doi: 10.14232/actasm-013-004-y

Acta Sci. Math. (*Szeged*)
80 (2014), 553–572

Global dynamics of a compartmental system modeling ectoparasite-borne diseases

Attila Dénes and Gergely Röst

Dedicated to Professor László Hatvani on the occasion of his 70^{th} *birthday*

Communicated by T. Krisztin

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

Received January 9, 2013.
AMS Subject Classifications: 37B25, 37C70, 92D30.
Key words and phrases: compartmental system; ectoparasites; global dynamics; Lyapunov function; persistence; global attractor.

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 β_Q, and denote the transmission rate for non-infectious parasites (to susceptibles) by β_T. The rate of disinfestation is denoted by μ for the infected compartment and by θ 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 reinfestation 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 α 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:

$$
\begin{aligned}
S'(t) &= -\beta_T S(t)T(t) - \beta_Q S(t)Q(t) + \theta T(t) + \alpha I(t) + b - bS(t),\\
T'(t) &= \beta_T S(t)T(t) - \beta_Q Q(t)T(t) - \theta T(t) - bT(t),\\
Q'(t) &= \beta_Q S(t)Q(t) + \beta_Q Q(t)T(t) - \mu Q(t) - bQ(t),\\
I'(t) &= \mu Q(t) - \alpha I(t) - bI(t).
\end{aligned}
\tag{1}
$$

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

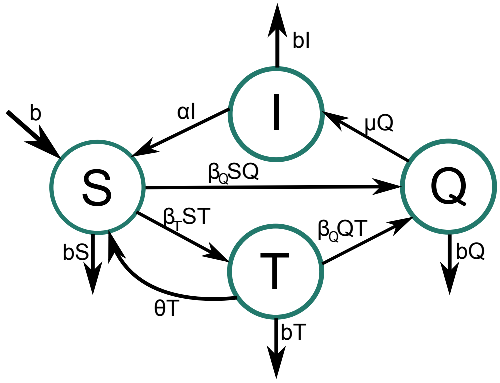

Figure 1.1. Transmission diagram.

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

$$\begin{aligned}
0 &= -\beta_T S^* T^* - \beta_Q S^* Q^* + \theta T^* + \alpha I^* + b - bS^*,\\
0 &= \beta_T S^* T^* - \beta_Q Q^* T^* - \theta T^* - bT^*,\\
0 &= \beta_Q S^* Q^* + \beta_Q Q^* T^* - \mu Q^* - bQ^*,\\
0 &= \mu Q^* - \alpha I^* - bI^*.
\end{aligned}$$

We get the four equilibria

$$
\begin{aligned}
E_S &= (1,0,0,0),\\
E_T &= \Big(\frac{b+\theta}{\beta_T}, 1-\frac{b+\theta}{\beta_T}, 0, 0\Big),\\
E_{QI} &= \Big(\frac{b+\mu}{\beta_Q}, 0, \frac{(b+\alpha)(\beta_Q-b-\mu)}{\beta_Q(b+\alpha+\mu)}, \frac{\mu(\beta_Q-b-\mu)}{\beta_Q(b+\alpha+\mu)}\Big)
\end{aligned}
$$

and

$$
\begin{aligned}
&E_{TQI}\\
&\quad=\Big(\frac{(b+\alpha)(\beta_Q+\theta)+\mu(\theta-\alpha)}{\beta_T(b+\alpha+\mu)},\\
&\qquad\frac{(b+\mu)(b+\alpha+\mu)\beta_T-(b+\theta)(b+\alpha+\mu)\beta_Q-\beta_Q(b+\alpha)(\beta_Q-(\mu+b))}{\beta_Q\beta_T(b+\alpha+\mu)},\\
&\qquad\frac{(b+\alpha)(\beta_Q-b-\mu)}{\beta_Q(b+\alpha+\mu)}, \frac{\mu(\beta_Q-b-\mu)}{\beta_Q(b+\alpha+\mu)}\Big).
\end{aligned}
$$

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: $\lambda_1 = -b$, $\lambda_2 = -b-\alpha$,

$\lambda_3 = -b - \theta + \beta_T = (b+\theta)(R_1 - 1)$ 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 λ_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:

$$\lambda_1 = -b, \qquad \lambda_2 = -\theta + \frac{\beta_T(b+\mu)}{\beta_Q} - \frac{(b+\alpha)\beta_Q - \alpha\mu}{b+\alpha+\mu}$$

and

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

The relation $R_2 < 1$ is necessary for the existence of the equilibrium E_{QI}. If we add the terms in λ_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 λ_3 and λ_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 then zero, as from $R_2 > 1$ we have $\beta_Q > b + \mu$. From this follows that λ_3 and λ_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:

$$\lambda_1 = -b, \qquad \lambda_2 = \theta - \frac{\beta_T(b+\mu)}{\beta_Q} + \frac{(b+\alpha)\beta_Q - \alpha\mu}{b+\alpha+\mu}$$

and

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

i.e. λ_1, λ_3 and λ_4 are the same as the corresponding eigenvalues in case (iii). The eigenvalue λ_2 is the negative of the second eigenvalue in case (iii). This yields the statement of the proposition.

■

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 $\rho\colon X \to \mathbb{R}_+$. A semiflow $\Phi\colon \mathbb{R}_+ \times X \to X$ is called *uniformly weakly ρ-persistent*, if there exists some $\varepsilon > 0$ such that

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

Φ is called *uniformly (strongly) ρ-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 ρ-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 Φ 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_∞ 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 $S(t)$:

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

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

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

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 ω-limit set of a point $x \in X$ is defined in the usual way by

$$\omega(x) := \{y \in X : \exists\{t_n\}_{n\ge1} \text{ such that } t_n \to \infty,\ \Phi(t_n,x) \to y \text{ as } n \to \infty\}.$$

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 $\Omega := \cup_{x\in X_T}\omega(x)$.

Substituting $S(t) = 1 - Q(t) - I(t)$, on the extinction space our system takes the form

$$\begin{aligned} Q'(t) &= \beta_Q(1 - Q(t) - I(t))Q(t) - \mu Q(t) - bQ(t), \\ I'(t) &= \mu Q(t) - \alpha I(t) - bI(t). \end{aligned} \tag{2}$$

This system has two possible equilibria, $(0,0)$ and $((b+\alpha)(\beta_Q - (b+\mu))/(\beta_Q(b+\alpha+\mu)),\ \mu(\beta_Q-(b+\mu))/(\beta_Q(b+\alpha+\mu)))$, 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

$$\frac{\partial}{\partial Q}\frac{(\beta_Q(1-Q-I)Q - \mu Q - bQ)}{Q} + \frac{\partial}{\partial I}\frac{\mu Q - \alpha I - bI}{Q} = -\frac{b+\alpha+Q\beta_Q}{Q} < 0,$$

if $Q > 0$, which, using Dulac's criterion implies that system (2) has no periodic solutions.

First we show weak ρ-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 ρ-repelling, then by [6, Chapter 8], the weak persistence follows.

Let us suppose that M_1 is not ρ-repelling, i.e. there exists a solution such that $\lim_{t\to\infty}(S(t),T(t),Q(t),I(t) = (1,0,0,0)$ 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 ε 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 ρ-repelling.

First assume that M_1 is not weakly ρ-repelling, so there exists a solution such that $\lim_{t\to\infty}(S(t),T(t),Q(t),I(t)) = (1,0,0,0)$ 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. $\beta_T(b+\alpha+\mu) > (b+\theta)(b+\alpha+\mu)+(b+\alpha)(\beta_Q-(b+\mu)) > (b+\theta)(b+\alpha+\mu)$, 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 ε 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

$$\lim_{t\to\infty}(S(t),T(t),Q(t),I(t)) = \Big(\frac{b+\mu}{\beta_Q}, 0, \frac{(b+\alpha)(\beta_Q-b-\mu)}{\beta_Q(b+\alpha+\mu)}, \frac{\mu(\beta_Q-b-\mu)}{\beta_Q(b+\alpha+\mu)}\Big)$$

and $T(t) > 0$. Similarly to the previous case, for any $\varepsilon > 0$, for t large enough we can estimate $T'(t)$ as

$$\begin{aligned}
T'(t) &= T(t)(\beta_T S(t) - \beta_Q Q(t) - \theta - b) \\
&> T(t)\Big(\beta_T\Big(\frac{b+\mu}{\beta_Q} - \varepsilon\Big) - \beta_Q\Big(\frac{(b+\alpha)(\beta_Q-b-\mu)}{\beta_Q(b+\alpha+\mu)} + \varepsilon\Big) - \theta - b\Big) \\
&> T(t)\Big(\frac{\beta_T(b+\mu)(b+\alpha+\mu) - (b+\alpha)(\beta_Q-(b+\mu))\beta_Q}{\beta_Q(b+\alpha+\mu)} - \\
&\qquad\qquad - \frac{(b+\theta)(b+\alpha+\mu)\beta_Q}{\beta_Q(b+\alpha+\mu)} - (\beta_T+\beta_Q)\varepsilon\Big),
\end{aligned}$$

which is positive for sufficiently small ε 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 $R_1 \le 1$ 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 Ω 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

$$\begin{aligned}
S'(t) &= -\beta_T S(t)T(t) + \theta T(t) + b - bS(t), \\
T'(t) &= \beta_T S(t)T(t) - \theta T(t) - bT(t).
\end{aligned} \tag{3}$$

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 $R_1\le 1$, and

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

if $R_1>1$, where

$$M_1 = \{(1,0,0,0)\} \quad \text{and} \quad M_2 = \Big\{\Big(\frac{b+\theta}{\beta_T}, 1-\frac{b+\theta}{\beta_T}, 0, 0\Big)\Big\}.$$

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 $R_1\le 1$ and $\{M_1, M_2\}$ is acyclic if $R_1>1$.

We can prove that M_1 is weakly ρ-repelling similarly in the two cases $R_1\le 1$ 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 ε 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 ρ-repelling, i.e. there exists a solution such that

$$\lim_{t\to\infty}(S(t),T(t),Q(t),I(t)) = \Big(\frac{b+\theta}{\beta_T}, 1-\frac{b+\theta}{\beta_T}, 0, 0\Big)$$

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 $Q'(t)$:

$$\begin{aligned} Q'(t) &= Q(t)(\beta_Q S(t) + \beta_Q T(t) - \mu - b) \\ &> Q(t)\Big(\beta_Q\Big(\frac{b+\theta}{\beta_T} - \varepsilon\Big) + \beta_Q\Big(1 - \frac{b+\theta}{\beta_T} - \varepsilon\Big) - \mu - b\Big) \\ &= Q(t)(\beta_Q - (\mu+b) - 2\beta_Q\varepsilon) > 0 \end{aligned}$$

for ε 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

$$I'(t) > \mu\varepsilon - \alpha I(t) - bI(t). \tag{4}$$

Let I_∞ 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 $I(t)$. ∎

4 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.

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

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

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

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 $R_1 \leq 1$.

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 $R_2\le 1$. 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

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

along the solutions. This is less than or equal to zero as $R_2\le 1$ and $S+T\le 1$. 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 $R_3\le 1$ and $R_1\le 1$, then E_{QI} is globally asymptotically stable on $X\setminus X_Q$ and E_S is globally asymptotically stable on X_Q.*

(ii) *If $R_3\le 1$ 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:

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

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

$$\Big\{\Big(S, T, \frac{(b+\alpha)(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)}, \frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)}\Big) \in \mathbb{R}^4_+ : S + T = \frac{b+\mu}{\beta_Q}\Big\}.$$

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

$$\begin{aligned} S'(t) = &-\beta_T S(t)T(t) - \beta_Q S(t)\frac{(b+\alpha)(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)} + \theta T(t) + \\ &\qquad + \alpha\frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)} + b - bS(t), \qquad (5) \\ T'(t) = &\,\beta_T S(t)T(t) - \beta_Q T(t)\frac{(b+\alpha)(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)} - \theta T(t) - bT(t) \end{aligned}$$

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

$$\begin{aligned} &\frac{\partial}{\partial S}\frac{-\beta_T ST - \beta_Q S\frac{(b+\alpha)(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)} + \alpha\frac{\mu(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)} + b - bS}{T} + \\ &\qquad + \frac{\partial}{\partial T}\frac{\beta_T ST - \beta_Q T\frac{(b+\alpha)(\beta_Q - b - \mu)}{\beta_Q(b+\alpha+\mu)} - \mu T(t) - bT}{T} = \\ &\qquad\qquad = -\frac{b}{T} - b_T - \frac{(b+\alpha)(\beta_Q - \mu - b)}{(b+\alpha+\mu)T} < 0, \end{aligned}$$

showing that there is no periodic solution in the region $\{(S,T) \in \mathbb{R}^2_+\}$. This means that in the case $R_3 \le 1$ 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 $R_3 \le 1$. 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_{QI} 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. ∎

	Reproduction number	Existing equilibria	Global stability
(i)	$R_1 \leq 1, R_2 \leq 1$	E_S	E_S GAS
(ii)	$R_1 > 1, R_2 \leq 1$	E_S, E_T	E_T GAS on $X \setminus X_T$, E_S GAS on X_T
(iii)	$R_1 \leq 1, R_2 > 1$, $R_3 \leq 1$	E_S, E_{QI}	E_{QI} GAS on $X \setminus X_Q$, E_S GAS on X_Q
(iv)	$R_1 > 1, R_2 > 1$, $R_3 \leq 1$	E_S, E_T, E_{QI}	E_{QI} GAS on $X \setminus X_Q$, E_T GAS on X_Q
(v)	$R_1 > 1, R_2 > 1$, $R_3 > 1$	E_S, E_T, E_{QI}, E_{TQI}	E_{TQI} GAS on $X \setminus (X_T \cup X_Q)$, E_T GAS on X_Q, E_Q GAS on X_T

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 γ_1 is a connecting orbit from E_S to E_T.*

(iii) *If* $R_2 > 1$, $R_3 \le 1$ *and* $R_1 \le 1$, *then* $\mathcal{A} = \{E_S, E_{QI}\} \cup \gamma_2$ *where* γ_2 *is a connecting orbit from* E_S *to* E_{QI}.

(iv) *If* $R_2 > 1$, $R_3 \le 1$ *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* γ_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* $\mathcal{A} = \{E_S, E_T, E_{QI}, E_{TQI}\} \cup \gamma_1 \cup \gamma_2 \cup \gamma_4 \cup \gamma_5 \cup \mathcal{A}_2$, *where* γ_4 *is a connecting orbit from* E_{QI} *to* E_{TQI}, γ_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

$$\begin{aligned} T'(t) &= \beta_T(1 - T(t) - Q(t))T(t) - \beta_Q Q(t)T(t) - \theta T(t) - bT(t), \\ Q'(t) &= \beta_Q(1 - T(t) - Q(t))Q(t) + \beta_Q Q(t)T(t) - \mu Q(t) - bQ(t), \\ I'(t) &= \mu Q(t) - \alpha I(t) - bI(t). \end{aligned} \tag{6}$$

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}. γ_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 $\mathcal{A}_1$ consists of heteroclinic orbits connecting E_S and E_{QT}. From Theorem 4.3 it is clear that a solution started from an arbitrary pont 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 γ_1, γ_2 and γ_3. If we apply the Poincaré–Bendixson theorem to the two-dimensional surface $\mathcal{A}_1$, 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 γ_4 from E_T to E_{TQI} and a connecting orbit γ_5 from E_{QI} to E_{TQI}. We can show that the two-dimensional domain $\mathcal{A}_2$ consists of connecting orbits from E_S to E_{TQI} similarly to the previous case. ∎

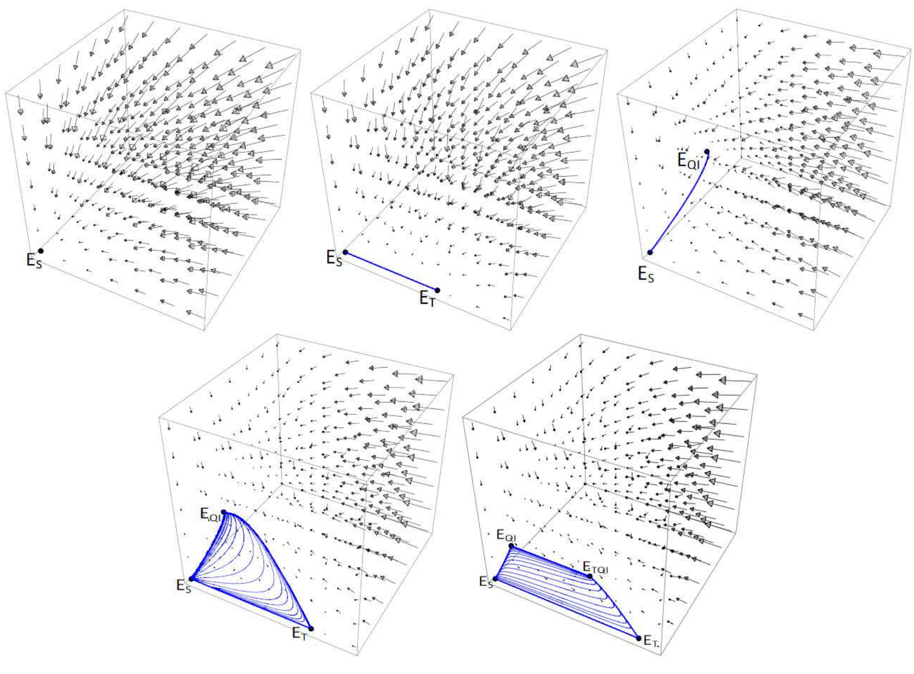

Figure 5.1. Representation of the flow on the TQI-space in the five cases (see Table 4.1). Dots denote equilibria.

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 β_T or increasing μ) 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 β_Q or increasing μ. 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

G. Röst was supported by ERC Starting Grant Nr. 259559, by Hungarian Scientific Research Fund OTKA K109782 and by the European Union and co-funded by the European Social Fund under the project TÁMOP-4.2.2.A-11/1/KONV-2012-0073 "Telemedicine-focused research activities on the field of Mathematics, Informatics and Medical sciences". A. Dénes was supported by the European Union and the State of Hungary, co-financed by the European Social Fund in the framework of TÁMOP-4.2.4.A/2-11/1-2012-0001 'National Excellence Program'.

	Equilibria and corresponding eigenvalues and eigenvectors
E_S	$\lambda_{S,1} = -b-\alpha,\ \ v_{S,1} = (0,0,1)$ $\lambda_{S,2} = \beta_T - (b+\theta),\ \ v_{S,2} = (1,0,0)$ $\lambda_{S,3} = \beta_Q - (b+\mu),\ \ v_{S,3} = \left(0, \frac{\beta_Q+\alpha-\mu}{\mu}, 1\right)$
E_T	$\lambda_{T,1} = -b-\alpha,\ \ v_{T,1} = \left(\frac{\beta_T-(b+\theta)}{2b+\alpha+\theta-\beta_T}, 0, 1\right)$ $\lambda_{T,2} = b+\theta-\beta_T,\ \ v_{T,2} = (1,0,0)$ $\lambda_{T,3} = \beta_Q - (b-\mu),\ \ v_{T,3} = \left(\frac{(b+\theta-\beta_T)(\alpha\beta_Q+\beta_Q^2+\alpha\beta_T+\beta_Q\beta_T-\beta_Q\mu)}{\beta_T(-2b+\beta_Q+\beta_T-\theta-\mu)\mu}, \frac{\beta_Q+\alpha-\mu}{\mu}, 1\right)$
E_{QI}	$\lambda_{QI,1} = -\theta + \frac{\beta_T(b+\mu)}{\beta_Q} - \frac{(b+\alpha)\beta_Q-\alpha\mu}{b+\alpha+\mu},\ \ v_{QI,1} = (1,0,0)$ $\lambda_{QI,2} = -\frac{(b+\alpha)(\alpha+\beta_Q)+\sqrt{b+\alpha}\sqrt{(b+\alpha)(2b+\alpha-\beta_Q)^2+4(b+\alpha)(3b+\alpha-2\beta_Q)\mu+4(3b+2\alpha-\beta_Q)\mu^2+4\mu^3}}{2(b+\alpha+\mu)}$ $v_{QI,2} = \left(0, \frac{(b+\alpha)(2b+\alpha-\beta_Q+2\mu)-\sqrt{b+\alpha}\sqrt{(b+\alpha)(2b+\alpha-\beta_Q)^2+4(b+\alpha)(3b+\alpha-2\beta_Q)\mu+4(3b+2\alpha-\beta_Q)\mu^2+4\mu^3}}{2\mu(b+\alpha+\mu)}, 1\right)$ $\lambda_{QI,3} = -\frac{(b+\alpha)(\alpha+\beta_Q)-\sqrt{b+\alpha}\sqrt{(b+\alpha)(2b+\alpha-\beta_Q)^2+4(b+\alpha)(3b+\alpha-2\beta_Q)\mu+4(3b+2\alpha-\beta_Q)\mu^2+4\mu^3}}{2(b+\alpha+\mu)}$ $v_{QI,3} = \left(0, \frac{(b+\alpha)(2b+\alpha-\beta_Q+2\mu)+\sqrt{b+\alpha}\sqrt{(b+\alpha)(2b+\alpha-\beta_Q)^2+4(b+\alpha)(3b+\alpha-2\beta_Q)\mu+4(3b+2\alpha-\beta_Q)\mu^2+4\mu^3}}{2\mu(b+\alpha+\mu)}, 1\right)$
E_{TQI}	$\lambda_{TQI,1} = \theta - \frac{\beta_T(b+\mu)}{\beta_Q} + \frac{(b+\alpha)\beta_Q-\alpha\mu}{b+\alpha+\mu},\ \ v_{TQI,1} = (1,0,0)$ $\lambda_{TQI,2} = -\frac{(b+\alpha)(\alpha+\beta_Q)+\sqrt{b+\alpha}\sqrt{(b+\alpha)(2b+\alpha-\beta_Q)^2+4(b+\alpha)(3b+\alpha-2\beta_Q)\mu+4(3b+2\alpha-\beta_Q)\mu^2+4\mu^3}}{2(b+\alpha+\mu)}$ $v_{TQI,2} = \Big(-\frac{((b+\alpha)(b\beta_T-\beta_Q(\beta_Q+\theta))+(2b\beta_T+\alpha(\beta_Q+\beta_T)-\beta_Q\theta)\mu+\beta_T\mu^2)}{\beta_T\mu(b+\alpha+\mu)} \times$ $\times \frac{-b(3\alpha-\beta_Q)(\beta_Q+\beta_T)+\alpha\beta_Q(\beta_Q+\beta_T)-2b(\beta_Q+2\beta_T)\mu-2\alpha(\beta_Q+2\beta_T)\mu-2\beta_T\mu^2+(\beta_Q+\beta_T)\left(\sqrt{A}-2b^2-\alpha^2\right)}{\alpha^2\beta_Q-2b^2\beta_T+\alpha\beta_Q(3\beta_Q+2\theta)-2\alpha(\beta_Q+\beta_T)\mu+2\beta_Q\theta\mu-2\beta_T\mu^2+b\left(3\beta_Q^2+\alpha(\beta_Q-2\beta_T)+2\beta_Q\theta-4\beta_T\mu\right)+\beta_Q\sqrt{A}}, \ \frac{(b+\alpha)(2b+\alpha-\beta_Q+2\mu)-\sqrt{A}}{2\mu(b+\alpha+\mu)}, 1\Big)$ $\lambda_{TQI,3} = -\frac{(b+\alpha)(\alpha+\beta_Q)-\sqrt{b+\alpha}\sqrt{(b+\alpha)(2b+\alpha-\beta_Q)^2+4(b+\alpha)(3b+\alpha-2\beta_Q)\mu+4(3b+2\alpha-\beta_Q)\mu^2+4\mu^3}}{2(b+\alpha+\mu)}$ $v_{TQI,3} = \Big(\frac{((b+\alpha)(b\beta_T-\beta_Q(\beta_Q+\theta))+(2b\beta_T+\alpha(\beta_Q+\beta_T)-\beta_Q\theta)\mu+\beta_T\mu^2)}{\beta_T\mu(b+\alpha+\mu)} \times$ $\times \frac{b(3\alpha-\beta_Q)(\beta_Q+\beta_T)-\alpha\beta_Q(\beta_Q+\beta_T)+2b(\beta_Q+2\beta_T)\mu+2\alpha(\beta_Q+2\beta_T)\mu+2\beta_T\mu^2+(\beta_Q+\beta_T)\left(\sqrt{A}+2b^2+\alpha^2\right)}{\alpha^2\beta_Q-2b^2\beta_T+\alpha\beta_Q(3\beta_Q+2\theta)-2\alpha(\beta_Q+\beta_T)\mu+2\beta_Q\theta\mu-2\beta_T\mu^2+b\left(3\beta_Q^2+\alpha(\beta_Q-2\beta_T)+2\beta_Q\theta-4\beta_T\mu\right)-\beta_Q\sqrt{A}}, \ \frac{(b+\alpha)(2b+\alpha-\beta_Q+2\mu)+\sqrt{A}}{2\mu(b+\alpha+\mu)}, 1\Big)$ with $A = (b+\alpha)\left((b+\alpha)(2b+\alpha-\beta_Q)^2 + 4(b+\alpha)(3b+\alpha-2\beta_Q)\mu + 4(3b+2\alpha-\beta_Q)\mu^2 + 4\mu^3\right)$

Table 7.1. Equilibria, eigenvalues and eigenvectors

References

[1] P. Brouqui and D. Raoult, Arthropod-Borne Diseases in Homeless, *Ann. N.Y. Acad. Sci.*, **1078** (2006), 223–235.

[2] A. Dénes and G. Röst, Global dynamics for the spread of ectoparasite-borne diseases, *Nonlinear Anal. Real World Appl.*, **18** (2014), 100–107.

[3] A. Dénes and G. Röst, Structure of the global attractors in a model for ectoparasite-borne diseases, *Biomath*, **1** (2012), Article ID A016 (1–5).

[4] H. Dulac, Recherche des cycles limites, *C. R. Acad. Sci. Paris*, **204** (1937), 1703–1706.

[5] L. Houhamdi, P. Parola and D. Raoult, Les poux et les maladies transmises à l'homme, *Med. Trop.*, **65** (2005), 13–23.

[6] H. L. Smith and H. R. Thieme, *Dynamical Systems and Population Persistence*, Graduate Studies in Mathematics **118**, Amer. Math. Soc., Providence, 2011.

[7] J. P. LaSalle and S. Lefschetz, *Stability by Liapunov's direct method, with applications*, Mathematics in Science and Engineering **4**, Academic Press, New York, 1961.

A. Dénes, Bolyai Institute, University of Szeged, Aradi vértanúk tere 1., Szeged, H-6720, Hungary; *e-mail*: denesa@math.u-szeged.hu

G. Röst, Bolyai Institute, University of Szeged, Aradi vértanúk tere 1., Szeged, H-6720, Hungary; *e-mail*: rost@math.u-szeged.hu