Coupled within-host and between-host dynamics and evolution of virulence

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1. Introduction

It has been shown that models that couple the disease dynamics at the population level and the cell-pathogen dynamics within hosts can generate new insights into host-pathogen interactions (e.g., \cite{1,7,8,10–12,15}). Gilchrist and Coombs demonstrated in \cite{11} that nested models can be used to derive the functional relationships between disease transmission and virulence at the population level, and these functions are helpful for studying the evolution of virulence. Particularly, based on the assumptions about the dependence of between-host transmission and disease-induced host mortality on the within-host variables (e.g., pathogen load and cell density), they illustrated the possible occurrence of a conflict between natural selection at the individual and population levels.

The examples considered in \cite{11} also provide specific functional forms for describing the trade-off relationships between disease transmission and pathogen virulence. In one of their examples, the disease transmission rate at the population level $\beta$ is assumed to be a power function of the within-host pathogen load $V$, i.e.,

$$\beta(V) = a_1 V^z, \quad z > 0.$$  \hfill (1)

where $a_1$ is a positive constant, while the disease-induced host mortality (virulence) $\alpha$ is assumed to be a function of the average density of target cells $T$ within a host given by

$$\alpha(T) = a_2 \left( \frac{1}{T} - \frac{1}{T_0} \right).$$  \hfill (2)

where $T_0$ is the density of target cells at the infection-free steady state and $a_2$ is a positive constant. Under the assumption that the within-host dynamics occur on a much faster time scale than the between-host dynamics, the variables $V$ in Eq. (1) and $T$ in Eq. (2) can be replaced by their values at the positive steady state, which leads to the following relationship between $\alpha$ and $\beta$:

$$\beta(\alpha) = a_1 \left( \frac{\Lambda \alpha}{a_2 k} \right)^z.$$  \hfill (3)

where $\Lambda$ and $k$ are parameters associated with the within-host system. Because the qualitative behavior of the function in Eq. (3) can be