1. Within-host Dynamics

Here is the within-host model. Solve for the endemic virus equilibrium:

In[∘]:=
```
Solve[{r * V - c * V * L == 0,  g0 + g * r * V - m * L == 0}, {V, L}]
```

Out[∘]=
$$\left\{\left\{V \to -\frac{c\ g0 - m\ r}{c\ g\ r},\ L \to \frac{r}{c}\right\},\ \left\{V \to 0,\ L \to \frac{g0}{m}\right\}\right\}$$

$$\text{Vstar} = \frac{m * r - c * g0}{g * c * r};$$

$$\text{Lstar} = \frac{r}{c};$$

Now, take those endemic, within-host equilibria and embed them in the virulence and transmission terms for the population model -- this gives some biological significance to r. w is motivated as host vulnerability to immunopathology (i.e. inflammation), so hosts with higher values for w are most susceptible to disease. We can try scaling this as the inverse of host lifespan corrected for body size (so values are higher for the shortest-lived hosts):

2. Both constant tolerance:

In[∘]:=
```
BetaT = zeta * Vstar;
alphaT = (v * r * Vstar / Tv) +  (w * (g * r * Vstar)) / Tw;

BetaT
```

Out[∘]=
$$\frac{(-c\ g0 + m\ r)\ zeta}{c\ g\ r}$$

In[∘]:=
```
alphaT
```

Out[∘]=
$$\frac{(-c\ g0 + m\ r)\ v}{c\ g\ Tv} + \frac{(-c\ g0 + m\ r)\ w}{c\ Tw}$$

Now, embed these transmission and virulence terms in the invasion fitness for a population-level S-I model:

In[∘]:=
```
InvasionFit = BetaT / (mu +  alphaT);
FullSimplify[InvasionFit]
```

Out[∘]=
$$\frac{(-c\ g0 + m\ r)\ Tv\ Tw\ zeta}{r\ Tw\ (c\ g\ mu\ Tv - c\ g0\ v + m\ r\ v) + g\ r\ (-c\ g0 + m\ r)\ Tv\ w}$$

2. Selection gradient on r

And now, differentiate with respect to r to get this for dInvasion Fitness/dr:

In[∘]:=
```
partialD = FullSimplify[D[InvasionFit, r]];
partialD
```

Out[∘]=
$$-\frac{Tv\ Tw\ \left(-c^2\ g\ g0\ mu\ Tv\ Tw + (c\ g0 - m\ r)^2\ Tw\ v + g\ (c\ g0 - m\ r)^2\ Tv\ w\right)\ zeta}{(r\ Tw\ (c\ g\ mu\ Tv - c\ g0\ v + m\ r\ v) + g\ r\ (-c\ g0 + m\ r)\ Tv\ w)^2}$$

And then set equal to 0 and solve for r*

In[∘]:=
```
FullSimplify[Solve[{partialD == 0}, {r}]]
```

Out[∘]=
$$\left\{\left\{r \to \frac{c\ g0\ m - \frac{\sqrt{c^2\ g\ g0\ m^2\ mu\ Tv\ Tw\ (Tw\ v + g\ Tv\ w)}}{Tw\ v + g\ Tv\ w}}{m^2}\right\}, \left\{r \to \frac{c\ g0\ m + \frac{\sqrt{c^2\ g\ g0\ m^2\ mu\ Tv\ Tw\ (Tw\ v + g\ Tv\ w)}}{Tw\ v + g\ Tv\ w}}{m^2}\right\}\right\}$$

$$rstar = \frac{c\ g0\ m + \frac{\sqrt{c^2\ g\ g0\ m^2\ mu\ Tv\ Tw\ (Tw\ v + g\ Tv\ w)}}{Tw\ v + g\ Tv\ w}}{m^2};$$

3. Checking stability

We can check that rstar is convergence stable and therefore a CSS by checking that the second derivative of d/dr is negative at rstar:

In[∘]:=
```
secondD = FullSimplify[D[partialD , r]];
secondD
```

Out[∘]=
$$-\Big(\Big(2\ Tv\ Tw\ \big(3\ c\ g0\ m^2\ r^2\ (Tw\ v + g\ Tv\ w)^2 - m^3\ r^3\ (Tw\ v + g\ Tv\ w)^2 - 3\ c^2\ g0\ m\ r\ (Tw\ v + g\ Tv\ w)\ (g0\ Tw\ v + g\ Tv\ (-mu\ Tw + g0\ w)) + c^3\ g0\ (g0\ Tw\ v + g\ Tv\ (-mu\ Tw + g0\ w))^2\big)\ zeta\Big) \Big/ \Big(r^3\ (-c\ g0\ Tw\ v + c\ g\ Tv\ (mu\ Tw - g0\ w) + m\ r\ (Tw\ v + g\ Tv\ w))^3\Big)\Big)$$

```
r = rstar;
```

In[∘]:=
```
FullSimplify[secondD]
```

Out[∘]=
$$-\Big(\Big(2\ c^2\ g\ g0\ m^8\ mu\ Tv^2\ Tw^2\ (Tw\ v + g\ Tv\ w)^3\ \Big(2\ \sqrt{c^2\ g\ g0\ m^2\ mu\ Tv\ Tw\ (Tw\ v + g\ Tv\ w)} + c\ m\ (g0\ Tw\ v + g\ Tv\ (mu\ Tw + g0\ w))\Big)\ zeta\Big) \Big/ \Big(\Big(c\ g\ m\ mu\ Tv\ Tw + \sqrt{c^2\ g\ g0\ m^2\ mu\ Tv\ Tw\ (Tw\ v + g\ Tv\ w)}\Big)^3\ \Big(c\ g0\ m\ (Tw\ v + g\ Tv\ w) + \sqrt{c^2\ g\ g0\ m^2\ mu\ Tv\ Tw\ (Tw\ v + g\ Tv\ w)}\Big)^3\Big)\Big)$$

This expression is clearly negative (also supported by the PIP), meaning that rstar is an ESS.

4. Virulence at optimal r in the reservoir host.*

We can also use the expression for r* to calculate an expression for alpha*, the virulence experienced by the reservoir host at optimal r*. To do this, we simply plug the within-host parameters into our expression for alpha, assuming r=r*.

This yields the following expression:

In[∘]:=
```
FullSimplify[alphaT]
```

Out[∘]=
$$\frac{c\ g0\ m\ mu\ (Tw\ v + g\ Tv\ w)}{\sqrt{c^2\ g\ g0\ m^2\ mu\ Tv\ Tw\ (Tw\ v + g\ Tv\ w)}}$$

$$\text{alpha}^* = \frac{c\ g0\ m\ mu\ (Tw\ v + g\ Tv\ w)}{\sqrt{c^2\ g\ g0\ m^2\ mu\ Tv\ Tw\ (Tw\ v + g\ Tv\ w)}}$$