

Predator-Prey Models

Lotka-Volterra Model

Model

prey model: $\frac{dV}{dt} = bV - aVP = f_1(V, P)$

predator model: $\frac{dP}{dt} = caVP - dP = f_2(V, P)$

Assumptions:

- density-independent exponential growth of the prey population V in the absence of predators, with intrinsic rate of increase b
- a constant predation rate a (fraction of the prey population eaten per predator), so that total predation is proportional to the abundance of prey and the abundance of predators; there is no slowing of predation at high prey abundance, and no interference among predators.
- a constant conversion rate c of eaten prey into new predator abundance
- a constant per capita mortality rate of predators, d .

Equilibrium

Assuming $V > 0$ and $P > 0$,

$$\frac{dV}{dt} = 0$$

$$(b - aP)V = 0$$

$$b - aP = 0$$

$$P^* = b/a$$

and

$$\frac{dP}{dt} = 0$$

$$(caV - d)P = 0$$

$$caV - d = 0$$

$$V^* = \frac{d}{ca}$$

Stability

From the preceding expressions for the equilibria it can be seen that the zero-growth isoclines are straight and perfectly horizontal (for prey) or vertical (for predators). This reflects the complete absence of self-density dependence in both species' dynamics.

$$\begin{aligned}
 J &= \begin{bmatrix} \frac{\partial f_1}{\partial V} & \frac{\partial f_1}{\partial P} \\ \frac{\partial f_2}{\partial V} & \frac{\partial f_2}{\partial P} \end{bmatrix}_{V^*, P^*} \\
 &= \begin{bmatrix} \frac{\partial}{\partial V}(b - aP)V & \frac{\partial}{\partial P}(b - aP)V \\ \frac{\partial}{\partial V}(kaV - d)P & \frac{\partial}{\partial P}(kaV - d)P \end{bmatrix}_{V^*, P^*} \\
 &= \begin{bmatrix} b - aP^* & -aV^* \\ caP^* & caV^* - d \end{bmatrix} \\
 &= \begin{bmatrix} b - a\left(\frac{b}{a}\right) & -a\left(\frac{d}{ka}\right) \\ ca\left(\frac{b}{a}\right) & ca\left(\frac{d}{ka}\right) - d \end{bmatrix} \\
 &= \begin{bmatrix} 0 & -\frac{d}{c} \\ cb & 0 \end{bmatrix}
 \end{aligned}$$

The **trace** of J therefore is exactly equal to 0, not meeting the stability condition that the trace is negative, so the equilibrium is **not stable**.

In fact (as shown to the right), the **eigenvalues are purely imaginary: their real parts are exactly 0**. This creates a kind of dynamics right on the cusp between stability and instability, called **neutral stability**: cycling with no trend either in towards the equilibrium or out away from it.

$$\begin{aligned}
 \det \begin{bmatrix} 0 - \lambda & -\frac{d}{c} \\ cb & 0 - \lambda \end{bmatrix} &= 0 \\
 (0 - \lambda)^2 - \left(-\frac{d}{c} \cdot cb\right) &= 0 \\
 \lambda^2 + db &= 0 \\
 \lambda^2 &= -db \\
 \lambda &= \sqrt{-db} \\
 &= \pm i\sqrt{db}
 \end{aligned}$$

Modifications to the Lotka-Volterra Model

Prey density dependence

Replacing the Lotka-Volterra model's exponential growth of the prey population by logistic growth with a carrying capacity K yields the model

$$\frac{dV}{dt} = bV\left(1 - \frac{V}{K}\right) - aVP = V\left[b\left(1 - \frac{V}{K}\right) - aP\right]$$

$$\frac{dP}{dt} = caVP - dP$$

Equilibrium:

Since the predator equation is the same as in the Lotka-Volterra model, it is still the case that

$$V^* = \frac{d}{ca}$$

With the new prey equation,

$$\frac{dV}{dt} = 0$$

$$\left[b\left(1 - \frac{V}{K}\right) - aP\right]V = 0$$

$$b\left(1 - \frac{V}{K}\right) - aP = 0$$

$$\begin{aligned} P^* &= \frac{b\left(1 - \frac{V^*}{K}\right)}{a} \\ &= \frac{b}{a}\left(1 - \frac{d}{caK}\right) \end{aligned}$$

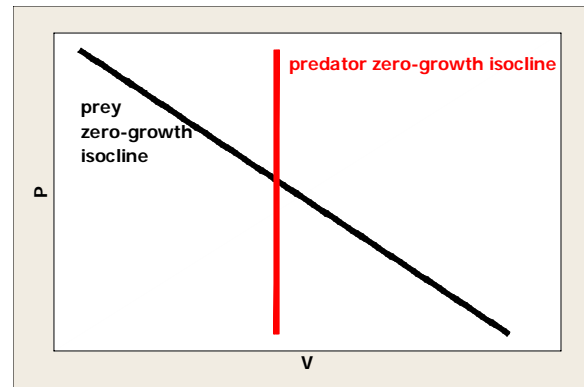
Stability:

Since the predator equation is unchanged from the Lotka-Volterra model, the predator zero-growth isocline still is a straight vertical line (at V^*).

The prey zero-growth isocline is given by the function $P = \frac{b}{a} \left(1 - \frac{V}{K}\right)$, which is a straight line,

decreasing from left to right with slope $-b/aK$.

When prey are abundant, the density dependence decreases their per capita rate of increase, so fewer predators are needed to eat enough of them to offset their population growth rate.



The density dependence in the prey's dynamics now causes the upper-left element of the Jacobian to be negative, so qualitatively:

$$J = \begin{bmatrix} - & - \\ + & 0 \end{bmatrix}$$

The **trace** therefore now is **negative** and the **determinant** is **positive**: the model is **stable** for any values of the parameters. What is happening is that the density-dependent regulation of the prey population suppresses the (neutrally stable) cycling of the Lotka-Volterra model.

Type 2 functional response

The “functional response” is the predation rate (per predator) as a function of the prey density. In the Lotka-Volterra model (and the model above with prey density dependence) it is assumed to be a constant proportion of the prey density, i.e. a straight upward sloping line in a graph of prey killed *vs.* prey density; this is called a Type 1 functional response.

A Type 2 functional response is one in which the predation rate (fraction of prey killed) decreases as prey density increases. This typically is caused by predators having to spend time capturing and consuming each prey, and perhaps from predators becoming satiated and ceasing to forage. On a graph of prey killed *vs.* prey density, a Type 2 functional response increases in initially nearly linear fashion, but gradually slows down and eventually asymptotes at a maximum feeding rate.

A common model for a Type 2 functional response replaces the constant predation rate parameter a of the Lotka-Volterra model with the function

$$\frac{a}{1 + aT_h V}$$

in which T_h is the so-called “handling time.”

The model then is

$$\frac{dV}{dt} = bV - \frac{a}{1 + aT_h V}VP = \left(b - \frac{a}{1 + aT_h V}P\right)V$$

$$\frac{dP}{dt} = \frac{ca}{1 + aT_h V}VP - dP = \left(\frac{ca}{1 + aT_h V}V - d\right)P$$

Equilibrium:

The predator equation gives

$$\frac{dP}{dt} = 0$$

$$\left(\frac{ca}{1 + aT_h V}V - d\right)P = 0$$

$$\frac{ca}{1 + aT_h V}V - d = 0$$

$$\frac{ca}{1 + aT_h V}V = d$$

$$caV = d(1 + aT_h V)$$

$$(ca - daT_h)V = d$$

$$\boxed{V^* = \frac{d}{ca - daT_h} = \frac{d}{a(c - dT_h)}}$$

The prey equation gives

$$\frac{dV}{dt} = 0$$

$$\left(b - \frac{a}{1 + aT_h V}P\right)V = 0$$

$$b - \frac{a}{1 + aT_h V}P = 0$$

$$P^* = b\left(\frac{1 + aT_h V^*}{a}\right)$$

$$= \frac{b}{a}\left(1 + aT_h\left[\frac{d}{a(c - dT_h)}\right]\right)$$

$$\boxed{P^* = \frac{b}{a}\left(1 + \frac{dT_h}{c - dT_h}\right)}$$

Stability:

The predator isocline yet again is a straight vertical line.

The prey isocline is given by the function

$$P = \frac{b}{a}(1 + aT_h V)$$

which is a straight line with positive slope bT_h .

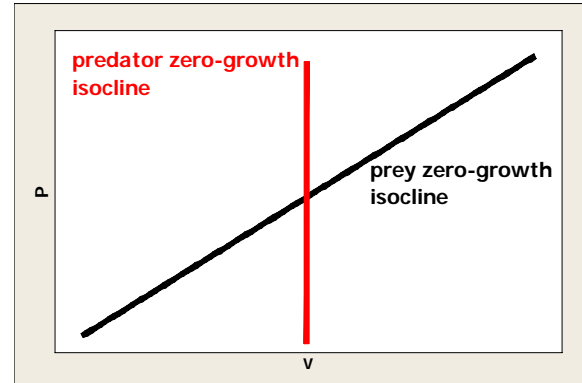
Because the per capita prey mortality (from predation) decreases with increasing prey density, the prey dynamics in model experience

positive feedback rather than negative, regulating density dependence. When prey are abundant, it takes more predators to eat enough of them to offset their intrinsic rate of population growth.

This inverse density dependence (decreasing per capita mortality at higher density) means that the upper-left element in the Jacobian matrix is now positive:

$$J = \begin{bmatrix} + & - \\ + & 0 \end{bmatrix}$$

The trace of this matrix is positive, so the model is **unstable** for any parameter values.



Nicholson-Bailey Model

The Nicholson-Bailey model is a close analogue in discrete time of the continuous-time Lotka-Volterra model. Because it typically is thought of as representing parasitoid-host interactions, I will follow case in using that terminology, and denoting the population abundances by H_t (hosts) and P_t (parasitoids).

Model

host model:
$$H_{t+1} = \lambda H_t e^{-aP_t} = g_1(H_t, P_t)$$

parasitoid model:
$$P_{t+1} = cH_t(1 - e^{-aP_t}) = g_2(H_t, P_t)$$

Assumptions:

- density-independent geometric growth of the host population V_t in the absence of parasitoids; λ is the finite rate of increase (not to be confused with an eigenvalue).
- each parasitoid parasitizes (and thus kills) a constant fraction of the host population; the fraction not killed is given by e^{-a} .
- parasitism by parasitoid individuals is independent, i.e. which fraction of the hosts a given parasitoid attacks is independent of which hosts any other parasitoid attacks; the probability any given host escapes parasitism by the population of P_t parasitoids thus is the probability it escapes parasitism by any one parasitoid, e^{-a} , raised to the P_t power: the fraction of hosts surviving is to reproduce is e^{-aP_t} .
- each parasitized host gives rise to c parasitoids in the next generation.

The fraction of hosts not parasitized, e^{-aP_t} , is equal to the **0 term** — i.e. the probability of a value of 0 — of a **Poisson distribution** with mean equal to aP_t . A Poisson distribution is closely related to a binomial distribution, and describes the frequency of counts of some rare event, when the events are independent of each other. In this application of the Poisson distribution, the rare events are parasitism of a particular host. The parameter a is the “area of discovery” — essentially, a search rate — of a parasitoid. We thus can think of there being a total of aP_t encounters of parasitoids with hosts, distributed randomly — each encounter independent of all the others — over the host population. The number of times each host is encountered will follow a Poisson distribution. The fraction of hosts which are not parasitized is the “zero term” of this distribution: the relative frequency of 0s.

Equilibrium

Assuming $H > 0$ and $P > 0$,

$$H^* = \lambda H^* e^{-aP^*}$$

$$1 = \lambda e^{-aP^*}$$

$$e^{aP^*} = \lambda$$

$$aP^* = \ln \lambda$$

$$P^* = \frac{\ln \lambda}{a}$$

and

$$P^* = cH^*(1 - e^{-aP^*})$$

$$\frac{\ln \lambda}{a} = cH^* \left(1 - e^{-a \left(\frac{\ln \lambda}{a} \right)} \right)$$

$$\frac{\ln \lambda}{a} = cH^*(1 - e^{-\ln \lambda})$$

$$\frac{\ln \lambda}{a} = cH^* \left(1 - \frac{1}{\lambda} \right)$$

$$\frac{\ln \lambda}{a} = cH^* \left(\frac{\lambda - 1}{\lambda} \right)$$

$$H^* = \frac{\lambda \ln \lambda}{ca(\lambda - 1)}$$

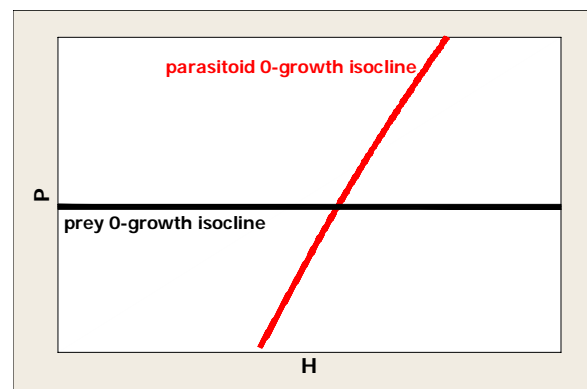
Stability

Isoclines:

The **host** zero-growth isocline is given by $1 = \lambda e^{-aP}$ or $P = \ln \lambda / a$: a straight horizontal line at a level determined by the host reproductive rate relative to the parasitism rate.

The **parasitoid** zero-growth isocline is given by $P = cH(1 - e^{-aP})$, which simplifies most easily into an equation for H as a function of

P : $H = \frac{P}{c(1 - e^{-aP})}$. This function curves to the right as it increases.



Stability analysis:

$$\begin{aligned}
J &= \begin{bmatrix} \frac{\partial g_1}{\partial H} & \frac{\partial g_1}{\partial P} \\ \frac{\partial g_2}{\partial H} & \frac{\partial g_2}{\partial P} \end{bmatrix}_{H^*, P^*} \\
&= \begin{bmatrix} \frac{\partial}{\partial H} \lambda H e^{-aP} & \frac{\partial}{\partial P} \lambda H e^{-aP} \\ \frac{\partial}{\partial H} cH(1 - e^{-aP}) & \frac{\partial}{\partial P} cH(1 - e^{-aP}) \end{bmatrix}_{V^*, P^*} \\
&= \begin{bmatrix} \lambda e^{-aP^*} & -a\lambda H^* e^{-aP^*} \\ c(1 - e^{-aP^*}) & acH^* e^{-aP^*} \end{bmatrix} \\
&= \begin{bmatrix} \lambda e^{-a\left(\frac{\ln \lambda}{a}\right)} & -a\lambda \left(\frac{\lambda \ln \lambda}{ca(\lambda - 1)}\right) e^{-a\left(\frac{\ln \lambda}{a}\right)} \\ c\left(1 - e^{-a\left(\frac{\ln \lambda}{a}\right)}\right) & ac\left(\frac{\lambda \ln \lambda}{ca(\lambda - 1)}\right) e^{-a\left(\frac{\ln \lambda}{a}\right)} \end{bmatrix} \\
&= \begin{bmatrix} 1 & -\frac{\lambda \ln \lambda}{c(\lambda - 1)} \\ \frac{c(\lambda - 1)}{\lambda} & \frac{\ln \lambda}{\lambda - 1} \end{bmatrix}
\end{aligned}$$

The trace of \mathbf{J} is $1 + \frac{\ln \lambda}{\lambda - 1}$ and the determinant is

$$\frac{\ln \lambda}{\lambda - 1} + \frac{\lambda \ln \lambda}{c(\lambda - 1)} \frac{c(\lambda - 1)}{\lambda} = \frac{\ln \lambda}{\lambda - 1} + \ln \lambda = \frac{\lambda \ln \lambda}{\lambda - 1}.$$

Notice that these terms — and thus the eigenvalues of the Jacobian — depend only on λ ; the other parameters (a and c) only determine the scale of the abundances, with no effect on the dynamics.

Proving it is complicated, but it turns out that the eigenvalues are complex, with **magnitudes greater than 1** for all λ for which the equilibrium even exists (all $\lambda > 1$). Thus the Nicholson-Bailey model is **always unstable**.