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.

```
In[8]:= dS1dt = r1 (S1 + I1r + I1m) (1 - (S1 + I1r + I1m)/K1) - β S1 (Pr + Pm);
        dS2dt = r2 (S2 + I2m) (1 - (S2 + I2m)/K2) - β S2 (Pr + Pm);
        dI1rdt = β S1 Pr - μ1 I1r;
        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;
```

The models differ in a number of ways that could affect the conclusions about the evolution of general-ism. 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); and (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).

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 $S_1 = \frac{\gamma \mu_1}{\beta(\lambda_1 - \mu_1)}$.

```
In[15]:= Eq = Solve[({dS1dt == 0, dI1rdt == 0, dPrdt == 0} /. {I1m → 0, Pm → 0}), {S1, I1r, Pr}];
         Eq[[4, 1]]
```

$$Out[16]= \quad S1 \to -\frac{\gamma \mu_1}{\beta(-\lambda_1 + \mu_1)}$$

When can a generalist parasite invade a system with a single specialist parasite, when parasites affect host population dynamics and only come in contact with susceptible hosts?

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 equilib-rium 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.

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_{1r} be the number of primary hosts infected by the resident parasite. The "mutant" parasite is a generalist, and we let I_{1m} and I_{2m} 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.

```
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 resident equilibrium *)
```

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 environ-ment. 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.

$$\left\{ -r1, \frac{1}{2}\left(-K1\,\beta - \gamma - \mu1 - \sqrt{(K1\,\beta + \gamma + \mu1)^2 - 4(-K1\,\beta\,\lambda1 + K1\,\beta\,\mu1 + \gamma\,\mu1)} \right), \right.$$
$$\left. \frac{1}{2}\left(-K1\,\beta - \gamma - \mu1 + \sqrt{(K1\,\beta + \gamma + \mu1)^2 - 4(-K1\,\beta\,\lambda1 + K1\,\beta\,\mu1 + \gamma\,\mu1)} \right) \right\}$$

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 $I_{1m} = 0$, $I_{2m} = 0$, 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 eigenval-ues 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 to be concerned about the eigenvalues of J_m, which is the submatrix dealing with the equations for the generalist parasite.

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:

In[8]:= `dS1dt = r1 (S1 + I1r + I1m)` $\left(1 - \dfrac{(S1 + I1r + I1m)}{K1}\right)$ `- β S1 (Pr + Pm);`

`dS2dt = r2 (S2 + I2m)` $\left(1 - \dfrac{(S2 + I2m)}{K2}\right)$ `- β S2 (Pr + 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 $S_1 = \frac{\gamma \mu_1}{\beta(\lambda_1 - \mu_1)}$.

In[15]:= `Eq = Solve[({dS1dt == 0, dI1rdt == 0, dPrdt == 0} /. {I1m → 0, Pm → 0}), {S1, I1r, Pr}];`
`Eq[[4, 1]]`

Out[16]= $S1 \to -\dfrac{\gamma \, \mu1}{\beta \, (-\lambda1 + \mu1)}$

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}]`

$\left\{-r1, \dfrac{1}{2}\left(-K1\,\beta - \gamma - \mu1 - \sqrt{(K1\,\beta + \gamma + \mu1)^2 - 4\,(-K1\,\beta\,\lambda1 + K1\,\beta\,\mu1 + \gamma\,\mu1)}\,\right),\right.$

$\left.\dfrac{1}{2}\left(-K1\,\beta - \gamma - \mu1 + \sqrt{(K1\,\beta + \gamma + \mu1)^2 - 4\,(-K1\,\beta\,\lambda1 + K1\,\beta\,\mu1 + \gamma\,\mu1)}\,\right)\right\}$

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.

In[24]:=
```
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};
```

In[51]:=
```
D[R0, a] // Simplify
D[R0, K2]
Simplify[D[R0, μ1]]
FullSimplify[D[R0, μ2]]
D[R0, γ]
```

Out[51]= $\dfrac{\lambda 1}{\lambda 1 - \mu 1}$

Out[52]= $\dfrac{K2\,\beta\,\lambda 2}{\gamma\,\mu 2^2}$

Out[53]= $\dfrac{\beta\,(a\,\lambda 2 - \mu 2)}{\gamma^2\,\mu 2}$

```
MatrixForm[
  J]
```

Out[25]//MatrixForm=

Out[54]= $\dfrac{\gamma\,\mu 1}{(-1 + a)\,\lambda 1}$

Out[55]= $\dfrac{(\gamma 1 - \mu 1)^2}{K2\,\beta\,\lambda 2}$

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

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

$$K = K_0\,e^{E/kT}\,W^{-0.75}$$

$$\mu = \mu_0\,e^{-E/kT}\,W^{-0.25}$$

for carrying capacity and mortality rate.

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

In[36]:= `F = {{0, 0, S1 β}, {0, 0, S2 β}, {a λ1, a λ2, 0}};`

Mechinger 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

$$\lambda = \lambda_0\,e^{-E/kT}\,W \text{ (for endoparasites)}$$

```
V[[5, 7]] = Pr β // Simplify
Eigenvalues[Dot[F, Inverse[V]]]
```

Out[38]= True

$$\lambda = \lambda_0\,e^{-E/kT}\,W^{5/12} \text{ (for ectoparasites)}.$$

The difference in scaling for endoparasites and ectoparasites is because these two parasites utilize

Out[39]= $\left\{-\dfrac{\sqrt{a}\,\sqrt{\beta}\,\sqrt{S2\,\lambda 2\,\mu 1 + S1\,\lambda 1\,\mu 2}}{\sqrt{S1\,\beta + S2\,\beta + \gamma}\,\sqrt{\mu 1}\,\sqrt{\mu 2}},\ \dfrac{\sqrt{a}\,\sqrt{\beta}\,\sqrt{S2\,\lambda 2\,\mu 1 + S1\,\lambda 1\,\mu 2}}{\sqrt{S1\,\beta + S2\,\beta + \gamma}\,\sqrt{\mu 1}\,\sqrt{\mu 2}}\right\}$

hosts differently: for endoparasites, abundance depends on host volume, whereas for ectoparasites, abundance depends on host surface area.

If the largest of these eigenvalues is larger than 1, then the generalist-absent equilibrium is unstable. We assume that the only difference between the two hosts is in terms of body size. We let W be the This is equivalent to requiring that $\frac{\beta(a\lambda 1 - \mu 1)}{\gamma\mu 1}S_1 + \frac{\beta(a\lambda 1 - \mu 2)}{\gamma\mu 2}S_2 > 1$, where S_1 and S_2 are the equilibrium mass of the primary host, and $r\,W$ be the mass of the secondary host; without loss of generality, we abundances of susceptible primary and secondary hosts when the generalist is absent. We can plug assume that $r \le 1$. 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 life: Notice that the derivatives of these expressions can be rewritten in terms of the expressions themselves. $R_0 > 1$, the generalist will spread through the host population.

In[41]:= `R0 = ( (β (a λ1 - μ1))/(γ μ1) S1 + (β (a λ2 - μ2))/(γ μ2) S2 ) /. {S1 → - (γ μ1)/(β (-λ1 + μ1)), S2 → K2}`

Out[41]= $-\dfrac{a\,\lambda 1 - \mu 1}{-\lambda 1 + \mu 1} + \dfrac{K2\,\beta\,(a\,\lambda 2 - \mu 2)}{\gamma\,\mu 2}$

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.

In[51]:=
```
D[R0, a] // Simplify
D[R0, K2]
Simplify[D[R0, μ1]]
FullSimplify[D[R0, μ2]]
D[R0, γ]
```

Out[51]= $\dfrac{\lambda 1}{\lambda 1 - \mu 1} + \dfrac{K2\,\beta\,\lambda 2}{\gamma\,\mu 2}$

Out[52]= $\dfrac{\beta\,(a\,\lambda 2 - \mu 2)}{\gamma\,\mu 2}$

Out[53]= $\dfrac{(-1 + a)\,\lambda 1}{(\lambda 1 - \mu 1)^2}$

Out[54]= $-\dfrac{a\,K2\,\beta\,\lambda 2}{\gamma\,\mu 2^2}$

Out[55]= $-\dfrac{K2\,\beta\,(a\,\lambda 2 - \mu 2)}{\gamma^2\,\mu 2}$

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
$K = K_0\,e^{E/kT}\,W^{-0.75}$
$\mu = \mu_0\,e^{-E/kT}\,W^{-0.25}$
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
$\lambda = \lambda_0\,e^{-E/kT}\,W^{0.75}$ (for endoparasites)
$\lambda = \lambda_0\,e^{-E/kT}\,W^{5/12}$ (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:

In[197]:=
In[71]:=
```
K3 [R0 / Exp[E / (k T)], (f W)^-3/4 [W], λ2 → λ2[W], μ2 → μ2[W], K2 → K2[W]}, W] /.
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] // Simplify
```

Out[71]= True

```
D[λ1, W] == (3 λ1)/(4 W) // Simplify

D[K2, W] == (3 K2)/(4 W) // Simplify
```

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.

In[124]:=
```
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],
(* Derivatives with respect to temperature *)
```

Out[124]=
$$\frac{\beta E K_2[T] (a \lambda_2[T] + \mu_2[T])}{k T^2 \gamma \mu_2[T]}$$

```
D[λ1, T] == E/(k T^2) λ1 // Simplify
```

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.

Out[192]= True

Ectoparasites

Out[193]= True

For endoparasites, we find that increasing host body size has a more complicated effect.

Out[194]= True

$\frac{dR_0}{dW} = \frac{2(1-a) \lambda_1 \mu_1}{3 W(\lambda_1 - \mu_1)} - \frac{\beta K_2(a \lambda_2 - 9 \mu_2)}{12 W \gamma \mu_2}$; the sign of this expression depends on the sign of $a \lambda_2 - 9 \mu_2$.

Out[195]= True

In[139]:=
Out[196]= True

```
(D[R0 /. {λ1 → λ1[W], μ1 → μ1[W], λ2 → λ2[W], μ2 → μ2[W], K2 → K2[W]}, W] /.
```

Out[197]= True
```
{μ1'[W] → -μ1[W]/(4 W), μ2'[W] → -μ2[W]/(4 W), K2'[W] → -3 K2[W]/(4 W),
```

Out[198]= True
```
λ1'[W] -> 5 λ1[W]/(12 W), λ2'[W] -> 5 λ2[W]/(12 W)}) ==
```

Out[199]= True
```
(2 (1-a) λ1[W] μ1[W])/(3 W (λ1[W] - μ1[W])) - (β K2[W] (a λ2[W] - 9 μ2[W]))/(12 W γ μ2[W]) // Simplify
```

We can then study how R_0 is affected by changes in host body size or temperature for endoparasites

Out[139]= True

and ectoparasites by differentiating R_0 with respect to host body size W and temperature T.

Endoparasites

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.

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

However, as host body size gets larger, $\frac{dR_0}{dW} < 0$.

```
In[148]:= Solve[(a λ2[W] λ1 w2[W]1 4 μ1[W], λ2 → λ2[W], μ2 → μ2[W], K2 → K2[W]}, 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]
{μ1'[W] → , μ2'[W] → , K2'[W] → ,
```

$$Out[148]= \left\{\left\{W \to -\frac{27 \mu0^{3/2}}{\lambda1^{3/2}}, ...\right\}\right\}$$

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

$$\frac{}{W (\lambda1[W] - \mu1[W])^2} + \frac{}{4 W \gamma \mu2[W]} \; //\; \text{Simplify}$$

Out[71]= 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.

```
In[124]:= 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
```

$$Out[124]= \frac{\beta \, E \, K2[T] \, (-a \, \lambda2[T] + \mu2[T])}{k \, T^2 \, \gamma \, \mu2[T]}$$

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 $a \lambda_2 - 9 \mu_2$.

```
In[139]:= (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
```

Out[139]= 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 $\frac{dR_0}{dW} < 0$.

In[148]:= `Solve[` $\left(\text{a } \lambda 2[W] - 9 \mu 2[W] \text{ /.}\right.$
$\left.\{\mu 2[W] \rightarrow \mu 0 \text{ Exp}[-E \text{ / } (k \text{ T})] \text{ } (f \text{ W})^{-1/4}, \lambda 2[W] \rightarrow \lambda 0 \text{ Exp}[-E \text{ / } (k \text{ T})] \text{ } (f \text{ W})^{5/12}\}\right) == 0, W]$

Out[148]= $\left\{\left\{W \rightarrow -\dfrac{27 \mu 0^{3/2}}{a^{3/2} f \lambda 0^{3/2}}\right\}, \left\{W \rightarrow \dfrac{27 \mu 0^{3/2}}{a^{3/2} f \lambda 0^{3/2}}\right\}\right\}$

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

When can a generalist parasite invade a system with two specialist parasites, when parasites affect host population dynamics and only come in contact with susceptible 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_{1r} and I_{2r} be the number of primary and secondary hosts infected by the resident parasites. The "mutant" parasite is a generalist, and we let I_{1m} and I_{2m} 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.

In[201]:= `dS1dt = r1 (S1 + I1r + I1m)` $\left(1 - \dfrac{(\text{S1} + \text{I1r} + \text{I1m})}{\text{K1}}\right)$ `- β1 S1 (P1r + P12m);`

`dI1rdt = β1 S1 P1r - μ1 I1r;`
`dP1rdt = λ1 I1r - β1 S1 P1r - γ1 P1r;`

`dS2dt = r2 (S2 + I2r + I2m)` $\left(1 - \dfrac{(\text{S2} + \text{I2r} + \text{I2m})}{\text{K2}}\right)$ `- 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_{1r}, and P_1 do not depend on S_2, I_{2r}, 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 $S_1 = \dfrac{\gamma_1 \mu_1}{\beta_1 (\lambda_1 - \mu_1)}$ and $S_2 = \dfrac{\gamma_2 \mu_2}{\beta_2 (\lambda_2 - \mu_2)}$.

In[213]:= `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]]`

Out[214]= $\left\{\text{S1} \rightarrow -\dfrac{\gamma 1 \mu 1}{\beta 1 (-\lambda 1 + \mu 1)}, \text{S2} \rightarrow -\dfrac{\gamma 2 \mu 2}{\beta 2 (-\lambda 2 + \mu 2)}\right\}$

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 $I_{1m} = 0$, $I_{2m} = 0$, 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]}};
```

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

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]]]
```

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

```
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, 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: