<u>Selection</u>

Consider two species x, y with reproductive rates + death rates & growth rates of a, b:

$\dot{x} = ax \qquad \dot{y} = by$

If a, b constant $x = x_0 e^{at}$ $y = y_0 e^{bt}$

Let $\rho = \frac{x}{y}$ be the ratio:

$$\dot{\rho} = \frac{\dot{x} y}{y^2} - \frac{x \dot{y}}{y^2} = \frac{axy - bxy}{y^2} = (a-b)\frac{x}{y} = (a-b)\rho$$

So if $a > b$ $\rho \to \infty$ x wins. If $a < b$ $\rho < 0$ y wins

Lets keep total pop constant: say

$x + y = 1$ $\Rightarrow$ ~~xxxx~~ for x, y <u>relative</u> abundance

$\dot{x} = x(a - \phi) \qquad \dot{y} = y(b - \phi)$

pick ϕ so that $x + y = 1$ for all time

$x + y = 1 \Rightarrow \dot{x} + \dot{y} = 0$

$\Rightarrow xa + yb - (x+y)\phi = 0$ but $x + y = 1$

$\Rightarrow \phi = (xa + yb)$ $\leftarrow$ mean growth rate so, since $x+y=1 \Rightarrow y=1-x$ so

$\phi = ax + b(\cancel{1-x})$

and $\dot{x} = x(a-\phi) = x(a-ax-b(\cancel{1-x}))$

$= x(1-x)(a-b)$

so if $a>b$ then $x \to 1$ if $a<b$ $x \to 0$

More generally f_i = "fitness"

$\dot{x}_i = \cancel{\phi}\ x_i f_i$

$\phi = \sum_{i=1}^{n} x_i f_i \leftarrow$ mean fitness suppose $\sum_{i=1}^{n} x_i = 1$

Then $\dot{x}_i = x_i(f_i - \phi)$

Recall that if x_i = prob of i then

$\sum x_i f_i$ = mean f_i (weighted sum)

If your fitness < mean die
> mean grow!

Verify $\sum_{i=1}^{n} \dot{x}_i = \sum_{i=1}^{n} x_i f_i - \phi \sum_{i=1}^{n} x_i = \phi - \phi \cdot 1 = 0$

Suppose $\dot{x} = ax^c - \phi x$ $\phi = ax^c + by^c$
$\dot{y} = by^c - \phi y$ to keep $x+y=1$

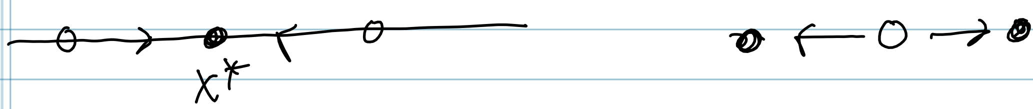
$\dot{x} = x(1-x)[ax^{c-1} - b(1-x)^{c-1}]$

If $c<1$ slower than exponential
$c>1$ greater " "

Verify 3 fixed points $x=0$, $x=1$
and $a x^{c-1} = b(1-x)^{c-1}$

$$\Rightarrow \left(\frac{a}{b}\right)^{\frac{1}{c-1}} x = (1-x) \rightarrow x^* = \frac{1}{1+\left(\frac{a}{b}\right)^{1/c-1}}$$

$c<1$ Neither win — $c>1$ one or other wins



$c>1$ favors whoever was bigger to start
$c<1$ " survival of all

Now lets look at evolutionary games

Game Theory invented by John von Neumann + Oskar Morgenstern

John Nash – "Nash equilibrium"

1 page paper in PNAS 1950
Nobel prize Economics 1994

By then he was mentally ill

Evolutionary game theory does not rely on rationality, rather individuals employ strategies that are fixed, interact & the payoffs are added up. payoff is fitness)

Example two phenotypes A, B

A can move, B cannot

A pays a cost to move eg using energy, but gains so suppose fitness of A is 1.1 & B is 1

Then A wins & eventually takes over

(cf. earlier)

Suppose fitness is density dependent.

Like if there are lots of A or B around moving doesn't do much good, so then fitness B ~~>~~ fitness A.

x_A = ~~fitness~~ freq of A x_B = ~~fitness~~ freq of B

$\vec{x} = (x_A, x_B)$

$\dot{x}_A = x_A(f_A(\vec{x}) - \phi)$ $\phi = x_A f_A(\vec{x}) + x_B f_B(\vec{x})$

$\dot{x}_B = x_B(f_B(\vec{x}) - \phi)$

Let $x = x_A$ $\quad 1-x = x_B$ $\quad$ Then: $f_A(\vec{x}) = f_A(x)$

$f_B(\vec{x}) = f_B(x)$

$\dot{x} = x(1-x)[f_A(x) - f_B(x)]$

Equilibria $x = 0$, $x = 1$, $\quad x^*$ $\quad f_A(x^*) = f_B(x^*)$

Stability: of $\bar{x}$

$$\dot{y} = \Big[(1-\bar{x})[f_A(\bar{x}) - f_B(\bar{x})] - \bar{x}[f_A(\bar{x}) - f_B(\bar{x})] + \bar{x}(1-\bar{x})[f_A'(\bar{x}) - f_B'(\bar{x})]\Big]y$$

$\bar{x} = 0$

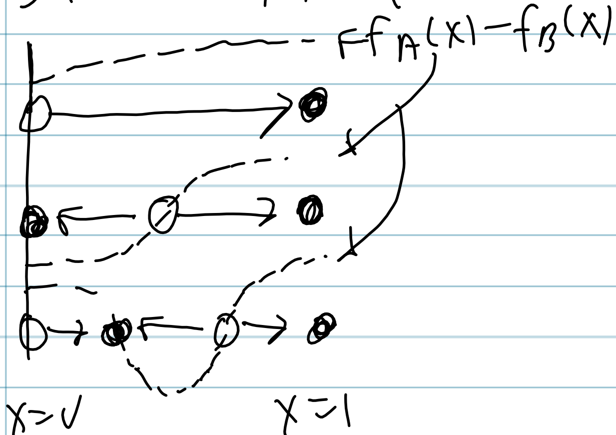
$\dot{y} = [f_A(0) - f_B(0)]y$ $\quad$ if $f_A(0) < f_B(0)$ stable

$\bar{x} = 1$, $\dot{y} = [f_B(1) - f_A(1)]y$ $\quad$ stable if $f_A(1) > f_B(1)$

$x = x^*$

$\dot{y} = x^*(1-x^*)[f_a'(x^*) - f_B'(x^*)]y$

stable iff $f_a'(x^*) < f_B'(x^*)$



Two player game.

strategies are A + B

When A plays A ~~A~~ both get payoff a

when A plays B A gets b, B gets c

when B plays B ~~A~~, both get d

$$\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array}$$

Let x_A = freq playing A

x_B = freq playing B

If play A expected payoff is

$f_A = a x_A + b x_B$

$f_B = c x_A + d x_B$

$f_A(x) = ax + b(1-x)$

$f_B(x) = cx + d(1-x)$

$$\boxed{f_A(x) - f_B(x) = (a - b - c + d)x + b - d}$$

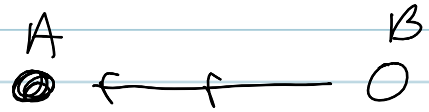
$\dot{x} = x(1-x)\left[(a-b-c+d)x + b-d\right]$

There are five possibilities for the two strategies

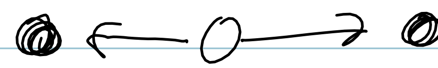
$a>c$ $\quad b>d$ (strategy A pays better no matter what

A dominates B

(1)

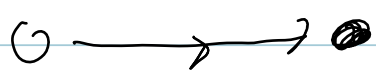


$a>c$ $\quad d>b$ (3) bistable



B dominates A

(2) $c>a$, $\quad d>b$



$a<c$ $\quad b>d$ (4) coexist

(5) $a=c$ $\quad b=d$ (5) neutral

(1) No matter what, it is best to play A payoff for playing A is always better

(2) payoff for B always better

(3) Always best to play same strategy as other player ("Nash equilibrium" more later)

Note $$x^* = \frac{(d-b)}{a-c+d-b} \in (0,1)$$

(4) $$x^* = \frac{b-d}{b-d+c-a} \in (0,1)$$

Homework due Friday Nov 5

① — #31 page 265

② — ~~Find equilibria and stability for~~ Consider epidemic model with Vital Dynamics:

$$\dot{S} = \delta(N-S) - \beta I S + \gamma R$$
$$\dot{I} = -\delta I + \beta I S - \nu I$$
$$\dot{R} = \nu I - \gamma R - \delta R$$

δ = death rate.

(a) Show $\frac{d}{dt}(S+I+R) = \delta(N-(S+I+R))$

and conclude that $S+I+R \to N$ as $t \to \infty$

(b) Since $S+I+R \to N$ set $R = N-(S+I)$ use this to reduce the model to 2 variables S, I

(c) Find equilibria & stability

What is the reproduction rate σ?

③ — $\dot{x} = (a x^{r-1}) x$ Here Fitness is $a x^{r-1}$, $b y^{r-1}$

$\dot{y} = (b y^{r-1}) y$ Let $\phi = a x^{r-1} x + b y^{r-1} y$

& consider $\dot{x} = x[a x^{r-1} - \phi]$, $\dot{y} = y[b y^{r-1} - \phi]$

Study equilibria + stability for $0 \leq r < \infty$

HAWK/DOVE

Dove is bad name since two doves will fight to the death!

But in many scenarios, animals are more likely to display & threaten than to actually fight

In H/D Hawks fight while doves posture & one will retreat

The gain is G & the cost of battle is C

	if it meets a hawk	if it meets dove
a hawk receives	$\frac{G-C}{2}$ "a"	G "b"
a dove receives	0 "c"	$\frac{G}{2}$ "d"

Lets look - If $C > G$ then it hurts a lot when hawk meets hawk, but still could be good in low densities of Hawks since gain is quite high when meeting dove

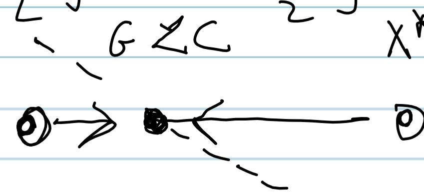
If $C < G$ then it is always better to be a Hawk. Let x = P Hawk & $1-x$ = dove

So ~~F~~

$$\dot{x} = x(1-x)\left[\left(\frac{G-C}{2} - G - 0 + \frac{G}{2}\right)x + G - \frac{G}{2}\right]$$

$$= x(1-x)\left[-\frac{C}{2}x + \frac{G}{2}\right]$$

$x^* = \frac{G}{C} \in (0,1)$



Multi player Games

"Battle of the sexes"

Parental responsibility.

Game is rigged against Females since They produce few large gametes & males many small.

Females are more committed so for males a better strategy could be to desert.

Female counterstrategy is "coyness" to insist on long engagement. So rather than going through second long engagement, male might stay home. Thus with lots of coy females, faithful might be best. But as more males become faithful females might want to be "fast" & this would lead to more "philandering" males & so on!

Two types of males: E_1 philandering E_2 faithful

Two types " females: F_1 coy F_2 fast

C = parental investment G = successful offspring
E = engagement, costs both

Faithful male + coy female $G-\frac{C}{2}-E$ for both since share duty

Faithful male + fast female $G-\frac{C}{2}$ (skip engagement)

Philander male + fast female G for him $G-C$ for her!

Philand male + coy female 0

Let x = faithful males $1-x$ = philan

y = coy female $1-y$ = ~~coy~~ fast

Average fitness for ~~fast~~ ~~fait~~ male

$$\left[\left(G-\frac{C}{2}-E\right)y+\left(G-\frac{C}{2}\right)(1-y)\right]x+$$

Fitness for faithful

philan

$$\left[0\cdot y+(G)(1-y)\right](1-x)$$

ϕ_M

Average fitness for female y:

coy

$$\left[\left(G-\frac{C}{2}-E\right)x+0(1-x)\right]y+$$

$$\left[\left(G-\frac{C}{2}\right)x+(G-C)(1-x)\right](1-y)$$

$$\dot{x}=x\left[\left(G-\frac{C}{2}-E\right)y+\left(G-\frac{C}{2}\right)(1-y)-\phi_M\right]$$

$$\dot{y}=y\left[\left(G-\frac{C}{2}-E\right)x-\phi_F\right]$$

You guys can simulate this for HW!

$$0<E<G<C<2(G-E)$$

Enzyme kinetics, ~~mass~~ + pseudosteady state hypothesis

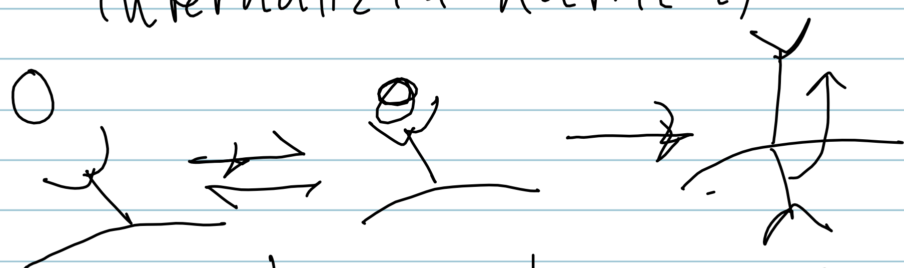
In chemostat model we assumed

$$k(C) = \frac{k_{max} C}{k_n + C}$$

Where does this come from?

Nutrients have to bind to external receptors be brought inside cell & then the receptors are recycled

C = nutrient X_0 = unoccupied receptor
X_1 = nutrient-Receptor complex, P = internalized nutrient



$$C + X_0 \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} X_1 \xrightarrow{k_2} P + X_0$$

$$\longrightarrow r - X_1$$

$$\frac{dC}{dt} = -k_1 C X_0 + k_{-1} X_1$$

$$\frac{dX_0}{dt} = -k_1 C X_0 + k_{-1} X_1 + k_2 X_1$$

$$\frac{dX_1}{dt} = k_1 C X_0 - k_{-1} X_1 - k_2 X_1$$

$$\frac{dP}{dt} = k_2 X_1$$

Note $\frac{d}{dt}(X_0+X_1) = 0 \Rightarrow X_0 + X_1 = r$ total receptor

$$\frac{dc}{dt} = -k_1 c r + (k_{-1} + k_1 c) X_1$$

$$\frac{dX_1}{dt} = k_1 r c - (k_{-1} + k_2 + k_1 c) X_1$$

One can justify the following that we will not prove it. Since there are few receptors compared to C, X_0 is rapidly completely bound to C to form X_1 so $dX_1/dt \simeq 0$ after a brief transient.

$$\Rightarrow k_1 r c - (k_{-1} + k_2 + k_1 c) X_1 = 0$$

$$\Rightarrow X_1 = \frac{k_1 r c}{k_1 c + k_2 + k_{-1}} = \frac{rc}{c + \frac{k_2 + k_{-1}}{k_1}}$$

$$\Rightarrow \frac{dc}{dt} = -k_1 c r + (k_1 + k_{-1} c) \frac{rc}{c + \frac{k_2 + k_{-1}}{k_1}}$$

$$= -\frac{k_2 r c}{c + \frac{k_2 + k_{-1}}{k_1}} \equiv -\frac{V_{max}\, c}{c + K_m}$$

Sigmoidal kinetics

$$2C + X_0 \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} X_2 \xrightarrow{k_2} X_0 + 2P$$

$$X_2 + X_0 = r$$

$$\frac{dc}{dt} = -k_1 c^2 X_0 + k_{-1} X_2$$

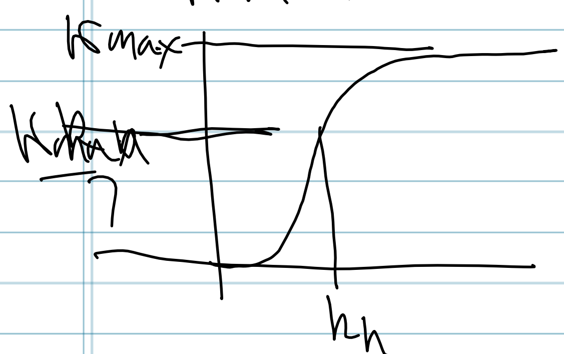
$$\cancel{\frac{dX_0}{dt} = -k_1 c^2 X_0 + k_{-1} X_2 + k_2 X_2}$$

$$\cancel{\text{set}} \quad \frac{dX_2}{dt} = k_1 X_0 c^2 - k_{-1} X_2 - k_2 X_2$$

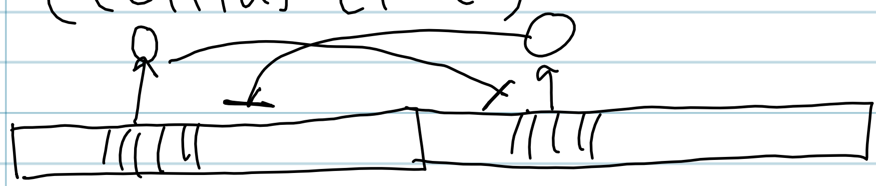
$$\text{set } \frac{dX_2}{dt} = 0 \ \& \ X_2 + X_0 = r$$

$$\Rightarrow \frac{dc}{dt} = -\frac{k_{max}\, c^2}{k_n^2 + c^2}$$

$$k_{max} = k_2 r \qquad k_n = \sqrt{\frac{k_{-1} + k_2}{k_1}}$$



~~Genetic~~ Molecular switch
(Collins et al)



Gene 1 makes product P_1 which suppresses Gene 2 + vice versa

production

Decay

$$\frac{dP_1}{dt} = \frac{A_1}{1+\alpha_1 P_2^2} - \mu_1 P_1$$

suppression

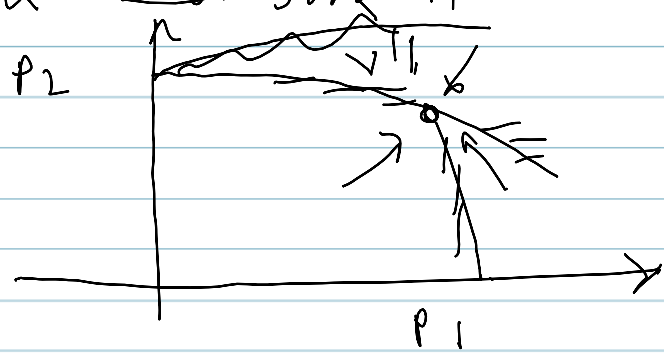
$$\frac{dP_2}{dt} = \frac{A_2}{1+\alpha_2 P_1^2} - \mu_2 P_2$$

Lets make life simple $A = A_1 = A_2$ + $\alpha_1 = \alpha_2$

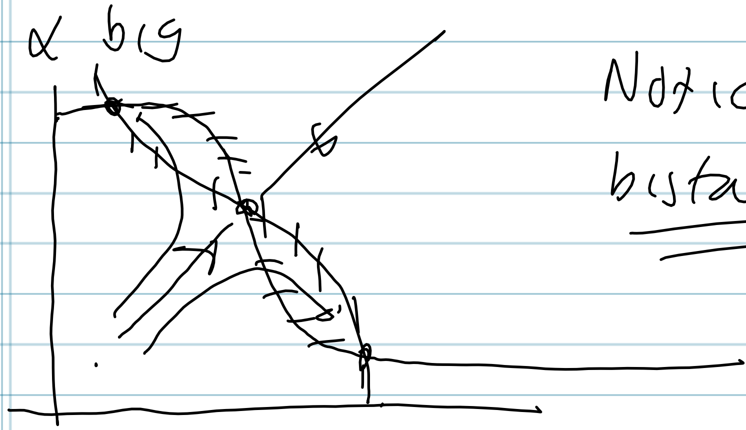
make it all dimensionless $\mu_1 = \mu_2 = \mu$

$$\frac{dP_1}{dt} = \frac{A}{1+\alpha P_2^2} - P_1 \qquad \frac{dP_2}{dt} = \frac{A}{1+\alpha P_1^2} - P_2$$

α ~~≈ 0~~ or small



α big



Notice we have bistability Now

If you change A_1 or A_2 you shift to make one or the other more likely.

One more example That is pretty Hard

Let X_1, X_2, X_3 produce products Y_1, Y_2, Y_3 & Y_1 suppresses X_2, Y_2 suppresses X_3 Y_3 suppresses X_1

This was built into a bacteria & generated oscillations.

$$\dot{X}_1 = \frac{A}{1+Y_3^2} - X_1 \qquad \dot{Y}_1 = \beta[X_1 - Y_1]$$

$$\dot{X}_2 = \frac{A}{1+Y_1^2} - X_2 \qquad \dot{Y}_2 = \beta[X_2 - Y_2]$$

$$\dot{X}_3 = \frac{A}{1+Y_2^2} - X_3 \qquad \dot{Y}_3 = \beta[X_3 - Y_3]$$

How to analyze this?

Tricky but simple when you know the trick since we can exploit symmetry

Same for grad course!

Homework

① simulate Rock paper scissors with

when playing

	R	P	S
R gets	0	$-a$	1
P gets	1	0	$-a$
S gets	$-a$	1	0

as follows:

Let x = Rock, y = Paper z = Scissors

Note $z = 1-x-y$

(a) What is rocks average payoff?

What is scissors, paper's average payoff

call these f_x, f_y, f_z

Let $\phi = x f_x + y f_y + z f_z$ be the average fitness of all

(b) $\dot{x} = x(f_x - \phi)$

$\dot{y} = y(f_y - \phi)$

Substitute $z = 1-x-y$

This is a two-dimensional system

(c) Start with $x = .2, y = .3$ + solve equations for:

$a = 1, \quad a = .9, \quad a = 1.1$

you may have to solve for a while

(d) Sketch the solution in the x-y phase plane. I will provide an XPP file if you want to use it.

(2) Lets consider the Hawk-Dove game again

	Hawk	Dove	Mixed
Hawk	$\frac{b-c}{2}$	b	$p\left(\frac{b-c}{2}\right)+(1-p)b$
Dove	0	$\frac{b}{2}$	☆
Mixed	$p\left(\frac{b-c}{2}\right)+(1-p)0$	☆	☆

The <u>mixed</u> strategy is as follows. With probability p, it takes the Hawk strategy & with prob $1-p$ it takes the dove strategy

So, for example when ~~mixed~~ Hawk plays Mixed it receives $p \cdot \frac{b-c}{2}+(1-p)b$.

When mixed plays Hawk, it receives

$$\underset{\text{playing as Hawk}}{p\left(\frac{b-c}{2}\right)} + \underset{\text{playing as dove}}{(1-p)\,0}$$

Try to fill in the rest of these values.

Note mixed vs mixed is tricky

There are 4 scenarios that you have to keep track of. For example mixed playing as Hawk vs mixed playing as Dove occurs at a rate $2p(1-p)$ (the 2 is there because the first can be dove, second hawk or hawk/dove.