# Predator-prey models 

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## Introduction

Consider a population of two species, e.g., foxes ("predator") and rabbits ("prey").

- $P_{t}=$ size of prey.
- $Q_{t}=$ size of predator.

The change in population size of each is a function of both population sizes:

$$
\Delta P=F(P, Q), \quad \Delta Q=G(P, Q)
$$

## Question

What would happen if the predator or the prey disappeared?

- Prey, without predators: $\Delta P=r\left(P\left(1-P_{t} / M\right)\right)$.

■ Predators, without prey: $\Delta Q=-u Q$, where $u \in(0,1)$ is per-capita death rate.

## Simple predator-prey model

$$
\left\{\begin{array}{l}
\Delta P=r P(1-P / M)-s P Q \\
\Delta Q=-u Q+v P Q
\end{array} \quad r, s, u, v, K>0, u<1\right.
$$

## Predator-prey model

## Alternate form

$$
\left\{\begin{array}{l}
P_{t+1}=P_{t}(1+r(1-P / M))-s P_{t} Q_{t} \\
Q_{t+1}=(1-u) Q_{t}+v P_{t} Q_{t}
\end{array} \quad r, s, u, v, K>0, u<1\right.
$$

The $-s P Q$ and $v P Q$ are called mass-action terms. Roughly speaking:
■ $-s P Q$ describes a negative effect of the predator-prey interaction on the prey,
■ $v P Q$ describes a positive effect of the predator-prey interaction on the predator.
Qualitatively, larger values of $s$ and $v$ indicate stronger predator-prey interaction.
We can plot the solutions of these equations several ways:
■ time plots: $P_{t}$ vs. $t$, and $Q_{t}$ vs. $t$

- phase plots: $Q_{t}$ vs. $P_{t}$.

Time plots and phase plots
Consider the following predator-prey model:

$$
\left\{\begin{array}{l}
P_{t+1}=P_{t}\left(1+1.3\left(1-P_{t}\right)\right)-.5 P_{t} Q_{t} \\
Q_{t+1}=.3 Q_{t}+1.6 P_{t} Q_{t}
\end{array}\right.
$$

Solutions can be graphed using a time plot (left) or a phase plot (right):



## Equilibria

To find steady-state population(s), we set $P_{t}=P_{t+1}=P^{*}$ and $Q_{t}=Q_{t+1}=Q^{*}$.

$$
\left\{\begin{array} { r l } 
{ P _ { t + 1 } } & { = P _ { t } ( 1 + 1 . 3 ( 1 - P _ { t } ) ) - . 5 P _ { t } Q _ { t } } \\
{ Q _ { t + 1 } } & { = . 3 Q _ { t } + 1 . 6 P _ { t } Q _ { t } }
\end{array} \leadsto \leadsto \left\{\begin{array}{l}
P^{*}=P^{*}\left(1+1.3\left(1-P^{*}\right)\right)-.5 P^{*} Q^{*} \\
Q^{*}=.3 Q^{*}+1.6 P^{*} Q^{*}
\end{array}\right.\right.
$$

Via simple algebra, this reduces to the following system

$$
\left\{\begin{array}{l}
0=P^{*}\left(1.3-1.3 P^{*}-.5 Q^{*}\right) \\
0=Q^{*}\left(-.7+1.6 P^{*}\right)
\end{array}\right.
$$

If $Q^{*}=0$, then $P^{*}=0$ or $P^{*}=1$.
Alternatively, $P^{*}=.4375$, which would force $Q^{*}=1.4625$.
Thus, there are three equilibria:

$$
\left(P^{*}, Q^{*}\right)=(0,0), \quad(1,0), \quad(.4375,1.4625) .
$$

## Equilibria and nullclines

For the general predator-prey model:

$$
\left\{\begin{array}{l}
P_{t+1}=P_{t}\left(1+r\left(1-P_{t} / M\right)\right)-s P_{t} Q_{t} \\
Q_{t+1}=(1-u) Q_{t}+v P_{t} Q_{t}
\end{array} \quad r, s, u, v, K>0, u<1\right.
$$

the equilibrium equations (set $P_{t}=P_{t+1}=P^{*}$ and $Q_{t}=Q_{t+1}=Q^{*}$ ) are

$$
\left\{\begin{array}{l}
0=P^{*}\left(r\left(1-P^{*}\right)-s Q^{*}\right) \\
0=Q^{*}\left(-u+v P^{*}\right)
\end{array}\right.
$$

For Equation 2 to be satisfied, $Q^{*}=0$ or $-u+v P^{*}=0$.
Furthermore, Equation 1 is satisfied if $P^{*}=0$ or $r\left(1-P^{*}\right)-s Q^{*}=0$.

By simple algebra, we get three equilibria:

$$
\left(P^{*}, Q^{*}\right)=(0,0), \quad(1,0), \quad\left(\frac{u}{v}, \frac{r}{s}\left(1-\frac{u}{v}\right)\right)
$$

A nullcline is a line on which either $\Delta P=0$ or $\Delta Q=0$. In our example:

$$
P=0, \quad Q=\frac{r}{s}(1-P), \quad Q=0, \quad P=\frac{u}{v}
$$

## Nullclines

We can plot the nullclines on the $P Q$-plane to help visualize the dynamics.


- $\Delta P>0$ occurs below $Q=\frac{r}{s}(1-P)$.
- $\Delta Q>0$ occurs to the right of $P=\frac{u}{v}$.

Do you see how we determine the direction of the green arrows? Can we tell whether it spirals inward or outward?

## Nullclines

## Remark

Changing $r$ or $s$ doesn't affect the $Q$-nullcline.


Suppose the predator was an insect and the prey was an agricultural crop.
One might want to introduce a new crop variety with higher $r$, to try to "outgrow" the predator.

Unfortunately, this won't work: $P^{*}$ is unchanged, but $Q^{*}$ increases. (Why?)

## Linearization

Suppose $\left(P^{*}, Q^{*}\right)$ is a fixed point whose stability we wish to understand.
We can plug the following "perturbation" back into the original system:

$$
P_{t}=P^{*}+p_{t}, \quad P_{t+1}=P^{*}+p_{t+1}, \quad Q_{t}=Q^{*}+q_{t}, \quad Q_{t+1}=Q^{*}+q_{t+1}
$$

Consider the fixed point $\left(P^{*}, Q^{*}\right)=(.4375,1.4625)$ of our previous example. Plugging

$$
P_{t}=.4375+p_{t}, \quad P_{t+1}=.4375+p_{t+1}, \quad Q_{t}=1.4625+q_{t}, \quad Q_{t+1}=1.4625+q_{t+1}
$$

$$
\text { into } \quad\left\{\begin{array}{l}
P_{t+1}=P_{t}\left(1+1.3\left(1-P_{t}\right)\right)-.5 P_{t} Q_{t} \\
Q_{t+1}=.3 Q_{t}+1.6 P_{t} Q_{t}
\end{array}\right.
$$

and simplifying yields

$$
\left\{\begin{array}{l}
p_{t+1}=.43125 p_{t}-.21875 q_{t}-1.3 p_{t}^{2}-.5 p_{t} q_{t} \\
q_{t+1}=2.34 p_{t}+q_{t}+1.6 p_{t} q_{t}
\end{array}\right.
$$

For small perturbations ( $p_{t}, q_{t}$ ), we can neglect the nonlinear terms (e.g., $p_{t}^{2}, q_{t}^{2}$, and $p_{t} \boldsymbol{q}_{t}$ ) which are $\approx 0$, leaving a linear system $\mathbf{p}_{t+1} \approx \mathbf{A} \mathbf{p}_{t}$.

## Linearization (cont.)

Thus, given a small perturbation $\left(p_{t}, q_{t}\right)$ at time $t$, it can be described at time $t+1$ by a linear equation $\mathbf{p}_{t+1} \approx \mathbf{A p}_{t}$ :

$$
\left[\begin{array}{c}
p_{t+1} \\
q_{t+1}
\end{array}\right] \approx\left[\begin{array}{cc}
.43125 & -.21875 \\
2.34 & 1
\end{array}\right]\left[\begin{array}{l}
p_{t} \\
q_{t}
\end{array}\right]
$$

The eigenvalues of $\mathbf{A}$ are $\lambda=.7156 \pm .6565 i$, which have norm

$$
|\lambda|=\sqrt{(.7156)^{2}+(.6565)^{2}}=.9711<1
$$

Thus, this perturbation from the steady-state is shrinking. The population will spiral back into the steady-state $\left(P^{*}, Q^{*}\right)=(.4375,1.4625)$.

Types of equilibrium points
■ $\left|\lambda_{1}\right|<1,\left|\lambda_{2}\right|<1, \quad$ stable
■ $\left|\lambda_{1}\right|>1,\left|\lambda_{2}\right|>1$, unstable
■ $\left|\lambda_{1}\right|<1,\left|\lambda_{2}\right|>1$, saddle

## Other interaction models

- Competition: 2 species fill the same niche in an environment.

$$
\left\{\begin{array}{l}
\Delta P=r P(1-(P+Q) / K) \\
\Delta Q=r Q(1-(P+Q) / K)
\end{array}\right.
$$

Question: Does one species "win"? Or can the co-exist?

- Competition with predator/prey: $\left\{\begin{array}{l}\Delta P=r P(1-(P+Q) / K)-s P Q \\ \Delta Q=r Q(1-(P+Q) / K) \pm v P Q\end{array}\right.$

■ Mutualism: e.g., $P=$ sharks, $Q=$ feeder fish. $\left\{\begin{array}{l}\Delta P=r P(1-P / K)+s P Q \\ \Delta Q=-u Q+v P Q\end{array}\right.$

- Immune system vs. infective agent:

$$
\begin{aligned}
& P: \text { immune cells } \\
& Q: \text { level of infection }
\end{aligned} \quad\left\{\begin{array}{l}
\Delta P=r Q-s P Q \\
\Delta Q=u Q-v P Q
\end{array}\right.
$$

- $-s P Q$ : negative effect on immune system from fighting
- $-s P Q$ : limited effect on immune system from fighting
- $r Q$ : immune response is proportional to infection level

