Global dynamics of a compartmental system modeling ectoparasite-borne diseases

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Dedicated to Professor László Hatvani on the occasion of his 70th birthday

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Abstract. We analyse a four-dimensional compartmental system that describes the spread of ectoparasites and a disease carried by them in a population. We identify three threshold parameters that determine which of the four potential equilibria exist. These parameters completely characterize the stability properties of the equilibria and also the global behaviour of solutions. We provide a detailed description of the global attractor in each possible scenario. The key mathematical tools of the proofs are Lyapunov–LaSalle theory, persistence theory, Poincaré–Dulac criteria and unstable manifolds. In the most complicated case, the global attractor consists of four equilibria and various heteroclinic orbits connecting those equilibria, forming a two-dimensional manifold in the phase space.

1 Introduction

Lice, fleas, mites and other ectoparasites cause serious problems in many human and animal populations. Besides infestation, these parasites also carry various diseases through the contact network of the population [1,5]. A basic model with three compartments was outlined and analysed in [2,3] for the spread of ectoparasite-borne diseases. Here we extend our previous work by incorporating an additional compartment, thus our model becomes a system of four nonlinear differential equations. We consider a single population that is invaded by infectious and non-infectious
parasites, so we distinguish infestation and infection. The four compartments are
the following: susceptibles (those who are neither infested nor infected, denoted by
$S(t)$), those who are infested by non-infectious parasites (denoted by $T(t)$), those
who are infested by infectious parasites, and thus infected with the disease as well
(denoted by $Q(t)$), and those who are infected with the disease but not infested by
the parasites, denoted by $I(t)$. Accordingly, we shall use the phrase $Z$-individual,
where $Z \in \{S, T, Q, I\}$.

For the transmission dynamics of the parasites and the disease, we assume
the following. A $T$-individual can transmit the parasites to susceptibles, while a
$Q$-individual can transmit both the parasites and the disease to susceptibles. Thus
$S$-individuals, upon adequate contact with a $T$- or $Q$-individual, become $T$- or $Q$-
type. We assume that an infested individual is infected by the disease if and only
if infested by infectious parasites. Hence, a $T$-individual can become $Q$-individual
after being in contact with a $Q$-individual that transmits the infected parasites to
the already infested individual. We assume that $Q$-individuals transmit the disease
at the same rate to $S$- and to $T$-individuals. Denote this transmission rate by $\beta_Q$,
and denote the transmission rate for non-infectious parasites (to susceptibles) by
$\beta_T$. The rate of disinfestation is denoted by $\mu$ for the infected compartment and by
$\theta$ for the non-infected compartment. After disinfestation, a $T$-individual moves back
to the $S$-class, while a $Q$-individual becomes $I$-individual before recovering from the
disease. We exclude reinfection of $I$-individuals, which is a reasonable assumption:
after disinfestation a still infected individual can be assumed to be kept isolated
from the source of parasites until recovery. The recovery rate for the compartment
$I$ is denoted by $\alpha$ and $b$ stands for the natural birth and death rates. We assume
that the disease is not fatal, thus the population size is constant. Without loss of
generality we can assume that $N(t) = S(t) + T(t) + Q(t) + I(t) = 1$ holds for the
total population. In the model equations we use mass action incidence.

Summarizing, we have the following system of differential equations, with all
parameters being positive:

\begin{align*}
S'(t) &= -\beta_T S(t) T(t) - \beta_Q S(t) Q(t) + \theta T(t) + \alpha I(t) + b - b S(t), \\
T'(t) &= \beta_T S(t) T(t) - \beta_Q Q(t) T(t) - \theta T(t) - b T(t), \\
Q'(t) &= \beta_Q S(t) Q(t) + \beta_Q Q(t) T(t) - \mu Q(t) - b Q(t), \\
I'(t) &= \mu Q(t) - \alpha I(t) - b I(t).
\end{align*}

Figure 1.1 shows the transmission diagram of the model. All solutions with
nonnegative initial values remain nonnegative for all forward time.
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Figure 1.1. Transmission diagram.

In previous works [2, 3] it was assumed that upon disinfestation an infected individual immediately recovers from the disease as well. However, it is expected that it takes some time until such an individual fully recovers from the disease after the parasites are removed. To make the basic model more realistic, here we introduce the I-compartment to account for this phenomenon. This way, the new the model is higher dimensional. While many of the techniques used in [2, 3] (Lyapunov functions, LaSalle’s invariance principle, persistence theory) can be applied to system (1) in an analogous, but more complicated manner, due to the increased number of dimensions we need some new methods as well, such as Dulac’s criterion and Poincaré–Bendixson theorem to analyse the dynamics on the extinction spaces. In this paper we provide a complete description of the global dynamics and the global attractors for this four-dimensional system, characterized by three threshold parameters which have clear biological interpretation.

2 Equilibria, reproduction numbers, local stability

To determine the positive equilibria of system (1), we solve the system of algebraic equations

\[
0 = -\beta_T S^* T^* - \beta_Q S^* Q^* + \theta T^* + \alpha I^* + b - b S^*,
\]

\[
0 = \beta_T S^* T^* - \beta_Q Q^* T^* - \theta T^* - b T^*,
\]

\[
0 = \beta_Q S^* Q^* + \beta_Q Q^* T^* - \mu Q^* - b Q^*,
\]

\[
0 = \mu Q^* - \alpha I^* - b I^*.
\]
We get the four equilibria

\[ E_S = (1, 0, 0, 0), \]
\[ E_T = \left( \frac{b + \theta}{\beta_T}, 1 - \frac{b + \theta}{\beta_T}, 0, 0 \right), \]
\[ E_{QI} = \left( \frac{b + \mu}{\beta_Q}, 0, \frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)}, \frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} \right), \]

and

\[ E_{TQI} = \left( \frac{(b + \alpha)(\beta_Q + \theta) + \mu(\theta - \alpha)}{\beta_T(b + \alpha + \mu)}, \frac{(b + \mu)(b + \alpha + \mu)\beta_T - (b + \theta)(b + \alpha + \mu)\beta_Q - \beta_Q(b + \alpha)(\beta_Q - (\mu + b))}{\beta_Q\beta_T(b + \alpha + \mu)}, \frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)}, \frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} \right). \]

Various reproduction numbers can be calculated by introducing a single infested (infectious or non-infectious) individual into a completely susceptible population \( E_S \), into a population where only non-infected parasites \( E_T \) or only infected parasites are present \( E_{QI} \), and calculating the expected number of secondary cases generated by this individual.

By introducing a \( T \)-individual into the disease- and infestation-free equilibrium \( E_S \), we obtain the reproduction number

\[ R_1 = \frac{\beta_T}{b + \theta}, \]

as a product of the average time spent in the \( T \) compartment and the transmission rate. Similarly, by introducing a \( Q \)-individual into the same equilibrium we get the reproduction number

\[ R_2 = \frac{\beta_Q}{b + \mu}. \]

We obtain exactly the same reproduction number \( R_2 \) by calculating the expected number of secondary infections caused by the introduction of a \( Q \)-individual into a population in the equilibrium \( E_T \) as the transmission rate from \( Q \)-individuals is the same for the \( S \)- and \( T \)-compartment.

To calculate the last reproduction number, we introduce a \( T \)-individual into a population in the equilibrium \( E_{QI} \). Then by (1), the expected sojourn time in the \( T \)-compartment is \((\beta_Q Q^* + \theta + b)^{-1}\), and the number of generated new \( T \)-cases
by this single individual per unit time is $\beta_T S^*$. Multiplying these two expressions and substituting the values of $Q^*$ and $S^*$ at the equilibrium $E_{QI}$, we obtain the reproduction number

$$R_3 = \frac{\beta_T(b + \mu)(b + \alpha + \mu)}{\beta_Q(b + \theta)(b + \alpha + \mu) + \beta_Q(b + \alpha)(\beta_Q - (b + \mu))}.$$ 

**Proposition 2.1.** The equilibrium $E_S$ always exists. The equilibrium $E_T$ exists if and only if $R_1 > 1$. The equilibrium $E_{QI}$ exists if and only if $R_2 > 1$. The equilibrium $E_{TQI}$ exists if and only if $R_2 > 1$ and $R_3 > 1$.

**Proof.** The first coordinate of $E_T$ is less than 1 if and only if $R_1 > 1$. In this case also the second coordinate of $E_T$ is between 0 and 1. For the first coordinate of $E_{QI}$ to be less than 1, we need $R_2 > 1$. If this holds, then the third and fourth coordinates are both positive, and as the sum of all coordinates is equal to 1, all of the coordinates of $E_{QI}$ are between 0 and 1. As the last two coordinates of $E_{TQI}$ are the same as those of $E_{QI}$, the condition $R_2 > 1$ is necessary and sufficient for them to be between 0 and 1, and the sum of the first and the second coordinates is $(b + \mu)/\beta_Q < 1$. It remained to prove that these two coordinates are positive if and only if $R_3 > 1$. The first coordinate can be written as

$$\frac{\theta}{\beta_T} + \frac{b\beta_Q + \alpha\beta_Q - \alpha\mu}{\beta_T(b + \alpha + \mu)},$$

which is positive as $\beta_Q > b + \mu$ follows from $R_2 > 1$. The denominator of the second coordinate is always positive, while one can check that the positivity of the numerator is equivalent to $R_3 > 1$.

**Proposition 2.2.** The local stability of the four equilibria is determined by the reproduction numbers in the following way.

(i) $E_S$ is locally asymptotically stable if $R_1 < 1$ and $R_2 < 1$, and unstable if $R_1 > 1$ or $R_2 > 1$.

(ii) $E_T$ is locally asymptotically stable if $R_1 > 1$ and $R_2 < 1$, and unstable if $R_2 > 1$.

(iii) $E_{QI}$ is locally asymptotically stable if $R_2 > 1$ and $R_3 < 1$, and unstable if $R_3 > 1$.

(iv) $E_{TQI}$ is locally asymptotically stable if $R_2 > 1$ and $R_3 > 1$ (i.e. always when it exists).

**Proof.** (i) To prove the first statement, we compute the eigenvalues of the Jacobian of the linearized equation around the equilibrium $E_S$: $\lambda_1 = -b$, $\lambda_2 = -b - \alpha$, 

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\( \lambda_3 = -b - \theta + \beta_T = (b + \theta)(R_1 - 1) \) and \( \lambda_4 = -b - \mu + \beta_Q = (b + \mu)(R_2 - 1) \). The first two eigenvalues are always negative, while the last two are negative if \( R_1 < 1 \) and \( R_2 < 1 \), and one of them is positive if \( R_1 > 1 \) or \( R_2 > 1 \).

(ii) The Jacobian of the linearized equation at the equilibrium \( E_T \) has the four eigenvalues \( \lambda_1 = -b \), \( \lambda_2 = -b - \alpha \), \( \lambda_3 = b + \theta - \beta_T = (b + \theta)(1 - R_1) \), \( \lambda_4 = -b - \mu + \beta_Q = (b + \mu)(R_2 - 1) \), i.e. the same as in case (i) with the exception of \( \lambda_3 \), which means that we can prove the second statement of the proposition in a similar way as in the first case.

(iii) If we linearize around the steady state \( E_{QI} \) we get the following eigenvalues of the Jacobian:

\[
\lambda_1 = -b, \quad \lambda_2 = -\theta + \frac{\beta_T(b + \mu)}{\beta_Q} - \frac{(b + \alpha)\beta_Q - \alpha\mu}{b + \alpha + \mu}
\]

and

\[
\lambda_{3,4} = -\frac{(b + \alpha)(\alpha + \beta_Q)}{2(b + \alpha + \mu)} \pm \frac{\sqrt{b + \alpha}}{2(b + \alpha + \mu)} \sqrt{(b + \alpha)(2b + \alpha - \beta_Q)^2 + 4(b + \alpha)(3b + \alpha - 2\beta_Q)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^4}.
\]

The relation \( R_2 < 1 \) is necessary for the existence of the equilibrium \( E_{QI} \). If we add the terms in \( \lambda_2 \), some calculations show that the numerator of the fraction is the difference of the numerator and the denominator of the reproduction number \( R_3 \), which means that it is negative if and only if \( R_3 < 1 \). As for \( \lambda_3 \) and \( \lambda_4 \), by taking the difference of the squares of the first resp. the second term of the nominator, we obtain \( 4(b + \alpha)(b + \alpha + \mu)^2(\beta_Q - (b + \mu)) \), which is greater than zero, as from \( R_2 > 1 \) we have \( \beta_Q > b + \mu \). From this follows that \( \lambda_3 \) and \( \lambda_4 \) always have negative real parts for \( R_2 > 1 \).

(iv) Local stability properties of the fourth equilibrium \( E_{TQI} \) can be seen in a similar way as in case (iii). By linearization we obtain the following eigenvalues of the Jacobian:

\[
\lambda_1 = -b, \quad \lambda_2 = \theta - \frac{\beta_T(b + \mu)}{\beta_Q} + \frac{(b + \alpha)\beta_Q - \alpha\mu}{b + \alpha + \mu}
\]

and

\[
\lambda_{3,4} = -\frac{(b + \alpha)(\alpha + \beta_Q)}{2(b + \alpha + \mu)} \pm \frac{\sqrt{b + \alpha}}{2(b + \alpha + \mu)} \sqrt{(b + \alpha)(2b + \alpha - \beta_Q)^2 + 4(b + \alpha)(3b + \alpha - 2\beta_Q)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^4},
\]

i.e. \( \lambda_1 \), \( \lambda_3 \) and \( \lambda_4 \) are the same as the corresponding eigenvalues in case (iii). The eigenvalue \( \lambda_2 \) is the negative of the second eigenvalue in case (iii). This yields the statement of the proposition.
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3 Persistence

To prove various persistence results, we use some definitions and results from [6].

Definition 3.1. Let $X$ be a nonempty set and $\rho: X \to \mathbb{R}_+^+$. A semiflow $\Phi: \mathbb{R}_+^+ \times X \to X$ is called uniformly weakly $\rho$-persistent, if there exists some $\varepsilon > 0$ such that

$$\limsup_{t \to \infty} \rho(\Phi(t, x)) > \varepsilon \quad \text{for all } x \in X, \rho(x) > 0.$$ 

$\Phi$ is called uniformly (strongly) $\rho$-persistent if there exists some $\varepsilon > 0$ such that

$$\liminf_{t \to \infty} \rho(\Phi(t, x)) > \varepsilon \quad \text{for all } x \in X, \rho(x) > 0.$$ 

A set $M \subseteq X$ is called weakly $\rho$-repelling if there is no $x \in X$ such that $\rho(x) > 0$ and $\Phi(t, x) \to M$ as $t \to \infty$.

System (1) generates a continuous flow $\Phi$ on the feasible state space

$$X := \{(S, T, Q, I) \in \mathbb{R}_+^4 : S + T + Q + I = 1\} \subset \mathbb{R}_+^4.$$ 

Theorem 3.1. $S(t)$ is always uniformly persistent. $T(t)$ is uniformly persistent if $R_1 > 1$ and $R_2 < 1$ as well as if $R_2 > 1$ and $R_3 > 1$. $Q(t)$ and $I(t)$ are uniformly persistent if $R_2 > 1$.

Proof. We use the method of fluctuation to prove the persistence of $S(t)$ (see e.g. Appendix A of [6]). We denote by $S_\infty$ the limit inferior of $S(t)$ ($t \to \infty$). Using the fluctuation lemma it follows that there exists a sequence $t_k \to \infty$ such that $S(t_k) \to S_\infty$ and $S'(t_k) \to 0$ as $k \to \infty$. We apply this for the equation for $S(t)$:

$$S'(t_k) + \beta_T S(t_k)T(t_k) + \beta_Q S(t_k)Q(t_k) + b S(t_k) = \theta T(t_k) + \alpha I(t_k) + b,$$

and using $0 \leq T(t_k), Q(t_k) \leq 1$ we obtain

$$(\beta_T + \beta_Q + b)S_\infty \geq b, \quad \text{i.e. } S_\infty \geq \frac{b}{\beta_T + \beta_Q + b} > 0.$$ 

To prove the persistence of $T(t)$ and $Q(t)$ we use some theory from [6]. For the sake of simplicity, for the state of the system we use the notation $x = (S, T, Q, I) \in X$. The $\omega$-limit set of a point $x \in X$ is defined in the usual way by

$$\omega(x) := \{y \in X : \exists \{t_n\}_{n \geq 1} \text{ such that } t_n \to \infty, \Phi(t_n, x) \to y \text{ as } n \to \infty\}.$$ 

Let $\rho(x) = T$ and consider the extinction space

$$X_T := \{x \in X : \rho(x) = 0\} = \{(S, 0, Q, I) \in \mathbb{R}_+^4 : S + Q + I = 1\}.$$
Clearly $X_T$ is invariant. Following [6, Chapter 8], we examine the set $\Omega := \bigcup_{x \in X_T} \omega(x)$.

Substituting $S(t) = 1 - Q(t) - I(t)$, on the extinction space our system takes the form
\[
\begin{align*}
Q'(t) &= \beta_Q(1 - Q(t) - I(t))Q(t) - \mu Q(t) - bQ(t), \\
I'(t) &= \mu Q(t) - \alpha I(t) - bI(t).
\end{align*}
\]
This system has two possible equilibria, $(0, 0)$ and $((b + \alpha)(\beta_Q - (b + \mu)))/\beta_Q(b + \alpha + \mu)$, corresponding to $E_S$ and $E_{QI}$. We claim that the limit of each solution of the reduced system is one of these two equilibria. According to the Poincaré–Bendixson theorem, all we have to prove is that system (2) does not have periodic solutions. To show this, we will use Dulac's criterion [4] using the Dulac function $D(Q, J) = 1/Q$. Then
\[
\frac{\partial}{\partial Q} (\beta_Q(1 - Q - I)Q - \mu Q - bQ) + \frac{\partial}{\partial I} \mu Q - \alpha I - bI = -\frac{b + \alpha + Q\beta_Q}{Q} < 0,
\]
if $Q > 0$, which, using Dulac’s criterion implies that system (2) has no periodic solutions.

First we show weak $\rho$-persistence for the case $R_1 > 1$ and $R_2 < 1$. To apply Theorem 8.17 of [6], we let $M_1 = \{E_S\}$ as in this case $E_{QI}$ does not exist. Then $\Omega \subset M_1$, and $M_1$ is isolated (by Proposition 2.2), compact, invariant and acyclic. It remained to show that $M_1$ is weakly $\rho$-repelling, then by [6, Chapter 8], the weak persistence follows.

Let us suppose that $M_1$ is not $\rho$-repelling, i.e. there exists a solution such that $\lim_{t \to 0} (S(t), T(t), Q(t), I(t)) = (1, 0, 0, 0)$ and $T(t) > 0$. Then for any $\varepsilon > 0$, for sufficiently large $t$, $S(t) > 1 - \varepsilon$, $Q(t) < \varepsilon$ and $I(t) < \varepsilon$ hold and we can give the following estimation for $T'(t)$:
\[
T'(t) = T(t)(\beta_T S(t) - \beta_Q Q(t) - \theta - b) > T(t)(\beta_T - \beta_T \varepsilon - \beta_Q \varepsilon - \theta - b).
\]
$R_1 > 1$ means $\beta_T > b + \theta$, so if $\varepsilon$ is small enough then $\beta_T - \beta_T \varepsilon - \beta_Q \varepsilon - \theta - b > 0$, contradicting $T(t) \to 0$.

Let us now suppose that $R_2$ and $R_3$ are both greater than 1. We proceed similarly as before. In this case also $E_{QI}$ exists, so $\Omega = \{E_S, E_{QI}\}$. We let $M_1 = \{E_S\}$ and $M_2 = \{E_{QI}\}$. Then $\Omega \subset M_1 \cup M_2$ and $\{M_1, M_2\}$ is acyclic and $M_1$ and $M_2$ are invariant, isolated and compact. Similarly to the previous case, we have to show that $M_1$ and $M_2$ are both weakly $\rho$-repelling.

First assume that $M_1$ is not weakly $\rho$-repelling, so there exists a solution such that $\lim_{t \to 0} (S(t), T(t), Q(t), I(t)) = (1, 0, 0, 0)$ and $T(t) > 0$. From
\[
R_2 = \frac{\beta_Q}{b + \mu} > 1 \quad \text{and} \quad R_3 = \frac{\beta_T(b + \mu)(b + \alpha + \mu)}{\beta_Q(b + \theta)(b + \alpha + \mu) + \beta_Q(b + \alpha)(\beta_Q - (b + \mu))} > 1
\]
we have
\[ R_2R_3 = \frac{\beta_T(b + \alpha + \mu)}{(b + \theta)(b + \alpha + \mu) + (b + \alpha)(\beta_Q - (b + \mu))} > 1, \]
i.e. \( \beta_T(b + \alpha + \mu) > (b + \theta)(b + \alpha + \mu) + (b + \alpha)(\beta_Q - (b + \mu)) \)
from which \( \beta_T > b + \theta \) follows. As for any \( \varepsilon > 0 \), for \( t \) large enough \( S(t) > 1 - \varepsilon \)
and \( Q(t) < \varepsilon \) hold, similarly to the previous case we can estimate \( T'(t) \):
\[ T'(t) = T(t)(\beta_T S(t) - \beta_Q Q(t) - \theta - b) > T(t)(\beta_T - \beta_T \varepsilon - \beta_Q \varepsilon - \theta - b) > 0 \]
for \( \varepsilon \) small enough, as \( R_2 > 1 \), contradicting to \( T(t) \to 0 \).

To show the repelling property of \( M_2 \), assume that there exists a solution such that
\[ \lim_{t \to \infty} (S(t), T(t), Q(t), I(t)) = \left( \frac{b + \mu}{\beta_Q}, 0, \frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)}, \beta_Q(b + \alpha + \mu) \right) \]
and \( T(t) > 0 \). Similarly to the previous case, for any \( \varepsilon > 0 \), for \( t \) large enough we can estimate \( T'(t) \) as
\[ T'(t) = T(t)(\beta_T S(t) - \beta_Q Q(t) - \theta - b) \]
\[ > T(t)\left(\beta_T \left(\frac{b + \mu}{\beta_Q} - \varepsilon\right) - \beta_Q \left(\frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} + \varepsilon\right) - \theta - b\right) \]
\[ > T(t)\left(\beta_T(b + \mu)(b + \alpha + \mu) - (b + \alpha)(\beta_Q - (b + \mu))\beta_Q \right) \]
\[ - \frac{(b + \theta)(b + \alpha + \mu)\beta_Q}{\beta_Q(b + \alpha + \mu)} - (\beta_T + \beta_Q)\varepsilon, \]
which is positive for sufficiently small \( \varepsilon \) as the positivity of the first term in the last line follows from \( R_3 > 1 \). This contradicts \( T(t) \to 0 \).

To prove the persistence of \( Q(t) \), we choose \( \rho(x) = Q \). We have the equilibrium \( E_S \) if \( R_1 \leq 1 \) and the two equilibria \( E_S \) and \( E_T \) if \( R_1 > 1 \). We define the extinction space as
\[ X_Q := \{ x \in X : \rho(x) = 0 \} = \{(S, T, 0, I) \in \mathbb{R}^4_+ : S + T + I = 1\}. \]
Similarly to the previous case, we will show that \( \Omega \) consists of \( E_S \) or \( E_S \) and \( E_T \). It is easy to see that if \( Q(t) = 0 \), then \( \lim_{t \to \infty} I(t) = 0 \), i.e. \( \Omega \subset \{(S, T, 0, 0) \in \mathbb{R}^4_+ : S + T = 1\} \). On this set, our system takes the form
\[ S'(t) = -\beta_T S(t) T(t) + \theta T(t) + b - b S(t), \]
\[ T'(t) = \beta_T S(t) T(t) - \theta T(t) - b T(t), \] (3)
This system has two equilibria, the unstable equilibrium \((1, 0)\) and for \(R_1 > 1\) the locally stable equilibrium \(((b + \theta)/\beta_T, 1 - (b + \theta)/\beta_T)\). If \(T = 0\), then \(S = 1\). If \(T > 0\), then \(T\) is decreasing if \(S < (b + \theta)/\beta_T\), i.e. if \(T > 1 - (b + \theta)/\beta_T\) and increasing if \(S > (b + \theta)/\beta_T\), i.e. if \(T < 1 - (b + \theta)/\beta_T\), thus we obtain that

\[
\Omega := \bigcup_{x \in X_T} \omega(x) = M_1
\]

if \(R_1 \leq 1\), and

\[
\Omega := \bigcup_{x \in X_Q} \omega(x) = M_1 \cup M_2
\]

if \(R_1 > 1\), where

\[
M_1 = \{(1, 0, 0, 0)\} \quad \text{and} \quad M_2 = \left\{ \left( \frac{b + \theta}{\beta_T}, 1 - \frac{b + \theta}{\beta_T}, 0, 0 \right) \right\}.
\]

Similarly, as in the proof of the persistence of \(T(t)\), \(M_1\) and \(M_2\) contain only one equilibrium, which means that these sets are invariant. These two equilibria are isolated in \(X_T\); \(M_1\) is acyclic if \(R_1 \leq 1\) and \(\{M_1, M_2\}\) is acyclic if \(R_1 > 1\).

We can prove that \(M_1\) is weakly \(\rho\)-repelling similarly in the two cases \(R_1 \leq 1\) and \(R_1 > 1\). Assume it does not hold, i.e. there exists a solution such that \(\lim_{t \to \infty}(S(t), T(t), Q(t), I(t)) = (1, 0, 0, 0)\) with \(Q(t) > 0\). For any \(\varepsilon > 0\), for sufficiently large \(t\) we have \(S(t) > 1 - \varepsilon\), so we can estimate \(Q'(t)\):

\[
Q'(t) = Q(t)(\beta_Q S(t) + \beta_Q T(t) - \mu - b) > Q(t)(\beta_Q(1 - \varepsilon) - \mu - b) > 0
\]

for \(\varepsilon\) small enough, as \(R_2 > 1\), i.e. \(\beta_Q > b + \mu\). This contradicts \(Q(t) \to 0\).

Now let us consider the case \(R_1 > 1\), i.e. when also \(E_T\) exists. Suppose that \(M_2\) is not weakly \(\rho\)-repelling, i.e. there exists a solution such that

\[
\lim_{t \to \infty}(S(t), T(t), Q(t), I(t)) = \left( \frac{b + \theta}{\beta_T}, 1 - \frac{b + \theta}{\beta_T}, 0, 0 \right)
\]

and \(Q(t) > 0\). For any \(\varepsilon > 0\), for \(t\) large enough we have

\[
S(t) > \frac{b + \theta}{\beta_T} - \varepsilon, \quad T(t) > 1 - \frac{b + \theta}{\beta_T} - \varepsilon.
\]

Using these relations, we can give the following estimation for the derivative \(Q'(t)\):

\[
Q'(t) = Q(t)(\beta_Q S(t) + \beta_Q T(t) - \mu - b)
\]

\[
> Q(t) \left( \beta_Q \left( \frac{b + \theta}{\beta_T} - \varepsilon \right) + \beta_Q \left( 1 - \frac{b + \theta}{\beta_T} - \varepsilon \right) - \mu - b \right)
\]

\[
= Q(t)(\beta_Q - (\mu + b) - 2\beta_Q\varepsilon) > 0
\]
for $\varepsilon$ small enough, which follows from $R_2 > 1$, i.e. $\beta_Q > b + \mu$. This contradicts $Q(t) \to 0$.

We have proved uniform weak persistence for $T(t)$ resp. $Q(t)$ in all of the cases, and for the transition to uniform (strong) persistence, we use [6, Theorem 4.5].

Clearly, our flow is continuous, and the subspaces $X_T, X_Q, X \setminus X_T$ and $X \setminus X_Q$ are all invariant. The existence of a compact attractor is also obvious, as the phase space $X$ is compact. Thus, all the conditions of [6, Theorem 4.5] hold.

To prove the uniform persistence of $I(t)$, it is enough to show that the persistence of $Q(t)$ implies that of $I(t)$. If $Q(t)$ is persistent, then there exists an $\varepsilon > 0$ such that $Q(t) > \varepsilon$ for all $t > t^*$ for some $t^* > 0$. Thus from the equation for $I'(t)$ we obtain

$$I'(t) > \mu \varepsilon - \alpha I(t) - b I(t).$$

Let $I_\infty$ denote the limit inferior of $I(t)$ ($t \to \infty$). From the fluctuation lemma it follows that there exists a sequence $t_k \to \infty$ such that $I(t_k) \to I_\infty$ and $I'(t_k) \to 0$ as $k \to \infty$. Applying this to (4) we obtain

$$I_\infty \geq \frac{\varepsilon \mu}{b + \alpha},$$

which shows the uniform persistence of $I(t)$.

\section{Global stability}

In this section we extend the statements about local stability in Section 2 to global asymptotic stability by means of Lyapunov functions and LaSalle’s invariance principle, where we also apply the persistence results of the previous section.

\textbf{Theorem 4.1.} Equilibrium $E_S$ is globally asymptotically stable if $R_1 \leq 1$ and $R_2 \leq 1$.

\textbf{Proof.} Let us choose $V_1(S, T, Q, I) = T + Q$ as a Lyapunov function. The derivative of the Lyapunov function along solutions of (1) is

$$\dot{V}_1 = T\beta_T \left( S - \frac{b + \theta}{\beta_T} \right) + Q\beta_Q \left( S - \frac{b + \mu}{\beta_Q} \right) \leq T\beta_T \left( 1 - \frac{1}{R_1} \right) + Q\beta_Q \left( 1 - \frac{1}{R_2} \right),$$

which is less than or equal to zero if $R_1 \leq 1$ and $R_2 \leq 1$. From LaSalle’s invariance principle [7] we know that the limit set of each solution is a subset of the set $\dot{V}_1 = 0$. The first term of the derivative can be equal to zero if and only if $T$ is zero or $S = (b + \theta)/\beta_T$. The latter case is only possible if $(b + \theta)/\beta_T = S = 1$, as $R_1 \leq 1$. 

\hspace{1cm} $\blacksquare$
However this also implies $T = 0$. Similarly, the second term is equal to zero if $Q = 0$ or $S = (b + \mu)/\beta Q$. The latter case only holds if $(b + \mu)/\beta Q = S = 1$ which yields $Q = 0$. The only remaining possibility for $\dot{V}_1 = 0$ is that $T = Q = I = 0$. Thus, the limit set of any solution is the equilibrium $E_S$.  

**Theorem 4.2.** Equilibrium $E_T$ is globally asymptotically stable on $X \setminus X_T$ if $R_1 > 1$ and $R_2 \leq 1$. On $X_T$, $E_S$ is globally asymptotically stable.

**Proof.** We choose the Lyapunov function $V_2(S, T, Q, I) = Q^2$, the derivative of which is

$$\dot{V}_2 = -2Q^2\beta Q \left(\frac{b + \mu}{\beta Q} - (S + T)\right)$$

along the solutions. This is less than or equal to zero as $R_2 \leq 1$ and $S + T \leq 1$. Thus $\dot{V}_2 = 0$ if $Q = 0$ or $(b + \mu)/\beta Q - (S + T) = 0$. The second case is only possible if $R_2 = 1$ and $S + T = 1$, from which $Q = I = 0$ follows. Hence, $\dot{V}_2$ is equal to zero if and only if $Q = 0$. We use LaSalle’s invariance principle to get that the limit set of each solution is a subset of the set $\dot{V}_2 = 0$.

For $Q = 0$ we know that $\lim_{t \to \infty} I(t) = 0$, i.e. the limit set lies in the set $\{(S, T, Q, I) \in \mathbb{R}_+^4 : S + T = 1\}$. On this set, the equations for $S$ and $T$ have the form (3). We have already shown in Theorem 3.1 how the solutions of this system behave: if $T = 0$, then $S = 1$, while if $T > 0$, then $T$ is decreasing if $S < (b + \theta)/\beta T$, i.e. if $T > 1 - (b + \theta)/\beta T$ and increasing if $S > (b + \theta)/\beta T$, i.e. $T < 1 - (b + \theta)/\beta T$.  

**Theorem 4.3.** Assume $R_2 > 1$. Then the following statements hold:

(i) If $R_3 \leq 1$ and $R_1 \leq 1$, then $E_{QI}$ is globally asymptotically stable on $X \setminus X_Q$ and $E_S$ is globally asymptotically stable on $X_Q$.

(ii) If $R_3 \leq 1$ and $R_1 > 1$, then $E_{QI}$ is globally asymptotically stable on $X \setminus X_Q$ and $E_T$ is globally asymptotically stable on $X_Q$.

(iii) If $R_3 > 1$, then $E_{TQI}$ is globally asymptotically stable on $X \setminus (X_Q \cup X_T)$, $E_T$ is globally asymptotically stable on $X_Q$ and $E_{QI}$ is globally asymptotically stable on $X_T$.

**Proof.** Let us rewrite the equation for $Q'(t)$ in the following way:

$$Q'(t) = \beta Q S(t) Q(t) + \beta Q T(t) Q(t) - \mu Q(t) - b Q(t) = \beta Q (1 - Q(t) - I(t)) - \mu Q(t) - b Q(t).$$

This way we get system (2) for $Q(t)$ and $I(t)$, which is independent from $S(t)$ and $T(t)$. In Theorem 3.1 we have already shown that the limit set of any solution of this system is one of the two equilibria $(0, 0)$ and $((b + \alpha)(\beta Q - (b + \mu))/(\beta Q(b + \alpha + \mu)), \mu(\beta Q - (b + \mu))/(\beta Q(b + \alpha + \mu)))$. However, in the same theorem we also proved that
$Q(t)$ and $I(t)$ are uniformly persistent if $R_2 > 1$, which excludes the equilibrium $(0, 0)$ for solutions started from $X \setminus X_Q$.

Thus, the limit set of each solution in $X \setminus X_Q$ of the four-dimensional system is contained in the set

$$\{ (S, T, \frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)}, \frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)}) : S + T = \frac{b + \mu}{\beta_Q} \}.$$ 

The equations for $S'(t)$ and $T'(t)$ take the form

$$S'(t) = -\beta T S(t) T(t) - \beta Q S(t) \frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} + \theta T(t) + \alpha \frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} + b - b S(t),$$

$$T'(t) = \beta T S(t) T(t) - \beta Q T(t) \frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} - \theta T(t) - b T(t)$$

on the limit set. This system might have two equilibria, one of them is $((b + \mu)/\beta_Q, 0)$, the other, which only exists for $R_3 > 1$ is $(S^*, T^*)$ with

$$S^* = \frac{(b + \alpha)(\beta_Q + \theta) + (-\alpha + \theta)\mu}{\beta_T(b + \alpha + \mu)}$$

and

$$T^* = \frac{(b + \alpha)(b\beta_T - \beta_Q(\beta_Q + \theta)) + (2b\beta_T + \alpha(\beta_Q + \beta_T) - \beta_Q\theta)\mu + \beta_T\mu^2}{\beta_Q\beta_T(b + \alpha + \mu)},$$

i.e. the first and second coordinates of the equilibrium $E_{TQI}$. Using Dulac’s criterion for system (5) with Dulac function $1/T$ we obtain

$$\frac{\partial}{\partial S} - \beta_T S T - \beta_Q S \frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} + \alpha \frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} + b - b S$$

$$+ \frac{\partial}{\partial T} \frac{\beta_T S T - \beta_Q T \frac{(b + \alpha)(\beta_Q - b - \mu)}{\beta_Q(b + \alpha + \mu)} - \mu T(t) - b T}{T} =$$

$$= -\frac{b}{T} - b T - \frac{(b + \alpha)(\beta_Q - \mu - b)}{(b + \alpha + \mu)T} < 0,$$

showing that there is no periodic solution in the region $\{(S, T) \in \mathbb{R}^2_+\}$. This means that in the case $R_3 \leq 1$ the only equilibrium $((b + \mu)/\beta_Q, 0)$ is globally asymptotically stable. This implies the global asymptotic stability of $E_{QI}$ in $X \setminus X_Q$ for the four-dimensional system in the case $R_3 \leq 1$. In the other case, if $R_3 > 1$, we know...
from Theorem 3.1 that $T(t)$ is uniformly persistent, which excludes the equilibrium $((b + \mu)/\beta Q, 0)$ as a limit set of any solution with $T(0) > 0$, and implies that for all such solutions the limit set is the equilibrium $(S^*, T^*)$, and thus $E_{TQI}$ is globally asymptotically stable on $X \setminus (X_Q \cup X_T)$. The solution with initial value $T(0) = 0$ is a constant solution for system (5), thus solutions started from $X_T$ tend to $E_{SI}$ in case (iii).

For $Q = 0$ we can proceed similarly as in the previous theorem: if $T = 0$, then $S = 1$, while if $T > 0$, then $T$ is decreasing if $S < (b + \theta)/\beta_T$, i.e. if $T > 1 - (b + \theta)/\beta_T$ and increasing if $S > (b + \theta)/\beta_T$, i.e. $T < 1 - (b + \theta)/\beta_T$. This means that for $R_1 \leq 1$ (case (i)), $T$ always decreases to 0, thus solutions started from $X_Q$ tend to $E_S$, while for $R_1 > 1$ (cases (ii) and (iii)), $T(t) \to 1 - (b + \theta)/\beta_T$, i.e. solutions started from $X_Q$ tend to $E_T$.

\[
\begin{array}{|c|c|c|}
\hline
\text{Reproduction number} & \text{Existing equilibria} & \text{Global stability} \\
\hline
(i) & R_1 \leq 1, R_2 \leq 1 & E_S & E_S \text{ GAS} \\
(ii) & R_1 > 1, R_2 \leq 1 & E_S, E_T & E_T \text{ GAS on } X \setminus X_T, \\
 & & & E_S \text{ GAS on } X_T \\
(iii) & R_1 \leq 1, R_2 > 1, & E_S, E_{QI} & E_{QI} \text{ GAS on } X \setminus X_Q, \\
 & R_3 \leq 1 & & E_S \text{ GAS on } X_Q \\
(iv) & R_1 > 1, R_2 > 1, & E_S, E_T, & E_{QI} \text{ GAS on } X \setminus X_Q, \\
 & R_3 \leq 1 & E_{QI} & E_T \text{ GAS on } X_Q \\
(v) & R_1 > 1, R_2 > 1, & E_S, E_T, & E_{TQI} \text{ GAS on } X \setminus (X_T \cup X_Q), \\
 & R_3 > 1 & E_{QI}, E_{TQI} & E_T \text{ GAS on } X_Q, \\
 & & & E_Q \text{ GAS on } X_T \\
\hline
\end{array}
\]

Table 4.1. Reproduction numbers and global stability: summary of Proposition 2.1 and Theorems 4.1, 4.2, 4.3.

5 Structure of the global attractor

In this section we give a complete description of the structure of the global attractor in all possible cases depending on the three reproduction numbers.

**Theorem 5.1.** The global attractor $\mathcal{A}$ for system (1) has the following structure:

(i) If $R_1 \leq 1$ and $R_2 \leq 1$ then $\mathcal{A} = \{E_S\}$.
(ii) If $R_1 > 1$ and $R_2 \leq 1$ then $\mathcal{A} = \{E_S, E_T\} \cup \gamma_1$ where $\gamma_1$ is a connecting orbit from $E_S$ to $E_T$. 


(iii) If $R_2 > 1$, $R_3 \leq 1$ and $R_1 \leq 1$, then $\mathcal{A} = \{E_S, E_{QI}\} \cup \gamma_2$ where $\gamma_2$ is a connecting orbit from $E_S$ to $E_{QI}$.

(iv) If $R_2 > 1$, $R_3 \leq 1$ and $R_1 > 1$ then $\mathcal{A} = \{E_S, E_T, E_{QI}\} \cup \gamma_1 \cup \gamma_2 \cup \gamma_3 \cup \mathcal{A}_1$, where $\gamma_3$ is a connecting orbit from $E_T$ to $E_{QI}$ and $\mathcal{A}_1$ is a two-dimensional manifold consisting of connecting orbits from $E_S$ to $E_{QI}$.

(v) If $R_2 > 1$, $R_3 > 1$ and $R_1 > 1$ then $\mathcal{A} = \{E_S, E_T, E_{QI}, E_{TQI}\} \cup \gamma_1 \cup \gamma_2 \cup \gamma_3 \cup \gamma_5 \cup \mathcal{A}_2$, where $\gamma_4$ is a connecting orbit from $E_{QI}$ to $E_{TQI}$, $\gamma_5$ is a connecting orbit from $E_T$ to $E_{TQI}$ and $\mathcal{A}_2$ is a two-dimensional manifold consisting of connecting orbits from $E_S$ to $E_{TQI}$.

**Proof.** (i) In the previous section we showed that $E_S$ is globally asymptotically stable on the whole phase space, from which it follows that the global attractor consists of the only point $E_S$.

For the proof of the further cases we substitute $S(t)$ by $1 - T(t) - Q(t) - I(t)$ to decrease the number of dimensions to three. We obtain the system

\[
\begin{align*}
T'(t) &= \beta_T(1 - T(t) - Q(t))T(t) - \beta_Q Q(t)T(t) - \theta T(t) - bT(t), \\
Q'(t) &= \beta_Q(1 - T(t) - Q(t))Q(t) + \beta_Q Q(t)T(t) - \mu Q(t) - bQ(t), \\
I'(t) &= \mu Q(t) - \alpha I(t) - bI(t).
\end{align*}
\]

(6)

Throughout this section we will denote the equilibria of this system by the same notation as the corresponding equilibria of system (1). The eigenvalues and eigenvectors of the Jacobian of the linearized system at the four equilibria are listed in Table 7.1.

(ii) If $R_1 > 1$ and $R_2 < 1$ then $E_S$ has the two stable eigenvectors $v_{s,1}$ and $v_{s,3}$ and the unstable eigenvector $v_{s,2}$, implying that $E_S$ has a one-dimensional unstable manifold, which coincides with the segment $(E_S, E_T)$ and a two-dimensional stable manifold coinciding with the extinction space $X_T$, while $E_T$ has three stable eigenvectors.

If $R_2 = 1$, then from Theorem 4.2 we know that all solutions started from $X_T$ tend to $E_S$, while those started from $X \setminus X_T$ tend to $X_T$, which means that the stable and unstable sets of the two equilibria are the same as for $R_2 < 1$.

(iii) If $R_2 > 1$, $R_3 < 1$ and $R_1 < 1$, then $E_S$ has two stable eigenvectors ($v_{s,1}$ and $v_{s,2}$) and the unstable eigenvector $v_{s,3}$, which lies in the $QI$-plane, while $E_{QI}$ has three stable eigenvectors. The second and third coordinates of the unstable eigenvector $v_{s,3}$ are positive for $R_2 > 1$, thus the vector points inside the phase space $X$. From this follows that the unstable manifold of $E_S$ intersects the phase space. A similar argument holds for $v_{s,3}$, $v_{T,3}$ and $v_{QI,1}$ in cases (iv) and (v).
If $R_1 = 1$ then $\lambda_{s,2} = 0$. In this case the equation for $T'(t)$ has the form
\[ T'(t) = -\beta_T T^2(t) < 0 \]
on the invariant extinction space $X_Q$ implying that all solutions on the center manifold belonging to the zero eigenvalue (i.e. the extinction space $X_Q$) tend to $E_S$.

If $R_3 = 1$ then the eigenvalue $\lambda_{QI,1}$ is zero with eigenvector $(1,0,0)$. The line given by the equations
\[ Q = \frac{(b+\alpha)(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)}, \]
\[ I = \frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)} \]
is invariant, this can be seen by substituting these values for $Q$ and $I$ into the equation for $Q'(t)$ and $I'(t)$. This means that the center manifold belonging to the zero eigenvalue coincides with this line. If $R_3 = 1$ then the equation for $T'(t)$ has the form
\[ T'(t) = -\beta_T T^2(t) < 0 \]
on this line. From this follows that all solutions started from this line tend to $E_{QI}$. $\gamma_2$ is the connecting orbit from $E_S$ to $E_{QI}$ lying in the $QI$-plane.

(iv) If $R_1 > 1$, $R_2 > 1$ and $R_3 \leq 1$, then $v_{s,2}$ becomes unstable and $v_{T,2}$ becomes stable. Thus, $E_S$ has a one-dimensional stable manifold and $E_T$ has a two-dimensional stable manifold coinciding with the extinction space $X_Q$. From Theorem 4.3 we know that all solutions started from the one-dimensional unstable manifold of $E_T$ tend to $E_{QI}$, from which the existence of a connecting orbit from $E_T$ to $E_{QI}$ follows. The eigenvectors belonging to $E_Q$ have the same stability as in case (iii). The independence of the equations for $Q'(t)$ and $I'(t)$ from $S(t)$ and $T(t)$ implies that the area bordered by the connecting orbits from $E_S$ to $E_{QI}$, from $E_S$ to $E_T$ and from $E_T$ to $E_{QT}$ is a two-dimensional surface. We have to show that this area $A_1$ consists of heteroclinic orbits connecting $E_S$ and $E_{QT}$. From Theorem 4.3 it is clear that a solution started from an arbitrary point $p$ in this area tends to $E_Q$. We have to show that the negative limit set $\alpha(p)$ is the equilibrium $E_S$. The existence and nonemptiness of the negative limit set follows from the fact that the backward orbit is bounded by $\gamma_1$, $\gamma_2$ and $\gamma_3$. If we apply the Poincaré–Bendixson theorem to the two-dimensional surface $A_1$, we have that $\alpha(p)$ is one of the three equilibria $E_S$, $E_T$ and $E_{QI}$ (the independence of the equations for $Q'(t)$ and $I'(t)$ from the equation for $T'(t)$ excludes the existence of periodic orbits). We can rule
out $E_{QI}$, as it has a three-dimensional stable manifold, while $E_T$ can be excluded by considering that it has a one-dimensional unstable manifold which coincides with the connecting orbit from $E_T$ to $E_{QI}$.

(v) The stability of the eigenvectors belonging to $E_S$ and $E_T$ is the same as in case (iv). The eigenvector $v_{QI,1}$ loses its stability implying that $E_{QI}$ has a two-dimensional stable manifold (coinciding with the $QI$-plane) and a one-dimensional unstable manifold. The equilibrium $E_{TQI}$ has three stable eigenvectors and thus a three-dimensional stable manifold. From Theorem 4.3 it follows that all solutions started from $X \setminus (X_T \cup X_Q)$ tend to $E_{TQI}$, which assures the existence of a connecting orbit $\gamma_4$ from $E_T$ to $E_{TQI}$ and a connecting orbit $\gamma_5$ from $E_{QI}$ to $E_{TQI}$. We can show that the two-dimensional domain $A_2$ consists of connecting orbits from $E_S$ to $E_{TQI}$ similarly to the previous case.

\[ \text{Figure 5.1. Representation of the flow on the } TQI\text{-space in the five cases (see Table 4.1). Dots denote equilibria.} \]
6 Discussion

In this paper we constructed a new, four-dimensional system of differential equations to simultaneously model the spread of an ectoparasite and a disease transmitted by it. The results described in the paper are an extension of our previous works [2,3]. In these papers we established and examined a basic model, which was made more realistic in the present work. Our paper is self-contained: we show the proofs in full detail.

We calculated three reproduction numbers and four potential equilibria of the system. We gave a complete description of the global dynamics of the system for all of the different cases provided by \( R_i \leq 1 \) or \( R_i > 1 \) for \( i = 1, 2, 3 \); we showed that all solutions of the system converge to one of the four equilibria, depending on the reproduction numbers as listed in Table 4.1. (The number of different cases is five, as four of the eight possibilities given by \( R_i \leq 1 \) or \( R_i > 1 \) for \( i = 1, 2, 3 \) are covered by cases (i) and (ii), while we showed that \( R_2 > 1 \) and \( R_3 > 1 \) imply \( R_1 > 1 \), thus excluding the case \( R_1 \leq 1, R_2 > 1, R_3 > 1 \).) The tools used in the proof include persistence theory, Lyapunov stability theory, LaSalle’s invariance principle and Dulac’s criterion. The different cases depending on the reproduction numbers are shown in Figure 2.

The biological interpretation of the stability results are the following: by decreasing \( R_1 \) to be less than or equal to 1 (possible by decreasing \( \beta_T \) or increasing \( \mu \)) we can eliminate the non-infectious parasites. To eradicate the disease, we have to decrease \( R_2 \) to be less than or equal to 1, which is possible by decreasing \( \beta_Q \) or increasing \( \mu \). If we have \( R_1 \leq 1 \) and \( R_2 \leq 1 \), we can eliminate both types of parasites and the disease as well. The reproduction number \( R_3 \) only determines whether besides infectious parasites non-infectious parasites are present as well.

7 Acknowledgement

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Equilibria and corresponding eigenvalues and eigenvectors

<table>
<thead>
<tr>
<th>$E_S$</th>
<th>$\lambda_{S,1} = -b - \alpha$, $v_{S,1} = (0, 0, 1)$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\lambda_{S,2} = \beta_T - (b + \theta)$, $v_{S,2} = (1, 0, 0)$</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{S,3} = \beta_Q - (b + \mu)$, $v_{S,3} = (0, \frac{\beta_Q + \alpha - \mu}{\mu}, 1)$</td>
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<table>
<thead>
<tr>
<th>$E_T$</th>
<th>$\lambda_{T,1} = -b - \alpha$, $v_{T,1} = \left(\frac{\beta_T - (b + \theta)}{2b + \alpha + \theta - \beta_T}, 0, 1\right)$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\lambda_{T,2} = b + \theta - \beta_T$, $v_{T,2} = (1, 0, 0)$</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{T,3} = \beta_Q - (b - \mu)$, $v_{T,3} = \left(\frac{(b + \theta - \beta_T)(\alpha \beta_Q + \beta_Q^2 + \alpha \beta_T + \beta_Q \beta_T - \beta_T \mu)}{\beta_T (2b + \beta_Q + \beta_T - \theta - \mu \mu)}, \frac{\beta_Q + \alpha - \mu}{\mu}, 1\right)$</td>
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<table>
<thead>
<tr>
<th>$E_QI$</th>
<th>$\lambda_{QI,1} = -\theta + \frac{\beta_T (b + \mu)}{\beta_Q} - \frac{(b + \alpha) \beta_Q - \alpha \mu}{b + \alpha + \mu}$, $v_{QI,1} = (1, 0, 0)$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\lambda_{QI,2} = \frac{(b + \alpha)(2b + \alpha - \beta_Q + 2\mu) - \sqrt{b + \alpha}(2b + \alpha - \beta_Q)^2 + 4(b + \alpha)(3b + \alpha - 2\beta_Q)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3}{2(b + \alpha + \mu)}$</td>
</tr>
<tr>
<td></td>
<td>$v_{QI,2} = \left(0, \frac{(b + \alpha)(2b + \alpha - \beta_Q + 2\mu) - \sqrt{b + \alpha}(2b + \alpha - \beta_Q)^2 + 4(b + \alpha)(3b + \alpha - 2\beta_Q)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3}{2(b + \alpha + \mu)}, 1\right)$</td>
</tr>
<tr>
<td></td>
<td>$\lambda_{QI,3} = \frac{(b + \alpha)(2b + \alpha - \beta_Q + 2\mu) + \sqrt{b + \alpha}(2b + \alpha - \beta_Q)^2 + 4(b + \alpha)(3b + \alpha - 2\beta_Q)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3}{2(b + \alpha + \mu)}$</td>
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<tr>
<td></td>
<td>$v_{QI,3} = \left(0, \frac{(b + \alpha)(2b + \alpha - \beta_Q + 2\mu) + \sqrt{b + \alpha}(2b + \alpha - \beta_Q)^2 + 4(b + \alpha)(3b + \alpha - 2\beta_Q)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3}{2(b + \alpha + \mu)}, 1\right)$</td>
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<th>$ETQI$</th>
<th>$\lambda_{TQI,1} = \theta - \frac{\beta_T (b + \mu)}{\beta_Q} + \frac{(b + \alpha) \beta_Q - \alpha \mu}{b + \alpha + \mu}$, $v_{TQI,1} = (1, 0, 0)$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\lambda_{TQI,2} = \frac{-b(3b - \beta_Q + \beta_T - 2\beta_T(3b + 2\beta_Q)\mu - 2\alpha(\beta_Q + 2\beta_T)\mu + 3b^2 \mu^2 + 2\beta_T \mu + 4(3b + \alpha)(\beta_Q - 2\beta_T)\mu + 2(3b + \alpha)(\beta_Q + 2\beta_T)\mu + 2\alpha(\beta_Q + 2\beta_T)\mu - 2\alpha(3b + 2\beta_T)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3}{2(b + \alpha + \mu)}$</td>
</tr>
<tr>
<td></td>
<td>$v_{TQI,2} = \left(\frac{-b(3b - \beta_Q + \beta_T - 2\beta_T(3b + 2\beta_Q)\mu - 2\alpha(\beta_Q + 2\beta_T)\mu + 3b^2 \mu^2 + 2\beta_T \mu + 4(3b + \alpha)(\beta_Q - 2\beta_T)\mu + 2(3b + \alpha)(\beta_Q + 2\beta_T)\mu + 2\alpha(\beta_Q + 2\beta_T)\mu - 2\alpha(3b + 2\beta_T)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3}{2(b + \alpha + \mu)}, \frac{\beta_Q + \alpha - \mu}{\mu}, 1\right)$</td>
</tr>
<tr>
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<td>$\lambda_{TQI,3} = \frac{-b(3b - \beta_Q + \beta_T - 2\beta_T(3b + 2\beta_Q)\mu - 2\alpha(\beta_Q + 2\beta_T)\mu + 3b^2 \mu^2 + 2\beta_T \mu + 4(3b + \alpha)(\beta_Q - 2\beta_T)\mu + 2(3b + \alpha)(\beta_Q + 2\beta_T)\mu + 2\alpha(\beta_Q + 2\beta_T)\mu - 2\alpha(3b + 2\beta_T)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3}{2(b + \alpha + \mu)}$</td>
</tr>
<tr>
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<td>$v_{TQI,3} = \left(\frac{-b(3b - \beta_Q + \beta_T - 2\beta_T(3b + 2\beta_Q)\mu - 2\alpha(\beta_Q + 2\beta_T)\mu + 3b^2 \mu^2 + 2\beta_T \mu + 4(3b + \alpha)(\beta_Q - 2\beta_T)\mu + 2(3b + \alpha)(\beta_Q + 2\beta_T)\mu + 2\alpha(\beta_Q + 2\beta_T)\mu - 2\alpha(3b + 2\beta_T)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3}{2(b + \alpha + \mu)}, \frac{\beta_Q + \alpha - \mu}{\mu}, 1\right)$</td>
</tr>
<tr>
<td></td>
<td>with $A = (b + \alpha)(2b + \alpha - \beta_Q)^2 + 4(b + \alpha)(3b + \alpha - 2\beta_Q)\mu + 4(3b + 2\alpha - \beta_Q)\mu^2 + 4\mu^3$</td>
</tr>
</tbody>
</table>

Table 7.1. Equilibria, eigenvalues and eigenvectors
References


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