Infectious Disease in Consumer Populations: Dynamic Consequences of Resource-mediated Transmission and Infectiousness

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Abstract

Non-host species can strongly affect the timing and progression of epidemics. One central interaction - between hosts, their resources, and parasites - remains surprisingly underdeveloped from a theoretical perspective. Furthermore, key epidemiological traits that govern disease spread are known to depend on resource density. We tackle both issues here using models that fuse consumer-resource and epidemiological theory. Motivated by recent studies of a phytoplankton-zooplankton-fungus system, we derive and analyze a family of dynamic models for parasite spread among consumers in which transmission depends on consumer (host) and resource densities. These models yield four key insights. First, host-resource cycling can lower mean host density and inhibit parasite invasion. Second, host-resource cycling can create Allee effects (bistability) if parasites increase mean host density by reducing the amplitude of host-resource cycles. Third, parasites can stabilize host-resource cycles; however, host-resource cycling can also cause disease cycling. Fourth, resource-dependence of epidemiological traits helps to govern the relative dominance of these different behaviors. However, these resource dependencies largely have quantitative rather than qualitative effects on these three-species dynamics. Given the extent of these results, host-resource-parasite interactions should become more fundamental components of the burgeoning theory for the community ecology of infectious diseases.

Introduction

This document is a trimmed down version of Hurtado et al. (2014), which you can find by clicking here.

LaTeXis wonderful at managing citations and figure/equation/table references! For example, we can cite some reference parenthetically (Hurtado et al. 2014), with a comment (e.g., like this; Hurtado et al. 2014), or in the text like Hurtado et al. (2014), or alternatively, like Hurtado et al. 2014. We can also reference Equation 2 like that or like Equation (2), Table B2, Figure 1, section or subsection 1.1, and even Appendix A.

There are a variety of environments for displaying equations. Some are automatically numbered, some not.

For example, note which of these gets a number vs not:

First, using double dollar signs to start and end an equation environment gives:

$$\frac{dx}{dt} = f(x,t)$$

Second, backslash before square brackets:

$$\frac{dx}{dt} = f(x,t)$$

Third, an `equation` environment:

$$\frac{dx}{dt} = f(x,t) \tag{1}$$

Fourth, an `equation*` environment:

$$\frac{dx}{dt} = f(x,t)$$

Noting which of these received labels (on the right) this should make sense: (), (), (1), ().

More about that “*” notation (note that I didn’t use these quotes: ”*”!) in the next section.

This Section Is Not Numbered

But...

1 This One Is

1.1 This Subsection is Labeled

Model 2 below is also labeled, and we can refer to it! We can also label and refer to individual equations 2a-2d. This model tracks changing densities of the resource population n, susceptible consumers (hereafter ‘hosts’), x, infected hosts, y, and infectious contagion (e.g., fungal spores), z, which are dispersed in the environment. For clarity we scaled the variables (see Appendix A) so that all population units are in resource equivalents (except a factor $\sigma(n)$ for spore density, z), and time has been scaled by the inverse of the consumer mortality rate (i.e., the average consumer lifetime in the absence of predation and disease).

$$\begin{aligned}
\frac{dn}{dt} &= rn(1-n) - \alpha(n)(x+y)n && \text{(2a)}\\
\frac{dx}{dt} &= \alpha(n)(x+fy)n - (1+m)x - \beta(n)xz && \text{(2b)}\\
\frac{dy}{dt} &= \beta(n)xz - (1+m\theta+\nu)y && \text{(2c)}\\
\frac{dz}{dt} &= \sigma(n)(1+\nu)y - \mu z. && \text{(2d)}
\end{aligned}$$

Results & Discussion

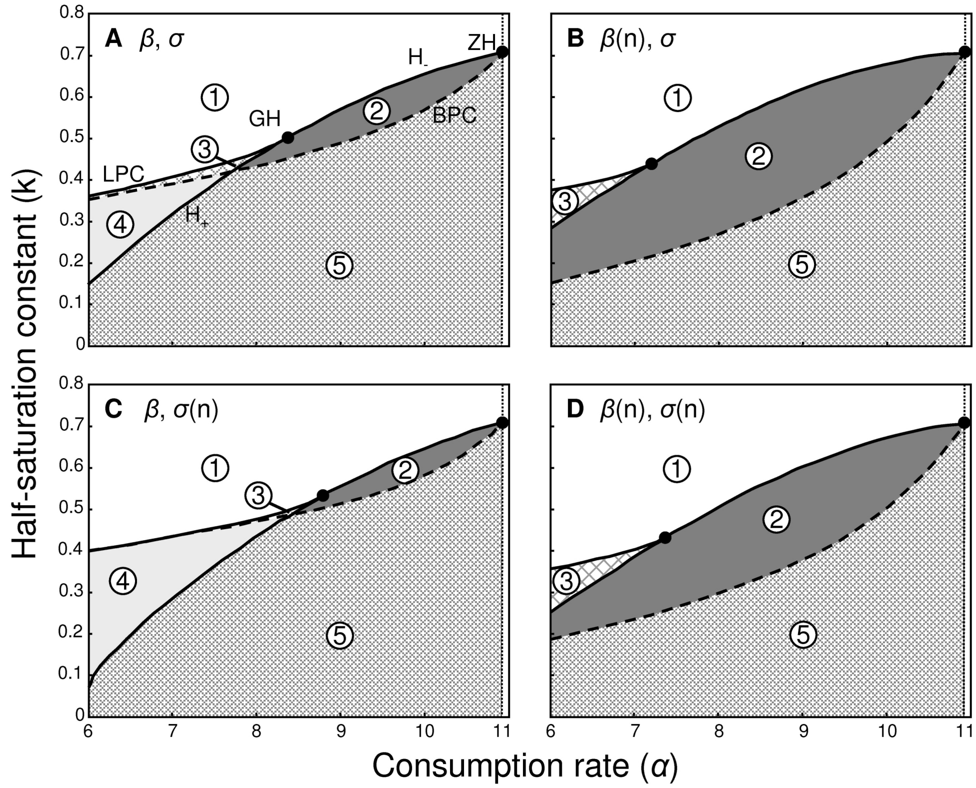

Figure 1: Comparison of model (2) dynamics with constant and resource-dependent rates of transmission $\beta(n)$ and spore production $\sigma(n)$. Panel **A** shows the constant-rates model bifurcation diagram. Panels **B** and **C** show the diagrams for model (2) with resource-dependence in either $\beta(n)$ or $\sigma(n)$, but not both. In panel **D**, both rates are resource-dependent.

THE END!

Appendix A Model Derivation

The general model (2) is a rescaled version of the following model, which is based on spore-based fungal parasitism of *Daphnia sp.*

As described in the text, we begin with a Rosenzweig-MacArthur model with a general predation rate $\tilde{\alpha}(N)N$. Among consumers, we incorporate constant rates of fish predation and a spore-based infectious disease using an "SIZ" model used previously for this system. Spore-based disease transmission largely follows the law of mass action in this systems and others (Ebert 2005, Ch. 8). Importantly, we allow for N-dependent contact rates between consumers and spores, and N-dependent production of spores by infected individuals by assuming general N-dependent rates $\tilde{\beta}(N)$, $\tilde{\sigma}(N)$ and $\tilde{C}(N)$. These yield the general (unscaled) model which has units of individuals L^{-1} and time in days.

$$\frac{dN}{d\tau} = \tilde{r}N(1 - N/K) - \tilde{\alpha}(N)N(X + \rho Y) \tag{A1a}$$
$$\frac{dX}{d\tau} = \chi\tilde{\alpha}(N)N(X + \tilde{f}\rho Y) - (d_x + \tilde{m})X - \tilde{\beta}(N)XZ \tag{A1b}$$
$$\frac{dY}{d\tau} = \tilde{\beta}(N)XZ - (d_x + \tilde{\nu} + \tilde{m})Y \tag{A1c}$$
$$\frac{dZ}{d\tau} = \tilde{\sigma}(N)(d_x + \tilde{\nu})Y - \tilde{\mu}Z - \eta\tilde{C}(N)Z(X + \rho Y) \tag{A1d}$$

Table B1 contains parameter descriptions, ranges and values. Note that to parameterize the N-dependent rates $\tilde{\beta}(N)$, $\tilde{\sigma}(N)$ and $\tilde{C}(N)$ we rescale the model assuming they are constant, then parameterize their N-dependent functional forms relative to their constant-rate counterparts. Finally, where parameter values were practically unknown, we attempted to choose values that are biologically plausible, and that yield dynamics consistent with field and laboratory observations.

The rescaled model (2) is given by: $t = \frac{\tau}{\frac{1}{d_x}}$, $r = \frac{\tilde{r}}{d_x}$, $\alpha = \frac{\chi\tilde{\alpha}}{d_x}$, $k = \tilde{k}/K$, $f = \tilde{f}\rho$, $m = \frac{\tilde{m}}{d_x}$, $C = \eta\tilde{C}\chi K\frac{1}{d_x}$, $C_c = \eta\tilde{C}_c\frac{\chi}{d_x}$, $\beta = \tilde{\beta}\chi K\frac{1}{d_x}$, $\nu = \frac{\tilde{\nu}}{d_x}$, $\sigma = \tilde{\sigma}$, $\mu = \frac{\tilde{\mu}}{d_x}$. This leaves the rescaled variables as $n = N/K$, $x = \frac{X}{\chi K}$, $y = \frac{Y}{\chi K}$, $z = \frac{Z}{\chi K}$. See Table B2 in the text for parameter descriptions.

Appendix B Parameter Values

Parameter values and ranges below were determined based upon their biological interpretations, using published values of those quantities when available. Other values come from previously published models of *Daphnia* parasitism or algae consumption. Within biologically plausible parameter ranges, certain parameter values were further specified in order to replicate observed phenomena or produce specific dynamic behaviors.

Variable	Value	Range	Description (Units)
N	–	–	Producer density (No. L^{-1})
X	–	–	Susceptible consumer density (No. L^{-1})
Y	–	–	Infected consumer density (No. L^{-1})
Z	–	–	Infectious spore density (Spores L^{-1})
τ	–	–	Time (days).
Parameter	**Value**	**Range**	**Description**
K	10^4	$10^2 - 10^9$	Algal carrying capacity (No. L^{-1}) (Porter et al. 1982, others)
$\tilde{r}$	2	$0.69 - 2.8$	Algal growth rate (No. d^{-1}) (Sorokin and Krauss 1958)
$\tilde{a}$	$3.16\text{x}10^2$	$\approx \frac{1}{100d} - \frac{1}{10d}$	Max. rate of consumption for type II $\alpha(n)$ (Hall et al. 2007)
$\tilde{k}$	$0.6\text{x}10^4$	–	Half saturation constant for type II $\alpha(n)$ (Hall et al. 2007)
ρ	1	–	Relative feeding rate of infected individuals
f	0.75	$0 - 1$	Relative fecundity of infected individuals
χ	$0.4\text{x}10^{-2}$	–	Births per consumed resource (Duffy et al. 2005)
d_x	0.05	$0.02 - 0.1$	*Daphnia* mortality $\approx$ lifetime^{-1} (No. day^{-1}) (Duffy et al. 2005)
$\tilde{m}$	0.03	$0 - 0.5$	Fish predation rate (Indiv day^{-1}) (Duffy et al. 2005)
$\tilde{C}$	0.1	≤ 0.1	Consumption rate (type-I $\alpha(n)$) (L day^{-1} consumer^{-1})
$\tilde{C}_c$	500	$0 - 1000$	Max. $C(n)$ (type II $\alpha(n)$) (Porter et al. 1982)
η	0.7	$0 - 1$	Spore consumption efficiency
$\tilde{\beta}$	–	≥ 0	Infection rate (fit to yield $\leq$20% prevalence) (Hall et al. 2006)
$\tilde{\beta}_c$	–	≥ 0	Per capita per spore infection rate
$\tilde{\nu}$	d_x	$\approx d_x$	Additional non-fish-related mortality for infecteds
θ	3	$1 - 10+$	Fish selectivity (Duffy et al. 2005; Hall et al. 2006)
$\tilde{\mu}$	0.033	≥ 0	Loss rate of infectious spores (No. L^{-1}) (Hall et al. 2006)
σ	$6.4\text{x}10^4$	$0 - 10^5$	Spores produced per dead infected individual (Hall et al. 2006)

Table B1: Paramter values and descriptions for the unscaled model. Units are individuals L^{-1}, time is in days. The broad range for d is based on the broad range of algal densities oberved in nature. Growth rate r based on a range of $1 - 4$ doublings per day. For other parameters, see the references indicated in the table.

Variable	Value	Description
n	–	Producer density (relative to consumer-free steady state)
x	–	Susceptible consumer density (scaled to resource equivalents)
y	–	Infected consumer density (scaled to resource equivalents)
z	–	Infectious spore density (scaled resource equivalents)
t	–	Time (units are disease-free consumer lifetime)
Parameter	Value	Description
r	40	Producer growth rate (day^{-1}) (Sorokin and Krauss 1958)
α	–	Type-I consumption rate (consumer^{-1} day^{-1})(Hall et al. 2007)
a	–	Maximum of type-II consumption rate $\alpha(n)$
k	–	Half saturation constant for type-II $\alpha(n)$ (Hall et al. 2007)
ρ	1	Relative feeding rate of infected individuals
f	0.75	Relative fecundity of infected individuals
m	0.6	Fish predation rate on susceptible *Daphnia* (Duffy et al. 2005)
β	–	Infection rate (susceptible^{-1} spore^{-1}) (Duffy et al. 2005)
ν	1	Additional mortality for infecteds unrelated to fish depredation
θ	3	Fish selectivity for infecteds (Duffy et al. 2005; Hall et al. 2006)
σ	–	Spore production rate (infected^{-1})
ϕ	0.5	Slope parameter for n-dependent spore production rate $\sigma(n)$
μ	0.66	Loss rate of infectious spores (L^{-1}) (Hall et al. 2006)
C	0	Spore consumption rate (day^{-1} consumer^{-1})

Table B2: Variables and parameters of the scaled model (2).

References

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