Impact of Excess Mortality on the Dynamics of Diseases Spread by Ectoparasites

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Abstract In this chapter, we generalize our earlier model for the spread of ectoparasites and diseases transmitted by them by including disease-induced mortality. The qualitative behavior of the system is similar to that of the original model: three reproduction numbers determine which of the four possible equilibria is globally asymptotically stable. We conclude that a moderate mortality decreases the size of the population, while a high mortality leads to the eradication of the infection. The main tools used for the proofs include persistence theory, Lyapunov–LaSalle theory and Dulac's criteria.

1 Introduction, Basic Properties of the Model

Ectoparasites are present in several regions of the world. Besides the problems caused by the infestation, they are also responsible for the transmission of several diseases like relapsing fever or murine typhus (for details see, e.g., [1]). The spread of these diseases is different from other vector-borne diseases, as in this case, the vectors themselves are transmitted like a disease through the human contact network. In [2], we established a basic model for the spread of ectoparasites and diseases transmitted by them and completely described the global dynamics of the model. Our basic model does not include disease mortality, however, as several ectoparasite-borne diseases are lethal (e.g., epidemic typhus or plague), it is a natural question to ask what happens if we also incorporate disease-induced mortality. In this chapter, we study the model with disease-induced mortality showing that the modified system has a similar behavior as the original one. Some of the proofs in [2] can be applied in an analogous way, however, several of them need some additional ideas or completely different methods.

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The present model is for one ectoparasite species, which might be a vector for a disease as well. The population is divided into three compartments: susceptibles (i.e., those who are not infested, denoted by $S(t)$), those who are infested by noninfectious parasites ($T(t)$) and those who are infested by infectious parasites ($Q(t)$). In the following, we will call an individual from compartment S (resp. T, Q) an S- (resp. T-, Q-) individual. A T-individual might infest an S-individual with noninfectious parasites, while a Q-individual might infest an S-individual or a T-individual with parasites which carry the disease. We assume that a person is infected by the disease, if and only if, he is infested by infectious parasites. We denote the transmission rate from Q to S and T by β_Q, while β_T stands for the transmission rate from T to S. The disinfestation rate is denoted by θ for compartment T and by μ for compartment Q. We denote by b the recruitment and removal rate, and d denotes disease-induced mortality. With these assumptions we obtain the following system of differential equations:

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

It is easy to see that all solutions are bounded and solutions with nonnegative initial values remain nonnegative.

Letting $S^* = \frac{(b+d)\theta - b\mu + b\beta_Q}{(b+d)\beta_T}$, the four equilibria can be calculated as:

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

By introducing a single infested, respectively, infested and infected individual into one of the equilibria E_S, E_T, and E_Q, we obtain three different reproduction numbers. By introducing a T-, resp. Q-individual into E_S, we get the reproduction numbers

$$
R_1 = \frac{\beta_T}{b+\theta}, \text{ resp. } R_2 = \frac{\beta_Q}{b+d+\mu}.
\tag{2}
$$

If we introduce a Q-individual into E_T, we get the same reproduction number R_2 again. Finally, by introducing a T-individual into E_Q, we obtain the reproduction number

$$
R_3 = \frac{\beta_T(b+d)(b+d+\mu)}{\beta_Q(b(\beta_Q+\theta-\mu)+d\theta)}.
\tag{3}
$$

The following proposition can easily be checked.

Proposition 1 *Equilibrium E_S always exists. Equilibrium E_T exists if and only if $R_1 > 1$. Equilibrium E_Q exists if and only if $R_2 > 1$. Equilibrium E_{QT} exists if and only if $R_2 > 1$ and $R_3 > 1$.*

Proposition 2 *Local stability of the four possible equilibria is determined by the reproduction numbers in the following way.*

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

(ii) *E_T is LAS if $R_1 > 1$ and $R_2 < 1$, and unstable if $R_2 > 1$.*

(iii) *E_Q is LAS if $R_2 > 1$ and $R_3 < 1$, and unstable if $R_3 > 1$.*

(iv) *E_{QT} is LAS if $R_2 > 1$ and $R_3 > 1$ (i.e., always when it exists).*

Proof (i) Calculating the eigenvalues of the Jacobian of the linearized equation around the equilibrium E_S we obtain $\lambda_{S_1} = -b$, $\lambda_{S_2} = -b - \theta + \beta_T = (b+\theta)(R_1 - 1)$, and $\lambda_{S_3} = -b - d - \mu + \beta_Q = (b + d + \mu)(R_2 - 1)$. All of the eigenvalues are negative if $R_1 < 1$ and $R_2 < 1$, while at least one of them is positive if $R_1 > 1$ or $R_2 > 1$.

(ii) If we linearize around the equilibrium E_T, we find the eigenvalues $\lambda_{T_1} = \lambda_{S_1}$, $\lambda_{T_2} = -\lambda_{S_2}$, and $\lambda_{T_3} = \lambda_{S_3}$, thus we can argue similarly as in case (i).

(iii) Linearization around the equilibrium E_Q yields the three eigenvalues $\lambda_{Q_1} = B(\mu - \beta_Q)/(b + d) + (b + d + \mu)\beta_T/\beta_Q - \theta$ and

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

$R_2 > 1$ is needed for the existence of E_Q. If we add the terms in λ_{Q_1}, it is easy to see 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 $R_3 < 1$. The absolute value of the term under the square root in the nominator of λ_{Q_2}, resp. λ_{Q_3} is less than that of the first term which itself is negative as $\beta_Q > \mu$ follows from $R_2 > 1$. Thus, the last two eigenvalues always have negative real parts if $R_2 > 1$.

(iv) Linearizing around E_{QT}, we get the eigenvalues $\lambda_{QT_1} = -\lambda_{Q_1}$, $\lambda_{QT_2} = \lambda_{Q_2}$, and $\lambda_{QT_3} = \lambda_{Q_3}$, from which the assertion follows.   □

2 Persistence and Global Stability

We shall use some notions and theorems from [3].

Definition 1 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

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

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

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

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

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

Proof The proof of the first assertion can be performed similarly as in [2, Theorem 4.3]. To prove the assertions about the persistence of $T(t)$ and $Q(t)$, we need some further theory from [3].

For the state of the system, we will use the notation $x = (S, T, Q) \in X$. We define the ω-limit set of a point $x \in X$ as usual 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 $\rho(x) = T$. Consider the invariant extinction space $X_T := \{x \in X : \rho(x) = 0\} = \{(S, 0, Q) \in \mathbb{R}^3_+\}$. The case $R_1 > 1$ and $R_2 < 1$ can be handled exactly as in [2, Theorem 4.3].

Let us now suppose that $R_2 > 1$ and $R_3 > 1$ hold. Following [3, Chap. 8], we examine the set $\Omega := \cup_{x \in X_T} \omega(x)$ for which in this case we have $\Omega = \{E_S, E_Q\}$. First we show weak ρ-persistence. To apply Theorem 8.17 of [3], we let $M_1 = \{E_S\}$ and $M_2 = \{E_Q\}$. We have $\Omega \subset M_1 \cup M_2$ and $\{M_1, M_2\}$ is acyclic and M_1 and M_2 are isolated, invariant and compact. We have to show that M_1 and M_2 are weakly ρ-repelling, then by [3, Chap. 8], the weak persistence follows.

Let us first assume that M_1 is not weakly ρ-repelling, i.e., there exists a solution with $\lim_{t \to \infty}(S(t), T(t), Q(t)) = (1, 0, 0)$ such that $T(t) > 0$. By $R_2 > 1$ and $R_3 > 1$,

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

i.e., $\beta_T > \theta + (\beta_Q - \mu)b/(b+d)$. For t large enough we have $S(t) > 1 - \varepsilon$ and $Q(t) < \varepsilon$, so we can give the following estimation for $T(t)$:

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

$$> T(t)\left(\frac{b}{b+d}(\beta_Q - \mu) - \varepsilon(\beta_T + \beta_Q) - b\right)$$

$$= T(t)\left(\frac{b}{b+d}(\beta_Q - \mu - b - d) - \varepsilon(\beta_T + \beta_Q)\right),$$

which is positive for ε small enough, since $R_2 > 1$ implies $\beta_Q > \mu + b + d$, thus $T(t) \to 0$ cannot hold.

Now we assume that M_2 is not weakly ρ-repelling, thus, there exists a solution with $\lim_{t \to \infty}(S(t), T(t), Q(t)) = (b+d+\mu)/\beta_Q, 0, b(\beta_Q - b - d - \mu)/(\beta_Q(b+d))$ and $T(t) > 0$. For any ε, for t large enough we can give the following estimations for $T'(t)$:

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

$$> T(t)\left(\beta_T\left(\frac{b+d+\mu}{\beta_Q} - \varepsilon\right) - \beta_Q\left(\frac{b(\beta_Q - b - d - \mu)}{(b+d)\beta_Q} + \varepsilon\right) - \theta - b\right)$$

$$= T(t) \left(\frac{\beta_T (b + d + \mu)}{\beta_Q} - \frac{b(\beta_Q - b - d - \mu)}{b + d} - \theta - b - \varepsilon(\beta_T + \beta_Q) \right),$$

which is positive for ε small enough, since $R_3 > 1$.

The persistence of $Q(t)$ for $R_2 > 1$ can be proved using the same methods. The steps are analogous to those of the corresponding part of [2, Theorem 4.3] with only a slight modification needed.   □

Using our theorem about persistence, in this section, we show that our LAS results extend to global asymptotic stability (GAS) results.

Theorem 2 *Equilibrium E_S is GAS if $R_1 \leq 1$ and $R_2 \leq 1$.*

Proof The proof is analogous to that of [2, Theorem 5.1]   □

Theorem 3 *Equilibrium E_T is GAS 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 The proof is analogous to that of [2, Theorem 5.2]   □

Theorem 4 *Let us suppose $R_2 > 1$. Then the following statements hold:*

(i) *If $R_3 \leq 1$ and $R_1 \leq 1$, then E_Q is GAS on $X \setminus X_Q$ and E_S is GAS on X_Q where $X_Q := \{x \in X : \{(S, T, 0) \in \mathbb{R}^3_+\}$, i.e., the extinction space of Q.*
(ii) *If $R_3 \leq 1$ and $R_1 > 1$, then E_Q is GAS on $X \setminus X_Q$ and E_T is GAS on X_Q.*
(iii) *If $R_3 > 1$, then E_{QT} is GAS on $X \setminus (X_Q \cup X_T)$, E_T is GAS on X_Q, E_Q is GAS on X_T.*

Proof Let us introduce the notation $F(t) := S(t) + T(t)$. With this notation, we can transcribe system (1) to the two-dimensional system

$$F'(t) = -\beta_Q F(t) Q(t) + \mu Q(t) + b - b F(t),$$
$$Q'(t) = \beta_Q F(t) Q(t) - \mu Q(t) - b Q(t) - d Q(t). \tag{4}$$

This system has the two positive equilibria $(1, 0)$ and

$$(F^*, Q^*) := \left(\frac{b + d + \mu}{\beta_Q}, \frac{b(\beta_Q - b - d - \mu)}{\beta_Q(b + d)} \right).$$

To show that the limit of each solution of this system is one of these two equilibria, according to the Poincaré–Bendixson theorem, all we have to prove is that system (4) does not have any periodic solutions. To show this, we apply Dulac's criterion using the Dulac function $D(Q, J) = 1/Q$. We have

$$\frac{\partial}{\partial F} \frac{-\beta_Q Q F + \mu Q + b - b F}{Q} + \frac{\partial}{\partial Q} \frac{-b Q - d Q + \beta_Q F Q - \mu Q}{Q} = -\frac{b + Q\beta_Q}{Q} < 0.$$

From the previous section, we know that $Q(t)$ is persistent for $R_2 > 1$; thus, the limit of each solution started in $X \setminus X_Q$ is a subset of the set $\{x \in X : \{(S, T, Q^*) \in$

$\mathbb{R}^3_+ : S + T = F^*\}$. Thus, on the limit set the equation for $T(t)$ takes the form

$$T'(t) = \beta_T(F^* - T(t))T(t) - \beta_Q T(t)Q^* - \theta T(t) - bT(t) = -\beta_T T^2(t) + \gamma T(t),$$

where $\gamma = \beta_T F^* - \beta_Q Q^* - \theta - b$. The solution started from $T(0) = 0$ is the function $T(t) \equiv 0$. The nontrivial solutions of this logistic equation are $T(t) = \gamma C e^{\gamma t}/\beta_T C e^{\gamma t} + 1$ for $C \in \mathbb{R}_+$. It is easy to see that $\gamma > 0$ if and only if $R_3 > 1$. Thus, for $R_3 \leq 1$, $\lim_{t\to\infty} T(t) = 0$ and the limit of solutions started in $X \setminus X_Q$ is E_Q.

In the case $R_3 > 1$, we have

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

thus we obtain that the limit of solutions started in $X \setminus (X_T \cup X_Q)$ is E_{QT}. Solutions started in X_T tend to E_Q.

The limit set of solutions of Eq. (4) started in X_Q is the equilibrium $(1, 0)$. Thus, in this case, the equation for $T(t)$ on the limit set has the form $T'(t) = -\beta_T T^2(t) + \delta T(t)$ with $\delta = \beta_T - (\theta + b)$. Similarly to the previous case, the nontrivial solutions of this equation have the form $T(t) = \delta C e^{\delta t}/\beta_T C e^{\delta t} + 1$ for $C \in \mathbb{R}_+$. We have $\delta > 0$ if and only if $R_1 > 1$. Thus, for $R_1 \leq 1$, $T(t) \to 0$ $(t \to \infty)$ and the limit of solutions started in X_Q is E_S, while for $R_1 > 1$ we obtain $\lim_{t\to\infty} T(t) = \delta/\beta_T = 1 - (\theta + b)/\beta_T$, i.e., solutions started in X_Q tend to E_T. To complete the proof of the theorem, we notice that $R_2 > 1$ and $R_3 > 1$ imply $R_1 > 1$:

$$1 < R_2 R_3 = \frac{\beta_T}{b+\theta} \frac{(b+d)(b+\theta)}{d\theta + b(\beta_Q + \theta - \mu)} = R_1 \frac{b^2 + db + b\theta + d\theta}{d\theta + b\theta + b\beta_Q - b\mu} < R_1.$$

$\square$

Finally, we comment on the impact of the disease-induced mortality d. For $d = 0$ we retrieve the results of [2]. Increasing d first decreases the total population without changing the qualitative dynamics. Sufficiently large d drives R_2 below 1. In this case, the disease dies out and the persistence of the parasites is determined by R_1.

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