For the host-parasite system presented in the main text and all other model variants, we use standard adaptive dynamics techniques to investigate when a generalist parasite that can infect both hosts can "invade" (mathematically, this means investigating the stability of the equilibrium where the generalist is absent - the generalist can invade if this equilibrium is unstable). For all of the models we study, four assumptions remain constant: there are two potential hosts; infections occur due to contact between susceptible hosts and parasites in the environment; infected hosts shed parasites into the environment throughout the infection; generalist parasites have a reduced shedding rate compared to specialist parasites.

The models differ in a number of ways that could affect the conclusions about the evolution of generalism. We explore models that differ in (1) the number of specialist parasites (either one or two); (2) the effect of parasitism on host population growth (dynamic versus constant population size); (3) the host-parasite contact process (parasites only come in contact with susceptible hosts; parasites come in contact with both susceptible and infected hosts; parasites come in contact with both host and non-host species); and (4) the parasite's life cycle (direct versus trophic transmission).

Case 1: Direct life cycle; one specialist parasite; parasite regulates host population size; active host seeking; avoidance of infected hosts

For this model, let S_1 and S_2 be the number of susceptible hosts of species 1 and 2, respectively. We will refer to these the "primary" and "secondary" hosts for simplicity. We assume that the "resident" parasite is a specialist on the primary host, and let $I_{1\,r}$ be the number of primary hosts infected by the resident parasite. The "mutant" parasite is a generalist, and we let $I_{1\,m}$ and $I_{2\,m}$ be the number of primary and secondary hosts infected by the mutant parasite. We let P_r and P_m be the number of resident (specialist) and mutant (generalist) parasites in the environment.

In the absence of any infection, the primary and secondary hosts population sizes reach species-specific carrying capacities K_1 and K_2. Infection, however, induces mortality that depends on host traits, quantified by the species-specific mortality rates μ_1 and μ_2. Infected hosts shed parasites into the environment. The rate of shedding depends on host traits and whether the host is infected by a generalist or a specialist. Primary hosts infected by the specialist parasite shed parasites at the rate λ_1 , whereas primary hosts infected by the generalist parasite shed parasites at the reduced rate $a\,\lambda_1$. Secondary hosts infected by the generalist parasite shed at the rate $a\,\lambda_2$ (where λ_2 is the rate that a specialist parasite would be shed). We assume that the parasite controls the infection process and can detect whether a host is infected or not, so that parasites in the environment come in contact with susceptible hosts at the rate β. Finally, we assume that parasites are lost from the environment (whether due to death or washout) at the rate γ.

Note that we have assumed that specialist and generalist parasites differ only in the rate that they are shed from infected hosts, rather than assuming that they differ in transmission (β) or mortality (μ). The model for this system is given below:

```
dS1dt = r1 (S1 + I1r + I1m) (1 - (S1 + I1r + I1m)/K1) - β S1 (Pr + Pm);
dS2dt = r2 (S2 + I2m) (1 - (S2 + I2m)/K2) - β S2 Pm;
dI1rdt = β S1 Pr - μ1 I1r;
dPrdt = λ1 I1r - β S1 Pr - γ Pr;
dI1mdt = β S1 Pm - μ1 I1m;
dI2mdt = β S2 Pm - μ2 I2m;
dPmdt = a λ1 I1m + a λ2 I2m - β S1 Pm - β S2 Pm - γ Pm;
```

For an invasion analysis, we assume that the resident parasite comes to an ecological equilibrium with the host. Since it does not parasitize the second host, it will go to its carrying capacity: $S_2 = K_2$. The density of the exploited host at equilibrium will be $S_1 = \frac{\gamma \mu_1}{\beta(\lambda_1 - \mu_1)}$.

```
Eq = Solve[({dS1dt == 0, dI1rdt == 0, dPrdt == 0} /. {I1m → 0, Pm → 0}), {S1, I1r, Pr}];
Eq[[4, 1]]
```

$$\text{S1} \to -\frac{\gamma\, \mu 1}{\beta\, (-\lambda 1 + \mu 1)}$$

While evaluating the stability of the endemic equilibrium is somewhat challenging, it is obvious that, for there to be any chance for the endemic parasite equilibrium to be stable, the parasite extinction equilibrium must be unstable. This requires $\frac{\beta K(\lambda_1 - \mu)}{\gamma \mu} > 1$. Notice that this is the reciprocal of the equilibrium host abundance at the endemic equilibrium, as expected.

```
Jres = {{D[dS1dt, S1], D[dS1dt, I1r], D[dS1dt, Pr]},
    {D[dI1rdt, S1], D[dI1rdt, I1r], D[dI1rdt, Pr]},
    {D[dPrdt, S1], D[dPrdt, I1r], D[dPrdt, Pr]}} /. {I1m → 0, Pm → 0};
(* Eigenvalues for the parasite-free equilibrium *)
Eigenvalues[Jres /. {I1r → 0, Pr → 0, S1 → K1}]
```

$$\left\{-\text{r1},\ \frac{1}{2}\left(-\text{K1}\,\beta - \gamma - \mu 1 - \sqrt{\left((\text{K1}\,\beta + \gamma + \mu 1)^2 - 4\ (-\text{K1}\,\beta\,\lambda 1 + \text{K1}\,\beta\,\mu 1 + \gamma\,\mu 1)\right)}\right),\right.$$
$$\left.\frac{1}{2}\left(-\text{K1}\,\beta - \gamma - \mu 1 + \sqrt{\left((\text{K1}\,\beta + \gamma + \mu 1)^2 - 4\ (-\text{K1}\,\beta\,\lambda 1 + \text{K1}\,\beta\,\mu 1 + \gamma\,\mu 1)\right)}\right)\right\}$$

To determine whether the generalist parasite can invade, we need to examine the stability of the full system when the generalist parasite is absent (i.e., when $I_{1,m} = 0$, $I_{2,m} = 0$, and $P_m = 0$). The Jacobian matrix for this is given below. Note that this matrix has a very simple structure:

$$J = \begin{pmatrix} J_s & M \\ 0 & J_m \end{pmatrix}$$

This structure is actually quite convenient - J is an upper-triangular matrix, which means that its eigenvalues are given by the eigenvalues of J_s and J_m. The eigenvalues of J_s determine the stability of the endemic equilibria for the system with only the specialist parasite. By assumption, these eigenvalues are negative. Thus, we only need be concerned about the eigenvalues of J_m, which is the submatrix dealing with the equations for the generalist parasite.

```
J = {{D[dS1dt, S1], D[dS1dt, S2], D[dS1dt, I1r],
      D[dS1dt, Pr], D[dS1dt, I1m], D[dS1dt, I2m], D[dS1dt, Pm]},
     {D[dS2dt, S1], D[dS2dt, S2], D[dS2dt, I1r], D[dS2dt, Pr],
      D[dS2dt, I1m], D[dS2dt, I2m], D[dS2dt, Pm]},
     {D[dI1rdt, S1], D[dI1rdt, S2], D[dI1rdt, I1r], D[dI1rdt, Pr],
      D[dI1rdt, I1m], D[dI1rdt, I2m], D[dI1rdt, Pm]},
     {D[dPrdt, S1], D[dPrdt, S2], D[dPrdt, I1r], D[dPrdt, Pr],
      D[dPrdt, I1m], D[dPrdt, I2m], D[dPrdt, Pm]},
     {D[dI1mdt, S1], D[dI1mdt, S2], D[dI1mdt, I1r], D[dI1mdt, Pr],
      D[dI1mdt, I1m], D[dI1mdt, I2m], D[dI1mdt, Pm]},
     {D[dI2mdt, S1], D[dI2mdt, S2], D[dI2mdt, I1r], D[dI2mdt, Pr],
      D[dI2mdt, I1m], D[dI2mdt, I2m], D[dI2mdt, Pm]},
     {D[dPmdt, S1], D[dPmdt, S2], D[dPmdt, I1r], D[dPmdt, Pr], D[dPmdt, I1m],
      D[dPmdt, I2m], D[dPmdt, Pm]}} /. {I1m → 0, I2m → 0, Pm → 0};
MatrixForm[
 J]
```

$$\begin{pmatrix} -\frac{r1\,(I1r+S1)}{K1}+r1\left(1-\frac{I1r+S1}{K1}\right)-Pr\,\beta & 0 & -\frac{r1\,(I1r+S1)}{K1}+r1\left(1-\frac{I1r+S1}{K1}\right) & -S1\,\beta & -\frac{r1}{} \\ 0 & -\frac{r2\,S2}{K2}+r2\left(1-\frac{S2}{K2}\right) & 0 & 0 & \\ Pr\,\beta & 0 & -\mu 1 & S1\,\beta & \\ -Pr\,\beta & 0 & \lambda 1 & -S1\,\beta-\gamma & \\ 0 & 0 & 0 & 0 & \\ 0 & 0 & 0 & 0 & \\ 0 & 0 & 0 & 0 & \end{pmatrix}$$

However, rather than calculating these eigenvalues directly (which are difficult to interpret), we apply the next generation theorem.

```
F = {{0, 0, S1 β}, {0, 0, S2 β}, {a λ1, a λ2, 0}};
V = {{μ1, 0, 0}, {0, μ2, 0}, {0, 0, S1 β + S2 β + γ}};
J[[5 ;; 7, 5 ;; 7]] == F - V // Simplify
Eigenvalues[Dot[F, Inverse[V]]]
```

```
True
```

$$\left\{0,\ -\frac{\sqrt{a}\ \sqrt{\beta}\ \sqrt{S2\ \lambda 2\ \mu 1+S1\ \lambda 1\ \mu 2}}{\sqrt{S1\ \beta+S2\ \beta+\gamma}\ \sqrt{\mu 1}\ \sqrt{\mu 2}},\ \frac{\sqrt{a}\ \sqrt{\beta}\ \sqrt{S2\ \lambda 2\ \mu 1+S1\ \lambda 1\ \mu 2}}{\sqrt{S1\ \beta+S2\ \beta+\gamma}\ \sqrt{\mu 1}\ \sqrt{\mu 2}}\right\}$$

If the largest of these eigenvalues is larger than 1, then the generalist-absent equilibrium is unstable. This is equivalent to requiring that $\frac{\beta(a\lambda_1-\mu_1)}{\gamma\mu_1}\hat{S}_1+\frac{\beta(a\lambda_1-\mu_2)}{\gamma\mu_2}\hat{S}_2>1$, where $\hat{S}_1$ and $\hat{S}_2$ are the equilibrium abundances of susceptible primary and secondary hosts when the generalist is absent. We can plug these equilibria into the stability condition. We define the left-hand side of this expression as R_0, the "invasion fitness" of the generalist parasite. Analogous to the canonical R_0 for an infectious disease, if $R_0>1$, the generalist will spread through the host population.

```
R0 = (β (a λ1 - μ1)/(γ μ1) S1 + β (a λ2 - μ2)/(γ μ2) S2) /. {S1 → -γ μ1/(β (-λ1 + μ1)), S2 → K2}
```

$$-\frac{a\,\lambda 1-\mu 1}{-\lambda 1+\mu 1}+\frac{K2\,\beta\,(a\,\lambda 2-\mu 2)}{\gamma\,\mu 2}$$

We can explore how changing parameters of the model affect the magnitude of R_0 to see how these parameters affect the evolution of generalism. In particular, reducing the cost of generalism (increasing a) increases R_0; increasing the abundance of the secondary host (K_2) increases R_0; increasing the mortality induced by infection (μ_1 or μ_2) reduces R_0; increasing the parasite loss rate in the environment

reduces R_0. None of these effects are surprising. However, in reality, many of these parameters are linked with one another by aspects of host physiology.

```
D[R0, a] // Simplify
D[R0, K2]
Simplify[D[R0, μ1]]
FullSimplify[D[R0, μ2]]
D[R0, γ]
```

$$\frac{\lambda 1}{\lambda 1 - \mu 1} + \frac{K2\ \beta\ \lambda 2}{\gamma\ \mu 2}$$

$$\frac{\beta\ (a\ \lambda 2 - \mu 2)}{\gamma\ \mu 2}$$

$$\frac{(-1 + a)\ \lambda 1}{(\lambda 1 - \mu 1)^2}$$

$$-\frac{a\ K2\ \beta\ \lambda 2}{\gamma\ \mu 2^2}$$

$$-\frac{K2\ \beta\ (a\ \lambda 2 - \mu 2)}{\gamma^2\ \mu 2}$$

In particular, carrying capacity, mortality rate, and shedding rate are all likely to be affected by host body size and temperature. Savage et al. 2004 suggested a scaling of
$K = K_0\, e^{E/k\,T}\, W^{-0.75}$
$\mu = \mu_0\, e^{-E/k\,T}\, W^{-0.25}$
for carrying capacity and mortality rate.

Hechinger 2012 suggested that within-host abundance correlates with body size and temperature. If we assume that shedding rate is a linear function of abundance, then
$\lambda = \lambda_0\, e^{-E/k\,T}\, W^{0.75}$ (for endoparasites)
$\lambda = \lambda_0\, e^{-E/k\,T}\, W^{5/12}$ (for ectoparasites).
The difference in scaling for endoparasites and ectoparasites is because these two parasites utilize hosts differently: for endoparasites, abundance depends on host volume, whereas for ectoparasites, abundance depends on host surface area.

We assume that the only difference between the two hosts is in terms of body size. We let W be the mass of the primary host, and $f\,W$ be the mass of the secondary host; without loss of generality, we assume that $0 < f < 1$.

Notice that the derivatives of these expressions can be rewritten in terms of the expressions themselves:

```
K2 = K0 Exp[E / (k T)] (f W)^(-3/4);
μ1 = μ0 Exp[-E / (k T)] W^(-1/4);
μ2 = μ0 Exp[-E / (k T)] (f W)^(-1/4);
λ1 = λ0 Exp[-E / (k T)] W^(3/4);
λ2 = λ0 Exp[-E / (k T)] (f W)^(3/4);
(* Derivatives with respect to mass *)
D[μ1, W] == (-μ1)/(4 W) // Simplify
D[λ1, W] == (3 λ1)/(4 W) // Simplify
D[K2, W] == (-3 K2)/(4 W) // Simplify
D[μ2, W] == (-μ2)/(4 W) // Simplify
D[λ2, W] == (3 λ2)/(4 W) // Simplify
(* Derivatives with respect to temperature *)
D[μ1, T] == E/(k T^2) μ1 // Simplify
D[λ1, T] == E/(k T^2) λ1 // Simplify
D[K2, T] == -E/(k T^2) K2 // Simplify
Clear[μ2, K2, λ2, μ1, λ1]
```

```
True

True

True

True

True

True

True

True
```

We can then study how R_0 is affected by changes in host body size or temperature for endoparasites and ectoparasites by differentiating R_0 with respect to host body size W and temperature T.

Endoparasites

For endoparasites, we find that increasing host body size always increases R_0 because $\frac{dR_0}{dW} = \frac{(1-a)\lambda_1\mu_1}{W(\lambda_1-\mu_1)} + \frac{\beta K_2(a\lambda_2+3\mu_2)}{4W\gamma\mu_2}$, which is always positive.

```
(D[R0 /. {λ1 → λ1[W], μ1 → μ1[W], λ2 → λ2[W], μ2 → μ2[W], K2 → K2[W]}, W] /.
    {μ1'[W] → -μ1[W]/(4 W), μ2'[W] → -μ2[W]/(4 W), K2'[W] → -3 K2[W]/(4 W),
     λ1'[W] -> 3 λ1[W]/(4 W), λ2'[W] -> 3 λ2[W]/(4 W)}) ==
  (1 - a) λ1[W] μ1[W]/(W (λ1[W] - μ1[W])^2) + β K2[W] (a λ2[W] + 3 μ2[W])/(4 W γ μ2[W]) // Simplify
True
```

We find that increasing temperature always decreases R_0 because $\frac{dR_0}{dT} = \frac{-\beta E K_2 (a \lambda_2 - \mu_2)}{k T^2 \gamma \mu_2}$, which is always negative.

```
D[R0 /. {λ1 → λ1[T], μ1 → μ1[T], λ2 → λ2[T], μ2 → μ2[T], K2 → K2[T]}, T] /.
  {μ1'[T] → E/(k T^2) μ1[T], λ1'[T] → E/(k T^2) λ1[T], K2'[T] -> -E/(k T^2) K2[T],
   μ2'[T] → E/(k T^2) μ2[T], λ2'[T] → E/(k T^2) λ2[T]} // Simplify
β E K2[T] (-a λ2[T] + μ2[T])/(k T^2 γ μ2[T])
```

Thus, for endoparasites, we have that increasing the mass of the hosts (or making the masses more similar - since increasing *f* would increase the mass of the second host, it has the same sign as $\frac{dR_0}{dW}$) makes the evolution of generalism more likely, whereas increasing the temperature makes the evolution of generalism less likely.

Ectoparasites

For endoparasites, we find that increasing host body size has a more complicated effect. $\frac{dR_0}{dW} = \frac{2(1-a)\lambda_1 \mu_1}{3 W(\lambda_1 - \mu_1)} - \frac{\beta K_2 (a \lambda_2 - 9 \mu_2)}{12 W \gamma \mu_2}$; the sign of this expression depends on the sign of $a \lambda_2 - 9 \mu_2$.

```
(D[R0 /. {λ1 → λ1[W], μ1 → μ1[W], λ2 → λ2[W], μ2 → μ2[W], K2 → K2[W]}, W] /.
    {μ1'[W] → -μ1[W]/(4 W), μ2'[W] → -μ2[W]/(4 W), K2'[W] → -3 K2[W]/(4 W),
     λ1'[W] -> 5 λ1[W]/(12 W), λ2'[W] -> 5 λ2[W]/(12 W)}) ==
  2 (1 - a) λ1[W] μ1[W]/(3 W (λ1[W] - μ1[W])^2) - β K2[W] (a λ2[W] - 9 μ2[W])/(12 W γ μ2[W]) // Simplify
True
```

We find that this expression will be negative whenever $W < \frac{27}{f}\left(\frac{\mu_0}{a \lambda_0}\right)^{3/2}$, meaning that the derivative $\frac{dR_0}{dW} > 0$. So, if host body size is small, increasing host size will make it easier for a generalist to invade. However, as host body size gets larger, eventually $\frac{dR_0}{dW} < 0$.

```
Solve[(a λ2[W] - 9 μ2[W] /.
    {μ2[W] → μ0 Exp[-E / (k T)] (f W)^-1/4, λ2[W] → λ0 Exp[-E / (k T)] (f W)^5/12}) == 0, W]
```

$$\left\{\left\{W \to -\frac{27\,\mu 0^{3/2}}{a^{3/2}\,f\,\lambda 0^{3/2}}\right\}, \left\{W \to \frac{27\,\mu 0^{3/2}}{a^{3/2}\,f\,\lambda 0^{3/2}}\right\}\right\}$$

Increasing temperature has the same effect for an ectoparasite as an endoparasite.

Case 2: Direct life cycle; two specialist parasites; parasite regulates host population size; active host seeking; avoidance of infected hosts

For this model, let S_1 and S_2 be the number of susceptible hosts of species 1 and 2, respectively. We will refer to these the "primary" and "secondary" hosts for simplicity. We assume that there are two "resident" parasites, one specializing on the primary host and the other specializing on the secondary host. We let $I_{1\,r}$ and $I_{2\,r}$ be the number of primary and secondary hosts infected by the resident parasites. The "mutant" parasite is a generalist, and we let $I_{1\,m}$ and $I_{2\,m}$ be the number of primary and secondary hosts infected by the mutant parasite. We let P_1, P_2 and P_m be the number of resident (specialist) and mutant (generalist) parasites in the environment.

The model for this system is given below.

```
dS1dt = r1 (S1 + I1r + I1m) (1 - (S1 + I1r + I1m)/K1) - β1 S1 (P1r + P12m);
dI1rdt = β1 S1 P1r - μ1 I1r;
dP1rdt = λ1 I1r - β1 S1 P1r - γ1 P1r;

dS2dt = r2 (S2 + I2r + I2m) (1 - (S2 + I2r + I2m)/K2) - β2 S2 (P2r + P12m);
dI2rdt = β2 S2 P2r - μ2 I2r;
dP2rdt = λ2 I2r - β2 S2 P2r - γ2 P2r;

dI1mdt = β1 S1 P12m - μ1 I1m;
dI2mdt = β2 S2 P12m - μ2 I2m;
dP12mdt = a λ1 I1m + a λ2 I2m - β1 S1 P12m - β2 S2 P12m - γ P12m;
```

Note that the specialist parasites do not have any interaction with one another (i.e., the dynamics of S_1, $I_{1\,r}$, and P_1 do not depend on S_2, $I_{2\,r}$, or P_2). Since, for an invasion analysis, we assume that the resident parasites come to an ecological equilibrium with their hosts, we can solve for these equilibria easily, finding that $S_1 = \frac{\gamma_1 \mu_1}{\beta_1 (\lambda_1 - \mu_1)}$ and $S_2 = \frac{\gamma_2 \mu_2}{\beta_2 (\lambda_2 - \mu_2)}$.

```
Eq = Solve[({dS1dt == 0, dS2dt == 0, dI1rdt == 0, dI2rdt == 0, dP1rdt == 0, dP2rdt == 0} /.
      {I1m → 0, I2m → 0, P12m → 0}), {S1, S2, I1r, I2r, P1r, P2r}];
Eq[[
 13,
 1
  ;;
  2]]
```

$$\left\{S1 \to -\frac{\gamma 1\,\mu 1}{\beta 1\,(-\lambda 1 + \mu 1)}, S2 \to -\frac{\gamma 2\,\mu 2}{\beta 2\,(-\lambda 2 + \mu 2)}\right\}$$

To determine whether the generalist parasite can invade, we need to examine the stability of the full system when the generalist parasite is absent (i.e., when $I_{1\,m} = 0$, $I_{2\,m} = 0$, and $P_{12,m} = 0$). The Jacobian

matrix for this is given below. Note that this matrix has a very simple structure:

$$J = \begin{pmatrix} J_1 & 0 & M_1 \\ 0 & J_2 & M_2 \\ 0 & 0 & J_m \end{pmatrix}$$

This structure is actually quite convenient - J is an upper-triangular matrix, which means that its eigenvalues are given by the eigenvalues of J_1, J_2, and J_m. The eigenvalues J_1 and J_2 determine the stability of the endemic equilibria for the two specialist parasite. By assumption, these eigenvalues are negative. Thus, we only need be concerned about the eigenvalues of J_m, which is the submatrix dealing with the equations for the generalist parasite.

```
J = {{D[dS1dt, S1], D[dS1dt, I1r], D[dS1dt, P1r], D[dS1dt, S2], D[dS1dt, I2r],
      D[dS1dt, P2r], D[dS1dt, I1m], D[dS1dt, I2m], D[dS1dt, P12m]},
     {D[dI1rdt, S1], D[dI1rdt, I1r], D[dI1rdt, P1r], D[dI1rdt, S2], D[dI1rdt, I2r],
      D[dI1rdt, P2r], D[dI1rdt, I1m], D[dI1rdt, I2m], D[dI1rdt, P12m]},
     {D[dP1rdt, S1], D[dP1rdt, I1r], D[dP1rdt, P1r], D[dP1rdt, S2], D[dP1rdt, I2r],
      D[dP1rdt, P2r], D[dP1rdt, I1m], D[dP1rdt, I2m], D[dP1rdt, P12m]},
     {D[dS2dt, S1], D[dS2dt, I1r], D[dS2dt, P1r], D[dS2dt, S2], D[dS2dt, I2r],
      D[dS2dt, P2r], D[dS2dt, I1m], D[dS2dt, I2m], D[dS2dt, P12m]},
     {D[dI2rdt, S1], D[dI2rdt, I1r], D[dI2rdt, P1r], D[dI2rdt, S2], D[dI2rdt, I2r],
      D[dI2rdt, P2r], D[dI2rdt, I1m], D[dI2rdt, I2m], D[dI2rdt, P12m]},
     {D[dP2rdt, S1], D[dP2rdt, I1r], D[dP2rdt, P1r], D[dP2rdt, S2], D[dP2rdt, I2r],
      D[dP2rdt, P2r], D[dP2rdt, I1m], D[dP2rdt, I2m], D[dP2rdt, P12m]},
     {D[dI1mdt, S1], D[dI1mdt, I1r], D[dI1mdt, P1r], D[dI1mdt, S2], D[dI1mdt, I2r],
      D[dI1mdt, P2r], D[dI1mdt, I1m], D[dI1mdt, I2m], D[dI1mdt, P12m]},
     {D[dI2mdt, S1], D[dI2mdt, I1r], D[dI2mdt, P1r], D[dI2mdt, S2], D[dI2mdt, I2r],
      D[dI2mdt, P2r], D[dI2mdt, I1m], D[dI2mdt, I2m], D[dI2mdt, P12m]},
     {D[dP12mdt, S1], D[dP12mdt, I1r], D[dP12mdt, P1r], D[dP12mdt, S2],
      D[dP12mdt, I2r], D[dP12mdt, P2r], D[dP12mdt, I1m],
      D[dP12mdt, I2m], D[dP12mdt, P12m]}} /. {I1m → 0, I2m → 0, P12m → 0};
MatrixForm[J[[1 ;; 3, 1 ;; 3]]]
```

$$\begin{pmatrix} -\frac{r1\,(I1r+S1)}{K1} + r1\left(1 - \frac{I1r+S1}{K1}\right) - P1r\,\beta 1 & -\frac{r1\,(I1r+S1)}{K1} + r1\left(1 - \frac{I1r+S1}{K1}\right) & -S1\,\beta 1 \\ P1r\,\beta 1 & -\mu 1 & S1\,\beta 1 \\ -P1r\,\beta 1 & \lambda 1 & -S1\,\beta 1 - \gamma 1 \end{pmatrix}$$

```
MatrixForm[J[[1 ;; 3, 4 ;; 6]]]
```

$$\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

```
MatrixForm[J[[1 ;; 3, 7 ;; 9]]]
```

$$\begin{pmatrix} -\frac{r1\,(I1r+S1)}{K1} + r1\left(1 - \frac{I1r+S1}{K1}\right) & 0 & -S1\,\beta 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

```
MatrixForm[J[[4 ;; 6, 1 ;; 3]]]
```

$$\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

```
MatrixForm[J[[4 ;; 6, 4 ;; 6]]]
```

$$\begin{pmatrix} -\frac{r2\,(I2r+S2)}{K2}+r2\left(1-\frac{I2r+S2}{K2}\right)-P2r\,\beta2 & -\frac{r2\,(I2r+S2)}{K2}+r2\left(1-\frac{I2r+S2}{K2}\right) & -S2\,\beta2 \\ P2r\,\beta2 & -\mu2 & S2\,\beta2 \\ -P2r\,\beta2 & \lambda2 & -S2\,\beta2-\gamma2 \end{pmatrix}$$

```
MatrixForm[J[[4 ;; 6, 7 ;; 9]]]
```

$$\begin{pmatrix} 0 & -\frac{r2\,(I2r+S2)}{K2}+r2\left(1-\frac{I2r+S2}{K2}\right) & -S2\,\beta2 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

```
MatrixForm[J[[1 ;; 3, 7 ;; 9]]]
```

$$\begin{pmatrix} -\frac{r1\,(I1r+S1)}{K1}+r1\left(1-\frac{I1r+S1}{K1}\right) & 0 & -S1\,\beta1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

```
MatrixForm[J[[4 ;; 6, 7 ;; 9]]]
```

$$\begin{pmatrix} 0 & -\frac{r2\,(I2r+S2)}{K2}+r2\left(1-\frac{I2r+S2}{K2}\right) & -S2\,\beta2 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

The eigenvalues of this matrix determine the stability of the generalist-absent system.

```
MatrixForm[J[[7 ;; 9, 7 ;; 9]]]
```

$$\begin{pmatrix} -\mu1 & 0 & S1\,\beta1 \\ 0 & -\mu2 & S2\,\beta2 \\ a\,\lambda1 & a\,\lambda2 & -S1\,\beta1-S2\,\beta2-\gamma \end{pmatrix}$$

Applying the next generation theorem, we find that the stability of the system depends on the magnitude of $\frac{\sqrt{a}\ \sqrt{S2\,\beta2\,\lambda2\,\mu1+S1\,\beta1\,\lambda1\,\mu2}}{\sqrt{S1\,\beta1+S2\,\beta2+\gamma}\ \sqrt{\mu1}\ \sqrt{\mu2}}$ - if this is greater than 1, then the generalist-absent equilibrium is unstable and the generalist can invade.

```
F = {{0, 0, S1 β1}, {0, 0, S2 β2}, {a λ1, a λ2, 0}};
V = {{μ1, 0, 0}, {0, μ2, 0}, {0, 0, S1 β1 + S2 β2 + γ}};
Eigenvalues[Dot[F, Inverse[V]]]
```

$$\left\{0,\ -\frac{\sqrt{a}\ \sqrt{S2\,\beta2\,\lambda2\,\mu1+S1\,\beta1\,\lambda1\,\mu2}}{\sqrt{S1\,\beta1+S2\,\beta2+\gamma}\ \sqrt{\mu1}\ \sqrt{\mu2}},\ \frac{\sqrt{a}\ \sqrt{S2\,\beta2\,\lambda2\,\mu1+S1\,\beta1\,\lambda1\,\mu2}}{\sqrt{S1\,\beta1+S2\,\beta2+\gamma}\ \sqrt{\mu1}\ \sqrt{\mu2}}\right\}$$

This condition can be rewritten as
$\frac{(a\lambda_1-\mu_1)\beta_1}{\mu_1\gamma}\hat{S}_1+\frac{(a\lambda_2-\mu_2)\beta_2}{\mu_2\gamma}\hat{S}_2>1,$
where $\hat{S}_1$ and $\hat{S}_2$ are the endemic equilibrium reached when only the specialist parasites are present. Interestingly, $\frac{(a\lambda_1-\mu_1)\beta_1}{\mu_1\gamma}$ is the reciprocal of the equilibrium abundance of the first host if the generalist parasite was the only parasite in the system and it only infected the first host; similarly, $\frac{(a\lambda_2-\mu_2)\beta_2}{\mu_2\gamma}$ is the reciprocal of the equilibrium abundance of the second host, if the generalist parasite was the only parasite in the system and it only infected the second host. Plugging in the equilibrium values for $\hat{S}_1$ and $\hat{S}_2$, the invasion condition simplifies to
$\frac{a\lambda_1-\mu_1}{\lambda_1-\mu_1}+\frac{a\lambda_2-\mu_2}{\lambda_2-\mu_2}>1.$

Notice that there are only three factors that influence whether a generalist parasite can invade or not:

the cost of generalism a, the shedding rates λ_1 and λ_2, and the host mortality rates μ_1 and μ_2. In this model, the abundance of the hosts matters not at all, contrary to simple verbal theories for the evolution of generalism. Of course, this is because we assume that the parasite regulates the host population size. If that is not the case, we have a different model, one in which parasites can move hosts into an infected class, but do not cause mortality.

Regardless, we can use a similar analysis to study how changing the host body size or temperature will affect the ability of the generalist parasite to invade. Notice that because increasing the mass of the hosts increases shedding rates and decreases mortality rates, increasing host body size will still increase the likelihood that the generalist can invade, for both endoparasites and ectoparasites.

Effect of increasing body size for a generalist endoparasite:

```
Simplify[
 D[(a λ1[W] - μ1[W])/(λ1[W] - μ1[W]), W] /. {K1'[W] -> (-3 K1[W])/(4 W), μ1'[W] -> (-μ1[W])/(4 W), λ1'[W] -> (3 λ1[W])/(4 W)}]
Simplify[D[(a λ2[W] - μ2[W])/(λ2[W] - μ2[W]), W] /.
  {K2'[W] -> (-3 K2[W])/(4 W), μ2'[W] -> (-μ2[W])/(4 W), λ2'[W] -> (3 λ2[W])/(4 W)}]
-((-1 + a) λ1[W] μ1[W])/(W (λ1[W] - μ1[W])^2)
-((-1 + a) λ2[W] μ2[W])/(W (λ2[W] - μ2[W])^2)
```

Effect of increasing body size for a generalist ectoparasite:

```
Simplify[
 D[(a λ1[W] - μ1[W])/(λ1[W] - μ1[W]), W] /. {K1'[W] -> (-3 K1[W])/(4 W), μ1'[W] -> (-μ1[W])/(4 W), λ1'[W] -> (5 λ1[W])/(12 W)}]
Simplify[D[(a λ2[W] - μ2[W])/(λ2[W] - μ2[W]), W] /.
  {K2'[W] -> (-3 K2[W])/(4 W), μ2'[W] -> (-μ2[W])/(4 W), λ2'[W] -> (5 λ2[W])/(12 W)}]
-((2 (-1 + a) λ1[W] μ1[W])/(3 W (λ1[W] - μ1[W])^2))
-((2 (-1 + a) λ2[W] μ2[W])/(3 W (λ2[W] - μ2[W])^2))
```

However, for both endoparasites and ectoparasites, the invasion fitness is independent of temperature (because shedding rate and mortality rate scale with temperature in the same way):

```
D[(a λ1 - μ1)/(λ1 - μ1) + (a λ2 - μ2)/(λ2 - μ2) /. {μ1 -> μ0 Exp[-E/(k T)] W^(-1/4), μ2 -> μ0 Exp[-E/(k T)] (f W)^(-1/4),
    λ1 -> λ0 Exp[-E/(k T)] W^(3/4), λ2 -> λ0 Exp[-E/(k T)] (f W)^(3/4)}, T] // Simplify
0
```

Case 3: Direct life cycle; two specialist parasites; constant host population size;

active host seeking; avoidance of infected hosts

For this model, we assume that the primary and secondary host population sizes are constant at K_1 and K_2, respectively. As such, we do not need to keep track of the dynamics of both susceptible and infected hosts - we can simply track the prevalence of infection. We define I_{1r} and I_{2r} as the fraction of primary and secondary hosts infected by the specialist parasites, respectively.

The dynamics of parasites in the environment are governed by shedding and loss, as before. The rate of shedding depends on the *number* of infected hosts, e.g., $I_{1r}K_1$. Similarly, loss due to contact with susceptible hosts depends on the *number* of susceptible hosts, e.g., $(1 - I_{1r} - I_{1m})\,K_1$.

The model is given below:

```
dI1rdt = β1 (1 - I1r - I1m) P1r - μ1 I1r;
dP1rdt = λ1 I1r K1 - β1 (1 - I1r - I1m) K1 P1r - γ P1r;

dI2rdt = β2 (1 - I2r - I2m) P2r - μ2 I2r;
dP2rdt = λ2 I2r K2 - β2 (1 - I2r - I2m) K2 P2r - γ P2r;

dI1mdt = β1 (1 - I1r - I1m) P12m - μ1 I1m;
dI2mdt = β2 (1 - I2r - I2m) P12m - μ2 I2m;
dP12mdt =
  a λ1 I1m K1 + a λ2 I2m K2 - β1 (1 - I1r - I1m) K1 P12m - β2 (1 - I2r - I2m) K2 P12m - γ P12m;
```

In the absence of the generalist parasite, the equilibrium prevalences of infection are $I_{1,r} = 1 - \frac{\gamma\,\mu_1}{\beta_1\,K_1(\lambda_1-\mu_1)}$ and $I_{2,r} = 1 - \frac{\gamma\,\mu_2}{\beta_2\,K_2(\lambda_2-\mu_2)}$, implying that the equilibrium number of susceptibles are $\frac{\gamma\,\mu_1}{\beta_1\,K_1(\lambda_1-\mu_1)}$ and $\frac{\gamma\,\mu_2}{\beta_2\,K_2(\lambda_2-\mu_2)}$.

```
Eq = Solve[({dI1rdt == 0, dP1rdt == 0, dI2rdt == 0, dP2rdt == 0} /. {I1m → 0, I2m → 0}),
    {I1r, P1r, I2r, P2r}] // Simplify;
Eq[[
 4]]
```

$$\left\{\text{I1r} \to \frac{\text{K1}\,\beta 1\,\lambda 1 - \text{K1}\,\beta 1\,\mu 1 - \gamma\,\mu 1}{\text{K1}\,\beta 1\,\lambda 1 - \text{K1}\,\beta 1\,\mu 1},\ \text{P1r} \to \frac{\text{K1}\,\beta 1\,(\lambda 1 - \mu 1) - \gamma\,\mu 1}{\beta 1\,\gamma},\right.$$
$$\left.\text{I2r} \to \frac{\text{K2}\,\beta 2\,\lambda 2 - \text{K2}\,\beta 2\,\mu 2 - \gamma\,\mu 2}{\text{K2}\,\beta 2\,\lambda 2 - \text{K2}\,\beta 2\,\mu 2},\ \text{P2r} \to \frac{\text{K2}\,\beta 2\,(\lambda 2 - \mu 2) - \gamma\,\mu 2}{\beta 2\,\gamma}\right\}$$

The Jacobian matrix for the full system is:

```
J = {{D[dI1rdt, I1r], D[dI1rdt, P1r], D[dI1rdt, I2r],
      D[dI1rdt, P2r], D[dI1rdt, I1m], D[dI1rdt, I2m], D[dI1rdt, P12m]},
     {D[dP1rdt, I1r], D[dP1rdt, P1r], D[dP1rdt, I2r], D[dP1rdt, P2r],
      D[dP1rdt, I1m], D[dP1rdt, I2m], D[dP1rdt, P12m]},
     {D[dI2rdt, I1r], D[dI2rdt, P1r], D[dI2rdt, I2r], D[dI2rdt, P2r],
      D[dI2rdt, I1m], D[dI2rdt, I2m], D[dI2rdt, P12m]},
     {D[dP2rdt, I1r], D[dP2rdt, P1r], D[dP2rdt, I2r], D[dP2rdt, P2r],
      D[dP2rdt, I1m], D[dP2rdt, I2m], D[dP2rdt, P12m]},
     {D[dI1mdt, I1r], D[dI1mdt, P1r], D[dI1mdt, I2r], D[dI1mdt, P2r],
      D[dI1mdt, I1m], D[dI1mdt, I2m], D[dI1mdt, P12m]},
     {D[dI2mdt, I1r], D[dI2mdt, P1r], D[dI2mdt, I2r], D[dI2mdt, P2r],
      D[dI2mdt, I1m], D[dI2mdt, I2m], D[dI2mdt, P12m]},
     {D[dP12mdt, I1r], D[dP12mdt, P1r], D[dP12mdt, I2r], D[dP12mdt, P2r], D[dP12mdt,
       I1m], D[dP12mdt, I2m], D[dP12mdt, P12m]}} /. {I1m → 0, I2m → 0, P12m → 0};
MatrixForm[
 J]
```

$$\begin{pmatrix} -\text{P1r}\,\beta 1-\mu 1 & (1-\text{I1r})\,\beta 1 & 0 & 0 & -\text{P1r}\,\beta 1 & 0 \\ \text{K1 P1r}\,\beta 1+\text{K1}\,\lambda 1 & -(1-\text{I1r})\,\text{K1}\,\beta 1-\gamma & 0 & 0 & \text{K1 P1r}\,\beta 1 & 0 \\ 0 & 0 & -\text{P2r}\,\beta 2-\mu & (1-\text{I2r})\,\beta 2 & 0 & -\text{P2r}\,\beta 2 \\ 0 & 0 & \text{K2 P2r}\,\beta 2+\text{K2}\,\lambda 2 & -(1-\text{I2r})\,\text{K2}\,\beta 2-\gamma & 0 & \text{K2 P2r}\,\beta 2 \\ 0 & 0 & 0 & 0 & -\mu 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & -\mu 2 \\ 0 & 0 & 0 & 0 & \text{a K1}\,\lambda 1 & \text{a K2}\,\lambda 2 \end{pmatrix}$$

As before, this has a upper block triangular structure, and whether the generalist can invade is entirely determined by the bottom left submatrix:

```
MatrixForm[J[[5 ;; 7, 5 ;; 7]]]
```

$$\begin{pmatrix} -\mu 1 & 0 & (1-\text{I1r})\,\beta 1 \\ 0 & -\mu 2 & (1-\text{I2r})\,\beta 2 \\ \text{a K1}\,\lambda 1 & \text{a K2}\,\lambda 2 & -(1-\text{I1r})\,\text{K1}\,\beta 1-(1-\text{I2r})\,\text{K2}\,\beta 2-\gamma \end{pmatrix}$$

Applying the next generation matrix theorem, the generalist will be able to invade if the eigenvalue is greater than 1.

```
F = {{0, 0, (1 - I1r) β1}, {0, 0, (1 - I2r) β2}, {a λ1 K1, a λ2 K2, 0}};
V = {{μ1, 0, 0}, {0, μ2, 0}, {0, 0, (1 - I1r) K1 β1 + (1 - I2r) K2 β2 + γ}};
Eigenvalues[Dot[F, Inverse[V]]] // Simplify
```

$$\left\{0,\ -\left(\left(\sqrt{\text{a}}\ \sqrt{((-1+\text{I2r})\,\text{K2}\,\beta 2\,\lambda 2\,\mu 1+(-1+\text{I1r})\,\text{K1}\,\beta 1\,\lambda 1\,\mu 2)}\right)\Big/\left(\sqrt{((-1+\text{I1r})\,\text{K1}\,\beta 1+(-1+\text{I2r})\,\text{K2}\,\beta 2-\gamma)\ \sqrt{\mu 1}\ \sqrt{\mu 2}}\right)\right),\ \left(\sqrt{\text{a}}\ \sqrt{((-1+\text{I2r})\,\text{K2}\,\beta 2\,\lambda 2\,\mu 1+(-1+\text{I1r})\,\text{K1}\,\beta 1\,\lambda 1\,\mu 2)}\right)\Big/\left(\sqrt{((-1+\text{I1r})\,\text{K1}\,\beta 1+(-1+\text{I2r})\,\text{K2}\,\beta 2-\gamma)\ \sqrt{\mu 1}\ \sqrt{\mu 2}}\right)\right\}$$

This condition can be simplified to

$\frac{\beta_1 K_1(a\lambda_1-\mu_1)}{\gamma\mu_1}(1-I_{1,r})+\frac{\beta_2 K_2(a\lambda_2-\mu_2)}{\gamma\mu_2}(1-I_{2,r})>1,$

which, after plugging in the generalist-free endemic equilibria for $I_{1,r}$ and $I_{2,r}$, simplifies to

$\frac{a\lambda_1-\mu_1}{\lambda_1-\mu_1}+\frac{a\lambda_2-\mu_2}{\lambda_2-\mu_2}>1$

```
Simplify[(β1 K1 (a λ1 - μ1))/(γ μ1) (1 - I1r) /. {I1r -> (K1 β1 λ1 - K1 β1 μ1 - γ μ1)/(K1 β1 λ1 - K1 β1 μ1)}]
Simplify[(β2 K2 (a λ2 - μ2))/(γ μ2) (1 - I2r) /. {I2r -> (K2 β2 λ2 - K2 β2 μ2 - γ μ2)/(K2 β2 λ2 - K2 β2 μ2)}]
```

$$\frac{a\,\lambda 1 - \mu 1}{\lambda 1 - \mu 1}$$

$$\frac{a\,\lambda 2 - \mu 2}{\lambda 2 - \mu 2}$$

We can again see how changing host body size and temperature will affect invasion by looking at the derivatives of the invasion condition with respect to body size and temperature, after substituting in the allometric scaling relationships. Note that now you have a contravailing pressure of increasing body size on invasion fitness for the generalist: increasing host body size increases shedding rate, but decreases carrying capacity.

For an endoparasite, the derivative of the invasion fitness with respect to host body size is always positive because $\frac{dR_0}{dW} = \frac{(1-a)}{W}\left(\frac{\lambda_1 \mu_1}{(\lambda_1-\mu_1)^2} + \frac{\lambda_2 \mu_2}{(\lambda_2-\mu_2)^2}\right)$.

```
(D[(a λ1[W] - μ1[W])/(λ1[W] - μ1[W]) + (a λ2[W] - μ2[W])/(λ2[W] - μ2[W]), W] /.
    {μ1'[W] -> -μ1[W]/(4 W), λ1'[W] -> 3 λ1[W]/(4 W), μ2'[W] -> -μ2[W]/(4 W), λ2'[W] -> 3 λ2[W]/(4 W)}) ==
  (1 - a)/W (λ1[W] μ1[W]/(λ1[W] - μ1[W])^2 + λ2[W] μ2[W]/(λ2[W] - μ2[W])^2) // Simplify
```

```
True
```

Similarly, for an ectoparasite, the derivative of the invasion fitness with respect to host body size is always positive beacuse $\frac{dR_0}{dW} = \frac{2(1-a)}{3W}\left(\frac{\lambda_1 \mu_1}{(\lambda_1-\mu_1)^2} + \frac{\lambda_2 \mu_2}{(\lambda_2-\mu_2)^2}\right)$.

```
Simplify[D[(a λ1[W] - μ1[W])/(λ1[W] - μ1[W]) + (a λ2[W] - μ2[W])/(λ2[W] - μ2[W]), W] /.
    {μ1'[W] -> -μ1[W]/(4 W), λ1'[W] -> 5 λ1[W]/(12 W), μ2'[W] -> -μ2[W]/(4 W), λ2'[W] -> 5 λ2[W]/(12 W)}] ==
  2 (1 - a)/(3 W) (λ1[W] μ1[W]/(λ1[W] - μ1[W])^2 + λ2[W] μ2[W]/(λ2[W] - μ2[W])^2) // Simplify
```

```
True
```

For both endoparasites and ectoparasites, the derivative of the invasion fitness with respect to temperature is zero, as before.

```
D[(a λ1[T] - μ1[T])/(λ1[T] - μ1[T]) + (a λ2[T] - μ2[T])/(λ2[T] - μ2[T]), T] /. {μ2'[T] -> E μ2[T]/(k T^2),
    λ2'[T] -> E λ2[T]/(k T^2), μ1'[T] -> E μ1[T]/(k T^2), λ1'[T] -> E λ1[T]/(k T^2)} // Simplify
```

```
0
```

Case 4: Direct life cycle; two specialist parasites; constant host population size;

active host seeking; no avoidance of infected hosts

The only change with the model above involves the loss of parasites due to contact with hosts. Since the parasite cannot determine whether a host is infected or not, the loss rate is, e.g., βK_1. Parasite consumption by an infected individual has no effect on infection status; if the parasite ends up in an already-infected host, it is simply lost from the system.

```
dI1rdt = β1 (1 - I1r - I1m) P1r - μ1 I1r;
dP1rdt = λ1 I1r K1 - β1 K1 P1r - γ P1r;

dI2rdt = β2 (1 - I2r - I2m) P2r - μ2 I2r;
dP2rdt = λ2 I2r K2 - β2 K2 P2r - γ P2r;

dI1mdt = β1 (1 - I1r - I1m) P12m - μ1 I1m;
dI2mdt = β2 (1 - I2r - I2m) P12m - μ2 I2m;
dP12mdt = a λ1 I1m K1 + a λ2 I2m K2 - β1 K1 P12m - β2 K2 P12m - γ P12m;
```

In the absence of the generalist parasite, the equilibrium prevalences of infection are $I_{1,r} = 1 - \frac{(K1\,\beta1+\gamma)\,\mu1}{K1\,\beta1\,\lambda1}$ and $I_{2,r} = 1 - \frac{(K2\,\beta2+\gamma)\,\mu2}{K2\,\beta2\,\lambda2}$.

```
Solve[({dI1rdt == 0, dP1rdt == 0, dI2rdt == 0, dP2rdt == 0} /. {I1m → 0, I2m → 0}),
  {I1r, P1r, I2r, P2r}] // Simplify
```

$$\left\{\{\text{I1r} \to 0, \text{P1r} \to 0, \text{I2r} \to 0, \text{P2r} \to 0\},\right.$$
$$\left\{\text{I1r} \to 1 - \frac{(\text{K1}\,\beta1 + \gamma)\,\mu1}{\text{K1}\,\beta1\,\lambda1}, \text{P1r} \to \frac{\text{K1}\,\beta1\,(\lambda1 - \mu1) - \gamma\,\mu1}{\beta1\,(\text{K1}\,\beta1 + \gamma)}, \text{I2r} \to 0, \text{P2r} \to 0\right\},$$
$$\left\{\text{I1r} \to 0, \text{P1r} \to 0, \text{I2r} \to 1 - \frac{(\text{K2}\,\beta2 + \gamma)\,\mu2}{\text{K2}\,\beta2\,\lambda2}, \text{P2r} \to \frac{\text{K2}\,\beta2\,(\lambda2 - \mu2) - \gamma\,\mu2}{\beta2\,(\text{K2}\,\beta2 + \gamma)}\right\},$$
$$\left\{\text{I1r} \to 1 - \frac{(\text{K1}\,\beta1 + \gamma)\,\mu1}{\text{K1}\,\beta1\,\lambda1}, \text{P1r} \to \frac{\text{K1}\,\beta1\,(\lambda1 - \mu1) - \gamma\,\mu1}{\beta1\,(\text{K1}\,\beta1 + \gamma)},\right.$$
$$\left.\left.\text{I2r} \to 1 - \frac{(\text{K2}\,\beta2 + \gamma)\,\mu2}{\text{K2}\,\beta2\,\lambda2}, \text{P2r} \to \frac{\text{K2}\,\beta2\,(\lambda2 - \mu2) - \gamma\,\mu2}{\beta2\,(\text{K2}\,\beta2 + \gamma)}\right\}\right\}$$

Skipping ahead to the calculation of the Jacobian for the full system:

```
J = {{D[dI1rdt, I1r], D[dI1rdt, P1r], D[dI1rdt, I2r],
      D[dI1rdt, P2r], D[dI1rdt, I1m], D[dI1rdt, I2m], D[dI1rdt, P12m]},
     {D[dP1rdt, I1r], D[dP1rdt, P1r], D[dP1rdt, I2r], D[dP1rdt, P2r],
      D[dP1rdt, I1m], D[dP1rdt, I2m], D[dP1rdt, P12m]},
     {D[dI2rdt, I1r], D[dI2rdt, P1r], D[dI2rdt, I2r], D[dI2rdt, P2r],
      D[dI2rdt, I1m], D[dI2rdt, I2m], D[dI2rdt, P12m]},
     {D[dP2rdt, I1r], D[dP2rdt, P1r], D[dP2rdt, I2r], D[dP2rdt, P2r],
      D[dP2rdt, I1m], D[dP2rdt, I2m], D[dP2rdt, P12m]},
     {D[dI1mdt, I1r], D[dI1mdt, P1r], D[dI1mdt, I2r], D[dI1mdt, P2r],
      D[dI1mdt, I1m], D[dI1mdt, I2m], D[dI1mdt, P12m]},
     {D[dI2mdt, I1r], D[dI2mdt, P1r], D[dI2mdt, I2r], D[dI2mdt, P2r],
      D[dI2mdt, I1m], D[dI2mdt, I2m], D[dI2mdt, P12m]},
     {D[dP12mdt, I1r], D[dP12mdt, P1r], D[dP12mdt, I2r], D[dP12mdt, P2r], D[dP12mdt,
       I1m], D[dP12mdt, I2m], D[dP12mdt, P12m]}} /. {I1m → 0, I2m → 0, P12m → 0};
MatrixForm[
 J]
```

$$\begin{pmatrix} -\text{P1r}\,\beta 1-\mu 1 & (1-\text{I1r})\,\beta 1 & 0 & 0 & -\text{P1r}\,\beta 1 & 0 & 0 \\ \text{K1}\,\lambda 1 & -\text{K1}\,\beta 1-\gamma & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\text{P2r}\,\beta 2-\mu 2 & (1-\text{I2r})\,\beta 2 & 0 & -\text{P2r}\,\beta 2 & 0 \\ 0 & 0 & \text{K2}\,\lambda 2 & -\text{K2}\,\beta 2-\gamma & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & -\mu 1 & 0 & (1-\text{I1r})\,\beta 1 \\ 0 & 0 & 0 & 0 & 0 & -\mu 2 & (1-\text{I2r})\,\beta 2 \\ 0 & 0 & 0 & 0 & \text{a K1}\,\lambda 1 & \text{a K2}\,\lambda 2 & -\text{K1}\,\beta 1-\text{K2}\,\beta 2-\gamma \end{pmatrix}$$

As before, this has a upper block triangular structure, and whether the generalist can invade is entirely determined by the bottom left submatrix:

```
MatrixForm[J[[5 ;; 7, 5 ;; 7]]]
```

$$\begin{pmatrix} -\mu 1 & 0 & (1-\text{I1r})\,\beta 1 \\ 0 & -\mu 2 & (1-\text{I2r})\,\beta 2 \\ \text{a K1}\,\lambda 1 & \text{a K2}\,\lambda 2 & -\text{K1}\,\beta 1-\text{K2}\,\beta 2-\gamma \end{pmatrix}$$

Applying the next generation matrix theorem, the generalist will be able to invade if the eigenvalue is greater than 1. This expression simplifies to

```
F = {{0, 0, (1 - I1r) β1}, {0, 0, (1 - I2r) β2}, {a λ1 K1, a λ2 K2, 0}};
V = {{μ1, 0, 0}, {0, μ2, 0}, {0, 0, K1 β1 + K2 β2 + γ}};
Eigenvalues[Dot[F, Inverse[V]]] // Simplify
```

$$\left\{0,\ -\left(\left(\text{i}\sqrt{\text{a}}\ \sqrt{((-1+\text{I2r})\ \text{K2}\,\beta 2\,\lambda 2\,\mu 1+(-1+\text{I1r})\ \text{K1}\,\beta 1\,\lambda 1\,\mu 2)}\right)\Big/\left(\sqrt{\text{K1}\,\beta 1+\text{K2}\,\beta 2+\gamma}\ \sqrt{\mu 1}\ \sqrt{\mu 2}\right)\right),\ \left(\text{i}\sqrt{\text{a}}\ \sqrt{((-1+\text{I2r})\ \text{K2}\,\beta 2\,\lambda 2\,\mu 1+(-1+\text{I1r})\ \text{K1}\,\beta 1\,\lambda 1\,\mu 2)}\right)\Big/\left(\sqrt{\text{K1}\,\beta 1+\text{K2}\,\beta 2+\gamma}\ \sqrt{\mu 1}\ \sqrt{\mu 2}\right)\right\}$$

Notice that if you square the second eigenvalue, you get a positive real number - this is R_0 for the generalist for this system.

$$\left(-\left(\left(\text{i}\sqrt{\text{a}}\ \sqrt{((-1+\text{I2r})\ \text{K2}\,\beta 2\,\lambda 2\,\mu 1+(-1+\text{I1r})\ \text{K1}\,\beta 1\,\lambda 1\,\mu 2)}\right)\Big/\left(\sqrt{\text{K1}\,\beta 1+\text{K2}\,\beta 2+\gamma}\ \sqrt{\mu 1}\ \sqrt{\mu 2}\right)\right)\right)^2$$

$$-((\text{a}\ ((-1+\text{I2r})\ \text{K2}\,\beta 2\,\lambda 2\,\mu 1+(-1+\text{I1r})\ \text{K1}\,\beta 1\,\lambda 1\,\mu 2))\ /\ ((\text{K1}\,\beta 1+\text{K2}\,\beta 2+\gamma)\,\mu 1\,\mu 2))$$

If you plug in the equilibrium values of I_{1r} and I_{2r}, you end up with a *very* simple expression, which is the cost of generalism multiplied by 1 plus the probability that a parasite in the environment is lost rather than consumed $\left(\frac{\gamma}{\beta_1 K_1+\beta_2 K_2+\gamma}\right)$.

```
Simplify[
    -((a ((-1 + I2r) K2 β2 λ2 μ1 + (-1 + I1r) K1 β1 λ1 μ2)) / ((K1 β1 + K2 β2 + γ) μ1 μ2)) /.
     {I1r → 1 - (K1 β1 + γ) μ1 / (K1 β1 λ1), I2r → 1 - (K2 β2 + γ) μ2 / (K2 β2 λ2)}] ==
  a (1 + γ / (β1 K1 + β2 K2 + γ)) // Simplify
```

```
True
```

For an endoparasite, we again see that increasing body size increases the magnitude of the invasion exponent (because increasing body size decreases the carrying capacity, thereby increasing the probability that a parasite in the environment will be lost rather than consumed - this increases the benefit to being a generalist).

```
Simplify[
  D[a (1 + γ / (β1 K1[W] + β2 K2[W] + γ)), W] /. {K1'[W] -> -3 K1[W] / (4 W), K2'[W] -> -3 K2[W] / (4 W)}]
```

$$\frac{3\,a\,\gamma\,(\beta 1\,K1[W]+\beta 2\,K2[W])}{4\,W\,(\gamma+\beta 1\,K1[W]+\beta 2\,K2[W])^2}$$

This is true for endoparasites as well:

```
Simplify[
  D[a (1 + γ / (β1 K1[W] + β2 K2[W] + γ)), W] /. {K1'[W] -> -5 K1[W] / (12 W), K2'[W] -> -5 K2[W] / (12 W)}]
```

$$\frac{5\,a\,\gamma\,(\beta 1\,K1[W]+\beta 2\,K2[W])}{12\,W\,(\gamma+\beta 1\,K1[W]+\beta 2\,K2[W])^2}$$

Interestingly, now increasing temperature actually *increases* the likelihood that the generalist parasite can invade - warmer temperatures decrease carrying capacity, thereby making it more likely that a parasite in the environment ends up not infecting any host.

```
Simplify[
  D[a (1 + γ / (β1 K1[T] + β2 K2[T] + γ)), T] /. {K1'[T] -> -E K1[W] / (k T^2), K2'[T] -> -E K2[W] / (k T^2)}]
```

$$\frac{a\,\gamma\,E\,(\beta 1\,K1[W]+\beta 2\,K2[W])}{k\,T^2\,(\gamma+\beta 1\,K1[T]+\beta 2\,K2[T])^2}$$

Case 5: Direct life cycle; two specialist parasites; constant host population size; passive host seeking; no avoidance of infected hosts

For this model, we assume that both hosts remove both parasites from the environment, but only compatible host-parasite pairs trigger infection. That is, specialists on the primary host are also “consumed” by secondary hosts (and vice versa). Intuively, you would expect this to increase the likelihood that a generalist can invade.

```
dI1rdt = β1 (1 - I1r - I1m) P1r - μ1 I1r;
dP1rdt = λ1 I1r K1 - β1 K1 P1r - β2 K2 P1r - γ P1r;

dI2rdt = β2 (1 - I2r - I2m) P2r - μ2 I2r;
dP2rdt = λ2 I2r K2 - β1 K1 P2r - β2 K2 P2r - γ P2r;

dI1mdt = β1 (1 - I1r - I1m) P12m - μ1 I1m;
dI2mdt = β2 (1 - I2r - I2m) P12m - μ2 I2m;
dP12mdt = a λ1 I1m K1 + a λ2 I2m K2 - β1 K1 P12m - β2 K2 P12m - γ P12m;
```

In the absence of the generalist parasite, the equilibrium prevalences of infection are $I_{1,r} = \frac{K1\,\beta1\,(\lambda1-\mu1)-(K2\,\beta2+\gamma)\,\mu1}{K1\,\beta1\,\lambda1}$ and $I_{2,r} = \frac{K2\,\beta2\,(\lambda2-\mu2)-(K1\,\beta1+\gamma)\,\mu2}{K2\,\beta2\,\lambda2}$.

```
Solve[({dI1rdt == 0, dP1rdt == 0, dI2rdt == 0, dP2rdt == 0} /. {I1m → 0, I2m → 0}),
  {I1r, P1r, I2r, P2r}] // Simplify
```

$$\left\{\{\text{I1r} \to 0, \text{P1r} \to 0, \text{I2r} \to 0, \text{P2r} \to 0\}, \left\{\text{I1r} \to \frac{\text{K1}\,\beta1\,(\lambda1-\mu1)-(\text{K2}\,\beta2+\gamma)\,\mu1}{\text{K1}\,\beta1\,\lambda1},\right.\right.$$
$$\text{P1r} \to \frac{\text{K1}\,\beta1\,(\lambda1-\mu1)-(\text{K2}\,\beta2+\gamma)\,\mu1}{\beta1\,(\text{K1}\,\beta1+\text{K2}\,\beta2+\gamma)}, \text{I2r} \to 0, \text{P2r} \to 0\Big\}, \Big\{\text{I1r} \to 0, \text{P1r} \to 0,$$
$$\text{I2r} \to \frac{\text{K2}\,\beta2\,(\lambda2-\mu2)-(\text{K1}\,\beta1+\gamma)\,\mu2}{\text{K2}\,\beta2\,\lambda2}, \text{P2r} \to \left.\frac{\text{K2}\,\beta2\,(\lambda2-\mu2)-(\text{K1}\,\beta1+\gamma)\,\mu2}{\beta2\,(\text{K1}\,\beta1+\text{K2}\,\beta2+\gamma)}\right\},$$
$$\left\{\text{I1r} \to \frac{\text{K1}\,\beta1\,(\lambda1-\mu1)-(\text{K2}\,\beta2+\gamma)\,\mu1}{\text{K1}\,\beta1\,\lambda1}, \text{P1r} \to \frac{\text{K1}\,\beta1\,(\lambda1-\mu1)-(\text{K2}\,\beta2+\gamma)\,\mu1}{\beta1\,(\text{K1}\,\beta1+\text{K2}\,\beta2+\gamma)},\right.$$
$$\left.\left.\text{I2r} \to \frac{\text{K2}\,\beta2\,(\lambda2-\mu2)-(\text{K1}\,\beta1+\gamma)\,\mu2}{\text{K2}\,\beta2\,\lambda2}, \text{P2r} \to \frac{\text{K2}\,\beta2\,(\lambda2-\mu2)-(\text{K1}\,\beta1+\gamma)\,\mu2}{\beta2\,(\text{K1}\,\beta1+\text{K2}\,\beta2+\gamma)}\right\}\right\}$$

Skipping ahead to the calculation of the Jacobian for the full system:

```
J = {{D[dI1rdt, I1r], D[dI1rdt, P1r], D[dI1rdt, I2r],
      D[dI1rdt, P2r], D[dI1rdt, I1m], D[dI1rdt, I2m], D[dI1rdt, P12m]},
     {D[dP1rdt, I1r], D[dP1rdt, P1r], D[dP1rdt, I2r], D[dP1rdt, P2r],
      D[dP1rdt, I1m], D[dP1rdt, I2m], D[dP1rdt, P12m]},
     {D[dI2rdt, I1r], D[dI2rdt, P1r], D[dI2rdt, I2r], D[dI2rdt, P2r],
      D[dI2rdt, I1m], D[dI2rdt, I2m], D[dI2rdt, P12m]},
     {D[dP2rdt, I1r], D[dP2rdt, P1r], D[dP2rdt, I2r], D[dP2rdt, P2r],
      D[dP2rdt, I1m], D[dP2rdt, I2m], D[dP2rdt, P12m]},
     {D[dI1mdt, I1r], D[dI1mdt, P1r], D[dI1mdt, I2r], D[dI1mdt, P2r],
      D[dI1mdt, I1m], D[dI1mdt, I2m], D[dI1mdt, P12m]},
     {D[dI2mdt, I1r], D[dI2mdt, P1r], D[dI2mdt, I2r], D[dI2mdt, P2r],
      D[dI2mdt, I1m], D[dI2mdt, I2m], D[dI2mdt, P12m]},
     {D[dP12mdt, I1r], D[dP12mdt, P1r], D[dP12mdt, I2r], D[dP12mdt, P2r], D[dP12mdt,
       I1m], D[dP12mdt, I2m], D[dP12mdt, P12m]}} /. {I1m → 0, I2m → 0, P12m → 0};
MatrixForm[
 J]
```

$$\begin{pmatrix}
-\text{P1r}\,\beta1-\mu1 & (1-\text{I1r})\,\beta1 & 0 & 0 & -\text{P1r}\,\beta1 & 0 & 0 \\
\text{K1}\,\lambda1 & -\text{K1}\,\beta1-\text{K2}\,\beta2-\gamma & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & -\text{P2r}\,\beta2-\mu2 & (1-\text{I2r})\,\beta2 & 0 & -\text{P2r}\,\beta2 & 0 \\
0 & 0 & \text{K2}\,\lambda2 & -\text{K1}\,\beta1-\text{K2}\,\beta2-\gamma & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & -\mu1 & 0 & (1-\text{I1r})\,\beta \\
0 & 0 & 0 & 0 & 0 & -\mu2 & (1-\text{I2r})\,\beta \\
0 & 0 & 0 & 0 & \text{a K1}\,\lambda1 & \text{a K2}\,\lambda2 & -\text{K1}\,\beta1-\text{K2}\,\beta
\end{pmatrix}$$

As before, this has a upper block triangular structure, and whether the generalist can invade is entirely determined by the bottom left submatrix:

```
MatrixForm[J[[5 ;; 7, 5 ;; 7]]]
```

$$\begin{pmatrix} -\mu 1 & 0 & (1-\text{I1r})\,\beta 1 \\ 0 & -\mu 2 & (1-\text{I2r})\,\beta 2 \\ \text{a K1}\,\lambda 1 & \text{a K2}\,\lambda 2 & -\text{K1}\,\beta 1-\text{K2}\,\beta 2-\gamma \end{pmatrix}$$

Applying the next generation matrix theorem, the generalist will be able to invade if the eigenvalue is greater than 1.

```
F = {{0, 0, (1 - I1r) β1}, {0, 0, (1 - I2r) β2}, {a λ1 K1, a λ2 K2, 0}};
V = {{μ1, 0, 0}, {0, μ2, 0}, {0, 0, K1 β1 + K2 β2 + γ}};
Eigenvalues[Dot[F, Inverse[V]]] // Simplify
```

$$\left\{0,\ -\left(\left(i\sqrt{a}\ \sqrt{((-1+\text{I2r})\ \text{K2}\ \beta 2\ \lambda 2\ \mu 1+(-1+\text{I1r})\ \text{K1}\ \beta 1\ \lambda 1\ \mu 2)}\right)\Big/\left(\sqrt{\text{K1}\ \beta 1+\text{K2}\ \beta 2+\gamma}\ \sqrt{\mu 1}\ \sqrt{\mu 2}\right)\right),\ \left(i\sqrt{a}\ \sqrt{((-1+\text{I2r})\ \text{K2}\ \beta 2\ \lambda 2\ \mu 1+(-1+\text{I1r})\ \text{K1}\ \beta 1\ \lambda 1\ \mu 2)}\right)\Big/\left(\sqrt{\text{K1}\ \beta 1+\text{K2}\ \beta 2+\gamma}\ \sqrt{\mu 1}\ \sqrt{\mu 2}\right)\right\}$$

Squaring the second eigenvalue yields a positive real number, which is R_0 for the generalist in this model:

```
(-((i Sqrt[a] Sqrt[((-1 + I2r) K2 β2 λ2 μ1 + (-1 + I1r) K1 β1 λ1 μ2)]) /
      (Sqrt[K1 β1 + K2 β2 + γ] Sqrt[μ1] Sqrt[μ2])))^2
-((a ((-1 + I2r) K2 β2 λ2 μ1 + (-1 + I1r) K1 β1 λ1 μ2)) / ((K1 β1 + K2 β2 + γ) μ1 μ2))
```

Interestingly, if you plug in the equilibria, you end up with a *very* simple expression, which is that the only thing that matters is the cost of generalism. Thus, host body size and temperature have no effect on anything in this model.

```
-((a ((-1 + I2r) K2 β2 λ2 μ1 + (-1 + I1r) K1 β1 λ1 μ2)) / ((K1 β1 + K2 β2 + γ) μ1 μ2)) /.
  {I1r → (K1 β1 (λ1 - μ1) - (K2 β2 + γ) μ1) / (K1 β1 λ1), I2r → (K2 β2 (λ2 - μ2) - (K1 β1 + γ) μ2) / (K2 β2 λ2)} // Simplify
```

$$2\,a$$

Case 6: Trophic transmission; one specialist parasite; parasites regulate definitive host population sizes; active seeking of intermediate hosts; avoidance of infected intermediate hosts

Let D_1 and D_2 be two definitive hosts and N be prey of both and the intermediate host. One touchy bit is how to deal with the effect of ingestion on both the dynamics of predator (the definitive host) and prey (the intermediate host). One possibility is that infection is embedded within a classic predator-prey model, where both predator and prey growth are impacted by one another. Such a model is quite different from the direct life cycle model studied in the main text, and is also very difficult to analyze. A second possibility is that prey density is constant; in this model you cannot assume that predator growth is entirely determined by prey ingestion (as in a classic predator-prey model) because the predator population will either grow or decay exponentially. We consider two possibilities: that the predator population is growing logistically or that it is constant.

Here we assume that the intermediate host (the prey) has a constant population size. We let N_T be the total population size, and $N_{I,r}$ and $N_{I,m}$ be the abundance of intermedate host infected with the resident (specialist) and mutant (generalist) parasites, respectively. We don't need to track the number of suscep-

tible intermediate hosts. The two definitive hosts both grow logistically in the absence of infection, with no direct effect of prey ingestion on their growth rate. One way to justify this assumption is to assume that the predators are eating lots of different prey items, so that their dynamics are largely independent of this particular prey item. However, infection is assumed to have an effect on the growth of the definitive host. We let $D_{1,S}$ and $D_{2,S}$ to be the number of primary and secondary definitive hosts that are susceptible to infection; $D_{1,I,r}$ is the number of primary definitive hosts infected by the specialist (resident) parasite; we assume that the secondary definitive host is not infected by its own specialist parasite. $D_{1,I,m}$ and $D_{2,I,m}$ are the numbers of primary and secondary definitive hosts infected by the generalist (mutant) parasite. Definitive hosts shed parasite back into the environment, with P_r and P_m the abundance of specialist and generalist in the environment. These parasites are consumed by the intermediate host, which can then transmit the parasite to the definitive host upon ingestion.

Note that there is no need to consider active vs. passive host seeking here, as there is only a single intermediate host that is assumed to contact parasites in the environment.

The full system is given below.

$$\mathbf{dNirdt} = \beta\,(\mathbf{NT}-\mathbf{Nir}-\mathbf{Nim})\,\mathbf{Pr} - \mathbf{a1}\,(\mathbf{D1s}+\mathbf{D1ir}+\mathbf{D1im})\,\mathbf{Nir} - \mathbf{a2}\,(\mathbf{D2s}+\mathbf{D2im})\,\mathbf{Nir};$$

$$\mathbf{dNimdt} = \beta\,(\mathbf{NT}-\mathbf{Nir}-\mathbf{Nim})\,\mathbf{Pm} - \mathbf{a1}\,(\mathbf{D1s}+\mathbf{D1ir}+\mathbf{D1im})\,\mathbf{Nim} - \mathbf{a2}\,(\mathbf{D2s}+\mathbf{D2im})\,\mathbf{Nim};$$

$$\mathbf{dD1sdt} = \mathbf{r1}\,(\mathbf{D1s}+\mathbf{D1ir}+\mathbf{D1im})\left(1-\frac{(\mathbf{D1s}+\mathbf{D1ir}+\mathbf{D1im})}{\mathbf{K1}}\right) - \mathbf{a1}\,\mathbf{D1s}\,(\mathbf{Nir}+\mathbf{Nim});$$

$$\mathbf{dD2sdt} = \mathbf{r2}\,(\mathbf{D2s}+\mathbf{D2im})\left(1-\frac{(\mathbf{D2s}+\mathbf{D2im})}{\mathbf{K2}}\right) - \mathbf{a2}\,\mathbf{D2s}\,\mathbf{Nim};$$

$$\mathbf{dD1irdt} = \mathbf{a1}\,\mathbf{D1s}\,\mathbf{Nir} - \mu\mathbf{1}\,\mathbf{D1ir};$$

$$\mathbf{dD1imdt} = \mathbf{a1}\,\mathbf{D1s}\,\mathbf{Nim} - \mu\mathbf{1}\,\mathbf{D1im};$$

$$\mathbf{dD2imdt} = \mathbf{a2}\,\mathbf{D2s}\,\mathbf{Nim} - \mu\mathbf{2}\,\mathbf{D2im};$$

$$\mathbf{dPrdt} = \lambda\mathbf{1}\,\mathbf{D1ir} - \beta\,(\mathbf{NT}-\mathbf{Nir}-\mathbf{Nim})\,\mathbf{Pr} - \gamma\,\mathbf{Pr};$$

$$\mathbf{dPmdt} = \mathbf{c}\,\lambda\mathbf{1}\,\mathbf{D1im} + \mathbf{c}\,\lambda\mathbf{2}\,\mathbf{D2im} - \beta\,(\mathbf{NT}-\mathbf{Nir}-\mathbf{Nim})\,\mathbf{Pm} - \gamma\,\mathbf{Pm};$$

The Jacobian matrix for this system is quite large, but has the same block triangular structure that we have observed previously.

```
J = {{D[dD1sdt, D1s], D[dD1sdt, D2s], D[dD1sdt, Nir], D[dD1sdt, D1ir], D[dD1sdt, Pr],
    D[dD1sdt, Nim], D[dD1sdt, D1im], D[dD1sdt, D2im], D[dD1sdt, Pm]},
   {D[dD2sdt, D1s], D[dD2sdt, D2s], D[dD2sdt, Nir], D[dD2sdt, D1ir], D[dD2sdt, Pr],
    D[dD2sdt, Nim], D[dD2sdt, D1im], D[dD2sdt, D2im], D[dD2sdt, Pm]},
   {D[dNirdt, D1s], D[dNirdt, D2s], D[dNirdt, Nir], D[dNirdt, D1ir], D[dNirdt, Pr],
    D[dNirdt, Nim], D[dNirdt, D1im], D[dNirdt, D2im], D[dNirdt, Pm]},
   {D[dD1irdt, D1s], D[dD1irdt, D2s], D[dD1irdt, Nir], D[dD1irdt, D1ir], D[dD1irdt,
     Pr], D[dD1irdt, Nim], D[dD1irdt, D1im], D[dD1irdt, D2im], D[dD1irdt, Pm]},
   {D[dPrdt, D1s], D[dPrdt, D2s], D[dPrdt, Nir], D[dPrdt, D1ir], D[dPrdt, Pr],
    D[dPrdt, Nim], D[dPrdt, D1im], D[dPrdt, D2im], D[dPrdt, Pm]},
   {D[dNimdt, D1s], D[dNimdt, D2s], D[dNimdt, Nir], D[dNimdt, D1ir], D[dNimdt, Pr],
    D[dNimdt, Nim], D[dNimdt, D1im], D[dNimdt, D2im], D[dNimdt, Pm]},
   {D[dD1imdt, D1s], D[dD1imdt, D2s], D[dD1imdt, Nir], D[dD1imdt, D1ir], D[dD1imdt,
     Pr], D[dD1imdt, Nim], D[dD1imdt, D1im], D[dD1imdt, D2im], D[dD1imdt, Pm]},
   {D[dD2imdt, D1s], D[dD2imdt, D2s], D[dD2imdt, Nir], D[dD2imdt, D1ir], D[dD2imdt,
     Pr], D[dD2imdt, Nim], D[dD2imdt, D1im], D[dD2imdt, D2im], D[dD2imdt, Pm]},
   {D[dPmdt, D1s], D[dPmdt, D2s], D[dPmdt, Nir], D[dPmdt, D1ir], D[dPmdt, Pr],
    D[dPmdt, Nim], D[dPmdt, D1im], D[dPmdt, D2im], D[dPmdt, Pm]}
  };
MatrixForm[J /. {Nim → 0, D1im → 0, D2im → 0, Pm → 0}]
```

$$\begin{pmatrix} -a1\,Nir + \left(1 - \frac{D1ir+D1s}{K1}\right) r1 - \frac{(D1ir+D1s)\,r1}{K1} & 0 & -a1\,D1s & \left(1 \\ 0 & \left(1 - \frac{D2s}{K2}\right) r2 - \frac{D2s\,r2}{K2} & 0 & \\ -a1\,Nir & -a2\,Nir & -a1\left(D1ir + D1s\right) - a2\,D2s - Pr\,\beta & \\ a1\,Nir & 0 & a1\,D1s & \\ 0 & 0 & Pr\,\beta & \\ 0 & 0 & 0 & \\ 0 & 0 & 0 & \\ 0 & 0 & 0 & \\ 0 & 0 & 0 & \end{pmatrix}$$

Because **J** is upper triangular, the eigenvalues are given by the eigenvalues of the submatrices that fall on the diagonal of **J**. Whether invasion can happen or not depends entirely on the eigenvalues of the lower triangular matrix, given below.

```
MatrixForm[J[[6 ;; 9, 6 ;; 9]] /. {Nim → 0, D1im → 0, D2im → 0, Pm → 0}]
```

$$\begin{pmatrix} -a1\left(D1ir + D1s\right) - a2\,D2s & 0 & 0 & \left(-Nir + NT\right)\beta \\ a1\,D1s & -\mu1 & 0 & 0 \\ a2\,D2s & 0 & -\mu2 & 0 \\ 0 & c\,\lambda1 & c\,\lambda2 & -\left(-Nir + NT\right)\beta - \gamma \end{pmatrix}$$

We can apply the next generation matrix theorem to determine the stability.

```
F = {{0, 0, 0, β (NT - Nir)}, {a1 D1s, 0, 0, 0}, {a2 D2s, 0, 0, 0}, {0, c λ1, c λ2, 0}};
V = {{a1 (D1ir + D1s) + a2 D2s, 0, 0, 0},
    {0, μ1, 0, 0}, {0, 0, μ2, 0}, {0, 0, 0, β (NT - Nir) + γ}};
(J[[6 ;; 9, 6 ;; 9]] /. {Nim → 0, D1im → 0, D2im → 0, Pm → 0}) == F - V // Simplify
Eigenvalues[Dot[F, Inverse[V]]]
```

True

$$\left\{0,\ \left(c^{1/3}\ (\text{Nir}-\text{NT})^{1/3}\ \beta^{1/3}\ (\text{a2 D2s}\ \lambda 2\ \mu 1+\text{a1 D1s}\ \lambda 1\ \mu 2)^{1/3}\right)\Big/\right.$$
$$\left.\left((\text{a1 D1ir}+\text{a1 D1s}+\text{a2 D2s})^{1/3}\ (\text{Nir}\ \beta-\text{NT}\ \beta-\gamma)^{1/3}\ \mu 1^{1/3}\ \mu 2^{1/3}\right),\right.$$
$$-\left(\left((-1)^{1/3}\ c^{1/3}\ (\text{Nir}-\text{NT})^{1/3}\ \beta^{1/3}\ (\text{a2 D2s}\ \lambda 2\ \mu 1+\text{a1 D1s}\ \lambda 1\ \mu 2)^{1/3}\right)\Big/\right.$$
$$\left.\left((\text{a1 D1ir}+\text{a1 D1s}+\text{a2 D2s})^{1/3}\ (\text{Nir}\ \beta-\text{NT}\ \beta-\gamma)^{1/3}\ \mu 1^{1/3}\ \mu 2^{1/3}\right)\right),$$
$$\left((-1)^{2/3}\ c^{1/3}\ (\text{Nir}-\text{NT})^{1/3}\ \beta^{1/3}\ (\text{a2 D2s}\ \lambda 2\ \mu 1+\text{a1 D1s}\ \lambda 1\ \mu 2)^{1/3}\right)\Big/$$
$$\left.\left((\text{a1 D1ir}+\text{a1 D1s}+\text{a2 D2s})^{1/3}\ (\text{Nir}\ \beta-\text{NT}\ \beta-\gamma)^{1/3}\ \mu 1^{1/3}\ \mu 2^{1/3}\right)\right\}$$

Note that $-(-1)^{1/3} = -0.5 - 0.866025\,i$ and $(-1)^{2/3} = -0.5 + 0.866025\,i$, so whether the parasite-free equilibrium is stable or not depends entirely on the second eigenvalue, which can be rewritten as $R_0 = \frac{\beta N_s N_T}{\beta N_s N_T+\gamma}\left(\frac{a_1 D_{1,S}}{a_1 D_{1,S}+a_1 D_{1,I,r}+a_2 D_{2,S}}\ \frac{c\,\lambda_1}{\mu_1} + \frac{a_2 D_{2,S}}{a_1 D_{1,S}+a_1 D_{1,I,r}+a_2 D_{2,S}}\ \frac{c\,\lambda_2}{\mu_2}\right)$, which has a nice intuitive meaning: $\frac{\beta(N_T-N_{I\,r})}{\beta(N_T-N_{I\,r})+\gamma}$ is the probability that a parasite in the environment is ingested by a susceptible intermediate host; $\frac{a_1 D_{1,S}}{a_1 D_{1,S}+a_1 D_{1,I,r}+a_2 D_{2,S}}$ is the probability that an infected intermediate host is ingested by a susceptible primary definitive host; $\frac{a_2 D_{2,S}}{a_1 D_{1,S}+a_1 D_{1,I,r}+a_2 D_{2,S}}$ is the probability that an infected intermediate host is ingested by a suceptible secondary definitive host; $\frac{c\,\lambda_1}{\mu_1}$ and $\frac{c\,\lambda_2}{\mu_2}$ are the expected number of parasites shed from infected primary and secondary definitive hosts, respectively.

```
(Eigenvalues[Dot[F, Inverse[V]]][[2]])^3 ==
  β (NT - Nir)/(β (NT - Nir) + γ) (a1 D1s/(a1 (D1s + D1ir) + a2 D2s) c λ1/μ1 + a2 D2s/(a1 (D1s + D1ir) + a2 D2s) c λ2/μ2) // Simplify
```

True

To determine how changing parameters affects R_0 for this model, we need to know the equilibrium values of N_s, $D_{1,S}$, $D_{1,I,r}$, and $D_{2,S}$ when the generalist parasite is not present. We know that $D_{2,S} = K_2$, the carrying capacity for the secondary host, but the other values are more difficult to determine.

```
PrEq = Simplify[Solve[(dNirdt /. {Nim → 0, D1im → 0, D2im → 0}) == 0, Pr]][[1]]
```

$$\left\{\text{Pr} \to -\frac{(\text{a1}\ (\text{D1ir}+\text{D1s})+\text{a2 D2s})\ \text{Nir}}{(\text{Nir}-\text{NT})\ \beta}\right\}$$

```
NirEq = Simplify[Solve[(dD1sdt /. {Nim → 0, D1im → 0}) == 0, Nir]][[1]]
```

$$\left\{\text{Nir} \to -\frac{(\text{D1ir}+\text{D1s})\ (\text{D1ir}+\text{D1s}-\text{K1})\ \text{r1}}{\text{a1 D1s K1}}\right\}$$

```
D1sEq = Assuming[K1 > 0, Simplify[Solve[(dD1irdt /. NirEq) == 0, D1s][[2]]]]
```

$$\left\{\text{D1s} \to \frac{1}{2\ \text{r1}}\left(-2\ \text{D1ir r1}+\text{K1 r1}+\sqrt{\text{K1 r1}\ (\text{K1 r1}-4\ \text{D1ir}\ \mu 1)}\right)\right\}$$

```
D1irEq = Solve[Numerator[Simplify[dPrdt /. PrEq /. NirEq /. D1sEq]] == 0, D1ir]
```

```
{{D1ir → 0}, {D1ir → ⋯ 1 ⋯}, ⋯ 1 ⋯,
 {D1ir → -((⋯ 47 ⋯ + a1^2 K1 r1 β^2 μ1^5) / (3 (a1^4 NT^2 r1^2 β^2 λ1^2 + 2 a1^3 NT r1^2 β^2 λ1^2 μ1 +
                a1^2 r1^2 β^2 λ1^2 μ1^2))) + (⋯ 1 ⋯)/(⋯ 1 ⋯) - ((1 + i √3) ⋯ 1 ⋯ ⋯ 1 ⋯)/(6 × 2^⋯ 1 ⋯ (⋯ 1 ⋯)))}}
```

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Because of the complexity of these expressions for the equilibria, we cannot explore the question of how changing parameters affects R_0 analytically. Instead, we will use numerical exploration to see whether changing mass/temperature have any effect on invasion fitness. As before, we use simple allometric scaling relationships to relate key processes to host body size and temperature. Additionally, we assume that the growth rate of the definitive host (r) depends on body size as well.

$r = r_0\, e^{E/k\,T}\, W^{-0.25}$
$K = K_0\, e^{E/k\,T}\, W^{-0.75}$
$\mu = \mu_0\, e^{-E/k\,T}\, W^{-0.25}$
$\lambda = \lambda_0\, e^{-E/k\,T}\, W^{0.75}$ (for endoparasites)
$\lambda = \lambda_0\, e^{-E/k\,T}\, W^{5/12}$ (for ectoparasites).

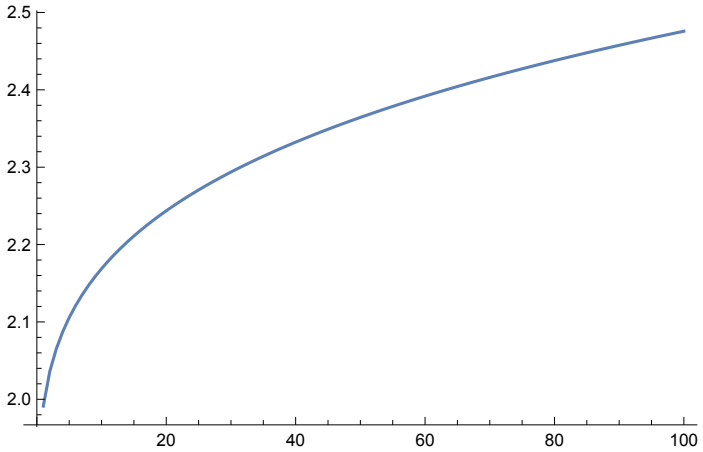
Values for \.08\.08E, k, r_0, K_0, and μ_0 that are appropriate for fish come from Savage et al. 2004. The estimate of λ_0 is modified from Poulin & George-Nascimento 2007.

The function below uses numerical simulation to determine the equilibrium values of N_s, $D_{1,S}$, $D_{1,I,r}$, and $D_{2,S}$ for the specified parameters. These values are then plugged into the R_0 expression to calculate the invasion fitness.

```
NumSolInvFit = Function[{W, T, c, f, NTot, B, g, a},
  allom = {K1 → K0 Exp[E/(k T)] W^(-3/4), K2 → K0 Exp[E/(k T)] (f W)^(-3/4),
    μ1 → μ0 Exp[-E/(k T)] W^(-1/4), μ2 → μ0 Exp[-E/(k T)] (f W)^(-1/4), λ1 → λ0 Exp[-E/(k T)] W^(3/4),
    λ2 → λ0 Exp[-E/(k T)] (f W)^(3/4), r1 → r0 Exp[-E/(k T)] W^(-1/4)};
  pars = {E → 0.45`, k → 8.617`/10^5, K0 → 2.984`/10^9, μ0 → 1.785` × 10^8,
    λ0 → 2 × 10^8, r0 → 2.21 × 10^10, β → B, γ → g, a1 → a, a2 → a, NT → NTot};
  DOPRIamat = {{1 / 5}, {3 / 40, 9 / 40}, {44 / 45, -56 / 15, 32 / 9}, {19 372 / 6561,
     -25 360 / 2187, 64 448 / 6561, -212 / 729}, {9017 / 3168, -355 / 33, 46 732 / 5247, 49 /
      176, -5103 / 18 656}, {35 / 384, 0, 500 / 1113, 125 / 192, -2187 / 6784, 11 / 84}};
  DOPRIbvec = {35 / 384, 0, 500 / 1113, 125 / 192, -2187 / 6784, 11 / 84, 0};
  DOPRIcvec = {1 / 5, 3 / 10, 4 / 5, 8 / 9, 1, 1};
  DOPRIevec = {71 / 57 600, 0, -71 / 16 695, 71 / 1920, -17 253 / 339 200, 22 / 525, -1 / 40};
  DOPRICoefficients[5, p_] := N[{DOPRIamat, DOPRIbvec, DOPRIcvec, DOPRIevec}, p];
  Soln = NDSolve[({
      Nir'[t] == β (NT - Nir[t]) Pr[t] - a1 (D1s[t] + D1ir[t]) Nir[t] - a2 K2 Nir[t],
      D1s'[t] == r1 (D1s[t] + D1ir[t]) (1 - (D1s[t] + D1ir[t])/K1) - a1 D1s[t] Nir[t],
      D1ir'[t] == a1 D1s[t] Nir[t] - μ1 D1ir[t],
      Pr'[t] == λ1 D1ir[t] - β (NT - Nir[t]) Pr[t] - γ Pr[t],
      Nir[0] == 0,
      D1s[0] == 0.1,
      D1ir[0] == 0,
      Pr[0] == 1} /. allom /. pars),
    {Ns, Nir, D1s, D1ir, Pr}, {t, 0, 1000},
    Method → {"ExplicitRungeKutta", "DifferenceOrder" → 5,
      "Coefficients" → DOPRICoefficients, "StiffnessTest" → False}];
  (* Print[{Ns→(Ns[1000]/.Soln)[[1]],Nir→(Nir[1000]/.Soln)[[1]],
     D1s→(D1s[1000]/.Soln)[[1]],D1ir→(D1ir[1000]/.Soln)[[1]],
     Pr→(Pr[1000]/.Soln)[[1]]}];*)
  β (NT - Nir)/(β (NT - Nir) + γ) (a1 D1s/(a1 (D1s + D1ir) + a2 D2s) c λ1/μ1 + a2 D2s/(a1 (D1s + D1ir) + a2 D2s) c λ2/μ2) /.
    {Nir → (Nir[1000] /. Soln)[[1]], D1s → (D1s[1000] /. Soln)[[1]],
     D1ir → (D1ir[1000] /. Soln)[[1]]} /. D2s → K2 /. allom /. pars
];
```

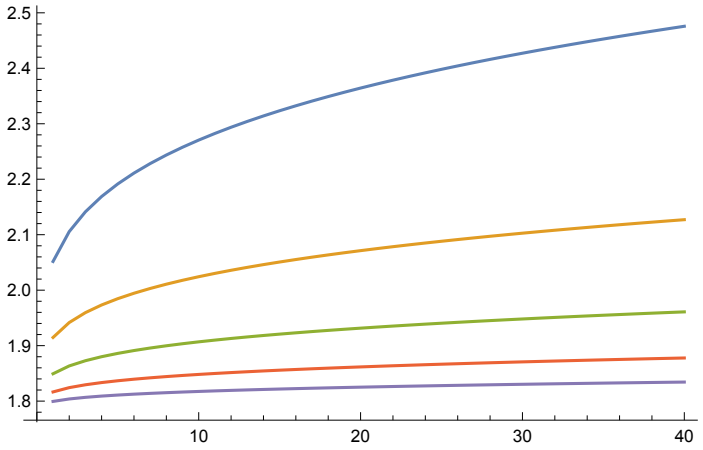
For these parameters, increasing body mass increases R_0:

```
InvFitAcrossW =
  Table[NumSolInvFit[W, 270, 0.9, 0.9, 1, 0.1, 0.01, 0.1], {W, 10, 1000, 10}];
ListLinePlot[InvFitAcrossW]
```



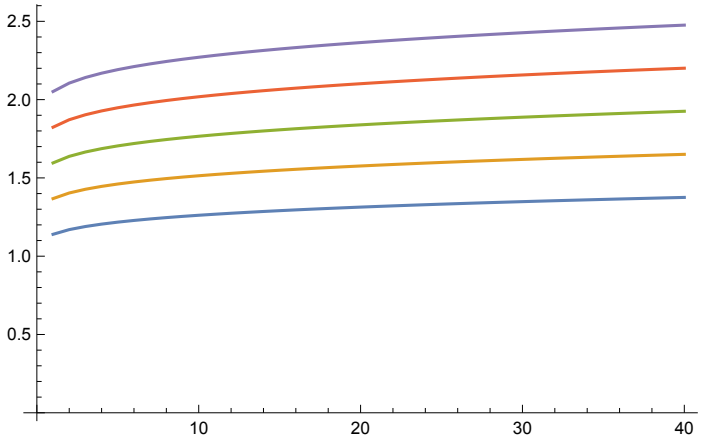
This is true if you increase the temperature (here increasing temperature from 270 to 310). Notice, however, that R_0 is lower for higher temperatures, indicating that increasing temperature negatively affects R_0.

```
InvFitAcrossWT =
  Table[Table[NumSolInvFit[W, T, 0.9, 0.9, 1, 0.1, 0.01, 0.1], {W, 25, 1000, 25}],
   {T, 270, 310, 10}];
ListLinePlot[InvFitAcrossWT]
```



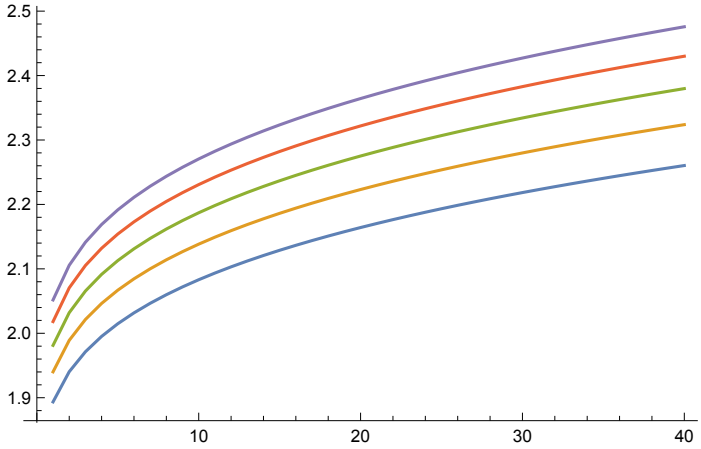
It also holds if you increase the cost of generalism (here decreasing *c* from 0.9 to 0.5):

```
InvFitAcrossWc =
 Table[Table[NumSolInvFit[W, 270, c, 0.9, 1, 0.1, 0.01, 0.1], {W, 25, 1000, 25}],
  {c, 0.5, 0.9, 0.1}]; ListLinePlot[InvFitAcrossWc]
```



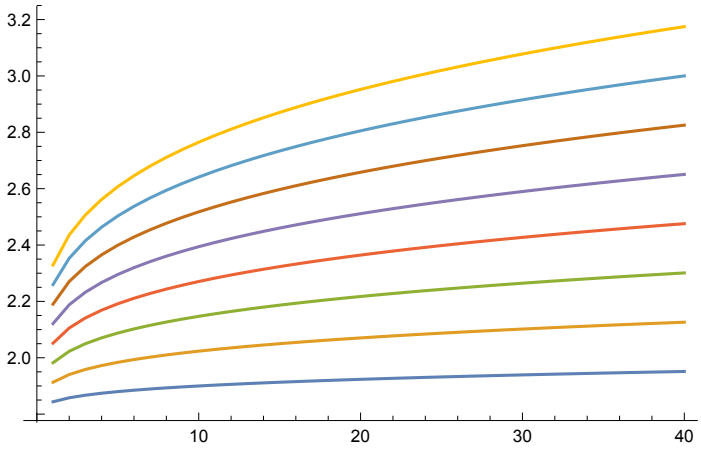
It also holds if you reduce the size of the secondary host (here decreasing *f* from 0.9 to 0.5):

```
InvFitAcrossWf =
  Table[Table[NumSolInvFit[W, 270, 0.9, f, 1, 0.1, 0.01, 0.1], {W, 25, 1000, 25}],
   {f, 0.5, 0.9, 0.1}];
ListLinePlot[InvFitAcrossWf]
```



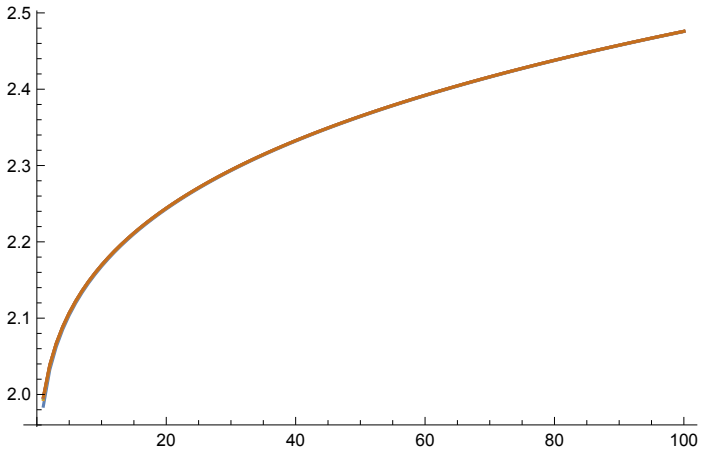
It also holds if you reduce the number of intermediate hosts (here N_T ranges from 0.25 to 2):

```
InvFitAcrossWNT =
  Table[Table[NumSolInvFit[W, 270, 0.9, 0.9, NT, 0.1, 0.01, 0.1], {W, 25, 1000, 25}],
   {NT, 0.25, 2, 0.25}];
ListLinePlot[InvFitAcrossWNT]
```



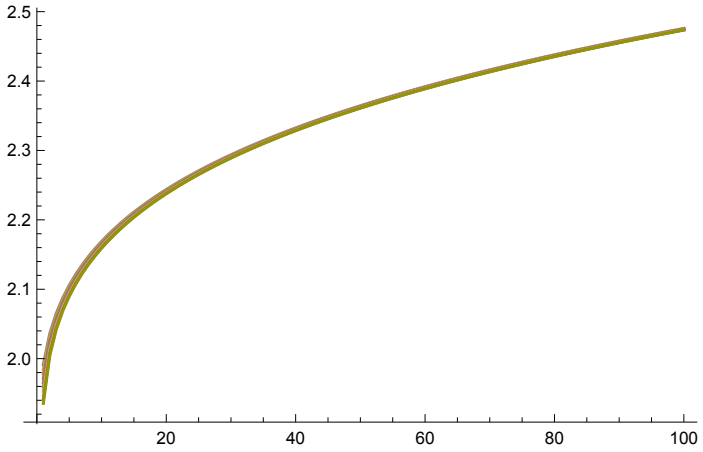
It also holds if you change the transmission rate to intermediate hosts (here β ranges from 0.05 to 0.55):

```
InvFitAcrossWB =
  Table[Table[NumSolInvFit[W, 270, 0.9, 0.9, 1, B, 0.01, 0.1], {W, 10, 1000, 10}],
   {B, 0.05, 0.55, 0.1}];
ListLinePlot[InvFitAcrossWB]
```



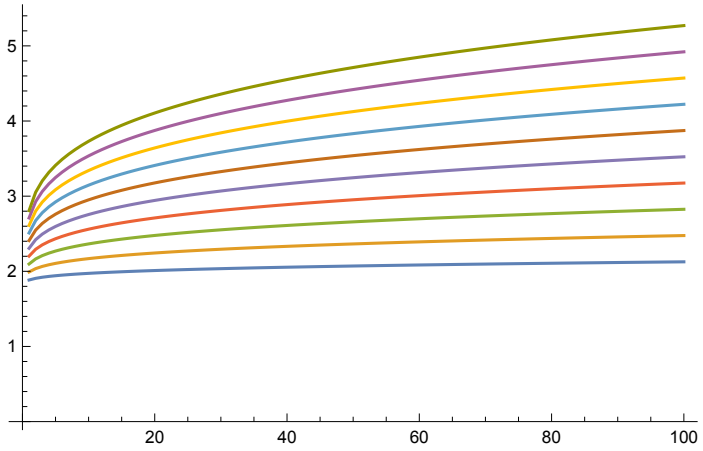
It also holds if you change the rate parasites are lost from the environment (here γ ranges from 0.01 to 0.1):

```
InvFitAcrossWg =
  Table[Table[NumSolInvFit[W, 270, 0.9, 0.9, 1, 0.1, g, 0.1], {W, 10, 1000, 10}],
   {g, 0.01, 0.1, 0.01}];
ListLinePlot[InvFitAcrossWg]
```



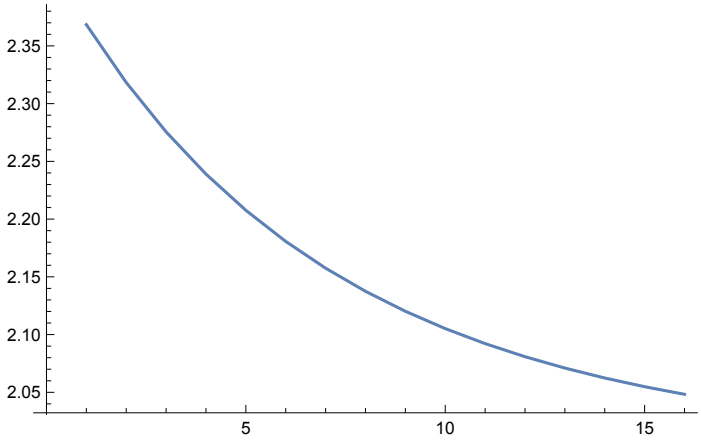
It also holds if you change the ingestion rate of the definitive hosts:

```
InvFitAcrossWa =
  Table[Table[NumSolInvFit[W, 270, 0.9, 0.9, 1, 0.1, 0.01, a], {W, 10, 1000, 10}],
   {a, 0.05, 0.5, 0.05}];
ListLinePlot[InvFitAcrossWa]
```



Increasing temperature decreases R_0:

```
InvFitAcrossT = Table[NumSolInvFit[100, T, 0.9, 0.9, 1], {T, 270, 300, 2}];
ListLinePlot[InvFitAcrossT]
```



Case 7: Trophic transmission; two specialist parasites; parasites regulate definitive host population sizes; active seeking of intermediate hosts; avoidance of infected intermediate hosts

Now we assume that there are two specialist parasites exploiting the same intermediate host, but infecting different definitive hosts. We let N_{2Ir} track the number of intermediate hosts infected with the second specialist parasite and D_{2Ir} track the number of secondary definitive hosts infected by the second specialist parasite.

```
dN1irdt =
  β (NT - N1ir - N2ir - Nim) P1r - a1 (D1s + D1ir + D1im) N1ir - a2 (D2s + D2ir + D2im) N1ir;
dN2irdt = β (NT - N1ir - N2ir - Nim) P2r - a1 (D1s + D1ir + D1im) N2ir -
    a2 (D2s + D2ir + D2im) N2ir;
dNimdt = β (NT - N1ir - N2ir - Nim) Pm - a1 (D1s + D1ir + D1im) Nim - a2 (D2s + D2ir + D2im) Nim;

dD1sdt = r1 (D1s + D1ir + D1im) (1 - (D1s + D1ir + D1im)/K1) - a1 D1s (N1ir + Nim);
dD2sdt = r2 (D2s + D2ir + D2im) (1 - (D2s + D2ir + D2im)/K2) - a2 D2s (N2ir + Nim);
dD1irdt = a1 D1s N1ir - μ1 D1ir;
dD2irdt = a2 D2s N2ir - μ2 D2ir;
dD1imdt = a1 D1s Nim - μ1 D1im;
dD2imdt = a2 D2s Nim - μ2 D2im;

dP1rdt = λ1 D1ir - β (NT - N1ir - N2ir - Nim) P1r - γ P1r;
dP2rdt = λ2 D2ir - β (NT - N1ir - N2ir - Nim) P2r - γ P2r;
dPmdt = c λ1 D1im + c λ2 D2im - β (NT - N1ir - N2ir - Nim) Pm - γ Pm;
```

To determine whether the generalist can invade this system, we again look at the Jacobian.

```
J = {{D[dN1irdt, N1ir], D[dN1irdt, D1s], D[dN1irdt, D1ir], D[dN1irdt, P1r],
      D[dN1irdt, N2ir], D[dN1irdt, D2s], D[dN1irdt, D2ir], D[dN1irdt, P2r],
      D[dN1irdt, Nim], D[dN1irdt, D1im], D[dN1irdt, D2im], D[dN1irdt, Pm]},
     {D[dD1sdt, N1ir], D[dD1sdt, D1s], D[dD1sdt, D1ir], D[dD1sdt, P1r],
      D[dD1sdt, N2ir], D[dD1sdt, D2s], D[dD1sdt, D2ir], D[dD1sdt, P2r],
      D[dD1sdt, Nim], D[dD1sdt, D1im], D[dD1sdt, D2im], D[dD1sdt, Pm]},
     {D[dD1irdt, N1ir], D[dD1irdt, D1s], D[dD1irdt, D1ir], D[dD1irdt, P1r],
      D[dD1irdt, N2ir], D[dD1irdt, D2s], D[dD1irdt, D2ir], D[dD1irdt, P2r],
      D[dD1irdt, Nim], D[dD1irdt, D1im], D[dD1irdt, D2im], D[dD1irdt, Pm]},
     {D[dP1rdt, N1ir], D[dP1rdt, D1s], D[dP1rdt, D1ir], D[dP1rdt, P1r],
      D[dP1rdt, N2ir], D[dP1rdt, D2s], D[dP1rdt, D2ir], D[dP1rdt, P2r],
      D[dP1rdt, Nim], D[dP1rdt, D1im], D[dP1rdt, D2im], D[dP1rdt, Pm]},
     {D[dN2irdt, N1ir], D[dN2irdt, D1s], D[dN2irdt, D1ir], D[dN2irdt, P1r],
      D[dN2irdt, N2ir], D[dN2irdt, D2s], D[dN2irdt, D2ir], D[dN2irdt, P2r],
      D[dN2irdt, Nim], D[dN2irdt, D1im], D[dN2irdt, D2im], D[dN2irdt, Pm]},
     {D[dD2sdt, N1ir], D[dD2sdt, D1s], D[dD2sdt, D1ir], D[dD2sdt, P1r],
      D[dD2sdt, N2ir], D[dD2sdt, D2s], D[dD2sdt, D2ir], D[dD2sdt, P2r],
      D[dD2sdt, Nim], D[dD2sdt, D1im], D[dD2sdt, D2im], D[dD2sdt, Pm]},
     {D[dD2irdt, N1ir], D[dD2irdt, D1s], D[dD2irdt, D1ir], D[dD2irdt, P1r],
      D[dD2irdt, N2ir], D[dD2irdt, D2s], D[dD2irdt, D2ir], D[dD2irdt, P2r],
      D[dD2irdt, Nim], D[dD2irdt, D1im], D[dD2irdt, D2im], D[dD2irdt, Pm]},
     {D[dP2rdt, N1ir], D[dP2rdt, D1s], D[dP2rdt, D1ir], D[dP2rdt, P1r],
      D[dP2rdt, N2ir], D[dP2rdt, D2s], D[dP2rdt, D2ir], D[dP2rdt, P2r],
      D[dP2rdt, Nim], D[dP2rdt, D1im], D[dP2rdt, D2im], D[dP2rdt, Pm]},
     {D[dNimdt, N1ir], D[dNimdt, D1s], D[dNimdt, D1ir], D[dNimdt, P1r],
      D[dNimdt, N2ir], D[dNimdt, D2s], D[dNimdt, D2ir], D[dNimdt, P2r],
      D[dNimdt, Nim], D[dNimdt, D1im], D[dNimdt, D2im], D[dNimdt, Pm]},
     {D[dD1imdt, N1ir], D[dD1imdt, D1s], D[dD1imdt, D1ir], D[dD1imdt, P1r],
      D[dD1imdt, N2ir], D[dD1imdt, D2s], D[dD1imdt, D2ir], D[dD1imdt, P2r],
      D[dD1imdt, Nim], D[dD1imdt, D1im], D[dD1imdt, D2im], D[dD1imdt, Pm]},
     {D[dD2imdt, N1ir], D[dD2imdt, D1s], D[dD2imdt, D1ir], D[dD2imdt, P1r],
      D[dD2imdt, N2ir], D[dD2imdt, D2s], D[dD2imdt, D2ir], D[dD2imdt, P2r],
      D[dD2imdt, Nim], D[dD2imdt, D1im], D[dD2imdt, D2im], D[dD2imdt, Pm]},
     {D[dPmdt, N1ir], D[dPmdt, D1s], D[dPmdt, D1ir], D[dPmdt, P1r],
      D[dPmdt, N2ir], D[dPmdt, D2s], D[dPmdt, D2ir], D[dPmdt, P2r],
      D[dPmdt, Nim], D[dPmdt, D1im], D[dPmdt, D2im], D[dPmdt, Pm]}} /.
   {Nim → 0, D1im → 0, D2im → 0, Pm → 0};
```

As before, this matrix is upper block triangular. The upper left submatrix determines the stability of the system that doesn't include the generalist parasite. It will be helpful to look at the eigenvalues of this submatrix at the parasite-free equilibrium when both specialist parasites are absent ($N_{1\,Ir} = 0,\ N_{2\,Ir} = 0,\ D_{1\,S} = K_1,\ D_{1\,Ir} = 0,\ D_{2\,S} = K_2,\ D_{2\,Ir} = 0,\ P_1 = 0,\ P_2 = 0$)? In particular, we want all of these eigenvalues to be positive to guarantee that the specialist parasites can both persist in the system. Notice that this matrix is block diagonal, so we can simply look at the eigenvalues of each submatrix to determine the eigenvalues of the full matrix.

```
J[[1 ;; 8, 1 ;; 8]] /. {N1ir → 0, N2ir → 0, D1s → K1,
    D1ir → 0, D2s → K2, D2ir → 0, P1r → 0, P2r → 0} // MatrixForm
```

$$\begin{pmatrix} -a1\,K1 - a2\,K2 & 0 & 0 & NT\,\beta & 0 & 0 & 0 & 0 \\ -a1\,K1 & -r1 & -r1 & 0 & 0 & 0 & 0 & 0 \\ a1\,K1 & 0 & -\mu 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \lambda 1 & -NT\,\beta - \gamma & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & -a1\,K1 - a2\,K2 & 0 & 0 & NT\,\beta \\ 0 & 0 & 0 & 0 & -a2\,K2 & -r2 & -r2 & 0 \\ 0 & 0 & 0 & 0 & a2\,K2 & 0 & -\mu 2 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \lambda 2 & -NT\,\beta - \gamma \end{pmatrix}$$

Applying the next generation matrix, we find that for the specialist-absent system to be unstable, we require that

$\frac{\beta N_T}{\beta N_T+\gamma}\left(\frac{a_1 K_1}{a_1 K_1+a_2 K_2}\,\frac{\lambda_1}{\mu_1}\right) > 1$ and $\frac{\beta N_T}{\beta N_T+\gamma}\left(\frac{a_2 K_2}{a_1 K_1+a_2 K_2}\,\frac{\lambda_2}{\mu_2}\right) > 1$

```
F1 = {{0, 0, 0, NT β}, {0, 0, 0, 0}, {a1 K1, 0, 0, 0}, {0, 0, λ1, 0}};
V1 = {{a1 K1 + a2 K2, 0, 0, 0}, {a1 K1, r1, r1, 0}, {0, 0, μ1, 0}, {0, 0, 0, NT β + γ}};
(J[[1 ;; 4, 1 ;; 4]] /.
    {N1ir → 0, N2ir → 0, D1s → K1, D1ir → 0, D2s → K2, D2ir → 0, P1r → 0, P2r → 0}) == F1 - V1
Eigenvalues[Dot[F1, Inverse[V1]]]
(Eigenvalues[Dot[F1, Inverse[V1]]][[2]])^3 == β NT/(β NT + γ) (a1 K1/(a1 K1 + a2 K2) λ1/μ1)
F2 = {{0, 0, 0, NT β}, {0, 0, 0, 0}, {a2 K2, 0, 0, 0}, {0, 0, λ2, 0}};
V2 = {{a1 K1 + a2 K2, 0, 0, 0}, {a2 K2, r2, r2, 0}, {0, 0, μ2, 0}, {0, 0, 0, NT β + γ}};
(J[[5 ;; 8, 5 ;; 8]] /.
    {N1ir → 0, N2ir → 0, D1s → K1, D1ir → 0, D2s → K2, D2ir → 0, P1r → 0, P2r → 0}) == F2 - V2
Eigenvalues[Dot[F2, Inverse[V2]]]
(Eigenvalues[Dot[F2, Inverse[V2]]][[2]])^3 == β NT/(β NT + γ) (a2 K2/(a1 K1 + a2 K2) λ2/μ2)
```

```
True
```

$$\left\{0,\ \frac{a1^{1/3}\,K1^{1/3}\,NT^{1/3}\,\beta^{1/3}\,\lambda 1^{1/3}}{(a1\,K1 + a2\,K2)^{1/3}\,(NT\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}},\right.$$
$$\left. -\frac{(-1)^{1/3}\,a1^{1/3}\,K1^{1/3}\,NT^{1/3}\,\beta^{1/3}\,\lambda 1^{1/3}}{(a1\,K1 + a2\,K2)^{1/3}\,(NT\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}},\ \frac{(-1)^{2/3}\,a1^{1/3}\,K1^{1/3}\,NT^{1/3}\,\beta^{1/3}\,\lambda 1^{1/3}}{(a1\,K1 + a2\,K2)^{1/3}\,(NT\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}}\right\}$$

```
True
```

```
True
```

$$\left\{0,\ \frac{a2^{1/3}\,K2^{1/3}\,NT^{1/3}\,\beta^{1/3}\,\lambda 2^{1/3}}{(a1\,K1 + a2\,K2)^{1/3}\,(NT\,\beta+\gamma)^{1/3}\,\mu 2^{1/3}},\right.$$
$$\left. -\frac{(-1)^{1/3}\,a2^{1/3}\,K2^{1/3}\,NT^{1/3}\,\beta^{1/3}\,\lambda 2^{1/3}}{(a1\,K1 + a2\,K2)^{1/3}\,(NT\,\beta+\gamma)^{1/3}\,\mu 2^{1/3}},\ \frac{(-1)^{2/3}\,a2^{1/3}\,K2^{1/3}\,NT^{1/3}\,\beta^{1/3}\,\lambda 2^{1/3}}{(a1\,K1 + a2\,K2)^{1/3}\,(NT\,\beta+\gamma)^{1/3}\,\mu 2^{1/3}}\right\}$$

```
True
```

We assume that both of those inequalities are satisfied. Whether the generalist can invade the system depends on the eigenvalues of the lower right submatrix of **J**:

```
MatrixForm[J[[9 ;; 12, 9 ;; 12]]]
```

$$\begin{pmatrix} -a1\,(D1ir+D1s)-a2\,(D2ir+D2s) & 0 & 0 & (-N1ir-N2ir+NT)\,\beta \\ a1\,D1s & -\mu1 & 0 & 0 \\ a2\,D2s & 0 & -\mu2 & 0 \\ 0 & c\,\lambda1 & c\,\lambda2 & -(-N1ir-N2ir+NT)\,\beta-\gamma \end{pmatrix}$$

Using the next generation matrix theorem, the Jacobian will have a positive eigenvalue whenever the second value is greater than 1.

```
F = {{0, 0, 0, (NT - N1ir - N2ir) β},
    {a1 D1s, 0, 0, 0}, {a2 D2s, 0, 0, 0}, {0, c λ1, c λ2, 0}};
V = {{a1 (D1ir + D1s) + a2 (D2ir + D2s), 0, 0, 0}, {0, μ1, 0, 0},
    {0, 0, μ2, 0}, {0, 0, 0, (NT - N1ir - N2ir) β + γ}};
J[[9 ;; 12, 9 ;; 12]] == F - V // Simplify
Eigenvalues[Dot[F, Inverse[V]]]
```

```
True
```

$$\left\{0,\ \left(c^{1/3}\,(N1ir+N2ir-NT)^{1/3}\,\beta^{1/3}\,(a2\,D2s\,\lambda2\,\mu1+a1\,D1s\,\lambda1\,\mu2)^{1/3}\right)\Big/\left((a1\,D1ir+a1\,D1s+a2\,D2ir+a2\,D2s)^{1/3}\,(N1ir\,\beta+N2ir\,\beta-NT\,\beta-\gamma)^{1/3}\,\mu1^{1/3}\,\mu2^{1/3}\right),\right.$$
$$-\left(\left((-1)^{1/3}\,c^{1/3}\,(N1ir+N2ir-NT)^{1/3}\,\beta^{1/3}\,(a2\,D2s\,\lambda2\,\mu1+a1\,D1s\,\lambda1\,\mu2)^{1/3}\right)\Big/\left((a1\,D1ir+a1\,D1s+a2\,D2ir+a2\,D2s)^{1/3}\,(N1ir\,\beta+N2ir\,\beta-NT\,\beta-\gamma)^{1/3}\,\mu1^{1/3}\,\mu2^{1/3}\right)\right),$$
$$\left((-1)^{2/3}\,c^{1/3}\,(N1ir+N2ir-NT)^{1/3}\,\beta^{1/3}\,(a2\,D2s\,\lambda2\,\mu1+a1\,D1s\,\lambda1\,\mu2)^{1/3}\right)\Big/$$
$$\left.\left((a1\,D1ir+a1\,D1s+a2\,D2ir+a2\,D2s)^{1/3}\,(N1ir\,\beta+N2ir\,\beta-NT\,\beta-\gamma)^{1/3}\,\mu1^{1/3}\,\mu2^{1/3}\right)\right\}$$

This eigenvalue is equivalent to the expression given below:

```
((c^1/3 (N1ir + N2ir - NT)^1/3 β^1/3 (a2 D2s λ2 μ1 + a1 D1s λ1 μ2)^1/3)) /
      ((a1 D1ir + a1 D1s + a2 D2ir + a2 D2s)^1/3 (N1ir β + N2ir β - NT β - γ)^1/3 μ1^1/3 μ2^1/3))^3 ==
  (NT - N1ir - N2ir) β / ((NT - N1ir - N2ir) β + γ) (a1 D1s / (a1 (D1ir + D1s) + a2 (D2ir + D2s)) c λ1 / μ1 +
    a2 D2s / (a1 (D1ir + D1s) + a2 (D2ir + D2s)) c λ2 / μ2) // Simplify
```

```
True
```

As before, it is impossible to make headway analytically, so we must resort to numerical solutions.

```
NumSolInvFit = Function[{W, T, c, f, NTot, B, g, a},
    allom = {K1 → K0 Exp[E / (k T)] W^-3/4, K2 → K0 Exp[E / (k T)] (f W)^-3/4,
      μ1 → μ0 Exp[-E / (k T)] W^-1/4, μ2 → μ0 Exp[-E / (k T)] (f W)^-1/4, λ1 → λ0 Exp[-E / (k T)] W^3/4,
      λ2 → λ0 Exp[-E / (k T)] (f W)^3/4, r1 → r0 Exp[-E / (k T)] W^-1/4, r2 → r0 Exp[-E / (k T)] (f W)^-1/4};
    pars = {E → 0.45`, k → 8.617` / 10^5, K0 → 2.984` / 10^9, μ0 → 1.785` × 10^8,
      λ0 → 2 × 10^8, r0 → 2.21 × 10^10, β → B, γ → g, a1 → a, a2 → a, NT → NTot};
```

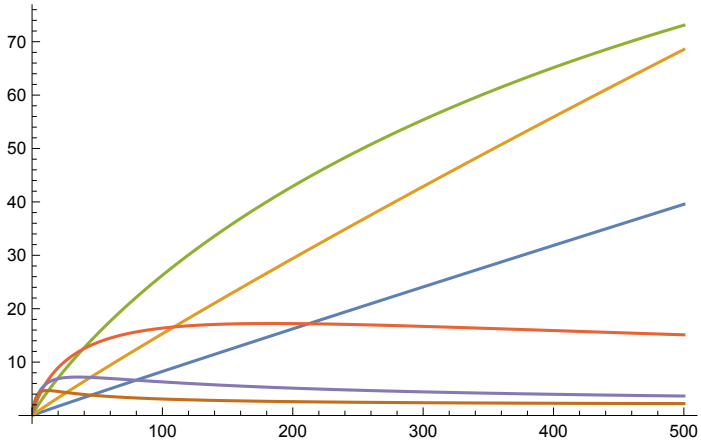
```
(*Print[ β NT/(β NT+γ) (a1 K1/(a1 K1+a2 K2)  λ1/μ1) /.allom/.pars];*)
(*Print[ β NT/(β NT+γ) (a2 K2/(a1 K1+a2 K2)  λ2/μ2) /.allom/.pars];*)
DOPRIamat = {{1 / 5}, {3 / 40, 9 / 40}, {44 / 45, -56 / 15, 32 / 9},
  {19 372 / 6561, -25 360 / 2187, 64 448 / 6561, -212 / 729},
  {9017 / 3168, -355 / 33, 46 732 / 5247, 49 / 176, -5103 / 18 656},
  {35 / 384, 0, 500 / 1113, 125 / 192, -2187 / 6784, 11 / 84}};
DOPRIbvec = {35 / 384, 0, 500 / 1113, 125 / 192, -2187 / 6784, 11 / 84, 0};
DOPRIcvec = {1 / 5, 3 / 10, 4 / 5, 8 / 9, 1, 1};
DOPRIevec = {71 / 57 600, 0, -71 / 16 695, 71 / 1920, -17 253 / 339 200, 22 / 525, -1 / 40};
DOPRICoefficients[5, p_] := N[{DOPRIamat, DOPRIbvec, DOPRIcvec, DOPRIevec}, p];
Soln = NDSolve[({
      N1ir'[t] == β (NT - N1ir[t] - N2ir[t]) P1r[t] -
        a1 (D1s[t] + D1ir[t]) N1ir[t] - a2 (D2s[t] + D2ir[t]) N1ir[t],
      N2ir'[t] == β (NT - N1ir[t] - N2ir[t]) P2r[t] -
        a1 (D1s[t] + D1ir[t]) N2ir[t] - a2 (D2s[t] + D2ir[t]) N2ir[t],
      D1s'[t] == r1 (D1s[t] + D1ir[t]) (1 - (D1s[t] + D1ir[t])/K1) - a1 D1s[t] N1ir[t],
      D2s'[t] == r2 (D2s[t] + D2ir[t]) (1 - (D2s[t] + D2ir[t])/K2) - a2 D2s[t] N2ir[t],
      D1ir'[t] == a1 D1s[t] N1ir[t] - μ1 D1ir[t],
      D2ir'[t] == a2 D2s[t] N2ir[t] - μ1 D2ir[t],
      P1r'[t] == λ1 D1ir[t] - β (NT - N1ir[t] - N2ir[t]) P1r[t] - γ P1r[t],
      P2r'[t] == λ1 D1ir[t] - β (NT - N1ir[t] - N2ir[t]) P2r[t] - γ P2r[t],
      N1ir[0] == 0, N2ir[0] == 0,
      D1s[0] == 0.1, D2s[0] == 0.1,
      D1ir[0] == 0, D2ir[0] == 0,
      P1r[0] == 1, P2r[0] == 1} /. allom /. pars),
  {N1ir, N2ir, D1s, D1ir, D2s, D2ir, P1r, P2r}, {t, 0, 1000},
  Method → {"ExplicitRungeKutta", "DifferenceOrder" → 5,
    "Coefficients" → DOPRICoefficients, "StiffnessTest" → False}];
(* Print[{N1ir→(N1ir[1000]/.Soln)[[1]],N2ir→(N2ir[1000]/.Soln)[[1]],
  D1s→(D1s[1000]/.Soln)[[1]],D1ir→(D1ir[1000]/.Soln)[[1]],
  D2s→(D2s[1000]/.Soln)[[1]],D2ir→(D2ir[1000]/.Soln)[[1]]}] *);
(NT - N1ir - N2ir) β / ((NT - N1ir - N2ir) β + γ) ((a1 D1s) / (a1 (D1ir + D1s) + a2 (D2ir + D2s))) c λ1/μ1 +
    ((a2 D2s) / (a1 (D1ir + D1s) + a2 (D2ir + D2s))) c λ2/μ2) /.
  {N1ir → (N1ir[1000] /. Soln)[[1]], N2ir → (N2ir[1000] /. Soln)[[1]],
   D1s → (D1s[1000] /. Soln)[[1]], D1ir → (D1ir[1000] /. Soln)[[1]], D2s →
    (D2s[1000] /. Soln)[[1]], D2ir → (D2ir[1000] /. Soln)[[1]]} /. allom /. pars
];
```

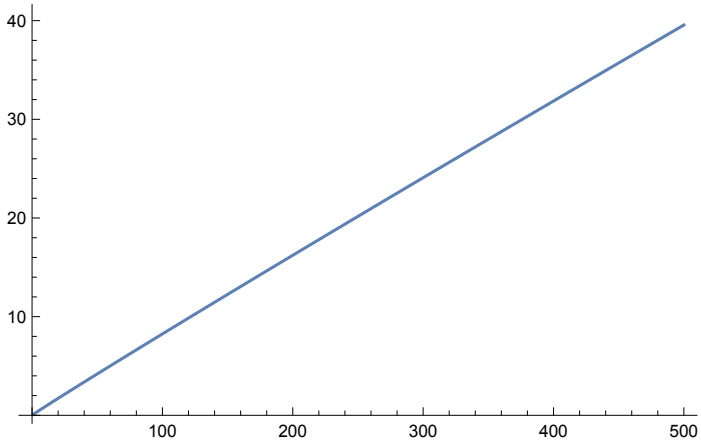
One case is sufficient to demonstrate that the response of the generalist's R_0 to changes in host body size is much more complex here. Consider the effect of changing the definitive host body sizes across a gradient of intermediate host abundance. You can see very clearly that the responses depend on the value of N_T: when N_T is small, increasing host mass increases R_0; when N_T is large, increasing host

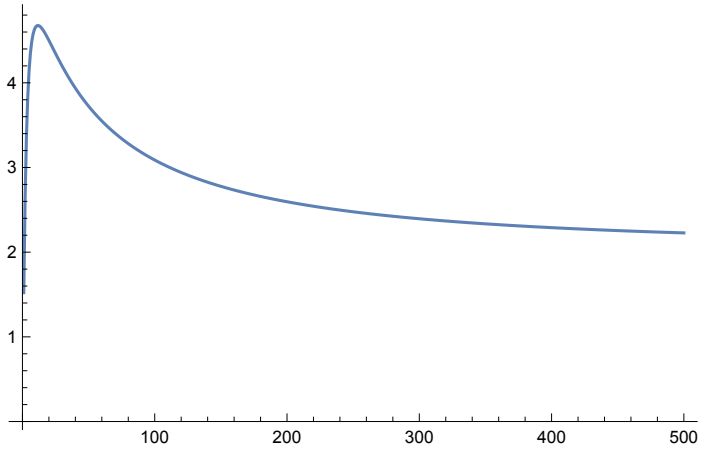
mass first increases, then decreases R_0.

In reality, the abundance of the definitive host's prey is likely to be related to the size of the definitive host: in general, larger-bodied hosts are more likely to consume larger-bodied prey, whose carrying capacities would decrease commensurately. That is, as definitive host body size goes up, you would expect intermediate host carrying capacity to go down.

```
InvFitAcrossWNT =
  Table[Table[NumSolInvFit[W, 270, 0.9, 0.9, NT, 0.01, 0.1, 0.01], {W, 10, 5000, 10}],
   {NT, {0.1, 0.2, 0.5, 1, 1.5, 2}}];
ListLinePlot[InvFitAcrossWNT]
ListLinePlot[InvFitAcrossWNT[[1]]]
ListLinePlot[InvFitAcrossWNT[[6]]]
```

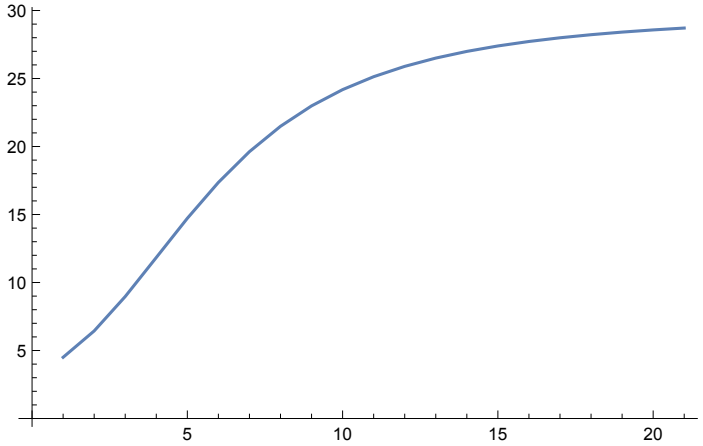




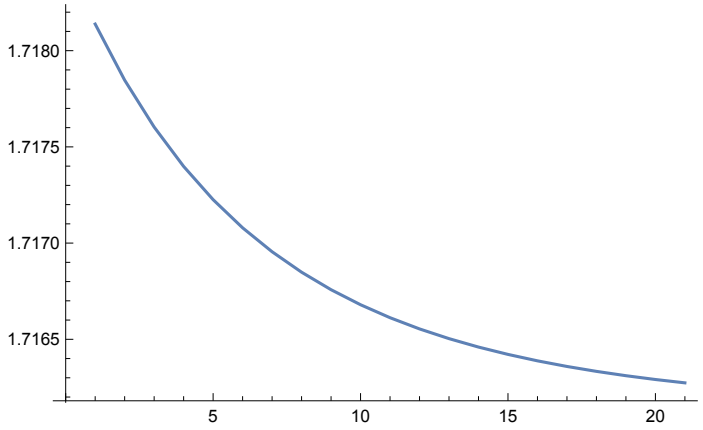


Increasing temperature also has a much more complex effect on R_0: when N_T is large, increasing temperature increases R_0, but when N_T is small, increasing temperature decreases R_0.

```
InvFitAcrossWT =
  Table[NumSolInvFit[200, T, 0.9, 0.9, 2, 0.01, 0.1, 0.01], {T, 270, 310, 2}];
ListLinePlot[InvFitAcrossWT]
```




```
InvFitAcrossWT =
  Table[NumSolInvFit[200, T, 0.9, 0.9, 0.1, 0.01, 0.1, 0.01], {T, 270, 310, 2}];
ListLinePlot[InvFitAcrossWT]
```



Case 8: Trophic transmission; two specialist parasites; constant definitive host population sizes; active seeking of intermediate hosts; avoidance of infected intermediate hosts

We assume that both the intermediate and definitive hosts have constant population size. Let K_N be the total number of intermediate hosts; let $N_{1,r}$ be the number of intermediate hosts infected by the first specialist parasite; let $N_{2,r}$ be the number of intermediate hosts infected by the second specialist parasite, and let $N_{12,m}$ be the fraction of intermediate hosts infected by the generalist parasite. Then $K_N - N_{1,r} - N_{2,r}$ is the number of susceptible intermediate hosts - we assume that each intermediate host can only be infected by a single parasite. Let K_1 be the abundance of the first definitive host population and let K_2 be the abundance of the second definitive host population. Let $I_{1,r}$ and $I_{2,r}$ be the numbers of the first and second definitive host populations, respectively, that are infected by the specialist parasites, and let $I_{1,m}$ and $I_{2,m}$ be the numbers of the definitive host populations infected by the generalist parasite. Let $P_{1,r}$ and $P_{2,r}$ be the numbers of the two specialist parasites in the environment and let $P_{12,m}$ be the number of generalist parasites in the environment.

```
dN1rdt = β (KN - N1r - N2r - N12m) P1r - a N1r (K1 + K2);
dN2rdt = β (KN - N1r - N2r - N12m) P2r - a N2r (K1 + K2);
dN12mdt = β (KN - N1r - N2r - N12m) P12m - a N12m (K1 + K2);

dI1rdt = a (K1 - I1r - I1m) N1r - μ1 I1r;
dI2rdt = a (K2 - I2r - I2m) N2r - μ2 I2r;
dI1mdt = a (K1 - I1r - I1m) N12m - μ1 I1m;
dI2mdt = a (K2 - I2r - I2m) N12m - μ2 I2m;

dP1rdt = λ1 I1r - β P1r (KN - N1r - N2r - N12m) - γ P1r;
dP2rdt = λ2 I2r - β P2r (KN - N1r - N2r - N12m) - γ P2r;
dP12mdt = c λ1 I1m + c λ2 I2m - β P12m (KN - N1r - N2r - N12m) - γ P12m;
```

The Jacobian is needed to inform us about the stability of the system.

```
J = {{D[dN1rdt, N1r], D[dN1rdt, N2r],
     D[dN1rdt, I1r], D[dN1rdt, I2r], D[dN1rdt, P1r], D[dN1rdt, P2r],
     D[dN1rdt, N12m], D[dN1rdt, I1m], D[dN1rdt, I2m], D[dN1rdt, P12m]},
    {D[dN2rdt, N1r], D[dN2rdt, N2r], D[dN2rdt, I1r], D[dN2rdt, I2r],
     D[dN2rdt, P1r], D[dN2rdt, P2r], D[dN2rdt, N12m],
     D[dN2rdt, I1m], D[dN2rdt, I2m], D[dN2rdt, P12m]},
    {D[dI1rdt, N1r], D[dI1rdt, N2r], D[dI1rdt, I1r], D[dI1rdt, I2r],
     D[dI1rdt, P1r], D[dI1rdt, P2r], D[dI1rdt, N12m],
     D[dI1rdt, I1m], D[dI1rdt, I2m], D[dI1rdt, P12m]},
    {D[dI2rdt, N1r], D[dI2rdt, N2r], D[dI2rdt, I1r], D[dI2rdt, I2r],
     D[dI2rdt, P1r], D[dI2rdt, P2r], D[dI2rdt, N12m],
     D[dI2rdt, I1m], D[dI2rdt, I2m], D[dI2rdt, P12m]},
    {D[dP1rdt, N1r], D[dP1rdt, N2r], D[dP1rdt, I1r], D[dP1rdt, I2r],
     D[dP1rdt, P1r], D[dP1rdt, P2r], D[dP1rdt, N12m],
     D[dP1rdt, I1m], D[dP1rdt, I2m], D[dP1rdt, P12m]},
    {D[dP2rdt, N1r], D[dP2rdt, N2r], D[dP2rdt, I1r], D[dP2rdt, I2r],
     D[dP2rdt, P1r], D[dP2rdt, P2r], D[dP2rdt, N12m],
     D[dP2rdt, I1m], D[dP2rdt, I2m], D[dP2rdt, P12m]},
    {D[dN12mdt, N1r], D[dN12mdt, N2r], D[dN12mdt, I1r], D[dN12mdt, I2r],
     D[dN12mdt, P1r], D[dN12mdt, P2r], D[dN12mdt, N12m],
     D[dN12mdt, I1m], D[dN12mdt, I2m], D[dN12mdt, P12m]},
    {D[dI1mdt, N1r], D[dI1mdt, N2r], D[dI1mdt, I1r], D[dI1mdt, I2r],
     D[dI1mdt, P1r], D[dI1mdt, P2r], D[dI1mdt, N12m],
     D[dI1mdt, I1m], D[dI1mdt, I2m], D[dI1mdt, P12m]},
    {D[dI2mdt, N1r], D[dI2mdt, N2r], D[dI2mdt, I1r], D[dI2mdt, I2r],
     D[dI2mdt, P1r], D[dI2mdt, P2r], D[dI2mdt, N12m],
     D[dI2mdt, I1m], D[dI2mdt, I2m], D[dI2mdt, P12m]},
    {D[dP12mdt, N1r], D[dP12mdt, N2r], D[dP12mdt, I1r], D[dP12mdt, I2r],
     D[dP12mdt, P1r], D[dP12mdt, P2r], D[dP12mdt, N12m],
     D[dP12mdt, I1m], D[dP12mdt, I2m], D[dP12mdt, P12m]}};
```

Before we can investigate whether the generalist can invade or not, we need to establish the conditions necessary for the specialist parasites to be able to persist in the system. That is, we are interested in the stability of the equilibrium where N_{1r}, N_{2r}, I_{1r}, I_{2r}, P_{1r} and P_{2r} are all equal to 0.

```
J[[1 ;; 6, 1 ;; 6]] /. {N1r → 0, N2r → 0, I1r → 0, I2r → 0,
    P1r → 0, P2r → 0, N12m → 0, I1m → 0, I2m → 0, P12m → 0} // MatrixForm
```

$$\begin{pmatrix} -a\,(K1+K2) & 0 & 0 & 0 & KN\,\beta & 0 \\ 0 & -a\,(K1+K2) & 0 & 0 & 0 & KN\,\beta \\ a\,K1 & 0 & -\mu 1 & 0 & 0 & 0 \\ 0 & a\,K2 & 0 & -\mu 2 & 0 & 0 \\ 0 & 0 & \lambda 1 & 0 & -KN\,\beta-\gamma & 0 \\ 0 & 0 & 0 & \lambda 2 & 0 & -KN\,\beta-\gamma \end{pmatrix}$$

Applying the next generation matrix theorem:

```
F = {{0, 0, 0, 0, KN β, 0}, {0, 0, 0, 0, 0, KN β}, {a K1, 0, 0, 0, 0, 0},
    {0, a K2, 0, 0, 0, 0}, {0, 0, λ1, 0, 0, 0}, {0, 0, 0, λ2, 0, 0}};
V = {{a (K1 + K2), 0, 0, 0, 0, 0}, {0, a (K1 + K2), 0, 0, 0, 0}, {0, 0, μ1, 0, 0, 0},
    {0, 0, 0, μ2, 0, 0}, {0, 0, 0, 0, KN β + γ, 0}, {0, 0, 0, 0, 0, KN β + γ}};
(J[[1 ;; 6, 1 ;; 6]] /. {N1r → 0, N2r → 0, I1r → 0, I2r → 0, P1r → 0,
     P2r → 0, N12m → 0, I1m → 0, I2m → 0, P12m → 0}) == F - V
Eigenvalues[Dot[F, Inverse[V]]]
```

```
True
```

$$\left\{\frac{K2^{1/3}\,KN^{1/3}\,\beta^{1/3}\,\lambda2^{1/3}}{(K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu2^{1/3}},\ -\frac{(-1)^{1/3}\,K2^{1/3}\,KN^{1/3}\,\beta^{1/3}\,\lambda2^{1/3}}{(K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu2^{1/3}},\right.$$
$$\frac{(-1)^{2/3}\,K2^{1/3}\,KN^{1/3}\,\beta^{1/3}\,\lambda2^{1/3}}{(K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu2^{1/3}},\ \frac{K1^{1/3}\,KN^{1/3}\,\beta^{1/3}\,\lambda1^{1/3}}{(K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu1^{1/3}},$$
$$\left.-\frac{(-1)^{1/3}\,K1^{1/3}\,KN^{1/3}\,\beta^{1/3}\,\lambda1^{1/3}}{(K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu1^{1/3}},\ \frac{(-1)^{2/3}\,K1^{1/3}\,KN^{1/3}\,\beta^{1/3}\,\lambda1^{1/3}}{(K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu1^{1/3}}\right\}$$

This equilibrium will be unstable, allowing both specialists to persist, as long as both $\frac{K1\,KN\,\beta\,\lambda1}{(K1+K2)\,(KN\,\beta+\gamma)\,\mu1} > 0$ and $\frac{K2\,KN\,\beta\,\lambda2}{(K1+K2)\,(KN\,\beta+\gamma)\,\mu2} > 0$.

To determine whether the generalist can invade, we need to evaluate the stability of the generalist-free equilibrium (i.e., the equilibrium when $N_{12,m}$, $I_{1,m}$, $I_{2,m}$, and $P_{12,m}$ are all equal to 0).

Stability is determined by the eigenvalues of the submatrix in the bottom right block.

```
MatrixForm[J[[7 ;; 10, 7 ;; 10]] /. {N12m → 0, I1m → 0, I2m → 0, P12m → 0}]
```

$$\begin{pmatrix} -a\,(K1+K2) & 0 & 0 & (KN-N1r-N2r)\,\beta \\ a\,(-I1r+K1) & -\mu1 & 0 & 0 \\ a\,(-I2r+K2) & 0 & -\mu2 & 0 \\ 0 & c\,\lambda1 & c\,\lambda2 & -(KN-N1r-N2r)\,\beta-\gamma \end{pmatrix}$$

Noting that $K_N - N_{1,r} - N_{2,r}$ is just the number of susceptible intermediate hosts (N_S), $K_1 - I_{1,r}$ is the number of susceptible definitive hosts of the first species (S_1), and $K_2 - I_{2,r}$ is the number of susceptible definitive hosts of the second species (S_2), we can rewrite this matrix slightly and then apply the next generation matrix theorem to determine the stability condition for the generalist-free system.

```
F = {{0, 0, 0, Ns β}, {a S1, 0, 0, 0}, {a S2, 0, 0, 0}, {0, c λ1, c λ2, 0}};
V = {{a (K1 + K2), 0, 0, 0}, {0, μ1, 0, 0}, {0, 0, μ2, 0}, {0, 0, 0, β Ns + γ}};
MatrixForm[F - V]
Eigenvalues[Dot[F, Inverse[V]]]
```

$$\begin{pmatrix} -a\,(K1+K2) & 0 & 0 & Ns\,\beta \\ a\,S1 & -\mu1 & 0 & 0 \\ a\,S2 & 0 & -\mu2 & 0 \\ 0 & c\,\lambda1 & c\,\lambda2 & -Ns\,\beta-\gamma \end{pmatrix}$$

$$\left\{0,\ \frac{c^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda2\,\mu1+S1\,\lambda1\,\mu2)^{1/3}}{(K1+K2)^{1/3}\,(Ns\,\beta+\gamma)^{1/3}\,\mu1^{1/3}\,\mu2^{1/3}},\right.$$
$$-\left((-1)^{1/3}\,c^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda2\,\mu1+S1\,\lambda1\,\mu2)^{1/3}\right)\Big/\left((K1+K2)^{1/3}\,(Ns\,\beta+\gamma)^{1/3}\,\mu1^{1/3}\,\mu2^{1/3}\right),$$
$$\left.\left((-1)^{2/3}\,c^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda2\,\mu1+S1\,\lambda1\,\mu2)^{1/3}\right)\Big/\left((K1+K2)^{1/3}\,(Ns\,\beta+\gamma)^{1/3}\,\mu1^{1/3}\,\mu2^{1/3}\right)\right\}$$

Note that $(-1)^{1/3} = -0.5 + 0.866025\,i$ and $(-1)^{2/3} = -0.5 + 0.866025\,i$, so whether the parasite-free equilibrium is stable or not depends entirely on the second eigenvalue. The condition for the generalist-absent equilibrium to be unstable is that this eigenvalue is greater than 1; this condition can be rewritten in a more biologically meaningful way:

$$\frac{c\,\beta N_s\,(\lambda_2 S_2 \mu_1 + \lambda_1 S_1 \mu_2)}{(K_1+K_2)(\beta N_S+\gamma)\,\mu_1 \mu_2} > 1$$

$$c\,\lambda\,\beta N_s\,(\lambda_2 S_2 \mu_1 + \lambda_1 S_1 \mu_2) > (K_1+K_2)(\beta K_N+\gamma)\,\mu_1 \mu_2$$

$$\frac{\beta N_s}{\beta N_S+\gamma}\,(c\,\lambda_2 \mu_1 S_2 + c\,\lambda_1 \mu_2 S_1) > (K_1+K_2)\,\mu_1 \mu_2$$

$$\frac{\beta N_s}{\beta N_S+\gamma}\left(\frac{S_1}{K_1+K_2}\,\frac{c\,\lambda_1}{\mu_1} + \frac{S_2}{K_1+K_2}\,\frac{c\,\lambda_2}{\mu_2}\right) > 1$$

where

$\frac{\beta N_s}{\beta N_S+\gamma}$ is the probability that a parasite in the environment is ingested by a susceptible intermediate host;

$\frac{S_1}{K_1+K_2}$ and $\frac{S_1}{K_1+K_2}$ are the probabilities that an infected intermediate host is ingested by a susceptible individual of the first and second susceptible definitive host, respectively;

$\frac{c\,\lambda_1}{\mu_1}$ and $\frac{c\,\lambda_2}{\mu_2}$ are the expected number of parasites shed from infected definitive hosts of the first and second species, respectively.

We define this expression as R_0, the invasion fitness of the generalist.

```
R0 = β Ns / (β Ns + γ) (S1 / (K1 + K2) c λ1 / μ1 + S2 / (K1 + K2) c λ2 / μ2);
```

To find the generalist-free equilibrium, we first make use of the fact that $\frac{dP_{1r}}{dt} = 0$ implies that $\beta P_{1r}(K_N - N_{1r} - N_{2r}) = \lambda_1 I_{1r} - \gamma P_{1r}$ and that $\frac{dP_{2r}}{dt} = 0$ implies that $\beta P_{2r}(K_N - N_{1r} - N_{2r}) = \lambda_2 I_{2r} - \gamma P_{2r}$.

```
I1rEq = Solve[λ1 I1r - γ P1r - c N1r (K1 + K2) == 0, I1r][[1, 1, 2]]
I2rEq = Solve[λ2 I2r - γ P2r - c N2r (K1 + K2) == 0, I2r][[1, 1, 2]]
```

$$\frac{c\,K1\,N1r + c\,K2\,N1r + P1r\,\gamma}{\lambda 1}$$

$$\frac{c\,K1\,N2r + c\,K2\,N2r + P2r\,\gamma}{\lambda 2}$$

```
P1rEq = Solve[(dI1rdt /. {I1r → I1rEq, I1m → 0}) == 0, P1r][[1, 1, 2]]
P2rEq = Solve[(dI2rdt /. {I2r → I2rEq, I2m → 0}) == 0, P2r][[1, 1, 2]]
```

$$\left(-a\,c\,K1\,N1r^2 - a\,c\,K2\,N1r^2 + a\,K1\,N1r\,\lambda 1 - c\,K1\,N1r\,\mu 1 - c\,K2\,N1r\,\mu 1\right) \Big/ (\gamma\,(a\,N1r + \mu 1))$$

$$\left(-a\,c\,K1\,N2r^2 - a\,c\,K2\,N2r^2 + a\,K2\,N2r\,\lambda 2 - c\,K1\,N2r\,\mu 2 - c\,K2\,N2r\,\mu 2\right) \Big/ (\gamma\,(a\,N2r + \mu 2))$$

```
I1rEq = I1rEq /. P1r → P1rEq // Simplify
I2rEq = I2rEq /. P2r → P2rEq // Simplify
```

$$\frac{a\,K1\,N1r}{a\,N1r + \mu 1}$$

$$\frac{a\,K2\,N2r}{a\,N2r + \mu 2}$$

```
N1rEq = Solve[(dP1rdt /. I1r → I1rEq /. P1r → P1rEq /. {N12m → 0}) == 0, N1r]
```

$$\Big\{\{\text{N1r} \to 0\},$$

$$\Big\{\text{N1r} \to \frac{1}{2\,(-\text{a c K1}\,\beta - \text{a c K2}\,\beta)}\Big(-\text{a c K1 KN}\,\beta - \text{a c K2 KN}\,\beta + \text{a c K1 N2r}\,\beta + \text{a c K2 N2r}\,\beta -$$
$$\text{a c K1}\,\gamma - \text{a c K2}\,\gamma - \text{a K1}\,\beta\,\lambda 1 + \text{c K1}\,\beta\,\mu 1 + \text{c K2}\,\beta\,\mu 1 -$$
$$\sqrt{\Big((\text{a c K1 KN}\,\beta + \text{a c K2 KN}\,\beta - \text{a c K1 N2r}\,\beta - \text{a c K2 N2r}\,\beta + \text{a c K1}\,\gamma + \text{a c K2}\,\gamma + \text{a K1}\,\beta\,\lambda 1 -$$
$$\text{c K1}\,\beta\,\mu 1 - \text{c K2}\,\beta\,\mu 1)^2 - 4\,(-\text{a c K1}\,\beta - \text{a c K2}\,\beta)\,(-\text{a K1 KN}\,\beta\,\lambda 1 + \text{a K1 N2r}\,\beta\,\lambda 1 +$$
$$\text{c K1 KN}\,\beta\,\mu 1 + \text{c K2 KN}\,\beta\,\mu 1 - \text{c K1 N2r}\,\beta\,\mu 1 - \text{c K2 N2r}\,\beta\,\mu 1 + \text{c K1}\,\gamma\,\mu 1 + \text{c K2}\,\gamma\,\mu 1)\Big)\Big)\Big\},$$

$$\Big\{\text{N1r} \to \frac{1}{2\,(-\text{a c K1}\,\beta - \text{a c K2}\,\beta)}\Big(-\text{a c K1 KN}\,\beta - \text{a c K2 KN}\,\beta + \text{a c K1 N2r}\,\beta +$$
$$\text{a c K2 N2r}\,\beta - \text{a c K1}\,\gamma - \text{a c K2}\,\gamma - \text{a K1}\,\beta\,\lambda 1 + \text{c K1}\,\beta\,\mu 1 + \text{c K2}\,\beta\,\mu 1 +$$
$$\sqrt{\Big((\text{a c K1 KN}\,\beta + \text{a c K2 KN}\,\beta - \text{a c K1 N2r}\,\beta - \text{a c K2 N2r}\,\beta + \text{a c K1}\,\gamma + \text{a c K2}\,\gamma + \text{a K1}\,\beta\,\lambda 1 -$$
$$\text{c K1}\,\beta\,\mu 1 - \text{c K2}\,\beta\,\mu 1)^2 - 4\,(-\text{a c K1}\,\beta - \text{a c K2}\,\beta)\,(-\text{a K1 KN}\,\beta\,\lambda 1 + \text{a K1 N2r}\,\beta\,\lambda 1 +$$
$$\text{c K1 KN}\,\beta\,\mu 1 + \text{c K2 KN}\,\beta\,\mu 1 - \text{c K1 N2r}\,\beta\,\mu 1 - \text{c K2 N2r}\,\beta\,\mu 1 + \text{c K1}\,\gamma\,\mu 1 + \text{c K2}\,\gamma\,\mu 1)\Big)\Big)\Big\}\Big\}$$

```
N2rEq = Solve[
  (dP2rdt /. I2r → I2rEq /. P2r → P2rEq /. {N12m → 0} /. N1r → N1rEq[[3, 1, 2]]) == 0, N2r]
```

$$\left\{\{N2r \to 0\},\right.$$

$$\left\{N2r \to \frac{1}{2\left(c^2\,K1\,\beta\,\lambda1 + c^2\,K2\,\beta\,\lambda2\right)}\left(c^2\,K2\,KN\,\beta\,\lambda2 + c^2\,K2\,\gamma\,\lambda2 + c\,K1\,\beta\,\lambda1\,\lambda2 - \frac{c\,K1^2\,\beta\,\lambda1\,\lambda2}{K1+K2} - \right.\right.$$
$$c\,K1\,\beta\,\lambda2^2 + c\,K2\,\beta\,\lambda2^2 + \frac{c\,K1^2\,\beta\,\lambda2^2}{K1+K2} + c\,K2\,\beta\,\lambda2\,\mu1 - 2\,c\,K1\,\beta\,\lambda1\,\mu2 - c\,K2\,\beta\,\lambda2\,\mu2 -$$
$$\sqrt{\left(\left(-c^2\,K2\,KN\,\beta\,\lambda2 - c^2\,K2\,\gamma\,\lambda2 - c\,K1\,\beta\,\lambda1\,\lambda2 + \frac{c\,K1^2\,\beta\,\lambda1\,\lambda2}{K1+K2} + c\,K1\,\beta\,\lambda2^2 - \right.\right.$$
$$\left.c\,K2\,\beta\,\lambda2^2 - \frac{c\,K1^2\,\beta\,\lambda2^2}{K1+K2} - c\,K2\,\beta\,\lambda2\,\mu1 + 2\,c\,K1\,\beta\,\lambda1\,\mu2 + c\,K2\,\beta\,\lambda2\,\mu2\right)^2 -$$
$$4\left(c^2\,K1\,\beta\,\lambda1 + c^2\,K2\,\beta\,\lambda2\right)\left(-c\,K1\,KN\,\beta\,\lambda2^2 + c\,K2\,KN\,\beta\,\lambda2^2 + \frac{c\,K1^2\,KN\,\beta\,\lambda2^2}{K1+K2} - \right.$$
$$K1\,\beta\,\lambda2^2\,\mu1 + K2\,\beta\,\lambda2^2\,\mu1 + \frac{K1^2\,\beta\,\lambda2^2\,\mu1}{K1+K2} - c\,K2\,KN\,\beta\,\lambda2\,\mu2 - c\,K2\,\gamma\,\lambda2\,\mu2 -$$
$$\left.\left.\left.\left.K1\,\beta\,\lambda1\,\lambda2\,\mu2 + \frac{K1^2\,\beta\,\lambda1\,\lambda2\,\mu2}{K1+K2} - K2\,\beta\,\lambda2\,\mu1\,\mu2 + K1\,\beta\,\lambda1\,\mu2^2\right)\right)\right)\right\},$$

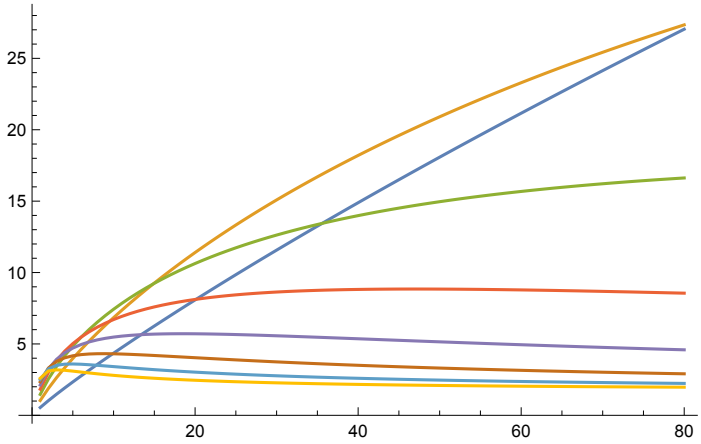
$$\left\{N2r \to \frac{1}{2\left(c^2\,K1\,\beta\,\lambda1 + c^2\,K2\,\beta\,\lambda2\right)}\left(c^2\,K2\,KN\,\beta\,\lambda2 + c^2\,K2\,\gamma\,\lambda2 + c\,K1\,\beta\,\lambda1\,\lambda2 - \frac{c\,K1^2\,\beta\,\lambda1\,\lambda2}{K1+K2} - \right.\right.$$
$$c\,K1\,\beta\,\lambda2^2 + c\,K2\,\beta\,\lambda2^2 + \frac{c\,K1^2\,\beta\,\lambda2^2}{K1+K2} + c\,K2\,\beta\,\lambda2\,\mu1 - 2\,c\,K1\,\beta\,\lambda1\,\mu2 - c\,K2\,\beta\,\lambda2\,\mu2 +$$
$$\sqrt{\left(\left(-c^2\,K2\,KN\,\beta\,\lambda2 - c^2\,K2\,\gamma\,\lambda2 - c\,K1\,\beta\,\lambda1\,\lambda2 + \frac{c\,K1^2\,\beta\,\lambda1\,\lambda2}{K1+K2} + c\,K1\,\beta\,\lambda2^2 - \right.\right.$$
$$\left.c\,K2\,\beta\,\lambda2^2 - \frac{c\,K1^2\,\beta\,\lambda2^2}{K1+K2} - c\,K2\,\beta\,\lambda2\,\mu1 + 2\,c\,K1\,\beta\,\lambda1\,\mu2 + c\,K2\,\beta\,\lambda2\,\mu2\right)^2 -$$
$$4\left(c^2\,K1\,\beta\,\lambda1 + c^2\,K2\,\beta\,\lambda2\right)\left(-c\,K1\,KN\,\beta\,\lambda2^2 + c\,K2\,KN\,\beta\,\lambda2^2 + \frac{c\,K1^2\,KN\,\beta\,\lambda2^2}{K1+K2} - \right.$$
$$K1\,\beta\,\lambda2^2\,\mu1 + K2\,\beta\,\lambda2^2\,\mu1 + \frac{K1^2\,\beta\,\lambda2^2\,\mu1}{K1+K2} - c\,K2\,KN\,\beta\,\lambda2\,\mu2 - c\,K2\,\gamma\,\lambda2\,\mu2 -$$
$$\left.\left.\left.\left.K1\,\beta\,\lambda1\,\lambda2\,\mu2 + \frac{K1^2\,\beta\,\lambda1\,\lambda2\,\mu2}{K1+K2} - K2\,\beta\,\lambda2\,\mu1\,\mu2 + K1\,\beta\,\lambda1\,\mu2^2\right)\right)\right)\right\}\right\}$$

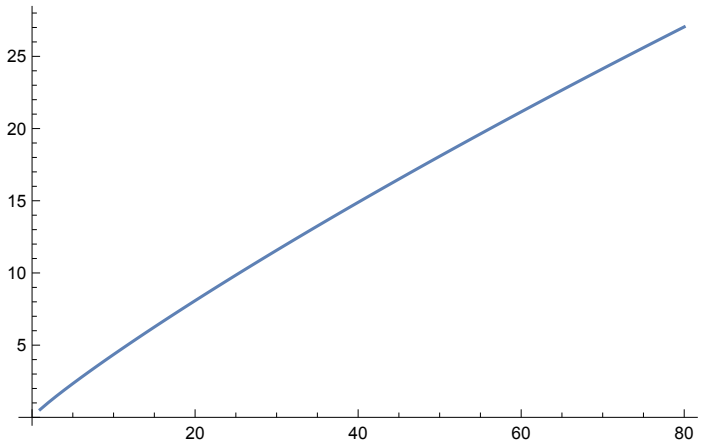
Based on the complexity of these two expression, we are unlikely to be able to make any headway analytically.

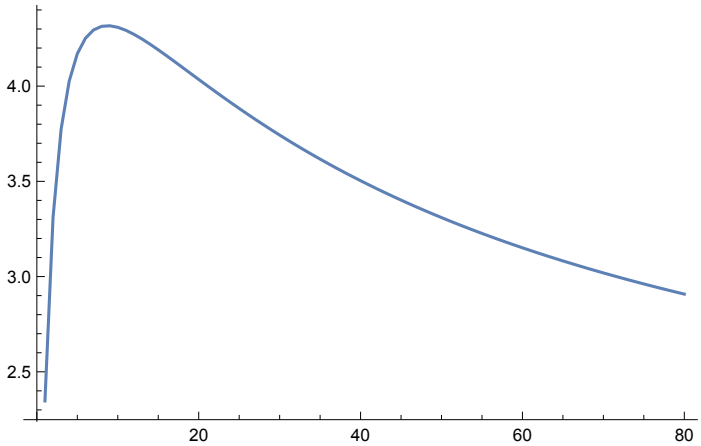
```
NumSolInvFit = Function[{W, T, c, f, NTot, B, g, a},
    allom = {K1 → K0 Exp[E/(k T)] W^(-3/4), K2 → K0 Exp[E/(k T)] (f W)^(-3/4),
      μ1 → μ0 Exp[-E/(k T)] W^(-1/4), μ2 → μ0 Exp[-E/(k T)] (f W)^(-1/4), λ1 → λ0 Exp[-E/(k T)] W^(3/4),
      λ2 → λ0 Exp[-E/(k T)] (f W)^(3/4), r1 → r0 Exp[-E/(k T)] W^(-1/4), r2 → r0 Exp[-E/(k T)] (f W)^(-1/4)};
    pars = {E → 0.45`, k → 8.617`/10^5, K0 → 2.984`/10^9, μ0 → 1.785` × 10^8,
      λ0 → 2 × 10^8, r0 → 2.21 × 10^10, β → B, γ → g, a1 → a, a2 → a, NT → NTot};
    DOPRIamat = {{1 / 5}, {3 / 40, 9 / 40}, {44 / 45, -56 / 15, 32 / 9},
      {19 372 / 6561, -25 360 / 2187, 64 448 / 6561, -212 / 729},
      {9017 / 3168, -355 / 33, 46 732 / 5247, 49 / 176, -5103 / 18 656},
      {35 / 384, 0, 500 / 1113, 125 / 192, -2187 / 6784, 11 / 84}};
    DOPRIbvec = {35 / 384, 0, 500 / 1113, 125 / 192, -2187 / 6784, 11 / 84, 0};
    DOPRIcvec = {1 / 5, 3 / 10, 4 / 5, 8 / 9, 1, 1};
    DOPRIevec = {71 / 57 600, 0, -71 / 16 695, 71 / 1920, -17 253 / 339 200, 22 / 525, -1 / 40};
    DOPRICoefficients[5, p_] := N[{DOPRIamat, DOPRIbvec, DOPRIcvec, DOPRIevec}, p];
    Soln = NDSolve[({
          N1r'[t] == -a (K1 + K2) N1r[t] + β (NT - N1r[t] - N2r[t]) P1r[t],
          N2r'[t] == -a (K1 + K2) N2r[t] + β (NT - N1r[t] - N2r[t]) P2r[t],
          I1r'[t] == -μ1 I1r[t] + a (K1 - I1r[t]) N1r[t],
          I2r'[t] == -μ2 I2r[t] + a (K2 - I2r[t]) N2r[t],
          P1r'[t] == λ1 I1r[t] - γ P1r[t] - β (NT - N1r[t] - N2r[t]) P1r[t],
          P2r'[t] == λ2 I2r[t] - γ P2r[t] - β (NT - N1r[t] - N2r[t]) P2r[t],
          N1r[0] == 0, N2r[0] == 0,
          I1r[0] == 0, I2r[0] == 0,
          P1r[0] == 1, P2r[0] == 1} /. allom /. pars),
      {N1r, N2r, I1r, I2r, P1r, P2r}, {t, 0, 1000},
      Method → {"ExplicitRungeKutta", "DifferenceOrder" → 5,
        "Coefficients" → DOPRICoefficients, "StiffnessTest" → False}];
    (* Print[{N1ir→(N1ir[1000]/.Soln)[[1]],N2ir→(N2ir[1000]/.Soln)[[1]],
      D1s→(D1s[1000]/.Soln)[[1]],D1ir→(D1ir[1000]/.Soln)[[1]],
      D2s→(D2s[1000]/.Soln)[[1]],D2ir→(D2ir[1000]/.Soln)[[1]]}] *);
    β (NT - N1r - N2r) / (β (NT - N1r - N2r) + γ) ((K1 - I1r) / (K1 + K2) c λ1 / μ1 + (K2 - I2r) / (K1 + K2) c λ2 / μ2) /.
      {N1r → (N1r[1000] /. Soln)[[1]], N2r → (N2r[1000] /. Soln)[[1]], I1r →
        (I1r[1000] /. Soln)[[1]], I2r → (I2r[1000] /. Soln)[[1]]} /. allom /. pars
  ];
```

As with the preceding model, there is not a simple relationship between R_0 and mass. For example, when intermediate host abundance is small, increasing mass increases R_0, but when intermediate host abundance is high, increasing host mass first increases, and then decreases, R_0.

```
InvFitAcrossWNT =
  Table[Table[NumSolInvFit[W, 270, 0.9, 0.9, NT, 0.01, 0.1, 0.01], {W, 25, 2000, 25}],
   {NT, 0.25, 2, 0.25}];
ListLinePlot[InvFitAcrossWNT]
ListLinePlot[InvFitAcrossWNT[[1]]]
ListLinePlot[InvFitAcrossWNT[[6]]]
```

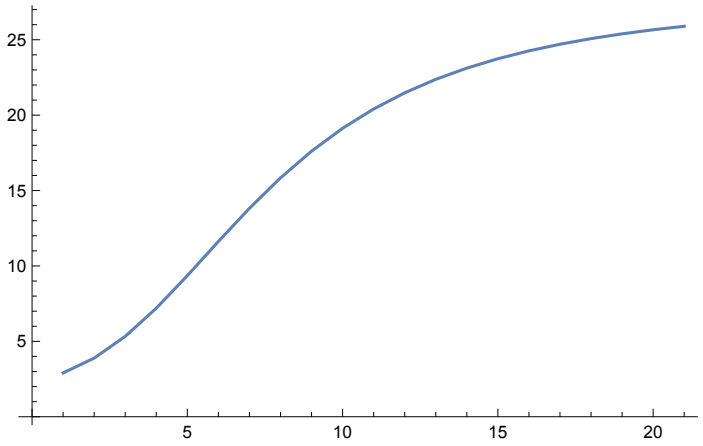




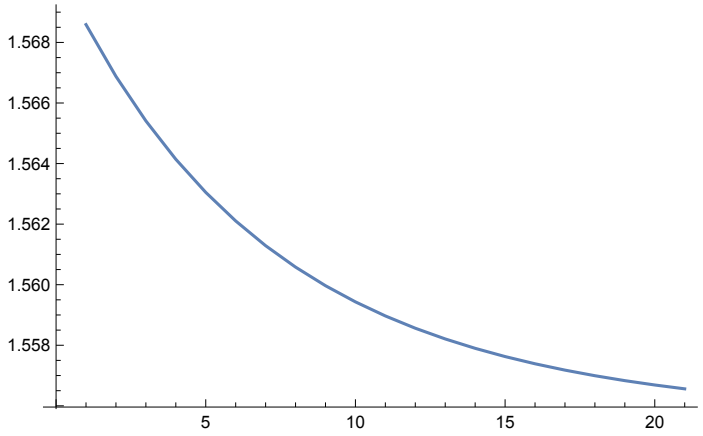


Increasing temperature also has a much more complex effect on R_0: when N_T is large, increasing temperature increases R_0, but when N_T is small, increasing temperature decreases R_0.

```
InvFitAcrossWT =
  Table[NumSolInvFit[200, T, 0.9, 0.9, 2, 0.01, 0.1, 0.01], {T, 270, 310, 2}];
ListLinePlot[InvFitAcrossWT]
```

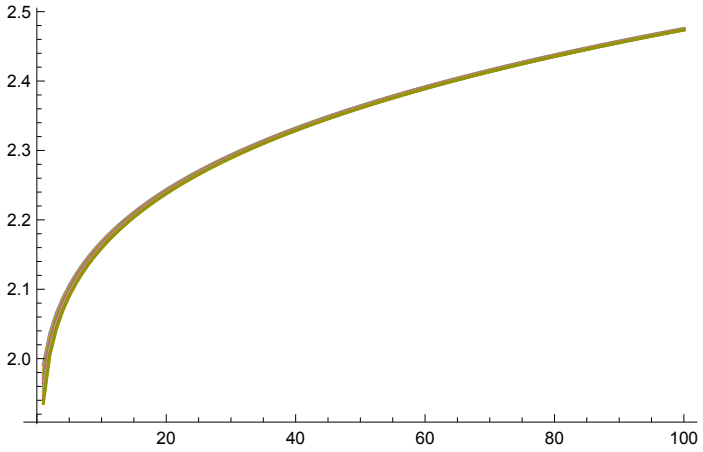



```
InvFitAcrossWT =
  Table[NumSolInvFit[200, T, 0.9, 0.9, 0.1, 0.01, 0.1, 0.01], {T, 270, 310, 2}];
ListLinePlot[InvFitAcrossWT]
```



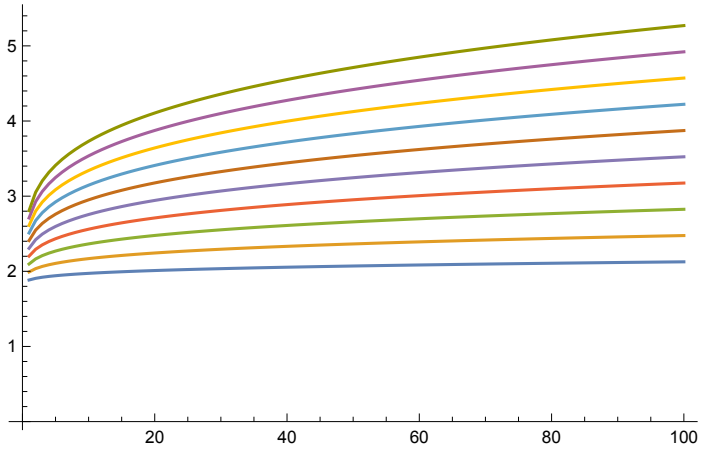
It also holds if you change the rate parasites are lost from the environment (here γ ranges from 0.01 to 0.1):

```
InvFitAcrossWg =
  Table[Table[NumSolInvFit[W, 270, 0.9, 0.9, 1, 0.1, g, 0.1], {W, 10, 1000, 10}],
   {g, 0.01, 0.1, 0.01}];
ListLinePlot[InvFitAcrossWg]
```



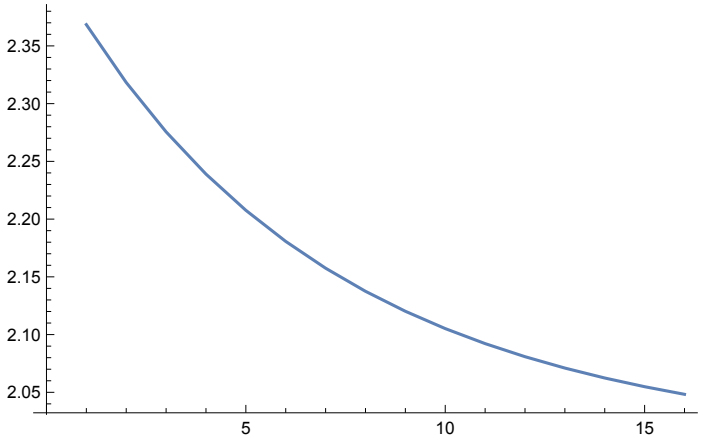
It also holds if you change the ingestion rate of the definitive hosts:

```
InvFitAcrossWa =
  Table[Table[NumSolInvFit[W, 270, 0.9, 0.9, 1, 0.1, 0.01, a], {W, 10, 1000, 10}],
   {a, 0.05, 0.5, 0.05}];
ListLinePlot[InvFitAcrossWa]
```



Increasing temperature decreases R_0:

```
InvFitAcrossT = Table[NumSolInvFit[100, T, 0.9, 0.9, 1], {T, 270, 300, 2}];
ListLinePlot[InvFitAcrossT]
```



Case 9: Trophic transmission; two specialist parasites; constant host population size; active seeking of intermediate hosts; no avoidance of infected intermediate hosts

We have assumed that parasites in the environment are consumed by *all* intermediate hosts, even though they only cause new infections in susceptible intermediate hosts. This makes the problem very analytically tractable.

```
dN1rdt = β (KN - N1r - N2r - N12m) P1r - c N1r (K1 + K2);
dN2rdt = β (KN - N1r - N2r - N12m) P2r - c N2r (K1 + K2);
dN12mdt = β (KN - N1r - N2r - N12m) P12m - c N12m (K1 + K2);

dI1rdt = c (K1 - I1r - I1m) N1r - μ1 I1r;
dI2rdt = c (K2 - I2r - I2m) N2r - μ2 I2r;
dI1mdt = c (K1 - I1r - I1m) N12m - μ1 I1m;
dI2mdt = c (K2 - I2r - I2m) N12m - μ2 I2m;

dP1rdt = λ1 I1r - β P1r KN - γ P1r;
dP2rdt = λ2 I2r - β P2r KN - γ P2r;
dP12mdt = a λ1 I1m + a λ2 I2m - β P12m KN - γ P12m;
```

Find the equilibria (the brute force, all at once technique failed for this model):

```
I1rEq = Solve[dP1rdt == 0, I1r][[1, 1, 2]]
I2rEq = Solve[dP2rdt == 0, I2r][[1, 1, 2]]
```

$$\frac{KN\ P1r\ \beta + P1r\ \gamma}{\lambda 1}$$

$$\frac{KN\ P2r\ \beta + P2r\ \gamma}{\lambda 2}$$

```
N1rEq = Solve[(dI1rdt /. {I1r → I1rEq, I1m → 0}) == 0, N1r][[1, 1, 2]]
N2rEq = Solve[(dI2rdt /. {I2r → I2rEq, I2m → 0}) == 0, N2r][[1, 1, 2]]
```

$$-\frac{(\mathrm{KN}\,\mathrm{P1r}\,\beta + \mathrm{P1r}\,\gamma)\,\mu 1}{\mathbf{c}\,(\mathrm{KN}\,\mathrm{P1r}\,\beta + \mathrm{P1r}\,\gamma - \mathrm{K1}\,\lambda 1)}$$

$$-\frac{(\mathrm{KN}\,\mathrm{P2r}\,\beta + \mathrm{P2r}\,\gamma)\,\mu 2}{\mathbf{c}\,(\mathrm{KN}\,\mathrm{P2r}\,\beta + \mathrm{P2r}\,\gamma - \mathrm{K2}\,\lambda 2)}$$

```
P1rEq =
 Simplify[Solve[(dN1rdt /. {N1r → N1rEq, N2r → N2rEq, N12m → 0}) == 0, P1r]][[2, 1, 2]]
P2rEq =
 Simplify[Solve[(dN2rdt /. {N1r → N1rEq, N2r → N2rEq, N12m → 0} /. {P1r → P1rEq}) == 0,
    P2r]][[2, 1, 2]]
```

$$(-\mathbf{c}\,(\mathrm{KN}\,\mathrm{P2r}\,\beta + \mathrm{P2r}\,\gamma - \mathrm{K2}\,\lambda 2)\,(\mathrm{K2}\,(\mathrm{KN}\,\beta + \gamma)\,\mu 1 + \mathrm{K1}\,(\gamma\,\mu 1 + \mathrm{KN}\,\beta\,(-\lambda 1 + \mu 1))) + \mathrm{K1}\,\mathrm{P2r}\,\beta\,(\mathrm{KN}\,\beta + \gamma)\,\lambda 1\,\mu 2) \,/\, (\beta\,(\mathrm{KN}\,\beta + \gamma)\,(\mathbf{c}\,\mathrm{KN}\,(\mathrm{KN}\,\mathrm{P2r}\,\beta + \mathrm{P2r}\,\gamma - \mathrm{K2}\,\lambda 2) + \mathrm{P2r}\,\gamma\,\mu 1 - \mathrm{K2}\,\lambda 2\,\mu 1 + \mathrm{P2r}\,\gamma\,\mu 2 + \mathrm{KN}\,\mathrm{P2r}\,\beta\,(\mu 1 + \mu 2)))$$

$$(\beta\,(\mathrm{K2}\,\lambda 2\,\mu 1 - \mathrm{K1}\,\lambda 1\,\mu 2) - \mathbf{c}\,(\mathrm{K1}\,(\mathrm{KN}\,\beta + \gamma)\,\mu 2 + \mathrm{K2}\,(\gamma\,\mu 2 + \mathrm{KN}\,\beta\,(-\lambda 2 + \mu 2)))) \,/\, (\beta\,(\mathrm{KN}\,\beta + \gamma)\,(\mathbf{c}\,\mathrm{KN} + \mu 1 + \mu 2))$$

The number of susceptible intermediate hosts at the generalist-free equilibrium is $N_S = K_N - N_{1,r} - N_{2,r}$:

```
NsEq = Simplify[KN - Simplify[
     Simplify[N1rEq /. P1r → P1rEq /. P2r → P2rEq] + Simplify[N2rEq /. P2r → P2rEq]]]
```

$$\frac{(\mathrm{K1} + \mathrm{K2})\,(\mathrm{KN}\,\beta + \gamma)\,(\mathbf{c}\,\mathrm{KN} + \mu 1 + \mu 2)}{\mathbf{c}\,(\mathrm{K1} + \mathrm{K2})\,(\mathrm{KN}\,\beta + \gamma) + \beta\,(\mathrm{K1}\,\lambda 1 + \mathrm{K2}\,\lambda 2)}$$

The number of susceptible definitive hosts of species 1 and 2 at the generalist free-equilibrium are $S_1 = K_1 - I_{1,r}$ and $S_2 = K_2 - I_{2,r}$, respectively:

```
S1Eq = Simplify[(K1 - I1r) /. I1r → I1rEq /. P1r → P1rEq /. P2r → P2rEq]
S2Eq = Simplify[(K2 - I2r) /. I2r → I2rEq /. P2r → P2rEq]
```

$$((\mathbf{c}\,(\mathrm{K1} + \mathrm{K2})\,(\mathrm{KN}\,\beta + \gamma) + \beta\,(\mathrm{K1}\,\lambda 1 + \mathrm{K2}\,\lambda 2))\,\mu 1) \,/\, (\beta\,\lambda 1\,(\mathbf{c}\,\mathrm{KN} + \mu 1 + \mu 2))$$

$$((\mathbf{c}\,(\mathrm{K1} + \mathrm{K2})\,(\mathrm{KN}\,\beta + \gamma) + \beta\,(\mathrm{K1}\,\lambda 1 + \mathrm{K2}\,\lambda 2))\,\mu 2) \,/\, (\beta\,\lambda 2\,(\mathbf{c}\,\mathrm{KN} + \mu 1 + \mu 2))$$

To determine whether the generalist can invade, we need to evaluate the stability of the generalist-free equilibrium (i.e., the equilibrium when $N_{12,m}$, $I_{1,m}$, $I_{2,m}$, and $P_{12,m}$ are all equal to 0).

```
J = {{D[dN1rdt, N1r], D[dN1rdt, N2r],
      D[dN1rdt, I1r], D[dN1rdt, I2r], D[dN1rdt, P1r], D[dN1rdt, P2r],
      D[dN1rdt, N12m], D[dN1rdt, I1m], D[dN1rdt, I2m], D[dN1rdt, P12m]},
     {D[dN2rdt, N1r], D[dN2rdt, N2r], D[dN2rdt, I1r], D[dN2rdt, I2r],
      D[dN2rdt, P1r], D[dN2rdt, P2r], D[dN2rdt, N12m],
      D[dN2rdt, I1m], D[dN2rdt, I2m], D[dN2rdt, P12m]},
     {D[dI1rdt, N1r], D[dI1rdt, N2r], D[dI1rdt, I1r], D[dI1rdt, I2r],
      D[dI1rdt, P1r], D[dI1rdt, P2r], D[dI1rdt, N12m],
      D[dI1rdt, I1m], D[dI1rdt, I2m], D[dI1rdt, P12m]},
     {D[dI2rdt, N1r], D[dI2rdt, N2r], D[dI2rdt, I1r], D[dI2rdt, I2r],
      D[dI2rdt, P1r], D[dI2rdt, P2r], D[dI2rdt, N12m],
      D[dI2rdt, I1m], D[dI2rdt, I2m], D[dI2rdt, P12m]},
     {D[dP1rdt, N1r], D[dP1rdt, N2r], D[dP1rdt, I1r], D[dP1rdt, I2r],
      D[dP1rdt, P1r], D[dP1rdt, P2r], D[dP1rdt, N12m],
      D[dP1rdt, I1m], D[dP1rdt, I2m], D[dP1rdt, P12m]},
     {D[dP2rdt, N1r], D[dP2rdt, N2r], D[dP2rdt, I1r], D[dP2rdt, I2r],
      D[dP2rdt, P1r], D[dP2rdt, P2r], D[dP2rdt, N12m],
      D[dP2rdt, I1m], D[dP2rdt, I2m], D[dP2rdt, P12m]},
     {D[dN12mdt, N1r], D[dN12mdt, N2r], D[dN12mdt, I1r], D[dN12mdt, I2r],
      D[dN12mdt, P1r], D[dN12mdt, P2r], D[dN12mdt, N12m],
      D[dN12mdt, I1m], D[dN12mdt, I2m], D[dN12mdt, P12m]},
     {D[dI1mdt, N1r], D[dI1mdt, N2r], D[dI1mdt, I1r], D[dI1mdt, I2r],
      D[dI1mdt, P1r], D[dI1mdt, P2r], D[dI1mdt, N12m],
      D[dI1mdt, I1m], D[dI1mdt, I2m], D[dI1mdt, P12m]},
     {D[dI2mdt, N1r], D[dI2mdt, N2r], D[dI2mdt, I1r], D[dI2mdt, I2r],
      D[dI2mdt, P1r], D[dI2mdt, P2r], D[dI2mdt, N12m],
      D[dI2mdt, I1m], D[dI2mdt, I2m], D[dI2mdt, P12m]},
     {D[dP12mdt, N1r], D[dP12mdt, N2r], D[dP12mdt, I1r], D[dP12mdt, I2r],
      D[dP12mdt, P1r], D[dP12mdt, P2r], D[dP12mdt, N12m], D[dP12mdt, I1m],
      D[dP12mdt, I2m], D[dP12mdt, P12m]}} /. {N12m → 0, I1m → 0, I2m → 0, P12m → 0};
```

Stability is determined by the eigenvalues of the submatrix in the bottom right block.

```
MatrixForm[J[[7 ;; 10, 7 ;; 10]]]
```

$$\begin{pmatrix} -c\,(K1+K2) & 0 & 0 & (KN-N1r-N2r)\,\beta \\ c\,(-I1r+K1) & -\mu 1 & 0 & 0 \\ c\,(-I2r+K2) & 0 & -\mu 2 & 0 \\ 0 & a\,\lambda 1 & a\,\lambda 2 & -KN\,\beta-\gamma \end{pmatrix}$$

Noting that $K_N - N_{1,r} - N_{2,r}$ is just the number of susceptible intermediate hosts (N_S), $K_1 - I_{1,r}$ is the number of susceptible definitive hosts of the first species (S_1), and $K_2 - I_{2,r}$ is the number of susceptible definitive hosts of the second species (S_2), we can rewrite this matrix slightly and then apply the next generation matrix theorem to determine the stability condition for the generalist-free system.

```
F = {{0, 0, 0, Ns β}, {c S1, 0, 0, 0}, {c S2, 0, 0, 0}, {0, a λ1, a λ2, 0}};
V = {{c (K1 + K2), 0, 0, 0}, {0, μ1, 0, 0}, {0, 0, μ2, 0}, {0, 0, 0, β KN + γ}};
MatrixForm[F - V]
Eigenvalues[Dot[F, Inverse[V]]]
```

$$\begin{pmatrix} -c\,(K1+K2) & 0 & 0 & Ns\,\beta \\ c\,S1 & -\mu 1 & 0 & 0 \\ c\,S2 & 0 & -\mu 2 & 0 \\ 0 & a\,\lambda 1 & a\,\lambda 2 & -KN\,\beta-\gamma \end{pmatrix}$$

$$\left\{0,\ \frac{a^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda 2\,\mu 1+S1\,\lambda 1\,\mu 2)^{1/3}}{(K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}\,\mu 2^{1/3}},\right.$$
$$-\left(\left(-1\right)^{1/3}a^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda 2\,\mu 1+S1\,\lambda 1\,\mu 2)^{1/3}\right)\Big/\left((K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}\,\mu 2^{1/3}\right),$$
$$\left.\left(\left(-1\right)^{2/3}a^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda 2\,\mu 1+S1\,\lambda 1\,\mu 2)^{1/3}\right)\Big/\left((K1+K2)^{1/3}\,(KN\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}\,\mu 2^{1/3}\right)\right\}$$

Note that $(-1)^{1/3} = -0.5 + 0.866025\,i$ and $(-1)^{2/3} = -0.5 + 0.866025\,i$, so whether the parasite-free equilibrium is stable or not depends entirely on the second eigenvalue. The condition for the generalist-absent equilibrium to be unstable is that this eigenvalue is greater than 1; this condition can be rewritten in a more biologically meaningful way:

$$\frac{a\,\beta\,N_s\,(\lambda_2\,S_2\,\mu_1+\lambda_1\,S_1\,\mu_2)}{(K_1+K_2)\,(\beta\,K_N+\gamma)\,\mu_1\,\mu_2} > 1$$

$$a\,\lambda\,\beta\,N_s\,(\lambda_2\,S_2\,\mu_1+\lambda_1\,S_1\,\mu_2) > (K_1+K_2)\,(\beta\,K_N+\gamma)\,\mu_1\,\mu_2$$

$$\frac{\beta N_s}{\beta K_N+\gamma}\,(a\,\lambda_2\,\mu_1\,S_2+a\,\lambda_1\,\mu_2\,S_1) > (K_1+K_2)\,\mu_1\,\mu_2$$

$$\frac{\beta N_s}{\beta K_N+\gamma}\left(\frac{S_1}{K_1+K_2}\,\frac{a\,\lambda_1}{\mu_1}+\frac{S_2}{K_1+K_2}\,\frac{a\,\lambda_2}{\mu_2}\right) > 1$$

where

$\frac{\beta N_s}{\beta K_N+\gamma}$ is the probability that a parasite in the environment is ingested by a susceptible intermediate host;

$\frac{S_1}{K_1+K_2}$ and $\frac{S_1}{K_1+K_2}$ are the probabilities that an infected intermediate host is ingested by a susceptible individual of the first and second susceptible definitive host, respectively;

$\frac{a\,\lambda_1}{\mu_1}$ and $\frac{a\,\lambda_2}{\mu_2}$ are the expected number of parasites shed from infected definitive hosts of the first and second species, respectively.

We define this expression as R_0, the invasion fitness of the generalist.

```
R0 = β Ns / (β KN + γ) (S1 / (K1 + K2) a λ1 / μ1 + S2 / (K1 + K2) a λ2 / μ2);
```

If you plug in the equilibrium values of N_S, S_1 and S_2, however, you get an incredibly simple expression for the invasion fitness:

```
Simplify[R0 /. {Ns → NsEq, S1 → S1Eq, S2 → S2Eq}]
```

```
2 a
```

What this indicates is that as long as the fraction that shedding is reduced for the generalist (the cost of generalism) is less than 0.5, the generalist will be able to invade.

Case 10: Trophic transmission; two specialist parasites; constant host population size; passive host seeking; no avoidance of infected intermediate hosts

For this model, we have assumed that parasites in the environment are consumed by *all* hosts (both

definitive and intermediate), even though they only cause new infections in susceptible intermediate hosts.

```
dN1rdt = β (KN - N1r - N2r - N12m) P1r - c N1r (K1 + K2);
dN2rdt = β (KN - N1r - N2r - N12m) P2r - c N2r (K1 + K2);
dN12mdt = β (KN - N1r - N2r - N12m) P12m - c N12m (K1 + K2);

dI1rdt = c (K1 - I1r - I1m) N1r - μ1 I1r;
dI2rdt = c (K2 - I2r - I2m) N2r - μ2 I2r;
dI1mdt = c (K1 - I1r - I1m) N12m - μ1 I1m;
dI2mdt = c (K2 - I2r - I2m) N12m - μ2 I2m;

dP1rdt = λ1 I1r - β P1r (KN + K1 + K2) - γ P1r;
dP2rdt = λ2 I2r - β P2r (KN + K1 + K2) - γ P2r;
dP12mdt = a λ1 I1m + a λ2 I2m - β P12m (KN + K1 + K2) - γ P12m;
```

Find the equilibria (the brute force, all at once technique failed for this model):

```
I1rEq = Solve[dP1rdt == 0, I1r][[1, 1, 2]]
I2rEq = Solve[dP2rdt == 0, I2r][[1, 1, 2]]
```

$$\frac{\text{K1 P1r}\,\beta + \text{K2 P1r}\,\beta + \text{KN P1r}\,\beta + \text{P1r}\,\gamma}{\lambda 1}$$

$$\frac{\text{K1 P2r}\,\beta + \text{K2 P2r}\,\beta + \text{KN P2r}\,\beta + \text{P2r}\,\gamma}{\lambda 2}$$

```
N1rEq = Solve[(dI1rdt /. {I1r → I1rEq, I1m → 0}) == 0, N1r][[1, 1, 2]]
N2rEq = Solve[(dI2rdt /. {I2r → I2rEq, I2m → 0}) == 0, N2r][[1, 1, 2]]
```

$$-\left(\left(\left(\text{K1 P1r}\,\beta + \text{K2 P1r}\,\beta + \text{KN P1r}\,\beta + \text{P1r}\,\gamma\right)\mu 1\right) \Big/ \left(\text{c}\left(\text{K1 P1r}\,\beta + \text{K2 P1r}\,\beta + \text{KN P1r}\,\beta + \text{P1r}\,\gamma - \text{K1}\,\lambda 1\right)\right)\right)$$

$$-\left(\left(\left(\text{K1 P2r}\,\beta + \text{K2 P2r}\,\beta + \text{KN P2r}\,\beta + \text{P2r}\,\gamma\right)\mu 2\right) \Big/ \left(\text{c}\left(\text{K1 P2r}\,\beta + \text{K2 P2r}\,\beta + \text{KN P2r}\,\beta + \text{P2r}\,\gamma - \text{K2}\,\lambda 2\right)\right)\right)$$

```
P1rEq =
 Simplify[Solve[(dN1rdt /. {N1r → N1rEq, N2r → N2rEq, N12m → 0}) == 0, P1r]][[2, 1, 2]]
P2rEq =
 Simplify[Solve[(dN2rdt /. {N1r → N1rEq, N2r → N2rEq, N12m → 0} /. {P1r → P1rEq}) == 0,
    P2r]][[2, 1, 2]]
```

$$\Big(-\text{c}\left(\text{K1 P2r}\,\beta + \text{K2 P2r}\,\beta + \text{KN P2r}\,\beta + \text{P2r}\,\gamma - \text{K2}\,\lambda 2\right)\left(\text{K1}^2\,\beta\,\mu 1 + \text{K2}\left(\text{K2}\,\beta + \text{KN}\,\beta + \gamma\right)\mu 1 + \text{K1}\left(\left(2\,\text{K2}\,\beta + \gamma\right)\mu 1 + \text{KN}\,\beta\left(-\lambda 1 + \mu 1\right)\right)\right) + \text{K1 P2r}\,\beta\left(\text{K1}\,\beta + \text{K2}\,\beta + \text{KN}\,\beta + \gamma\right)\lambda 1\,\mu 2\Big) \Big/ \left(\beta\left(\text{K1}\,\beta + \text{K2}\,\beta + \text{KN}\,\beta + \gamma\right)\left(\text{c KN}\left(\text{K1 P2r}\,\beta + \text{K2 P2r}\,\beta + \text{KN P2r}\,\beta + \text{P2r}\,\gamma - \text{K2}\,\lambda 2\right) + \text{K2 P2r}\,\beta\,\mu 1 + \text{KN P2r}\,\beta\,\mu 1 + \text{P2r}\,\gamma\,\mu 1 - \text{K2}\,\lambda 2\,\mu 1 + \text{K2 P2r}\,\beta\,\mu 2 + \text{KN P2r}\,\beta\,\mu 2 + \text{P2r}\,\gamma\,\mu 2 + \text{K1 P2r}\,\beta\left(\mu 1 + \mu 2\right)\right)\right)$$

$$\Big(\beta\left(\text{K2}\,\lambda 2\,\mu 1 - \text{K1}\,\lambda 1\,\mu 2\right) - \text{c}\left(\text{K2}^2\,\beta\,\mu 2 + \text{K1}\left(\text{K1}\,\beta + \text{KN}\,\beta + \gamma\right)\mu 2 + \text{K2}\left(\left(2\,\text{K1}\,\beta + \gamma\right)\mu 2 + \text{KN}\,\beta\left(-\lambda 2 + \mu 2\right)\right)\right)\Big) \Big/ \left(\beta\left(\text{K1}\,\beta + \text{K2}\,\beta + \text{KN}\,\beta + \gamma\right)\left(\text{c KN} + \mu 1 + \mu 2\right)\right)$$

The number of susceptible intermediate hosts at the generalist-free equilibrium is $N_S = K_N - N_{1,r} - N_{2,r}$:

```
NsEq = Simplify[KN - Simplify[
    Simplify[N1rEq /. P1r → P1rEq /. P2r → P2rEq] + Simplify[N2rEq /. P2r → P2rEq]]]
```

$$\left(\left(\text{K1} + \text{K2}\right)\left(\text{K1}\,\beta + \text{K2}\,\beta + \text{KN}\,\beta + \gamma\right)\left(\text{c KN} + \mu 1 + \mu 2\right)\right) \Big/ \left(\text{c}\left(\text{K1} + \text{K2}\right)\left(\text{K1}\,\beta + \text{K2}\,\beta + \text{KN}\,\beta + \gamma\right) + \beta\left(\text{K1}\,\lambda 1 + \text{K2}\,\lambda 2\right)\right)$$

The number of susceptible definitive hosts of species 1 and 2 at the generalist free-equilibrium are $S_1 = K_1 - I_{1,r}$ and $S_2 = K_2 - I_{2,r}$, respectively:

```
S1Eq = Simplify[(K1 - I1r) /. I1r → I1rEq /. P1r → P1rEq /. P2r → P2rEq]
S2Eq = Simplify[(K2 - I2r) /. I2r → I2rEq /. P2r → P2rEq]
```

```
((c (K1 + K2) (K1 β + K2 β + KN β + γ) + β (K1 λ1 + K2 λ2)) μ1) / (β λ1 (c KN + μ1 + μ2))
```

```
((c (K1 + K2) (K1 β + K2 β + KN β + γ) + β (K1 λ1 + K2 λ2)) μ2) / (β λ2 (c KN + μ1 + μ2))
```

To determine whether the generalist can invade, we need to evaluate the stability of the generalist-free equilibrium (i.e., the equilibrium when $N_{12,m}$, $I_{1,m}$, $I_{2,m}$, and $P_{12,m}$ are all equal to 0).

```
J = {{D[dN1rdt, N1r], D[dN1rdt, N2r],
      D[dN1rdt, I1r], D[dN1rdt, I2r], D[dN1rdt, P1r], D[dN1rdt, P2r],
      D[dN1rdt, N12m], D[dN1rdt, I1m], D[dN1rdt, I2m], D[dN1rdt, P12m]},
     {D[dN2rdt, N1r], D[dN2rdt, N2r], D[dN2rdt, I1r], D[dN2rdt, I2r],
      D[dN2rdt, P1r], D[dN2rdt, P2r], D[dN2rdt, N12m],
      D[dN2rdt, I1m], D[dN2rdt, I2m], D[dN2rdt, P12m]},
     {D[dI1rdt, N1r], D[dI1rdt, N2r], D[dI1rdt, I1r], D[dI1rdt, I2r],
      D[dI1rdt, P1r], D[dI1rdt, P2r], D[dI1rdt, N12m],
      D[dI1rdt, I1m], D[dI1rdt, I2m], D[dI1rdt, P12m]},
     {D[dI2rdt, N1r], D[dI2rdt, N2r], D[dI2rdt, I1r], D[dI2rdt, I2r],
      D[dI2rdt, P1r], D[dI2rdt, P2r], D[dI2rdt, N12m],
      D[dI2rdt, I1m], D[dI2rdt, I2m], D[dI2rdt, P12m]},
     {D[dP1rdt, N1r], D[dP1rdt, N2r], D[dP1rdt, I1r], D[dP1rdt, I2r],
      D[dP1rdt, P1r], D[dP1rdt, P2r], D[dP1rdt, N12m],
      D[dP1rdt, I1m], D[dP1rdt, I2m], D[dP1rdt, P12m]},
     {D[dP2rdt, N1r], D[dP2rdt, N2r], D[dP2rdt, I1r], D[dP2rdt, I2r],
      D[dP2rdt, P1r], D[dP2rdt, P2r], D[dP2rdt, N12m],
      D[dP2rdt, I1m], D[dP2rdt, I2m], D[dP2rdt, P12m]},
     {D[dN12mdt, N1r], D[dN12mdt, N2r], D[dN12mdt, I1r], D[dN12mdt, I2r],
      D[dN12mdt, P1r], D[dN12mdt, P2r], D[dN12mdt, N12m],
      D[dN12mdt, I1m], D[dN12mdt, I2m], D[dN12mdt, P12m]},
     {D[dI1mdt, N1r], D[dI1mdt, N2r], D[dI1mdt, I1r], D[dI1mdt, I2r],
      D[dI1mdt, P1r], D[dI1mdt, P2r], D[dI1mdt, N12m],
      D[dI1mdt, I1m], D[dI1mdt, I2m], D[dI1mdt, P12m]},
     {D[dI2mdt, N1r], D[dI2mdt, N2r], D[dI2mdt, I1r], D[dI2mdt, I2r],
      D[dI2mdt, P1r], D[dI2mdt, P2r], D[dI2mdt, N12m],
      D[dI2mdt, I1m], D[dI2mdt, I2m], D[dI2mdt, P12m]},
     {D[dP12mdt, N1r], D[dP12mdt, N2r], D[dP12mdt, I1r], D[dP12mdt, I2r],
      D[dP12mdt, P1r], D[dP12mdt, P2r], D[dP12mdt, N12m], D[dP12mdt, I1m],
      D[dP12mdt, I2m], D[dP12mdt, P12m]}} /. {N12m → 0, I1m → 0, I2m → 0, P12m → 0};
```

Stability is determined by the eigenvalues of the submatrix in the bottom right block.

```
MatrixForm[J[[7 ;; 10, 7 ;; 10]]]
```

$$\begin{pmatrix} -c\,(K1+K2) & 0 & 0 & (KN-N1r-N2r)\,\beta \\ c\,(-I1r+K1) & -\mu 1 & 0 & 0 \\ c\,(-I2r+K2) & 0 & -\mu 2 & 0 \\ 0 & a\,\lambda 1 & a\,\lambda 2 & -(K1+K2+KN)\,\beta-\gamma \end{pmatrix}$$

Noting that $K_N - N_{1,r} - N_{2,r}$ is just the number of susceptible intermediate hosts (N_S), $K_1 - I_{1,r}$ is the number of susceptible definitive hosts of the first species (S_1), and $K_2 - I_{2,r}$ is the number of susceptible definitive hosts of the second species (S_2), we can rewrite this matrix slightly and then apply the next generation matrix theorem to determine the stability condition for the generalist-free system.

```
F = {{0, 0, 0, Ns β}, {c S1, 0, 0, 0}, {c S2, 0, 0, 0}, {0, a λ1, a λ2, 0}};
V = {{c (K1 + K2), 0, 0, 0}, {0, μ1, 0, 0}, {0, 0, μ2, 0}, {0, 0, 0, β (KN + K1 + K2) + γ}};
MatrixForm[F - V]
Eigenvalues[Dot[F, Inverse[V]]]
```

$$\begin{pmatrix} -c\,(K1+K2) & 0 & 0 & Ns\,\beta \\ c\,S1 & -\mu 1 & 0 & 0 \\ c\,S2 & 0 & -\mu 2 & 0 \\ 0 & a\,\lambda 1 & a\,\lambda 2 & -(K1+K2+KN)\,\beta-\gamma \end{pmatrix}$$

$$\Big\{0,\ \left(a^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda 2\,\mu 1+S1\,\lambda 1\,\mu 2)^{1/3}\right)\Big/\left((K1+K2)^{1/3}\,(K1\,\beta+K2\,\beta+KN\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}\,\mu 2^{1/3}\right),$$
$$-\left(\left((-1)^{1/3}\,a^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda 2\,\mu 1+S1\,\lambda 1\,\mu 2)^{1/3}\right)\Big/\left((K1+K2)^{1/3}\,(K1\,\beta+K2\,\beta+KN\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}\,\mu 2^{1/3}\right)\right),$$
$$\left((-1)^{2/3}\,a^{1/3}\,Ns^{1/3}\,\beta^{1/3}\,(S2\,\lambda 2\,\mu 1+S1\,\lambda 1\,\mu 2)^{1/3}\right)\Big/\left((K1+K2)^{1/3}\,(K1\,\beta+K2\,\beta+KN\,\beta+\gamma)^{1/3}\,\mu 1^{1/3}\,\mu 2^{1/3}\right)\Big\}$$

Note that $(-1)^{1/3} = -0.5 + 0.866025\,i$ and $(-1)^{2/3} = -0.5 + 0.866025\,i$, so whether the parasite-free equilibrium is stable or not depends entirely on the second eigenvalue. The condition for the generalist-absent equilibrium to be unstable is that this eigenvalue is greater than 1; this condition can be rewritten in a more biologically meaningful way:

$$\frac{\beta N_s}{\beta(K_N+K_1+K_2)+\gamma}\left(\frac{S_1}{K_1+K_2}\,\frac{a\lambda_1}{\mu_1}+\frac{S_2}{K_1+K_2}\,\frac{a\lambda_2}{\mu_2}\right)>1$$

where

$\frac{\beta N_s}{\beta(K_N+K_1+K_2)+\gamma}$ is the probability that a parasite in the environment is ingested by a susceptible intermediate host;

$\frac{S_1}{K_1+K_2}$ and $\frac{S_1}{K_1+K_2}$ are the probabilities that an infected intermediate host is ingested by a susceptible individual of the first and second susceptible definitive host, respectively;

$\frac{a\lambda_1}{\mu_1}$ and $\frac{a\lambda_2}{\mu_2}$ are the expected number of parasites shed from infected definitive hosts of the first and second species, respectively.

We define this expression as R_0, the invasion fitness of the generalist.

```
R0 = β Ns / (β (KN + K1 + K2) + γ) (S1 / (K1 + K2) a λ1 / μ1 + S2 / (K1 + K2) a λ2 / μ2);
```

If you plug in the equilibrium values of N_S, S_1 and S_2, however, you get an incredibly simple expression for the invasion fitness:

```
Simplify[R0 /. {Ns → NsEq, S1 → S1Eq, S2 → S2Eq}]
```

```
2 a
```

What this indicates is that as long as the fraction that shedding is reduced for the generalist (the cost of generalism) is less than 0.5, the generalist will be able to invade.