium is (0.18, 4.59, 1.62) and discounted profit is 605.7 (Fig. 2).

CONCLUDING REMARKS

An important and one of the interesting questions in mathematical ecology is persistence or permanence, which ensures the survival of biological species and exclude extinction of species for all positive initial conditions. The question of permanence of biological species is of particular interest to fishery. If it known that a system exhibits such a permanent behaviour, then ecological planning based on a fixed eventual population can be carried out. Realizing the problem we have obtained the conditions for persistence of the solutions of our systems.

We have studied how the weights should be divided between two fleets to maximize the harvesting returns from the fishery. We are aware of the simplification involved in converting a highly complex situation into a theoretical model. However, the model that has been developed in the current paper would be a guidelines for the future research.

Before ending this article, we would like to mention that there is still tremendous amount of work to do in this model. For example,

- One can consider the stage-structure of prey population.
- Gestation period for predator is also an important characteristic to be considered. We leave it for future considerations.
- Uncertainties is another important point to be considered.

APPENDIX

The Hamiltonian for the weighted average objective function is

$$H = e^{-\delta t}[\beta(p_1 q_1 x_2 - c_1)E_1 + (1-\beta)(p_2 q_2 x_3 - c_2)E_2] + \lambda_1[ax_1 - x^2 - bx_1 x_3] + \lambda_2[x_3 - x_2 - q_1 E_1 x_2]$$
$$+ \lambda_3[-cx_3 + dx_1 x_3 + ex_2 - fx_3^2 - q_2 E_2 x_3]$$

where λ_1, λ_2 and λ_3 are adjoint variables.

The control variables E_1 and E_2 appear linearly in the Hamiltonian function H. Therefore, optimal control will be a combination of bang-bang control and singular control. The optimal control $E_i(t)$ which maximizes H, must satisfy the following conditions:

$$E_1 = \begin{cases} E_{1_{max}}, \text{ when } \lambda_2 e^{\delta t} < p_1 - \dfrac{c_1}{q_1 x_2} \\ 0, \quad \text{when } \lambda_2 e^{\delta t} > p_1 - \dfrac{c_1}{q_1 x_2} \\ \text{see below, when } \lambda_2 e^{\delta t} = p_1 - \dfrac{c_1}{q_1 x_2} \end{cases}$$

$$E_2 = \begin{cases} E_{2_{max}}, \text{ when } \lambda_3 e^{\delta t} < p_2 - \dfrac{c_2}{q_2 x_3} \\ 0, \quad \text{when } \lambda_3 e^{\delta t} > p_2 - \dfrac{c_2}{q_2 x_3} \\ \text{see below, when } \lambda_3 e^{\delta t} = p_2 - \dfrac{c_2}{q_2 x_3} \end{cases}$$

For the singular control we have,

$$\frac{\partial H}{\partial E_i} = 0, \quad i = 1, 2.$$

Now

$$\frac{\partial H}{\partial E_1} = 0 \Rightarrow \lambda_1 = e^{-\delta t}\beta(p_1 - \frac{c_1}{q_1 x_2}) \qquad (A.1)$$

and

$$\frac{\partial H}{\partial E_2} = 0 \Rightarrow \lambda_2 = e^{-\delta t}(1-\beta)(p_2 - \frac{c_2}{q_2 x_3}) \qquad (A.2)$$

We intend to derive here an optimal equilibrium solution of the problem. Since we are considering an equilibrium solution, x, y and E are to be treated as constants in the subsequent steps.

Now the adjoint equations are

$$\frac{d\lambda_1}{dt} = -\frac{\partial H}{\partial x_1} = -\left[-\lambda_1 x_1 + \lambda_3 d x_3\right] \tag{A.3}$$

$$\frac{d\lambda_2}{dt} = -\frac{\partial H}{\partial x_2} = -\left[e^{-\delta t}\beta p_1 q_1 E_1 + \lambda_2(-1 - q_1 E_1) + \lambda_3 e\right] \tag{A.4}$$

and

$$\frac{d\lambda_3}{dt} = -\frac{\partial H}{\partial x_3} = -\left[(1-\beta)e^{-\delta t} p_2 q_2 E_2 - \lambda_1 b x_1 + \lambda_2 + \lambda_3(-c + d x_1 - 2 f x_3 - q_2 E_2\right] \tag{A.5}$$

Substituting λ_2 and λ_3 in (A.4) we get

$$\beta(p_1 - \frac{c_1}{q_1 x_2})(-\delta - 1 - q_1 E_1) + e(1-\beta)(p_2 - \frac{c_2}{q_2 x_3}) + \beta p_1 q_1 E_1 = 0.$$

Again substituting λ_2 and λ_3 in (A.5) we get

$$\lambda_1 = e^{-\delta t}\frac{1}{b x_1}[(1-\beta)p_2 q_2 E_2 + \beta(p_1 - \frac{c_1}{q_1 x_2}) + (1-\beta)(p_2 - \frac{c_2}{q_2 x_2)})(-c + d x_1 - 2 f x_3 - q_2 E_2 - \delta)]$$

Substituting λ_1 and λ_3 in (A.3) we get

$$[(1-\beta)p_2 q_2 E_2 + \beta(p_1 - \frac{c_1}{q_1 x_2}) + (1-\beta)(p_2 - \frac{c_2}{q_2 x_3})(-c - \delta + d x_1 - 2 f x_3 - q_2 E_2)]$$
$$(\frac{\delta}{x_1} + 1) - b d x_3 (1-\beta)(p_2 - \frac{c_2}{q_2 x_3}) = 0$$

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