Modelling and control of coffee berry borer infestation

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ABSTRACT. In this paper, we developed a mathematical model that describes the infestation dynamics of coffee berry by *Hypothenemus hampei* (CBB). This model takes into account control some integrated pest management strategies which are used by coffee growers to eradicate CBB in plantations, represented by two functions depending on time. We design these functional controls to maximize the yield of healthy berries at the end of the cropping season, while minimising the borer population for the next cropping season and the control costs. By using optimal control theory, we show that an optimal control exists for this problem and Pontryagin's maximum principle is used to characterize an optimal control. Numerical simulations are provided to illustrate our results.

RÉSUMÉ. Dans ce papier, nous développons un modèle mathématique qui décrit la dynamique d'infestation des baies du caféier par les scolytes (CBB). Ce modèle prend en compte certaines stratégies de lutte intégrée utilisées par les caféiculteurs pour éradiquer les CBB dans les plantations, représentées par deux fonctions dépendantes du temps. Nous concevons ces contrôles fonctionnels pour maximiser le rendement des baies saines à la fin de la saison, tout en minimisant la population de CBB pour la prochaine saison et les coûts de contrôle. En utilisant la théorie du contrôle optimal, nous montrons qu'un contrôle optimal existe pour ce problème et le principe du maximun de Pontryagin est utilisé pour caractériser ce contrôle optimal. Des simulations numériques sont faites pour illustrer nos résultats.

KEYWORDS : *Hypothenemus hampei*, optimal control, numerical simulations

MOTS-CLÉS : *Hypothenemus hampei*, contrôle optimal, simulations numériques

1. Introduction

Coffee plays an important role in the economic growth of many developing countries such as Brazil, Cameroon, Ethiopia, Ivory Coast, Mexico, Viet Nam and many others. Coffee production throughout the world is affected by several pests and diseases. Among these pests, the coffee berry borer (CBB), *Hypothenemus hampei*, is considered as the most important pest economically [2, 1, 9]. The CBB feeds and spends its entire development cycle in the berries, developing in the berry of the coffee tree in all maturation stages. It causes direct loss such as a reduction of coffee production and indirect losses such as a lowering of the quality of the coffee berries. Sibling mating inside the berry makes this insect quite difficult to control. The levels of infestation of CBB in coffee growing areas are estimated at 60% in Mexico, $50 - 90\%$ in Malaysia, 60% in Colombia, 75% in Jamaica, 80% in Uganda and 90% in Tanzania [8]. It is now present in almost all of the major coffee producing countries. It lives the greatest part of its life cycle inside the coffee berry, which involves egg laying followed by the emergence of adult females from the berry. The life cycle of the CBB is composed of four stages: eggs, larvae, nymphs and adults. Mature females are responsible for the dispersal of the population: they emerge from the berries to colonize and lay their eggs in new berries, while males and larvae stages remain inside the berries. Faced with the extent of the damages, several programs and control methods have been developed by the coffee growers, such as improved cultural practices, chemical and biological control and trapping [2, 1, 9]. In this paper, we propose an epidemiological model to describe the dynamics of infestation of coffee berries by CBB. This model takes into account several control strategies. Our aim is to design an optimal strategy, that maximizes the yield of healthy berries at the end of the cropping season, while minimizing the CBB population for the next season.

After a formulation of the model and the control problem in Section 2, we study the stability of equilibrium points in the absence of control in Section 3. In Section 4, we prove the existence of the optimal control which is later characterized in Section 5. We illustrate these analytical results by simulations in Section 6 and conclude our work.

2. The model

We propose an epidemiological model of infestation of coffee berries by CBB. We subdivide the total number of coffee berries into two compartments: the healthy coffee berries s, and the infested coffee berries i. We assume that the new coffee berries are produced at a constant rate Λ and we place ourselves during a cropping season. We assume that adult males are not limited, so we only consider female CBB, which are responsible for dispersal and host selection. We subdivide the female population in two compartments: the colonizing females or host-searching females which emerge from the berries and search for a new host denoted by y and the infesting females who can find and infested the coffee berry and denoted by z. The healthy berries are submitted to a force of infestation $\beta\frac{y}{y+d}$ by colonizing females, which compete for this resource, hence the saturation term. We denote by μ and δ the natural mortality of healthy and infested coffee berries respectively. According to the biology of CBB, we assume that the average number of new colonizing females produced is taken proportional of the number of infesting females. Let ϕ be that average number per unit of time. We denote by μ_y and μ_z the natural mortality rates of colonizing and infesting females respectively. We denote by ε

the conversion parameter from the coffee berries to CBB population, that is the number of CBB colonizing females that can infest one unit of healthy berry. Usually $\varepsilon = 1$, but if the infestation process fails, $\varepsilon < 1$. The first control u represents the efforts made to reduce the infestation of healthy coffee berries. In practice, this control function represents the biological control using entomopathogenic fungi such as *Beauveria bassiana*, that is applied to the surface of the coffee berries and that kills the colonizing females of CBB when they drill an entry hole into the coffee berries [1]. The second control v represents the efforts made to reduce the colonizing females. It consists mainly of the use of chemicals, traps and the parasitoids. We associate to these control functions, the parameters $\alpha_i \in (0, 1)$, $i = u, v$ which measure the effectiveness of control u and v respectively. The dynamics of CBB is given by the following nonlinear differential equations:

$$\begin{cases} s' = \Lambda - (1 - \alpha_u u)\beta \dfrac{sy}{y + d} - \mu s \\[2mm] i' = (1 - \alpha_u u)\beta \dfrac{sy}{y + d} - \delta i \\[2mm] y' = \phi z - \varepsilon \beta \dfrac{sy}{y + d} - (\mu_y + \alpha_v v)\, y \\[2mm] z' = (1 - \alpha_u u)\varepsilon \beta \dfrac{sy}{y + d} - \mu_z z \end{cases} \qquad (1)$$

Since variable i does not interact with the other variables of system (1), its dynamics can be decoupled from the system. We will focus on the dynamics of the other three variables. Thus we obtain the following system:

$$\begin{cases} s' = \Lambda - (1 - \alpha_u u)\beta \dfrac{sy}{y + d} - \mu s \\[2mm] y' = \phi z - \varepsilon \beta \dfrac{sy}{y + d} - (\mu_y + \alpha_v v)\, y \\[2mm] z' = (1 - \alpha_u u)\varepsilon \beta \dfrac{sy}{y + d} - \mu_z z \end{cases} \qquad (2)$$

The goal of coffee farmers is the production of high quality coffee at the best market price produced at lowest cost. So our problem consists in maximizing the yield at the end of the cropping season, while minimizing the coffee berry borer population for the next season. Since all these methods of control are expensive and require a lot of energy in their implementation. We propose the following objective function:

$$\mathcal{J}(u, v) = \int_0^{t_f} \frac{1}{2} \left[C_u u^2(t) + C_v v^2(t) \right] dt - D_s s(t_f) + D_y y(t_f) \qquad (3)$$

where t_f represents the time at the end of the cropping season and the parameters, C_u and C_v measure the relative cost of interventions associated with controls u and v respectively; D_s and D_y represent the weights of healthy coffee berries and of colonizing females at the end of the season respectively. The set of admissible controls is defined as follows

$$\mathcal{U} = \left\{ u, v \in L^1(0, t_f) / (u, v) \in [0, 1] \times [0, 1], \forall t \in [0, t_f] \right\} \qquad (4)$$

Table 1. *Biological meaning and value of parameters (with s in number of berries and y, z in number of females).*

symbol	Description	value
Λ	Production rate of new coffee berries	1200 berries day^{-1}
μ	Natural mortality rate of healthy coffee berries	0.01 day^{-1}
ϕ	Emergence of new colonizing females	2 day^{-1}
β	Infestation rate	0.0125 day^{-1}
d	Saturation constant	2 females
ε	Conversion rate from coffee berries to CBB	1 female berry^{-1}
μ_y	Natural mortality rate of colonizing females	1/81 day^{-1}
μ_z	Natural mortality rate of infesting females	1/28 day^{-1}
α_u	Effectiveness rate of control $u(t)$	0.62
α_v	Effectiveness rate of control $v(t)$	0.31

The problem now is to find the control pair $(u^\star, v^\star)$ satisfying:

$$\mathcal{J}(u^\star, v^\star) = \min_{(u,v)\in\mathcal{U}} \mathcal{J}(u,v) \tag{5}$$

3. Basic properties

For model (2) to be biologically acceptable, it is important to show that all these variables are always positive when time evolves.

Theorem 1 *If the initial condition $(s(0), y(0), z(0)) \in \mathbb{R}_+^3$, then the solution $(s(t), y(t), z(t))$ of system (2) are non negative for all time $t > 0$ and bounded. Moreover, the compact set*

$$\Omega = \left\{ (s, y, z) \in \mathbb{R}_+^3 / s \leq \frac{\Lambda}{\mu}, \; \varepsilon s + z \leq \frac{\varepsilon\Lambda}{\xi}, \; y \leq \frac{\varepsilon\phi\Lambda}{\xi\mu_y} \right\}$$

where $\xi = \min\{\mu, \mu_z\}$, is positively invariant for the model system (2).

Proof: See Appendix A.

In the absence of controls ($u = v = 0$), system (2) has one trivial equilibrium $\mathcal{E}^0 = (s^0, 0, 0)$ where $s^0 = \frac{\Lambda}{\mu}$, which corresponds to a plantation without infestation. Thereafter, we will define the basic offspring number which is the average number of new females originated from a single infesting female in the healthy coffee berries in plantation. The basic offspring number is defined by

$$\mathcal{N} = \frac{\varepsilon\phi\beta\frac{s^0}{d}}{\mu_z \left(\varepsilon\beta\frac{s^0}{d} + \mu_y\right)}. \tag{6}$$

Lemma 1 *There exists another coexistence equilibrium $\mathcal{E}^* = (s^*, y^*, z^*)$ which is biologically realistic when $\mathcal{N} > 1$:*

$$s^* = \frac{\Lambda + \frac{\mu_y d}{\varepsilon\mathcal{T}}}{\beta + \mu}, \quad y^* = \frac{\mu_z}{\mu_y}\mathcal{T}z^*, \quad z^* = \frac{\mu d \left(\frac{\varepsilon\beta s^0}{d} + \mu_y\right)}{\mu_z(\beta + \mu)\mathcal{T}}(\mathcal{N} - 1) \quad with \quad \mathcal{T} = \frac{\phi}{\mu_z} - 1.$$

It is easy to prove that $\mathcal{N} > 1$ implies $\mathcal{T} > 0$.

The long term behavior of model system (2) without controls is given by:

Proposition 1 *1) The trivial equilibrium $\mathcal{E}^0$ is locally asymptotically stable whenever $\mathcal{N} < 1$, and unstable otherwise.*

2) The coexistence equilibrium $\mathcal{E}^*$ exists and is locally asymptotically stable whenever $\mathcal{N} > 1$.

Proof: See Appendix B.

The aim of our control problem is to prove the existence of the optimal control and uniqueness of the optimality system and the characterisation of the optimal control.

4. Existence of an optimal control

The existence of an optimal control is obtained by the theorem of Fleming and Richer [4].

Theorem 2 *There exists an optimal control pair $(u^\star, v^\star)$ and a corresponding solution $(s^\star, y^\star, z^\star)$ of the initial value problem (2) that minimizes the cost function $\mathcal{J}$ in $\mathcal{U}$ such that*

$$\mathcal{J}(u^\star, v^\star) = \min_{(u,v) \in \mathcal{U}} \mathcal{J}(u,v) \tag{7}$$

Proof: we use Theorem 4.1 in Fleming and Ricker [4] which gives the conditions of existence of optimal control for the optimal system (2), which we recall here for self-containeness:

(i) the set of controls and corresponding state variables is non-empty;

(ii) the control set $\mathcal{U}$ is convex and closed;

(iii) the right hand side of the state system (2) is bounded by a linear function in the state and control variable;

(iv) there exist constants $\zeta_1, \zeta_2 > 0$ and $\beta > 1$ such that the integrand function define by f^0 of the objective functional satisfies $f^0(t, \tilde{x}, \tilde{u}) \geq \zeta_1 \|\tilde{u}\|^\beta - \zeta_2$ for all $t \in [0, t_f]$.

The existence of the solution of system (2) is obtained in using the result from Lukes [5](Theorem 9.2.1), since system (2) has bounded coefficients and any solution is bounded on the finite interval time $[0, t_f]$, so condition (i) is satisfied. By definition, the control set $\mathcal{U}$ is convex and closed, so condition (ii) is satisfied. The right hand side of the state system satisfies condition (iii) since we have a linear dependence of the state equations on controls u and v. Finally, the integrand function f^0 of the objective functional is clearly convex in the controls since it is quadratic. Moreover, since all states are bounded, it is easy to find $\zeta > 0$ such that we have $f^0(t, \tilde{x}, \tilde{u}) = \frac{1}{2}(C_u u^2 + C_v v^2) \geq \frac{1}{2} \min\{C_u, C_v\}(u^2 + v^2) - \zeta \geq \frac{1}{2} \min\{C_u, C_v\}\|\tilde{u}\|^2 - \zeta$ which proves property (iv). We conclude that there exists an optimal control pair $(u^\star, v^\star)$ that minimizes the cost function $\mathcal{J}$ in $\mathcal{U}$.

5. Characterization of the optimal control

Since an optimal control minimizing the objective function (3) exists, we use Pontryagin's principle [7] to have the necessary conditions for the optimal control $u^\star$ and

$v^\star$ of our control problem . Let $\tilde{x} = (s, y, z)$ and $\tilde{u} = (u, v) \in \mathcal{U}$. According to this principle, there exists a nontrivial absolutely continuous mapping $\lambda : [0, t_f] \longrightarrow \mathbb{R}^3$, $t \longmapsto \lambda(t) = (\lambda_1(t), \lambda_2(t), \lambda_3(t))$ called the adjoint vector containing the adjoint variables. We define the Hamiltonian by

$$\mathcal{H}(\tilde{x}, \lambda, \tilde{u}) = \frac{1}{2}\left[C_u u^2 + C_v v^2\right] + \lambda_1 \left[\Lambda - (1 - \alpha_u u)\beta\frac{sy}{y+d} - \mu s\right]$$
$$+ \lambda_2 \left[\phi z - \varepsilon\beta\frac{sy}{y+d} - (\mu_y + \alpha_v v)y\right] + \lambda_3 \left[(1 - \alpha_u u)\varepsilon\beta\frac{sy}{y+d} - \mu_z z\right].$$

Theorem 3 *Given an optimal control $(u^\star, v^\star)$ and corresponding solutions $(x^\star, y^\star, z^\star)$, there exist adjoint variables $\lambda_i(t)$ for $i = 1, 2, 3$ satisfying the following system of linear differential equation*

$$\begin{cases} \lambda_1' = \left[(\lambda_1 - \varepsilon\lambda_3)(1 - \alpha_u u) + \varepsilon\lambda_2\right]\beta\frac{y}{y+d} + \mu\lambda_1 \\[3mm] \lambda_2' = \left[(\lambda_1 - \varepsilon\lambda_3)(1 - \alpha_u u) + \varepsilon\lambda_2\right]\beta\frac{ds}{(y+d)^2} + \lambda_2(\mu_y + \alpha_v v) \qquad (8) \\[3mm] \lambda_3' = -\lambda_2\phi + \mu_z\lambda_3 \end{cases}$$

for almost all $t \in [0, t_f]$, with transversality conditions $\lambda_1(t_f) = -D_s$, $\lambda_2(t_f) = D_y$ and $\lambda_3(t_f) = 0$. Furthermore, we can characterize the optimal control pair by

$$u^\star(t) = \min\left\{\max\left\{0, \frac{1}{C_u}(\varepsilon\lambda_3 - \lambda_1)\alpha_u\beta\frac{sy}{y+d}\right\}, 1\right\};$$
$$v^\star(t) = \min\left\{\max\left\{0, \frac{\alpha_v}{C_v}\lambda_2 y\right\}, 1\right\}.$$

Proof: We use the direct application of Pontryagin's maximum principle for bounded control [7]. The differential equations governing these adjoint variables $(\lambda_i)_{i=\{1,2,3\}}$ are obtained by differentiation of the Hamiltonian (8), evaluated at the optimal control:

$$\lambda_1' = -\frac{\partial\mathcal{H}}{\partial s}, \quad \lambda_2' = -\frac{\partial\mathcal{H}}{\partial y}, \quad and \quad \lambda_3' = -\frac{\partial\mathcal{H}}{\partial z}$$

and the traversality conditions are obtained by $\lambda_1(t_f) = \left[\frac{\partial\Theta}{\partial s}\right]_{t=t_f}$, $\lambda_2(t_f) = \left[\frac{\partial\Theta}{\partial y}\right]_{t=t_f}$ and $\lambda_3(t_f) = \left[\frac{\partial\Theta}{\partial z}\right]_{t=t_f}$ with the function $\Theta(\tilde{x}) = -D_s s + D_y y$. To determine an explicit expression for the optimal control $(u^\star, v^\star)$, we use the standard optimality technique given in [6]. On the set $I_1 = \{t \in [0, t_f] : 0 < u^\star(t) < 1 \qquad 0 < v^\star(t) < 1\}$; The minimum condition is

$$\frac{\partial\mathcal{H}}{\partial u} = C_u u + (\lambda_1 - \varepsilon\lambda_3)\alpha_u\beta\frac{sy}{y+d} = 0, \qquad \frac{\partial\mathcal{H}}{\partial v} = C_v v - \alpha_v\lambda_2 y = 0;$$

Thus, the controls have the explicit expression given by:

$$u^\star(t) = \frac{1}{C_u}(\varepsilon\lambda_3 - \lambda_1)\alpha_u\beta\frac{sy}{y+d} \quad and \quad v^\star(t) = \frac{\alpha_v}{C_v}\lambda_2 y.$$

On the set $I_2 = \{t \in [0, t_f] : u^\star(t) = 0\}$, the minimum condition of control $u^\star$ is given by $\frac{\partial \mathcal{H}}{\partial u} \geq 0$, which implies that $\frac{1}{C_u}(\varepsilon\lambda_3 - \lambda_1)\alpha_u\beta\frac{sy}{y+d} \leq 0$.

On the set $I_3 = \{t \in [0, t_f] : u^\star(t) = 1\}$, then the minimum condition of control $u^\star$ is $\frac{\partial \mathcal{H}}{\partial u} \leq 0$, which implies that $\frac{1}{C_u}(\varepsilon\lambda_3 - \lambda_1)\alpha_u\beta\frac{sy}{y+d} \geq 0$. All these criteria on the control $u^\star$ can be written in the compact form given in the theorem. The characterization of control $v^\star$ is obtained in a similar way.

6. Numerical simulations

In this section, we present the numerical solution of our control problem and compare it with the solution in the absence of controls. We use the forward-backward sweep method to solve numerically our optimal model[6]. The process begins by using an initial guess on the control variable, then the state variables are solved simultaneously forward in time with a semi-implicit finite difference method developed and the adjoint equations are solved using the backward semi-implicit finite difference method. The controls are updated by inserting the new values of state and adjoint variables into its characterization. We assume that the implementation costs of these controls are C_u=3 day^{-1} and C_v= 1 day^{-1} and we use the following weights, $D_s = 1$ berry^{-1} and D_y=1 female^{-1} with initial values $(s(0), y(0), z(0)) = (0, 20, 0)$. The other parameter values are given in Table 1. Since coffee berries become mature after 8–9 months, we simulate the system (2) over a period $t_f = 250$ days.

The simulations plots are given in figure 1. We compare the cases with (dashed red curves) and without (plain blue curves) controls in the presence of pests. We observe that the control $u(t)$ (lower-right panel: black curve) significantly reduces infestation (lower-left panel) and increases at its maximum value at almost mid-season, while control $v(t)$ (lower-right panel: magenta curve) greatly reduces colonizing females at the end of season (upper-right panel: 6×10^4 females instead of 2.5×10^6 at t_f). The fairly long and high application of these controls, especially of $u(t)$, is due to the relatively low costs of the controls. The yield increases with the controls (upper-left) but, due to the limited effectiveness of the controls (parameters α_u and α_v), it remains below its value in the pest-free case (plain green curve).

7. Conclusion

In this paper, we formulate a deterministic epidemiological control model that describes the infestation of coffee berries by the CBB. We have designed an optimal control problem that consists in maximizing the yield of healthy berries at the end of the cropping season, while minimizing the CBB population for the next season. We have computed the basic offspring number and investigated the existence and stability of equilibria in the absence of controls. We have showed that an optimal control exists and that it can be characterized using the Pontryagin's maximum principle. Furthermore, we have solved numerically the system to assess the role of controls on dynamics of CBB population. This numerical result shows that, the application of these controls reduce the CBB population and increase the healthy berries at the end of the cropping season.
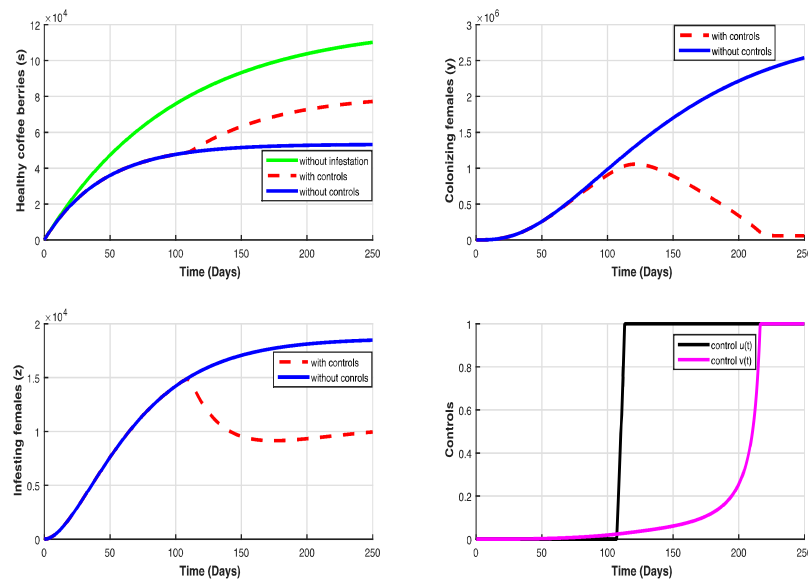
Figure 1. *Simulations of system (2) with (plain blue curves) or without (dashed red curves) controls. Upper-left panel: healthy coffee berries s (plain green curve: pest-free case); Upper-right: colonizing females y; Lower-left: infesting females z; Lower-right: evolution of controls $u(t)$ (plain black curve) and $v(t)$ (plain magenta curve).*

8. References

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Appendix. A:

For any initial condition $(s(0), y(0), z(0)) \in \mathbb{R}^3_+$, the corresponding solution $(s(t), y(t), z(t))$ of system (1) lies in $\mathbb{R}^3_+$, since we have $s'_{\big|_{s=0}} = \Lambda > 0$, $y'_{\big|_{y=0}} = \phi z \geq 0$ and $z'_{\big|_{z=0}} = (1 - \alpha_u u)\varepsilon\beta\frac{sy}{y+d} \geq 0$. Therefore, all solutions of system (2) with initial positive condition stay in first quadrant. Hence, $\mathbb{R}^3_+$ is positively invariant.

Since all variables are nonnegative for all $t > 0$, then $s'(t) \leq \Lambda - \mu s(t)$. It can be shown that using a standard comparison principle, that

$$s(t) \leq s(0)e^{-\mu t} + \frac{\Lambda}{\mu}\left(1 - e^{-\mu t}\right) \tag{9}$$

from which we deduce that $s \leq \frac{\Lambda}{\mu}$ if $s(0) \leq \frac{\Lambda}{\mu}$ and we have $\overline{\lim}\, s(t) \leq \frac{\Lambda}{\mu_S}$.

Let $\tilde{z}(t) = \varepsilon s(t) + z(t)$ and $\xi = \min\{\mu, \mu_z\}$, then adding the first and third equation of model system (2), we obtain

$$\tilde{z}(t) = \varepsilon\Lambda - \varepsilon\mu y - \mu_z z \leq \varepsilon\Lambda - \xi\tilde{z}(t). \tag{10}$$

In particular $\tilde{z}(t) \leq \frac{\varepsilon\Lambda}{\xi}$ if $z(0) \leq \frac{\varepsilon\Lambda}{\xi}$ and we have $\limsup_{t\to\infty} \tilde{z}(t) \leq \frac{\varepsilon\Lambda}{\xi}$. Now, using the second equation of model system (2), we have

$$y'(t) \leq \phi z(t) - \mu_y y \leq \frac{\phi\varepsilon\Lambda}{\xi} - \mu_y y. \tag{11}$$

proceeding in the same way as previously, then $y(t) \leq \frac{\phi\varepsilon\Lambda}{\xi\mu_y}$ if $y(0) \leq \frac{\phi\varepsilon\Lambda}{\xi\mu_y}$ and we have $\limsup_{t\to\infty} y(t) \leq \frac{\phi\varepsilon\Lambda}{\xi\mu_y}$.

Appendix. B:

A method for computing the basic reproduction number in epidemiological models which corresponds to the number of secondary infections produced by a single infectious individual in a susceptible population was developed in [3]. We use the same technique to compute the basic offspring number for model system (2 in absence of controls.

Let $\tilde{x} = (s, y, z)$ be the set of state variables. The system (2) can be rewritten as $\frac{d\tilde{x}_i}{dt} = F_i(\tilde{x}) - V_i(\tilde{x})$, where F_i is the rate of new recruits (birth of new colonizing females) in compartment i, $V_i = V_i^- - V_i^+$, where V_i^+ representing the rate of transfer into a compartment i by all other means, and V_i^- is the rate of transfer out the compartment i. For this model, F and V are given by

$$F = \begin{bmatrix} 0 \\ \phi z \\ 0 \end{bmatrix}; \qquad V = \begin{bmatrix} -\Lambda + \beta\frac{sy}{y+d} + \mu s \\ \varepsilon\beta\frac{sy}{y+d} + \mu_y y \\ -\varepsilon\beta\frac{sy}{y+d} + \mu_z z \end{bmatrix}.$$

To obtain the next generation matrix, we compute the Jacobian matrices of F and V denoted by $R = \mathcal{J}_F(\mathcal{E}^0)$ and $T = \mathcal{J}_V(\mathcal{E}^0)$. Here, we have

$$R = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & \phi \\ 0 & 0 & 0 \end{pmatrix}; \qquad T = \begin{pmatrix} \mu & \beta\frac{s^0}{d} & 0 \\ 0 & \varepsilon\beta\frac{s^0}{d} + \mu_y & 0 \\ 0 & -\varepsilon\beta\frac{s^0}{d} & \mu_z \end{pmatrix}.$$

The basic offspring is obtained by computing the spectral radius of the next generation matrix RT^{-1}:

$$\mathcal{N} = \rho(RT^{-1}) = \frac{\varepsilon\phi\beta\frac{s^0}{d}}{\mu_z\left(\varepsilon\beta\frac{s^0}{d} + \mu_y\right)}.$$ (12)

The immediate consequence of the next generation method is that, the equilibrium $\mathcal{E}_0$ is locally asymptotically stable if $\mathcal{N} < 1$ and unstable otherwise.

The Jacobian matrix associated with system (2) at equilibrium point $\mathcal{E}^*$ is given by:

$$\mathcal{J} = \begin{pmatrix} -\beta\frac{y^*}{y^*+d} - \mu & -\beta\frac{s^*d}{(y^*+d)^2} & 0 \\ -\varepsilon\beta\frac{y^*}{y^*+d} & -\varepsilon\beta\frac{s^*d}{(y^*+d)^2} - \mu_y & \phi \\ \varepsilon\beta\frac{y^*}{y^*+d} & \varepsilon\beta\frac{s^*d}{(y^*+d)^2} & -\mu_z \end{pmatrix}.$$

The characteristic equation of which is

$$\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0 = 0.$$

where

$$a_0 = \mu_y\mu_z\beta\frac{y^*}{y^*+d} + \mu\mu_y\mu_z\left(1 - \frac{d}{y^*+d}\right);$$

$$a_1 = \left(\mu + \frac{\beta y^*}{y^*+d}\right)(\mu_z + \mu_y) + \mu\varepsilon\frac{\beta s^*d}{(y^*+d)^2} + \mu_y\mu_z\left(1 - \frac{d}{y^*+d}\right);$$

$$a_2 = \mu_z + \mu + \mu_y + \frac{\beta y^*}{y^*+d} + \frac{\varepsilon\beta s^*d}{(y^*+d)^2}.$$

Since a_2, a_1 and a_0 are positive, The Routh-Hurwitz criterion for stability only imposes the $a_2 a_1 - a_0 > 0$ needs to be positives, which can easily be shown. This implies that $\mathcal{E}^*$ exists and is asymptotically stable if and only if $\mathcal{N} > 1$.