MA 331

Differential Equations for the Life Sciences

Fall 2018

Lectures 12 and 13

Moving Beyond One Dimensional Models

Now that we have more than one state variable, our phase space is no longer the line.

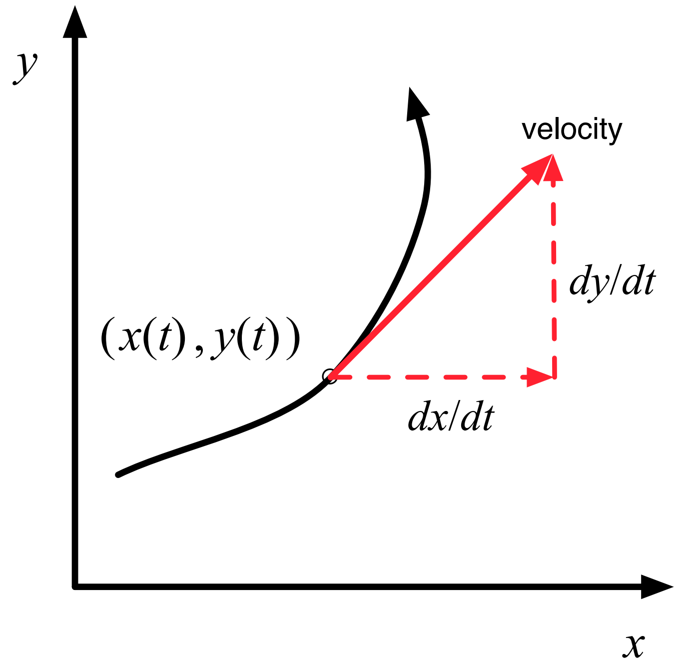
For a two dimensional model, we have the phase plane

(we will typically stick to 2D, because sketching things gets more difficult for 3+ dimensions)

$$\frac{dx}{dt} = f(t, x, y)$$

$$\frac{dy}{dt} = g(t, x, y)$$

We look at the point (*x*,*y*), and how this changes with time



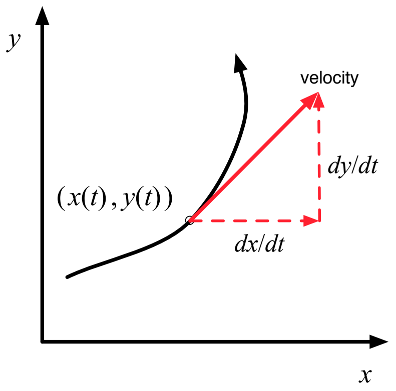
Solution traces out a curve in the phase plane

Velocity vector at time *t* is tangent to solution curve at that point

Velocity vector has two components, one in *x* direction, one in *y* direction, given by *dx/dt* and *dy/dt*, respectively

Vector Fields for Two Dimensional Models

Consider an autonomous two dimensional model
$$\frac{dx}{dt} = f(x,y)$$
$$\frac{dy}{dt} = g(x,y)$$



Right hand side of the differential equation does not depend explicitly on time, so there is a unique velocity, (*dx*/*dt*, *dy*/*dt*), associated with each point (*x*,*y*) in the phase plane

Create vector field:

1. Take a grid of points in the phase plane and calculate velocity at each
2. Draw arrows that depict these velocities

Each arrow is tangent to the solution curve passing through that point

By following arrows we can get a very good idea of what solution curves look like

Length of an arrow tells us about speed of motion, signs of components and their relative sizes tell us about direction of motion

An important consequence of having a unique velocity at each point:
solution curves cannot cross

Vector Fields for Two Dimensional Models

Example:

$$\frac{dx}{dt} = x(3-2y)$$

$$\frac{dy}{dt} = y(2x-1)$$

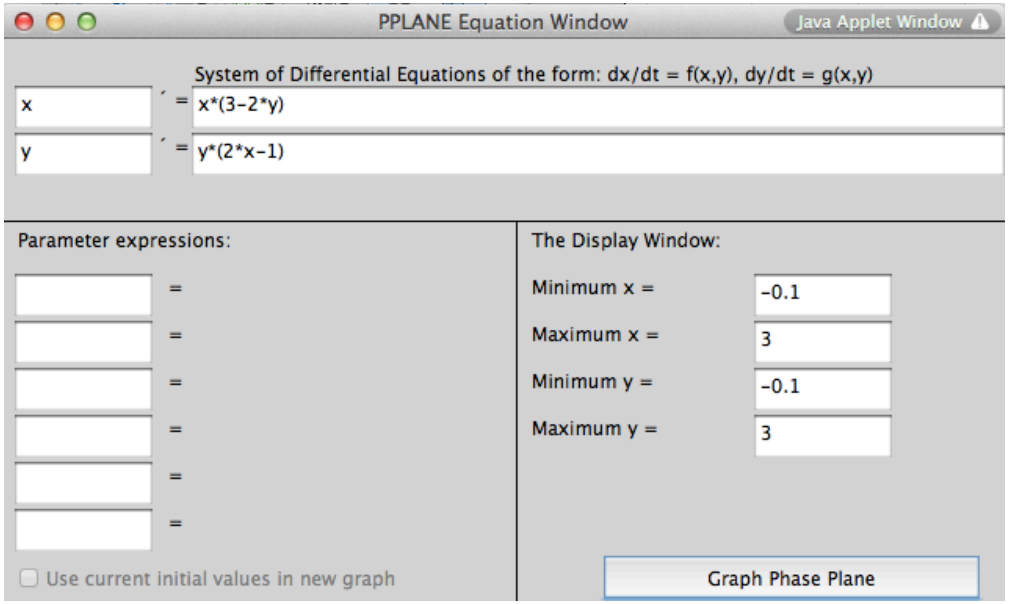
(This is a model for a predator-prey interaction, but we shall talk about that later…)

Use **PPLANE** web app to create vector field:

Link is on “resources” page on course website; then click on PPLANE button

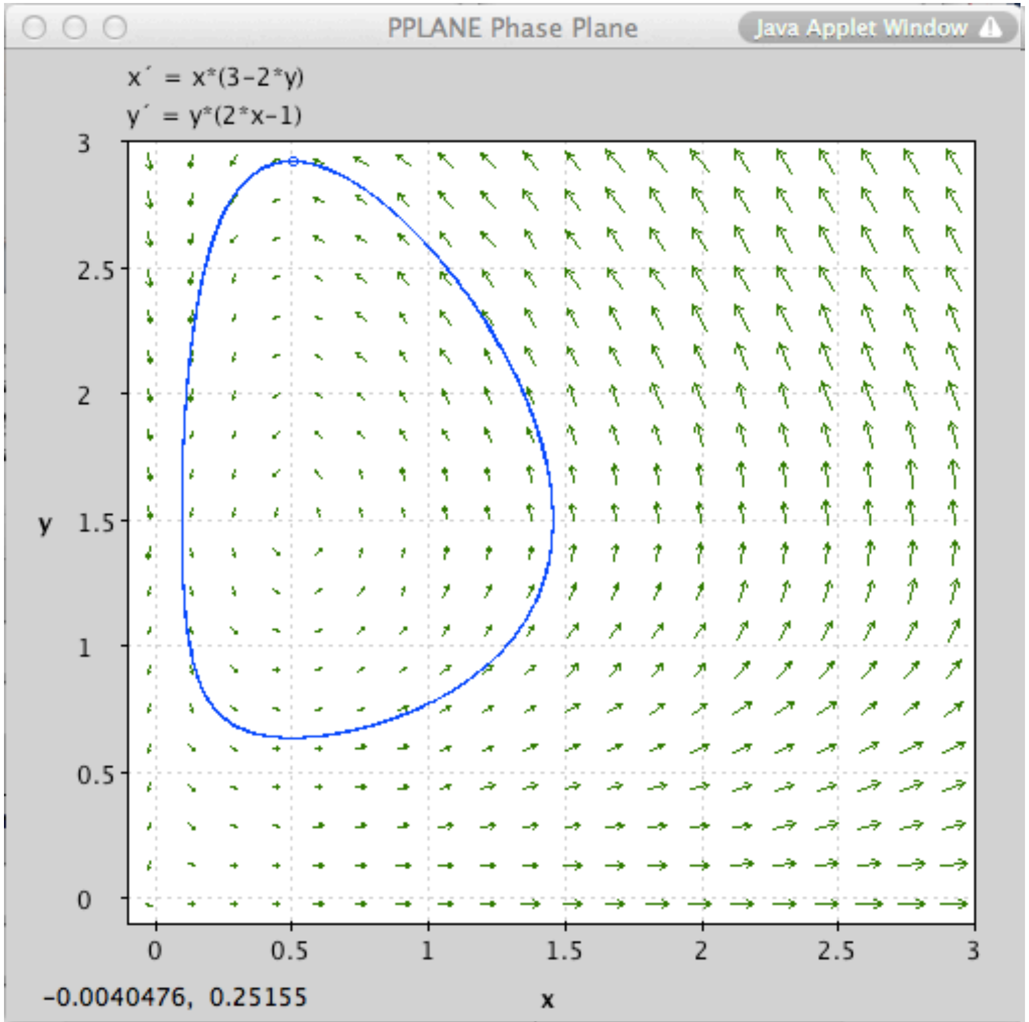
Type equations into boxes (note * for multiply), select ranges for *x* and *y* axes, then click “Graph Phase Plane”

One nice feature of PPLANE: you can use state variables other than *x* and *y*… enter different symbols in the boxes before the primes



PPLANE: Vector Fields for 2D Models

$$\frac{dx}{dt} = x(3-2y)$$
$$\frac{dy}{dt} = y(2x-1)$$



Click on graph and PPLANE will draw the solution curve (trajectory) through that point.

By default, PPLANE draws curves forward and backward in time

Can change this: "Options->Solution Direction"

(Another interesting option: "Options->Delay Time Per Point" allows you to see curve being traced out over time)

Notice: solution curve returns to its starting point… then behavior will repeat. **Oscillatory solution** … possible in 2D because you can return to a point without backtracking (unlike on the line)

Lotka-Volterra Predator Prey Model

Two species: one is a predator, the other its prey

$$\frac{dN}{dt} = N\left(a - bP\right) \qquad \text{prey}$$

$$\frac{dP}{dt} = P\left(cN - d\right) \qquad \text{predator}$$

a, b, c, d are positive constants

Per-capita growth rate of prey (N) is $a-bP$ … depends on the number of predators (P)

Per-capita growth rate of predators is $cN-d$ … depends on the number of prey

Model Assumptions:

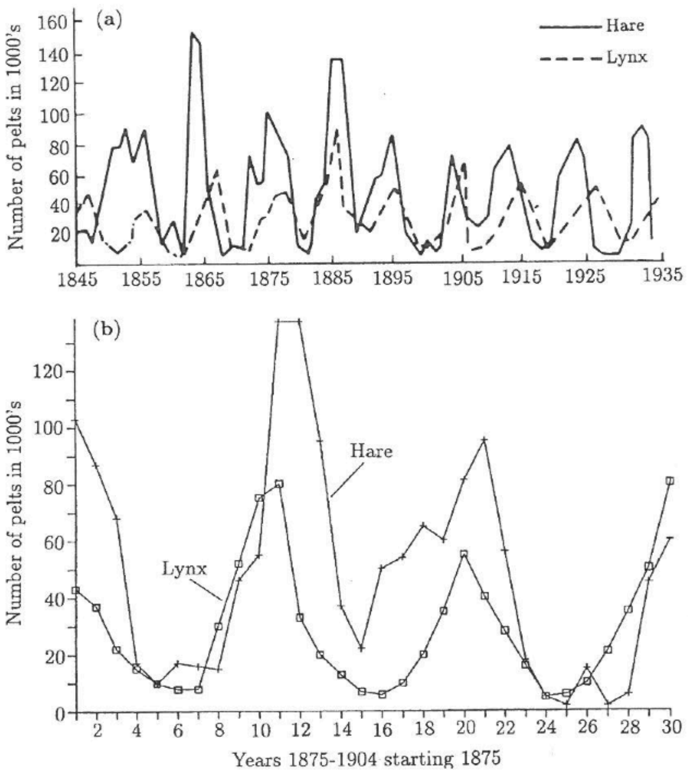
1. In the absence of predators, prey grow exponentially with per-capita growth rate a
2. Predation reduces per-capita growth rate of prey in a linear fashion (slope b)
3. In the absence of prey, predator population declines exponentially, per-capita decay rate d
4. Consumption of prey increases growth rate of predators in a linear fashion (slope c)

We will return to discuss these assumptions later on…

Canada Lynx-Snowshoe Hare

Often given as an example of a predator-prey system

Numbers of hares and lynx oscillate with (approximately) ten year period:



Lotka-Volterra Predator Prey Model

$$\frac{dN}{dt} = N\left(a - bP\right)$$ prey

$$\frac{dP}{dt} = P\left(cN - d\right)$$ predator

a, *b*, *c*, *d* are positive constants

How much understanding can we get about the behavior of the model?

As we discussed some time ago, there are three ways to analyze a model:

1. Analytic: we cannot find formulae for $N(t)$ and $P(t)$
(although there is some analysis that we can do… see later)

2. Numerical: we already saw a numerically-obtained solution curve
one issue with this approach: we have to choose values for *a*, *b*, *c*, *d*

3. Graphical/qualitative analysis: Can we understand the nature of the vector field and get a fair idea of behavior without solving numerically?

Analysis of the Lotka-Volterra Predator Prey Model

$$\frac{dN}{dt} = N\left(a - bP\right)$$ prey

$$\frac{dP}{dt} = P\left(cN - d\right)$$ predator

a, *b*, *c*, *d* are positive constants

Constant solutions? Require **both** *dN*/*dt* **and** *dP*/*dt* to equal zero

$$\frac{dN}{dt} = 0 \quad \text{means} \quad N\left(a - bP\right) = 0$$

so either *N* = 0 or *a* – *bP* = 0

(1) Either *N* = 0 or ***P* = *a*/*b***

$$\frac{dP}{dt} = 0 \quad \text{means} \quad P\left(cN - d\right) = 0$$

(2) Either *P* = 0 or ***N* = *d*/*c***

For both *dN*/*dt* = 0 and *dP*/*dt* = 0, pick combinations of conditions, one from (1) and one from (2)

Four possibilities, but two are incompatible:
N cannot equal both 0 and *d*/*c*; *P* cannot equal both *a*/*b* and 0

Leaves two equilibria: (*N*,*P*) = (0,0) and (*d*/*c*, *a*/*b*)

First: neither present; second: co-existence

Analysis of the Lotka-Volterra Predator Prey Model

Can we figure out anything about the directions of arrows on the vector field?

$$\frac{dN}{dt} = N(a - bP) \qquad \text{prey}$$

$$\frac{dP}{dt} = P(cN - d) \qquad \text{predator}$$

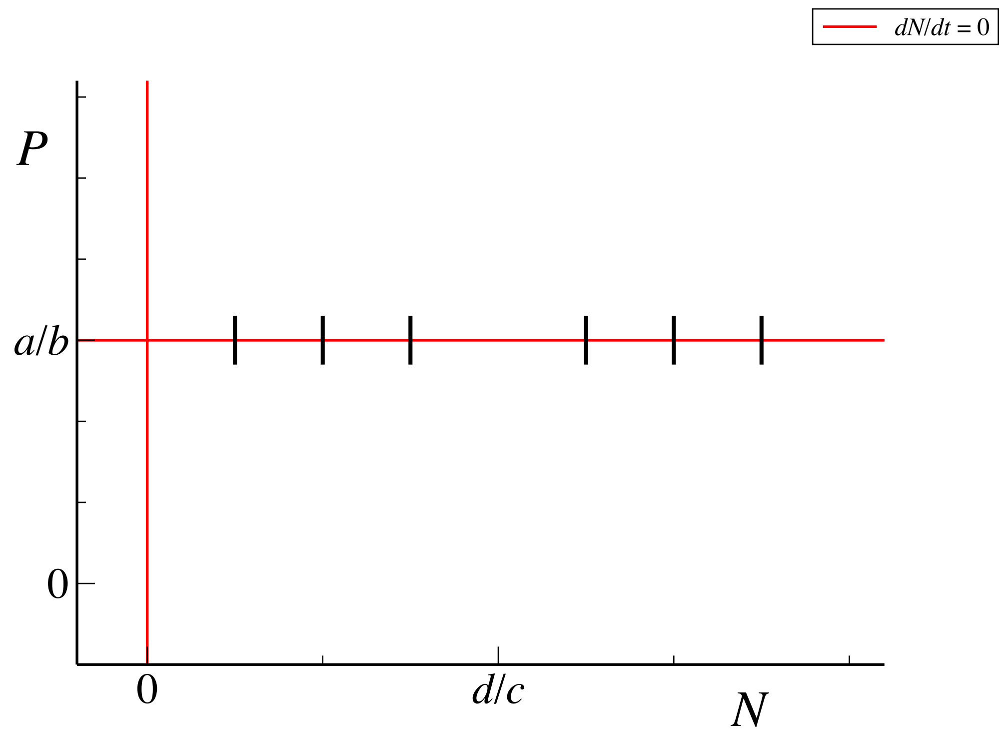
Nullclines: curves where **either** *dN*/*dt* = 0 (“*N* nullcline”) **or** *dP*/*dt* = 0 (“*P* nullcline”)

Notice: *N* and *P* nullclines intersect at equilibrium points

dN/*dt* = 0 means horizontal component of velocity is zero: motion is purely vertical at such points

We just saw that this occurs when either *N* = 0 or *P* = *a*/*b*

We will focus on non-negative values of *N* and *P*, but similar reasoning can be applied to explore behavior when one or both is/are negative



Analysis of the Lotka-Volterra Predator Prey Model

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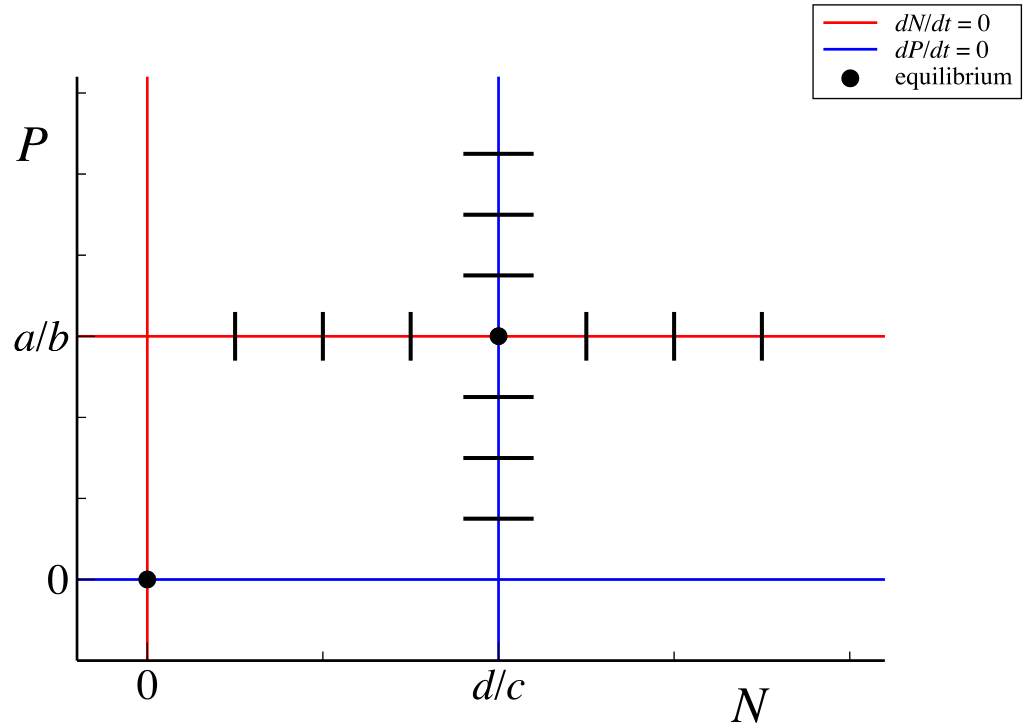
Nullclines: curves where **either** *dN/dt* = 0 (“*N* nullcline”) **or** *dP/dt* = 0 (“*P* nullcline”)

dP/dt = 0 means vertical component of velocity is zero: motion is purely horizontal at such points

We just saw that this occurs when either *P* = 0 or *N* = *d/c*

Notice equilibria at intersections between *N* and *P* nullclines



Analysis of the Lotka-Volterra Predator Prey Model

$$\frac{dN}{dt} = N\left(a - bP\right) \qquad \text{prey}$$

$$\frac{dP}{dt} = P\left(cN - d\right) \qquad \text{predator}$$

N nullcline: $dN/dt = 0$, so either $N = 0$ or $P = a/b$

The sign of dN/dt changes as you cross the N nullcline:

dN/dt is the product of N and $a - bP$

sign of N changes as you cross $N = 0$

sign of $a - bP$ changes between $P < a/b$ and $P > a/b$

P nullcline: $dP/dt = 0$, so either $P = 0$ or $N = d/c$

The sign of dP/dt changes as you cross the P nullcline:

dP/dt is the product of P and $cN - d$

sign of P changes as you cross $P = 0$

sign of $cN - d$ changes between $N < d/c$ and $N > d/c$

Analysis of the Lotka-Volterra Predator Prey Model

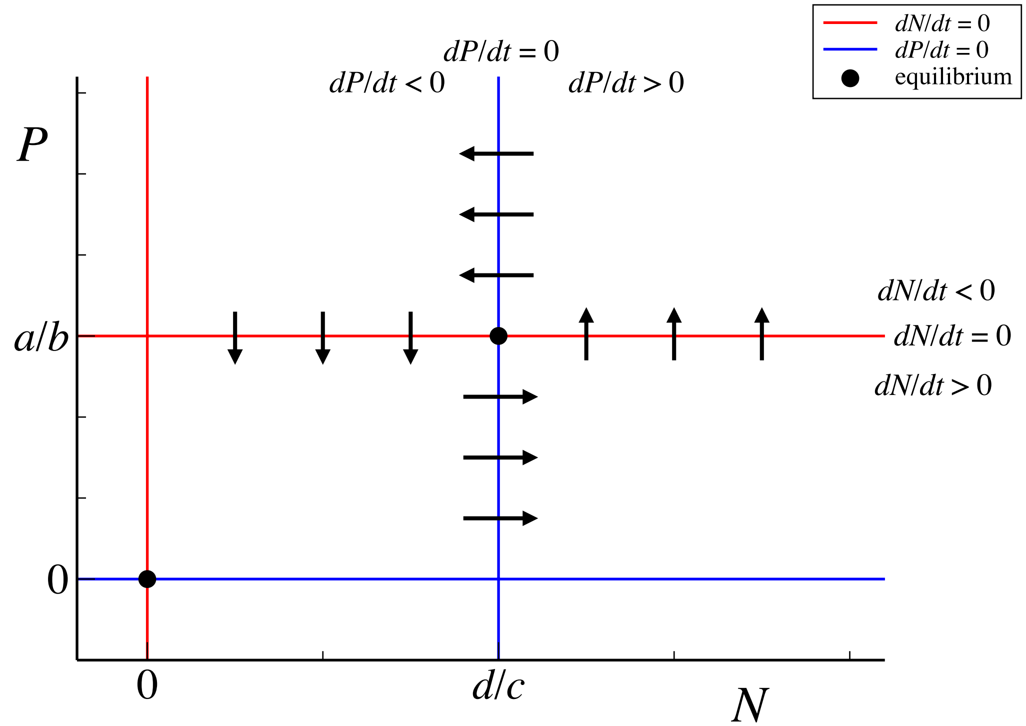
$$\frac{dN}{dt} = N(a - bP) \qquad \text{prey}$$

$$\frac{dP}{dt} = P(cN - d) \qquad \text{predator}$$

The sign of *dN/dt* changes as you cross the *N* nullcline

The sign of *dP/dt* changes as you cross the *P* nullcline

Can fill in directions on line segments



Analysis of the Lotka-Volterra Predator Prey Model

The sign of *dN/dt* changes as you cross the *N* nullcline $\frac{dN}{dt} = N\left(a - bP\right)$ prey

The sign of *dP/dt* changes as you cross the *P* nullcline $\frac{dP}{dt} = P\left(cN - d\right)$ predator

Conclusion: nullclines divide up the phase plane into regions where arrows share a common orientation

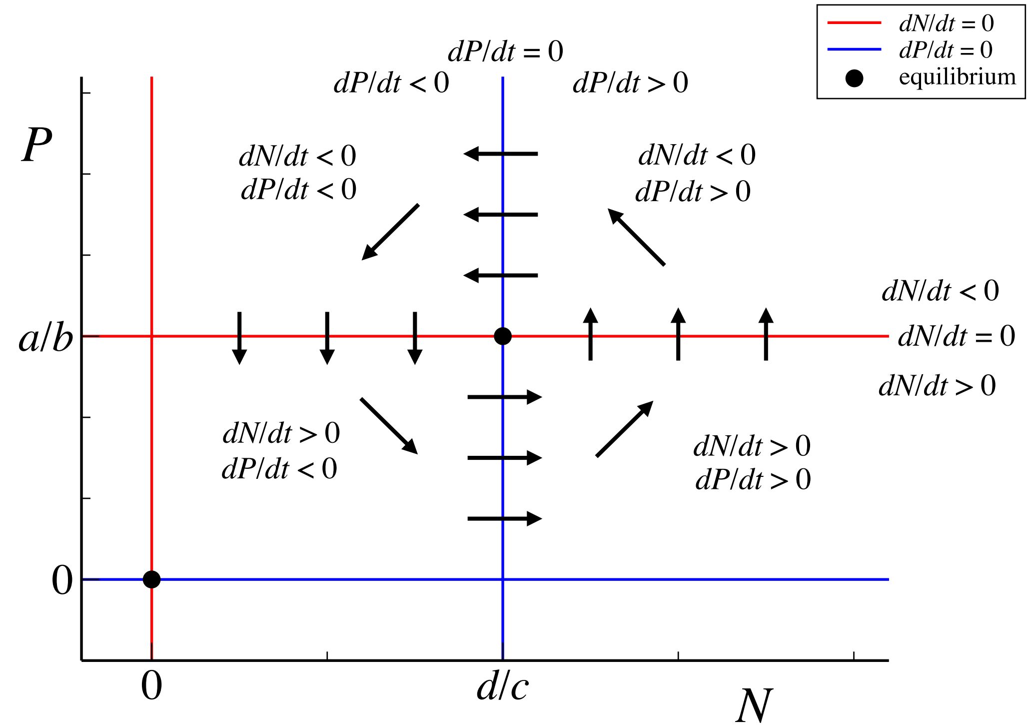
e.g. $dN/dt > 0$, $dP/dt > 0$:

arrows are up and to the right

$dN/dt < 0$, $dP/dt > 0$:

arrows are up and to the left

and so on…



Analysis of the Lotka-Volterra Predator Prey Model

Nullclines divide up the phase plane into regions where arrows share a common orientation

$$\frac{dN}{dt} = N\left(a - bP\right) \qquad \text{prey}$$

$$\frac{dP}{dt} = P\left(cN - d\right) \qquad \text{predator}$$

Finally, fill in directions on axes

Note decay of predator when prey absent, growth of prey when predator absent

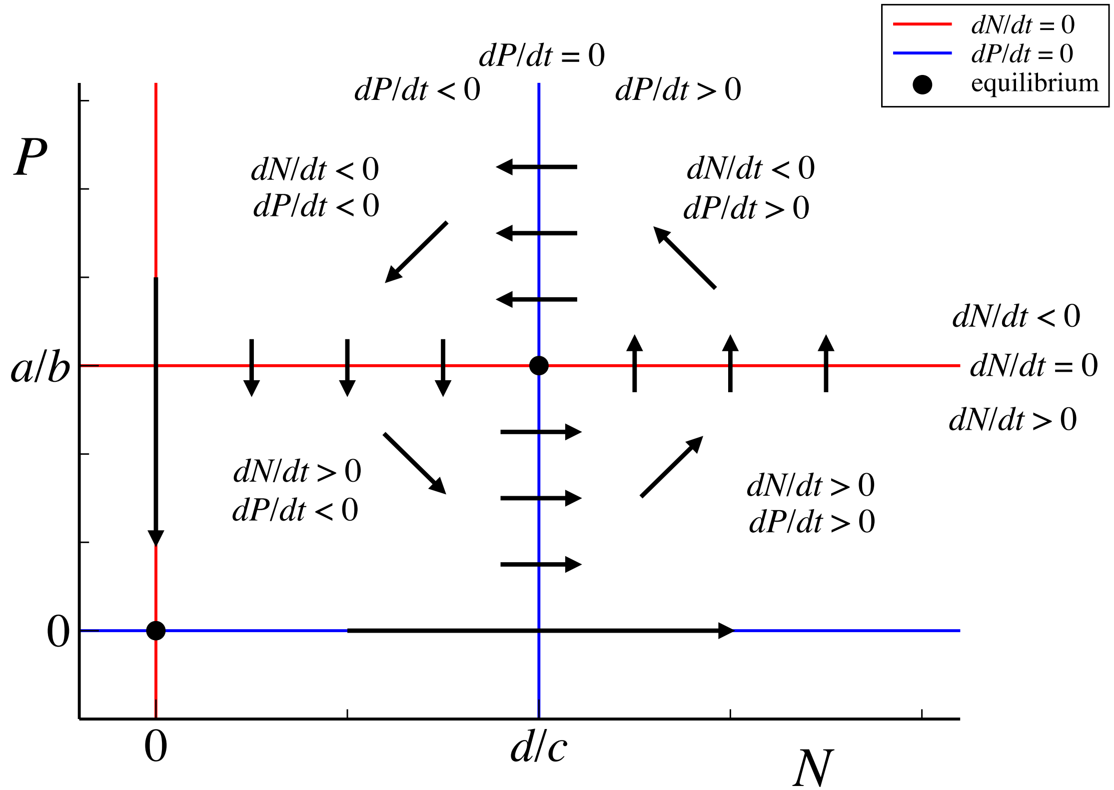
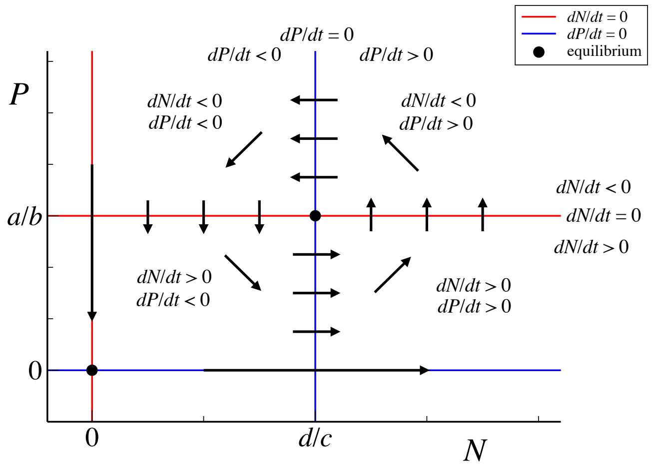


Diagram gives us a pretty good idea of behavior! It suggests the possibility of oscillations, but our nullcline analysis doesn't give enough information for us to be sure

Biological Comments on Lotka-Volterra Predator Prey Model



$$\frac{dN}{dt} = N\left(a - bP\right) \qquad \text{prey}$$

$$\frac{dP}{dt} = P\left(cN - d\right) \qquad \text{predator}$$

Direction of the arrows, the oscillatory behavior and its **anti-clockwise direction** make sense biologically:

What happens when prey are abundant, predators are few?

Prey will increase, predators will increase (arrow up and to the right)

When both predator and prey are abundant, predator numbers will increase, prey will decrease (arrow up and to the left)

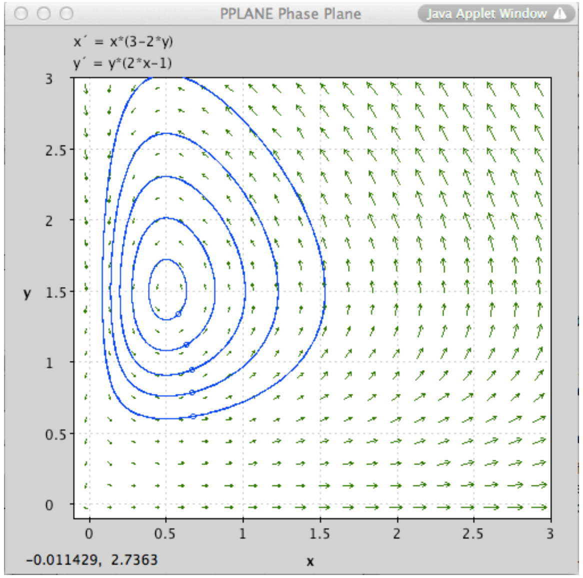
When predator is abundant and prey few, both predator and prey numbers will decrease (arrow down and to the left)

When predator and prey are both few, prey will increase, predators will decrease (arrow down and to the right)

Cycle repeats…

This broad behavior, with anti-clockwise oscillatory motion (possibly damped), is common to many predator-prey models/systems

Oscillations in the Lotka-Volterra Predator Prey Model



$$\frac{dN}{dt} = N(a - bP) \qquad \text{prey}$$

$$\frac{dP}{dt} = P(cN - d) \qquad \text{predator}$$

An odd thing: whatever your initial condition (provided you aren't on the axes or at the equilibrium), the solution curve loops around and returns to its starting point

Infinitely many periodic solutions

On average, solution curves neither approach nor move away from the co-existence equilibrium

Neutral stability

Neutral stability is a fairly uncommon phenomenon in biological models.

Interesting fact: there is a class of physical models where neutral stability is common… e.g., when you have conservation of energy

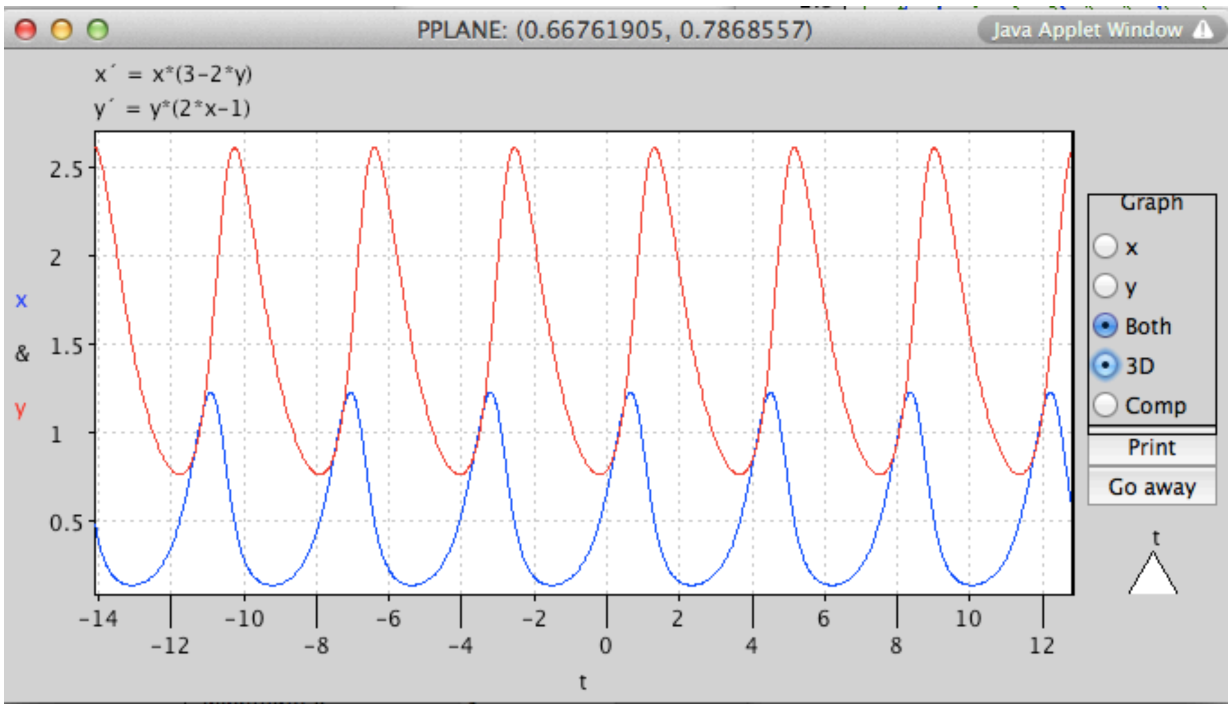
Oscillations in the Lotka-Volterra Predator Prey Model

What do oscillations look like when plotted as *N* and *P* vs time?

In PPLANE, select “Graph -> Both x-t and y-t”

$$\frac{dN}{dt} = N(a - bP) \qquad \text{prey}$$

$$\frac{dP}{dt} = P(cN - d) \qquad \text{predator}$$



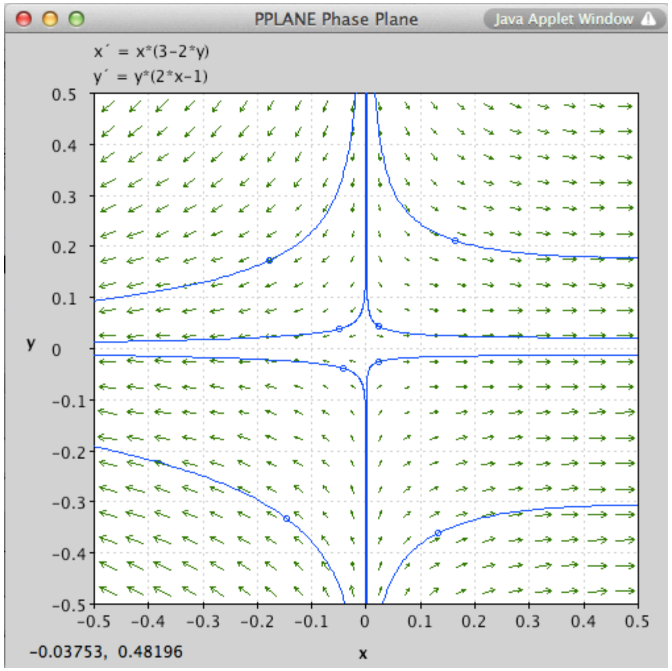
Blue: prey (*N*)
Red: predators (*P*)

Notice: prey numbers start increasing before predator numbers do; prey numbers fall before predators do

Predator oscillation is “behind” prey oscillation

in agreement with the verbal argument we gave before

Behavior Near the Other Equilibrium



$$\frac{dN}{dt} = N(a - bP) \qquad \text{prey}$$

$$\frac{dP}{dt} = P(cN - d) \qquad \text{predator}$$

In addition to the neutrally stable co-existence equilibrium, there is an equilibrium at (0,0)

Solution curves move upwards or downwards towards P = 0, but left or right away from N = 0

… first moving towards (0,0), then away from it

This type of equilibrium is known as a “saddle” – we will talk about this later in the course

Some Analysis of the Lotka-Volterra Predator Prey Model

Mentioned earlier that it is possible to do some analysis of this model

$$\frac{dN}{dt} = N\left(a - bP\right) \qquad \text{prey}$$

$$\frac{dP}{dt} = P\left(cN - d\right) \qquad \text{predator}$$

Cannot solve for *N*(*t*) and *P*(*t*), but can get a relationship between *N* and *P*, eliminating time

Calculate *dP*/*dN* … Chain Rule says that $\frac{dP}{dN} = \frac{dP}{dt} \cdot \frac{dt}{dN} = \frac{dP}{dt} \Big/ \frac{dN}{dt}$

$$\frac{dP}{dN} = \frac{P\left(cN - d\right)}{N\left(a - bP\right)}$$

This is a separable differential equation

$$\frac{\left(a - bP\right)}{P}\frac{dP}{dN} = \frac{cN - d}{N}$$

$$\int \frac{\left(a - bP\right)}{P}\frac{dP}{dN}\,dN = \int \frac{cN - d}{N}\,dN$$

$$\int \left(\frac{a}{P} - b\right) dP = \int \left(c - \frac{d}{N}\right) dN$$

$$a \ln P - bP = cN - d \ln N + k$$

k : constant of integration

if we focus on *N*, *P* > 0, we don't need |*N*|, |*P*| inside logs

Some Analysis of the Lotka-Volterra Predator Prey Model

$$\frac{dN}{dt} = N\left(a - bP\right) \qquad \text{prey}$$

$$\frac{dP}{dt} = P\left(cN - d\right) \qquad \text{predator}$$

Solution curves satisfy

$$a\ln P - bP = cN - d\ln N + k$$

Can write this as $a\ln P - bP - cN + d\ln N = k$

Different values of the constant of integration, *k* , pick out different solution curves, i.e. correspond to different initial conditions

Solution curves correspond to contours of the function $F(N,P) = a\ln P - bP - cN + d\ln N$

(This analysis confirms that solution curves form closed curves, in addition to providing us a way of graphing solution curves without integrating numerically)

Canada Lynx-Snowshoe Hare Revisited

Replot data as a phase plane plot

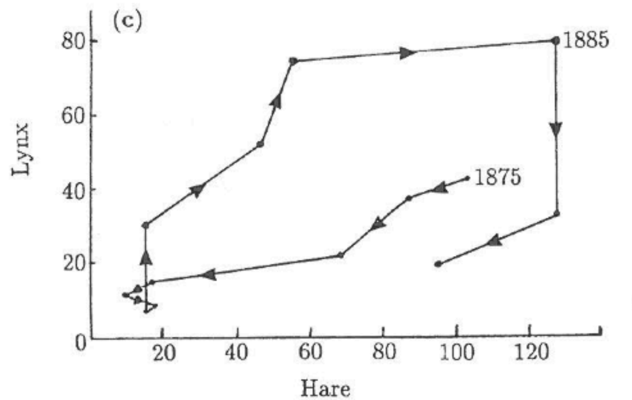


Figure 3.3. (**a**) Fluctuations in the number of pelts sold by the Hudson Bay Company. (Redrawn from Odum 1953) (**b**) Detail of the 30-year period starting in 1875, based on the data from Elton and Nicholson (1942). (**c**) Phase plane plot of the data represented in (**b**). (After Gilpin 1973)

Trajectories move clockwise! (Compare to anti-clockwise motion that we saw previously)
From time series plot, the numbers of lynx often peak before the numbers of hare…

… lynx are the prey and hares are the predators ??? !!!

… not the simple predator-prey system that is often claimed!
(see Krebs et al., 2001, for more discussion)

Notice: the mathematical analysis provides an important insight into this ecological system

Criticisms of Lotka-Volterra Predator Prey Model

Recall model's assumptions:

1. In the absence of predators, prey grow exponentially with per-capita growth rate *a*
2. Predation reduces per-capita growth rate of prey in a linear fashion (slope *b*)
3. In the absence of prey, predator population declines exponentially, per-capita decay rate *d*
4. Consumption of prey increases growth rate of predators in a linear fashion (slope *c*)

Exponential growth of prey is unrealistic : logistic growth might be more appropriate

Predation term is linear in the number of prey : unrealistic because a given number of predators can only eat a certain number of prey : predation is likely a saturating function of the number of prey (c.f. harvesting model)

Improved model:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{BNP}{N+D}$$

$$\frac{dP}{dt} = \frac{bNP}{N+D} - cP$$

Parameter *D* measures how quickly predation saturates with increasing number of prey

More Realistic Predator Prey Model

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{BNP}{N+D}$$

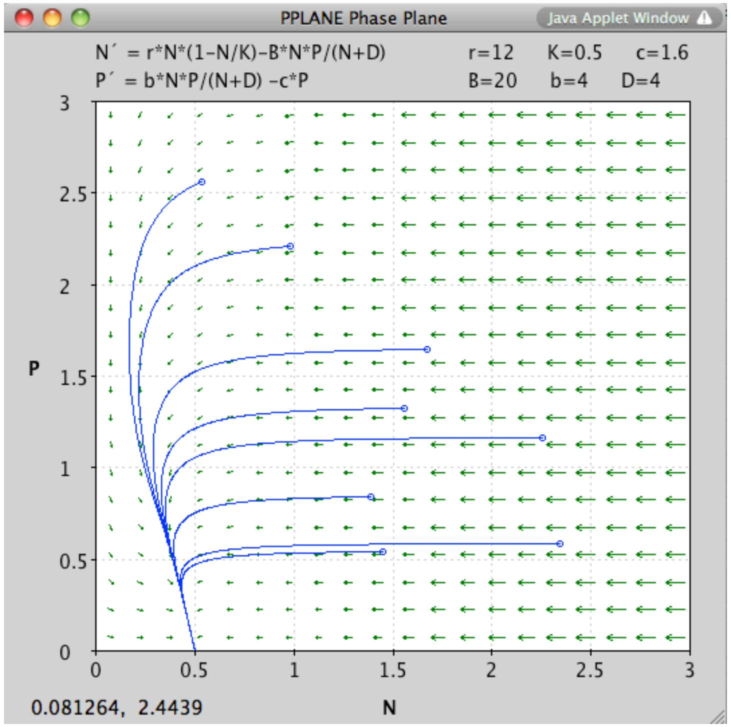
$$\frac{dP}{dt} = \frac{bNP}{N+D} - cP$$

Not so easy to do analysis on this model

Use PPLANE to carry out a numerical analysis

Fix *r* = 12, *c* = 1.6, *B* = 20, *b* = 4, *D* = 4, and examine behavior for different values of *K*

Low prey carrying capacity: *K* = 0.5



All trajectories go to a (stable) equilibrium with *N* = 0.5, *P* = 0

Prey at their carrying capacity, predators are extinct

Prey carrying capacity is too low to support predators

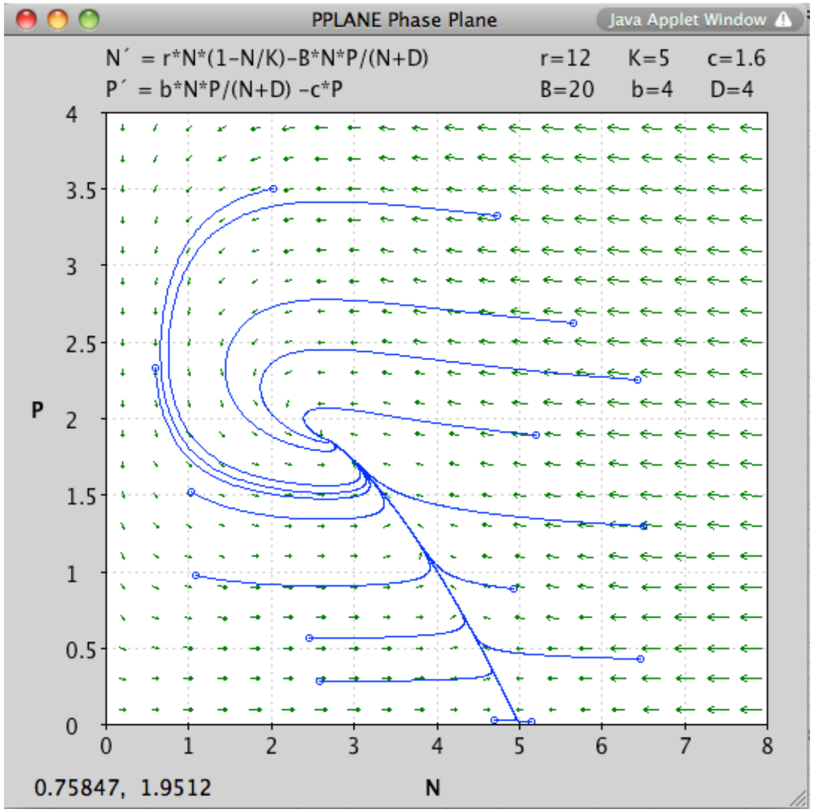
More Realistic Predator Prey Model

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{BNP}{N+D}$$

$$\frac{dP}{dt} = \frac{bNP}{N+D} - cP$$

Fix r = 12, c = 1.6, B = 20, b = 4, D = 4, and examine behavior for different values of K

Higher prey carrying capacity: K = 5



All trajectories go to a stable interior equilibrium: stable co-existence

Prey-only equilibrium (K,0) is no longer stable

What type of bifurcation happened between K = 0.5 and K = 5 ?

More Realistic Predator Prey Model

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{BNP}{N+D}$$
$$\frac{dP}{dt} = \frac{bNP}{N+D} - cP$$

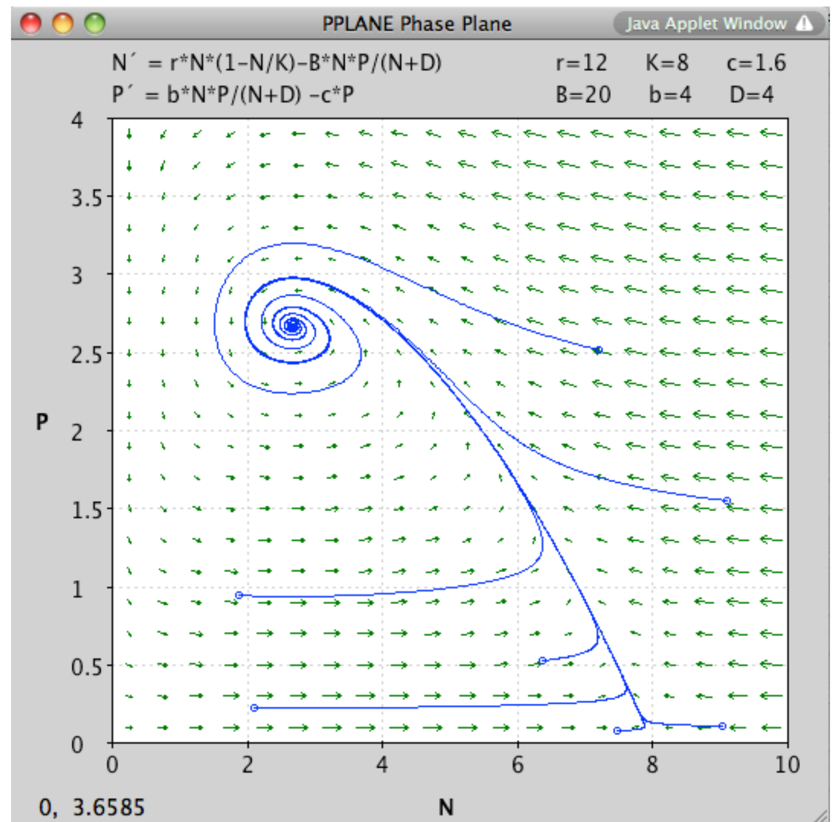
Fix r = 12, c = 1.6, B = 20, b = 4, D = 4, and examine behavior for different values of K

Higher prey carrying capacity: K = 8

All trajectories go to a stable interior equilibrium: stable co-existence

Notice oscillatory approach to this equilibrium: curves spiral in towards equilibrium, and in an anti-clockwise direction

This type of equilibrium is known as a stable spiral (or stable focus)



More Realistic Predator Prey Model

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{BNP}{N+D}$$

$$\frac{dP}{dt} = \frac{bNP}{N+D} - cP$$

Fix r = 12, c = 1.6, B = 20, b = 4, D = 4, and examine behavior for different values of K

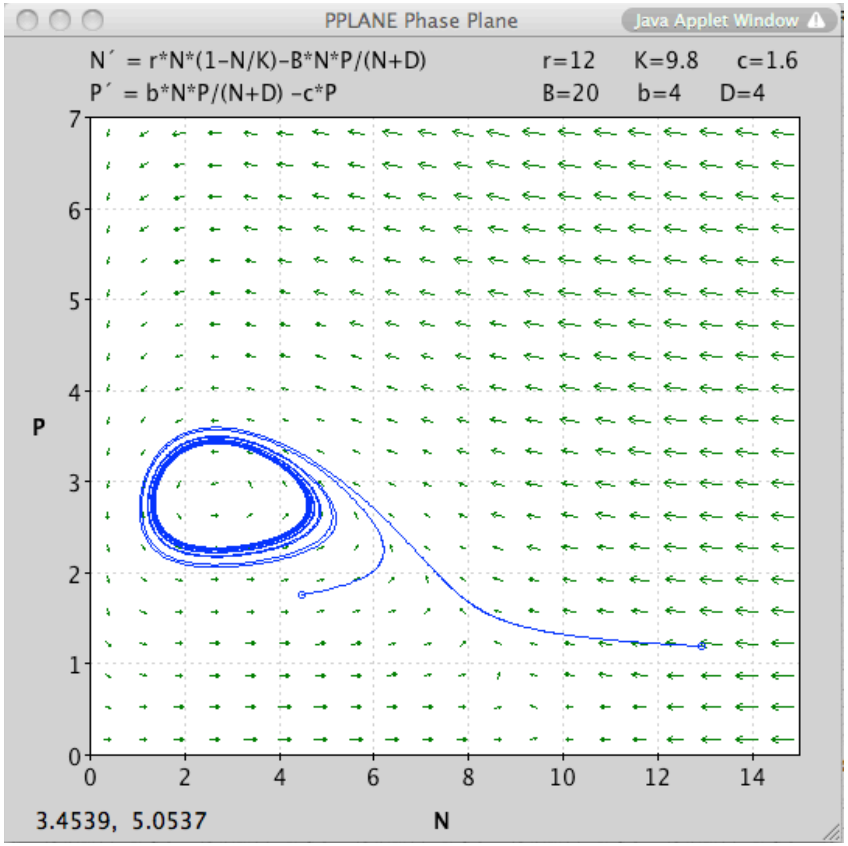
Higher prey carrying capacity: K = 9.8

Trajectories approach a single oscillatory solution (closed loop)

Co-existence equilibrium is now unstable
Inside the closed loop, trajectories spiral towards the closed loop

(the bifurcation that occurred–a Hopf bifurcation–is one that we shall discuss later in the course)

Notice anti-clockwise motion of solution curves



More Realistic Predator Prey Model

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{BNP}{N+D}$$

$$\frac{dP}{dt} = \frac{bNP}{N+D} - cP$$

Fix r = 12, c = 1.6, B = 20, b = 4, D = 4, and examine behavior for different values of K

Higher prey carrying capacity: K = 12

Trajectories approach a single oscillatory solution (closed loop)

Amplitude of oscillations increases