

Ecology and evolution of sterilizing infections: roles of mating and fecundity-longevity trade-off

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Outline

- Intro: Sterilizing and sexually transmitted infections
- Sterilizing infections and fecundity-longevity trade-off
- Host-pathogen dynamics
- Evolution of sterilization efficiency
- Sexually transmitted infections and willingness to mate
- Host-pathogen dynamics
- Evolution of mating avoidance

Sterilizing and sexually transmitted infections

Basic characteristics

- **Ubiquitous** among animals
- Sexually transmitted infections (STIs) **commonly sterilizing**
- Infection-induced **mortality often negligible**
- Recovery relatively rare
- STI transmission often assumed **frequency-dependent**: number of mating encounters per unit time constant regardless of population density

Sterilizing and sexually transmitted infections

Conventional model of host-pathogen dynamics

$$\begin{aligned}\frac{dS}{dt} &= \beta(S + (1 - \sigma)I) - \Phi(N) \frac{SI}{N} - (\mu + dN)S \\ \frac{dI}{dt} &= \Phi(N) \frac{SI}{N} - (\mu + dN)I - \alpha I\end{aligned}$$

- Disease-induced fecundity reduction
- Disease-induced mortality
- Pathogen transmission

$\Phi(N)$... generic per-capita rate of contacts between hosts as a function of population density: frequency-dependent (FD), density-dependent (DD), or asymptotic (AS)

Sterilizing and sexually transmitted infections

Conventional model of host-pathogen dynamics

Up to three equilibria:

■ **disease-free equilibrium** - is stable if $R_0 = \Phi(N)/(\beta + \alpha) < 1$

■ **endemic equilibrium** - exists and is stable if (DD, AS) $R_0 > 1$ or (FD) $1 < R_0 < R_0^c$, where

$$R_0^c = 1 + \frac{\beta(1 - \sigma)(\beta - \mu)}{(\beta + \alpha)(\alpha + \mu - \beta(1 - \sigma))}$$

■ (FD) **disease-induced extinction equilibrium** - exists if $R_0 > 1$ and is stable when $R_0 > R_0^c$

Part 1

Sterilizing infections and fecundity-longevity trade-off

Host-pathogen dynamics

Janouskova and Berec (2018), J Theor Biol 450, 76-85

Evolution of sterilization efficiency

Janouskova and Berec (2020), Am Nat 195, 95-106

Sterilizing infections

Fecundity-longevity trade-off

- Life history theory is based on the concept of **trade-offs**
- **Fecundity-longevity trade-off**: increased reproductive activity at a cost of reduced survival
- **Sterilizing pathogens**: reduced fecundity or even full sterility might let infected individuals live longer than susceptible ones
- Neglected in epidemiological modeling (Berec and Maxin, 2012)
- **Plasmodium-mosquito interaction**: relative to uninfected *Culex pipiens* mosquitoes, those infected by the avian malaria parasite *Plasmodium relictum* had reduced fecundity traded off by increased longevity (Vézilier et al., 2012)

Sterilizing infections

Fecundity-longevity trade-off

- Sterilizing (or castrating) pathogens commonly **suggested as potentially effective control agents**: with fecundity-longevity trade-off, infected pests may live for an extended period of time and their expected regulating effect may thus be weakened

Sterilizing infections

Fecundity-longevity trade-off

■ Sterilizing (or castrating) pathogens commonly **suggested as potentially effective control agents**: with fecundity-longevity trade-off, infected pests may live for an extended period of time and their expected regulating effect may thus be weakened

Question: How does the presence of fecundity-longevity trade-off in hosts affected by sterilizing pathogens impact dynamics of this host-pathogen interaction?

Sterilizing infections

Fecundity-longevity trade-off

Fecundity-longevity trade-off $\delta(\sigma)$

$$\begin{aligned}\frac{dS}{dt} &= \beta(S + (1 - \sigma)I) - \Phi(N) \frac{SI}{N} - (\mu + dN)S \\ \frac{dI}{dt} &= \Phi(N) \frac{SI}{N} - (\delta(\sigma)\mu + dN)I\end{aligned}$$

Sterilizing infections

Fecundity-longevity trade-off

Fecundity-longevity trade-off $\delta(\sigma)$

$$\begin{aligned}\frac{dS}{dt} &= \beta(S + (1 - \sigma)I) - \Phi(N) \frac{SI}{N} - (\mu + dN)S \\ \frac{dI}{dt} &= \Phi(N) \frac{SI}{N} - (\delta(\sigma)\mu + dN)I\end{aligned}$$

Ecology: $0 \leq \sigma \leq 1$, $\Delta \equiv \delta(\sigma)$, $0 \leq \Delta \leq 1$

$$\begin{aligned}\frac{dS}{dt} &= \beta(S + (1 - \sigma)I) - \Phi(N) \frac{SI}{N} - (\mu + dN)S \\ \frac{dI}{dt} &= \Phi(N) \frac{SI}{N} - (\Delta\mu + dN)I\end{aligned}$$

Sterilizing infections

Fecundity-longevity trade-off

Existence and stability of endemic equilibria:

Number	Existence	Stable
<i>Density-dependent transmission</i>		
One	$N^* < K$ $R_0 > 1$ and $b\sigma - d(1 - \Delta) > 0$	If exists
One	$N^* > K$ $R_0 > 1$ and $b\sigma - d(1 - \Delta) < 0$	If exists
Two	$N^* > K$ $R_0 < 1$ and $b\sigma - d(1 - \Delta) < 0$ and $D_{DT} > 0$ and $N^* > N_{0(DT)}$	$N^* > N_s$
<i>Frequency-dependent transmission</i>		
One	$N^* < K$ $R_0 > 1$ and $b\sigma - d(1 - \Delta) > 0$ and $i^* < \frac{b-d}{b\sigma - d(1 - \Delta)}$	If exists
One	$N^* > K$ $R_0 > 1$ and $b\sigma - d(1 - \Delta) < 0$	If exists
<i>Asymptotic transmission</i>		
One	$N^* < K$ $R_0 > 1$ and $b\sigma - d(1 - \Delta) > 0$	If exists
One	$N^* > K$ $R_0 > 1$ and $b\sigma - d(1 - \Delta) < 0$	If exists
Two	$N^* > K$ $R_0 < 1$ and $\beta > b - d(1 - \Delta)$ and $b\sigma - d(1 - \Delta) < 0$ and $D_{AT} > 0$ and $N^* > N_{0(AT)}$	$\det J_{AT} > 0$

Sterilizing infections

Fecundity-longevity trade-off

The enhancement condition $b\sigma - d(1 - \Delta) < 0$

- Population density in endemic equilibrium larger than carrying capacity in the absence of infection
- Endemic equilibrium exists and is stable for $R_0 < 1$ (bistability)

Reduction of fecundity in infected individuals is overcompensated by increase in their longevity

This would disqualify such pathogen as efficient control agent

Sterilizing infections

Fecundity-longevity trade-off

Fecundity-longevity trade-off is a **host characteristic**, $d(b)$

Action of sterilizing pathogen is to **deviate the host** along this trade-off from its pre-infection level

Evolution of **per-capita birth rate** b^* in the absence of infection

Adaptive dynamics: mutant invasion fitness

$$f(b_m, b_r) = (b_m - d(b_m)) - (b_r - d(b_r))$$

Host evolves maximum intrinsic per-capita growth rate $b - d(b)$

Sterilizing infections

Fecundity-longevity trade-off

Physiological upper bound on birth rate b_{\max} :

$$d(b) = d_0 + (d_{\max} - d_0) \left(\frac{b}{b_{\max}} \right)^{\theta}$$

Evolved per-capita birth rate b^* :

$$0 < \theta \leq \max\{1, \theta_c\}, \theta_c = b_{\max}/(d_{\max} - d_0) : b^* = b_{\max}$$

$$\theta > \max\{1, \theta_c\} : b^* = b_{\max} \left(\frac{b_{\max}}{\theta(d_{\max} - d_0)} \right)^{\frac{1}{\theta-1}}$$

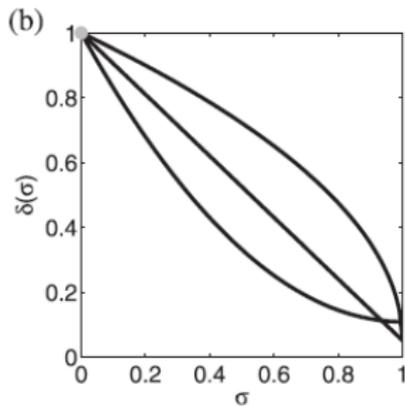
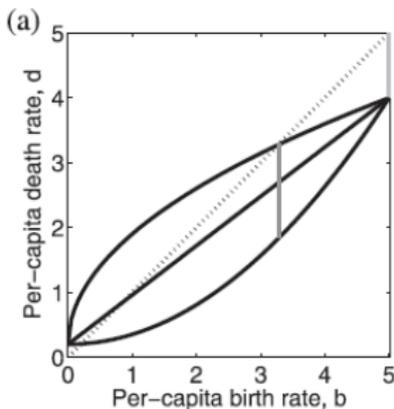
b^* is an **evolutionary attractor**

Sterilizing infections

Fecundity-longevity trade-off

Fecundity-longevity trade-off $\delta(\sigma)$ needs to be consistent with $d(b)$:

$$\delta(\sigma) d(b^*) = d((1 - \sigma)b^*) \Rightarrow \delta(\sigma) = \frac{d((1 - \sigma)b^*)}{d(b^*)}$$



Sterilizing infections

Fecundity-longevity trade-off

Host fecundity b^* in the absence of infection

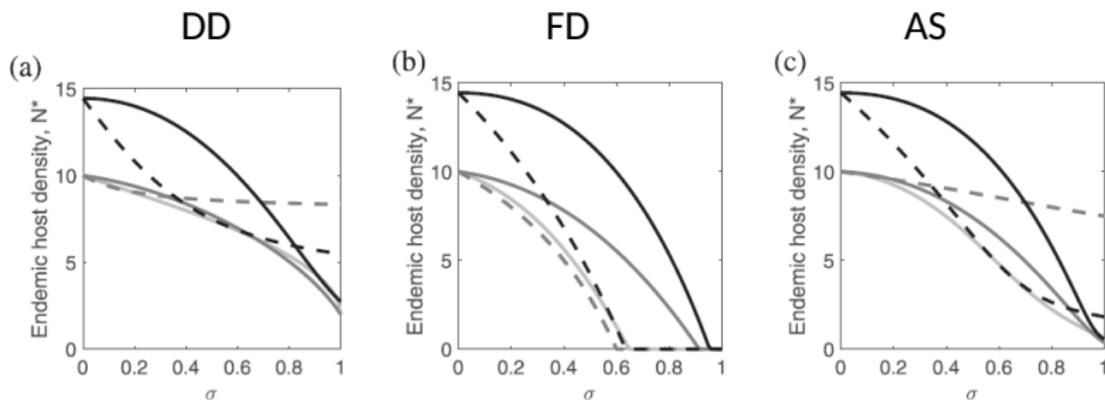
Trade-off curves always lie in the part of parameter space where
the enhancement condition does not hold

No situation with $N^* > K$ can occur

There is at most one endemic equilibrium with $N^* < K$

Sterilizing infections

Fecundity-longevity trade-off



Solid lines - with trade-off, dashed lines - without trade-off

Even then, fecundity-longevity trade-off mostly weakens efficiency of sterilizing pathogens in controlling hosts, unless fecundity reduction σ is sufficiently large and/or trade-off is not too convex ($\theta < \sim 1$)

Sterilizing infections: evolution

Fecundity-longevity trade-off

Evolution of sterilization efficiency

- Common occurrence of sterilizing pathogens, yet **studies of evolution of fecundity reduction are rare**
- Earlier models: **pathogens fully sterilize their hosts**
- **Observations:** many parasites sterilize their hosts only partially
- **Existing explanations:** spatial host population structure, sterility tolerance in hosts
- **No explanation in terms of pathogen evolution in well-mixed populations**

Sterilizing infections: evolution

Fecundity-longevity trade-off

Observation: many sterilizing infections are transmitted also vertically

Evolution of mortality virulence: **vertical transmission (VT) reduces infection fatality**

With VT, pathogens should have **no interest in full host sterilization**

Ferdy and Godelle (2005): **with VT, intermediate sterility virulence may evolve, provided that VT efficiency is sufficiently high**

Sterilizing infections: evolution

Fecundity-longevity trade-off

Question: What role does the fecundity-longevity trade-off play in evolution of sterility virulence under possibly vertical transmission?

$$\frac{dS}{dt} = bS + b(1 - \sigma)(1 - \nu)I - \Phi(N) \frac{SI}{N} - (d(b) + d_1 N) S$$
$$\frac{dI}{dt} = b(1 - \sigma)\nu I + \Phi(N) \frac{SI}{N} - (d(b(1 - \sigma)) + d_1 N) I - \alpha I$$

ν ... vertical transmission efficiency

Sterilizing infections: evolution

Fecundity-longevity trade-off

Physiological upper bound on birth rate b_{\max} :

$$d(b) = d_0 + (d_{\max} - d_0) \left(\frac{b}{b_{\max}} \right)^\theta$$

Evolved per-capita birth rate b^* :

$$0 < \theta \leq \max\{1, \theta_c\}, \theta_c = b_{\max}/(d_{\max} - d_0) : b^* = b_{\max}$$

$$\theta > \max\{1, \theta_c\} : b^* = b_{\max} \left(\frac{b_{\max}}{\theta(d_{\max} - d_0)} \right)^{\frac{1}{\theta-1}}$$

Transmission-virulence trade-off: $\sigma(\beta) = (\beta/\beta_{\max})^z$

Sterilizing infections: evolution

Fecundity-longevity trade-off

Adaptive dynamics (contact rate $\Phi(N) = \beta(\sigma) \Psi(N)$)

Mutant invasion fitness:

$$f(\sigma_m, \sigma_r) = b\nu(\sigma_r - \sigma_m) + \Psi(\hat{N}) \frac{\hat{S}}{\hat{N}} (\beta(\sigma_m) - \beta(\sigma_r)) + \\ + d((1 - \sigma_r)b) - d((1 - \sigma_m)b)$$

From left to right: the force of selection due to vertical transmission, the transmission-virulence trade-off $\beta(\sigma)$, and the fecundity-longevity trade-off $d(b)$

Sterilizing infections: evolution

Fecundity-longevity trade-off

No vertical transmission

Evolution towards $\sigma = 1$

For DD and AD this means **full host sterilization**

For FD it means **evolutionary suicide**

But STIs (that are sterilizing and presumably have FD) do exist!

Sterilizing infections: evolution

Fecundity-longevity trade-off

Vertical transmission but no fecundity-longevity trade-off

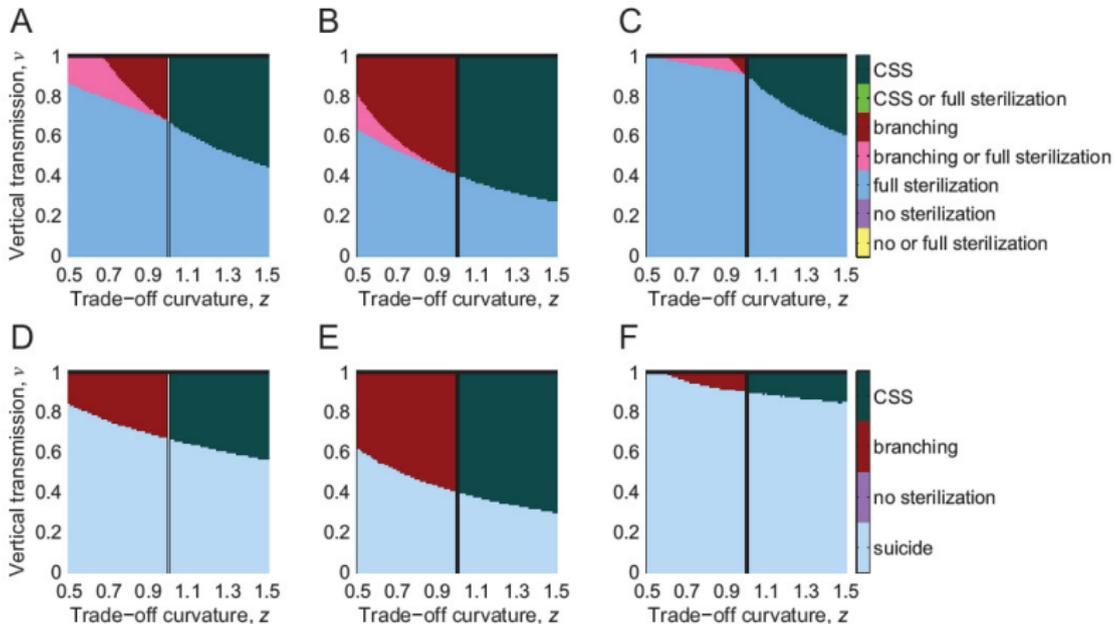
No transmission-virulence trade-off: evolution to no sterility virulence ($\sigma = 0$)

Transmission-virulence trade-off: singular point, if it exists, is evolutionary stable when $\beta(\sigma)$ is concave ($z > 1$) and evolutionary unstable when $\beta(\sigma)$ is convex ($z < 1$)

Sterilizing infections: evolution

Fecundity-longevity trade-off

Density-dependent (asymptotic) transmission



Frequency-dependent transmission

Sterilizing infections: evolution

Fecundity-longevity trade-off

Vertical transmission and fecundity-longevity trade-off

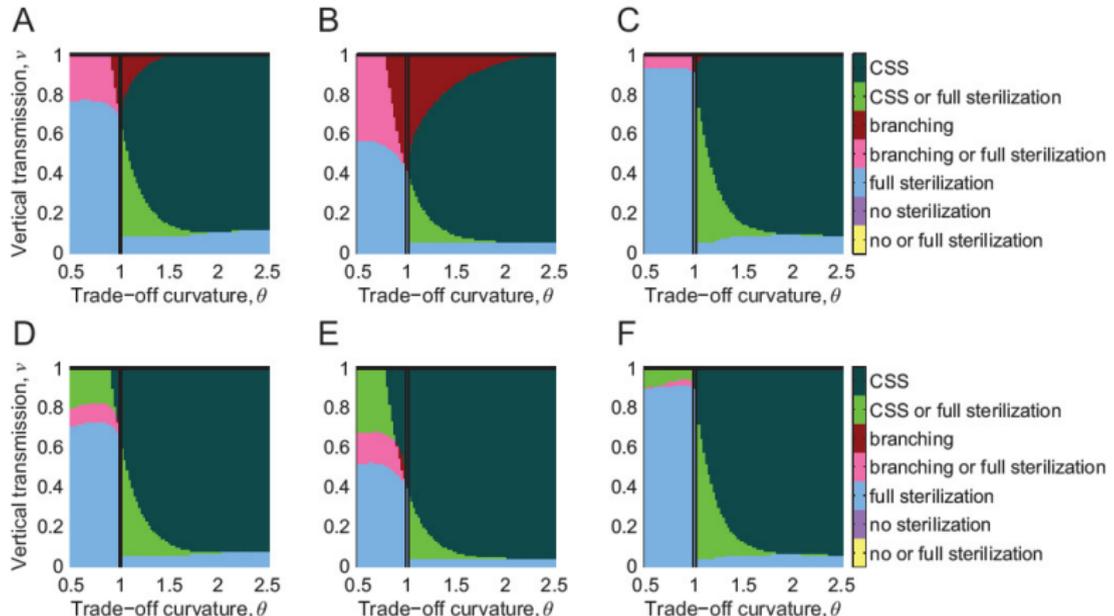
Tension between VT (evolution to low σ) and fecundity-longevity trade-off (speeding up evolution to high σ)

- Much higher VT efficacy ν required to prevent evolution of full sterilization under concave fecundity-longevity trade-off ($\theta < 1$) than under convex fecundity-longevity trade-off ($\theta > 1$)

Sterilizing infections: evolution

Fecundity-longevity trade-off

Density-dependent (asymptotic) transmission

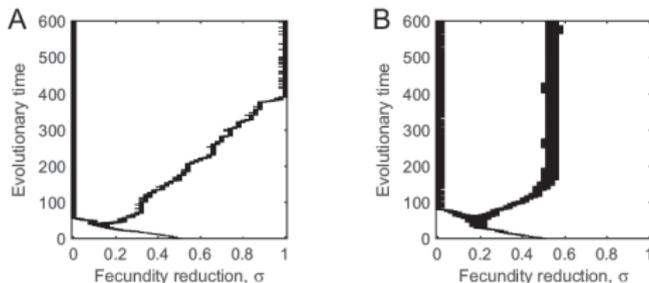


Frequency-dependent transmission

Sterilizing infections: evolution

Fecundity-longevity trade-off

Dimorphic population: one branch of pathogens evolving high sterilization (sometimes even full sterilization) and the other branch evolving only a negligible fecundity reduction effect



FD: fully sterilizing variants may survive as their effect on host population is compensated by presence of nearly avirulent ones

Sterilizing infections: conclusions

- The **enhancement condition** $b\sigma - d(1 - \Delta) < 0$
- Fecundity-longevity trade-off **itself cannot prevent** evolution of full sterilization
- Sufficiently **intense VT can prevent** evolution of full sterilization
- Fecundity-longevity trade-off **strongly modulates** threshold efficiency of VT above which partial sterilization may evolve
- Whereas **evolutionary branching** is important under concave fecundity-longevity trade-off, **evolutionary attractor** dominates under convex fecundity-longevity trade-off
- **Consistency across horizontal transmission**

Part 2

Sexually transmitted infections and willingness to mate

Host-pathogen dynamics

Theuer and Berc (2018), J Theor Biol 455, 64-74

Evolution of mating avoidance

*Theuer and Berc (2020), Theoretical Ecology. doi:
10.1007/s12080-020-00494-3*

Sexually transmitted infections

Mating avoidance

- Sexually transmitted infections (STIs) are **widespread in nature**
- **Mating is the key factor**: different mating strategies affect the way STIs spread and impact the host population
- STIs are likely to **shape host mating strategies**
- **Avoiding an infected mate** is a strategy that has benefits (not becoming infected) but also costs (lost mating opportunities)

Sexually transmitted infections

Mating avoidance

No evidence found of female mate choice based on male infection status (other theoretical studies remain silent about this):

■ **Webberley et al. (2002):** The two-spot ladybird *Adalia bipunctata* and its sexually transmitted mite *Coccipolipus hippodamiae*

■ **Luong & Kaya (2005):** The decorated cricket *Gryllodes sigillatus* and its sexually transmitted nematode *Mehdinema alii*

Many authors: STIs should generally evolve to become cryptic

Recently challenged: stable mating preferences, but also coevolutionary cycles (Ashby and Boots, 2015)

Sexually transmitted infections

Mating avoidance

Question: How do preferences for mating with healthy vs. infected mate affect host-STI dynamics?

ψ_{SS} ... probability that two S individuals mate upon encounter

ψ_{SI} ... probability that S and I individuals mate upon encounter

ψ_{II} ... probability that two I individuals mate upon encounter

Consistency between the processes of host reproduction and infection transmission, since mating mediates both

Sex-structured population model

Basic structure

Assumption: pairs are formed for just the purpose of mating

Only females give birth, mortality rates possibly sex-specific

Females (density N_F) and males (density N_M) discerned:

$$\frac{dN_F}{dt} = \gamma b(N_F, N_M) N_F - \mu_F(N_F, N_M) N_F$$

$$\frac{dN_M}{dt} = (1 - \gamma) b(N_F, N_M) N_F - \mu_M(N_F, N_M) N_M$$

γ ... sex ratio at birth (proportion of females)

Sex-structured population model

Full equations

Density-dependent mortality:

$$\mu_F(N_F, N_M) = \mu_F + d(N_F + N_M)$$

$$\mu_M(N_F, N_M) = \mu_M + d(N_F + N_M)$$

$$\frac{dN_F}{dt} = \gamma b w \mathcal{M}(N_F, N_M) - (\mu_F + d(N_F + N_M)) N_F$$

$$\frac{dN_M}{dt} = (1 - \gamma) b w \underbrace{\mathcal{M}(N_F, N_M)}_{\text{mating rate}} - \underbrace{(\mu_M + d(N_F + N_M)) N_M}_{\text{density-dependent mortality}}$$

$\underbrace{\hspace{10em}}_{\text{fertilization rate}}$

$\underbrace{\hspace{15em}}_{\text{birth rate}}$

Sex-structured population model

Sexually transmitted infection

$$\begin{aligned} \frac{dS_F}{dt} = & \gamma b w (\psi_{SS} \mathcal{M}(S_F, S_M) + \psi_{SI} \mathcal{M}(S_F, I_M) + \psi_{IS} \mathcal{M}(I_F, S_M) \\ & + \psi_{II} \mathcal{M}(I_F, I_M)) - \lambda \psi_{SI} \mathcal{M}(S_F, I_M) - (\mu_F + dN) S_F \end{aligned}$$

$$\begin{aligned} \frac{dS_M}{dt} = & (1 - \gamma) b w (\psi_{SS} \mathcal{M}(S_F, S_M) + \psi_{SI} \mathcal{M}(S_F, I_M) + \psi_{IS} \mathcal{M}(I_F, S_M) \\ & + \psi_{II} \mathcal{M}(I_F, I_M)) - \lambda \psi_{IS} \mathcal{M}(I_F, S_M) - (\mu_M + dN) S_M \end{aligned}$$

$$\frac{dI_F}{dt} = \lambda \psi_{SI} \mathcal{M}(S_F, I_M) - (\mu_F + dN) I_F - \alpha_F I_F$$

$$\frac{dI_M}{dt} = \lambda \psi_{IS} \mathcal{M}(I_F, S_M) - (\mu_M + dN) I_M - \alpha_M I_M$$

Sex-structured population model

Sexually transmitted infection

Assumption: **random mating** between individuals in the population

$$\mathcal{M}(X, Y) = \mathcal{M}(N_M, N_F) \frac{X}{N_M} \frac{Y}{N_F}, \quad X = S_M, I_M, \quad Y = S_F, I_F$$

$\mathcal{M}(N_M, N_F)$... total mating rate

X/N_F ... proportion of females of type X among all females

Y/N_M ... proportion of males of type Y among all males

Sex-structured population model

Sexually transmitted infection

Assumptions: 1:1 sex ratio at birth, sex-independent process rates

($\gamma = 0.5$, $\mu_F = \mu_M = \mu$, $\psi_{SI} = \psi_{IS}$, $\alpha_F = \alpha_M = \alpha$)

$S_F = S_M = S/2$ where $S = S_F + S_M$

$I_F = I_M = I/2$ where $I = I_F + I_M$, $N = N_F + N_M$

$$\frac{dS}{dt} = bw\mathcal{M} \left(\frac{N}{2}, \frac{N}{2} \right) \frac{\psi_{SS}S^2 + 2\psi_{SI}SI + \psi_{II}I^2}{N^2} - 2\lambda\psi_{SI}\mathcal{M} \left(\frac{N}{2}, \frac{N}{2} \right) \frac{SI}{N^2} - (\mu + dN)S$$

$$\frac{dI}{dt} = 2\lambda\psi_{SI}\mathcal{M} \left(\frac{N}{2}, \frac{N}{2} \right) \frac{SI}{N^2} - (\mu + dN)I - \alpha I$$

Sex-structured population model

Mating function $\mathcal{M}(N_F, N_M)$

Degree-one homogeneous mating function

$\mathcal{M}(ax, ay) = a \mathcal{M}(x, y)$ for any positive a, x, y

$\mathcal{M}(N_F, N_M)/N_F = \mathcal{M}(1, N_M/N_F)$... per female mating rate

Constant if N_M/N_F is fixed, regardless of $N = N_M + N_F$

$$\mathcal{M}(N/2, N/2) = (N/2) \mathcal{M}(1, 1)$$

Sex-structured population model

Degree-one homogeneous mating function

$\beta = b w \mathcal{M}(1, 1)/2$ and $\lambda = \Lambda \mathcal{M}(1, 1)$:

$$\frac{dS}{dt} = \beta \frac{\psi_{SS} S^2 + 2\psi_{SI} SI + \psi_{II} I^2}{N} - \psi_{SI} \lambda \frac{SI}{N} - (\mu + dN) S$$

$$\frac{dI}{dt} = \lambda \psi_{SI} \frac{SI}{N} - (\mu + dN) I - \alpha I$$

Frequency-dependent transmission

Complex reproduction term

$\psi_{SS} = \psi_{SI} = \psi_{II} = 1$... conventional STI model without sterility

Sexually transmitted infections

Mating avoidance

Extension to include sterility virulence

$$\frac{dS}{dt} = \beta \frac{\psi_{SS}S^2 + 2\psi_{SI}(1-\sigma)IS + \psi_{II}(1-\sigma)^2I^2}{N}$$

$$- \lambda\psi_{SI} \frac{SI}{N} - (\mu + dN)S$$

$$\frac{dI}{dt} = \lambda\psi_{SI} \frac{SI}{N} - (\mu + dN)I - \alpha I$$

Sexually transmitted infections

Mating avoidance

Individuals are able to recognize the infection status of their potential mating partners

- susceptible individuals mate with all susceptible partners, while accepting infected individuals as mates only with a probability ψ
- infected individuals are assumed not to lose anything by mating with other infected individuals and thus mate unselectively

$$\psi_{SS} = 1, \psi_{SI} = \psi, \psi_{II} = 1$$

ψ ... willingness of an individual to accept infection risk upon mating
(mating willingness parameter)

Sexually transmitted infections

Mating avoidance

$\psi = 0$: infection does not spread

$\psi = 1$: no mating preferences exist (model above)

$0 < \psi < 1$

$$\frac{dS}{dt} = \beta \frac{S^2 + 2\psi(1-\sigma)IS + (1-\sigma)^2 I^2}{N} - \lambda\psi \frac{SI}{N} - (\mu + dN)S$$

$$\frac{dI}{dt} = \lambda\psi \frac{SI}{N} - (\mu + dN)I - \alpha I$$

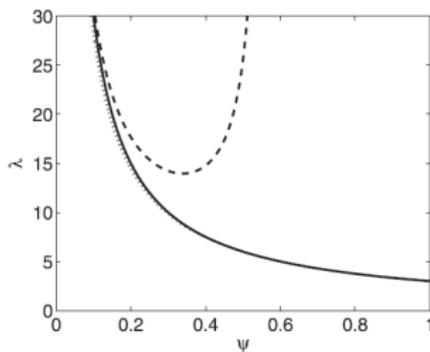
Basic reproduction number: $R_0 = \lambda \psi / (\beta + \alpha)$

When $\lambda > \beta + \alpha$, a decrease in ψ invokes a change from $R_0 > 1$ to $R_0 < 1$ at a critical value $\psi_c = (\beta + \alpha)/\lambda$

Sexually transmitted infections

Mating avoidance

Equilibrium	Existence	Stability
Extinction (0,0)	Always	Always unstable
Disease-free ($K, 0$)	Always	Stable for $R_0 < 1$, unstable for $R_0 > 1$
Disease-induced extinction ($0, i_2^c$)	$\psi < \frac{1}{2}$: $\max\{D, F\} < R_0 < 1$	Always unstable
Disease-induced extinction ($0, i_3^c$)	$\psi < \frac{1}{2}$: $R_0 > \max\{D, F\}$ $\psi > \frac{1}{2}$: $R_0 > 1$	Stable if it exists and (9) holds
Endemic (N_2^e, i_2^e)	$\psi < \frac{1}{2}$: $\max\{D, F\} < R_0 < 1$, (10)	Always unstable
Endemic (N_3^e, i_3^e)	$\psi < \frac{1}{2}$: $R_0 > \max\{D, F\}$, (10) $\psi > \frac{1}{2}$: $R_0 > 1$, (10)	Stable if it exists



Under solid curve: DFE

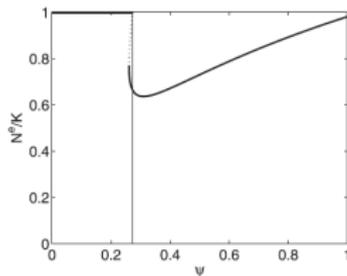
Above dashed curve: DIE

In between the two: END

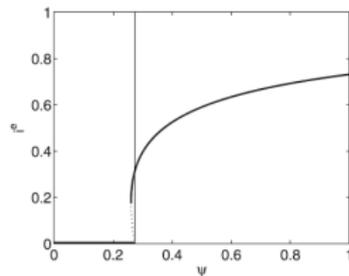
Small area: bistability

Sexually transmitted infections

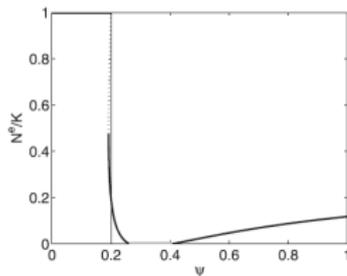
Mating avoidance



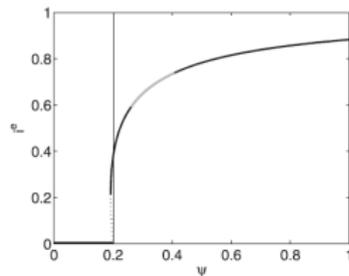
(a) $\alpha = 0.1$ and $\beta = 4$



(b) $\alpha = 0.1$ and $\beta = 4$



(c) $\alpha = 1.4$ and $\beta = 1.6$



(d) $\alpha = 1.4$ and $\beta = 1.6$

Sexually transmitted infections: evolution

Mating avoidance

Evolution of mating willingness

ψ ... willingness to accept infection risk upon encounter

We study evolution of ψ via adaptive dynamics

Cost-benefit analysis of infection avoidance:

- benefits always exceed costs: $\psi^* = 0$
- benefits are always lower than costs: $\psi^* = 1$
- benefits balance with costs at some $0 \leq \psi^* \leq 1$

Sexually transmitted infections: evolution

Mating avoidance

Host perspective: ψ ... probability of accepting infection risk upon mating with infected individual (can be recognized)

Pathogen perspective: ψ ... willingness to mate decreases with increasing visibility of infection (is it always in the best interest of parasite to become cryptic?)

Can partial infection avoidance evolve?

Can evolutionary suicide occur?

Sexually transmitted infections: evolution

Mating avoidance

Host perspective

Proxy sign-equivalent to mutant invasion fitness

$$f(\hat{\psi}, \psi) = \frac{(\hat{\psi} - \psi) ((1 - I^*(\psi)/N^*(\psi))(\lambda\psi - \beta) - \alpha)}{\psi (\lambda(\hat{\psi} - \psi)I^*(\psi)/N^*(\psi) + \lambda\psi - \alpha)}$$

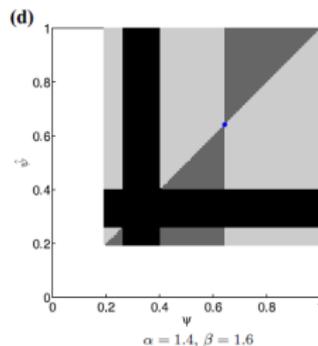
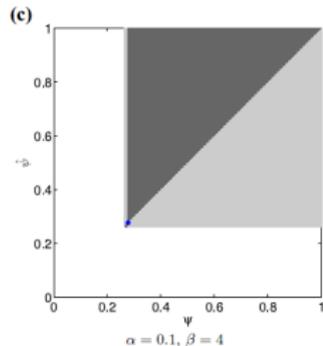
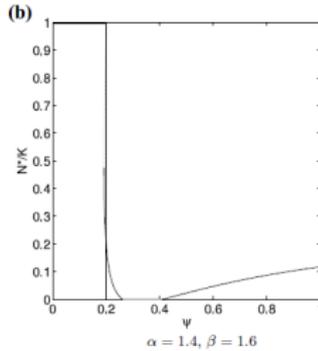
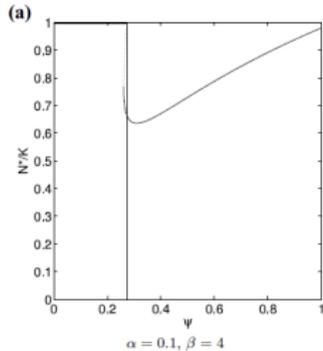
Evolutionary singular point

$$\psi^* = \frac{\beta(\alpha + \beta)(1 - \sigma)^2}{2\alpha\beta(1 - \sigma) + \lambda(\beta(1 - \sigma)^2 - \alpha)}$$

exists provided that $0 < \psi^* < 1$

Sexually transmitted infections: evolution

Host perspective



Bistability:

$\psi \rightarrow 1$

or down to
disease-free
equilibrium
or suicide

Sexually transmitted infections: evolution

Mating avoidance

Pathogen perspective

No trade-off

$$f(\hat{\psi}, \psi) = (\hat{\psi} - \psi) \lambda \frac{S^*}{N^*}$$

$\psi \rightarrow 1$ by evolution

Cryptic parasite, no signs of infectiousness

Sexually transmitted infections: evolution

Pathogen perspective

Transmissibility-visibility trade-off

Higher transmissibility means more conspicuous signs of infectiousness

$$\psi = e^{-A\lambda} \Rightarrow \lambda(\psi) = -\frac{\ln \psi}{A}$$

$$f(\hat{\psi}, \psi) = -\frac{1}{A} \frac{S^*}{N^*} (\hat{\psi} \ln \hat{\psi} - \psi \ln \psi)$$

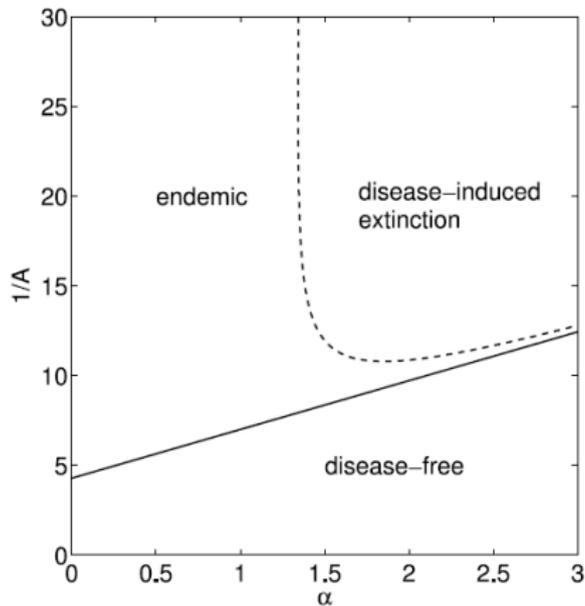
$\psi \rightarrow 1/e$ by evolution: evolutionary attractor

Independent of any host and parasite characteristic

Intermediate value of mating willingness: ecological output?

Sexually transmitted infections: evolution

Pathogen perspective



Sexually transmitted infections: evolution

Pathogen perspective

Virulence-visibility trade-off

More virulent infection means more conspicuous signs of infectiousness

$$\psi = e^{-A\alpha} \Rightarrow \alpha(\psi) = -\frac{\ln \psi}{A}$$

$$f(\hat{\psi}, \psi) = (\hat{\psi} - \psi) \lambda \frac{S^*}{N^*} + \frac{1}{A} (\ln \hat{\psi} - \ln \psi)$$

$\psi \rightarrow 1$ by evolution

Cryptic parasite, unharmed ($\alpha = 0$)

Sexually transmitted infections: evolution

Pathogen perspective

Analogous result for

$$\psi = e^{-A\sigma} \Rightarrow \sigma(\psi) = -\frac{\ln \psi}{A}$$

Invasion fitness does not depend on σ

$\psi \rightarrow 1$ by evolution

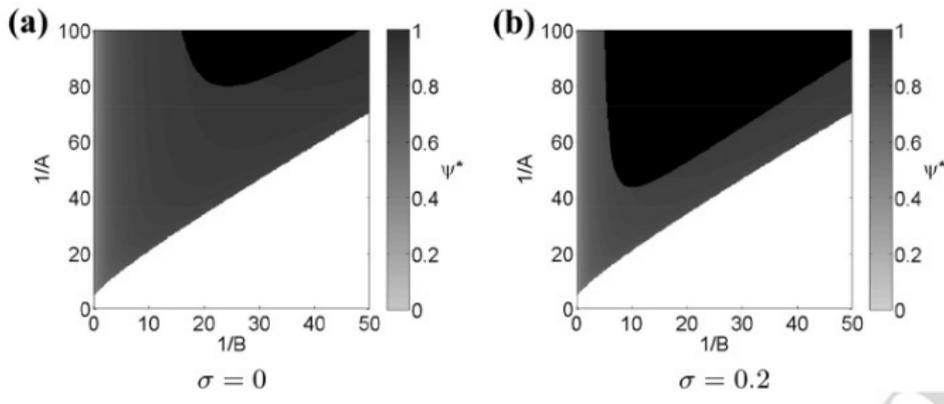
Cryptic parasite, unharmed ($\sigma = 0$)

Sexually transmitted infections: evolution

Pathogen perspective

Both trade-offs

$$\psi = e^{-A\lambda} \quad \text{and} \quad \psi = e^{-B\alpha}$$



Evolutionary attractor or suicide due to host extinction

Sexually transmitted infections: conclusions

- STI avoidance **impacts** host-pathogen dynamics
- Population perspective: best strategy is **not to avoid mating** with infected individuals or **completely avoid mating** with them
- **Disease-induced extinction** can be encountered on the way in between the two extremes → **evolutionary suicide** may occur
- STIs may evolve **to become cryptic** and thus undetectable for mate choice **or to some degree of recognizability**

Thank you!!!

Adaptive dynamics

Selection gradient $D(\lambda) = \left. \frac{\partial s(\lambda_r, \lambda_m)}{\partial \lambda_m} \right|_{\lambda_m = \lambda_r = \lambda}$ determines direction of evolution

Directed evolution stops where selection gradient = 0: **evolutionary singularity** λ^*

λ^* **evolutionarily stable** $\Leftrightarrow E = \left. \frac{\partial^2 s(\lambda_r, \lambda_m)}{(\partial \lambda_m)^2} \right|_{\lambda_m = \lambda_r = \lambda^*} < 0$

λ^* **convergence stable** $\Leftrightarrow C = E + \left. \frac{\partial^2 s(\lambda_r, \lambda_m)}{\partial \lambda_r \partial \lambda_m} \right|_{\lambda_m = \lambda_r = \lambda^*} < 0$

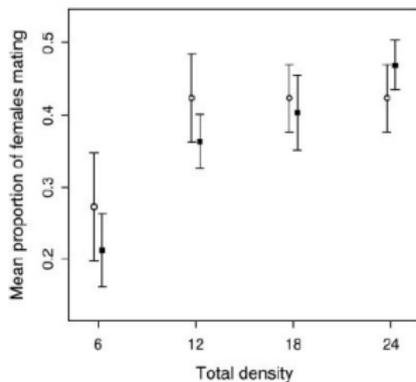
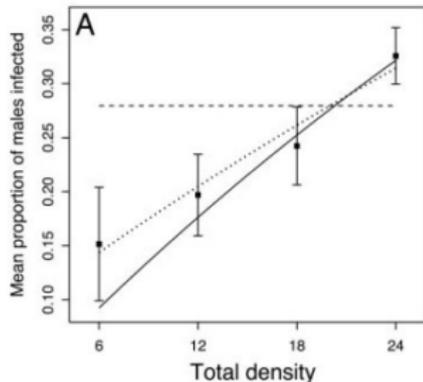
Attractor: evolutionarily stable + convergence stable

Branching point: evolutionarily unstable + convergence stable

Repeller: convergence unstable

Frequency-dependent STI transmission?

The mite *Coccipolipus hippodamiae* as a parasite transmitted sexually in the two-spot ladybird *Adalia bipunctata* (Ryder et al. 2005)



Density-dependent transmission?

Is it mating that mediates infection transmission?