```
> ##############################################################################
> # Coevolution: approximation to fast social information dynamics & fast parasite evolution #
> ##############################################################################
>
> restart :
> with(VectorCalculus) :
> with(LinearAlgebra) :
> interface(imaginaryunit = _I) :
>
> # Assume parasite evolves rapidly to maximise R0
> beta := kappa·sqrt(alpha) : # This is the transmission-virulence trade-off we are assuming
```

$$> A := 1 - \frac{\mathrm{sigma}}{\mathrm{tau} \cdot c \cdot c} :$$

$$> R0 := \frac{\mathrm{beta} \cdot c^2}{(d \cdot (1 - (1 - a) \cdot A) + \mathrm{alpha} + \mathrm{gamma})} :$$

```
>
> # Fitness gradient for the parasite
> R0_1 := simplify(diff(R0, alpha));
```

$$R0\_1 := \frac{\left(c^2 \left(a\, d - \alpha + \gamma\right) \tau - d\, \sigma \left(-1 + a\right)\right) \kappa\, c^4\, \tau}{2 \sqrt{\alpha} \left(c^2 \left(a\, d + \alpha + \gamma\right) \tau - d\, \sigma \left(-1 + a\right)\right)^2} \qquad \textbf{(1)}$$

```
> # Optimal virulence
> alpha_ss := simplify(solve(R0_1, alpha));
```

$$alpha\_ss := \frac{c^2 \left(a\, d + \gamma\right) \tau - d\, \sigma \left(-1 + a\right)}{c^2\, \tau} \qquad \textbf{(2)}$$

```
> # Optimal transmission
> beta_ss := subs(alpha = alpha_ss, beta);
```

$$beta\_ss := \kappa \sqrt{\frac{c^2 \left(a\, d + \gamma\right) \tau - d\, \sigma \left(-1 + a\right)}{c^2\, \tau}} \qquad \textbf{(3)}$$

```
>
>
> # Host evolution
> # First calculate information awareness in mutant when rare (Ams)
>
```

$$> dSAm := \frac{cm \cdot c}{N} \cdot (\mathrm{tau} \cdot SUm \cdot A \cdot N) - \mathrm{sigma} \cdot SAm :$$

$$> dIAm := \frac{cm \cdot c}{N} \cdot (\mathrm{tau} \cdot IUm \cdot A \cdot N) - \mathrm{sigma} \cdot IAm :$$

$$> dAm := \frac{1}{Nm} \cdot \left(\frac{cm \cdot c}{N} \cdot (\mathrm{tau} \cdot (1 - Am) \cdot Nm \cdot A \cdot N) - \mathrm{sigma} \cdot Am \cdot Nm \right) :$$

```
> Ams := solve(dAm, Am);
```

$$Ams := \frac{cm\,(\tau c^2 - \sigma)}{c^2\, cm\, \tau + \sigma c - cm\, \sigma} \quad \textbf{(4)}$$

\>

\> *# Now calculate resident equilibrium*

\> $dS := (b - q\cdot(S+I))\cdot(S+I) - \dfrac{\text{beta}\cdot c\cdot c\cdot S\cdot I}{(S+I)} - d\cdot(1-(1-a)\cdot A)\cdot S + \text{gamma}\cdot I:$

\> $dI := \dfrac{\text{beta}\cdot c\cdot c\cdot S\cdot I}{(S+I)} - (d\cdot(1-(1-a)\cdot A) + \text{alpha} + \text{gamma})\cdot I:$

\> $dN := (b - q\cdot N)\cdot N - d\cdot(1-(1-a)\cdot A)\cdot N - \text{alpha}\cdot I:$

\> $sol := solve([dS, dI], [S, I]):$

\> $eql := simplify(sol[2]):$

\> $Ns := simplify(subs(eql, S+I));$

$$Ns := \frac{1}{\kappa c^4 \tau q}\left(\alpha^{3/2} c^2 \tau + \left(c^2 (a d + \gamma)\tau - d\sigma(-1+a)\right)\sqrt{\alpha} + \kappa c^2\left(-\tau(a d + \alpha - b) c^2 + d\sigma(-1+a)\right)\right) \quad \textbf{(5)}$$

\>

\> *# Mutant dynamics*

\> $dSm := (b - q\cdot N)\cdot(Sm + \text{Im}) - \dfrac{\text{beta}\cdot cm\cdot c\cdot Sm\cdot I}{N} - d\cdot(1-(1-a)\cdot Ams)\cdot Sm + \text{gamma}\cdot\text{Im}:$

\> $dIm := \dfrac{\text{beta}\cdot cm\cdot c\cdot Sm\cdot I}{N} - (d\cdot(1-(1-a)\cdot Ams) + \text{alpha} + \text{gamma})\cdot\text{Im}:$

\>

\> *# Calculate the Jacobian*

\> $J := (Jacobian([dSm, dIm], [Sm, \text{Im}]));$

$$J := \left[\left[-q N + b - \frac{\kappa\sqrt{\alpha}\, cm\, c\, I}{N} - d\left(1 - \frac{(1-a)\, cm\,(\tau c^2 - \sigma)}{c^2\, cm\,\tau + c\,\sigma - cm\,\sigma}\right), -q N + b + \gamma\right], \left[\frac{\kappa\sqrt{\alpha}\, cm\, c\, I}{N}, -d\left(1 - \frac{(1-a)\, cm\,(\tau c^2 - \sigma)}{c^2\, cm\,\tau + c\,\sigma - cm\,\sigma}\right) - \alpha - \gamma\right]\right] \quad \textbf{(6)}$$

\>

\> *# Split the Jacobian into components F and V as follows*

\> $F := \langle\langle b - q\cdot N, 0\rangle | \langle b - q\cdot N, 0\rangle\rangle;$

$$F := \begin{bmatrix} -q N + b & -q N + b \\ 0 & 0 \end{bmatrix} \quad \textbf{(7)}$$

\> $V := F - J;$

$$V := \left[\left[\frac{\kappa\sqrt{\alpha}\, cm\, c\, I}{N} + d\left(1 - \frac{(1-a)\, cm\,(\tau c^2 - \sigma)}{c^2\, cm\,\tau + c\,\sigma - cm\,\sigma}\right), -\gamma\right], \quad \textbf{(8)}$$

$$\left[-\frac{\kappa\sqrt{\alpha}\ cm\ c\ I}{N},\ d\left(1-\frac{(1-a)\ cm\ \left(\tau c^2-\sigma\right)}{c^2\ cm\ \tau+c\ \sigma-cm\ \sigma}\right)+\alpha+\gamma\right]\right]$$

> *# Now calculate the next-generation matrix*

> $V1 := MatrixInverse(V):$

> $NG := simplify(F \cdot V1):$

>

> *# Fitness is equal to the largest eigenvalue of the NG matrix minus 1*

> $w := simplify(NG[1,1]) - 1;$

$$w := \left(\left(cm\ \kappa\left(\left(\tau c^2-\sigma\right) cm+c\ \sigma\right) c\ I\sqrt{\alpha}+N\left(-\left(-\tau c^2+\sigma\right)\left(a\ d+\alpha+\gamma\right) cm+\sigma c\left(\alpha+\gamma+d\right)\right)\right)\left(\left(\tau c^2-\sigma\right) cm+c\ \sigma\right)\left(q\ N-b\right)\right) \Big/ \left(-cm\ \kappa\left(\left(\tau c^2-\sigma\right) cm+c\ \sigma\right)^2 c\ I\ \alpha^{3/2}+\left(a\left(-\tau c^2+\sigma\right) cm-c\ \sigma\right)\left(cm\ \kappa\left(\left(\tau c^2-\sigma\right) cm+c\ \sigma\right) c\ I\sqrt{\alpha}+N\left(-\left(-\tau c^2+\sigma\right)\left(a\ d+\alpha+\gamma\right) cm+\sigma c\left(\alpha+\gamma+d\right)\right)\right) d\right)-1 \tag{9}$$

>

> *# Calculate the fitness gradient*

> $dw0 := simplify(subs(cm = c, diff(w, cm))):$

> $dw := simplify(subs(eql, (subs(N = Ns, dw0))));$

$$dw := \left(\left(-\alpha^{3/2} c^2\tau+\left(-c^2\left(a\ d+\gamma\right)\tau+d\ \sigma\left(-1+a\right)\right)\sqrt{\alpha}+\kappa c^2\left(\tau\left(a\ d+\alpha\right)c^2-d\ \sigma\left(-1+a\right)\right)\right)\left(-\alpha^{3/2} c^8\kappa\tau^3-\left(\tau^2\left(a\ d+\gamma\right)c^4-2\ d\ \tau\ \sigma\left(-1+a\right)c^2+d\ \sigma^2\left(-1+a\right)\right)\kappa c^4\tau\sqrt{\alpha}-d\ \tau^2\kappa^2\sigma\left(-1+a\right)c^8+\left(\left(a\ d+\alpha+\gamma\right)^2\tau^2+d\ \kappa^2\sigma^2\left(-1+a\right)\tau c^6-3\ d\ \tau^2\sigma\left(-1+a\right)\left(a\ d+\alpha+\gamma\right)c^4+3\ \sigma^2 d\left(-1+a\right)\left(\left(a-\frac{2}{3}\right)d+\frac{\alpha}{3}+\frac{\gamma}{3}\right)\tau c^2-d^2\sigma^3\left(-1+a\right)^2\right)\alpha\right)\Big/\left(\left(\alpha^{3/2}c^4\kappa\tau+d\ \kappa c^2\left(a\ c^2\tau-\sigma\left(-1+a\right)\right)\right)\sqrt{\alpha}-\left(c^2\left(a\ d+\alpha+\gamma\right)\tau-d\ \sigma\left(-1+a\right)\right)\alpha\right)^2\kappa c^7\tau^2\right) \tag{10}$$

>

> *# Calculate evolutionary stability (output hidden for brevity)*

> $E0 := simplify(subs(cm = c, diff(w, cm, cm))):$

> $E := simplify(subs(eql, (subs(N = Ns, E0)))):$

>

>

> *# Special case - 1) only information is viable*

>

> $eql := simplify(sol[1]);$

(11)

$$eql := \left[S = \frac{-c^2\,(a\,d - b)\,\tau + d\,\sigma\,(-1+a)}{c^2\,q\,\tau}, I = 0\right] \tag{11}$$

```
> Ns := simplify(subs(eql, S + I));
```

$$Ns := \frac{-c^2\,(a\,d - b)\,\tau + d\,\sigma\,(-1+a)}{c^2\,q\,\tau} \tag{12}$$

```
> # Mutant dynamics
> dSm := (b − q·S)Sm − d·(1 − (1 − a)·Ams)·Sm :
>
> # Invasion fitness
> w := simplify(subs(eql, dSm/Sm));
```

$$w := \frac{d\,\sigma\,(\tau\,c^2 - \sigma)\,(c - cm)\,(-1+a)}{\tau\,c^2\,(c^2\,cm\,\tau + c\,\sigma - cm\,\sigma)} \tag{13}$$

```
> # Fitness gradient
> dw := simplify(subs(cm = c, diff(w, cm)));
```

$$dw := -\frac{d\,\sigma\,(\tau\,c^2 - \sigma)\,(-1+a)}{\tau^2\,c^5} \tag{14}$$

```
>
>
> # Special case - 2) only disease is viable
>
> restart :
> with(VectorCalculus) :
> with(LinearAlgebra) :
> interface(imaginaryunit = _I) :
>
> # Assume parasite evolves rapidly to maximise R0
> beta := kappa·sqrt(alpha) : # This is the transmission-virulence trade-off we are assuming
> A := 0 :
> R0 := beta·c^2 / ((d·(1 − (1 − a)·A) + alpha + gamma)) :
>
> # Fitness gradient for the parasite
> R0_1 := simplify(diff(R0, alpha));
```

$$R0\_1 := \frac{\kappa\,c^2\,(-\alpha + \gamma + d)}{2\sqrt{\alpha}\,(d + \alpha + \gamma)^2} \tag{15}$$

```
> # Optimal virulence
> alpha_ss := simplify(solve(R0_1, alpha));
```

$$alpha\_ss := \gamma + d \tag{16}$$

> *# Optimal transmission*

> `beta_ss := subs(alpha = alpha_ss, beta);`

$$beta\_ss := \kappa \sqrt{\gamma + d} \tag{17}$$

>

> *# Host evolution*

> $Ams := 0:$

>

> *# Now calculate resident equilibrium*

> $dS := (b - q\cdot(S + I))\cdot(S + I) - \dfrac{\text{beta}\cdot c\cdot c\cdot S\cdot I}{(S + I)} - d\cdot(1 - (1 - a)\cdot A)\cdot S + \text{gamma}\cdot I:$

> $dI := \dfrac{\text{beta}\cdot c\cdot c\cdot S\cdot I}{(S + I)} - (d\cdot(1 - (1 - a)\cdot A) + \text{alpha} + \text{gamma})\cdot I:$

> $dN := (b - q\cdot N)\cdot N - d\cdot(1 - (1 - a)\cdot A)\cdot N - \text{alpha}\cdot I:$

> $sol := solve([dS, dI], [S, I]):$

> $eql := simplify(sol[2]):$

> $Ns := simplify(subs(eql, S + I));$

$$Ns := \frac{\alpha^{3/2} + (\gamma + d)\sqrt{\alpha} + (b - d - \alpha)\, c^2\, \kappa}{\kappa\, c^2\, q} \tag{18}$$

>

> *# Mutant dynamics*

> $dSm := (b - q\cdot N)\cdot(Sm + \text{Im}) - \dfrac{\text{beta}\cdot cm\cdot c\cdot Sm\cdot I}{N} - d\cdot(1 - (1 - a)\cdot Ams)\cdot Sm + \text{gamma}\cdot\text{Im}:$

> $dIm := \dfrac{\text{beta}\cdot cm\cdot c\cdot Sm\cdot I}{N} - (d\cdot(1 - (1 - a)\cdot Ams) + \text{alpha} + \text{gamma})\cdot\text{Im}:$

>

> *# Calculate Jacobian*

> $J := (Jacobian([dSm, dIm], [Sm, \text{Im}]));$

$$J := \begin{bmatrix} -q\,N + b - \dfrac{\kappa\sqrt{\alpha}\ cm\ c\ I}{N} - d & -q\,N + b + \gamma \\ \dfrac{\kappa\sqrt{\alpha}\ cm\ c\ I}{N} & -d - \alpha - \gamma \end{bmatrix} \tag{19}$$

> *# Split the Jacobian into components F and V as follows*

> $F := \langle\langle b - q\cdot N, 0\rangle | \langle b - q\cdot N, 0\rangle\rangle;$

$$F := \begin{bmatrix} -q\,N + b & -q\,N + b \\ 0 & 0 \end{bmatrix} \tag{20}$$

> $V := F - J;$

(21)

$$V := \begin{bmatrix} \frac{\kappa \sqrt{\alpha}\ cm\, c\, I}{N} + d & -\gamma \\ -\frac{\kappa \sqrt{\alpha}\ cm\, c\, I}{N} & d+\alpha+\gamma \end{bmatrix} \tag{21}$$

```
> # Now calculate the next-generation matrix
> V1 := MatrixInverse(V) :
> NG := simplify(F . V1) :
>
> # Fitness is equal to the largest eigenvalue of the NG matrix minus 1
> w := simplify(NG[1, 1]) - 1;
```

$$w := -\frac{\left(\kappa \sqrt{\alpha}\ cm\, c\, I + N\left(d+\alpha+\gamma\right)\right)\left(q\, N - b\right)}{I\, \alpha^{3/2}\, c\, cm\, \kappa + d\left(\kappa \sqrt{\alpha}\ cm\, c\, I + N\left(d+\alpha+\gamma\right)\right)} - 1 \tag{22}$$

```
> # Calculate the fitness gradient
> dw0 := simplify(subs(cm = c, diff(w, cm))) :
> dw := simplify(subs(eql, (subs(N = Ns, dw0))));
```

$$dw := -\frac{\left(\kappa\sqrt{\alpha}\ c^2 - \gamma - \alpha - d\right)\alpha\left(d+\alpha+\gamma\right)\left(-\alpha^{3/2} + \left(-d-\gamma\right)\sqrt{\alpha} + c^2\kappa\left(d+\alpha\right)\right)}{\kappa\, c^3\left(\alpha^{3/2}\, c^2\, \kappa + \sqrt{\alpha}\ c^2\, d\, \kappa - \alpha\left(d+\alpha+\gamma\right)\right)^2} \tag{23}$$

```
>
> # Calculate evolutionary stability
> E0 := simplify(subs(cm = c, diff(w, cm, cm))) :
> E := simplify(subs(eql, (subs(N = Ns, E0))));
```

$$E := \left(2\left(\kappa\sqrt{\alpha}\ c^2 - \gamma - \alpha - d\right)^2 \alpha\left(d+\alpha+\gamma\right)\left(-\alpha^{3/2} + \left(-d-\gamma\right)\sqrt{\alpha} + c^2\kappa\left(d+\alpha\right)\right)\left(d+\alpha\right)\right) \Big/ \left(\kappa\, c^4\left(\alpha^{3/2}\, c^2\, \kappa + \sqrt{\alpha}\ c^2\, d\, \kappa - \alpha\left(d+\alpha+\gamma\right)\right)^3\right) \tag{24}$$

```
>
>
>
```