



Global dynamics for the spread of ectoparasite-borne diseases



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ABSTRACT

A mathematical model is introduced to simultaneously study the dynamics of ectoparasite infestation and infectious diseases spread by those ectoparasites. The system has four potential equilibria. We identify three reproduction numbers that determine whether the infectious or the non-infectious parasites can invade the population, and whether a population already infested by non-infectious parasites can be invaded by the infection. By using Lyapunov functions and persistence theory, we show that the solutions always converge to one of the equilibria, depending on those three reproduction numbers. Hence the global dynamics is completely characterized by the reproduction numbers.

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1. Introduction

Ectoparasite infestations are widespread in several regions of the world, and these parasites may also be vectors for various diseases [1,2]. The transmission mechanism of these diseases is different from mosquito-borne diseases (e.g. malaria, West Nile virus), as they are transmitted through the human contact network.

Lice have been recognized as human parasites for a very long time, and they are now increasingly present in developed countries especially in homeless people or economically deprived population. Three of the more than 3000 louse species affect humans: *Pediculus humanus capitis* (head lice), *Pediculus humanus humanus* (body lice), and *Phthirus pubis* (pubic lice). *P. humanus capitis* affects all levels of society, *P. pubis* is transmitted sexually, and *P. humanus humanus* is associated with lack of hygiene and extreme poverty. The transmission of lice needs a close body-to-body connection, thus crowded environments usually facilitate infestation, especially when hygienic standards are lacking. We know three louse-borne diseases: trench fever, first described during World War I and caused by *B. quintana*, epidemic typhus caused by *R. prowazekii*, and relapsing fever caused by the spirochaete *B. recurrentis*.

Fleas are also widespread in the whole world. Flea species are not adapted to a specific host and may occasionally bite humans. Most common fleas that parasite humans are the cat, the rat, and the human fleas, *Ctenocephalides felis*, *Xenopsylla cheopis*, and *Pulex irritans*, respectively. Fleas transmit plague (spread by *Xenopsylla cheopis*, *Pulex irritans*), murine typhus (spread by *Xenopsylla cheopis*), flea-borne spotted rickettsiosis (*Rickettsia felis*, spread by *Ctenocephalides felis*, *Pulex irritans*), and maybe cat scratch disease (*Bartonella henselae*, spread by *Ctenocephalides felis*). There are diseases (such as rickettsialpox) that can be transmitted by mites.

For more information on louse, flea and mite species and the diseases transmitted by them, see [1,2] and references thereof.

The purpose of this paper is to establish and analyse a mathematical model that monitors a population infested by infectious and non-infectious parasites. We identify threshold quantities that determine whether the parasites can invade the population, and describe the asymptotic behaviour of solutions.

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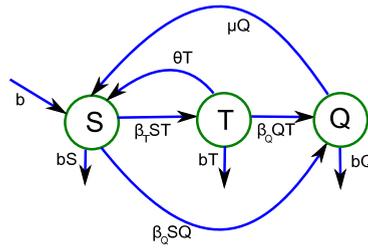


Fig. 1. Transmission diagram.

2. Derivation of the model

In our model we assume the presence of one ectoparasite species (for example lice) which is a vector for a disease as well and transmitted to a susceptible host only upon adequate contact with an infested host.

We divide a population into three compartments depending on the presence of the vectors and the disease transmitted by them: susceptibles (i.e. those who can be infested by the vector, denoted by $S(t)$), those who are infested by non-infectious vectors (denoted by $T(t)$) and those who are infested by infectious vectors, and thus infected with the disease (denoted by $Q(t)$). We have the following assumptions for the transmission of the parasites and the disease: someone infested by non-infectious vectors can transmit the parasites to susceptibles, while an individual infested by infectious vectors can transmit both the parasites and the disease to susceptibles. An individual infested by infectious vectors can transmit the infection to individuals infested by non-infectious vectors, i.e. a member of compartment T can move to compartment Q upon adequate contact with someone from compartment Q . We assume that a person is infected by the disease if and only if he is infested by infectious parasites. We assume that individuals infested by infected parasites transmit the disease at the same rate to susceptibles and to those who are already infested by non-infected parasites. Denote this transmission rate by β_Q , and denote the transmission rate for non-infectious vectors (to susceptibles) by β_T . The rate of disinfection is denoted by μ for the infested compartment and by θ for the non-infected compartment. We denote by b the natural birth and death rates, and we assume the disease is not fatal, thus the population size is constant. In the model equations we use mass action incidence (note that for constant population size it does not differ from standard incidence).

Then we have the following system of differential equations, where all the parameters are assumed to be positive:

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

The transmission chart of the model is depicted in Fig. 1. It is easy to see that any solution with nonnegative initial values remains nonnegative for all forward time. Without loss of generality, we can assume that the total population $N(t) = S(t) + T(t) + Q(t) = 1$.

3. Equilibria, reproduction numbers

By solving the algebraic equations

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

we can determine the four equilibria of system (1), one of which is disease- and infestation-free, one is disease-free with infestation, one is endemic where all vectors are infectious, and one is endemic where both infectious and non-infectious vectors are present:

$$\begin{aligned}
 E_S &= (1, 0, 0), \\
 E_T &= \left(\frac{b + \theta}{\beta_T}, 1 - \frac{b + \theta}{\beta_T}, 0 \right), \\
 E_Q &= \left(\frac{b + \mu}{\beta_Q}, 0, 1 - \frac{b + \mu}{\beta_Q} \right), \\
 E_{QT} &= \left(\frac{\theta - \mu + \beta_Q}{\beta_T}, \frac{b + \mu}{\beta_Q} - \frac{\theta - \mu + \beta_Q}{\beta_T}, 1 - \frac{b + \mu}{\beta_Q} \right).
 \end{aligned}$$

Due to the biological interpretation of the model, we are only interested in nonnegative equilibria. In the sequel, we say that a given equilibrium exists, if each of its three coordinates is between 0 and 1.

We can determine four reproduction numbers by introducing a single infested (infectious or non-infectious) individual into a population in which neither infected and non-infected parasites are present (E_S), only non-infected parasites are present (E_T) or only infected parasites are present (E_Q), and calculating the expected number of generated secondary cases.

If we introduce an infested, non-infectious individual into the disease- and infestation-free equilibrium, we obtain the reproduction number

$$R_1 = \frac{\beta_T}{b + \theta},$$

by introducing an infested and infectious individual into the same equilibrium we obtain the reproduction number

$$R_2 = \frac{\beta_Q}{b + \mu}.$$

Calculating the expected number of secondary infections caused by the introduction of an infectious infested individual into a population in the equilibrium E_T , we obtain the same reproduction number R_2 , as the transmission rate from Q -individuals is the same for the S - and T -compartment.

Now introduce a non-infectious infested individual into a population in the equilibrium E_Q . 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 $\beta_T S^*$. Taking the product of these two expressions and substituting the values of Q^* and S^* at the equilibrium E_Q , we obtain the reproduction number

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

We shall use later the fact that $R_2 \geq 1$ implies $R_3 > 0$. Indeed, $R_2 \geq 1$ is equivalent with $\beta_Q \geq b + \mu$, so in this case obviously $\beta_Q + \theta > \mu$ and thus $R_3 > 0$.

In the next proposition we show how the reproduction numbers determine the existence of the four equilibria.

Proposition 3.1. *The equilibrium E_S always exists. The equilibrium E_T exists if and only if $R_1 > 1$. The equilibrium E_Q exists if and only if $R_2 > 1$. The equilibrium E_{QT} 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 $R_1 > 1$. If this holds, also the second coordinate of this equilibrium is between 0 and 1. Similarly, we have that E_Q exists if and only if $R_2 > 1$. In the case of the equilibrium E_{QT} , the third coordinate being between 0 and 1 is equivalent to $R_2 > 1$. If $R_2 > 1$, then the second coordinate being positive is equivalent to $R_3 > 1$. Thus for the existence of E_{QT} , it is necessary that $R_2 > 1$ and $R_3 > 1$. To see the sufficiency, notice that $(R_2 R_3)^{-1} = (\beta_Q - \mu + \theta)/\beta_T$, which is the first coordinate, thus if $R_2 > 1$ and $R_3 > 1$ then all three coordinates of E_{QT} are between 0 and 1. \square

4. Local stability, persistence

Proposition 4.1. *The stability of equilibria is determined by the reproduction numbers as follows.*

- (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_Q is locally asymptotically stable if $R_2 > 1$ and $R_3 < 1$, and unstable if $R_3 > 1$.
- (iv) E_{QT} is locally asymptotically stable if $R_2 > 1$ and $R_3 > 1$ (i.e. always when it exists).

Proof. Calculating the eigenvalues of the Jacobian of the linearization at equilibria is straightforward, hence omitted, here we only discuss the consequences.

- (i) The eigenvalues of the Jacobian of the linearized equation around the equilibrium E_S are $-b$, $-b - \theta + \beta_T = (b + \theta)(R_1 - 1)$ and $-b - \mu + \beta_Q = (b + \mu)(R_2 - 1)$. All of these eigenvalues are negative if $R_1 < 1$ and $R_2 < 1$, and there is a positive one if $R_1 > 1$ or $R_2 > 1$.
- (ii) Linearizing at the equilibrium E_T , one finds the eigenvalues $-b$, $b + \theta - \beta_T = (b + \theta)(1 - R_1)$, $-b - \mu + \beta_Q = (b + \mu)(R_2 - 1)$. The statement follows as in case (i).
- (iii) Linearization around the steady state E_Q gives the following eigenvalues of the Jacobian: $-b$, $b + \mu - \beta_Q = (b + \mu)(1 - R_2)$, $-\theta + \mu - \beta_Q + (b + \mu)\beta_T/\beta_Q = (R_3 - 1)\beta_T/(R_2 R_3)$. If $R_2 < 1$ then E_Q does not exist, if $R_3 > 1$ then the third eigenvalue is positive. If $R_3 < 1$ then the second eigenvalue is negative, and the third eigenvalue is also negative since in this case from $R_2 > 1$ (which required for the existence of E_Q) we know that $R_3 > 0$.
- (iv) Finally, if we linearize the system around the equilibrium E_{QT} , we obtain the eigenvalues $-b$, $b + \mu - \beta_Q = (b + \mu)(1 - R_2)$ and $\theta - \mu + \beta_Q - (b + \mu)\beta_T/\beta_Q = (1 - R_3)\beta_T/(R_2 R_3)$, and the conclusion follows as in case (iii). \square

For the proof of persistence we use some notions and theorems from [3].

Definition 4.2. Let X be a nonempty set and $\rho : X \rightarrow \mathbb{R}_+$. A semiflow $\Phi : \mathbb{R}_+ \times X \rightarrow X$ is called *uniformly weakly ρ -persistent*, if there exists some $\varepsilon > 0$ such that

$$\limsup_{t \rightarrow \infty} \rho(\Phi(t, x)) > \varepsilon \quad \forall x \in X, \rho(x) > 0.$$

Φ is called *uniformly (strongly) ρ -persistent* if there exists some $\varepsilon > 0$ such that

$$\liminf_{t \rightarrow \infty} \rho(\Phi(t, x)) > \varepsilon \quad \forall x \in X, \rho(x) > 0.$$

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

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

$$X := \{(S, T, Q) \in \mathbb{R}_+^3 : S + T + Q = 1\} \subset \mathbb{R}_+^3.$$

Theorem 4.3. $S(t)$ 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 $R_3 > 1$. $Q(t)$ is uniformly persistent if $R_2 > 1$.

Proof. To prove the persistence of $S(t)$ we use the method of fluctuation (see for example Appendix A of [3]). Let S_∞ denote the limit inferior of $S(t)$ as $t \rightarrow \infty$. From the fluctuation lemma we know that there exists a sequence $t_k \rightarrow \infty$ such that $S(t_k) \rightarrow S_\infty$ and $S'(t_k) \rightarrow 0$ as $k \rightarrow \infty$. Using this for the first equation of our system,

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

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

$$(\beta_T + \beta_Q + b)S_\infty \geq b,$$

i.e.

$$S_\infty \geq \frac{b}{\beta_T + \beta_Q + b} > 0.$$

In proving the persistence of $T(t)$ and $Q(t)$ we will use some theory from [3]. For the sake of simplicity, for the state of the system we use the notation $x = (S, T, Q) \in X$. The ω -limit set of a point $x \in X$ is defined in the usual way by

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

Let us first suppose that $R_1 > 1$ and $R_2 < 1$ hold and let $\rho(x) = T$. Consider the extinction space

$$X_T := \{x \in X : \rho(x) = 0\} = \{(S, 0, Q) \in \mathbb{R}_+^3 : S + Q = 1\}.$$

Clearly X_T is invariant. Following [3, Chapter 8], we examine the set $\Omega := \cup_{x \in X_T} \omega(x)$. Since X_T is a one-dimensional closed segment and the solutions are bounded, $\Omega = \{E_S\}$. First we show weak ρ -persistence. To apply Theorem 8.17 of [3], we let $M_1 = \{E_S\}$. Then $\Omega \subset M_1$, and M_1 is isolated (by Proposition 4.1), compact, invariant and acyclic. It remained to show that M_1 is weakly ρ -repelling, then by [3, Chapter 8], the weak persistence follows.

Suppose that M_1 is not ρ -repelling, i.e. there exists a solution such that $\lim_{t \rightarrow \infty} (S(t), T(t), Q(t)) = (1, 0, 0)$ and $T(t) > 0$. Then for any $\varepsilon > 0$, for sufficiently large t , $S(t) > 1 - \varepsilon$ and $Q(t) < \varepsilon$ hold and we can give the following estimation for $T'(t)$:

$$T'(t) = T(t)(\beta_T S(t) - \beta_Q Q(t) - \theta - b) > T(t)(\beta_T - \beta_T \varepsilon - \beta_Q \varepsilon - \theta - b).$$

As $\beta_T > b + \theta$, if ε is small enough then $\beta_T - \beta_T \varepsilon - \beta_Q \varepsilon - \theta - b > 0$, contradicting to $T(t) \rightarrow 0$.

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_Q exists, so $\Omega = \{E_S, E_Q\}$. We let $M_1 = \{E_S\}$ and $M_2 = \{E_Q\}$. 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 $\lim_{t \rightarrow \infty} (S(t), T(t), Q(t)) = (1, 0, 0)$ and $T(t) > 0$. From

$$R_2 = \frac{\beta_Q}{b + \mu} > 1 \quad \text{and} \quad R_3 = \frac{\beta_T(b + \mu)}{\beta_Q(\beta_Q + \theta - \mu)} > 1$$

we have

$$R_2 R_3 = \frac{\beta_T}{\beta_Q + \theta - \mu} > 1,$$

i.e. $\beta_T > \beta_Q + \theta - \mu$. 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 $T'(t)$:

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

for ε small enough, as $R_2 > 1$, contradicting to $T(t) \rightarrow 0$.

To show the repelling property of M_2 , assume that there exists a solution such that

$$\lim_{t \rightarrow \infty} (S(t), T(t), Q(t)) = \left(\frac{b + \mu}{\beta_Q}, 0, 1 - \frac{b + \mu}{\beta_Q} \right)$$

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

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

as from the inequality $R_3 > 1$, for sufficiently small ε we have

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

contradicting to $T(t) \rightarrow 0$.

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

$$X_Q := \{x \in X : \rho(x) = 0\} = \{(S, T, 0) \in \mathbb{R}_+^3 : S + T = 1\},$$

i.e. in this case we have

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

if $R_1 \leq 1$, and

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

if $R_1 > 1$, where

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

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 ρ -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 $\lim_{t \rightarrow \infty} (S(t), T(t), Q(t)) = (1, 0, 0)$ 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 $Q(t) \rightarrow 0$.

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

$$\lim_{t \rightarrow \infty} (S(t), T(t), Q(t)) = \left(\frac{b + \theta}{\beta_T}, 1 - \frac{b + \theta}{\beta_T}, 0 \right)$$

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 $Q'(t)$:

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

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

We have proved uniform weak persistence in all of the cases, and for the transition to uniform (strong) persistence, we use [3, 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 [3, Theorem 4.5] hold. \square

5. Global stability

In this section we extend the statements about local stability in the previous section 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 5.1. *Equilibrium E_S is globally asymptotically stable if $R_1 \leq 1$ and $R_2 \leq 1$.*

Proof. Let us choose $V_1(S, T, Q) = T + Q$ 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 [4] we know that the limit set of each solution is a subset of the set $V_1 = 0$. 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, from this we have that $T = Q = 0$. Similarly, the second term is equal to zero if $Q = 0$ or $S = (b + \mu)/\beta_Q$. The latter case only holds if $(b + \mu)/\beta_Q = S = 1$. The remaining possibility for $\dot{V} = 0$ is that $T = Q = 0$. Thus, the limit set of any solution is the equilibrium E_S . \square

Theorem 5.2. *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. Let us choose the Lyapunov function $V_2(S, T, Q) = Q^2$. The derivative of this Lyapunov function along the solutions is

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

which is less than or equal to zero as $R_2 \leq 1$ and $S + T \leq 1$. We have $\dot{V}_2 = 0$ if $Q = 0$ or $(b + \mu)/\beta_Q - (S + T) = 0$. The latter can hold only if $R_2 = 1$ and $S + T = 1$, which implies $Q = 0$. Thus, \dot{V}_2 is equal to zero if and only if $Q = 0$. Using LaSalle’s invariance principle we have that the limit set of each solution is a subset of the set $V_2 = 0$.

For $Q = 0$ the equations for S and T have the form

$$\begin{aligned} S'(t) &= -\beta_T S(t)T(t) + \theta T(t) + b - bS(t) \\ T'(t) &= \beta_T S(t)T(t) - \theta T(t) - bT(t). \end{aligned} \tag{2}$$

This system has two equilibria, the unstable equilibrium $(1, 0)$ and 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 $T < 1 - (b + \theta)/\beta_T$. From this follows the assertion of the theorem. \square

Theorem 5.3. *Assume $R_2 > 1$. Then the following statements hold:*

- (i) *If $R_3 \leq 1$ and $R_1 \leq 1$, then E_Q 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_Q 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_{QT} is globally asymptotically stable on $X \setminus (X_Q \cup X_T)$, E_T is globally asymptotically stable on X_Q and E_Q is globally asymptotically stable on X_T .*

Proof. In proving all three statements, we apply the Lyapunov function

$$V_3(S, T, Q) = \left(Q - \left(1 - \frac{b + \mu}{\beta_Q} \right) \right)^2.$$

The derivative of this Lyapunov function along solutions of (1) is

$$\begin{aligned} \dot{V}_3 &= -2Q\beta_Q \left(\frac{b + \mu}{\beta_Q} - (S + T) \right) \left(\frac{b + \mu}{\beta_Q} - 1 + Q \right) \\ &= -2Q\beta_Q \left(\frac{b + \mu}{\beta_Q} - 1 + Q \right)^2 \leq 0. \end{aligned}$$

Again we use LaSalle’s invariance principle. This derivative is equal to zero if and only if $Q = 0$ or $Q = 1 - (b + \mu)/\beta_Q$. If $Q = 0$, then from the Eq. (2) we get that E_S is globally asymptotically stable on the extinction space X_Q if $R_1 \leq 1$ and E_T is globally asymptotically stable on X_Q if $R_1 > 1$. If $Q > 0$, then, using the persistence result of the previous section we have that $Q > 0$ holds also on the limit set. From this follows that for any solution of (1) in $X \setminus X_Q$ $\lim_{t \rightarrow \infty} Q(t) = 1 - (b + \mu)/\beta_Q > 0$ if $R_2 > 1$.

On the limit set, the solutions satisfy

$$S'(t) = -\beta_T S(t)T(t) - \beta_Q S(t) \left(1 - \frac{b + \mu}{\beta_Q}\right) + \theta T(t) + \mu \left(1 - \frac{b + \mu}{\beta_Q}\right) + b - bS(t),$$

$$T'(t) = \beta_T S(t)T(t) - \beta_Q \left(1 - \frac{b + \mu}{\beta_Q}\right) T(t) - \theta T(t) - bT(t),$$

$$0 = \left(1 - \frac{b + \mu}{\beta_Q}\right) (\beta_Q S(t) + \beta_Q T(t) - \mu - b).$$

From the last of these equations we obtain that $\beta_Q S(t) + \beta_Q T(t) - \mu - b = 0$, i.e. $S(t) = (b + \mu)/\beta_Q - T(t)$ holds on the limit set. Substituting this expression for S into the equation for T' we obtain

$$\begin{aligned} T'(t) &= \beta_T \left(\frac{b + \mu}{\beta_Q} - T(t)\right) T(t) - \beta_Q \left(1 - \frac{b + \mu}{\beta_Q}\right) T(t) - \theta T(t) - bT(t) \\ &= -\beta_T T^2(t) + \gamma T(t) \end{aligned}$$

on the limit set, where

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

The solution started from $T(0) = 0$ is the function $T(t) \equiv 0$. The nontrivial solutions of this logistic equation have the form

$$T(t) = \frac{\gamma C e^{\gamma t}}{\beta_T C e^{\gamma t} + 1}$$

for $C \in \mathbb{R}_+$. Notice that $\gamma > 0$ if and only if $R_3 > 1$. Therefore, if $R_3 \leq 1$ then on $X \setminus X_Q$ we have $\lim_{t \rightarrow \infty} T(t) = 0$, thus $\lim_{t \rightarrow \infty} S(t) = (b + \mu)/\beta_Q$, and we obtain the convergence to E_Q . On X_Q our system is reduced to (2), and for $R_1 > 1$ we have that E_T , while for $R_1 \leq 1$ we have that E_S is globally asymptotically stable on X_Q . We proved (i) and (ii).

If $R_3 > 1$ then

$$\lim_{t \rightarrow \infty} T(t) = \frac{\gamma}{\beta_T} = \frac{\mu - \theta - \beta_Q}{\beta_T} + \frac{b + \mu}{\beta_Q},$$

so on $X \setminus (X_Q \cup X_T)$, both $Q(t)$ and $T(t)$ converge to the corresponding coordinates of E_{QT} . On X_T , we have $S(t) = (b + \mu)/\beta_Q$ on the limit set, thus solutions converge to E_Q . If $R_3 > 1$ and $R_2 > 1$ then

$$1 < R_2 R_3 = R_1 \frac{b + \theta}{R_2(b + \mu) + \theta - \mu} < R_1,$$

and for $R_1 > 1$ we already established the global asymptotic stability of E_T on X_Q . The proof of (iii) is complete. \square

6. Discussion

We established a system of differential equations for the simultaneous modelling of the spread of an ectoparasite and a disease transmitted by it. We calculated three reproduction numbers and four potential equilibria of the system. The reproduction numbers R_i ($i = 1, 2, 3$) determine whether the infectious or the non-infectious parasites can invade the population, and whether a population already infested by non-infectious parasites can be invaded by the infection. By using Lyapunov functions and persistence theory, we showed that the solutions always converge to one of the equilibria, depending on those three reproduction numbers. The results are summarized in Table 1. Depending on $R_i \leq 1$ or $R_i > 1$ for $i = 1, 2, 3$, there are eight possible scenarios. Cases (a) and (b) include four of them. We showed that $R_2 > 1$ and $R_3 > 1$ imply $R_1 > 1$ (see the proof of Theorem 5.3), so one of the eight cases can be excluded. The remaining three possibilities are covered by (c), (d) and (e). Therefore we provide a complete characterization of the global dynamics in each possible scenario. We proved the global asymptotic stability of one of the equilibria in all of the five different cases by giving three Lyapunov functions. Depending on the reproduction numbers, we can determine which of the four equilibria is globally asymptotically stable. Each of the five cases can be realized as we illustrate the dynamics on the TQ -plane in Fig. 2. From our results we can see that to eradicate the disease, we have to decrease R_2 to be less than 1, which is possible by reducing β_Q or increasing μ . If we also want to eliminate the parasites, then besides decreasing R_2 , we also have to decrease R_1 (possible by reducing β_T or increasing θ). Decreasing only R_1 is not enough for the elimination of the parasites. The reproduction number R_3 is a threshold parameter which, in the case when the parasites persist, shows whether all of them become infectious or not.

It is natural to ask what happens if we incorporate disease induced mortality in our model. In this case the equation for $Q(t)$ has the form

$$Q'(t) = \beta_Q S(t)Q(t) + \beta_Q Q(t)T(t) - \mu Q(t) - bQ(t) - dQ(t),$$

Table 1
 Reproduction numbers and global stability: the complete characterization of the dynamics.

| Case | Reproduction numbers | Existing equilibria | Global stability |
|------|-----------------------------------|-------------------------|--|
| (a) | $R_1 \leq 1, R_2 \leq 1$ | E_S | E_S GAS |
| (b) | $R_1 > 1, R_2 \leq 1$ | E_S, E_T | E_T GAS on $X \setminus X_T$, E_S GAS on X_T |
| (c) | $R_1 \leq 1, R_2 > 1, R_3 \leq 1$ | E_S, E_Q | E_Q GAS on $X \setminus X_Q$, E_S GAS on X_Q |
| (d) | $R_1 > 1, R_2 > 1, R_3 \leq 1$ | E_S, E_T, E_Q | E_Q GAS on $X \setminus X_Q$, E_T GAS on X_Q |
| (e) | $R_1 > 1, R_2 > 1, R_3 > 1$ | E_S, E_T, E_Q, E_{QT} | E_{QT} GAS on $X \setminus (X_Q \cup X_T)$, E_T GAS on X_Q , E_Q GAS on X_T |

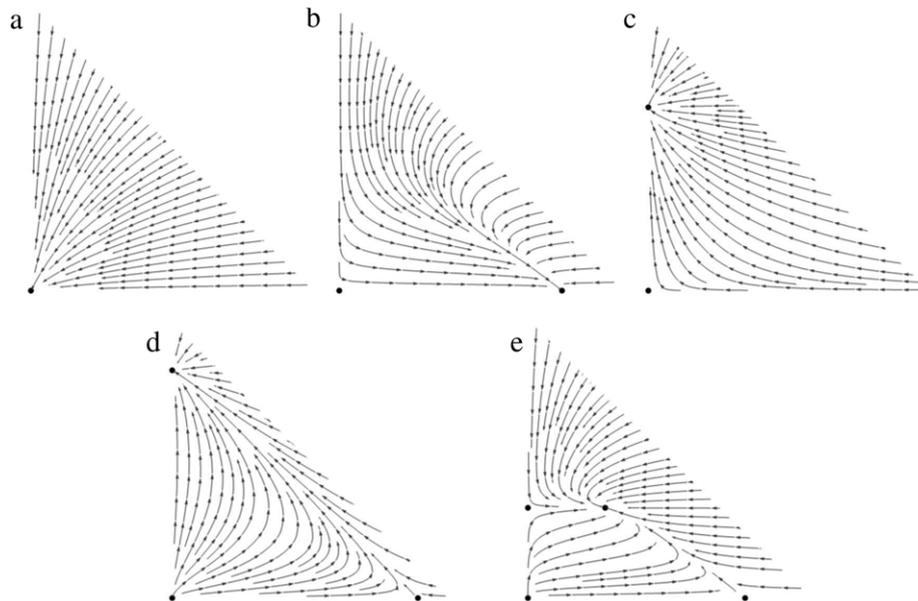


Fig. 2. Representation of the flow on the TQ -plane in the five cases (see Table 1). Dots denote equilibria.

where $d > 0$ denotes the excess mortality caused by the disease. Introducing d makes R_2 smaller, thus, disease mortality facilitates the elimination of the disease. On the other hand, if $Q(t)$ is persistent, then disease mortality reduces the total population in the long run. Numerical simulations suggest that the qualitative behaviour of the solutions of the modified model is similar to system (1). Some of our proofs can be performed in a similar, but more intricate way, however, as the total population is not constant any more, we cannot make the reduction to a planar system. As a consequence, one needs completely new proofs for some global stability results such as the ones in Theorem 5.3. We leave this problem as a future work.

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