#### 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.
- $Q_t = \text{size of predator.}$

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

$$\Delta P = F(P, Q), \qquad \Delta Q = G(P, Q).$$

#### Question

What would happen if the predator or the prey disappeared?

- Prey, without predators:  $\Delta P = r(P(1 P_t/M))$ .
- Predators, without prey:  $\Delta Q = -uQ$ , where  $u \in (0, 1)$  is per-capita death rate.

#### Simple predator-prey model

$$\begin{cases} \Delta P = rP(1 - P/M) - sPQ \\ \Delta Q = -uQ + vPQ \end{cases}$$

# Predator-prey model

#### Alternate form

$$\begin{cases} P_{t+1} = P_t(1 + r(1 - P/M)) - sP_tQ_t \\ Q_{t+1} = (1 - u)Q_t + vP_tQ_t \end{cases}$$
 r, s, u,

r,s,u,v,K>0, u<1

The -sPQ and vPQ are called mass-action terms. Roughly speaking:

- -sPQ describes a *negative* effect of the predator-prey interaction on the prey,
- *vPQ* 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:

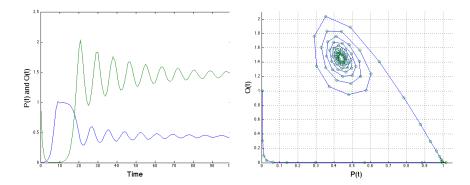
- **time plots**:  $P_t$  vs. t, and  $Q_t$  vs. t
- phase plots:  $Q_t$  vs.  $P_t$ .

## Time plots and phase plots

Consider the following predator-prey model:

$$\begin{cases} P_{t+1} = P_t (1 + 1.3(1 - P_t)) - .5P_t Q_t \\ Q_{t+1} = .3Q_t + 1.6P_t Q_t \end{cases}$$

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  $Q_t = Q_{t+1} = Q^*$ .

Via simple algebra, this reduces to the following system

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

If  $Q^* = 0$ , then  $P^* = 0$  or  $P^* = 1$ .

Alternatively,  $P^* = .4375$ , which would force  $Q^* = 1.4625$ .

Thus, there are three equilibria:

$$(P^*, Q^*) = (0, 0), (1, 0), (.4375, 1.4625).$$

## Equilibria and nullclines

For the general predator-prey model:

$$\begin{cases} P_{t+1} = P_t(1 + r(1 - P_t/M)) - sP_tQ_t \\ Q_{t+1} = (1 - u)Q_t + vP_tQ_t \end{cases} \quad r, s, u, v, K > 0, \quad u < 1 \end{cases}$$

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

$$\begin{cases} 0 = P^* (r(1 - P^*) - sQ^*) \\ 0 = Q^* (-u + vP^*). \end{cases}$$

For Equation 2 to be satisfied,  $Q^* = 0$  or  $-u + vP^* = 0$ .

Furthermore, Equation 1 is satisfied if  $P^* = 0$  or  $r(1 - P^*) - sQ^* = 0$ .

By simple algebra, we get three equilibria:

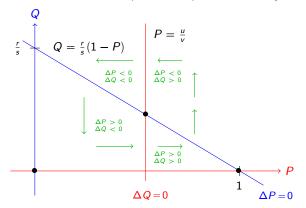
$$(P^*, Q^*) = (0, 0), \ (1, 0), \ \left(\frac{u}{v}, \frac{r}{s}(1 - \frac{u}{v})\right).$$

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

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

## Nullclines

We can plot the nullclines on the PQ-plane to help visualize the dynamics.



•  $\Delta P > 0$  occurs below  $Q = \frac{r}{s}(1 - P)$ .

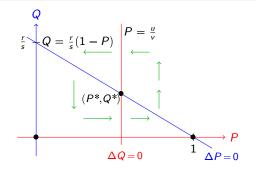
•  $\Delta Q > 0$  occurs to the right of  $P = \frac{u}{v}$ .

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  $(P^*, Q^*)$  is a fixed point whose stability we wish to understand.

We can plug the following "perturbation" back into the original system:

$$P_t = P^* + p_t$$
,  $P_{t+1} = P^* + p_{t+1}$ ,  $Q_t = Q^* + q_t$ ,  $Q_{t+1} = Q^* + q_{t+1}$ .  
Consider the fixed point  $(P^*, Q^*) = (.4375, 1.4625)$  of our previous example.  
Plugging

$$\begin{split} P_t &= .4375 + p_t \,, \quad P_{t+1} = .4375 + p_{t+1} \,, \quad Q_t = 1.4625 + q_t \,, \quad Q_{t+1} = 1.4625 + q_{t+1} \,. \\ & \\ & \text{into} \qquad \begin{cases} P_{t+1} = P_t (1 + 1.3(1 - P_t)) - .5P_t Q_t \\ Q_{t+1} = .3Q_t + 1.6P_t Q_t \end{cases} \end{split}$$

and simplifying yields

$$\begin{cases} p_{t+1} = .43125p_t - .21875q_t - 1.3p_t^2 - .5p_tq_t \\ q_{t+1} = 2.34p_t + q_t + 1.6p_tq_t \end{cases}$$

For small perturbations  $(p_t, q_t)$ , we can neglect the nonlinear terms (e.g.,  $p_t^2$ ,  $q_t^2$ , and  $p_t q_t$ ) 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  $(p_t, q_t)$  at time t, it can be described at time t + 1 by a linear equation  $\mathbf{p}_{t+1} \approx \mathbf{A}\mathbf{p}_t$ :

$$\begin{bmatrix} p_{t+1} \\ q_{t+1} \end{bmatrix} \approx \begin{bmatrix} .43125 & -.21875 \\ 2.34 & 1 \end{bmatrix} \begin{bmatrix} p_t \\ q_t \end{bmatrix}$$

The eigenvalues of **A** are  $\lambda = .7156 \pm .6565i$ , 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  $(P^*, Q^*) = (.4375, 1.4625)$ .

#### Types of equilibrium points

- $|\lambda_1| < 1$ ,  $|\lambda_2| < 1$ , stable
- $\bullet \ |\lambda_1|>1, \ |\lambda_2|>1, \ \text{ unstable}$
- $\ \ \, \|\lambda_1\|<1,\ |\lambda_2|>1, \ \ \, \text{saddle}$

#### Other interaction models

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

$$\begin{cases} \Delta P = rP(1 - (P + Q)/K) \\ \Delta Q = rQ(1 - (P + Q)/K) \end{cases}$$

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

• Competition with predator/prey:  $\begin{cases} \Delta P = rP(1 - (P + Q)/K) - sPQ \\ \Delta Q = rQ(1 - (P + Q)/K) + vPQ \end{cases}$ 

• Mutualism: e.g., 
$$P = \text{sharks}$$
,  $Q = \text{feeder fish}$ . 
$$\begin{cases} \Delta P = rP(1 - P/K) + sPQ \\ \Delta Q = -uQ + vPQ \end{cases}$$

- Immune system vs. infective agent:
  - $\begin{array}{l} P: \text{ immune cells} \\ Q: \text{ level of infection} \end{array} \begin{cases} \Delta P = rQ sPQ \\ \Delta Q = uQ vPQ \end{cases}$
  - -sPQ: negative effect on immune system from fighting
  - -sPQ: limited effect on immune system from fighting
  - rQ: immune response is proportional to infection level