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. 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).

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). An equivalent representation of this condition is

It is possible break down the terms of this expression a bit more carefully:

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, this condition 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.

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. Plugging these expressions into the invasion fitness and simplifying, the temperature- and body size-dependent invasion fitness is

We can do a similar analysis, this time asking how changing the masses of the two hosts and the temperature affect the invasion fitness. In particular, let , where *f* is a scalar and *W* is the mass of the first 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: