> ##

> # Host fitness for slow social information dynamics #

> ##

>

> restart :

> with(VectorCalculus) :

> with(LinearAlgebra) :

> interface(imaginaryunit = _I) :

>

> # Mutant dynamics

> $Nm := SUm + SAm + IUm + IAm$:

> $dSUm := (b - q \cdot N) \cdot Nm - \frac{cm \cdot c \cdot SUm}{N} \cdot (\text{beta} \cdot (IU + IA) + \text{tau} \cdot (SA + IA)) - d \cdot SUm + \text{gamma} \cdot IUm + \text{sigma} \cdot SAm$:

> $dSAm := \frac{cm \cdot c}{N} \cdot (\text{tau} \cdot SUm \cdot (SA + IA) - \text{beta} \cdot SAm \cdot (IU + IA)) - a \cdot d \cdot SAm + \text{gamma} \cdot IAm - \text{sigma} \cdot SAm$:

> $dIUm := \frac{cm \cdot c}{N} \cdot (\text{beta} \cdot SUm \cdot (IU + IA) - \text{tau} \cdot IUm \cdot (SA + IA)) - (d + \text{alpha} + \text{gamma}) \cdot IUm + \text{sigma} \cdot IAm$:

> $dIAm := \frac{cm \cdot c}{N} \cdot (\text{beta} \cdot SAm \cdot (IU + IA) + \text{tau} \cdot IUm \cdot (SA + IA)) - (a \cdot d + \text{alpha} + \text{gamma} + \text{sigma}) \cdot IAm$:

>

> # Calculate the Jacobian

> $J := (\text{Jacobian}([dSUm, dSAm, dIUm, dIAm], [SUm, SAm, IUm, IAm]))$;

$$J := \left[\left[-q\,N + b - \frac{cm\,c\,(\beta\,(IU + IA) + \tau\,(SA + IA))}{N} - d,\ -q\,N + b + \sigma,\ -q\,N + b + \gamma,\ -q\,N + b\right],\right.$$
$$\left[\frac{cm\,c\,\tau\,(SA + IA)}{N},\ -\frac{cm\,c\,\beta\,(IU + IA)}{N} - a\,d - \sigma,\ 0,\ \gamma\right],$$
$$\left[\frac{cm\,c\,\beta\,(IU + IA)}{N},\ 0,\ -\frac{cm\,c\,\tau\,(SA + IA)}{N} - d - \alpha - \gamma,\ \sigma\right],$$
$$\left.\left[0,\ \frac{cm\,c\,\beta\,(IU + IA)}{N},\ \frac{cm\,c\,\tau\,(SA + IA)}{N},\ -a\,d - \alpha - \gamma - \sigma\right]\right] \tag{1}$$

>

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

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

(2)

$$F := \begin{bmatrix} -q\,N + b & -q\,N + b & -q\,N + b & -q\,N + b \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} \qquad \textbf{(2)}$$

>

> $V := F - J;$

$$V := \left[\left[\frac{cm\,c\,(\beta\,(IU + IA) + \tau\,(SA + IA))}{N} + d,\ -\sigma,\ -\gamma,\ 0\right], \left[-\frac{cm\,c\,\tau\,(SA + IA)}{N},\ \frac{cm\,c\,\beta\,(IU + IA)}{N} + a\,d + \sigma,\ 0,\ -\gamma\right], \left[-\frac{cm\,c\,\beta\,(IU + IA)}{N},\ 0,\ \frac{cm\,c\,\tau\,(SA + IA)}{N} + d + \alpha + \gamma,\ -\sigma\right], \left[0,\ -\frac{cm\,c\,\beta\,(IU + IA)}{N},\ -\frac{cm\,c\,\tau\,(SA + IA)}{N},\ a\,d + \alpha + \gamma + \sigma\right]\right] \qquad \textbf{(3)}$$

>

> *# 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*

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

$$w := -\Bigg(\Bigg(\Bigg((a\,d + \sigma)\,(d + \alpha + \gamma)\,(a\,d + \alpha + \gamma + \sigma)\,N^3 + cm\,c\,\Bigg((a + 1)\,(\beta\,(IU + IA) + \tau\,(SA + IA))\,a\,d^2 + \Bigg(2\left(\left((\alpha + \gamma + \sigma)\,a + \frac{\alpha}{2} + \frac{\sigma}{2}\right)(IU + IA)\,\beta + 2\left(\left(\alpha + \gamma + \frac{\sigma}{2}\right)a + \frac{\alpha}{2} + \frac{\gamma}{2} + \frac{\sigma}{2}\right)(SA + IA)\,\tau\right)d + \left(\alpha^2 + (\gamma + 2\,\sigma)\,\alpha + 2\,\gamma\,\sigma + \sigma^2\right)(IU + IA)\,\beta + \tau\,(SA + IA)\,(\alpha + \gamma)\,(\alpha + \gamma + 2\,\sigma)\Bigg)N^2 + cm^2\Bigg(\Bigg(a\,(IU + IA)^2\,\beta^2 + 2\,(SA + IA)\left(a + \frac{1}{2}\right)\tau\,(IU + IA)\,\beta + \tau^2\,a\,(SA + IA)^2\Bigg)d + (IU + IA)^2\,(\alpha + \sigma)\,\beta^2 + 2\,\tau\,(SA + IA)\,(IU + IA)\,(\alpha + \gamma + \sigma)\,\beta + \tau^2\,(SA + IA)^2\,(\alpha + \gamma)\Bigg)c^2\,N + \beta\,(\beta\,(IU + IA) + \tau\,(SA + IA))\,(SA + IA)\,\tau\,c^3\,(IU + IA)\,cm^3\Bigg)(q\,N - b)\Bigg) \Bigg/ \Bigg(\beta\,(\beta\,(IU + IA) + \tau\,(SA + IA))\,(SA + IA)\,\tau\,(a\,d + \alpha)\,c^3\,(IU + IA)\,cm^3 \qquad \textbf{(4)}$$

$$+N\left(a\left((IU+IA)^2\beta^2+\tau(SA+IA)(IU+IA)(a+2)\beta+\tau^2 a(SA+IA)^2\right)d^2\right.$$
$$+\left((IU+IA)^2(a\alpha+\alpha+\sigma)\beta^2+2(SA+IA)\left(\left(\alpha+\gamma+\frac{\sigma}{2}\right)a+\alpha+\frac{\sigma}{2}\right)\tau(IU\right.$$
$$\left.+IA)\beta+\tau^2 a(SA+IA)^2(\alpha+\gamma)\right)d+\beta\left((IU+IA)(\alpha+\sigma)\beta+\tau(SA+IA)(\alpha\right.$$
$$\left.\left.+\gamma+2\sigma)\right)\alpha(IU+IA)\right)c^2 cm^2+N^2\left(2\left(\frac{(IU+IA)(a+1)\beta}{2}+\tau a(SA\right.\right.$$
$$\left.+IA)\right)a d^3+\left(\left(\alpha a^2+(2\alpha+2\gamma+2\sigma)a+\alpha+\sigma\right)(IU+IA)\beta+(SA\right.$$
$$\left.+IA)\tau a\left((\alpha+\gamma)a+2\alpha+2\gamma+2\sigma\right)\right)d^2+\left(\left(\alpha(\alpha+\gamma+2\sigma)a+\alpha^2+(\gamma\right.\right.$$
$$\left.\left.+2\sigma)\alpha+2\gamma\sigma+\sigma^2\right)(IU+IA)\beta+(SA+IA)(\alpha+\gamma)\tau\left((\alpha+\gamma+\sigma)a+\sigma\right)\right)d$$
$$\left.+\beta\alpha\sigma(IU+IA)(\alpha+\gamma+\sigma)\right)c\,cm+N^3 d(a d+\sigma)(d+\alpha+\gamma)(a d+\alpha+\gamma$$
$$\left.+\sigma)\right)-1$$

\>

\> *# Calculate the fitness gradient (output hidden for brevity)*

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

\>

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

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

\>

\>

\> *# Special case - 1) R0_I<1*

\>

\> $dw1 := simplify(subs(\{SA=0, IA=0, N=SU+IU\}, dw))$;

$$dw1 := -\frac{(SU+IU)\beta\alpha IU(d+\alpha+\gamma)(-q\,IU-q\,SU+b)c}{\left(\left(d^2+(\beta c^2+\alpha+\gamma)d+c^2\beta\alpha\right)IU+d\,SU(d+\alpha+\gamma)\right)^2} \quad (5)$$

\>

\> *# Intuitively if R0_D>1 and alpha>0, this is always negative (since $b > q\cdot N$)*

\>

\>

\> *# Special case - 2) R0_D<1*

\>

\> $dw1 := simplify(subs(\{IU=0, IA=0, N=SU+SA\}, dw))$;

$$dw1 := -\frac{c(-q\,SA-q\,SU+b)(a d+\sigma)\tau(a-1)SA(SU+SA)}{d\left(\left((c^2\tau+d)a+\sigma\right)SA+SU(a d+\sigma)\right)^2} \quad (6)$$

\>

\> *# Intuitively if R0_I>1 and a<1, this is always positive (since $b > q\cdot N$)*

>

>

> # Special case - 3) R0_I, R0_D <1

>

> dw1 := simplify(subs({SA = 0, IU = 0, IA = 0, N = SU}, dw));

$$dw1 := 0 \tag{7}$$

>

> # Trivial: cm does not feature in invasion fitness, so dw=0 for all c

>

```
> ###########################################################
> # Host fitness for approximation to fast social information dynamics #
> ###########################################################
>
> restart :
> with(VectorCalculus) :
> with(LinearAlgebra) :
> interface(imaginaryunit = _I) :
>
> # First calculate information awareness in mutant when rare (Ams)
```

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

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

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

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

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

$$Ams := \frac{cm\left(\tau c^{2} - \sigma\right)}{c^{2}\, cm\, \tau + \sigma c - cm\, \sigma} \tag{1}$$

```
>
> # Now calculate resident equilibrium
```

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

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

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

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

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

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

$$Ns := \frac{-\tau \beta (a d + \alpha - b) c^{4} + \left(\alpha (a d + \alpha + \gamma) \tau + \sigma d \beta (-1 + a)\right) c^{2} - \sigma d \alpha (-1 + a)}{\beta c^{4} \tau q} \tag{2}$$

```
> # Mutant dynamics
```

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

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

```
>
```

> # Calculate the Jacobian

> J := (Jacobian([dSm, dIm], [Sm, Im]));

$$J := \left[\left[-q\,N+b-\frac{\beta\,cm\,c\,I}{N}-d\left(1-\frac{(1-a)\,cm\,(c^2\,\tau-\sigma)}{c^2\,cm\,\tau+c\,\sigma-cm\,\sigma}\right), -q\,N+b+\gamma\right], \left[\frac{\beta\,cm\,c\,I}{N}, -d\left(1-\frac{(1-a)\,cm\,(c^2\,\tau-\sigma)}{c^2\,cm\,\tau+c\,\sigma-cm\,\sigma}\right)-\alpha-\gamma\right]\right] \quad \textbf{(3)}$$

>

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

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

$$F := \begin{bmatrix} -q\,N+b & -q\,N+b \\ 0 & 0 \end{bmatrix} \quad \textbf{(4)}$$

> V := F − J;

$$V := \left[\left[\frac{\beta\,cm\,c\,I}{N}+d\left(1-\frac{(1-a)\,cm\,(c^2\,\tau-\sigma)}{c^2\,cm\,\tau+c\,\sigma-cm\,\sigma}\right), -\gamma\right], \left[-\frac{\beta\,cm\,c\,I}{N}, d\left(1-\frac{(1-a)\,cm\,(c^2\,\tau-\sigma)}{c^2\,cm\,\tau+c\,\sigma-cm\,\sigma}\right)+\alpha+\gamma\right]\right] \quad \textbf{(5)}$$

> # 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;

$$w := -\left(\left((c^2\,\tau-\sigma)\,cm+c\,\sigma\right)(q\,N-b)\left(-I\,\beta\,c\,(-c^2\,\tau+\sigma)\,cm^2+\left((I\,\beta\,\sigma+N\,\tau\,(a\,d+\alpha+\gamma))\,c^2-\sigma\,N\,(a\,d+\alpha+\gamma)\right)cm+\sigma\,N\,c\,(\alpha+\gamma+d)\right)\right) \Big/ \left(I\,\beta\,c\,(-c^2\,\tau+\sigma)^2\,(a\,d+\alpha)\,cm^3-2\left(\left(\left(\left(\frac{a}{2}+\frac{1}{2}\right)d+\alpha\right)I\,\beta\,\sigma+\frac{N\,a\,d\,\tau\,(a\,d+\alpha+\gamma)}{2}\right)c^2-\frac{\sigma\,N\,a\,d\,(a\,d+\alpha+\gamma)}{2}\right)(-c^2\,\tau+\sigma)\,cm^2+c\left(\left(I\,\beta\,(\alpha+d)\,\sigma+d\,N\,\tau\,(2\,a\,d+(a+1)\,(\alpha+\gamma))\right)c^2-d\,N\,\sigma\,(2\,a\,d+(a+1)\,(\alpha+\gamma))\right)\sigma\,cm+\sigma^2\,N\,c^2\,d\,(\alpha+\gamma+d)\right)-1 \quad \textbf{(6)}$$

>

> # Calculate the fitness gradient

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

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

$$dw := \Big(-\beta\,(\alpha\,(a\,d+\alpha+\gamma)\,\tau+\sigma\,d\,\beta\,(-1+a))\,\tau^2\,c^8+\big(\alpha\,(a\,d+\alpha+\gamma)^2\,\tau^2 \quad \textbf{(7)}$$

$$+ 2\, d\, \beta\, \alpha\, \sigma\, (-1 + a)\, \tau + d\, \beta^2\, \sigma^2\, (-1 + a) \Big)\, \tau\, c^6 - 3\, \alpha\, \sigma\, \tau\, (-1 + a) \Big(\big(a\, d + \alpha + \gamma \big)\, \tau + \frac{\beta\, \sigma}{3} \Big)\, d\, c^4 + 3\, \alpha\, \sigma^2\, \tau\, (-1 + a) \left(\frac{\alpha}{3} + \left(a - \frac{2}{3} \right) d + \frac{\gamma}{3} \right) d\, c^2 - d^2\, \alpha\, \sigma^3\, (-1 + a)^2 \Big) \Big/ \Big(\beta\, c^7\, \tau^2 \big(\tau\, \beta\, (a\, d + \alpha)\, c^4 + (-\alpha\, (a\, d + \alpha + \gamma)\, \tau - \sigma\, d\, \beta\, (-1 + a))\, c^2 + \sigma\, d\, \alpha\, (-1 + a) \big) \Big)$$

```
>
> # 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) R0_I<1
>
> restart :
> with(VectorCalculus) :
> with(LinearAlgebra) :
> interface(imaginaryunit = _I) :
>
> A := 0 :
> Ams := 0 :
> dS := (b - q·(S + I))·(S + I) - beta·c·c·S·I/(S + I) - d·(1 - (1 - a)·A)·S + gamma·I :
> dI := beta·c·c·S·I/(S + I) - (d·(1 - (1 - a)·A) + alpha + gamma)·I :
> dN := (b - q·N)·N - d·(1 - (1 - a)·A)·N - alpha·I :
> sol := solve([dS, dI], [S, I]) :
> eql := simplify(sol[2]) :
> Ns := simplify(subs(eql, S + I));
```

$$Ns := \frac{\alpha^2 + \left(-\beta\, c^2 + d + \gamma \right) \alpha + c^2\, \beta\, (b - d)}{\beta\, c^2\, q} \tag{8}$$

```
> # Mutant dynamics
> dSm := (b - q·N)·(Sm + Im) - beta·cm·c·Sm·I/N - d·(1 - (1 - a)·Ams)·Sm + gamma
      ·Im :
> dIm := beta·cm·c·Sm·I/N - (d·(1 - (1 - a)·Ams) + alpha + gamma)·Im :
>
> # Calculate the Jacobian
> J := (Jacobian([dSm, dIm], [Sm, Im]));
```

$$J := \begin{bmatrix} -q\,N + b - \frac{\beta\,cm\,c\,I}{N} - d & -q\,N + b + \gamma \\ \frac{\beta\,cm\,c\,I}{N} & -d - \alpha - \gamma \end{bmatrix} \quad \textbf{(9)}$$

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

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

$$F := \begin{bmatrix} -q\,N + b & -q\,N + b \\ 0 & 0 \end{bmatrix} \quad \textbf{(10)}$$

> $V := F - J;$

$$V := \begin{bmatrix} \frac{\beta\,cm\,c\,I}{N} + d & -\gamma \\ -\frac{\beta\,cm\,c\,I}{N} & d + \alpha + \gamma \end{bmatrix} \quad \textbf{(11)}$$

> # 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

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

$$w := -\frac{((d + \alpha + \gamma)\,N + I\,\beta\,c\,cm)\,(q\,N - b)}{d\,(d + \alpha + \gamma)\,N + I\,c\,cm\,\beta\,(d + \alpha)} - 1 \quad \textbf{(12)}$$

> # Calculate the fitness gradient

> $dw1 := simplify(subs(cm = c, diff(w, cm)));$

$$dw1 := \frac{I\,\beta\,c\,(q\,N - b)\,N\,\alpha\,(d + \alpha + \gamma)}{(d\,(d + \alpha + \gamma)\,N + I\,c^2\,\beta\,(d + \alpha))^2} \quad \textbf{(13)}$$

> # Intuitively if R0_D>1 and alpha>0, this is always negative $(since\ b > q\cdot N)$

>

>

> # Special case - 2) R0_D<1

>

> $restart:$

> $with(VectorCalculus):$

> $with(LinearAlgebra):$

> $interface(imaginaryunit = \_I):$

>

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

```
> Ams := cm (τ c^2 − σ) / (c^2 cm τ + σ c − cm σ) :
>
> dS := (b − q·S)·S − d·(1 − (1 − a)·A)·S :
> dSm := (b − q·S)·Sm − d·(1 − (1 − a)·Ams)·Sm :
> sol := solve(dS, S) :
> eql := simplify(sol[2]);
```

$$eql := \frac{-c^2 \left(a\, d - b\right) \tau + d\, \sigma \left(-1 + a\right)}{c^2\, q\, \tau} \tag{14}$$

```
> # Fitness is straightforward in this case
> w := simplify(dSm / Sm);
```

$$w := \frac{\left(\left(q\, S + a\, d - b\right) cm - c\left(q\, S - b + d\right)\right)\sigma - c^2\, cm\, \tau\left(q\, S + a\, d - b\right)}{\left(c - cm\right)\sigma + c^2\, cm\, \tau} \tag{15}$$

```
> # Calcualte the fitness gradient
> dw1 := simplify(subs(cm = c, subs(S = eql, diff(w, cm))));
```

$$dw1 := -\frac{d\, \sigma\left(-1 + a\right)\left(\tau\, c^2 - \sigma\right)}{c^5\, \tau^2} \tag{16}$$

```
> # Intuitively if R0_I>1 & a<1, then dw>0 for all c
>
>
> # Special case - 3) R0_I, R0_D<1
>
> # Trivial: cm does not feature in invasion fitness, so dw=0 for all c
>
```

```
> ##############################################################################
> # 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));
```

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

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

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

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

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

```
>
>
> # 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);
```

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

```
>
> # Now calculate resident equilibrium
```

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

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

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

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

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

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

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

```
>
> # Mutant dynamics
```

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

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

```
>
> # Calculate the Jacobian
```

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

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

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

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

$$F := \begin{bmatrix} -q\,N+b & -q\,N+b \\ 0 & 0 \end{bmatrix} \tag{7}$$

$$> V := F-J;$$

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

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

```
> # 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;
```

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

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

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

```
>
> # 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)

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

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

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

> *# Mutant dynamics*

> $dSm := (b - q\cdot S)Sm - d\cdot(1 - (1-a)\cdot Ams)\cdot Sm :$

>

> *# Invasion fitness*

> $w := simplify\left(subs\left(eql, \frac{dSm}{Sm}\right)\right);$

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

> *# Fitness gradient*

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

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

>

>

> *# Special case - 2) only disease is viable*

>

> $restart:$

> $with(VectorCalculus):$

> $with(LinearAlgebra):$

> $interface(imaginaryunit = \_I):$

>

> *# Assume parasite evolves rapidly to maximise R0*

> $\mathrm{beta} := \mathrm{kappa}\cdot\mathrm{sqrt}(\mathrm{alpha}):$ *# This is the transmission-virulence trade-off we are assuming*

> $A := 0:$

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

>

> *# Fitness gradient for the parasite*

> $R0\_1 := simplify(diff(R0, \mathrm{alpha}));$

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

> *# Optimal virulence*

> $alpha\_ss := simplify(solve(R0\_1, \mathrm{alpha}));$

$$alpha\_ss := \gamma + d \quad \textbf{(16)}$$

```
> # 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
```

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

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

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

```
> 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
```

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

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

```
>
> # Calculate Jacobian
> J := (Jacobian([dSm, dIm], [Sm, Im]));
```

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

```
> # Split the Jacobian into components F and V as follows
> F := <<b - q·N, 0>|<b - q·N, 0>>;
```

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

```
> 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))));
```

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

```
>
>
>
```