This model assumes environmental transmission, but where the parasite actively seeks out hosts. Contact is thus controlled by the parasite (so quantifies both the contact and infection processes), and contact is assumed to remove parasites from the environment. There are two hosts. I assume that the resident parasite strain exploits a single host and ask whether a mutant that exploits both hosts can invade. I assume that the cost of this generalism is that the shedding rate from both hosts is reduced by a factor *a*.

I am going to explore the consequence of varying the carrying capacity and host mortality rate on the evolution of generalism. As such, I will let and be the carrying capacities of the first and second host, respectively; similarly, will be the mortality rates for each host and and will be the shedding rates from each host. For simplicity, I will assume that all other parameters (traits) are equal between the hosts and parasites.

The full system is then

For the invasion analysis, we assume that the resident parasite comes to its ecological equilibrium with the hosts. Since it does not parasitize the second host, will go to its carrying capacity. The endemic equilibrium host densities are

Evaluating the stability of this equilibrium is a pain, but for it to have any hope of being stable (which invasion analysis usually assumes the equilibrium is), the extinction equilibrium must be unstable. This equilibrium is unstable if

This defines for this parasite (note that is the fraction of the host population that remains susceptible at equilibrium). An equivalent representation of this condition is

where is the probability that a spore in the environment infects a host and is the expected number of spores produced per infected host.

To determine whether a mutant parasite can invade the system, we are essentially asking whether the mutant parasite-free equilibrium of the full system is unstable. To evaluate at this, we can take advantage of the fact that the Jacobian matrix at this equilibrium is upper block-triangular (that is, it can be written as)

The eigenvalues of this matrix (which determine the stability of the equilibrium) are given by the eigenvalues of the matrices and . The eigenvalues of determine the stability of the resident-only system – by assumption, the resident-only system is stable. Thus, we only need to look at the eigenvalues of :

Applying the next-generation matrix theorem, we can determine that will have a positive eigenvalue (and thus, the mutant-free equilibrium will be unstable) if

From this, it is clear that if the invading parasite is capable of persisting on the second host alone, it will be able to displace the resident (because is the condition for instability of the parasite extinction equilibrium in the system). As before, an equivalent representation of this condition is

where is the probability that a spore in the environment infects host 1 and is the expected number of spores produced per infected host 1; the second set of terms have an analogous interpretation for host 2. Thus the invasion criterion is simply that, between the two hosts, each spore in the environment is expected to produce more than one new spore in the environment.

If we plug in the resident parasite endemic equilibrium into Eq. 1 (which is a bit simpler and easier to work with), it can be rewritten as

Note that the term on the left must be less than one, since by definition as the cost of generalism. Thus, we require that for invasion to have anychance of succeeding.

At this point, we can plug in values for the different parameters and investigate under what combinations of cost and host traits a generalist can invade. But we can also get a bit more insight by considering how changing the values of host and parasite traits affect the magnitude of the invasion fitness (the expression on the left side of the invasion criterion). That is, we can look at the derivatives of the invasion fitness with respect to host and parasite traits. For example, the derivative of the invasion fitness (let’s call it *r* for simplicity) with respect to *a* is just

which is always positive ( > 1). What this means is that, as the cost of generalism goes down (*a* increases), the invasion fitness increases, meaning that invasion is more likely. This result is, of course, intuitive.

If you increase the carrying capacity of the second host, you also get a very simple effect:

Since we require , this is always positive, implying that generalism is more likely when the alternative host is very abundant. A further implication that you can draw from this is that an abundant host is very unlikely to be unexploited, which is intuitive.

If you increase the mortality rate of infected individuals of the first host, on the other hand, you make it harder for a generalist to invade (this term is always negative because the first term ).

Similarly, if you increase the mortality rate of infected individuals of the second host, it is harder for a generalist to invade.

If you increase the mortality rate of parasites in the environment (), you make it harder for a generalist to invade. In other words, specialism is more likely in harsher environments.

|  |  |
| --- | --- |
| Parameter | Effect of increasing the parameter value on invasion fitness |
| Cost of generalism *a* | Increases |
| Parasite shedding | Increases |
| Second host carrying capacity | Increases |
| Host mortality rates | Decreases |
| Parasite environmental mortality rate | Decreases |

None of these results are surprising, which is itself not surprising – invasion analyses are typically only surprising when there are trade-offs between parameters of the model. For this system, there actually are some potential trade-offs between parameters that are not being considered at the moment.

**Allometric and temperature scaling of host and parasite traits**

In particular, metabolic scaling theory predicts that host body size and temperature will simultaneously affect both host carrying capacity and host mortality rate. Savage et al. (2004) predict the following scaling relationships:

where is the Boltzmann factor, which describes how temperature affects reaction kinetics (e.g., metabolic rate), *W* is body mass*,* and are proportionality constants. *E* is the average activation energy of rate-limiting biochemical metabolic reactions and *k* is Boltzmann’s constant. It is worth noting at this point that increasing mass will decrease the carrying capacity and mortality rate, whereas increasing temperature decreases carrying capacity and increases mortality rate.

Shedding rate also scales with host body size. This is because larger hosts support larger abundances of parasites. Metabolic scaling theory (Poulin & George-Nascimento 2007, Hechinger 2013) predicts that parasite abundance should scale with host body mass to the 3/4 power for endoparasites and with host body mass to the 5/12 power for ectoparasites. (However, in an empirical dataset, Poulin & George-Nascimento calculated that, across 34 species of fish hosts, parasite abundance scaled linearly with host body mass.) Thus, assuming that shedding rate is a linear function of parasite abundance, then

If we plug these allometric functions into our expressions for invasion fitness (e.g., Eq. 1), we can again use the derivatives of the invasion fitness equation with respect to host mass and temperature to see how those affect the likelihood of invasion. For notational simplicity, we will let , where *f* is a scalar and *W* is the mass of the primary host.

To determine how mass affects invasion,

This implies that increasing the masses of the hosts will always make invasion easier. In other words, **it is easier for generalists to invade if the available hosts are large-bodied.** A corollary of this prediction is that **large-bodied hosts are more likely to be infected by generalist than specialist parasites.**

where is the probability that a spore infects host *i* (which depends on the masses of both hosts) and is the expected spore production from each infected host of type *i.*

Notice that for an endoparasite,

whereas for an ectoparasite,

From this we can immediately see that **a generalist endoparasite is more likely to be able to invade than a generalist ectoparasite** because they can attain a higher abundance and thus shed more.

We can again use the derivatives of the invasion fitness equation with respect to host mass and temperature to see how those affect the likelihood of invasion. For notational simplicity, we will let , where *f* is a scalar and *W* is the mass of the primary host.

and

From here, you can also write

However, since ,

and

As discussed previously, , which implies that both and . So, if , then ; however, if

From this, it is clear that either or vice versa, meaning that at least

meaning that the signs of and are indeterminate.

and since , as discussed before, as well. Thus, increasing the size of the host decreases the abundance of susceptible hosts at equilibrium.

On the other hand, because , as mentioned above. So the effect of increasing mass of the host on the probability of contact with host

The derivative of invasion fitness with respect to host mass has a complicated expression, but every term of the expression is positive with the possible exception of . If that term is negative, it is possible for increasing the size of the hosts to decrease the likelihood of invasion by a generalist. If, however, this term is positive, then increasing the size of the hosts is guaranteed to increase the likelihood of invasion.

Similarly, the sign of the derivative of invasion fitness with respect to the scalar *f* depends on the value of . If this term is negative, then increasing the value of *f* decreases the likelihood of invasion; otherwise it increases it.

These two results suggest two predictions about the influence of host body size on the evolution of generalism: specialism is more likely when the parasite exploits a very large bodied host (large and generalism is more likely when the parasite exploits hosts of very different sizes (small *f*).

We can also look at the effects of temperature on the likelihood of invasion, which also has a complex dependence. There are more potentially negative terms here, so my sense is that increasing temperature is likely to cause the derivative to be negative, implying that specialism is more likely in warm temperatures, and generalism is more likely in cool temperatures.

If we want to be more quantitative, Allen e t al. 2002 report the following empirical relationship (Fig. 2) between temperature *T* (in Kelvin), population density *N*, and mass *W*:

Savage et al. (2004) also presents data on the relationship between temperature, mass, and instantaneous mortality rate for 175 fishes. They report the following relationship (Fig. 3b):

and report the value of *E* for fish to be , with

We can rearrange to find size- and temperature-dependent expressions for carrying capacity and mortality rate:

Some other notes:

For the resident parasite to be able to persist, the

Defining and , then the derivative of the persistence condition is equal to . But

and

Since and , this means that the two terms move the derivative are changing in opposite directions. In particular, it can be shown that if , then increasing *W* will decrease , thereby making it harder for the parasite to persist as the primary host gets larger. Biologically, what this implies is that the probability of contacting a host ( decreases faster than the spore production per infected host () increases. This makes evaluating the influence of host body mass on the evolution of generalism complicated because increasing body mass makes it harder for the specialist to persist. This is one of the reasons why it makes sense to also consider the host mass-dependence of shedding rate as well.