

The purpose of this document is to outline some models that could potentially be used to study the factors that push parasites towards generalism or specialism. I will propose two approaches to this problem, an evolutionary approach based on game theory and an ecological approach based on optimal foraging theory. I will discuss the evolutionary approach first, as it was the one I originally suggested in Wales.

1. EVOLUTION OF PARASITE PREFERENCE

The approach that I suggest is fairly simple: for any set of ecological conditions (where “ecological conditions” is used loosely to refer to any change in model parameters that might shift the relative costs and benefits of generalism/specialism), what is the evolutionarily stable transmission strategy?

Consider an environmentally transmitted parasite that can potentially transmit to two hosts. For simplicity of formulation, I will assume that infections, once acquired, are lifelong. The two host populations are subdivided into susceptible (S_1, S_2) and infected (I_1, I_2) classes. The parasite (P) is transmitted through the environment by parasites shed from infected hosts of each species. A simple model for the dynamics is:

$$\begin{aligned}\frac{dS_1}{dt} &= r_1 N_1 \left(\frac{1 - N_1}{K_1} \right) - \beta_1 S_1 P \\ \frac{dS_2}{dt} &= r_2 N_2 \left(\frac{1 - N_2}{K_2} \right) - \beta_2 S_2 P \\ \frac{dI_1}{dt} &= \beta_1 S_1 P - (\mu_1 + \nu_1) I_1 \\ \frac{dI_2}{dt} &= \beta_2 S_2 P - (\mu_2 + \nu_2) I_2 \\ \frac{dP}{dt} &= \lambda_1 I_1 + \lambda_2 I_2 - \delta P,\end{aligned}$$

where $N_i = S_i + I_i$. In the absence of infection, both host populations grow logistically at per-capita rates r_1 and r_2 to the carrying capacities K_1 and K_2 , respectively. Both susceptible and infected individuals are assumed to have equal birth rates, and all individuals are born susceptible. The infection rates per parasite in the environment are β_1 and β_2 ; note that we assume that all parasites in the environment are equivalent (that is, it doesn't matter whether the parasite was shed from host 1 or host 2). I also assume that β_1 and β_2 are determined by the host, not the parasite - the parasite is passive in the environment. In some circumstances, it might make more sense to assume that parasites shed from host 1 have a higher transmission rate in host 1 (if, for example, the two hosts have slightly different environmental preferences; ?). Infected hosts suffer mortality due to natural causes at the rates μ_1 and μ_2 and due to infection at the rates ν_1 and ν_2 . Infected hosts shed parasites into the environment at the rates λ_1 and λ_2 , and these are lost at the rate δ .

The R_0 for a parasite invading a fully susceptible host community will be (??):

$$R_0 = \sqrt{\frac{\lambda_1 \beta_1 K_1}{\gamma(\mu_1 + \nu_1)} + \frac{\lambda_2 \beta_2 K_2}{\gamma(\mu_2 + \nu_2)}}. \quad (1)$$

If $R_0 > 1$, the parasite can invade. Note that this expression is equivalent to $\sqrt{R_{0,1} + R_{0,2}}$, where $R_{0,i}$ is the R_0 of a parasite due to transmission only in host i . The implication here is that the parasite could have an R_0 less than 1 in each individual host, so long as the sum is greater than 1. Moreover,

this simple model can be extended to consider many host species; in general, the fitness of a parasite infection n host species will be

$$\sqrt{\sum_{i=1}^n R_{0,i}}. \quad (2)$$

We can define the ratio $R_{0,i}/R_0$ to evaluate how important each individual host is to the overall fitness of the parasite. Without any loss of generality, we can assume that the potential hosts are ordered by their $R_{0,i}$ values (i.e., $R_{0,1} > R_{0,2} > \dots > R_{0,n}$): the parasite has the highest single-host R_0 in the first host, and the lowest in the n^{th} host. These differences in $R_{0,i}$ can be set by a single parameter (e.g., holding all parameters constant across hosts except K_i would produce this pattern) or by covarying multiple parameters. The choice of how to vary the single-host R_0 could potentially be motivated by how we choose to implement any evolutionary trade-offs.

A similar analysis can be used to determine whether a mutant parasite that parasitizes a different number of hosts can invade. To make this concrete, consider that there is a community of three hosts; the resident parasite infects two of these hosts. A mutant parasite that infects all three hosts can invade if

$$\sqrt{\frac{\lambda_1\beta_1\hat{S}_1}{\gamma(\mu_1+\nu_1)} + \frac{\lambda_2\beta_2\hat{S}_2}{\gamma(\mu_2+\nu_2)} + \frac{\lambda_3\beta_3K_3}{\gamma(\mu_3+\nu_3)}} > 1, \quad (3)$$

where \hat{S}_1 and \hat{S}_2 are the equilibrium abundances of susceptible hosts, set by the resident parasite.

The key to making this analysis interesting are the potential trade-offs between traits that might affect the number of hosts utilized by the parasite. In particular, let's define η to be the number of hosts the parasite utilizes. Effects of η on other parameters of the model that might be interesting to consider are:

- a trade-off between η and λ_i : the more hosts the parasite infects, the less its shedding rate in each host;
- a trade-off between η and ν_i : the more hosts the parasite infects, the greater its virulence in each host;
- a trade-off between η and γ : the more hosts a parasite infects, the less hardy each parasite is in the environment;
- a trade-off between η and β_i : the more hosts a parasite infects, the less transmissible each parasite is.

Any of these trade-offs might be interesting to explore, as each seems biologically reasonable: the first essentially posits that transmitting to many hosts compromises within-host replication ability; the third and fourth essentially posit that transmitting to many hosts compromises the quality or viability of parasites in the environment; the second is probably the most tenuous, positing that transmitting to many hosts makes the parasite more harmful to each one. More complicated relationships could also be considered: for example, if increasing the number of infected hosts decreases within-host replication, then increasing η might simultaneously decrease λ_i and ν_i (a classic transmission–virulence trade-off controlled by the parasite's generality).

This evolutionary model can help us make predictions about how ecological conditions might affect the evolution of generality. For example, the invasion criterion (Eq. 3) can be rearranged to yield

$$\sqrt{\frac{\lambda_1\beta_1\hat{S}_1}{\mu_1+\nu_1} + \frac{\lambda_2\beta_2\hat{S}_2}{\mu_2+\nu_2} + \frac{\lambda_3\beta_3K_3}{\mu_3+\nu_3}} > \sqrt{\gamma}. \quad (4)$$

Thus, the higher the mortality rate in the environment, the harder it will be for a mutant parasite that infects more hosts to invade. This suggests that parasites living in high-mortality environments might be more likely to be specialists.

2. ECOLOGY OF PARASITE PREFERENCE

The ecological approach is slightly different, in that it takes many things as given and has less concern about dynamics. In particular, this approach is based on classic optimal foraging theory (?). Classic optimal foraging theory deals with prey selection by a predator. It assumes that there are many different prey items that could potentially be included in the diet, $i = 1, \dots, n$. Each prey item has a profitability to the predator of E_i (which can be thought of as the energy content of the prey). The search time (or, inversely, the encounter rate) for prey type i is s_i . The handling time for prey type i is h_i . The prey types are ordered in decreasing profitability, so $E_1/h_1 > E_2/h_2 > E_3/h_3 > \dots$. Assume that the predator currently predaes on prey types 1 thru n - should it include the $(n + 1)^{\text{th}}$ prey item? Optimal foraging theory says that this prey item will be included if

$$\frac{E_{n+1}}{h_{n+1}} > \frac{\bar{E}}{\bar{h} + \bar{s}}. \quad (5)$$

The intuition behind this equation is as follows: imagine that the predator has encountered an individual of type $n + 1$: should it eat it or keep searching for other prey items? It should eat it only if the rate it gains energy from that prey item (the profitability divided by the time to handle it) is greater than the average rate it gains energy from searching for and handling all other items in the diet.

It remains to relate these to parameters to the situation of an environmentally transmitted parasite. Although this particular question has not been tackled, other authors have considered applying optimal foraging theory to parasitoids (??) and lytic phages (?). The following is my best first attempt at making this relation. Let's consider the processes we want to include in the model. To start as simply as possible, let's assume that the profitability is the shedding rate times the duration of infection, the search time depends on the transmission (encounter) rate and the abundance of the host (which we will assume is constant), and the handling time depends on the development rate of the parasite (assuming that eggs are ingested from the environment and must develop from larvae into adults before shedding begins). Let λ_i be the shedding rate from host i ; let μ_i be the mortality rate of host i ; let β_i be the encounter rate with host i ; let H_i be the abundance of host i ; and let γ_i be the development rate of the parasite. Then

$$E_i = \frac{\lambda_i}{\mu_i} \frac{\gamma_i}{\gamma_i + \mu_i}, \quad (6)$$

$$s_i = \frac{1}{\beta_i H_i}, \quad (7)$$

$$h_i = \frac{1}{\gamma_i}. \quad (8)$$

Note that the profitability is scaled by the probability that the parasite matures before the host dies ($\gamma_i/(\gamma_i + \mu_i)$).

Under this very simple model, the $(n + 1)^{\text{th}}$ host will be included if (refer to 5):

$$\frac{\lambda_{n+1} \gamma_{n+1}^2}{\mu_{n+1} (\gamma_{n+1} + \mu_{n+1})} > \frac{\sum_{i=1}^n \frac{\lambda_i}{\mu_i} \frac{\gamma_i}{\gamma_i + \mu_i}}{1 / \sum_{i=1}^n \beta_i H_i + 1 / \sum_{i=1}^n \gamma_i}. \quad (9)$$

- (1) The profitability of a host is the parasite shedding rate from that host (λ_i) times the expected duration of an infection. In general, infections can end three ways (from the perspective of the parasite):
- (a) the host could die (at a rate μ_i);
 - (b) the host could recover (at a rate γ_i);
 - (c) the parasite could be displaced by competitively superior parasite. This seems like a worthwhile consideration, since competitive dominance in coinfection seems likely to influence whether a parasite is a generalist or specialist. The rate that a parasite is displaced by a competitive dominant depends on the rate that such parasites are encountered $\beta_i \sum_j P_j$, where β_i is the encounter rate of the host with parasites in the environment and $\sum_j P_j$ is the total abundance of competitively dominant parasites in the environment.

Thus, the profitability of host i is

$$E_i = \frac{\lambda_i}{\mu_i + \gamma_i + \beta_i \sum_j P_j}. \quad (10)$$

- (2) The expected search time for host type i is $(\beta_i H_i)^{-1}$.
- (3) The handling time for host type i depends on the development rate of the parasite. I am assuming we are dealing with a helminth parasite, so eggs are what is encountered and the parasite must hatch and go through its juvenile period before it actually profits from the host. Let α_i be the development rate of the parasite in host i .

This almost specifies the model, but we haven't considered the possibility of mortality during e helminths parasites, where eggs are ingested from the environment and there is a