Dynamics of an infectious disease including fleas, rodents and humans

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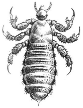
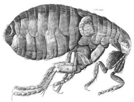
Ectoparasite-borne diseases harboured by rodents

Ectoparasites

- parasites that live on or in the skin but not within the body
- lice, fleas, mites
- long been known as vectors of several infectious diseases including epidemic typhus and plague
- in several cases, ectoparasites are transmitted to humans from animals, most often by rodents


Ectoparasite-borne diseases harboured by rodents

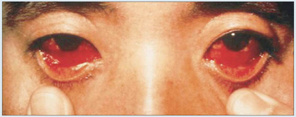
Plague

- tranmitted by fleas
- caused by the bacterium *Yersinia pestis*
- harboured by rats

Ectoparasite-borne diseases harboured by rodents

Omsk hemorrhagic fever

- tranmitted by ticks
- caused by a Flavivirus
- harboured by water voles and muskrats



Ectoparasite-borne diseases harboured by rodents

Rickettsialpox

- tranmitted by mites
- caused by caused by the bacteria *Rickettsia akari*
- harboured by mice

Murine typhus

- tranmitted by fleas
- caused by caused by the bacteria *Rickettsia typhi*
- harboured by rats

Scrub typhus

- tranmitted by trombiculid mites
- caused by the bacteria *Orientia tsutsugamushi*
- harboured by mice
- more than a million cases annually in Asia with more than a billion people being at risk

Mathematical model – assumptions

- an infectious disease caused by a pathogen spread by ectoparasites which are harboured by rodents
- ectoparasites might be infectious or non-infectious
- a given rodent/human can be infested only by one type of the ectoparasite (infectious or non-infectious)
- a human can be infested (infected) through adequate contact with an infested (infected) rodent or another human
- ectoparasites are not transmitted back from humans to the rodents
- due to disinfestation and/or treatment, infested and infected humans may become susceptible again

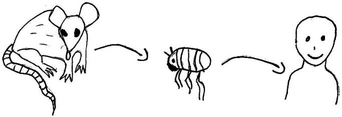


Figure: courtesy of Júlia Röst

Mathematical model – notations

Rodent compartments

- $R(t)$ – susceptible rodents
- $T(t)$ – rodents infested by non-infectious parasites
- $Q(t)$ – rodents infested by infectious parasites

Human compartments

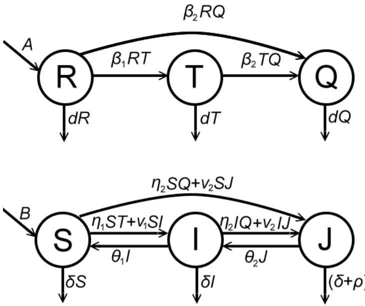
- $S(t)$ – susceptible humans
- $I(t)$ – humans infested by non-infectious parasites
- $J(t)$ – humans infested by infectious parasites

Mathematical model – notations

- A – birth rate of rodents
- d – death rate of rodents
- β_1 – transmission rate between R and T
- β_2 – transmission rate between R and Q, resp. T and Q
- B – birth rate of humans
- δ – death rate of humans
- ϱ – disease-induced death rate of humans
- ν_1 – transmission rate between S and I
- ν_2 – transmission rate between S and J, resp. I and J
- η_1 – transmission rate between T and S
- η_2 – transmission rate between Q and S, resp. Q and I
- θ_1 – disinfestation rate from I
- θ_2 – disinfestation/recovery rate from J

Mathematical model

$$
\begin{aligned}
R'(t) &= A - \beta_1 R(t)T(t) - \beta_2 R(t)Q(t) - dR(t),\\
T'(t) &= \beta_1 R(t)T(t) - \beta_2 T(t)Q(t) - dT(t),\\
Q'(t) &= \beta_2 R(t)Q(t) + \beta_2 T(t)Q(t) - dQ(t),\\
S'(t) &= B - \eta_1 S(t)T(t) - \eta_2 S(t)Q(t) - \nu_1 S(t)I(t) - \nu_2 S(t)J(t)\\
&\quad - \delta S(t) + \theta_1 I(t) + \theta_2 J(t),\\
I'(t) &= \eta_1 S(t)T(t) + \nu_1 S(t)I(t) - \eta_2 I(t)Q(t) - \nu_2 I(t)J(t) - \delta I(t) - \theta_1 I(t),\\
J'(t) &= \eta_2 S(t)Q(t) + \eta_2 I(t)Q(t) + \nu_2 S(t)J(t) + \nu_2 I(t)J(t)\\
&\quad - \delta J(t) - \rho J(t) - \theta_2 J(t),
\end{aligned}
$$



The rodent subsystem

$$
\begin{aligned}
R'(t) &= A - \beta_1 R(t)T(t) - \beta_2 R(t)Q(t) - dR(t),\\
T'(t) &= \beta_1 R(t)T(t) - \beta_2 T(t)Q(t) - dT(t),\\
Q'(t) &= \beta_2 R(t)Q(t) + \beta_2 T(t)Q(t) - dQ(t)
\end{aligned}
$$

Equilibria

$$E_R = \left(\tfrac{A}{d}, 0, 0\right), \qquad E_T = \left(\frac{d}{\beta_1}, \frac{A}{d} - \frac{d}{\beta_1}, 0\right)$$

$$E_Q = \left(\frac{d}{\beta_2}, 0, \frac{A}{d} - \frac{d}{\beta_2}\right), \qquad E_{TQ} = \left(\frac{A\beta_2}{d\beta_1}, \frac{d}{\beta_2} - \frac{A\beta_2}{d\beta_1}, \frac{A}{d} - \frac{d}{\beta_2}\right).$$

The rodent subsystem

Reproduction numbers

$$r_1 = \frac{A\beta_1}{d^2}, \qquad r_2 = \frac{A\beta_2}{d^2}, \qquad r_3 = \frac{\beta_1 d^2}{\beta_2^2 A}$$

Local stability

- E_R is LAS if $r_1 < 1$ and $r_2 < 1$ and unstable if $r_1 > 1$ or $r_2 > 1$
- E_T is LAS if $r_1 > 1$ and $r_2 < 1$
- E_Q is LAS if $r_2 > 1$ and $r_3 < 1$
- E_{TQ} is LAS if $r_2 > 1$ and $r_3 > 1$

The rodent subsystem – persistence

Definition

$X \neq \emptyset$ and $\rho \colon X \to \mathbb{R}_+$
$\Phi \colon \mathbb{R}_+ \times X \to X$ is *uniformly weakly ρ-persistent*, if $\exists\, \varepsilon > 0$:

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

Φ is *uniformly (strongly) ρ-persistent* if $\exists\, \varepsilon > 0$:

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

Definition

$M \subseteq X$ is *weakly ρ-repelling* if $\nexists\, x \in X : \rho(x) > 0$ and $\Phi(t,x) \to M$ as $t \to \infty$.

The rodent subsystem – persistence

Theorem

$R(t)$ 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

$R(t)$: method of fluctuation

$\exists\, t_k \to \infty : R(t_k) \to R_\infty := \liminf_{t\to\infty} R(t)$ and $R'(t_k) \to 0$ as $k \to \infty$

$\Rightarrow R'(t_k) + \beta_1 R(t_k) T(t_k) + \beta_2 R(t_k) Q(t_k) = A$

using $0 \leq T^\infty \leq \frac{A}{d}$ and $0 \leq Q^\infty \leq \frac{A}{d}$ we obtain $R_\infty \geq \frac{d}{\beta_1+\beta_2}$

The rodent subsystem – persistence

Proof

$T(t)$ and $Q(t)$: persistence theory (Smith & Thieme)

$X_T := \{(R,T,Q) \in \mathbb{R}^3 : T = 0\}$ extinction space

$\Omega := \bigcup_{X_T} \omega(R,T,Q)$

$\Omega = \{E_R\}$ or $\Omega = \{E_R, E_Q\}$: acyclic, invariant, isolated, compact

$\{E_R\}$, $\{E_Q\}$ is weakly T-repelling, i.e. $\nexists$ solution with $\lim_{t\to\infty}(R,T,Q) = E_R$ (or E_Q) with $T(t) > 0$

The rodent subsystem – global stability

Theorem

- E_R is GAS if $r_1 < 1$ and $r_2 < 1$.
- E_T is GAS on $X \setminus X_T$ if $r_1 > 1$ and $r_2 < 1$. E_R is GAS on X_T.
- E_Q is GAS on $X \setminus X_Q$ if $r_2 > 1$ and $r_3 < 1$. E_R is GAS on X_Q if $r_1 < 1$ and E_T is GAS on X_Q if $r_1 > 1$.
- E_{TQ} is GAS on $X \setminus (X_T \cup X_Q)$ if $r_2 > 1$ and $r_3 > 1$. E_T is GAS on X_Q and E_Q is GAS on X_T.

Proof

Introduce $F(t) := R(t) + T(t)$ to obtain

$$F'(t) = A - \beta_2 F(t) Q(t) - dF(t),$$
$$Q'(t) = \beta_2 F(t) Q(t) - dQ(t).$$

The rodent subsystem – global stability

Proof

Apply the Dulac function $1/Q$:

$$\frac{\partial}{\partial F}\frac{A-\beta_2 FQ-dF}{Q}+\frac{\partial}{\partial Q}\frac{\beta_2 FQ-dQ}{Q}=-\beta_2-\frac{d}{Q}<0.$$

to obtain that there is no periodic solution and all solutions tend to one of the two equilibria $\left(\frac{A}{d},0\right)$ and $\left(\frac{d}{\beta_2},\frac{A}{d}-\frac{d}{\beta_2}\right)$

If $r_2<1$, then only $\left(\frac{A}{d},0\right)$ exists $\Rightarrow Q(t)\to 0$ and $F(t)\to\frac{A}{d}\Rightarrow$

$$T'(t)=\gamma T(t)-\beta_1 T^2(t)\quad \text{with}\quad \gamma=\left(\frac{A\beta_1}{d}-d\right)$$

nontrivial solutions: $\frac{Ce^{\gamma t}}{1+\frac{\beta_1}{\gamma}Ce^{\gamma t}}$

If $r_1<1\Rightarrow T(t)\to 0$, if $r_1>1\Rightarrow T(t)\to\frac{A}{d}-\frac{d}{\beta_1}$

The rodent subsystem – global stability

Proof

If $r_2 > 1 \Rightarrow$ both equilibria exist

Persistence of $Q(t) \Rightarrow Q(t) \to \frac{A}{d} - \frac{d}{\beta_2} \Rightarrow$

$$T'(t) = \gamma T(t) - \beta_1 T^2(t) \quad \text{with} \quad \gamma = \left(\frac{d\beta_1}{\beta_2} - \frac{A\beta_2}{d}\right)$$

If $r_3 < 1 \Rightarrow T(t) \to 0$, if $r_3 > 1 \Rightarrow T(t) \to \frac{d}{\beta_2} - \frac{A\beta_2}{d\beta_1}$

The human subsystem

$$
\begin{aligned}
S'(t) &= B - \eta_1 T^* S(t) - \eta_2 Q^* S(t) - \nu_1 S(t) I(t) - \nu_2 S(t) J(t) \\
&\quad - \delta S(t) + \theta_1 I(t) + \theta_2 J(t), \\
I'(t) &= \eta_1 T^* S(t) + \nu_1 S(t) I(t) - \eta_2 Q^* I(t) - \nu_2 J(t) I(t) - \delta I(t) - \theta_1 I(t), \\
J'(t) &= \eta_2 Q^* S(t) + \eta_2 Q^* I(t) + \nu_2 S(t) J(t) + \nu_2 I(t) J(t) \\
&\quad - \delta J(t) - \rho J(t) - \theta_2 J(t)
\end{aligned}
$$

The human subsystem

$$
\begin{aligned}
S'(t) &= B - \eta_1 T^* S(t) - \eta_2 Q^* S(t) - \nu_1 S(t) I(t) - \nu_2 S(t) J(t) \\
&\quad - \delta S(t) + \theta_1 I(t) + \theta_2 J(t), \\
I'(t) &= \eta_1 T^* S(t) + \nu_1 S(t) I(t) - \eta_2 Q^* I(t) - \nu_2 J(t) I(t) - \delta I(t) - \theta_1 I(t), \\
J'(t) &= \eta_2 Q^* S(t) + \eta_2 Q^* I(t) + \nu_2 S(t) J(t) + \nu_2 I(t) J(t) \\
&\quad - \delta J(t) - \rho J(t) - \theta_2 J(t)
\end{aligned}
$$

Introduce $G(t) := S(t) + I(t)$ to obtain

$$
\begin{aligned}
G'(t) &= B - \eta_2 Q^* G(t) - \nu_2 G(t) J(t) - \delta G(t) + \theta_2 J(t), \\
J'(t) &= \eta_2 Q^* G(t) + \nu_2 G(t) J(t) - \delta J(t) - \rho J(t) - \theta_2 J(t).
\end{aligned}
$$

The human subsystem

Apply Bendixson–Dulac criterion with Dulac function $1/J$ and Poincaré–Bendixson theorem

$$\frac{\partial}{\partial G}\frac{B-\eta_2 Q^* G-\nu_2 GJ-\delta G+\theta_2 J}{J}+\frac{\partial}{\partial J}\frac{\eta_2 Q^* G+\nu_2 GJ-\delta J-\rho J-\theta_2 J}{J}$$
$$=-\frac{\eta_2 Q^*}{J}-\nu_2-\frac{\delta}{J}-\frac{\eta_2 G}{J^2}<0,$$

to obtain that all solutions tend to one of the two possible equilibria

$$E_1=\left(\frac{D+B\nu_2-\sqrt{(D-B\nu_2)^2+4B\eta_2 Q^*\nu_2(\delta+\rho)}}{2\delta\nu_2},\frac{-D+B\nu_2+\sqrt{(D-B\nu_2)^2+4B\eta_2 Q^*\nu_2(\delta+\rho)}}{2(\delta+\rho)\nu_2}\right)$$

and

$$E_2=\left(\frac{D+B\nu_2+\sqrt{(D-B\nu_2)^2+4B\eta_2 Q^*\nu_2(\delta+\rho)}}{2\delta\nu_2},\frac{-D+B\nu_2-\sqrt{(D-B\nu_2)^2+4B\eta_2 Q^*\nu_2(\delta+\rho)}}{2(\delta+\rho)\nu_2}\right)$$

with $D=\delta^2+Q^*\eta_2\rho+\delta(Q^*\eta_2+\theta_2+\rho)$

The human subsystem

Case 1: $r_2 > 1 \Leftrightarrow Q^* > 0$

only E_1 exists $\Rightarrow$ all solutions tend to E_1

Case 2: $r_2 \leq 1 \Leftrightarrow Q^* = 0$

The above system simplifies to

$$\begin{aligned} G'(t) &= B - \nu_2 G(t)J(t) - \delta G(t) + \theta_2 J(t), \\ J'(t) &= \nu_2 G(t)J(t) - \delta J(t) - \rho J(t) - \theta_2 J(t) \end{aligned}$$

which has the two equilibria

$e_1 := \left(\frac{B}{\delta}, 0\right)$ and $e_2 := \left(\frac{\delta+\theta_2+\rho}{\nu_2}, \frac{B\nu_2 - \delta(\delta+\theta_2+\rho)}{\nu_2(\delta+\rho)}\right)$

e_2 only exists if $\mathcal{R}_0^J := \frac{B\nu_2}{\delta(\delta+\theta_2+\rho)} > 1$

If $\mathcal{R}_0^J \leq 1 \Rightarrow$ all solutions tend to e_1

If $\mathcal{R}_0^J > 1 \Rightarrow J(t)$ strongly persistent $\Rightarrow$ all positive solutions tend to e_2

The human subsystem

Substitute the limit J^* into the first two equations of the human subsystem:

$$\begin{aligned} S'(t) &= B - \eta_1 T^* S(t) - \eta_2 Q^* S(t) - \nu_1 S(t) I(t) - \nu_2 J^* S(t) \\ &\qquad - \delta S(t) + \theta_1 I(t) + \theta_2 J^*, \\ I'(t) &= \eta_1 T^* S(t) + \nu_1 S(t) I(t) - \eta_2 Q^* I(t) - \nu_2 J^* I(t) - \delta I(t) - \theta_1 I(t) \end{aligned}$$

having two possible equilibria

$$\mathcal{E}_1 = \left(\frac{\nu_1(B+\theta_2 J^*)+P-\sqrt{(\nu_1(B+\theta_2 J^*)-P)^2+H}}{2\nu_1 K}, \frac{\nu_1(B+\theta_2 J^*)-P+\sqrt{(\nu_1(B+\theta_2 J^*)-P)^2+H}}{2\nu_1 K} \right)$$

and

$$\mathcal{E}_2 = \left(\frac{\nu_1(B+\theta_2 J^*)+P+\sqrt{(\nu_1(B+\theta_2 J^*)-P)^2+H}}{2\nu_1 K}, \frac{\nu_1(B+\theta_2 J^*)-P-\sqrt{(\nu_1(B+\theta_2 J^*)-P)^2+H}}{2\nu_1 K} \right)$$

with $K = (\delta + \eta_2 Q^* + \nu_2 J^*)$, $P = K(\delta + \theta_1 + \eta_1 T^* + \eta_2 Q^* + \nu_2 J^*)$ and $H = 4\eta_1 \nu_1 T^* (B + \theta_2 J^*) K$

The human subsystem

Apply Bendixson–Dulac criterion with Dulac function $1/I$ and Poincaré–Bendixson theorem to show that all solutions tend to an equilibrium:

$$\frac{\partial}{\partial S}\frac{B-\eta_1 T^* S-\eta_2 Q^* S-\nu_1 SI-\nu_2 J^* S-\delta S+\theta_1 I+\theta_2 J^*}{I}$$
$$+\frac{\partial}{\partial I}\frac{\eta_1 T^* S+\nu_1 SI-\eta_2 Q^* I-\nu_2 J^* I-\delta I-\theta_1 I}{I}$$
$$=\frac{-\eta_1 T^*}{I}-\frac{\eta_2 Q^*}{I}-\nu_1-\frac{\nu_2 J^*}{I}-\frac{\delta}{I}-\frac{\eta_1 T^* S}{I^2}<0$$

$\mathcal{E}_2$ only exists if $T^*=0$

The human subsystem

If $T^* > 0$ and $Q^* > 0 \Leftrightarrow r_2 > 1$ and $r_3 > 1 \Rightarrow$ all solutions tend to $(\mathcal{E}_1^1, \mathcal{E}_1^2, E_1^2)$

If $T^* > 0$ and $Q^* = 0$, $\Leftrightarrow r_1 > 1$ and $r_2 \leq 1 \Rightarrow \mathcal{R}_0^J$ determines the limit of $J(t)$

If $r_1 > 1$, $r_2 \leq 1$ and $\mathcal{R}_0^J \leq 1 \Leftrightarrow$ all solutions of tend to $\left(\mathcal{E}_1^1, \mathcal{E}_1^2, 0\right)$,

If $r_1 > 1$, $r_2 \leq 1$ and $\mathcal{R}_0^J > 1 \Leftrightarrow$ all solutions tend to

$$\left(\mathcal{E}_1^1, \mathcal{E}_1^2, \frac{B\nu_2 - \delta(\delta + \theta_2 + \rho)}{\nu_2(\delta + \rho)}\right)$$

The human subsystem

If $T^* = 0$ ($r_1 < 1$ and $r_2 < 1$), the system reduces to

$$\begin{aligned} S'(t) &= B - \eta_2 Q^* S(t) - \nu_1 S(t) I(t) - \nu_2 S(t) J^* \\ &\qquad - \delta S(t) + \theta_1 I(t) + \theta_2 J^*, \\ I'(t) &= \nu_1 S(t) I(t) - \eta_2 Q^* I(t) - \nu_2 I(t) J^* - \delta I(t) - \theta_1 I(t), \end{aligned}$$

having the two equilibria

$$\mathcal{E}_1 = \left(\frac{\eta_2 Q^* + \nu_2 J^* + \delta + \theta_1}{\nu_1}, \frac{\nu_1 (B + \theta_2 J^*) - (\eta_2 Q^* + \nu_2 J^* + \delta)(\eta_2 Q^* + \nu_2 J^* + \delta + \theta_1)}{\nu_1 (\eta_2 Q^* + \nu_2 J^* + \delta)} \right),$$

and

$$\mathcal{E}_2 = \left(\frac{B + \theta_2 J^*}{\eta_2 Q^* + \nu_2 J^* + \delta}, 0 \right),$$

with $\mathcal{E}_2$ only existing if

$$\mathcal{R}_0^I := \frac{\nu_1 (B + \theta_2 J^*)}{(\eta_2 Q^* + \nu_2 J^* + \delta)(\eta_2 Q^* + \nu_2 J^* + \delta + \theta_1)} > 1.$$

The human subsystem

If $\mathcal{R}_0^I \leq 1$, only $\mathcal{E}_2$ exists $\Rightarrow$ all solutions tend to $\left(\frac{B+\theta_2 J^*}{\eta_2 Q^* + \nu_2 J^* + \delta}, 0, J^*\right)$

If $\mathcal{R}_0^I > 1 \Rightarrow I(t)$ is strongly persistent $\Rightarrow$ all positive solutions of the SI system tend to $\mathcal{E}_1$

The human subsystem

If $Q^* > 0$ ($r_2 > 1$) $\Rightarrow \exists!$ equilibrium of the GJ system $\Rightarrow J(t)$ tends to E_1^2

If $r_2 > 1$ and $\mathcal{R}_0^I \leq 1 \Rightarrow$ all solutions tend to $\left(\frac{B+\theta_2 E_1^2}{\eta_2\left(\frac{A}{d}-\frac{d}{\beta_2}\right)+\nu_2 E_1^2+\delta}, 0, E_1^2 \right)$

If $r_2 > 1$ and $\mathcal{R}_0^I > 1$, all solutions tend to

$$\left(\frac{\eta_2 Q^* + \nu_2 E_1^2 + \delta + \theta_1}{\nu_1}, \frac{\nu_1 (B+\theta_2 E_1^2) - (\eta_2 Q^* + \nu_2 E_1^2 + \delta)(\eta_2 Q^* + \nu_2 E_1^2 + \delta + \theta_1)}{\nu_1 (\eta_2 Q^* + \nu_2 E_1^2 + \delta)}, E_1^2 \right)$$

with $Q^* = \left(\frac{A}{d} - \frac{d}{\beta_2}\right)$.

The human subsystem

If $r_2 \leq 1$ $(Q^* = 0) \Rightarrow \mathcal{R}_0^J$ determines $\lim_{t\to\infty} J(t)$.

If $r_1 \leq 1, r_2 \leq 1, \mathcal{R}_0^J \leq 1, \mathcal{R}_0^I \leq 1 \Rightarrow$ all solutions tend to

$$\left(\tfrac{B}{\delta}, 0, 0\right).$$

If $r_1 \leq 1, r_2 \leq 1, \mathcal{R}_0^J \leq 1, \mathcal{R}_0^I > 1$, all solutions tend to

$$\left(\tfrac{\delta+\theta_1}{\nu_1}, \frac{B}{\delta} - \frac{\delta+\theta_1}{\nu_1}, 0\right).$$

If $r_1 \leq 1, r_2 \leq 1, \mathcal{R}_0^J > 1, \mathcal{R}_0^I \leq 1$, all solutions tend to

$$\left(\tfrac{\delta+\theta_2+\rho}{\nu_2}, 0, \frac{\nu_2 B - \delta(\delta+\theta_2+\rho)}{\nu_2(\delta+\rho)}\right).$$

If $r_1 \leq 1, r_2 \leq 1, \mathcal{R}_0^J > 1, \mathcal{R}_0^I > 1$, all solutions tend to

$$\left(\tfrac{\nu_2 B+\theta_1\rho+\delta(\theta_1-\theta_2)}{\nu_1(\delta+\rho)}, \tfrac{\delta\theta_2-\nu_2 B}{\nu_1(\delta+\rho)} + \tfrac{\delta+\theta_2+\rho}{\nu_2} - \tfrac{\theta_1}{\nu_1}, \tfrac{\nu_2 B-\delta(\delta+\theta_2+\rho)}{\nu_2(\delta+\rho)}\right).$$

Possible ways to control

Three main ways to control the disease:

- decrease the transmission rates $\eta_{1,2}$ between humans and rodents
- increase the disinfestation rates $\theta_{1,2}$ of humans to shorten the duration of infestation of humans
- reduce d by culling of the rodents

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First two ways: only mitigation not sufficient to eradicate the disease – except the extreme case of decreasing $\eta_{1,2}$ to zero $\Rightarrow$ one may decrease human reproduction numbers below 1 by increasing $\theta_{1,2}$ and thus eliminate the infestation.

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Controlling the rodent population can reduce r_1, r_2 below 1 $\Rightarrow$ eliminate the infestation among rodents $\Rightarrow$ rodent$\rightarrow$human infestation can be eliminated and human repr. numbers determine global attractivity in human subsystem $\Rightarrow$ increasing the disinfestation rate among humans eliminates parasites and disease.