

**THE GEOMETRY OF A POPULATION CYCLE:
A MECHANISTIC MODEL OF SNOWSHOE HARE DEMOGRAPHY:
APPENDIX**

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A. NONDIMENSIONALIZATION OF THE MINIMAL MODEL.

A.1. Rescaling to reveal the Hamiltonian limit. For a wide range of parameter values, the autonomous dynamical system obtained by setting $\varepsilon_1 = \varepsilon_2 = 0$ in the minimal model (10) admits an interior equilibrium (B^*, H^*, P^*) , $B^*, H^*, P^* > 0$. When such an equilibrium exists, it is invariably unique. We rescale the phase variables B , H , P around this equilibrium by defining new state variables and time

$$x = \log \frac{B}{B^*} \quad y = \log \frac{H}{H^*} \quad z = \log \frac{P}{P^*} \quad t = \Omega T. \quad (\text{A.1})$$

Defining the dimensionless parameters

$$\begin{aligned} \gamma_b &= \frac{\bar{G}K}{\Omega B^*} & \gamma_h &= \frac{\bar{R}_H + \delta_1 \bar{D}_H}{\Omega} \frac{B^*}{B^* + X_B} & \gamma_p &= \frac{\bar{D}_P}{\Omega} \\ \alpha_b &= \frac{B^*}{K} & \alpha_h &= \frac{\bar{D}_H}{\bar{R}_H + \delta_1 \bar{D}_H} \frac{B^* + X_B}{B^*} \\ \eta_b &= \frac{B^*}{X_B} & \eta_h &= \frac{H^*}{X_H} \\ \beta_h &= \frac{\bar{R}_H}{\bar{R}_H + \delta_1 \bar{D}_H} & \beta_p &= \frac{\bar{R}_P}{\bar{R}_P + \delta_2 \bar{D}_P}, \end{aligned} \quad (\text{A.2})$$

we arrive at the rescaled system

$$\begin{aligned} \frac{dx}{dt} &= \gamma_b \left[(e^{-x} - \alpha_b) \phi_s(t) - (1 - \alpha_b) \phi_w(t) \frac{(1 + \eta_b)e^y}{1 + \eta_b e^x} \right] \\ \frac{dy}{dt} &= \gamma_h \left[(\beta_h \phi_s(t) + (1 - \beta_h)) \frac{(1 + \eta_b)e^x}{1 + \eta_b e^x} - \alpha_h - (1 - \alpha_h) \frac{(1 + \eta_h)e^z}{1 + \eta_h e^y} \right] \\ \frac{dz}{dt} &= \gamma_p \left[(\beta_p \phi_s(t) + (1 - \beta_p)) \frac{(1 + \eta_h)e^y}{1 + \eta_h e^y} - 1 \right]. \end{aligned} \quad (\text{A.3})$$

In terms of the dimensionless parameters (A.2), the conditions for co-existence of the three trophic levels are simply

$$\begin{aligned} \alpha_b &< 1 & \alpha_h &< 1 \\ \eta_b &> 0 & \eta_h &> 0. \end{aligned} \quad (\text{A.4})$$

Whether or not these conditions are satisfied, in the autonomous case, the equilibrium of (A.3) is located at the origin. A Hamiltonian limit is located at $\alpha_b = 1$, $\eta_h = 0$. At the Hamiltonian limit, the dynamics in the three dimensional phase space of (A.3) rapidly collapse to the two-dimensional submanifold $x = 0$. On this limiting submanifold, the dynamics are Hamiltonian. For a recent discussion of Hamiltonian dynamics in predator-prey models, see King et al. (1996). Hamiltonian

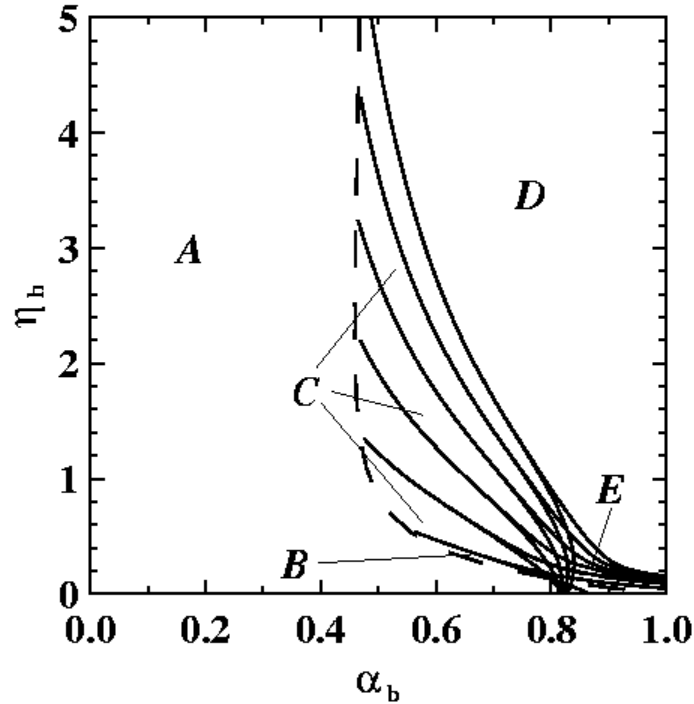


FIGURE A.1. Resonance horns emanating from the Hamiltonian limit at $\alpha_b = 1$, $\eta_h = 0$ in the rescaling of Eqns. (A.3). The labels A–E designate regimes of different periodicities as in Figs. 3–7. Other parameters are $\gamma_b = 0.2806$, $\gamma_h = 0.53496$, $\gamma_p = 0.25465$, $\alpha_h = 0.80327$, $\beta_h = \beta_p = 1$, $\eta_b = 6.23915$, $\varepsilon_1 = 1$, $\varepsilon_2 = 0$.

dynamics generally are discussed in Hénon (1983), Tabor (1989), and Lichtenberg & Lieberman (1992). For an introductory discussion of the nature and significance of Hamiltonian limits, see King & Schaffer (1999). It can be shown that this is the only such limit in (A.3). The fact that this special case lies on the boundary of the region of biologically meaningful solutions (A.4) neither stops us from investigating it nor prevents this singularity from making itself felt well within the regime of interest.

As we see in Fig. A.1, resonance horns, each one bounded by a surface of tangent (or saddle-node) bifurcations, emanate from the Hamiltonian limit into the dissipative regime and terminate on the surface of Neimark-Sacker bifurcations upon which the annual cycle changes stability. For a more detailed discussion of the global bifurcation structure, see King & Schaffer (1999).

A.2. Alternate rescaling. Although the rescaling (A.2) reveals the geometry underlying the dynamics of Eqns. (9), it obscures the biology. Modification of a single biological parameter such as K traces, via the equilibrium values B^* , H^* , P^* and (A.2), a curvilinear path through the full 13-dimensional parameter space. To facilitate Interpretation of our results we introduce a simpler,

more directly meaningful, rescaling, as follows. Let

$$\begin{aligned}
 b &= \frac{B}{K} & h &= \frac{k_B H}{X_B \Omega} & p &= \frac{k_H P}{X_H \Omega} \\
 \gamma_1 &= \frac{\bar{G}}{\Omega} & \gamma_2 &= \frac{\bar{R}_H}{\Omega} & \gamma_3 &= \frac{\bar{R}_P}{\Omega} \\
 \mu_1 &= \frac{\bar{D}_H}{\Omega} & \mu_2 &= \frac{\bar{D}_P}{\Omega} \\
 \eta_1 &= \frac{K}{X_B} & \eta_2 &= \frac{X_B \Omega}{k_B X_H}.
 \end{aligned} \tag{A.5}$$

Under this rescaling, with the same dimensionless time as before, Eqns. (9) become

$$\begin{aligned}
 \frac{db}{dt} &= \gamma_1 \phi_s(t)(1-b) - \phi_w(t) \frac{bh}{1+\eta_1 b} \\
 \frac{dh}{dt} &= (\gamma_2 \phi_s(t) + \delta_1 \mu_1) \frac{\eta_1 bh}{1+\eta_1 b} - \mu_1 h - \frac{hp}{1+\eta_2 h} \\
 \frac{dp}{dt} &= (\gamma_3 \phi_s(t) + \delta_2 \mu_2) \frac{\eta_2 hp}{1+\eta_2 h} - \mu_2 p.
 \end{aligned} \tag{A.6}$$

In performing the numerical computations leading to Figs. 3–7, we have used rescaling (A.5). We remark that the Hamiltonian limit does not exist in model (A.6) for finite values of the parameters.

LITERATURE CITED

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