Sexually transmitted infections,

and mate-finding Allee effect

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Allee effects

occur in rare populations when mean fitness increases with increasing population size or density



Vancouver Island marmot *Marmota vancouverensis*

Brashares et al. (2010)





Mate-finding Allee effect

occurs when females have increased difficulty to find mates as male density declines



Azuki bean weevil *Callosobruchus chinensis* Fauvergue (2013)





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While sex may have an advantage in providing genetic variation to combat coevolving pathogens, sex also has a major disadvantage in that it also provides a route for the sexual transmission of pathogens.

Antonovics et al. (2011)

Sexually transmitted infections

STIs are ubiquitous, and tend to ...

- cause sterility than mortality in the host
- ✓ cause less mortality than nonsexually transmitted infections
- ✓ be cryptic, with few overt symptoms
- \checkmark be persistent in the host

Antonovics et al. (2011)

Implications for modeling

✓ STIs affect fertility but less often mortality

 ✓ There is no recovery from infection or (less often) there is recovery to the susceptible class The association between STD and abortion or infertility is well known in animals; indeed, it is perhaps the major reason why veterinarians study these infections.

Oriel and Hayward (1974)

Sexually transmitted infections

Sexual contacts are likely to be relatively independent of overall population density:

- High densities: number of sexual contacts is limited by mating opportunity or breeding season length
- Low densities: organisms are extremely efficient at mate finding even at low densities due to a variety of adaptations

Antonovics et al. (2011)

Implications for modeling

Individuals have a fixed number of new sexual partners per unit time Frequency-dependent transmission

Force of infection

 $\beta c \frac{1}{N}$

β ... transmission probability per partnership
c ... rate at which individuals acquire new sexual partners
I ... density of infectious hosts
N ... total host density

Classic SI model with logistic host growth

$$\frac{dS}{dt} = b(S + \sigma I) - \beta c \frac{SI}{N} - (\mu + dN)S$$
$$\frac{dI}{dt} = \beta c \frac{SI}{N} - (\mu + dN)I - \alpha I$$

- Fecundity reduction
- Horizontal transmission
- Disease-induced mortality

No infection \rightarrow logistic host growth

Classic SI model with logistic host growth

Basic reproduction ratio

$$R_0 = \frac{\beta c}{b + \alpha}$$

Classic results:

✓ Disease-free equilibrium is stable when R₀ < 1
 ✓ Endemic equilibrium exists and is stable when 1 < R₀ < R₀^{crit}
 ✓ Disease-induced extinction equilibrium exists

if $R_0 > 1$ and is stable when $R_0 > R_0^{crit}$

Frequency-dependent transmission is the standard approach to modeling STD transmission in compartmental models.

Lloyd-Smith et al. (2004)

The two-spot ladybird *Adalia bipunctata* and its sexually transmitted mite *Coccipolipus hippodamiae*



The mean proportion of males that were infected at the end of the experiment at each density: 0.67 (A) and 0.33 (B) females infectious

Ryder et al. (2005)



The mean proportion of females that mated at each density. , 0.67 females infectious; , 0.33 females infectious. Ryder et al. (2005)

Berec et al. (in review 1): The mate-finding Allee effect gives rise to a density-dependent infection transmission

Berec et al. (in review 2): Evolution need not always select for extremely efficient mate finding strategies

Partnership dynamics

Partnership dynamics has been found a critical element of STI models

Heesterbeek and Metz (1993): asymptotic transmission function

Lloyd-Smith et al. (2004): frequencydependent transmission function suitable for chronic less transmissible STIs (chiefly viruses)

Changes have been suggested for the transmission term, but the host reproduction term remained unchanged



Reproduction-transmission consistency

Mating mediates both host reproduction and infection transmission It is also possible that the transmission process in STDs is partly density-dependent because mating frequency may decline with decreasing population density. Indeed, if densities fall to such low values that contact rates decline, it is likely that there would be a concomitant fall in reproductive success.

Antonovics et al. (1995)

Sex-structured population model

The core part is a mating function, which describes the rate at which males and females mate (number of females mating per unit time)

Notation: $\mathcal{M}(N_M, N_F)$... N_M and N_F are male and female densities

$$\frac{dN_F}{dt} = (1 - \gamma) b w \mathcal{M}(N_M, N_F) - (\mu_F + d(N_M + N_F)) N_F$$

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

$$\underbrace{\frac{dN_F}{dt}}_{\text{fertilization rate}} + \underbrace{\frac{dN_F}{dt}}_{\text{reproduction rate}} + \underbrace{\frac{dN_F}{dt}}_{\text{reproductio$$

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w ... proportion of matings that end up with giving birth

Sex-structured SI model

The core part is a transmission function, which describes the rate at which susceptible individuals get infected

Random mating – various pairs form at rates

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

 ξ_M , ξ_F ... probabilities of susceptible males / females getting infected upon mating with an infected male / female

 σ_M, σ_F ... fecundity reduction of males / females due to infection

Sex-structured SI model

$$\frac{dS_F}{dt} = (1 - \gamma) bw \mathcal{M}(N_M, N_F) \frac{S_M + \sigma_M I_M}{N_M} \frac{S_F + \sigma_F I_F}{N_F} - \xi_M \mathcal{M}(N_M, N_F) \frac{I_M}{N_M} \frac{S_F}{N_F} - (\mu_F + d(N_M + N_F)) S_F$$

$$\frac{dS_M}{dt} = \gamma bw \mathcal{M}(N_M, N_F) \frac{S_M + \sigma_M I_M}{N_M} \frac{S_F + \sigma_F I_F}{N_F} - \xi_F \mathcal{M}(N_M, N_F) \frac{S_M}{N_M} \frac{I_F}{N_F} - (\mu_M + d(N_M + N_F)) S_M$$

$$\frac{dI_F}{dt} = \xi_M \mathcal{M}(N_M, N_F) \frac{I_M}{N_M} \frac{S_F}{N_F} - (\mu_F + d(N_M + N_F))I_F - \alpha_F I_F$$
$$\frac{dI_M}{dt} = \xi_F \mathcal{M}(N_M, N_F) \frac{S_M}{N_M} \frac{I_F}{N_F} - (\mu_M + d(N_M + N_F))I_M - \alpha_M I_M$$

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Simplification

1:1 sex ratio at birth and sex-independent process rates ($\gamma = 0.5$, $\sigma_F = \sigma_M = \sigma$, $\xi_F = \xi_M = \xi$, $\mu_F = \mu_M = \mu$, $\alpha_F = \alpha_M = \alpha$)

$$S_F = S_M = S/2$$
 where $S = S_F + S_M$
 $I_F = I_M = I/2$ where $I = I_F + I_M$
 $N = N_F + N_M$

$$\frac{dS}{dt} = bw \mathcal{M}\left(\frac{N}{2}, \frac{N}{2}\right) \frac{(S+\sigma I)^2}{N^2} - 2\xi \mathcal{M}\left(\frac{N}{2}, \frac{N}{2}\right) \frac{SI}{N^2} - (\mu + dN) S$$
$$\frac{dI}{dt} = 2\xi \mathcal{M}\left(\frac{N}{2}, \frac{N}{2}\right) \frac{SI}{N^2} - (\mu + dN) I - \alpha I$$

Basic reproduction number R_0

No infection:

$$\frac{dN}{dt} = bw \mathcal{M}\left(\frac{N}{2}, \frac{N}{2}\right) - (\mu + dN)N \Rightarrow \text{ carrying capacity } K$$

Basic reproduction number R_0 :

$$R_0 = \frac{2\xi\mathcal{M}(N/2, N/2)/K}{\mu + dK + \alpha} = \frac{2\xi\mathcal{M}(N/2, N/2)}{bw\mathcal{M}(N/2, N/2) + \alpha K} = \frac{2\xi}{bw}\frac{\mu + dK}{\mu + dK + \alpha}$$

No disease-induced mortality ($\alpha = 0$): $R_0 = \frac{2\xi}{bw}$

For non-lethal STIs R_0 does not depend on the mating function

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

A variety of mating functions have been proposed

Common class: degree-one homogeneous functions $\mathcal{M}(ax, ay) = a\mathcal{M}(x, y)$ for any positive *a*, *x*, *y*

The per female mating rate is constant if the (operational) sex ratio stays constant, no matter how low male and female densities are

Questionable e.g. in presence of the mate-finding Allee effect

Mate-finding Allee effect:
$$\mathcal{M}(N_M, N_F) = N_F \frac{N_M}{N_M + \vartheta}$$
 for a positive ϑ

Degree-one homogeneous mating function

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

Berec and Maxin (2013)

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Degree-one homogeneous mating function

$$\mathcal{M}\left(\frac{N}{2},\frac{N}{2}\right) = \frac{N}{2}\mathcal{M}(1,1)$$

With $\beta := bw \mathcal{M}(1,1)/2$ and $\lambda := \xi \mathcal{M}(1,1)$, our model is

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

Frequency-dependent transmission!

But a non-standard reproduction term!

 $\sigma = 1$: common, linear reproduction term βN

 $\sigma = 0$: reproduction term is βSs , where s = S/N

Full sterilization ($\sigma = 0$), N = S + I, i = I/N, equilibria (N, i)

Transmission	$\lambda < \alpha$ low	$\frac{\alpha < \lambda < \alpha + \beta}{\text{intermediate}}$	$\lambda > lpha + eta$ high
$R_0 = \lambda/(\beta + \alpha)$	< 1	< 1	>1
(0,0) $((\beta - \mu)/d,0)$	unstable stable	unstable stable may or may not	unstable unstable
(<i>Ne, Ie</i>)	_	exist, unstable if it exists	_
(0, i _e)	-	unstable	-
(0,1)	unstable	stable	stable
Outcome	infection cannot invade	infection cannot invade but triggers <mark>bistability</mark>	disease- induced extinction

The bistability case

$$\alpha < \lambda < \alpha + \beta \iff 0 < \frac{\alpha}{\beta + \alpha} < R_0 < 1$$



 $\alpha = 0$: the bistability case covers the whole range $0 < R_0 < 1$

The bistability case

$$\alpha < \lambda < \alpha + \beta \iff 0 < \frac{\alpha}{\beta + \alpha} < R_0 < 1$$



Allee effect characterized by an invasion threshold for the parasite

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The bistability case

This kind of bistability also occurs when sterilization efficieency of the pathogen is incomplete but sufficiently large



Another type of bistability, between the disease-free equilibrium and endemic equilibrium, occurs at intermediate fecundity reduction values
Mate-finding Allee effect mating function

$$\mathcal{M}(N_M, N_F) = N_F \frac{N_M}{N_M + \vartheta}$$
 for a positive ϑ

Berec et al. (in review)

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Mate-finding Allee effect mating function

$$\mathcal{M}(N_M, N_F) = N_F \frac{N_M}{N_M + \vartheta} \Rightarrow \mathcal{M}\left(\frac{N}{2}, \frac{N}{2}\right) = \frac{N^2}{2(N + 2\vartheta)}$$

With $\beta := wb/2$, $\lambda := \xi$ and $\theta := 2\vartheta$, our model is

$$\frac{dS}{dt} = \beta \frac{N}{N+\theta} \frac{(S+\sigma I)^2}{N} - \lambda \frac{N}{N+\theta} \frac{SI}{N} - (\mu + dN)S$$
$$\frac{dI}{dt} = \lambda \frac{N}{N+\theta} \frac{SI}{N} - (\mu + dN)I - \alpha I$$

Asymptotic transmission!

Allee effect term $N/(N + \theta)$ affects both reproduction and transmission

Up to three endemic equilibria





Homoclinic and heteroclinic bifurcations

Possible extinction patterns



Oscillations may warn before host extinction

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Domestic cats infected by FIV





Bistability between endemic and extinction equilibria

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Mating enhancement as a strategy of sexually transmitted parasites

Berec and Maxin (2014)

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Evolution of ST parasites

ST parasites may increase their transmission efficiency by enhancing mating effort / sexual activity of infected individuals

STI-induced mating enhancement has been repeatedly proposed as a natural adaptation of ST parasites to manipulate their hosts

However, just a few examples have been documented so far and the strength of evidence remains weak

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No modeling study appears to have been conducted so far

Evolution of ST parasites

McLachlan (1999): Infestation by the mite Unionicola ypsilophora enhances mating success of males of the midge Paratrichocladius rufiventris

Abbott and Dill (2001): Males of the milkweed leaf beetle Labidomera clivicollis infected with the mite Chrysomelobia labidomera displace rival males from mating pairs more often than uninfected males

Webberley et al. (2002): No effect of a sexually transmitted mite Coccipolipus hippodamiae on willingness to mate in the two-spot ladybird Adalia bipunctata



Labidomera clivicollis

Paratrichocladius rufiventris

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Mating rate of infected individuals in these two species increased roughly 4.2 and 2 times, respectively

Is this phenomenon underexplored or is there any cost countering any potential increase in mating enhancement?

Sex-structured SI model

Parasites are assumed not to affect mate choice, but rather mating effort or sexual activity of their hosts

Random mating and independent contribution of each infected parent

 $\delta_{\rm F}, \delta_{\rm M}$... mating enhancement factor of infected females and males, respectively

 $\delta_F, \delta_M \geq 1$

 $\delta_F = \delta_M = 1 \dots$ no mating enhancement

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Sex-structured SI model

$$\frac{dS_F}{dt} = (1 - \gamma) bw \mathcal{M}(N_M, N_F) \frac{S_M + \delta_M I_M}{N_M} \frac{S_F + \delta_F I_F}{N_F} - \xi_M \delta_M \mathcal{M}(N_M, N_F) \frac{I_M}{N_M} \frac{S_F}{N_F} - (\mu_F + d(N_M + N_F)) S_F$$

$$\frac{dS_M}{dt} = \gamma bw \mathcal{M}(N_M, N_F) \frac{S_M + \delta_M I_M}{N_M} \frac{S_F + \delta_F I_F}{N_F} - \xi_F \delta_F \mathcal{M}(N_M, N_F) \frac{S_M}{N_M} \frac{I_F}{N_F} - (\mu_M + d(N_M + N_F)) S_M$$

$$\frac{dI_F}{dt} = \xi_M \delta_M \mathcal{M}(N_M, N_F) \frac{I_M}{N_M} \frac{S_F}{N_F} - (\mu_F + d(N_M + N_F)) I_F - \alpha_F I_F$$
$$\frac{dI_M}{dt} = \xi_F \delta_F \mathcal{M}(N_M, N_F) \frac{S_M}{N_M} \frac{I_F}{N_F} - (\mu_M + d(N_M + N_F)) I_M - \alpha_M I_M$$

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Simplification

1:1 sex ratio at birth and sex-independent process rates $(\gamma = 1/2, \delta_F = \delta_M = \delta, \xi_F = \xi_M = \xi, \mu_F = \mu_M = \mu, \alpha_F = \alpha_M = \alpha)$

$$S_M = S_F = S/2 \text{ with } S = S_M + S_F$$
$$I_M = I_F = I/2 \text{ with } I = I_M + I_F$$
$$N = N_M + N_F$$

$$\frac{dS}{dt} = bw\mathcal{M}\left(\frac{N}{2}, \frac{N}{2}\right)\frac{(S+\delta I)^2}{N^2} - 2\xi\delta\mathcal{M}\left(\frac{N}{2}, \frac{N}{2}\right)\frac{SI}{N^2} - (\mu + dN)S$$
$$\frac{dI}{dt} = 2\xi\delta\mathcal{M}\left(\frac{N}{2}, \frac{N}{2}\right)\frac{SI}{N^2} - (\mu + dN)I - \alpha I$$

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Degree-one homogeneous mating function

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

With $\beta := bw \mathcal{M}(1,1)/2$ and $\lambda := \xi \mathcal{M}(1,1)$, our model is

$$\frac{dS}{dt} = \beta \frac{(S+\delta I)^2}{N} - \lambda \delta \frac{SI}{N} - (\mu + dN) S$$
$$\frac{dI}{dt} = \lambda \delta \frac{SI}{N} - (\mu + dN) I - \alpha I$$

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Frequency-dependent transmission

Non-linear reproduction term

Evolution of mating enhancement factor δ

No cost to enhanced mating: runaway evolution $\delta \rightarrow \infty$

Reproduction-survival trade-off:

Mating rate δ can increase only at the cost of enhanced host mortality

 $\alpha(\delta) = k \, \delta^z, \, z > 1$



Evolution of mating enhancement factor δ

Mutant invasion fitness

 $(\hat{\delta} \text{ is the mutant's mating enhancement factor})$

$$f(\hat{\delta},\delta) = \lambda(\hat{\delta}-\delta)(1-i^*(\delta)) - k(\hat{\delta}^z - \delta^z)$$

z > 1:

$$\frac{\partial^2 f(\hat{\delta}, \delta)}{\partial \hat{\delta}^2} = -kz(z-1)\hat{\delta}^{z-2} < 0$$

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Any evolutionary singular point is evolutionary stable (no evolutionary branching can occur) Evolution of mating enhancement factor δ

z = 1: runaway evolution, mating enhancement constrained to a very small parameter range



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Effect of trade-off concavity z



The higher cost of mating enhancement *z* lowers the likelihood that disease-induced mating enhancement will evolve

Mating enhancement is more likely to evolve if:

- host reproduction rate and the baseline infection transmission rate both relatively large
- 2 cost of mating enhancement, that is, concavity and steepness of the transmission-virulence trade-off are relatively low
- 3 mating is enhanced in both sexes, as opposed to just in one sex

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4 polygyny in the host population increases (if mating is enhanced just in one sex)

Evolution of a trait affecting strength of the mate-finding Allee effect

Berec et al. (in review)

Evolution of the mate-finding Allee effect

- Low density: evolution is expected to promote traits that reduce strength of the matefinding Allee effect
- High density: evolution may make populations more vulnerable by promoting traits that increase strength of the mate-finding Allee effect



Population density

Density-dependent selection







Strongylocentrotus droebachiensis

Lowest density

Sperm limitation

Larger eggs

Slow, long-lived sperm

23% eggs fertilized

Strongylocentrotus franciscanus

Intermediate density

Intermediate gamete traits

Strongylocentrotus purpuratus

Highest density

Sperm competition

Smaller eggs

Fast, short-lived sperm

94% eggs fertilized

The mate-finding Allee effect still there

64% eggs fertilized

Levitan (1993, 2002)

Agent-based, eco-genetic model

We developed an agent-based, eco-genetic model to study evolution of a trait affecting strength of the mate-finding Allee effect

- Strength of the mate-finding Allee effect is determined by the variables affecting the area a searcher scans per breeding season (search rate, detection distance, movement regularity, breeding season length)
- ✓ Our evolving trait: rate at which individuals search for mates
- ✓ Discrete, non-overlapping generations
- ✓ Females mate only once

Agent-based, eco-genetic model

Scenarios:

- \checkmark Males or females are the searching sex
- There are no costs on mate search, fecundity costs or viability costs
- ✓ Males are either polygynous or monogamous
- ✓ Low, high or oscillating upper bound on male density

How do differences in mating systems and fitness trade-offs interact with changes in population density?



Any female has a certain probability to meet each male; area searched per breeding season: $A(q) = C \phi q$, P(female meets a male) = A(q) / habitat area; movement-viability trade-off

Poisson-distributed number of offspring, movement-fecundity trade-off

Quantitative genetic approach, continuous polygenic trait, additive allelic effects, recombination, mutation

Density-dependent juvenile probability to survive to adulthood

Fixed or alternating upper bound on male density

Males as the searching sex

Baseline scenario



Movement-fecundity trade-off **b**



Male monogamy

с



Movement-viability trade-off d



Time

Females as the searching sex

Baseline scenario



Movement-fecundity trade-off **b**



Male monogamy C



Movement-viability trade-off d



Conclusions and perspectives

- ✓ We propose a framework for modeling STI dynamics by considering that mating mediates both host reproduction and infection transmission: reproduction-transmission consistency assumption
- The question is how often is this assumption a sound description of the underlying processes
- ✓ We used this framework to address several issues related to STIs
- Non-trivial results arose relative to the results of the commonly used STI model formulations
- ✓ This happened mainly when STIs reduced fecundity of infectious individuals, a common assumption for STIs
- ✓ Studies may require full sex-structured models: STI commonly cause abortions which means that fecundity is reduced in just one sex

A recurring theme is the essential habit of re-examining our most basic assumptions: what is a 'contact'? How much detail on population structure is needed to address a given question? What biological processes have been oversimplified, and when are simpler representations appropriate?

Lloyd-Smith et al. (2004)



THANK YOU!



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Evolution of mate-finding Allee effect

- ✓ Negative effects of low density
- ✓ Pheromones, calling, ability to flight, etc.
- Could also have arisen to signal mate quality in high-density populations
- The challenge is to understand which mechanisms have evolved to counter the effects of low density on mating
- Are high density populations likely to lack or reverse such adaptations?

Mate-finding Allee effect

occurs when females have increased difficulty to find mates as male density declines



Azuki bean weevil *Callosobruchus chinensis* Fauvergue (2013)



Trade-offs

Movement-viability trade-off

 $\varphi(q) = \varphi_0 \exp\left(-aq^b\right)$

Movement-fecundity trade-off $b(q) = b_0 \exp(-\kappa q)$



Upper bound on male density oscillates between low and high values



Movement-fecundity trade-off **c**

d



Females are the searching sex

Baseline scenario: no trade-off, male polygyny





Conclusions

- When males are the searching sex, no costs or fecundity costs on mate search cause runaway selection or evolutionary suicide, respectively
- Male monogamy and viability costs on mate search tend to stabilize eco-evolutionary dynamics
- ✓ When females are the searching sex, no such outcomes arise
- ✓ Male monogamy and viability costs on mate search lead to different directions of density-dependent selection
- Possible extensions: metapopulation dynamics, sexual selection, polyandry
- ✓ Is there a possibility of evolutionary branching and dimorphism?

Conclusions and perspectives

- Many ST pathogens are also transmitted by alternative routes: vertically or by close contact (e.g. by aggressive interactions such as biting in primates)
- Exploration of evolution of transmission route as a response to changes in population density or contact rate
- Sexual selection should be a major determinant of how STIs spread through animal populations: ST parasites may respond to mating assortativity in their hosts by being more cryptic; Ashby and Boots (2015): possibility of incomplete crypticity and evolutionary cycling
- ✓ Spatial heterogeneity: higher local density → higher local mating rate → stronger local STI impact → STI-induced sterility / mortality will reduce local population density (metapopulation framework?)
Evolution in hosts

- Sexual selection should be a major determinant of how STIs spread through animal populations
- ✓ Absence of avoidance behavior indicates that STI risk is of secondary importance relative to other selective pressures operating in mating success
- Parasite-mediated sexual selection STI affecting expression of secondary sexual characteristics