Electronic Supporting Material for "Sexually transmitted infection and the evolution of serial monogamy"

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1 Wild-type population dynamics

The wild-type population dynamics are given by

$$\begin{aligned} \dot{S} &= b\,\frac{(S+\delta\,I)^2}{S+I}(1-S-I) - \frac{2\,\beta\,b\,S\,I}{S+I} - S \\ \dot{I} &= I\left(\frac{2\,\beta\,b\,S}{S+I} - \mu\right). \end{aligned} \tag{1}$$

The equations (1) admit three equilibria: population extinction, $(S,\, I) = (0,\, 0)$, the disease-free equilibrium (DFE), $(S,\, I) = (1 - 1/b,\, 0)$, and the endemic equilibrium (EE), given by

$$\begin{aligned} \bar{S} &= \frac{1}{R_0}\left(1 - \frac{2\,\beta\,(R_0 - 1 + 1/\mu)}{(1+\delta(R_0-1))^2}\right), \\ \bar{I} &= \bar{S}\,(R_0 - 1)\,, \end{aligned} \tag{2}$$

where $R_0 = 2\,\beta\,b/\mu$. For the DFE to exist in the positive quadrant, $b > 1$. For the EE to exist in the positive quadrant, $b > 1$, $R_0 > 1$ and $\delta > \delta_c$, where

$$\delta_c = \frac{-1 + \sqrt{2\,\beta\,(1/\mu + R_0 - 1)}}{R_0 - 1}. \tag{3}$$

Because the population is bounded by a carrying capacity, we are only interested in solutions with initial conditions contained in the solid closed triangle $\bar{\Delta} = \{(S, I) : S \in [0, 1],\, 0 \leq I \leq 1 - S\}$. Indeed, $\bar{\Delta}$ is forward invariant to solution trajectories of (1). To

see this, consider the phase plane of (1) (see Fig. 1). It is clear from (1) that if $S = 0$ and $I > 0$, all trajectories crossing the I-axis point into the triangle $\bar{\Delta}$ (see Fig. 1). Similarly, if $S + I = 1$, $\dot{S} < 0$, whereas $\dot{I} > 0$ (resp. $\dot{I} < 0$) if $S > 1/R_0$ (resp. $S < 1/R_0$). Therefore trajectories along the line $S+I = 1$ also remain in $\bar{\Delta}$ (see Fig. 1). Along the S-axis, if $b < 1$, then the trajectories move towards the origin. Hence if $b < 1$, the extinction equilibrium is globally asymptotically stable. If $b > 1$, then trajectories along the S-axis either move towards the extinction equilibrium or the DFE (see Fig. 1). For $I \ll 1$, trajectories move into the interior of $\bar{\Delta}$ provided $R_0 > 1$.

In general, when $b > 1$, the dynamics in the phase plane becomes more complex (see Fig. 1). To investigate, in what follows we examine the local stability of each of the equilibria in turn.

2 Local stability of equilibria

2.1 Extinction equilibrium

First consider the extinction equilibrium. There are two possible cases: i) $I \to 0$ more rapidly then $S \to 0$ as $(S,\, I) \to 0$ (i.e. $I/S \to 0$), or ii) $S \to 0$ more rapidly then $I \to 0$ as $(S,\, I) \to 0$ (i.e. $S/I \to 0$; the case when $S/I \to C < \infty$, where C is a positive constant, is the same). For case i), the Jacobian of (1) evaluated at the extinction equilibrium is

$$J_{00}^{i} = \begin{pmatrix} b-1 & * \\ 0 & 2\,\beta\, b - \mu \end{pmatrix},$$

and hence the extinction equilibrium is stable provided $b < 1$ and $R_0 = 2\,\beta\, b/\mu < 1$.

For case ii), the Jacobian of (1) evaluated at the extinction equilibrium is

$$J_{00}^{ii} = \begin{pmatrix} -b\,(1-\delta)^2 + b - 1 - 2\,\beta\, b & b\,\delta^2 \\ 2\,\beta\, b & -\mu \end{pmatrix}.$$

If $b \leq 1$, this is stable. If $b > 1$, this is locally stable provided $\delta < \delta_0$, where δ_0 is given by

$$\delta_0 = \frac{-1 + \sqrt{2\,\beta\,(1/\mu + R_0 - 1) + 1 - 1/b}}{R_0 - 1}. \tag{4}$$

Observe that $\delta_0 > \delta_c$ and that both δ_0 and δ_c approach 0 as $b \to \infty$. Hence for large b, $\delta_0 \approx \delta_c$.

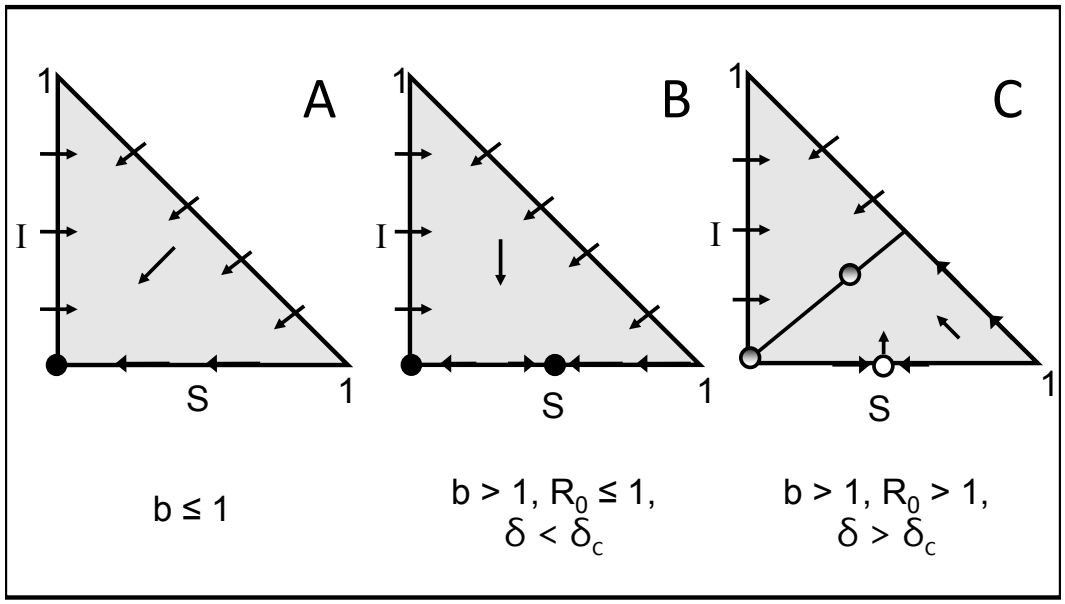

Figure S1: Changes in stability of equilibria of wild-type system. For panel A, the extinction equilibrium is globally asymptotically stable, while for panel B, both the extinction equilibrium and the disease-free equilibrium (DFE) are locally stable. Observe that for both panels A and B, the endemic equilibrium (EE) does not exist in $\bar{\Delta}$. For panel C, the DFE is unstable, while the stability of the EE and the extinction equilibrium vary (see text for further details).

2.2 Disease-free equilibrium

Now suppose $b > 1$, then the DFE, $(S,\, I) = (1 - 1/b,\, 0)$ exists. The Jacobian evaluated at the DFE is

$$J_{DFE} = \begin{pmatrix} -(b-1) & * \\ 0 & 2\,\beta\,b - \mu \end{pmatrix}.$$

Since $b > 1$, if $R_0 < 1$, the DFE is stable. Otherwise the DFE is a saddle and is unstable (see Fig. 1).

2.3 Endemic equilibrium

Now suppose $R_0 > 1$, $b > 1$ and $\delta > \delta_c$. Then the endemic equilibrium (EE) exists in the positive quadrant. The Jacobian evaluated at the EE is

$$J_{EE} = \begin{pmatrix} Y - X - R_0\,W^2 - 1/\mu & \delta\,Y - X - 1/R_0 \\ R_0\,W^2 & -W \end{pmatrix}, \tag{5}$$

where

$$X = b\,\frac{(1 + \delta\,(R_0 - 1))^2}{\mu\,R_0^2}, \quad Y = 2\frac{R_0 - 1 + 1/\mu}{1 + \delta\,(R_0 - 1)}, \quad \text{and} \quad W = \frac{R_0 - 1}{R_0}.$$

The determinant of J_{EE} is

$$\det\left(J_{EE}\right) = \frac{R_0 - 1}{\mu\,R_0^2}\left[b\,(R_0 - 1)^2\delta^2 + 2\,b\,(R_0 - 1)\delta + b - \mu\,R_0(R_0 + 1/\mu - 1)\right], \tag{6}$$

and by solving for the δ at which $\det\left(J_{EE}\right)$ changes sign, it can be shown that if $\delta > \delta_c$, $R_0 > 1$, and $b > 1$, this is strictly positive. Therefore the EE is not a saddle; furthermore, we can conclude that the local stability of the EE rests upon the sign of the trace of J_{EE}. We will first consider the cases when $\delta = 1$ and $\mu = 1$ separately before considering them in combination.

2.3.1 Pathogen only causes mortality ($\delta = 1$)

Suppose $\delta = 1$, that is infection does not cause sterility. Then

$$\mathrm{Tr}\left(J_{EE}\right) = -\left(\frac{(2 + R_0^2 - 3\,R_0)\,\mu + R_0(b+1) - 2}{R_0\,\mu}\right)$$

Notice from the numerator that there can be at most one root; moreover, since $\mathrm{Tr}\,(J_{EE})\,|_{\mu=0} > 0$, while $\mathrm{Tr}\,(J_{EE})\,|_{\mu=1} = -\,(b + R_0 - 2) < 0$, the root occurs on the interval $\mu \in (0, 1)$ and thus is not biologically relevant. Therefore, if the pathogen only causes mortality, the endemic equilibrium is LAS whenever it exists.

2.3.2 Pathogen only causes sterility ($\mu = 1$)

Suppose instead that $\mu = 1$, that is, the pathogen only causes sterility. Then

$$\mathrm{Tr}\,(J_{EE}) \propto -\left(b\,(R_0 - 1)^3\,\delta^3 + 3\,b\,(R_0 - 1)^2\,\delta^2 + (R_0 - 1)(R_0^3 + 3\,b)\,\delta + b - R_0^3\right),$$

where proportionality is with respect to a positive constant. If we assume $b < R_0^3$ (this will only be violated if $\beta \ll 1$, since $b < R_0^3 \Leftrightarrow 1 < 2\,\beta\,R_0^2$), there is exactly one $\delta \in \mathbb{R}^+$ at which $\mathrm{Tr}\,(J_{EE})$ changes sign; denote this value δ^*. As we have previously shown that $\mathrm{Tr}\,(J_{EE})\,|_{\delta=1} < 0$, to ensure that $\delta^* \in (\delta_c, 1)$, we must also have

$$\mathrm{Tr}\,(J_{EE})\,|_{\delta=\delta_c} = -1 - R_0 + 2\,\sqrt{b} > 0,$$

and it follows that if $1 < R_0 < 2\,\sqrt{b} - 1$, then $\delta^* \in (\delta_c, 1)$. Assuming δ^* exists, when $\delta < \delta^*$, the EE is unstable, while for $\delta > \delta^*$, the EE is LAS.

Suppose that $S/I \to 0$ as $(S,\, I) \to (0,\, 0)$ (case ii from the extinction equilibrium discussion), and that $\delta > \delta_0$, that is, the extinction equilibrium is unstable. Then for $\delta^* \in (\delta_0,\, 1)$, we must have

$$\mathrm{Tr}\,(J_{EE})\,|_{\delta=\delta_0} = -R_0 - 1 - \frac{b-1}{R_0^2} + 2\sqrt{\frac{b}{1 + R_0^2(b-1)}} > 0$$

so if we have

$$\sqrt{1 + R_0^2(b-1)}\left(R_0 + 1 + \frac{b-1}{R_0^2}\right) < 2\sqrt{b}$$

then $\delta^* \in (\delta_0,\, 1)$. Now, for $\delta_0 \le \delta < \delta^*$, all three equilibria are locally unstable. As $\bar{\Delta}$ is forward invariant, by Poincaré-Bendixson, we can conclude that there are periodic orbits in the phase plane.

2.3.3 Pathogen causes both sterility and mortality

Finally, suppose virulence affects both mortality and sterility. Then the trace of (5) is

$$\begin{aligned}\mathrm{Tr}\,(J_{EE}) = -A\,\big[b(R_0-1)^3\,\delta^3 + 3\,b\,(R_0-1)^2\delta^2 + (R_0-1)(\mu\,R_0^2(R_0-1) \\ + R_0^2 + 3\,b)\delta + b + \mu\,R_0^2 - R_0^2(\mu\,R_0+1)\big] \quad (7)\end{aligned}$$

where $A = 1/(\mu\,R_0^2[1+\delta(R_0-1)]) > 0$. $\mathrm{Tr}\,(J_{EE})$ can change sign on the interval $\delta \in (0,1)$ if R_0 satisfies

$$3\,\mu\,R_0 - 2(\mu-1) - R_0\,(b+\mu\,R_0) < R_0 < R_0\left(R_0 + \frac{1}{\mu}\right) - \frac{1}{2\,\beta}. \quad (8)$$

If (8) is satisfied, then there exists a δ^* on the interval (0, 1) at which the stability of the EE changes: for $\delta < \delta^*$, the EE is locally unstable, whereas for $\delta > \delta^*$, the EE is locally stable. Obviously, satisfying (8) requires consideration of a significantly restricted set of parameter space; and if (8) is not satisfied, then the EE is LAS. We also note that numerical results indicate that periodic orbits are possible; these of course can only occur when the EE exists.

In what follows, we assume that we are in a region of parameter space for which the endemic equilibrium is LAS.

3 Mutant subpopulation dynamics

Here we present a derivation of the mutant subpopulation dynamics. As mentioned in the main text, the invasion process is fully determined by heterozygous individuals and mutant-wild-type pairings. There are six mutant densities we need to track. We will denote these densities at time t as $q_{\widehat{I}}$, $q_{\widehat{S}}$, $p_{\widehat{S}S}$, $p_{\widehat{S}I}$, $p_{\widehat{I}S}$, and $p_{\widehat{I}I}$, where $q_{\widehat{k}}$ and $p_{\widehat{k}j}$ correspond to densities of singletons and pairs, respectively, and $\widehat{k}$ and $\widehat{kj}$ indicate the infection status of involved individuals. Mutants form pairs at a per-capita rate of $\varphi_{\widehat{kj}}(\rho)$. We suppose that pair-formation comes with a cost, in particular we let $\widehat{\nu}_k(\rho) \in [0,1]$ be the reduced fecundity of a solitary ($k = q$) or paired ($k = p$) mutant, and let $\widehat{\mu}_k(\rho) \geq 1$ be the increased mortality of a solitary ($k = q$) or paired ($k = p$) mutant. We have chosen both costs to be multiplicative to facilitate comparison, however, were we to use additive mortality costs instead, the qualitative results would not change. Both $\widehat{\nu}_k(\rho)$ and $\widehat{\mu}_k(\rho)$ have the property that $\widehat{\nu}_k(0) = \widehat{\mu}_k(0) = 1$.

A susceptible mutant singleton can expect to produce mutant susceptibles at a per-capita rate of $\theta_{\widehat{S}} = \widehat{\nu}_q(\rho)\,\theta_S$, where we assume that θ_S is now at the wild-type endemic equilibrium $(\bar{S}, \bar{I})$. Likewise, an infected singleton can expect to produce mutant susceptibles at a per-

capita rate of $\theta_{\widehat{I}} = \delta\,\theta_{\widehat{S}}$. As part of the different pairings, susceptible mutants are produced at the following rates: $\theta_{\widehat{S}S} = G + 1$, $\theta_{\widehat{S}I} = \delta\,G + \mu$, $\theta_{\widehat{I}S} = \delta\,G$, and $\theta_{\widehat{I}I} = \delta^2\,G$, where $G = \widehat{\nu}_p(\rho)\,b\left(1 - \bar{S} - \bar{I}\right)$, that is, $2\,G$ is the fecundity in the absence of infection; since the mutants are heterozygotes and rare, they can expect that half their reproductive output will also be mutant. Notice that $\theta_{\widehat{S}I}$ and $\theta_{\widehat{S}S}$ include production of susceptible mutants from pairing break up due to the death of the wild-type partner. Likewise, pairings involving infected mutants can also expect to produce infected mutant singletons through the death of the wild-type partner.

We assume that mutant behaviour does not explicitly alter the transmission process, so susceptible singletons become infected at a per-capita rate of λ, which is computed at wild-type equilibrium and hence $\lambda = 2\,\beta\,b - \mu$, whereas the STI is transmitted within $p_{\widehat{I}S}$ and $p_{\widehat{S}I}$ pairings at a per-capita rate of $\lambda_p = 2\,\beta\,b$. Finally, let $\tau_{\widehat{k}}$ denote the per-capita rate at which mutant singletons exit class $\widehat{k}$, and $\tau_{\widehat{k}j}$ denote the per-capita rate at which paired mutants exit the class $\widehat{k}j$. These are as follows

$$\begin{aligned}
\tau_{\widehat{S}} &= \widehat{\mu}_q(\rho) + \lambda + \varphi_{\widehat{S}I}(\rho) + \varphi_{\widehat{S}S}(\rho) & \qquad \tau_{\widehat{I}} &= \mu\,\widehat{\mu}_q(\rho) + \varphi_{\widehat{I}I}(\rho) + \varphi_{\widehat{I}S}(\rho) \\
\tau_{\widehat{S}S} &= \widehat{\mu}_p(\rho) + 1 & \qquad \tau_{\widehat{I}I} &= \mu\,\widehat{\mu}_p(\rho) + \mu \\
\tau_{\widehat{S}I} &= \widehat{\mu}_p(\rho) + \mu + \lambda_p & \qquad \tau_{\widehat{I}S} &= \mu\,\widehat{\mu}_p(\rho) + 1 + \lambda_p.
\end{aligned}$$

The dynamics of the mutant subpopulation can therefore be written in matrix-vector notation as

$$\begin{pmatrix} \dot{q}_{\widehat{S}} \\ \dot{q}_{\widehat{I}} \\ \dot{p}_{\widehat{I}I} \\ \dot{p}_{\widehat{I}S} \\ \dot{p}_{\widehat{S}I} \\ \dot{p}_{\widehat{S}S} \end{pmatrix} = \begin{pmatrix} \theta_{\widehat{S}} - \tau_{\widehat{S}} & \theta_{\widehat{I}} & \theta_{\widehat{I}I} & \theta_{\widehat{I}S} & \theta_{\widehat{S}I} & \theta_{\widehat{S}S} \\ \lambda & -\tau_{\widehat{I}} & \mu & 1 & 0 & 0 \\ 0 & \varphi_{\widehat{I}I}(\rho) & -\tau_{\widehat{I}I} & \lambda_p & \lambda_p & 0 \\ 0 & \varphi_{\widehat{I}S}(\rho) & 0 & -\tau_{\widehat{I}S} & 0 & 0 \\ \varphi_{\widehat{S}I}(\rho) & 0 & 0 & 0 & -\tau_{\widehat{S}I} & 0 \\ \varphi_{\widehat{S}S}(\rho) & 0 & 0 & 0 & 0 & -\tau_{\widehat{S}S} \end{pmatrix} \begin{pmatrix} q_{\widehat{S}} \\ q_{\widehat{I}} \\ p_{\widehat{I}I} \\ p_{\widehat{I}S} \\ p_{\widehat{S}I} \\ p_{\widehat{S}S} \end{pmatrix}, \tag{9}$$

where dots denote differentiation with respect to non-dimensionalized time.

4 Invasion condition

The Jacobian of (9) evaluated at the mutant free equilibrium (MFE) is simply the matrix in (9). Denote this matrix J_{MFE}. To assess stability of the MFE, we apply the next-generation method [1, 2]. This involves decomposing J_{MFE} into two matrices, F and V such that: i) $J_{MFE} = F - V$, ii) all entries of F are nonnegative, and iii) each eigenvalue of $-V$ must have negative real part. If F and V are selected in this way, then the MFE is stable if the

spectral radius of the matrix FV^{-1} is less than 1.

In general, F and V are chosen in a biologically specific way [2]. As we are concerned with host reproductive success, we focus on production of susceptible mutants. This production can occur in two ways: through reproduction or through the break up of $p_{\widehat{S}I}$ or $p_{\widehat{S}S}$ pairings through the death of the wild-type partner. Within the context of lifetime reproductive success (LRS), pairing break up can be viewed as an individual giving 'birth' to itself.

Define F as a 6×6 matrix whose first row is $\begin{pmatrix} \theta_{\widehat{S}} & \theta_{\widehat{I}} & \theta_{\widehat{I}I} & \theta_{\widehat{I}S} & \theta_{\widehat{S}I} & \theta_{\widehat{S}S} \end{pmatrix}$, and whose remaining entries are zero, and V as

$$V = \begin{pmatrix} \tau_{\widehat{S}} & 0 & 0 & 0 & 0 & 0 \\ -\lambda & \tau_{\widehat{I}}(\rho) & -\mu & -1 & 0 & 0 \\ 0 & -\varphi_{\widehat{I}I}(\rho) & \tau_{\widehat{I}I} & -\lambda_p & -\lambda_p & 0 \\ 0 & -\varphi_{\widehat{I}S}(\rho) & 0 & \tau_{\widehat{I}S} & 0 & 0 \\ -\varphi_{\widehat{S}I}(\rho) & 0 & 0 & 0 & \tau_{\widehat{S}I} & 0 \\ -\varphi_{\widehat{S}S}(\rho) & 0 & 0 & 0 & 0 & \tau_{\widehat{S}S} \end{pmatrix}.$$

All entries of F are nonnegative. It remains to show that the eigenvalues of V have positive real part (doing so implies that the eigenvalues of $-V$ have negative real part). V is block triangular: we have the blocks v_{11}, v_{66} and the inner 4×4 block; however, the inner 4×4 block is itself block triangular, with one of its blocks consisting of the entry v_{55}. Therefore three of the eigenvalues of V are given by the entries v_{11}, v_{55} and v_{66}, each of which is positive and real. The remaining three eigenvalues are determined by the matrix

$$M = \begin{pmatrix} \tau_{\widehat{I}} & -\mu & -1 \\ -\varphi_{\widehat{I}I} & \tau_{\widehat{I}I} & -\lambda_p \\ -\varphi_{\widehat{I}S} & 0 & \tau_{\widehat{I}S} \end{pmatrix}.$$

To show that the eigenvalues of M have positive real part, we use Gershgorin circle theorem [3]. Briefly, if we define the Gerschgorin disks of M

$$D_i = \{|z - m_{ii}| \leq R_i : z \in \mathbb{C}\}, \quad \text{with } R_I = \sum_{\substack{j=1 \\ j \neq i}}^{n} |m_{ji}|, \quad i = 1, 2, 3$$

and let the Gerschgorin domain of M, $D_M = \cup_{i=1}^{3} D_i \subset \mathbb{C}$, be the union of the disks, then all eigenvalues of the matrix M lie in its Gerschgorin domain D_M [3].

As each of the diagonal entries of M correspond to the total rate at which individuals exit a particular class while the off-diagonal column entries correspond to a subset of those rates, we necessarily have that the $D_i > R_i$ for each $i = 1, 2, 3$. Since for each D_i, the center

is greater than the radius, all points in each disk are strictly positive, hence all points in the union of the three discs are also strictly positive. It follows immediately that all eigenvalues of M have positive real part. Therefore we are justified in choosing F and V as we have.

Proceeding, we can compute FV^{-1}, which in this case is a matrix with all zero entries other than the first row. As a result, the stability of the MFE is determined by entry fv_{11}^{-1}. Specifically, if fv_{11}^{-1}, which represents LRS of a rare mutant, is greater than the wild-type LRS (which at equilibrium is equal to 1), then the mutant can invade. That is

$$\frac{\theta_{\widehat{S}}}{\tau_{\widehat{S}}} + \frac{\varphi_{\widehat{S}S}}{\tau_{\widehat{S}}}\frac{\theta_{\widehat{S}S}}{\tau_{\widehat{S}S}} + \frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\theta_{\widehat{S}I}}{\tau_{\widehat{S}I}} + \left(\frac{\lambda}{\tau_{\widehat{S}}} + \frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\lambda_p}{\tau_{\widehat{S}I}}\frac{\mu}{\tau_{\widehat{I}I}}\right)\mathcal{I}\frac{\theta_{\widehat{I}}}{\tau_{\widehat{I}}} + \left(\frac{\lambda}{\tau_{\widehat{S}}} + \frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\lambda_p}{\tau_{\widehat{S}I}}\frac{\mu}{\tau_{\widehat{I}I}}\right)\mathcal{I}\frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\theta_{\widehat{I}S}}{\tau_{\widehat{I}S}}$$
$$+ \left(\frac{\lambda}{\tau_{\widehat{S}}}\mathcal{I}\left[\frac{\varphi_{\widehat{I}I}}{\tau_{\widehat{I}}} + \frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\lambda_p}{\tau_{\widehat{I}S}}\right] + \underbrace{\frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\lambda_p}{\tau_{\widehat{S}I}}\left[1 - \frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{1}{\tau_{\widehat{I}S}}\right]}_{\mathrm{a}}\right)\frac{\theta_{\widehat{I}I}}{\tau_{\widehat{I}I}} > 1. \quad (10)$$

where $\mathcal{I}$ is

$$\mathcal{I} = \left(1 - \frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\lambda_p}{\tau_{\widehat{I}S}}\frac{\mu}{\tau_{\widehat{I}I}} - \frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{1}{\tau_{\widehat{I}S}} - \frac{\varphi_{\widehat{I}I}}{\tau_{\widehat{I}}}\frac{\mu}{\tau_{\widehat{I}I}}\right)^{-1}.$$

Recognizing that $\mathcal{I}$ is the sum of a infinite geometric series, following two applications of the binomial theorem, $\mathcal{I}$ can be rewritten as

$$\mathcal{I} = \sum_{n=0}^{\infty}\sum_{k=0}^{n}\binom{n}{k}\left(\frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\lambda_p}{\tau_{\widehat{I}S}}\frac{\mu}{\tau_{\widehat{I}I}}\right)^{k}\sum_{j=0}^{n-k}\binom{n-k}{j}\left(\frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{1}{\tau_{\widehat{I}S}}\right)^{j}\left(\frac{\varphi_{\widehat{I}I}}{\tau_{\widehat{I}}}\frac{\mu}{\tau_{\widehat{I}I}}\right)^{n-k-j}.$$

We also need to rewrite $\mathbf{a}$; to do so we use the definition of $\mathcal{I}$:

$$\mathbf{a} = \frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\lambda_p}{\tau_{\widehat{S}I}}\mathcal{I}\left(\mathcal{I}^{-1} + \frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\lambda_p}{\tau_{\widehat{I}S}}\frac{\mu}{\tau_{\widehat{I}I}} + \frac{\varphi_{\widehat{I}I}}{\tau_{\widehat{I}}}\frac{\mu}{\tau_{\widehat{I}I}}\right) = \frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\lambda_p}{\tau_{\widehat{S}I}}\left(1 + \frac{\mu}{\tau_{\widehat{I}I}}\mathcal{I}\left[\frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\lambda_p}{\tau_{\widehat{I}S}} + \frac{\varphi_{\widehat{I}I}}{\tau_{\widehat{I}}}\right]\right). \quad (11)$$

Then swapping $\mathbf{a}$ in (10), the invasion condition, partitioned to match with Figure 1 from

the main text is

$$\underbrace{\frac{\theta_{\widehat{S}}}{\tau_{\widehat{S}}}}_{\text{i}} + \underbrace{\frac{\varphi_{\widehat{S}S}}{\tau_{\widehat{S}}}\frac{\theta_{\widehat{S}S}}{\tau_{\widehat{S}S}}}_{\text{ii}} + \underbrace{\frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\theta_{\widehat{S}I}}{\tau_{\widehat{S}I}}}_{\text{iii}} + \underbrace{\left(\frac{\lambda}{\tau_{\widehat{S}}} + \frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\lambda_p}{\tau_{\widehat{S}I}}\frac{\mu}{\tau_{\widehat{I}I}}\right)\mathcal{I}\frac{\theta_{\widehat{I}}}{\tau_{\widehat{I}}}}_{\text{iv}} + \underbrace{\left(\frac{\lambda}{\tau_{\widehat{S}}} + \frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\lambda_p}{\tau_{\widehat{S}I}}\frac{\mu}{\tau_{\widehat{I}I}}\right)\mathcal{I}\frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\theta_{\widehat{I}S}}{\tau_{\widehat{I}S}}}_{\text{v}}$$
$$+ \underbrace{\left(\frac{\lambda}{\tau_{\widehat{S}}}\mathcal{I}\left[\frac{\varphi_{\widehat{I}I}}{\tau_{\widehat{I}}} + \frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\lambda_p}{\tau_{\widehat{I}S}}\right] + \frac{\varphi_{\widehat{S}I}}{\tau_{\widehat{S}}}\frac{\lambda_p}{\tau_{\widehat{S}I}}\left[1 + \frac{\mu}{\tau_{\widehat{I}I}}\mathcal{I}\left\{\frac{\varphi_{\widehat{I}S}}{\tau_{\widehat{I}}}\frac{\lambda_p}{\tau_{\widehat{I}S}} + \frac{\varphi_{\widehat{I}I}}{\tau_{\widehat{I}}}\right\}\right]\right)\frac{\theta_{\widehat{I}I}}{\tau_{\widehat{I}I}}}_{\text{vi}} > 1, \quad (12)$$

As a check of (12), observe that if the mutation is selectively neutral ($\rho = 0$), then $\varphi_{\widehat{k}j} = 0$, and the left-hand side of (12) simplifies to 1, as expected.

4.1 Weak selection approximation

Fix attention on the pairing function given by

$$\varphi_{\widehat{k}j}(\rho) = \rho\,\frac{\bar{j}}{\bar{I} + \bar{S}}.$$

As an aside, observe that were we to use our choice of $\varphi_{\widehat{k}j}(\rho)$ in (10) and assume that the wild-type population is at the DFE rather than the endemic equilibrium, when pair formation is cost free (i.e. $\widehat{\nu}_k(\rho) = 1$ and $\widehat{\mu}_k(\rho) = 0$), (12) simplifies to $\rho > 1$. That is, invasion is possible if the rate at which pairs form, ρ, exceeds the wild-type mortality. This is intuitive: if there is no STI present in the population and pair formation is cost free, forming pairs is only advantageous if it prolongs lifespan.

Now, applying a Maclaurin expansion to (12), while noting that $\mathcal{I}(0) = 1$, we obtain

$$1 + \left(\frac{1}{2}\left(\frac{R_0 - 1}{R_0}\right)\frac{a_2\delta^2 - a_1\delta + a_0}{\left((R_0 + 1/\mu)^2 - 1\right)\left(1 + \delta(R_0 - 1)\right)^2}\right.$$
$$\left. + \left.\frac{\mathrm{d}\widehat{\nu}_q}{\mathrm{d}\rho}\right|_{\rho=0} - \left(\frac{\delta(R_0 - 1)}{1 + \delta(R_0 - 1)} + \frac{1}{\mu\left(R_0 + 1/\mu - 1\right)}\right)\left.\frac{\mathrm{d}\widehat{\mu}_q}{\mathrm{d}\rho}\right|_{\rho=0}\right)\rho + O(\rho^2) > 1, \quad (13)$$

where

$$a_2 = \frac{1}{\mu}\left((R_0-1)^2\left(R_0+\frac{1}{\mu}\right)+\frac{R_0-1}{\mu^2}+\frac{R_0\,(R_0+1)}{\mu}\right)$$
$$a_1 = \frac{1}{\mu}\left(1+(R_0-1)\left(R_0+\frac{1}{\mu}\right)^2+3\,R_0\right)$$
$$a_0 = \left(R_0+\frac{1}{\mu}\right)\left(R_0+1-\frac{1}{\mu}\right).$$

Under weak selection, we can neglect $O(\rho^2)$ terms, and therefore invasion is determined by the selection gradient, which is the coefficient of ρ. The sign of the selection gradient determines the success of mutant invasion.

4.1.1 No infection induced mortality ($\mu = 1$)

Suppose $\mu = 1$. Then the LHS of (13) simplifies to

$$\frac{1}{2}\left(\frac{R_0-1}{R_0}\right)\frac{(1-\delta)(R_0+1-\delta(1+R_0^2))}{(R_0+2)(1+\delta(R_0-1))^2}. \tag{14}$$

We first want to understand the behaviour of (14) as we vary the rate of infection transmission, R_0 (manipulating β or b). (14) has two positive roots, $R_0 = 1$ and

$$R_0^* = \left(1+\sqrt{1+4\,\delta(1-\delta)}\right)/(2\,\delta) > 1.$$

Now the derivative of (14) at $R_0 = 1$ is $(1-\delta)^2/3 > 0$, while as $R_0 \to \infty$, (14) goes to 0 from below. Therefore for $R_0 \in (0,1)\cup(R_0^*,\infty)$, (14) is negative and is non-negative for $R_0 \in [1, R_0^*]$. By taking the derivative of (14), it can be shown that there are strictly two critical points; one on the interval $(1,\, R_0^*)$, and one on the interval $(R_0^*,\, \infty)$. Combining this information allows us to show the general behaviour of (14) as R_0 is varied in Figure 2.

Now consider (14) as a function of δ. It has roots at $\delta = 1$ and $\delta = (R_0+1)/(1+R_0^2)$. If we take the derivative of (14) with respect to δ, we obtain

$$\frac{1}{2}\frac{(R_0-1)\,(\delta(R_0+1)^2-(1+3R_0))}{(R_0+2)(1+\delta(R_0-1))^3},$$

and it follows that if $\delta > (1+3R_0)/(1+R_0)^2$, the function is increasing, whereas if $\delta < (1+3R_0)/(1+R_0)^2$, the function is decreasing. Evaluating (14) at $\delta = (1+3R_0)/(1+R_0)^2$

yields

$$-\frac{1}{16}\frac{(R_0-1)^3}{R_0^2(R_0+2)}<0,$$

so invasion is only possible for $\delta \in (\delta_c, [R_0+1]/[1+R_0^2])$, where δ_c is the critical value of δ below which the population is driven to extinction. As δ increases on this interval, the likelihood of the evolution of monogamy declines. Of course, as noted in the main text, it is not necessarily true that $(R_0+1)/(1+R_0^2) > \delta_c$. If this is not satisfied, then invasion is not possible.

If we suppose that $\widehat{\nu}_q'(0) = 0$ and $\widehat{\mu}_q'(0) \neq 0$, then we can divide through by the multiplier in (13) giving the invasion condition, when $\mu = 1$ as

$$\frac{1}{2}\frac{(R_0-1)(1-\delta)(R_0+1-\delta(1+R_0^2))}{(R_0+2)(1+\delta(R_0-1))(\delta R_0^2+1-\delta)} > \left|\widehat{\mu}_q'(0)\right| \tag{15}$$

Following some elementary calculus, it can be shown that the shape of (14) and (15) are qualitatively similar; it is also clear that from inspection that they differ simply by one of the denominator terms ((15) has $\delta R_0^2 + 1 - \delta$, while (14) has $R_0(1+\delta(R_0-1))$). Since

$$\delta R_0^2 + 1 - \delta < \delta R_0^2 + R_0(1-\delta) = R_0(1+\delta(R_0-1)),$$

the LHS of (15) is greater than the LHS of (14), so monogamy is more advantageous when the trade-off is with mortality rather than fecundity.

4.1.2 No infection induced sterility ($\delta = 1$)

Suppose $\delta = 1$. Then the LHS of (13) simplifies to

$$\frac{1}{2}\left(\frac{R_0-1}{R_0^2}\right)\frac{(1-1/\mu)(R_0+1-1/\mu)}{(R_0+1+1/\mu)(R_0-1+1/\mu)}. \tag{16}$$

As $\mu > 1$, (16) has a single positive root with respect to R_0, at $R_0 = 1$. Also note that as $R_0 \to \infty$, (16) approaches 0 from above and as $R_0 \to 0$, (16) approaches ∞. There is also a discontinuity when $R_0 = 1 - 1/\mu$ (which is mathematically relevant, but not biologically, since R_0, $\mu > 1$). When $R_0 \to (1-1/\mu)^+$, (16) $\to -\infty$, whereas when $R_0 \to (1-1/\mu)^-$, (16) $\to \infty$. By taking the derivative with respect to R_0, it can be shown that (16) has two critical points. Hence, combining all of the above information allows us to deduce the general form of the curve given by (16), which is shown in Figure 2. Of course,we have assumed that the RHS of (13) is equal to zero; if it is not, then the invasion curve is translated downward.

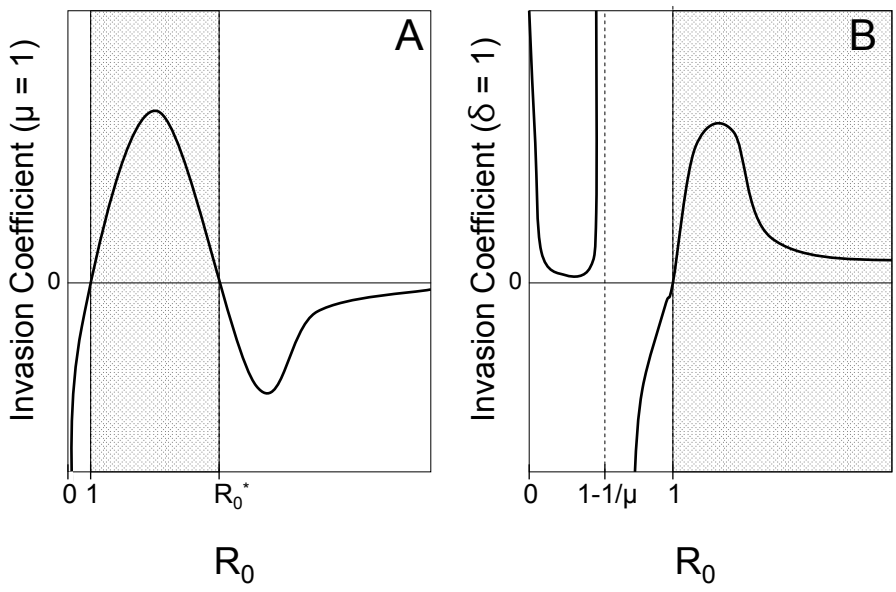

Figure S2: General qualitative behaviour of invasion coefficients when pathogen virulence exclusively causes sterility (panel A) or exclusively causes mortality (panel B). The shaded region of each plot represents the biologicallly relevant section of parameter space in which invasion is possible.

If we suppose that $\widehat{\nu}'_q(0) = 0$ and $\widehat{\mu}'_q(0) \neq 0$, then dividing through by the multiplier in (13) gives the revised version of (16) as

$$\frac{1}{2}\left(\frac{R_0 - 1}{R_0}\right)\frac{(1 - 1/\mu)\,(R_0 + 1 - 1/\mu)}{(R_0 + 1 + 1/\mu)\,(R_0^2 - (1 - 1/\mu)(2\,R_0 - 1))}. \tag{17}$$

As before, by elementary calculus, it can be shown that this curve qualitatively matches that of (16). However, (17) has $R_0^2 - (1 - 1/\mu)(2R_0 - 1)$ in the denominator, whereas (16) has $R_0(R_0 - 1 + 1/\mu)$. Thus (17) is greater than or equal to (16), so monogamy is more advantageous when the trade-off is with mortality rather than fecundity.

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