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 *K* be the carrying capacity of the first host and *kK* be the carrying capacity of the second host; similarly, will be the mortality rates for hosts 1 and 2, respectively. 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

is the number of new mutant parasite infections generated per infected host 1, when the mutant parasite is invading a fully susceptible host population (and only infecting this host); similarly, is the number of new mutant parasite infections generated per infected host 2.

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 *any* chance 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 (parameters) 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. 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 host carrying capacity, you also get a very simple effect (because host carrying capacity only shows up in one place in the invasion fitness):

Since we require , this is always positive, implying that generalism is more likely when hosts are very abundant.

If you increase the mortality rate of infected hosts, on the other hand, you make it 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 |
| Host carrying capacity *K* | Increases |
| Host background mortality rate | Decreases |
| Parasite 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 trade-offs that are not being considered at the moment. In particular, metabolic scaling theory predicts that host body size and temperature will both simultaneously affect both host carrying capacity and host mortality rate. Savage et al. 2004 suggests that carrying capacity should scale as

where *E* is the “average activation energy of rate-limiting biochemical metabolic reactions”, *k* is Boltzmann’s constant, *T* is the temperature (in Kelvin)*,* and *W* is mass. He reports that, for fish, eV and Boltzmann’s constant is Savage et al. (2004) presents data on the relationship between temperature *T*, mass *W*, and instantaneous mortality rate for 175 fishes. They report the following relationship (Fig. 3b):

This simplifies to the following expression for mortality rate: