Appendix for Malishev, M & Civitello, DJ Linking bioenergetics and parasite transmission models suggests mismatch between snail host density and production of human schistosomes

Model construction

We built an individual-based disease transmission and dynamic energy budget model for schistosomiasis infection (SIDEB) of a size-structured *Biomphalaria glabrata* host population and its human infectious parasite *Schistosoma mansoni*. The SIDEB model is informed by two sub models: a complete dynamic energy and mass budget (DEB) model for *B. glabrata*, including energy and mass compartments for *S. mansoni* parasite biomass and a disease transmission model.

Table A1. Key dynamic energy budget state variables for individual hosts and within-host parasite biomass (bold). Equations refer to the equation numbers listed under 'Dynamic energy budget for *B. glabrata*'. Dimensions and units: —, dimensionless; C, carbon; d, day; L, length; mg, milligrams; mm, millimeters.

Parameter	Definition	Dimension(unit)	Equation
L	structural length	mm	Eq. 2
e	scaled reserve density	—	Eq. 3
D	host development	$mg\ C$	Eq. 4
R_H	energy in reproduction buffer	$mg\ C$	Eq. 5
δ	damage density (infection and starvation costs)	d^{-1}	Eq. 8
H	starvation-related hazard rate	d^{-1}	Eq. 9
L_G	shell length	$L\ (mm)$	—
age	age of egg (hatches at 10 days)	d	—
$\boldsymbol{P}$	**parasite biomass**	$\boldsymbol{mg\ C}$	**Eq. 6**
R_P	**energy in parasite reproduction**	$\boldsymbol{mg\ C}$	**Eq. 7**

Table A2. Definitions of model state variables for the simulation model environment. Dimensions and units: #, number; C, carbon; g, grams; L, liter; mg, milligrams.

Parameter	Definition	Dimension(unit)
F_a	algae resource density	$mg\ C\ L^{-1}d^{-1}$
F_d	detritus resource density	$mg\ C\ L^{-1}d^{-1}$
M	total number of miracidia	$\#\ L^{-1}$
C	cercarial density	$\#\ 0.1\ L^{-1}$
G	total number of host eggs	$\#\ L^{-1}$

Table A3. Parameters and compound functions for the bioenergetic model of within-host infection dynamics.

(A) Primary parameters (Host)

Quantity	Description	Units
i_M	Surface area-specific maximum host ingestion rate	$mg\ C\ d^{-1}\ mm^{-2}$
F_h	Host (Type-II) foraging half saturation constant	$mg\ C$
Y_{EF}	Yield of reserve on resources	dimensionless
Y_{VE}	Yield of structure on reserve	dimensionless
κ	Proportion of mobilized reserve allocated to soma	dimensionless
m_D	Maintenance rate for maturity	d^{-1}
L_M	Maximum physical host length	mm
χ	Ratio of structural biomass to physical length cubed	$mg\ C\ mm^{-3}$
E_M	Maximum host reserve biomass relative to structural biomass	dimensionless
D_R	Host maturity threshold for reproduction	$mg\ C$
ε_H	Carbon content of host offspring	$mg\ C$

(B) Primary parameters (Parasite)

Y_{AE}	Yield of parasite assimilate on host reserve	dimensionless
Y_{PA}	Yield of parasite biomass on assimilate	dimensionless
Y_{RP}	Yield of parasite offspring biomass on assimilate	dimensionless
i_{PM}	Parasite maximum mass-specific ingestion rate	$mg\ C\ d^{-1}$
e_h	Parasite ingestion half saturation constant	dimensionless
p_h	Parasite allocation half-saturation constant	dimensionless
α	Parasite manipulation of host allocation rule	$mg\ C^{-1}$
m_P	Mass-specific maintenance rate for parasites	d^{-1}

ε_P	Carbon content of parasite offspring	*mg C*

(C) Primary parameters (Damage, hazard, and survivorship)

k_R	Damage repair rate constant	d^{-1}
Θ	Intensity of parasite-induced damage	dimensionless
h_b	Background hazard rate	d^{-1}
h_δ	Hazard coefficient of damage	d^{-1}
m_R	Scaled energy expenditure rate for damage repair	d^{-1}
δ_0	Damage density threshold	dimensionless

(D) Derived parameters and functions

Equation	Description	Units
$a_M = i_M Y_{EF}$	Maximum host assimilation rate	$mg\ C\ d^{-1}\ mm^{-2}$
$g = \frac{1}{\kappa^* Y_{VE} E_m}$	Cost of structural growth relative to maximum possible allocation to soma	dimensionless
$r_P = \frac{\frac{P}{\chi L^3}^2}{{p_h}^2 + \frac{P}{\chi L^3}^2}$	Proportional allocation of parasite assimilate to reproduction	dimensionless
$Y_{PE} = Y_{PA} Y_{AE}$	Yield of parasite biomass on host reserve	dimensionless
$\gamma_{RP} = \frac{Y_{RP}}{Y_{PA}}$	Relative yield of parasite reproduction on parasite assimilate	dimensionless
$C = \left(\frac{ge}{g+e}\right)\left(a_M L^2 + \frac{(m_V + m_R E_M \delta)\chi L^3}{\kappa^* g}\right)$	Commitment/mobilization rate of reserve	$mg\ C\ d^{-1}$
$m_V = \frac{\kappa a_M}{\chi L_M}$	Mass-specific maintenance rate for structure	d^{-1}
$\mu_D = \frac{m_D}{m_V}$	Scaled maturity maintenance rate	dimensionless

$M = \chi(1 + E_M)$	Volume-biomass coefficient for hosts	*mg C mm*$^{-3}$
$\kappa^* = min(\kappa + \alpha P, 1)$	Realized proportion of mobilized reserve allocated to soma	dimensionless
$f_H = \frac{F}{F_h + F}$	Scaled host functional response	dimensionless
$f_P = \frac{e}{e_h + e}$	Scaled parasite functional response	dimensionless

Table A4. Parameter estimates used in this simulation study.

Parameter	Description	Estimate[1,2,3]	Units
Host parameters			
κ	Proportional allocation to soma	0.91	—
M	Mass:volume relationship	$5.46 \cdot 10^{-3}$	$mg\ C\ mm^{-3}$
E_M	Maximum host reserve biomass relative to structural biomass	1.32	$mg\ C$
L_M	Maximum physical host length	55.8	mm
i_M	Surface area-specific maximum host ingestion rate	$3.06 \cdot 10^{-2}$	$mg\ C\ d^{-1}\ mm^{-2}$
F_h	Host (Type-II) foraging half saturation constant	2.00	$mg\ C\ L^{-1}$
Y_{EF}	Yield of reserve on resources	0.279	—
Y_{VE}	Yield of structure on reserve	0.269	—
μ_D	Maintenance rate for maturity	0.139	—
D_R	Host maturity threshold for reproduction	0.633	$mg\ C$
ε_H	Carbon content of host offspring	0.015	$mg\ C$
Parasite parameters			
α	Parasite manipulation of host allocation rule	1.88	$mg\ C^{-1}$
i_{PM}	Parasite maximum mass-specific ingestion rate	0.592	$mg\ C\ d^{-1}$
Y_{PE}	Yield of parasite biomass on reserve	0.937	—
Y_{RP}	Yield of parasite offspring biomass on assimilate	0.824	—
e_h	Parasite ingestion half saturation constant	$2.17 \cdot 10^{-2}$	—
m_P	Mass-specific maintenance rate for parasites	0.317	d^{-1}
p_h	Parasite allocation half-saturation constant	0.132	—
ε_P	Carbon content of parasite offspring	$4 \cdot 10^{-5}$	$mg\ C$

Damage, hazard, survival, and repair parameters			
k_R	Damage repair rate constant	$3.14 \cdot 10^{-2}$	d^{-1}
δ_0	Damage density threshold	$9.12 \cdot 10^{-2}$	—
h_δ	Hazard coefficient of damage	$2.06 \cdot 10^{-3}$	d^{-1}
h_b	Background hazard rate	$7.76 \cdot 10^{-4}$	d^{-1}
Θ	Intensity of parasite-induced damage	259	—
m_R	Scaled energy expenditure rate for damage repair	$5.57 \cdot 10^{-5}$	d^{-1}
Transmission model			
ε	Snail-miracidia contact rate	20.0	$L\ d^{-1}$
σ	Miracidial infection probability given contact	0.50	—
M_{in}	Miracidial input rate	10	$L^{-1}\ d^{-1}$
m_M	Mortality rate of miracidia	1	d^{-1}
Environmental/Resource parameters			
ENV	Volume of environment	500	L
r	Algal maximum growth rate	varied	d^{-1}
K	Algal carrying capacity	5	$mg\ C\ L^{-1}$
det	Detritus subsidy rate	varied	$mg\ C\ L^{-1}\ d^{-1}$
M_Z	Mortality rate of cercariae	1	d^{-1}

1. All DEB parameter estimates rounded to three significant figures.
2. Transmission model parameters rounded from estimates in Civitello and Rohr (2014).
3. Environmental/resource parameters chosen to reflect a $1\text{m}^2 \cdot 0.5$ m deep volume of habitat, realistic quantities of algal growth or detrital input, and rates of parasite mortality.

Dynamic energy budget sub-model for *B. glabrata*.

We outline the energy and mass budget equations for the dynamic energy and mass budget state variables for the intermediate snail host *Biomphalaria glabrata*. Equation number in brackets refers to the equation references in Civitello *et al.* (2018).

Resource, F, growth in the environment (Eq. 1)

$$\frac{dF}{dt} = -i_M L^2 f_H$$

where i_M is the maximum ingestion rate per individual host, L is host length (cm), and f_H is the host functional feeding response.

Host body length, L (growth) (Eq. 2)

$$\frac{dL}{dt} = \frac{gY_{VE}}{3\chi} \cdot \left(\frac{\kappa^* a_M e - (m_V + m_R E_M \delta)\chi L}{e+g} \right)$$

where g is the energy investment ratio per unit of biomass cm^3, Y_{VE} is yield of structure on host energy reserve, χ is the ratio of structural biomass to physical length (mg C mm^{-3}), κ is the allocation of mobilized energy reserve e to somatic maintenance m_V and growth, a_M is the maximum assimilation rate of food converted into energy, m_R is maintenance of infected (damaged) biomass, E_M is maximum reserve (per unit of structural biomass V), and δ is scaled damage density.

Scaled host energy reserve, e (Eq. 3)

$$\frac{de}{dt} = (f_H - e)\frac{a_M}{\chi E_M L} - \frac{P}{\chi L^3}\left(\frac{i_{PM} f_P}{E_M}\right)$$

where P is the within-host parasite biomass (growth of parasite), i_{PM} is the maximum mass-specific within-host parasite ingestion rate, and f_P is the parasite functional feeding response.

The $\frac{P}{\chi L^3}\left(\frac{i_{PM} f_P}{E_M}\right)$ term equals the depleted energy reserve of infected hosts by parasites.

Host development, D (Eq. 4)

$$\frac{dD}{dt} = \begin{cases} \text{if } D < D_R, & (1-\kappa^*)C - m_D D \\ \text{if } D \geq D_R, & \min[\ 0,\ (1-\kappa^*)C - m_D D\ ] \end{cases}$$

where D_R is the maturity threshold for host reproduction, C is the rate of mobilized host reserve, and m_D is the rate of host maturity maintenance.

The $\min[\ 0,\ (1-\kappa^*)C - m_D D\ ]$
term allows the host to 'regress' back to a previous maturity stage when volume-specific reserve becomes too low under starvation conditions, i.e. the shrinking and regression starvation rule (Kooijman 2010).

Host reproduction, R_H (Eq. 5)

$$\frac{dR_H}{dt} = \begin{cases} \text{if } D < D_R, & 0 \\ \text{if } D \geq D_R, & (1-\kappa^*)C - m_D D \end{cases}$$

Within-host parasite biomass, P (growth) (Eq. 6)

$$\frac{dP}{dt} = P(Y_{PE} i_{PM} f_P (1 - r_P) - m_P)$$

where Y_{PE} is the yield of parasite biomass on host energy reserve, r_P is the allocated parasite biomass assimilated to new parasite offspring (proportional to parasite biomass), and m_P is the mass-specific rate of parasite maturity maintenance.

Parasite reproduction, R_P (Eq. 7)

$$\frac{dR_P}{dt} = \gamma_{RP} Y_{PE} i_{PM} f_P r_P$$

where γ_{RP} is the relative yield of parasite offspring biomass from assimilated parasite reserve.

Host damage density, δ (Eq. 8)

$$\frac{d\delta}{dt} = \frac{\Theta}{\chi L^3} \cdot \frac{dR_P}{dt} + k_R(1-e) - k_R\delta - \frac{3\delta}{L} \cdot \frac{dL}{dt}$$

where Θ is the intensity of parasite-induced damage to the host and k_R is a constant for the rate of damage repair via reserve depletion. The $\frac{3\delta}{L} \cdot \frac{dL}{dt}$ term is host "dilution by growth": as the host adds new biomass, this reduces the damage density to its overall biomass.

Cumulative hazard for host, H (Eq. 9)

$$\frac{dH}{dt} = h_b + h_\delta \cdot \max(0,\ \delta - \delta_0)$$

where h_b is the background hazard rate, h_δ is the hazard coefficient, and δ_0 is the linear function for damage density.

Host survival probability (Eq. 10)

$$P(\text{Survival})[t] = e^{-H(t)}$$

Simulation model code for the within-host DEB model, the between-host disease transmission model, and the individual-based simulation model

All model code is found at https://github.com/darwinanddavis/MalishevCivitello_SICB.

Required files

```
"DEB_IBM.R"
"DEB_INF_GUTS_IBM.nlogo"
"FullStarve_shrink_dilute_damage3.Rda"
"IndividualModel_IBM3.c"
"IndividualModel_IBM3.so" # Mac OSX. generated from C
"IndividualModel_IBM3.o" # Mac OSX. generated from C
"IndividualModel_IBM.dll" # Windows. generated from C
```

Bibliography

Civitello DJ, Rohr JR. 2014. Disentangling the effects of exposure and susceptibility on transmission of the zoonotic parasite Schistosoma mansoni. Journal of Animal Ecology 83(6):1379-1386.

Civitello DJ, Fatima H, Johnson LR, Nisbet RM, Rohr JR. 2018. Bioenergetic theory predicts infection dynamics of human schistosomes in intermediate host snails across ecological gradients. Ecology Letters 21(5):692-701.

End Appendix