3506 Mathematical Ecology Notes

Based on the 2012 autumn lectures by Dr S A Baigent

General Overview

Continuous Time

Single species models
- time dependent ODEs

 1st order, 1 variable

explicitly intergrate, graphical analysis

Two species models
- 1st order, time independent

 pairs of ODEs in 2 variables

explicitly solve, phase plane analysis

Discrete Time

Single species discrete time models
- $N_{t+1} = f(N_t)$

Age structured models
- $\underline{N}_{t+1} = L\underline{N}_t$

Last part: General models of n species interacting (pairwise), continuous time. Main tool = Lyapunov function. all qualitative.

Single Species Models

Some basic probability

Proposition:
For δt small let $p(t)\delta t + O(\delta t^2)$ be the probability that some event E occurs in $[t, t+\delta t]$. Also assume events in disjoint time intervals are independent. Then the probability that No event occurs in $[0,t)$ is
$$\exp\left(-\int_0^t p(s)\,ds\right)$$

Proof: $P(t) = \text{prob}\{\text{no event occurs in } [0,t)\}$

$P(t+\delta t) = \text{prob}\{\text{no E in } [0, t+\delta t)\}$

$= \text{prob}\{\text{no E in } [0,t)\}$ and $\text{prob}\{\text{no E in } [t, t+\delta t)\}$

$= \text{prob}\{\text{no E in } [0,t)\} \times \text{prob}\{\text{no E in } [t, t+\delta t)\}$ by independence.

$\Rightarrow P(t+\delta t) = P(t) \times (1 - p(t)\delta t) + O(\delta t^2)$

$= P(t) - p(t)P(t)\delta t + O(\delta t^2)$

$\underbrace{\frac{P(t+\delta t) - P(t)}{\delta t}} = -p(t)P(t)\delta t + O(\delta t^2)$

Take limit $\delta t \to 0$.

$\Rightarrow P'(t) = -p(t)P(t)$

$P(0) = 1$ certain that no E happens in no time

$$P'(t) = -p(t)P(t), \quad P(0)=1 \quad t \geq 0$$

$$\int \frac{P'(t)}{P(t)}\,dt = \int -p(t)\,dt$$

$$\Rightarrow \int_1^{P'} \frac{dP}{P} = -\int_0^t p(s)\,ds$$

$$\Big[\log P\Big]_1^{P(t)} = -\int_0^t p(s)\,ds$$

$$\log P(t) = -\int_0^t p(s)\,ds$$

$$\Rightarrow \cancel{p}\,P(t) = \exp\left(-\int_0^t p(s)\,ds\right)$$

Expected waiting time till first event.

Assumption: $p(t)$ satisfies $\lim_{t\to\infty} t \times \exp\left(-\int_0^t p(s)\,ds\right) = 0$

Probability that 1st event happens in $[t, t+\delta t] = \exp\left(-\int_0^t p(s)\,ds\right)p(t)\delta t + O(\delta t^2)$

Note that $\int_0^\infty p(t)\exp\left(-\int_0^t p(s)\,ds\right)dt \overset{?}{=} 1$

Note $\frac{d}{dt}\exp\left(-\int_0^t p(s)\,ds\right) = \exp\left(-\int_0^t p(s)\,ds\right)\frac{d}{dt}\left(-\int_0^t p(s)\,ds\right)$

$$= -p(t)\exp\left(-\int_0^t p(s)\,ds\right)$$

$$A = \int_0^\infty p(t)\exp\left(-\int_0^t p(s)\,ds\right)$$

$$= -\int_0^\infty \frac{d}{dt}\exp\left(-\int_0^t p(s)\,ds\right)dt$$

$$= -\left[\exp\left(-\int_0^t p(s)\,ds\right)\right]_0^\infty = -0+1 = 1$$

Since if $\lim_{t\to\infty} t\exp\left(-\int_0^t p(s)\,ds\right)=0$ then certainly $\lim_{t\to\infty}\exp\left(-\int_0^t p(s)\,ds\right)=0$

Expected time to 1st event

$$\bar{T} = \int_0^\infty t\,p(t)\exp\left(-\int_0^t p(s)\,ds\right)dt$$

Intergration by parts:

$$= -\int_0^\infty t\,\frac{d}{dt}\exp\left(-\int_0^t p(s)\,ds\right)dt$$

$$= -\left\{\Big[\underbrace{t\exp\left(-\int_0^t p(s)\,ds\right)}_{\to 0 \text{ by assumption}}\Big]_0^\infty - \int_0^\infty \exp\left(-\int_0^t p(s)\,ds\right)dt = \int_0^\infty \exp\left(-\int_0^t p(s)\,ds\right)dt\right.$$

Example:

$p(t) = \lambda$ constant

$$\overline{T} = \int_0^\infty \exp\left(-\int_0^t \lambda \, ds\right) dt$$

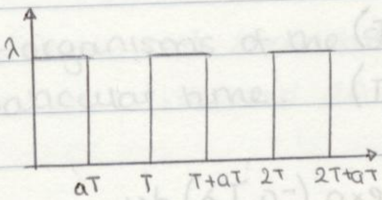
$$= \int_0^\infty \exp(-\lambda t)\, dt = \left[\frac{1}{\lambda}\exp(-\lambda t)\right]_\infty^0 = 1/\lambda.$$

Example:

Periodic $p(t)$

Take $a \in (0,1)$

period T for $p(t)$



k integer $$\int_0^{kT} p(s)\,ds = \sum_{r=1}^{k} \int_{(r-1)T}^{rT} p(s)\,ds$$

$$= \sum_{r=1}^{k} aT \times \lambda$$

$$= k\lambda aT$$

Define $$\overline{T}_k = \int_0^{kT} \exp\left(-\int_0^t p(s)\,ds\right) dt$$ since $\overline{T} = \lim_{k\to\infty} \overline{T}_k$

$$= \sum_{r=1}^{k} \int_{(r-1)T}^{rT} \exp\left(-\int_0^t p(s)\,ds\right) dt$$

Substitute $u = t-(r-1)T$

$$\Rightarrow \overline{T}_k = \sum_{r=1}^{k} \int_0^T \exp\left(-\int_0^{u+(r-1)T} p(s)\,ds\right) du$$

$$= \sum_{r=1}^{k} \int_0^T \exp\left(-\int_0^{(r-1)T} p(s)\,ds - \int_{(r-1)T}^{u+(r-1)T} p(s)\,ds\right) du.$$

$$= \sum_{r=1}^{k} \int_0^T \exp\left(-\int_0^{(r-1)T} p(s)\,ds\right) \times \exp\left(-\int_{(r-1)T}^{u+(r-1)T} p(s)\,ds\right) du$$

$$= \sum_{r=1}^{k} e^{-r\lambda aT} \times \int_0^T \exp\left(-\int_{(r-1)T}^{u+(r-1)T} p(s)\,ds\right) du$$

$$= \sum_{r=1}^{k} e^{-r\lambda aT} \times \int_0^T \exp\left(-\int_0^u p(s)\,ds\right) du$$

Let $$\overline{t} = \int_0^T \exp\left(-\int_0^u p(s)\,ds\right) du$$

$$\Rightarrow \overline{T}_k = \sum_{r=1}^{k} e^{-\lambda a r T}\, \overline{t}$$

$$= \overline{t}\left(\frac{1 - e^{-\lambda a T k}}{1 - e^{-\lambda a T}}\right)$$

So let $k \to \infty$ $$\overline{T} = \frac{\overline{t}}{1 - e^{-\lambda a t}}$$

$$\bar{t} = \int_0^T \exp\left(-\int_0^u p(s)\,ds\right) du$$

$$= \int_0^{aT} \exp\left(-\int_0^u p(s)\,ds\right) du + \int_{aT}^T \exp\left(-\int_0^u p(s)\,ds\right) du$$

$$= \int_0^{aT} \exp(-\lambda u)\,du + \int_{aT}^T \exp\left(-\int_0^u p(s)\,ds\right) du$$

$$\int_0^u p(s)\,ds = \begin{cases} u\lambda & u \in [0, aT) \\ aT\lambda & u \in (aT, T) \end{cases}$$

$$= \min(\lambda u, aT\lambda)$$

$$\int_{aT}^T \exp\left(-\int_0^u p(s)\,ds\right) du = \int_{aT}^T \exp(-aT\lambda)\,du$$

$$= (1-a)T\,e^{-\lambda aT}$$

$$\Rightarrow \bar{t} = \int_0^{aT} \exp(-\lambda u)\,du + (1-a)Te^{-\lambda aT}$$

$$= \left[\frac{e^{-\lambda u}}{\lambda}\right]_{aT}^{0} + (1-a)Te^{-\lambda aT}$$

$$\bar{t} = \frac{1}{\lambda}\left(1 - e^{-\lambda aT}\right) + (1-a)Te^{-\lambda aT}$$

Let $T \to \infty \Rightarrow \bar{T} = \frac{1}{\lambda}$ same as first example λ = constant

Population Biology: basic notions

Definition:

A species is a set of organisms capable of interbreeding.

Definition:

A population is a set of organisms of the same species occupying a particular place at a particular time.

Definition:

The population density N, is the number of individuals per unit area.

Process that can lead to change in population density.

- Birth
- Death
- Immigration
- Emmigration

Change in population density $= B - D - I + E$

Not considering I and E in this course.
Will be focusing on birth/death.

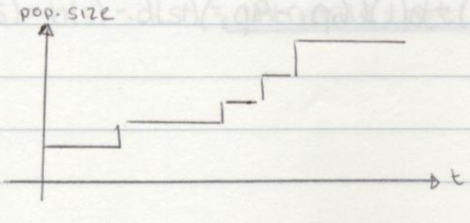
We will assume every individual in the population is identical (we can assume asexual reproduction or that male/female sex ratio is constant).

Simple Birth Models.

Take $b(t)\delta t + O(\delta t^2)$ = probability an individual gives birth in $[t, t+\delta t]$
We ignore deaths for now.

Find the mean population size at time t, given it at $t=0$.

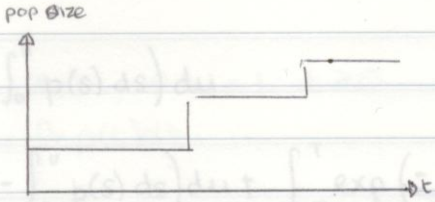
Exp 1



(time series)

time scale is $O(\delta t)$.

Exp 2



Do many experiments and look at average of whats happening.

$p_K(t)$ = proportion of experiments for which the population size was K at time t.

How do we find $\frac{dp_K(t)}{dt}$?

$p_0(t+\delta t) = p_0(t) = \bar{p}_0$ constant

$p_1(t+\delta t) = p_1(t) - b(t)\delta t\, p_1(t) + O(\delta t^2)$

$\frac{p_1(t+\delta t) - p_1(t)}{\delta t} = -b(t)\delta t\, p_1(t) + O(\delta t^2)$.

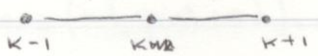
$\frac{dp_1(t)}{dt} = -b(t)p_1(t)$

$p_2(t+\delta t) = p_2(t) + b(t)\delta t\, p_1(t) - 2b(t)\delta p_2(t)$

pop size 1 → pop size 2   pop size 2 → pop size 3.

$\frac{p_2(t+\delta t) - p_2(t)}{\delta t} = b(t)p_1(t) - 2b(t)p_2(t) + O(\delta t)$.

$\Rightarrow \frac{dp_2}{dt} = b(t)(p_1(t) - 2p_2(t))$



$\frac{dp_K}{dt} = (K-1)b(t)p_{K-1} - Kb(t)p_K \quad K \geq 2$.

The mean population $N(t) = \sum_{K=0}^{\infty} Kp_K(t)$

$\frac{dN}{dt} = \sum_{r=0}^{\infty} K\frac{dp_K}{dt} = -b(t)p_1 + b(t)(2p_1 - 4p_2) + b(t)(6p_2 - 9p_3) + \dots$

$= b(t)(p_1 + 2p_2 + 3p_3 + \dots)$

$\frac{dN}{dt} = b(t)N$

initial condition $N(0) = N_0$

$N(t) = \exp\left(\int_0^t b(s)\,ds\right) N_0$ mean population at t.

If death is included we obtain $N(t) = \exp\left(\int_0^t b(s) - d(s)\,ds\right) N_0$

Definition:

A generation is the expected time ~~from birth~~ between the birth of an individual (choosen at random) and the time of their first offspring.

Definition:

Life expectancy is the expected time from birth of an individual to its death.

Using formulae for expected time for the first event.

$$T_{gen} = \text{generation time} = \int_0^\infty \exp\left(-\int_0^t b(s)\,ds\right) dt$$

$$T_{surv} = \text{life expectancy} = \int_0^\infty \exp\left(-\int_0^t d(s)\,ds\right) dt$$

For viability of the population we need $T_{surv} > T_{gen}$.

$$T_{surv} - T_{gen} = \int_0^\infty \left[\exp\left(\int_0^t -d(s)\,ds\right) - \exp\left(\int_0^t -b(s)\,ds\right)\right] dt$$

$$= \int_0^\infty \exp\left(\int_0^t -d(s)\,ds\right)\left[1 - \exp\left(\int_0^t b(s) - d(s)\right)\right] dt$$

Let $r(s) = b(s) - d(s)$

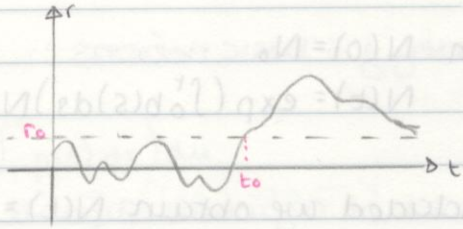
$$T_{surv} - T_{gen} = \int_0^\infty \left[\exp\left(-\int_0^t d(s)\,ds\right)\left(1 - \exp\left(\int_0^t r(s)\,ds\right)\right)\right] dt$$

So we need $r(s) > 0$ on average (to be made more precise later)

ie $-\int_0^t r(s)\,ds < 0$ and $1 > \exp\left(\int_0^t r(s)\,ds\right)$ and we get $T_{surv} - T_{gen} > 0$

Call $r(s) = b(s) - d(s)$ = intrinsic net repoductive rate

Example: Population explosion



$r(t) > r_0$ for $t > t_0$

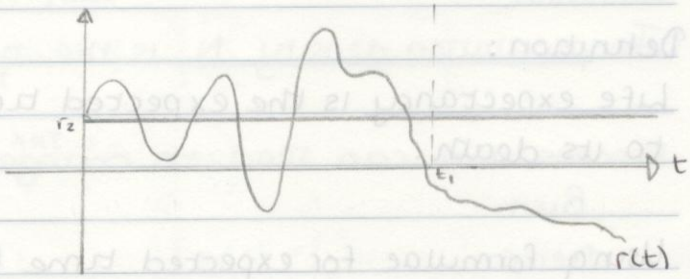
$N(t) = \exp\left(\int_0^t r(s)\,ds\right) N_0$

and $\int_0^t r(s)\,ds \uparrow$ for $t > t_0$

Here $N(t) \uparrow \infty$ as $t \to \infty$

Sufficent condition for $N(t) \uparrow \infty$ is $r(t) > r_0 > 0$ for all $t > t_0$.

Example: Extinction



$N(t) \to 0$ as $t \to \infty$ extinction

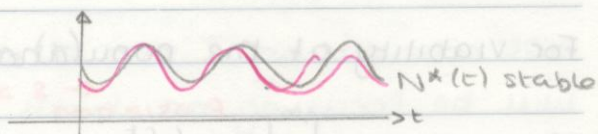
Sufficent condinition

for $t > t_1$, $r(t) < r_2 < 0$

so $\int_0^t r(s)\,ds \to -\infty$

$\Rightarrow \exp\left(\int_0^t r(s)\,ds\right) \to 0$ and have $N(t) \to 0,\ t \to \infty$ (population collapse)

Example: Stable population



Here $|N(t) - N^*(t)| \to 0$ as $t \to \infty$

$N^*(t)$ is "stable" population trajectory.

$|N(t) - N^*(t)| \to 0$ as $t \to \infty$.

eg. $r(t) \to 0$ as $t \to \infty$ st $\int_0^t |r(s)|\,ds < \infty$ then $N(t) \to N^*(t) = N^*$ constant

where $N^* = \exp\left(\int_0^\infty r(s)\,ds\right) N_0$ (sheet 1)

Example: Periodic

$r(t)$ is periodic, period T.

Define $R := \int_0^T r(s)\,ds$ "mean" net repoductive rate.

Consider $t = kT + s$ where $s \in [0, T)$.

$N(t) = N(kT + s)$

$= \exp\left(\int_0^{kT+s} r(u)\,du\right) N(0)$

$= \exp\left(\int_0^{kT} r(u)\,du + \int_{kT}^{kT+s} r(u)\,du\right) N_0$

$\int_0^{kT} r(u)\,du = k \cdot \int_0^T r(u)\,du = kR$.

$$\text{Hence } N(kT+s) = \exp\left(kR + \int_{kT}^{kT+s} r(u)\,du\right) N(0)$$
$$= e^{kR}\left[\exp\left(\int_0^s r(u)\,du\right) N(0)\right]$$
$$= e^{kR} N(s)$$

$$\int_{kT}^{kT+s} r(u)\,du = \int_0^s r(v+kT)\,dv = \int_0^s r(v)\,dv$$

$v = u - kT$ change variables

Thus $N(kT+s) = e^{kR} N(s)$

Hence if $R=0$ then $N(kT+s) = N(s)$ $(\forall k)$ $\Rightarrow$ periodic

$R<0$ then $e^{kR} \to 0$ as $k \to \infty \Rightarrow N(kT+s) \to 0$ as $k \to \infty$

$N(t) \to 0$ as $t \to \infty$ extinction.

$R>0$ then $e^{kR} \to \infty$ as $k \to \infty \Rightarrow N(kT+s) \to \infty$ as $k \to \infty$

population explosion.

Conclusion:

Simple models, make intuitive sense (mostly) but are not very enlightening, certainly not predicative.

Chapter 2: Single Species, Density dependent models.

We have $\underbrace{\frac{\dot{N}}{N}}_{\text{per capita growth rate}} = r(t)$ ie. per capita rate does not depend on current population density.

This leads to say, $\dot{N} = rN$
$\Rightarrow N = e^{rt}N(0) \longrightarrow \infty$ if $r>0$
because this assume that resources are unlimited and so no matter what the population density there are sufficent resources to grow at maximal rate.

Realistically resources (food, space, light, ... anything that controls population growth) are always limited

Intuitively high population density $\Rightarrow$ fewer resources per individual
or
less energy devoted to survival or fall in fecundity
(fecundity = ability to produce offspring)

Thus we expect the per capita growth rate to depend on the density N:

A $\frac{\dot{N}}{N} = \rho(t,N)$ density dependent growth
per capita net repoductive growth rate

Split $\rho(t,N) = \underbrace{\beta(t,N)}_{\text{birth rate}} - \underbrace{\delta(t,N)}_{\text{death rate}}$

A is a very general model, what properties should ρ exhibit?
- We expect $\beta(t,N)$ to be decreasing in N
  - increase in N $\Rightarrow$ fewer resources
    $\Rightarrow$ lower birth rate

$\Rightarrow \frac{\partial \beta}{\partial N}(t,N) < 0$

- $\delta(t,N)$ should be increasing with density N
  - increase in $N \Rightarrow$ less food, more competition, fights between mates etc.

Hence $\frac{\partial \rho}{\partial N}(t,N) = \underbrace{\frac{\partial}{\partial N}\beta(t,N)}_{<0} - \underbrace{\frac{\partial}{\partial N}\delta(t,N)}_{>0} < 0$

$\frac{\partial \rho}{\partial N} < 0$ basic requirement for per-capita growth.

Hence $\dot{N} = N\rho(t,N)$ where $\frac{\partial \rho}{\partial N} < 0$ gives $N(0) = N_0$

We have done $\rho(t,N) = \rho(t)$, so we look at the linear problem.
Do a maclaurian series of N:
$\rho(t,N) = \rho_0(t) +$

Thus we expect the per capita ~~rate~~ growth rate to depend on the density N:

- (A) $\quad \dfrac{\dot{N}}{N} = \rho(t,N)$ density dependent growth.

per capita net reproductive growth rate.

Split $\quad \rho(t,N) = \underbrace{\beta(t,N)}_{\text{birth rate}} - \underbrace{\delta(t,N)}_{\text{death rate}}$?

(A) is a very general model, what ~~purpose~~ properties should ρ exhibit?

- First. We expect $\beta(t,N)$ to be decreasing in N. - increase $N \Rightarrow$ less resources $\Rightarrow$ low birth rate

$$\Rightarrow \frac{\partial \beta}{\partial N}(t,N) < 0$$

Second $\quad \delta(t,N)$ should be increasing with density N - increase $N \Rightarrow$ less food more competitive fights between males. etc.

Hence $\dfrac{\partial \rho}{\partial N}(t,N) = \underbrace{\dfrac{\partial}{\partial N}\beta(t,N)}_{<0} - \underbrace{\left(\dfrac{\partial}{\partial N}\delta(t,N)\right)}_{>0} < 0$

- $\dfrac{\partial \rho}{\partial N} < 0$ basic requirement for per-capita growth.

Hence $\dot{N} = N\rho(t,N)$ where $\dfrac{\partial \rho}{\partial N} < 0$ gives $N(0) = N_0$

We have done $\rho(t,N) = \rho(t)$, so we look at the linear problem.

Do a maclaurin series of N.

$$\rho(t,N) = \rho_0(t) + \rho_1(t)\left(\frac{N}{N^*}\right) + \beta(t)\left(\frac{N^2}{N^*}\right) + \cdots$$

where N^* is the max population the system can manage. $N^* \gg 1$

But need $\dfrac{\partial \rho}{\partial N} < 0 \Rightarrow \dfrac{\partial \rho}{\partial N} = \rho_1(t)\dfrac{1}{N^*} + \rho_2(t)\dfrac{2N}{N^{*2}}$

- Need that $\rho_1(t) < 0$ (since we can choose $N=0$)

$\rho_0(t)$ could be any sign.

Rewrite truncated system $\dfrac{\dot{N}}{N} = \rho_0(t) + \rho_1(t)\dfrac{N}{N^*}$ (ie ignore second order terms)

Let $\rho(t) = \rho_0$ and $\dfrac{K(t) = \cancel{N}_{max} \rho d(t)}{\rho_1(t)}$

So that $\dfrac{\dot{N}}{N} = \rho(t)\left(1 - \dfrac{V}{K(t)}\right) \Rightarrow \dot{N} = \rho(t) N \left(1 - \dfrac{N}{K(t)}\right)$.

$\dot{N} = \rho(t) N \left(1 - \dfrac{N}{K(t)}\right)$ time dependent - Logistic equation

Try $M(t) = \exp\left(-\int_0^t \rho(s)\,ds\right) N(t)$ and find an ODE for M

$$N(t) = e^{\int_0^t \rho(s)\,ds} M(t)$$

$$\dot{N} = \dot{M} e^{\int_0^t \rho(s)\,ds} + M \frac{d}{dt}\left(e^{\int_0^t \rho(s)\,ds}\right).$$

$$= \dot{M} e^{\int_0^t \rho(s)\,ds} + M \rho(t) \cdot e^{\int_0^t \rho(s)\,ds}$$

But $\dot{N} = \rho(t) e^{\int_0^t \rho(s)\,ds} M \left(1 - \dfrac{M e^{\int_0^t \rho(s)\,ds}}{K(t)}\right)$.

Compare:

$$(\dot{M} + \rho(t) M) e^{\int_0^t \rho(s)\,ds} = \rho(t) e^{\int_0^t \rho(s)\,ds} M \left(1 - \frac{M e^{\int_0^t \rho(s)\,ds}}{K(t)}\right).$$

$$\dot{M} e^{\int_0^t \rho(s)\,ds} + \cancel{\rho(t) M e^{\int_0^t \rho(s)\,ds}} = \cancel{\rho(t) M e^{\int_0^t \rho(s)\,ds}} - \frac{\rho(t)}{K(t)} M^2 \cdot e^{2\int_0^t \rho(s)\,ds}$$

$$\Rightarrow \dot{M} e^{\int_0^t \rho(s)\,ds} = -\frac{\rho(t)}{K(t)} M^2 e^{2\int_0^t \rho(s)\,ds}$$

$$\Rightarrow \dot{M} = -\frac{\rho(t)}{K(t)} e^{\int_0^t \rho(s)\,ds} \cdot M^2$$

$$\frac{dM}{M^2} = -\frac{\rho(t)}{K(t)} e^{\int_0^t \rho(s)\,ds}\,dt$$

$$\int_{M(0)}^{M(t)} \frac{dM}{M^2} = -\int_0^t \left(\frac{\rho(\tau)}{K(\tau)} e^{\int_0^\tau \rho(s)\,ds}\right) d\tau$$

$$\left[-\frac{1}{M}\right]_{M(0)}^{M(t)} = -\int_0^t H(\tau)\,d\tau \quad \text{where} \quad H(t) = \frac{\rho(\tau)}{K(\tau)} e^{\int_0^\tau \rho(s)\,ds}.$$

$$\frac{1}{M(0)} - \frac{1}{M(t)} = -\int_0^t H(\tau)\,d\tau$$

$$\frac{1}{M(0)} + \int_0^t H(\tau)\,d\tau = \frac{1}{M(t)} \Rightarrow M(t) = \frac{1}{\frac{1}{M(0)} + \int_0^t H(t)\,d\tau}$$

Recall $M(t) = e^{-\int_0^t p(s)ds} N(t)$

$$e^{-\int_0^t p(s)ds} N(t) = \frac{1}{\frac{1}{M(0)} + \int_0^t H(\tau)\,d\tau}$$ but $M(0) = N(0) = N_0$ (say

$$N(t) = \frac{N_0 e^{\int_0^t p(s)ds}}{1 + N_0 \int_0^t H(\tau)\,d\tau}$$

Case ρ, K constants $\rho(t) = \rho$, $K(t) = K$.

$$\dot{N} = \rho N\left(1 - \frac{N}{K}\right)$$ Logistic Growth.

Many models we consider start from logistic growth and add on more terms.

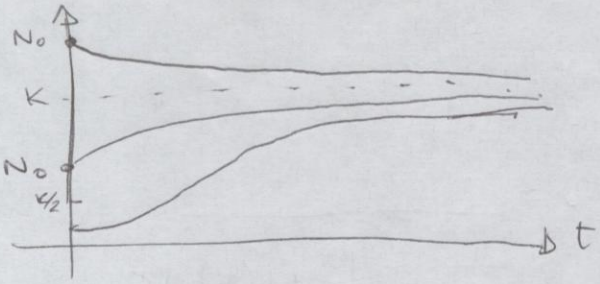
$$H(\tau) = \frac{\rho}{K} e^{\int_0^\tau \rho ds} = \frac{\rho}{K} e^{\rho\tau}$$

$$\Rightarrow N(t) = \frac{N_0 e^{\rho t}}{1 + N_0 \int_0^t \frac{\rho}{K} e^{\rho t} d\tau} = \frac{N_0 e^{\rho t}}{1 + \frac{N_0 \rho}{K}\left[\frac{1}{\rho} e^{\rho t}\right]_0^t}$$

$$= \frac{N_0 e^{\rho t}}{1 + \frac{N_0}{K}(e^{\rho t} - 1)}$$

$$N(t) = \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right)e^{-\rho t}}$$ logistic growth.

As $t \to \infty$, $N(t) \to \frac{N_0}{\frac{N_0}{K}} = K$ which is independent of N_0



for any $N_0 > 0$

$N(t) \to K$ as $t \to \infty$

K is the maximum stable population that the environment can support. K is called the <u>carrying capacity</u>

The effect of ~~hat~~ building in densinity dependence $\frac{\dot{N}}{N} = \rho\left(1 - \frac{N}{K}\right)$ is that the long term population $N(t)$ as $t \to \infty$ is always finite and $N(\infty) = 0$ if $N_0 = 0$; $N(\infty) = K$ if $N_0 > 0$.

density dependence

<u>Case</u> $K(t)$ constant $= K$, $\rho(t)$ some function of time

$$\dot{N} = \rho(t) N (1 - N/K)$$

set $\tau = \int_0^t \rho(s)\,ds \Rightarrow d\tau = \rho(t)\,dt$.

$$\frac{dN}{dt} = \frac{dN}{d\tau}\frac{d\tau}{dt} = \frac{dN}{d\tau}\rho(t)$$

$$\Rightarrow \frac{dN}{d\tau}\rho(t) = \rho(t) N\left(1 - \frac{N}{K}\right) \Rightarrow \frac{dN}{dt} = N\left(1 - \frac{N}{K}\right).$$

$$N(t) = \frac{N_0}{\frac{N_0}{K} - \left(1 - \frac{N_0}{K}\right)e^{-\tau}}$$ (using last formula)

$$N(t) = \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right)e^{-\int_0^t \rho(s)\,ds}}.$$

Suppose $\rho(t)$ is periodic, period T. split $t = kT + s$.

$$N(t) = N(kT+s) = \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{\int_0^{kT+s} \rho(\tau)\,d\tau}}$$

$$\int_0^{kT+s} \rho(\tau)\,d\tau = \int_0^{kT} \rho(\tau)\,d\tau + \int_{kT}^{kT+s} \rho(\tau)\,d\tau \qquad \text{set } R = \int_0^T \rho(s)\,ds$$

$$= kR + \int_0^s \rho(\tau)\,d\tau \quad \text{using peoridicy.}$$

$$N(t) = \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{kR} e^{\int_0^s \rho(\tau)\,d\tau}} \qquad (\text{here } t = kT+s).$$

Let $k \to \infty$ and define $N_\infty(s) = \lim_{k\to\infty} N(kT+s)$.

$$\lim_{k\to\infty} \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{kR} e^{\int_0^s \rho(\tau)\,d\tau}} = \begin{cases} K & \text{if } R < 0 \\ 0 & \text{if } R > 0 \\ \dfrac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{\int_0^s \rho(s)\,ds}} & \text{if } R = 0 \end{cases}$$

The case $R = 0$ $\quad N_\infty(s) = \dfrac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{\int_0^{s} \rho(\tau)\,d\tau}}$

What about $N_\infty(T+s) = \dfrac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{\int_0^{T+s} \rho(\tau)\,d\tau}}$ $\quad *$

But
$$\int_0^{T+s} \rho(t)\,dt = \int_0^T \rho(t)\,dt + \int_T^{T+s} \rho(\tau)\,d\tau$$
$$= R + \int_0^s \rho(t)\,d\tau$$
$$= \int_0^s \rho(t)\,d\tau \quad \text{since } R = 0$$

from $*$ $\quad N_\infty(T+s) = \dfrac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{\int_0^s \rho(t)\,dt}} = N_\infty(s) \Rightarrow$ when $k \to \infty$ N periodic

$$N(t) = \frac{N_0 e^{\int_0^t \rho(s)ds}}{1 + N_0 \int_0^t H(u)du} \qquad H(u) = \frac{\rho(u)}{K(u)} e^{\int_0^u \rho(s)ds} \qquad \text{sol to } \dot{N} = \rho(t) N \left(1 - \frac{N}{K(t)}\right)$$

Case ρ constant, $K(t)$ periodic, period T

$\Rightarrow H(u) = \frac{\rho}{K(u)} e^{\rho u}$: so H is periodic, period T

We need $\int_0^t H(u)du = \int_0^t \frac{\rho}{K(u)} e^{\rho u} du$

Divide $t = kT + s \quad s \in [0, T)$ so we need $\int_0^{kT+s} \frac{\rho}{K(u)} e^{\rho u} du = I$

Write $I = \int_0^{kT} \frac{\rho}{K(u)} e^{\rho u} du + \int_{kT}^{kT+s} \frac{\rho}{K(u)} e^{\rho u} du$

Now $\int_{kT}^{kT+s} \frac{\rho}{K(u)} e^{\rho u} du = \int_0^s \frac{\rho}{K(v+kT)} e^{(v+kT)\rho} du$ let $v = u - kT$

$$= \int_0^s \frac{\rho}{K(v)} e^{\rho v} \cdot e^{\rho kT} dv = e^{\rho kT} \int_0^s \frac{\rho}{K(v)} e^{\rho v} dv$$
$$= \int_0^s H(v) dv.$$

For $\int_0^{kT} \frac{\rho}{K(u)} e^{\rho u} du = \sum_{r=1}^{k} \int_{(r-1)T}^{rT} \frac{\rho}{K(u)} e^{\rho u} du$

$$= \sum_{r=1}^{k} \int_0^T \frac{\rho}{K(w+(r-1)T)} e^{\rho(w+(r-1)T)} dw \qquad w = u - (r-1)T$$

$$= \sum_{r=1}^{k} \int_0^T \frac{\rho}{K(w)} e^{\rho w} e^{(r-1)\rho T} dw$$

$$= \left(\sum_{r=1}^{k} e^{(r-1)\rho T}\right) \cdot \mathcal{K} \qquad \mathcal{K} = \int_0^T \frac{\rho}{K(w)} e^{\rho w} dw = \int_0^T H(w) dw$$

$$= \left(\frac{1 - e^{k\rho T}}{1 - e^{\rho T}}\right) \mathcal{K}$$

Write $I = \int_0^{kT} \frac{\rho}{K(u)} e^{\rho u} du + \int_{kT}^{kT+s} \frac{\rho}{K(u)} e^{\rho u} du$

$$\int_0^{kT+s} H(u) du = \left(\frac{1 - e^{\rho kT}}{1 - e^{\rho T}}\right) \mathcal{K} + e^{\rho kT} \int_0^s H(v) dv$$

$$N(t) = \frac{N_0 e^{\rho(kT+s)}}{1 + N_0 \left(\left(\frac{1 - e^{\rho kT}}{1 - e^{\rho T}}\right) \mathcal{K} + \left(\int_0^s H(u) du\right) e^{\rho kT} \right)} \qquad \text{where } t = kT + s.$$

$$= \frac{N_0 e^{\rho s}}{e^{-\rho kT} + N_0\left(\left(\frac{e^{-\rho kT}-1}{1-e^{\rho T}}\right)R + \int_0^s H(u)\,du\right)}$$

To see how $N(t) = N(kT+s)$ behaves as t gets large ($k \to \infty$) we set

$$N_\infty(s) = \lim_{k\to\infty} N(kT+s) = \frac{N_0 e^{\rho s}}{0 + N_0\left(\frac{-1}{1-e^{\rho T}}R + \int_0^s H(u)\,du\right)}$$

$$= \frac{e^{\rho s}}{R\left(\frac{1}{e^{\rho T}-1}\right) + \int_0^s H(u)\,du}$$

claim $N_\infty(s)$ is periodic

Need to prove $N_\infty(T+s) = N_\infty(s)$

$$N_\infty(T+s) = \frac{e^{\rho(T+s)}}{R\left(\frac{1}{e^{\rho T}-1}\right) + \int_0^{T+s} H(u)\,du}$$

But $\int_0^{T+s} H(u)\,du = \int_0^T H(u)\,du + \int_T^{T+s} H(u)\,du$

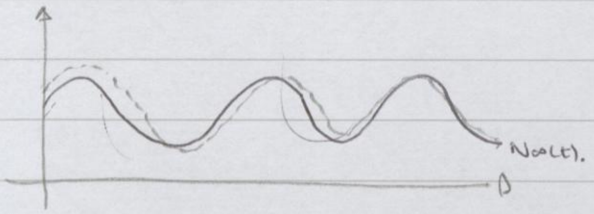
$$= R + e^{\rho T}\int_0^s H(v+T)\,dv$$

$$= R + e^{\rho T}\int_0^s H(v)\,dv$$

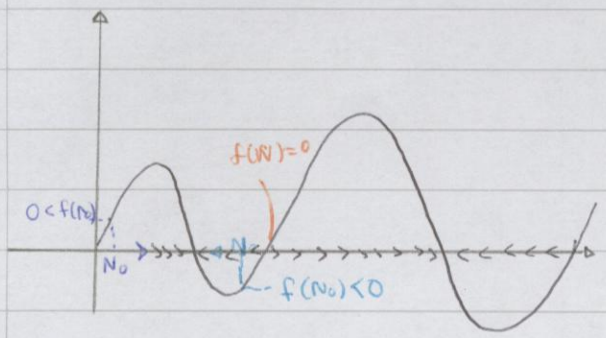
$$N_\infty(T+s) = \frac{e^{\rho T}e^{\rho s}}{R\left(\frac{1}{e^{\rho T}-1}\right) + R + e^{\rho T}\int_0^s H(u)\,du}$$

$$= \frac{e^{\rho T}e^{\rho s}}{R\left(\frac{1+e^{\rho T}-1}{e^{\rho T}-1}\right) + e^{\rho T}\int_0^s H(u)\,du}$$

$$= \frac{e^{\rho T}e^{\rho s}}{R\left(\frac{1}{e^{\rho T}-1}\right) + \int_0^s H(u)\,du} = N_\infty(s).$$



Graphical analysis of $\dot{N} = f(N)$ where $N \in \mathbb{R}$ & $f: \mathbb{R} \rightarrow \mathbb{R}$ as smooth as you like.



$\dot{N} = f(u)$ initial condition $N(0)=N_0$

$\Rightarrow$ solution $N(t)$, $t \geq 0$ with $N(0) = N_0$

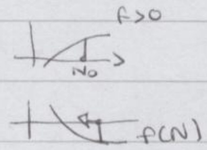
Want to know how $N(t)$ behaves as $t \rightarrow \infty$ for any N_0.

i) Suppose $N_0 > 0$ is very small ($N_0 \ll 1$)

Idea:

1. Plot f as function of N
2. Choose N
3. If $f(N) > 0$, N moves to the right

   < 0 left

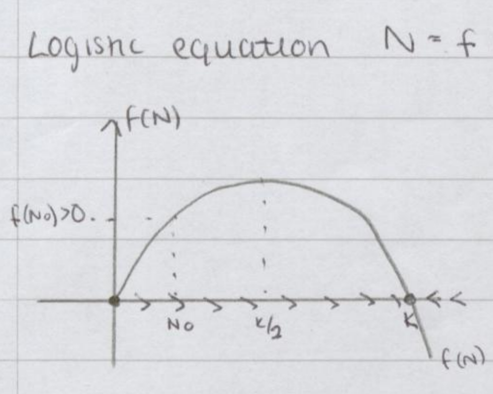


4. At points where $f(N) = 0$, N stays ~~the~~ still.

Points where $f(N) = 0$ are called steady states

ie steady states are where f crosses the "x" axis.

Logistic equation $\dot{N} = f(N) = \rho N(1 - N/K)$



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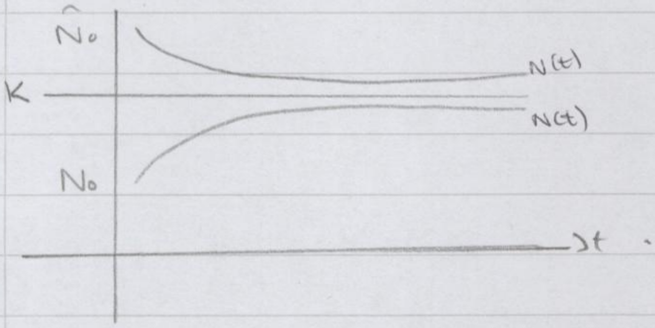
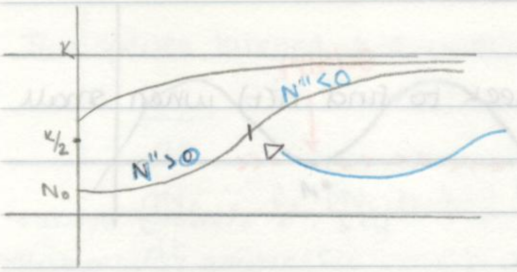
Two steady states $N=0$, $N=K$



for $N_0 \neq 0$

$N(t) \to K$ as $t \to \infty$

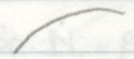
K is carrying capacity and if $N_0 \neq 0$ $N(t) \to K$.



For $N_0 < K/2$ there's a point of inflection: $N''=0$

There's a qualitative difference to $N(t)$ depending on whether $N_0 \leq K/2$ or $N_0 > K/2$

$N'' > 0$ is convex



$N'' < 0$ is concave

How do we find the convex/concave parts?

Know: $N'(t) = f(N(t)) = \rho N(t)\left(1 - \frac{N(t)}{K}\right)$

$\Rightarrow N''(t) = \frac{d}{dt}\left(f(N(t))\right) = f'(N(t))\frac{dN}{dt} = f'(N(t))f(N(t))$

So $N''(t) = 0$ if $f'(N(t)) = 0$ or $f(N(t)) = 0$ (or both)

If $N < K/2$, $f'(N) > 0$

$> K/2$, $f'(N) < 0$

So for $0 < N(t) < K/2$, $f'(N(t)) > 0$, $f(N(t)) > 0$

$\Rightarrow N''(t) = f'(N(t))f(N(t)) > 0$

$\Rightarrow N$ is a convex function of t if $0 < N(t) < K/2$

For $K/2 < N(t) < K$, $f'(N(t)) < 0$ $f(N(t)) > 0$

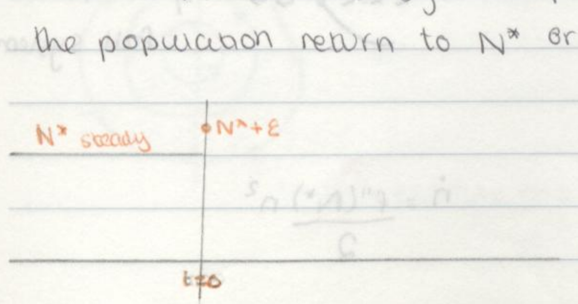
$\Rightarrow N''(t) < 0$

$\Rightarrow N$ is a concave function of t if $K/2 < N(t) < K$.

Linear Stability Analysis

Recall: $\dot{N} = f(N)$, points N^* where $f(N^*) = 0$ are called <u>steady states</u>

We would like to say something about the stability of these steady states ie If $N = N^*$ and the system ~~p~~ is perturbed by a small amount does the population return to N^* or grow?



For $t<0$, $N(t) = N^*$ steady

At $t=0$ N is perturbed from N^* by a small pertubation ε (>0 or ≤ 0) so that $N(0) = N^* + \varepsilon$

What happens to $N(t)$ for $t>0$?

We know $\dot{N} = f(N)$. Let $N(t) = N^* + n(t)$ and we seek to find $n(t)$ when small (certainly $n(0) = \varepsilon << 1$)

If $N(t) \to N^*$ then $n(t) \to 0$, $n(t)$ is the pertubation.

$N(t)$ is a solution of $\dot{N} = f(N)$

$\Rightarrow n(t)$ satisfies:

$$\frac{d}{dt}\left(N^* + n(t)\right) = f\left(N^* + n(t)\right)$$

$$\frac{dn}{dt} = f(N^* + n(t)) \quad \text{since } N^* \text{ is constant}$$

$$= f(N^*) + f'(N^*)n(t) + \frac{f''(N^*)}{2!}n(t)^2 + \dots$$

Since $n(0) \approx \varepsilon << 1$, then for small enough time, $n(t) << 1 \Rightarrow$ can ignore terms in n^2 and higher.

$\Rightarrow \frac{dn}{dt} = f(N^*) + f'(N^*)n(t)$ to first order in $n(t)$

Since N^* is a steady state, $f(N^*) = 0$

$\Rightarrow \frac{dn}{dt} = f'(N^*)n$

This gives a good approximation to the pertubation provided $n(t)$ is small

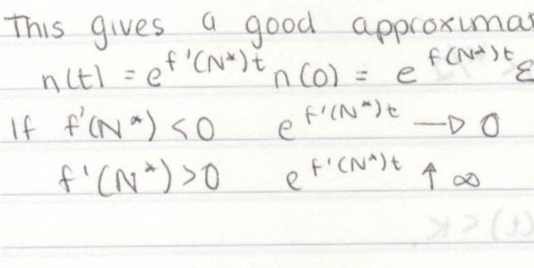
$n(t) = e^{f'(N^*)t} n(0) = e^{f(N^*)t}\varepsilon$

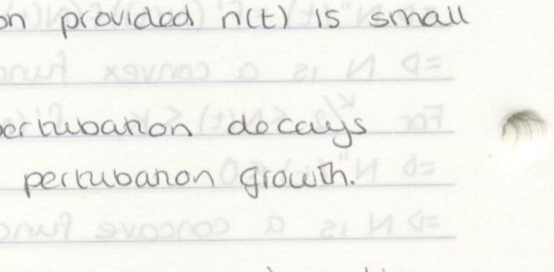
If $f'(N^*) < 0$ $\quad e^{f'(N^*)t} \to 0$ so $n(t) \to 0$ ie pertubation decays

$f'(N^*) > 0$ $\quad e^{f'(N^*)t} \uparrow \infty$ so $n(t)$ grows ie pertubation growth.

The case $f'(N^*) < 0$ where pertubation decays is called (locally) stable

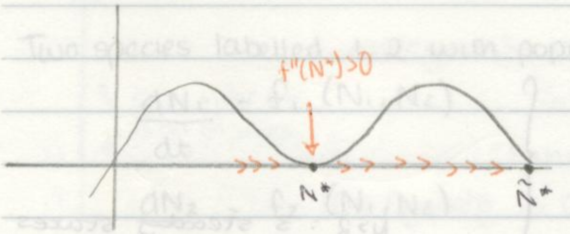
> 0 grows unstable





If $f'(N^*) = 0$ the linear term in Taylor's is zero:

$\dot{n} = 0 + 0 \cdot n + \frac{f''(N^*)}{2} n^2$ to second order. $\quad \dot{n} = \frac{f''(N^*)}{2} n^2$



Depends on which way the pertubation takes N. If $\varepsilon<0$, then $N(t)\to N^*$
$\varepsilon>0$, then $N(t)\to\tilde{N}^*$

Example:

Per-capita birth rate $\beta(N)=\dfrac{rN}{N^2+K}$, $\quad\delta(N)=d>0$ constant

So $\dfrac{\dot N}{N}=\beta(N)-\delta(N)=\dfrac{rN}{N^2+K}-d$

$\Rightarrow \dot N = N\left(\dfrac{rN}{N^2+K}-d\right)$

Find the steady states: $\Rightarrow N\left(\dfrac{rN}{N^2+K}-d\right)=0$

$\Rightarrow N=0$ and solutions to $\dfrac{rN}{N^2+K}=d$

$\Rightarrow dN^2-rN+dK=0$

$N_\pm=\dfrac{r}{2d}\pm\dfrac{1}{2d}(r^2-4d^2K)^{1/2}$

For populations need $N_\pm>0$ and real!

$N_\pm=\dfrac{r}{2d}\pm\dfrac{r}{2d}\left(1-\left(\dfrac{2d\sqrt{K}}{r}\right)^2\right)^{1/2}$ $\qquad$ here $r, d, K>0$

$=\dfrac{r}{2d}\left(1\pm\left(1-\dfrac{4}{\mu^2}\right)^{1/2}\right)$ $\quad$ where $\mu=\dfrac{r}{d\sqrt{K}}$

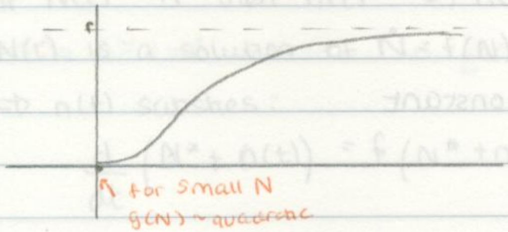
Hence: for real roots need $\mu\geq 2$. If $\mu=2$ we get $N_\pm=r/2d$ double root.
When $\mu>2$ we get real roots (and they're distinct)
Are they both >0?
Yes since $N_-=\dfrac{r}{2d}\left(1-\left(1-\dfrac{4}{\mu^2}\right)^{1/2}\right)$ and $0<1-4/\mu^2<1$ (and $N_+>N_->0$).

Hence if $\mu<2$ $\quad N=0$ is the unique steady state
$\mu>2$ $\quad$ The steady states are $N=0$ and 2 distinct N_-, N_+
$\mu=2$ $\quad N=0$ and $N_-=N_+$.

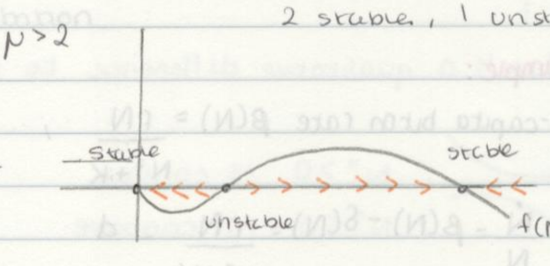
$$\dot{N} = N\left(\frac{rN}{N^2+K} - d\right) = \frac{rN^2}{N^2+K} - dN$$

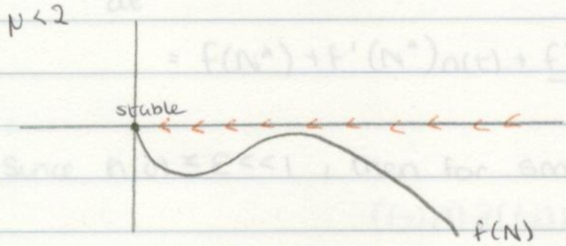
$$g(N) = \frac{r}{1+K/N^2} \longrightarrow r \text{ as } N \to \infty.$$

$\mu > 2$: 3 steady states
2 stable, 1 unstable.



Now subtract $\longrightarrow$ dN





for $\mu < 2$, $\exists$ a unique steady state $N = 0$ and $N_0 > 0$, $N(t) \to 0$ $t \to \infty$
Extinction is the only outcome.

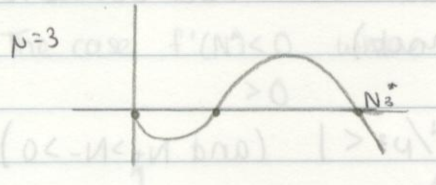
For $\mu > 2$ label the steady states: $0 = N_1^* < N_2^* < N_3^*$

If $N_0 \in (0, N_2^*)$ then $N(t) \to 0$ $t \to \infty$, extinction

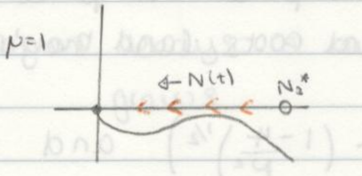
$N_0 \in (N_2^*, N_3^*)$ then $N(t) \to N_3^*$, $t \to \infty$

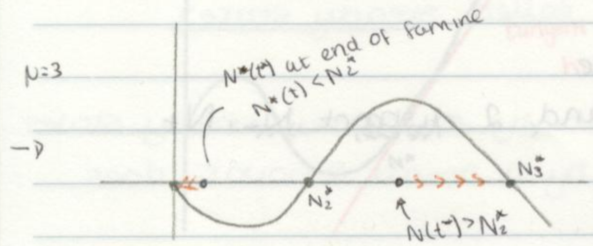
$N_0 \geq N_3^*$ then $N(t) \longrightarrow N_3^*$ as $t \to \infty$.

- Suppose $\mu = 3$ and $N(t) = N_3^*$. Then suppose that a sustained famine hits the population so that $\mu = 1$. Then after some time the famine lifts so that $\mu = 3$ again. What happens to the population?



famine $\longrightarrow$





If the famine is different at $t = t^*$ and $N(t^*) < N_2^*$ then $N(t) \longrightarrow 0$ as $t \to \infty$

If $N(t^*) > N_2^*$

Two Species Models

Two species labelled 1, 2 with population densities N_1, N_2

$$\left.\begin{aligned} \frac{dN_1}{dt} &= f_1(N_1, N_2) \\ \frac{dN_2}{dt} &= f_2(N_1, N_2) \end{aligned}\right\} \quad \begin{aligned} N_1(0) &= N_{10} \\ N_2(0) &= N_{20} \end{aligned}$$

The form of f_1, f_2 depends on how the two species interact eg compete, cooperate.

We expect $f_1(0, N_2) = 0 \quad \forall N_2 \geq 0$

$f_2(N_1, 0) = 0 \quad \forall N_1 \geq 0$

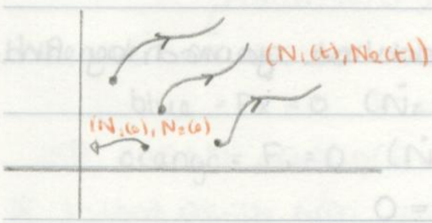
So $\exists$ $f_1(N_1, N_2) = N_1 F_1(N_1, N_2)$

$f_2(N_1, N_2) = N_2 F_2(N_1, N_2)$

$\dot{N}_1 = N_1 F_1(N_1, N_2), \quad \dot{N}_2 = N_2 F_2(N_1, N_2)$ * General model for two species

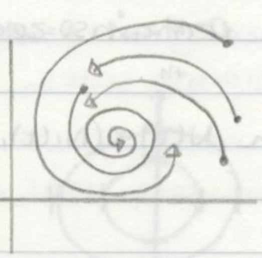
We want a qualitative picture of how $N_1(t), N_2(t)$ change with time for any $N_1(0), N_2(0)$.

Solution of * are curves $(N_1(t), N_2(t)) \in \mathbb{R}^2$ parametrised by t.



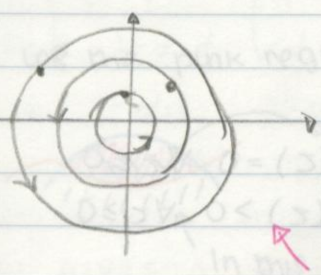
Through each initial point $(N_1(0), N_2(0))$ there is a solution curve.

Idea is to plot lots of initial points and draw the solution curves leaving each point.



With enough curves we can determine $(N_1(t), N_2(t))$ qualitatively for any $(N_1(0), N_2(0))$

Example: $\dot{N}_1 = -N_2, \quad \dot{N}_2 = N_1$ (not relevant to ecology).



$$\ddot{N}_1 = -\dot{N}_2 = -N_1 \Rightarrow N_1(t) = A\cos(t+\varepsilon)$$

$$N_2(t) = A\sin(t+\varepsilon)$$

example of a phase plane.

Plotting a phase plane: for $\dot{x} = f(x,y)$, $\dot{y} = g(x,y)$ planar system

Find nullclines:

These are curves where either $f(x,y)=0$ or $g(x,y)=0$

Steady states:

Points (x^*, y^*) where $f(x^*, y^*) = 0 = g(x^*, y^*)$

- In the previous example $f(x,y) = -y$, $g(x,y) = x$

$\Rightarrow$ nullclines are $y=0$ and $x=0$.

$\frac{\dot{N}_1}{N_1} = f_1(N_1, N_2)$ $\frac{\dot{N}_2}{N_2} = f(N_1, N_2)$ per capita growth rate.

The models are always of this form because if N_i is absent we expect no growth ie. $\dot{N}_i = 0$ and this implies that $F_i = N_i f_i(N_1, N_2)$ $i = 1, 2$ for fractions f_i

In terms of the phase plane this means that if N_0 belongs to the axes then $N(t)$ stays on the axes

So some useful information for the phase plane can be gained by finding what happens on the axes.

For example: If at $t=0$, $N_1(0) = N_{10} > 0$ but $N_2(0) = 0$

Then $\dot{N}_1(0) > 0$, $\dot{N}_2(0) = 0$. So N_1 increase but N_2 remains zero.

Note $\dot{N}_2(t) = N_2(t) f_2(N_1(t), N_2(t))$ along a solution $N(t) = (N_1(t), N_2(t))$

$\frac{\dot{N}_2}{N_2} = f_2(N_1(t), N_2(t))$

Intergrate over $t \in (0, \tau)$

$$[\log N_2(t)]_0^\tau = \int_0^\tau f_2(N_1(t), N_2(t))\,dt$$

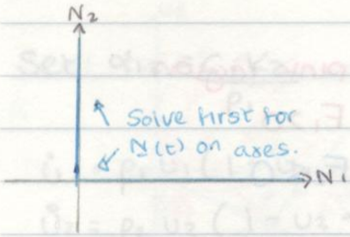
$$\log \frac{N_2(\tau)}{N_2(0)} = \int_0^\tau f_2(N_1(t), N_2(t))\,dt$$

$$N_2(\tau) = N_2(0) \exp\left(\int_0^\tau f_2(N_1(t), N_2(t))\,dt\right)$$

This provides a (sketch) proof that if $N_2(0) = 0$ then $N_2(\tau) = 0$ $\forall \tau \geq 0$

$N_2(0) > 0$ $N_2(\tau) > 0$ $\forall \tau \geq 0$

$\Rightarrow$ start with $N_2 = 0 \Rightarrow$ stay with $N_2 = 0$

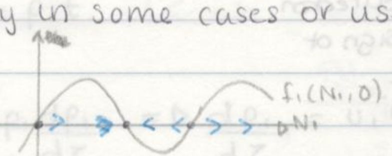


So set $N_2(0)=0$ then $N_2(t)=0 \ \forall t \geq 0$

So $\dot{N}_1(t) = N_1(t) f_1(N_1(t), 0)$

$\Rightarrow$ this is a simple ode for one variable N_1

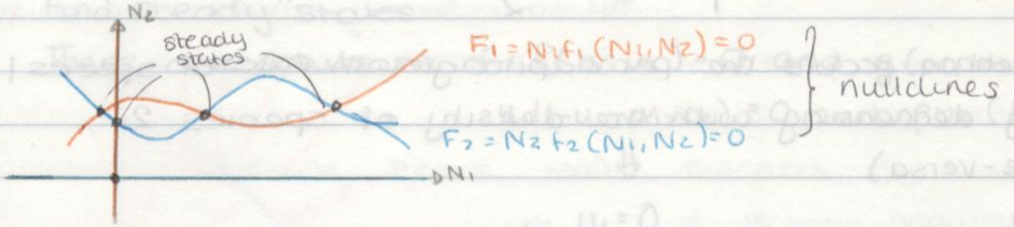
We can solve explicitly in some cases or use methods for single species models.



Ecologically the axis $N_2=0$ is the situation: How does species 1 behave if species 2 is absent?

The next step is to plot the nullclines $f_1(N_1,N_2)=0$, $f_2(N_1,N_2)=0$

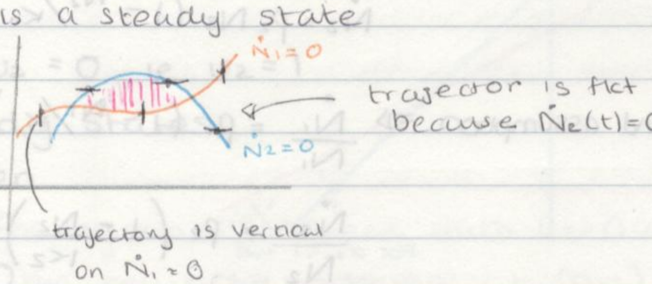
These are typically curves (but may have multiple branches)



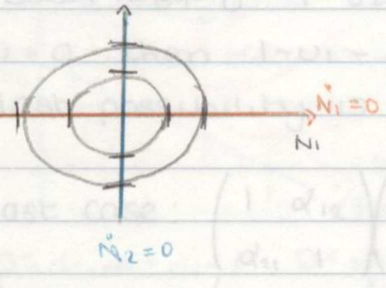
Whenever orange and blue cross there is a steady state

blue $= F_2 = 0$ $(\dot{N}_2 = 0)$

orange $= F_1 = 0$ $(\dot{N}_1 = 0)$



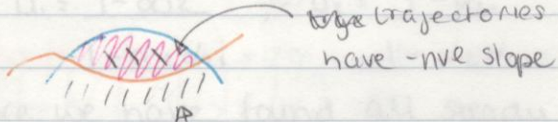
$\dot{N}_1 = \dot{N}_2 = 0$ $\dot{N}_2 = \dot{N}_1 = 0$



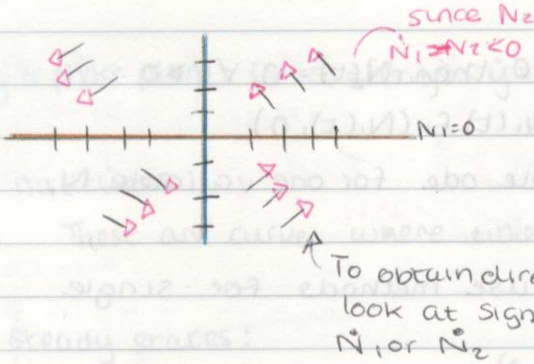
So for a trajectory $(N_1(t), N_2(t))$ in the blue pink region

$$\frac{dN_1}{dN_2} = \frac{\dot{N}_2}{\dot{N}_1} = \frac{F_2(N_1, N_2)}{F_1(N_1, N_2)} < 0$$

So in the pink region trajectories have negative slope



In this region $\frac{dF_2}{dF_1} > 0$ along a trajectory.



$\dot N_1 = F_1 = -N_2$
$\dot N_2 = F_2 = N_1$

In pink region
$F_1>0$
$F_2<0$

↑ Next question in which direction do trajectories go?
Are the clockwise or anticlockwise

Example: 2 competing species

Assume 1: In the absense of species 2, species 1 undergoes logistic growth
" 1 " 2 "

Assume 2: When competition occurs the per capita growth rate of species 1 is linearly decreasing with the density of species 2 (and vice-versa)

1st assumption $\Rightarrow$ $\dot N_1 = \rho_1 N_1 (1 - N_1/K_1)$ when not interacting
$\dot N_2 = \rho_2 N_2 (1 - N_2/K_0)$

2nd assumption $\Rightarrow$ $\dfrac{\dot N_1}{N_1} = \rho_1 (1 - N_1/K_1) - c N_2$ $\rho_i>0$ $K_i>0$ and $c_i>0$ for linearly decreasing growth rates.

$\dfrac{\dot N_2}{N_2} = \rho_2 \left(1 - \dfrac{N_2}{K_2}\right) - c_2 N_1$

Has 6 parameters $\Rightarrow$ now reduce to 3.

Define $u_1 = \dfrac{N_1}{K_1}$, $u_2 = \dfrac{N_2}{K_2}$

$\Rightarrow \dot N_1 = K_1 \dot u_1$

$\Rightarrow K_1 \dot u_1 = (K_1 u_1) \rho_1 (1 - \frac{K_1 u_1}{K_1}) - c_1 K_2 u_2 K_1 u_1$

$\dot u_1 = \rho_1 u_1 (1 - u_1) - K_2 c_1 u_1 u_2$

Also get

$\dot u_2 = \rho_2 u_2 (1 - u_2) - K_1 c_2 u_1 u_2$

$\dot u_1 = \rho_1 \left[u_1 (1 - u_1) - \frac{c_1 K_2}{\rho_1} u_1 u_2 \right]$

$\dot u_2 = \rho_2 \left[u_2 (1 - u_2) - \frac{c_2 K_1}{\rho_2} u_1 u_2 \right]$

Set $\alpha_{12} = \frac{c_1 K_2}{\rho_1}$ $\alpha_{21} = \frac{c_2 K_1}{\rho_2}$

$\dot{u}_1 = \rho_1 u_1 (1 - u_1 - \alpha_{12} u_2)$

$\dot{u}_2 = \rho_2 u_2 (1 - u_2 - \alpha_{21} u_1)$

Set $\rho = \frac{\rho_2}{\rho_1}$ and $\tau = \rho_1 t$

$\Rightarrow \frac{d\rho_1}{dt} = \frac{d\rho_1}{d\tau}\frac{d\tau}{dt} = \rho_1 \frac{d\rho_1}{d\tau} \Rightarrow \frac{d\rho_1}{d\tau} = u_1(1 - u_1 - \alpha_{12} u_2)$

and $\frac{d\rho_2}{d\tau} = \rho u_2 (1 - u_2 - \alpha_{21} u_1)$ 3 parameters

The effect of the scaling to u_1, u_2, τ is to stretch the axes of phase space $\Rightarrow$ general picture the same.

1. Find steady states

These are solutions of $f(u_1, u_2) = 0$ and $g(u_1, u_2) = 0$

$u_1(1 - u_1 - \alpha_{12} u_2) = 0$ and $\rho u_2 (1 - u_2 - \alpha_{21} u_1) = 0$

$\Downarrow$ $\Downarrow$

$u_1 = 0$ $u_2 = 0$

or $1 - u_1 - \alpha_{12} u_2 = 0$ or $1 - u_2 - \alpha_{21} u_1 = 0$

If $u_1 = 0$, then either $u_2 = 0$

or $1 - u_2 - \alpha_{12} u_1 = 1 - u_2 = 0$ ie $u_2 = 1$

$\Rightarrow (0,0)$ and $(0,1)$ are steady states.

If $1 - u_1 - \alpha_{12} u_2 = 0$ and $u_1 \neq 0$ then

either $u_2 = 0$

or $1 - u_2 - \alpha_{21} u_1 = 0$

If $u_2 = 0$ then $1 - u_1 - \alpha_{12} u_2 = 1 - u_1 = 0 \Rightarrow u_1 = 1 \Rightarrow (1,0)$ is a steady state

The last possibility is $\left.\begin{array}{l} 1 - u_2 - \alpha_{21} u_1 = 0 \\ 1 - u_1 - \alpha_{12} u_2 = 0 \end{array}\right\}$ *

This last case: $\begin{pmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{pmatrix}\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$ $\equiv$ *

$\begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \frac{1}{1 - \alpha_{12}\alpha_{21}} \begin{pmatrix} 1 & -\alpha_{12} \\ -\alpha_{21} & 1 \end{pmatrix}\begin{pmatrix} 1 \\ 1 \end{pmatrix}$

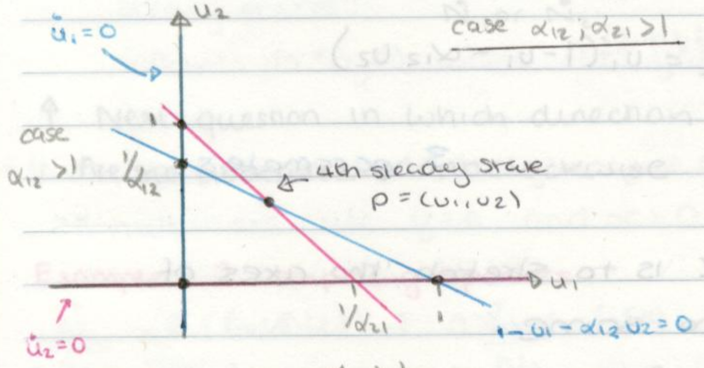
$\Rightarrow u_1 = \frac{1 - \alpha_{12}}{1 - \alpha_{12}\alpha_{21}}$, $u_2 = \frac{1 - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}}$ 4th possible steady state.

Since we have found all steady states with $u_1 = 0$ or $u_2 = 0$, this only gives a relevant steady state if $u_1 > 0$, $u_2 > 0$

If $1-\alpha_{12} \gtrless 0$ then for $u_1>0$ we must have $1-\alpha_{12}\alpha_{21} \gtrless 0$ and then for $u_2>0$ we must have $1-\alpha_{21} \gtrless 0$

Hence then for $\left(\dfrac{1-\alpha_{12}}{1-\alpha_{12}\alpha_{21}}, \dfrac{1-\alpha_{21}}{1-\alpha_{12}\alpha_{21}}\right)$ to be steady state

either $\alpha_{12}<1$, $\alpha_{21}<1$ or $\alpha_{12}>1$, $\alpha_{21}>1$



$u_1 = 0$ $1-u_1-\alpha_{12}u_2 = 0$ $\dot{u}_1 = 0$

$u_2 = 0$ $1-u_2-\alpha_{21}u_1 = 0$ $\dot{u}_2 = 0$

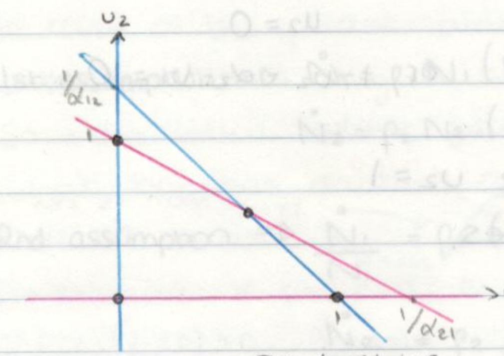
First line $1-u_1-\alpha_{12}u_2 = 0$

second $1-u_2-\alpha_{21}u_1 = 0$

P represents a coexistance state

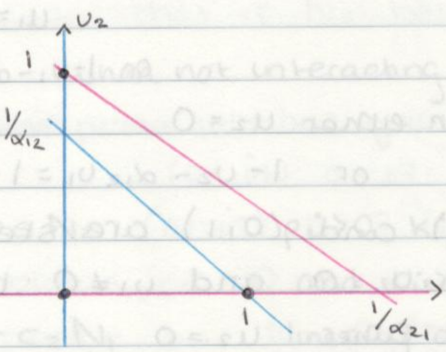
All other steady states have extinction for at least one species

Case $\alpha_{12}, \alpha_{21} < 1$



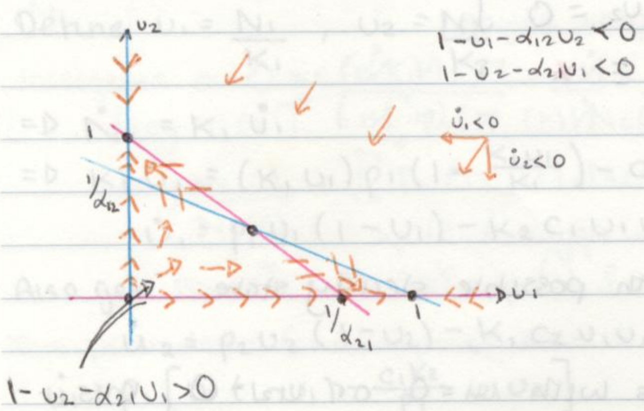
For $\alpha_{21}<1$ we cross over $u_1 = 1$

Case $\alpha_{21}<1$ $\alpha_{12}>1$



No interior steady state, so species cannot coexist.

4th case $\alpha_{21}>1$ $\alpha_{12}<1$ is as ↑ with lines swapped over.



$\alpha_{12}>1$ $\alpha_{21}>1$

$1-u_1-\alpha_{12}u_2 = 0$ $1-u_2-\alpha_{21}u_1 = 0$

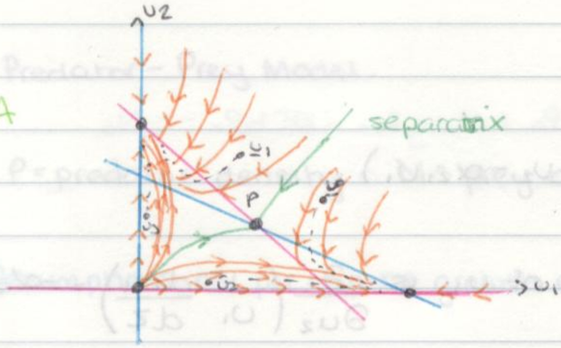
Look at axes

Look on $u_2 = 0$ $\dfrac{du_1}{dz} = u_1(1-u_1)$

On $x_1 = 0$ $\dfrac{du_2}{dz} = \rho u_2(1-u_2)$

This gives trajectory on axes

Fig A



$\alpha_{12} > 1, \alpha_{21} > 1$

This phase plane can be read to understand qualative behaviour for any initial condition

eg $\underline{u}_0 \to (1,0)$ $\quad \underline{u}_1 \to (0,1)$

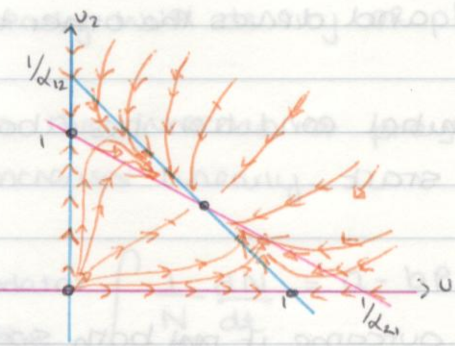
$\underline{u}_2 \to (1,0)$ $\quad \underline{u}_3 \to (0,1)$

If the initial condition lies above separatrix then end up at $(0,1)$

If the initial condition lies below separatrix then end up at $(1,0)$

Finally if the initial condition lies on the separatrix, end up at P.

Case $\alpha_{12} < 1$, $\alpha_{21} < 1$

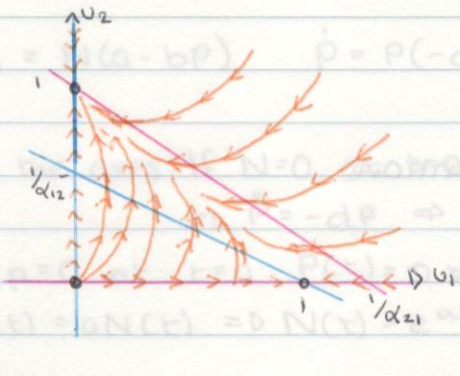


Now the picture has changed

For any initial condition not lying on the axes, the solution ends up at P.

ie if both populations start positive then the result is coexistance.

case $\alpha_{12} > 1$, $\alpha_{21} < 1$



For any initial condition with $u_2 > 0$ the solution ends up at $(0,1)$

No matter how small u_2 is in comparison to u_1 at $t = 0$, u_2 eventually drives u_1 extinct.

The case $\alpha_{12} < 1$, $\alpha_{21} > 1$ is the same a previous case but with $(0,1)$ replaced by $(1,0)$.

Conclusion:

~~Case I: $\alpha_{12} > 1, \alpha_{21} > 1$~~

~~$\frac{1}{u_1}\frac{du_1}{dz} = 1 - u_1 - \alpha_{12} u_2$~~

~~$\frac{1}{u_2}\frac{du_2}{dz} = \rho(1 - u_2 - \alpha_{21} u_1)$~~

Conclusion:

$$\frac{1}{u_1}\frac{du_1}{dz} = 1 - u_1 - \alpha_{12}u_2 \qquad \frac{1}{u_2}\frac{du_2}{dz} = \rho\left(1 - u_2 - \alpha_{21}u_1\right)$$

Effect of u_2 on the per capita growth of u_1 is $\frac{\partial}{\partial u_2}\left(\frac{1}{u_1}\frac{du_1}{dz}\right) = -\alpha_{12}$

and for u_1 on u_2 $\frac{\partial}{\partial u_1}\left(\frac{1}{u_2}\frac{du_2}{dz}\right) = -\rho\alpha_{21}$

Case I : $\alpha_{12} > 1, \alpha_{21} > 1$

Here $\frac{\partial}{\partial u_2}\left(\frac{1}{u_1}\frac{du_1}{dz}\right) = -\alpha_{12}$ is very negative, as is $\frac{\partial}{\partial u_1}\left(\frac{1}{u_2}\frac{du_2}{dz}\right)$

This is interpreted as strong ~~competition~~ competition.

Fig A shows one species always "wins" and drives the other to extinction.

Which species wins depends on whether the initial condition lies above the separatrix ie which has the head start.

Case II : $\alpha_{12} < 1, \alpha_{21} < 1$

Weak competition. Stable coexistance is outcome if ~~pop~~ both species start with positive populations.

Case III : $\alpha_{12} > 1, \alpha_{21} < 1$

$\Rightarrow$ effect of 2 on 1 is strong

effect of 1 on 2 is weak

$\Rightarrow$ species 2 "wins" and drives 1 to extinction.

Predator – Prey Model.

- P = predator density N = prey density.

Assumptions on per capita growth rates:

1. in the absence of predator, prey growth ~~follows a logistic growth law~~ ~~te.~~ is a positive constent.

2. in the absense of prey, predator per capita growth ~~rate~~ is a negative constant.

3. in the presence of predator, per capita growth rate of prey decreases linearly with density of predator.

4. In the presence of prey, the per capita growth of predator ~~grows~~ increases linearly.

Predator Prey Model
$$\begin{cases} \dfrac{1}{N}\dfrac{dN}{dt} = a - bP \\[2ex] \dfrac{1}{P}\dfrac{dP}{dt} = -d + cN \end{cases} \qquad a, b, c, d > 0$$

$$\dot{N} = N(a - bP) \qquad \dot{P} = P(-d + cN)$$

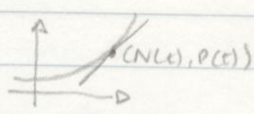
On the axes: If $N = 0$ at $t = 0$, $N(t) = 0 \ \forall t \geq 0$

$\Rightarrow \dot{P} = -dP \Rightarrow P(t) = e^{-dt}P(0) \longrightarrow 0$ exponentially.

If $P = 0$ at $t = 0$ $P(t) = 0 \ \forall t \geq 0$

$\dot{N}(t) = aN(t) \Rightarrow N(t) = e^{at}N(0) \Rightarrow$ exponential growth ⚠

$\dfrac{dP}{dN} = \dfrac{P(-d + cN)}{N(a - bP)}$ along a trajectory $(N(t), P(t))$



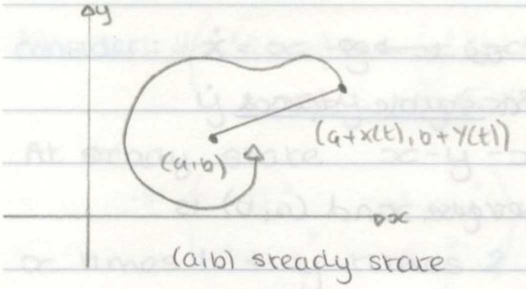
$\Rightarrow \dfrac{(a - bP)}{P} dP = \dfrac{(-d + cN)}{N} dN$

$$\int_{P_0}^{P(t)} \frac{a}{P} - b \, dP = \int_{N_0}^{N(t)} -\frac{d}{N} + c \, dN \qquad \text{where } N_0 = N(0) \quad P_0 = P(0)$$

$$\left[a\log P - bP\right]_{P_0}^{P(t)} = \left[-d\log N + cN\right]_{N_0}^{N(t)}$$

$$a\log P(t) + d\log N(t) - bP(t) - cN(t) = a\log P_0 + d\log N_0 - bP_0 - cN_0$$

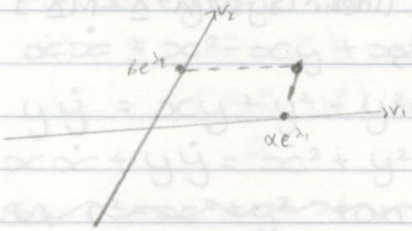
ie $\vartheta(t) : a\log P(t) + d\log N(t) - bP(t) - cN(t)$ is constant in time



$\dot{x} = f(x,y) \quad \dot{y} = g(x,y)$

A. $\dfrac{d\underline{X}}{dt} = M\underline{X}$ where $M = \left.\begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}\right|_{(a,b)}$

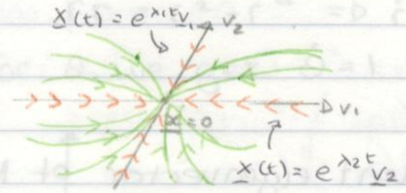
If M has real eigenvalues λ_1, λ_2 with respective eigenvectors $\underline{v}_1, \underline{v}_2$ then solution of A is $\underline{X}(t) = \alpha e^{\lambda_1 t}\underline{v}_1 + \beta e^{\lambda_2 t}\underline{v}_2$.



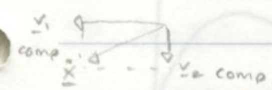
Case $\lambda_1 < \lambda_2 < 0$

Here $\left.\begin{array}{l} e^{\lambda_1 t} \to 0 \\ e^{\lambda_2 t} \to 0 \end{array}\right\}$ as $t \to \infty$

But $e^{\lambda_1 t} \to 0$ faster than $e^{\lambda_2 t}$ because $\lambda_1 < \lambda_2$



If $\underline{X}(0) = \underline{v}_1$ then $\underline{X}(t)$ stays on the line $k\underline{v}_1$, $k \in \mathbb{R}$.



$\underline{X}(t) = e^{\lambda_1 t}\underline{v}_1 \quad (\underline{X}(0) = \underline{v}_1)$

$\underline{\dot{X}} = \lambda_1 e^{\lambda_1 t}\underline{v}_1 = e^{\lambda_1 t}M\underline{v}_1$

$= M(e^{\lambda_1 t}\underline{v}_1) = M\underline{X}(t)$

$\Rightarrow \underline{X}(t) = e^{\lambda_1 t}\underline{v}_1$ lies on the line with direction $\underline{v}_1$ through $\underline{0}$

If $\lambda_1 < 0$, $\underline{X}(t) \to 0$ along this line.

(a,b) is called stable node. Stable because if $|\underline{X}(0)|$ is small $\underline{X}(t) \to \underline{0}$ as $t \to \infty$ and $\lambda_1, \lambda_2 < 0$.

If λ_1, λ_2 are positive the arrows reverse direction and then (a,b) is called unstable (node)

Case λ_1, λ_2 complex conjugate

Say $\lambda_1 = \mu + i\omega \quad \lambda_2 = \mu - i\omega \qquad (\mu, \omega \neq 0)$

Now $\underline{X}(t) = \mathrm{Re}\{e^{\mu t}\mathrm{Re}\{Ae^{i\omega t}\underline{v}_1 + Be^{-i\omega t}\underline{v}_2\}\}$

This gives $\underline{X}(t) = e^{\mu t}(\underline{\hat{A}}\cos\omega t + \underline{\tilde{B}}\sin(\omega t))$ $\quad \underline{\tilde{A}}, \underline{\tilde{B}}$ real vectors

Controls $|\underline{X}(t)|$ $\qquad$ controls polar angle.

Case where $\mu < 0 \Rightarrow e^{\mu t} \to 0$ as $t \to \infty$

The steady state is called a stable spiral

If $\mu > 0$ then the arrows reverse and (a,b) is unstable spiral.

If $\mu = 0$ then $e^{\mu t} = 1 \ \forall t$ so we only have the oscillatory component

The trajectories $\underline{x}(t)$ [of the linear system $\dot{\underline{x}} = M\underline{x}$]

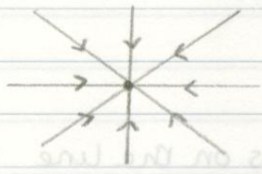
The trajectories are closed orbits

Called a centre

Case $\lambda_1 = \lambda_2$

Jordon normal form of M is $\begin{pmatrix} a & 0 \\ b & a \end{pmatrix}$ where $a = \lambda_1 = \lambda_2$ $(\neq 0)$

- Subcase A: $b = 0 \Rightarrow$ JF $\begin{pmatrix} a & 0 \\ 0 & a \end{pmatrix} \Rightarrow$ any $\underline{v} \neq 0$ is an eigenvector



Stable star $(a<0)$

- Subcase B: $b \neq 0$

In this case there is only one linearly independent eigenvector of M

Review

Here drawn is $a < 0$

stable (degenerate node)

~~Case~~ $\lambda_1\lambda_2 < 0$

Case $\lambda_1 \lambda_2 < 0$.

Take $\lambda_1 < 0$ $\lambda_2 > 0$

Saddle

Is unstable since pertubation grows in the direction that corresponds to the positive eigenvalue.

This covers all cases where $Re\{\lambda\} \neq 0$.

For this course we ignore cases where $Re\{\lambda\} = 0$ (except centres)

μ everywhere !

Consider: $\left.\begin{aligned} \dot{x} &= x - y - x(x^2+y^2) \\ \dot{y} &= x + y - y(x^2+y^2) \end{aligned}\right\}$ B

At steady state $x - y - x(x^2+y^2) = 0$ 1

$x + y - y(x^2+y^2) = 0$ 2

x times 1 + y times 2

$x^2 - xy - x^2(x^2+y^2) = 0$ if $x \neq 0$ $y \neq 0$

$xy + y^2 - y^2(x^2+y^2) = 0$

$x^2+y^2 - (x^2+y^2)^2 = 0$

$\Rightarrow x^2+y^2 = 0$ or $x^2+y^2 = 1$ $\Rightarrow x=0$ $y=0$ only steady state

$x\dot{x} = x^2 - xy + x^2(x^2+y^2)$

$y\dot{y} = xy + y^2 - y^2(x^2+y^2)$

$x\dot{x} + y\dot{y} = x^2 + y^2 - (x^2+y^2)^2$

~~set $r^2 = x^2+y^2$ $\tan\theta = y$~~

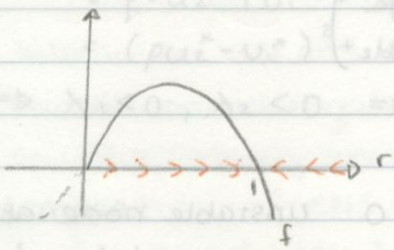
$\frac{d}{dt}\frac{1}{2}(x^2+y^2) = (x^2+y^2) - (x^2+y^2)^2$

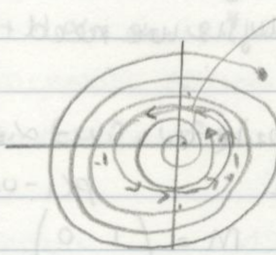
set $r^2 = x^2+y^2$ $\tan\theta = y/x$ polar coordinates

$\frac{d}{dt}\left(\frac{1}{2}r^2\right) = r^2 - (r^2)^2 = r^2 - r^4$

$r\dot{r} = r^2 - r^4 \Rightarrow \dot{r} = r(1-r^2)$

For θ we get $\dot{\theta} = 1$





$r=1 \Rightarrow \dot{r}=0 \Rightarrow$ a circle

$r>1$ $\dot{r}<0$ $\Rightarrow$ spiral in onto circle radius 1

$r<1$ spiral out to circle of radius 1.

Phase plane shows $\underline{0} = (0,0)$ is a unstable spiral.

Now do linear stability analysis for $\underline{0} = (0,0)$

$\dot{x} = \mu x - y - x(x^2+y^2) = f$ $\partial f/\partial x$:

$\dot{y} = x + \mu y - y(x^2+y^2) = g$

$\frac{\partial f}{\partial x} = \mu - (x^2+y^2) - 2x^2 = \mu$ at $(0,0)$

$\frac{\partial f}{\partial y} = -1 - 2xy = -1$ $\qquad \frac{\partial g}{\partial x} = 1 - 2xy = 1$

$\frac{\partial g}{\partial y} = \mu - (x^2+y^2) - 2y^2 = \mu$

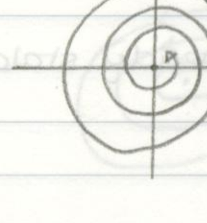
$\Rightarrow$ At $\underline{0}$ $M = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}$ $\det(M-\lambda I) = \left| \begin{pmatrix} \mu-\lambda & -1 \\ 1 & \mu-\lambda \end{pmatrix} \right| = (\mu-\lambda)^2+1$

$\Rightarrow \mu - \lambda = \pm i$

$\lambda = \mu \pm i$

case $\mu = 0 \Rightarrow \lambda = \pm i$

predicts centre, but what we get is a stable spiral at $(0,0)$



Competitive model Revisited.

$\dot{u}_1 = u_1(1-u_1-\alpha_{12}u_2) = f$

$\dot{u}_2 = \rho u_2(1-u_2-\alpha_{21}u_1) = g$

This system has 3 steady states on the axes: $(0,0)$; $(1,0)$; $(0,1)$

and has an interior steady state (u_1^*, u_2^*) provided that $\alpha_{12}, \alpha_{21} > 1$

or $\alpha_{12}, \alpha_{21} < 1$

The u_1^*, u_2^* satisfy $1-u_1^*-\alpha_{12}u_2^* = 0$, $1-u_2^*-\alpha_{21}u_1^* = 0$

For stability analysis we need $M = \begin{pmatrix} \partial f/\partial u_1 & \partial f/\partial u_2 \\ \partial g/\partial u_1 & \partial g/\partial u_2 \end{pmatrix}$

$M = \begin{pmatrix} (1-u_1-\alpha_{12}u_2) - u_1 & -\alpha_{12}u_1 \\ -\rho\alpha_{21}u_2 & \rho(1-u_2-\alpha_{21}u_1) - \rho u_2 \end{pmatrix}$

Look at $(0,0)$ $\Rightarrow$ $M = \begin{pmatrix} 1 & 0 \\ 0 & \rho \end{pmatrix}$ $\Rightarrow \lambda_1 = 1, \lambda_2 = \rho > 0$ unstable node at $(0,0)$.

At $(1,0)$ $M_{(1,0)} = \begin{pmatrix} -1 & -\alpha_{12} \\ 0 & \rho(1-\alpha_{21}) \end{pmatrix} \Rightarrow \lambda_1 = -1, \lambda_2 = \rho(1-\alpha_{21})$

If $\alpha_{21} > 1$, $\lambda_1, \lambda_2 < 0 \Rightarrow$ stable node

$\alpha_{21} < 1$ $\lambda_1 = -1, \lambda_2 > 0 \Rightarrow$ saddle (unstable)

At $(0,1)$ $\Rightarrow M = \begin{pmatrix} 1-\alpha_{12} & 0 \\ -\rho\alpha_{21} & -\rho \end{pmatrix} \Rightarrow \lambda_2 = -\rho < 0$

$\lambda_1 = 1-\alpha_{12}$

So $(0,1)$ is stable node if $\alpha_{12} > 1$

saddle if $\alpha_{12} < 1$

Last possibility is when (u_1^*, u_2^*) exists

ie when $\alpha_{12}, \alpha_{21} > 1$

or $\alpha_{12}, \alpha_{21} < 1$

$$M_{(u_1^*,u_2^*)} = \begin{pmatrix} \overbrace{(1-u_1^*-\alpha_{12}u_2^*)}^{=0}-u_1^* & -\alpha_{12}u_1^* \\ -\rho\alpha_{21}u_2^* & \rho\underbrace{(1-u_2^*-\alpha_{21}u_1^*)}_{=0}-\rho u_2^* \end{pmatrix}$$

$$= \begin{pmatrix} -u_1^* & -\alpha_{12}u_1^* \\ \rho\alpha_{21}u_2^* & -\rho u_2^* \end{pmatrix}$$

Eigenvalues satisfy $\begin{vmatrix} -u_1^*-\lambda & -\alpha_{12}u_1^* \\ \rho\alpha_{21}u_2^* & -\rho u_2^*-\lambda \end{vmatrix} = 0$

$(u_1^*+\lambda)(\rho u_2^*+\lambda) - \rho\alpha_{21}\alpha_{12}u_1^*u_2^* = 0$

$\lambda^2 + \lambda(\rho u_2^* + u_1^*) + \rho(1-\alpha_{21}\alpha_{12})u_1^*u_2^* = 0$

$\lambda_{1,2} = \dfrac{-(\rho u_2^*+u_1^*)}{2} \pm \dfrac{1}{2}\sqrt{(\rho u_2^*+u_1^*)-4\rho(1-\alpha_{12}\alpha_{21})u_1^*u_2^*}$ 1

Case $\alpha_{12}>1,\ \alpha_{21}>1 \Rightarrow \alpha_{12}\alpha_{21}>1$

$(\rho u_2^*+u_1^*)-4\rho(1-\alpha_{12}\alpha_{21})u_1^*u_2^* > (\rho u_2^*+u_1^*)^2$

From 1 we see that $\sqrt{\sim} > \rho u_2^*+u_1^*$

$\Rightarrow \lambda_1, \lambda_2$ are opposite signs $\Rightarrow$ saddle.

For $\alpha_{12}<1,\ \alpha_{21}<1$ $\quad 1-\alpha_{12}\alpha_{21}>0$ and so λ_1, λ_2 have both real parts <0.

$(\rho u_2^*+u_1^*)^2 - 4\rho(1-\alpha_{12}\alpha_{21})u_1^*u_2^*$

$\quad = \rho^2u_2^{*2}+u_1^{*2}\mp 2\rho u_1^*u_2^* - 4\rho\cancel{u_1^*}u_2^* + 4\alpha_{12}\alpha_{21}u_1^*u_2^*$

$\quad = (\rho u_2^*-u_1^*)^2 + 4\alpha_{12}\alpha_{21}u_1^*u_2^* > 0$

$\Rightarrow \lambda_1<0,\ \lambda_2<0 \Rightarrow$ stable node at (u_1^*, u_2^*)

Lemma:

Let M be a real 2×2 matrix with eigenvalues λ_1, λ_2

Then $\lambda_1\lambda_2 = \det M$

$\quad\lambda_1+\lambda_2 = \operatorname{trace} M$

Proof: $M = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$

$|M-\lambda I| = 0$

$\begin{vmatrix} a-\lambda & b \\ c & d-\lambda \end{vmatrix} = 0 \qquad \overset{+ad}{ad}-(a+d)\lambda+\lambda^2-bc = 0 = c(\lambda)$

$\qquad a+d = \operatorname{trace} M \quad ad-bc = \det M$

But $(\lambda-\lambda_1)(\lambda-\lambda_2) = c(\lambda)$

$\quad \lambda^2-(\lambda_1+\lambda_2)\lambda+\lambda_1\lambda_2 = c(\lambda)$

$\Rightarrow \lambda_1+\lambda_2 = a+d = \operatorname{trace} M \quad \lambda_1\lambda_2 = ad-bc = \det M.$

Recall: for (u_1^*, u_2^*) $M = \begin{pmatrix} -u_1^* & -\alpha_{12}u_1^* \\ -\rho\alpha_{21}u_2^* & -\rho u_2^* \end{pmatrix}$

Trace $M = \lambda_1 + \lambda_2$
$= -u_1^* - \rho u_2^* < 0$

Det $M = \lambda_1\lambda_2$
$= \rho(u_1^* u_2^*(1-\alpha_{12}\alpha_{21})$

If $\alpha_{12} > 1$, $\alpha_{21} > 1$ then $\det M = \lambda_1\lambda_2 < 0 \Rightarrow \lambda_1, \lambda_2$ real oppisite sign $\Rightarrow$ saddle.

$\alpha_{12} < 1$, $\alpha_{21} < 1$ then $\lambda_1\lambda_2 > 0$

If $\lambda_1\lambda_2 > 0$ then either $\lambda_1, \lambda_2 < 0$
or $\lambda_1, \lambda_2 > 0$
or $\lambda_1 = \overline{\lambda_2}$

But $\lambda_1 + \lambda_2 = \text{trace } M < 0 \Rightarrow$ rules out $\lambda_1, \lambda_2 > 0$

For remaining two cases, $\lambda_1 + \lambda_2 < 0 \Rightarrow \lambda_1, \lambda_2 < 0$ if λs real
$\lambda_1 + \lambda_2 = 2\mathrm{Re}(\lambda) < 0 \Rightarrow$ real parts of $\lambda_1 = \overline{\lambda_2}$ are negative

In either case, real parts $< 0 \Rightarrow$ stable

λ_1, λ_2 real $\Rightarrow$ stable node
complex $\Rightarrow$ stable spiral.

To increase realism of model introduce density dependence into growth rates

$$\frac{\dot N}{N} = a - bP - \underline{eN}$$

$$\frac{\dot P}{P} = -d + cN - \underline{fP}$$

intraspecific competition
ie competition between members of same species.

$a, b, c, d, e, f > 0$

Now if $P(0) = 0$

$\dot N = N(a - eN) \Rightarrow N(t) \longrightarrow \frac{a}{e} < \infty$ as $t \to \infty$ if $N(0) > 0$
(logistic growth)

Steady states

$\dot N = 0$ $\qquad \dot P = 0$

$N = 0$ $\qquad P = 0$

or $a - bP - eN = 0$ $\qquad$ or $-d + cN - fP = 0$

If $N=0$ then either $P=0$

or $-d-fP=0 \Rightarrow P=-\frac{d}{f}<0$ not relevant

If $a-bP-eN=0$ then either $P=0$ or $-d+cN-fP=0$

If $P=0$, $N=\frac{a}{e} \Rightarrow \left(\frac{a}{e},0\right)$ is a steady state

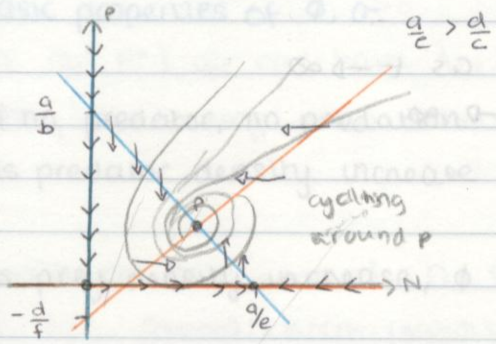
Last possibility is an interior steady state:

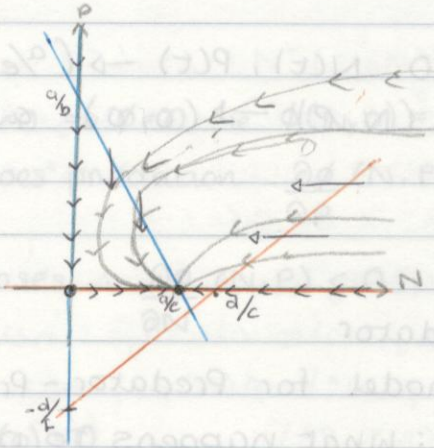
$a-bP-eN=0$

$-d+cN-fP=0$

$$\begin{pmatrix} e & b \\ c & -f \end{pmatrix}\begin{pmatrix} N \\ P \end{pmatrix}=\begin{pmatrix} a \\ d \end{pmatrix}$$

$$\begin{pmatrix} N \\ P \end{pmatrix}=\frac{-1}{ef+bc}\begin{pmatrix} -f & -b \\ -c & e \end{pmatrix}\begin{pmatrix} a \\ d \end{pmatrix}=\frac{1}{ef+bc}\begin{pmatrix} fa+bd \\ ca-ed \end{pmatrix}$$ exist only if $ca>ed$





$\dot{N}=0 \quad N(a-bP-eN)$

$\dot{P}=0 \quad P(-d+cN-fP)$

Without the eN and fP terms we had concentric periodic orbits around the interior steady states: is this preserved when $e>0$, $f>0$?

Do linear stability analysis:

$\dot{N}=N(a-bP-eN)=F$

$\dot{P}=P(-d+cN-fP)=G$

$$M=\begin{pmatrix} \frac{\partial F}{\partial N} & \frac{\partial F}{\partial P} \\ \frac{\partial G}{\partial N} & \frac{\partial G}{\partial P} \end{pmatrix}=\begin{pmatrix} (a-bP-eN)+N(-e) & -bN \\ cP & (-d+cN-fP)+P(-f) \end{pmatrix}$$

$$M_{(0,0)}=\begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix} \Rightarrow \lambda_1=a>0,\ \lambda_2=-d<0 \Rightarrow \text{saddle}$$

$$M\left(\frac{a}{e},0\right)=\begin{pmatrix} -a & -ba/c \\ 0 & \frac{ca}{e}-d \end{pmatrix}$$

If $ca>de$ (P exists) $\Rightarrow \lambda_1<0$, $\lambda_2>0$

If $ca<de$ (P not exists) $\lambda_1<0$, $\lambda_2<0 \Rightarrow$ stable node.

~~If ca>de P exists~~

PTO

If interior steady state exists $(ca > de)$

$$M = \begin{pmatrix} -eN^* & -bN^* \\ cP & -fP^* \end{pmatrix} \Rightarrow \begin{array}{l} \text{trace } M = -eN^* - fP^* < 0 \\ \det M = N^*P^*(ef + bc) > 0 \end{array} \quad \text{since } N^*>0 \ P^*>0 \ e,f=0$$

$\Rightarrow$ stable node or spiral.

Case $ca > de$

If $N(0) > 0$, $P(0) > 0$, $(N, P) \to$ interior steady states as $t \to \infty$

~~$N(0) > 0$ $P(0)$~~

$N(0)>0$ $P(0)=0$ $(N, P) \to (a/e, 0)$ as $t \to \infty$

$N(0)=0$ $P(0)=0$ $(N, P) \to (0,0)$ as $t \to \infty$

Case $ca < de$

Unless $N(0) = 0$ $N(t), P(t) \to (a/e, 0)$ as $t \to \infty$

If $N(0) = 0$, $(N, P) \to (0,0)$ as $t \to \infty$

Predator - Prey

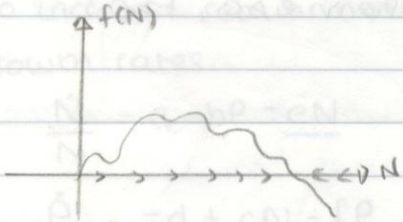
N = prey P = predator

Build general model for Predator - Prey interaction

Starting point: what happens to prey in absense of predator

If $P = 0$ we would have $\dot{N} = N\rho(N) = f(N)$

(We factor the N out since we want no growth when $N=0$



Sensible to suppose that if $P=0$, $N(0)>0$, then $N(t) \to$ carrying capicity $K>0$.

We can do this by insisting: $\rho(0) = 0$, $\rho(K) = 0$ and $\rho(N) \neq 0$ for $N \neq K$ $N \geq 0$ α

At 0, $f'(N) = \rho(N) + N\rho'(N)$

$f'(0) = \rho(0) \Rightarrow$ need $f'(0) = \rho(0) > 0$

These conditions (assuming smooth ρ) $\Rightarrow \rho'(K) < 0$

since $f'(K) = \underbrace{\rho(K)}_{=0} + K\rho'(K) = K\rho'(K)$

Conditions α say that if $P = 0$, $N(0) > 0$, then $N(t) \to K$ carrying capacity.

Now introduce predation:

$\dot{N} = N\rho(N) - N\phi(N,P)$ 1

So per capita growth $\frac{\dot{N}}{N} = \rho(N) - \underbrace{\phi(N,P)}_{\text{predation term}}$

For the predator $\frac{\dot{P}}{P} = -\mu + \sigma(N)$ $\mu > 0$ 2

if no food ($\sigma(N)$ absent) then $\dot{P} = -\mu P \Rightarrow P(t) = e^{-\mu t}P(0) \rightarrow 0$ extinction.

The $\sigma(N)$ term models the contribution to per capita growth of predator due to prey consumption.

Basic properties of ϕ, σ.

If no predator, no predation ie $P=0 \Rightarrow \phi = 0$ ie $\phi(N,0) = 0$ $\forall N \geq 0$.

As predator density increase so does predation $\frac{\partial\phi}{\partial P}(N,P) > 0$.

As prey density increase, ϕ decreases : $\frac{\partial\phi}{\partial N}(N,P) \leq 0$

because as N ↑ the chance of an individual being chosen for dinner decreases.

For σ :

No prey $\Rightarrow$ no food consumed : $\sigma(0) = 0$

As prey density increase, so does per capita consumption : $\sigma'(N) > 0$

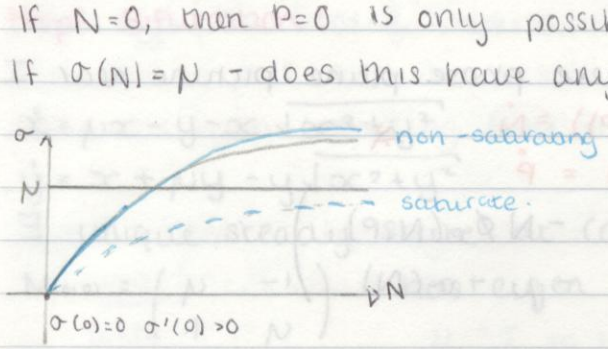
Steady states :

$N=0$ and $P=0$

or $\rho(N) - \phi(N,P) = 0$ or $\sigma(N) = \mu$ (>0)

If $N=0$, then $P=0$ is only possibility.

If $\sigma(N) = \mu$ - does this have any solutions?



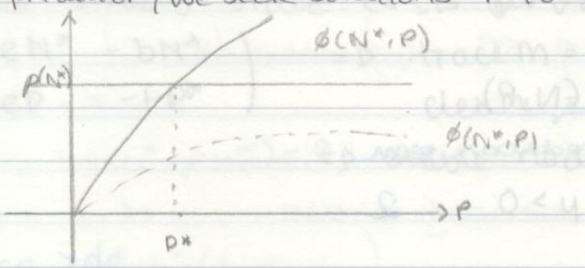
If σ does not saturate then there exists a unique N^* such that $\sigma(N^*) = \mu$

If σ saturates above μ then $\exists$ unique N^* with $\sigma(N^*) = \mu$

If σ saturates below μ, there is no solution

For the predator, we seek solutions P to $\phi(N^*, P) = \rho(N^*)$

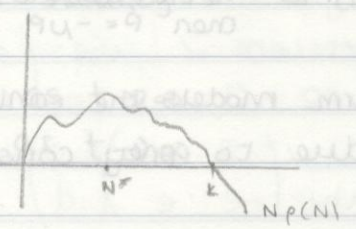
But



If ϕ saturates below $\rho(N^*)$ then no P^* exists

If ϕ saturates (or increases) above $\rho(N^*)$ then $\exists$ unique P^*.

To ensure $\rho(N^*) > 0 \Rightarrow N^* \in (0, K)$

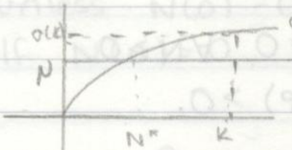


$\sigma(N^*) = \mu$

σ increase $\Rightarrow$ has inverse σ^{-1}.

$N^* = \sigma^{-1}(\mu) \in (0, K)$

$\Rightarrow \mu < \sigma(K)$

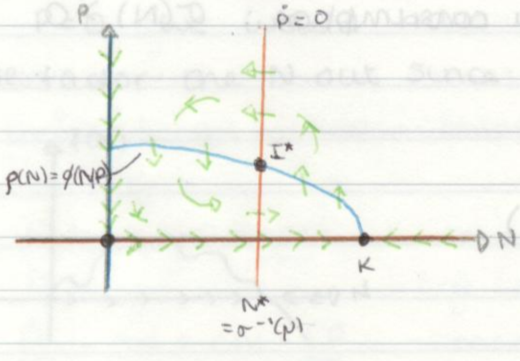


Indeed if $\sigma(K) > \mu$ then σ curve goes above μ $\Rightarrow N^*$ exists.

There is also a steady state when $N = K$, $P = 0$ (since $\rho(K) = 0$, $\phi(N, 0) = 0$)

Conclusion: steady states always include $(0,0)$ and $(K, 0)$

If $\sigma(K) > \mu$ and $\rho(N^*) = \phi(N^*, P)$ has a solution P^* then $\exists$ interior steady state (N^*, P^*).



there's a form of cycling around I^* but more analysis required to find details.

Linear stability analysis may help complete phase plane picture near I^*

$$M = \begin{pmatrix} F_N & F_P \\ G_N & G_P \end{pmatrix} \qquad F = N(\rho(N) - \phi(N,P)) = \dot{N} \qquad G = P(-\mu + \sigma(N)) = \dot{P}$$

$$= \begin{pmatrix} (\rho(N) - \phi(N,P)) + N(\rho'(N) - \phi_N(N,P)) & -N\phi_P(N,P) \\ P\sigma'(N) & -\mu + \sigma(N) \end{pmatrix}$$

$$M_{(0,0)} = \begin{pmatrix} \rho(0) & 0 \\ 0 & -\mu \end{pmatrix}$$

~~$\rho(0) > 0$~~ $\rho(0) > 0$, $\mu > 0 \Rightarrow$ ~~$\lambda_1 \lambda_2 < 0$~~ $\lambda_1 \lambda_2 < 0 \Rightarrow (0,0)$ is a saddle

$$M_{(K,0)} = \begin{pmatrix} K\rho'(K) & -K\phi_P(K,0) \\ 0 & -\mu + \sigma(K) \end{pmatrix}$$

$\lambda_1 = K\rho'(K) < 0$

$\lambda_2 = \sigma(K) - \mu > 0$

if interior steady state exists $\Rightarrow$ saddle

If $\sigma(K) < \mu$, so that interior steady state does not exist then $(K,0)$ is a steady node.

Interior steady state $I^* = (N^*, P^*)$ $N^* > 0$, $P^* > 0$ $(\sigma(K) > \mu)$

$$M(N^*,P^*) = \begin{pmatrix} N(\rho'(N^*) - \phi_N(N^*,P^*)) & -N^*\phi_P(N^*,P^*) \\ P^*\sigma'(N^*) & 0 \end{pmatrix}$$

using lemma on sum and product of eigenvalues:

$$tr(M) = \lambda_1 + \lambda_2$$
$$det(M) = \lambda_1\lambda_2$$

So $\lambda_1 + \lambda_2 = N^*(\rho'(N^*) - \phi_N(N^*,P^*))$

$\lambda_1\lambda_2 = N^*P^*\underbrace{\sigma'(N^*)}_{>0}\underbrace{\phi_P(N^*,P^*)}_{>0} > 0$

At (N^*,P^*) we can have λ_1,λ_2 real $\Rightarrow \lambda_1+\lambda_2 = N^*(\rho'(N^*) - \phi_P(N^*,P^*))$

$<0 \Rightarrow \lambda_1,\lambda_2$ negative stable node

$>0 \Rightarrow \lambda_1,\lambda_2$ positive unstable node.

If λ_1,λ_2 complex conjugates,

$$\lambda_1 + \lambda_2 = 2\,Re\{\lambda_1\}$$
$$= N^*(\rho'(N^*) - \phi_P(N^*,P^*))$$

$\Rightarrow$ if $\rho'(N^*) - \phi_P(N^*,P^*)$ <0 $Re\{\lambda_1\} = Re\{\lambda_2\} < 0 \Rightarrow$ stable spiral

>0 $Re\{\lambda_1\} = Re\{\lambda_2\} > 0 \Rightarrow$ unstable spiral.

If $\rho'(N^*) - \phi_P(N^*,P^*) = 0$ (can't have λ_1,λ_2 real since $\lambda_1\lambda_2 > 0$) and so $\lambda_1 = i\omega$, $\lambda_2 = -i\omega$ $\Rightarrow$ linear stability analysis suggest centre.

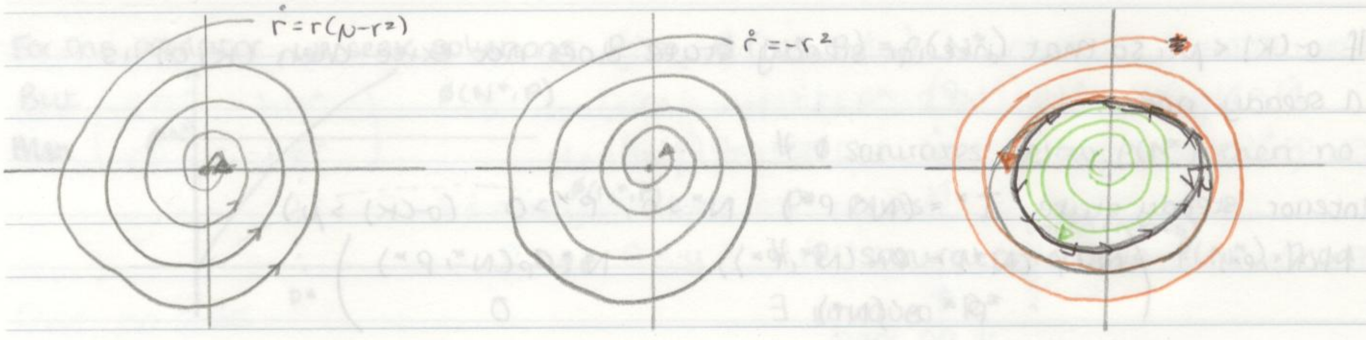
Hopf Bifurcation:

$$\dot{x} = \mu x - y - x\sqrt{x^2+y^2}$$
$$\dot{y} = x + \mu y - y\sqrt{x^2+y^2}$$

$\exists$ unique steady state at $(0,0)$

$M_{(0,0)} = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}$ has eigen values $\mu \pm i$

Polar coords give $\dot{r} = r(\mu - r^2)$, $\dot{\theta} = 1$



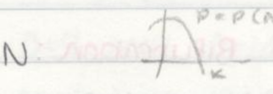
$\mu < 0$ $\qquad\qquad$ $\mu = 0$ $\qquad\qquad$ $\mu > 0$

Let $\dot{x} = f(x, y, \mu)$ $\quad \dot{y} = g(x, y, \mu)$ $*$ $(x, y) \in \mathbb{R}^2$ be a planar system.
f, g are analytic in x, y and μ.
Let (x_μ, y_μ) be a steady state of $*$ for $\mu \in (-\epsilon, \epsilon)$ with $\epsilon > 0$
Take $M = \begin{pmatrix} f_x & f_y \\ g_x & g_y \end{pmatrix}$

Suppose M has complex eigenvalues
$\lambda_\pm = \sigma(\mu) \pm i\omega(\mu)$ $\qquad \mu \in (-\epsilon, \epsilon)$
and assume $\sigma(\mu) < 0$ for $\mu \in (-\epsilon, 0)$
$\sigma(0) = 0$ for $\mu = 0$ $\qquad \omega(0) \neq 0$
$\sigma(\mu) > 0$ for $\mu \in (0, \epsilon)$
Finally we suppose that for $\mu = 0$, then (x_0, y_0) is (locally) stable and $\dfrac{d\sigma}{d\mu}(0) > 0$

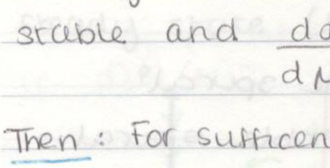
Then: For sufficiently small $\mu > 0$ the unstable steady state (x_μ, y_μ) is surrounded by an attracting periodic orbit, (which depends on μ). The period of oscillation is approximately $\dfrac{2\pi}{\omega(0)}$

The $\rho(N) = \phi(N, P)$ nullcline in more detail

On this nullcline, we can express P as a function of N 

So on the nullcline: $\rho(N) = \phi(N, P(N))$
and $\rho'(N) = \dfrac{\partial \phi}{\partial N}(N, P(N)) + \dfrac{\partial \phi}{\partial P}(N, P(N))\, P'(N)$ $\quad$ chain rule

$\Rightarrow P'(N) = \dfrac{\rho'(N) - \phi_N(N, P(N))}{\phi_P(N, P(N))}$



gradient of nullcline at I^* is

$$P'(N) = \frac{\rho'(N^*) - \phi_N(N^*, P(N))}{\phi_P(N^*, P^*)}$$

$$= \frac{1}{N^*} \frac{1}{\phi_P(N^*, P^*)} \text{ trace}(M)$$

At I^* $tr(M_{I^*}) = \lambda_1 + \lambda_2$

$$= N^* \phi_P(N^*, P(N^*)) \, p'(N^*)$$

But $N^* > 0$, $\phi_P > 0 \Rightarrow$ sign of $\lambda_1 + \lambda_2$ = sign of $p'(N^*)$

So to know if I^* is stable we only need to know ~~a~~ sign of gradient of nullcline at I^*.

Thus if $p'(N^*) < 0$ then $\lambda_1 + \lambda_2 < 0 \Rightarrow$ stable

$p'(N^*) > 0$ then $\lambda_1 + \lambda_2 > 0 \Rightarrow$ unstable.

1 $\dot{N} = N\rho(N) - N\phi(N, P)$ Prey

2 $\dot{P} = P(\sigma(N) - \mu)$ Predator

In 1 $N\phi(N,P)$ = density of prey removed by predator per unit time

$\frac{N\phi(N,P)}{P}$ = density of prey removed by predator per unit time per predator

= feeding rate of ~~pre~~ a predator

= ϖ say

Holling functional responses

3 types I, II, III

Type I $\varpi = \gamma N$, $\phi = \frac{P\varpi}{N}$

eg. $\dot{N} = N(\rho(N) - \gamma P) = N\rho(N) - \gamma NP$

$\phi(N,P) = \gamma P$

$\varpi = \frac{N\gamma P}{P} = \gamma N$.

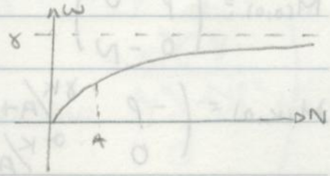
This says the feeding rate is increasing indefinitely with prey density. But this is not realistic since consumption rate of prey depends upon catching, handling time and eating $\Rightarrow$ feeding rate must be limited.

Type II Here the feeding rate ϖ saturates with N:

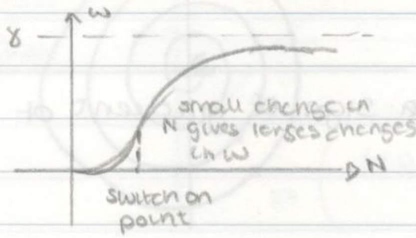
$\varpi = \frac{\gamma N}{A+N}$ $\gamma > 0$, $A > 0$

γ = maximum feeding rate

A = is the value of N at which ϖ is half maximal.



Type III : feeding rate saturates with N, but now there is a "switch on" point.



$$\omega = \frac{\gamma N^2}{A^2+N^2}$$

$$\sim \frac{\gamma N^2}{A^2} \text{ for small } N$$

saturates for large N.

Example:

Holling type II : $\omega = \frac{\gamma N}{A+N}$, $\sigma(N) = \frac{\sigma N}{P}$ $\sigma > 0$ and $P(N) = \rho(1 - N/K)$

$$\dot{N} = \rho N(1 - N/K) - \frac{\gamma N P}{A+N}$$

$$\dot{P} = P\left(\frac{\sigma N}{A+N} - \mu\right)$$

Let $f = \rho N\left(1 - \frac{N}{K}\right) - \frac{\gamma N P}{A+N}$, $g = P\left(\frac{\sigma N}{A+N} - \mu\right)$

steady states:

$N = 0$ and $P = 0$

or $\rho(1 - N/K) = \frac{\gamma P}{A+N}$ or $\frac{\sigma N}{A+N} = \mu$

Hence there are steady states at $(0,0)$ and $(K,0)$.

An interior steady state is at $\sigma N = \mu(A+N)$

$\Rightarrow N^* = \frac{\mu A}{\sigma - \mu} > 0$ if $\sigma > \mu$

But then $P^* = \frac{\rho}{\gamma}(A+N^*)\left(1 - \frac{N^*}{K}\right) > 0$ provided $N^* < K$

$\Rightarrow 0 < \frac{\mu A}{\sigma - \mu} < K$.

stability

$$M = \begin{pmatrix} f_N & f_P \\ g_N & g_P \end{pmatrix} = \begin{pmatrix} \left(\rho(1-N/K) - \gamma P/(A+N)\right) + N\left(-\rho/K + \gamma P/(A+N)^2\right) & -\gamma N/(A+N) \\ P A \sigma/(A+N)^2 & \left\{\sigma N/(A+N)\right\} - \mu \end{pmatrix}$$

$$M_{(0,0)} = \begin{pmatrix} \rho & 0 \\ 0 & -\mu \end{pmatrix} \quad \lambda_1 = \rho > 0, \ \lambda_2 = -\mu < 0 \Rightarrow \text{saddle}$$

$$M_{(K,0)} = \begin{pmatrix} -\rho & \gamma K/(A+K) \\ 0 & \sigma K/(A+K) - \mu \end{pmatrix}$$

$\lambda_1 = -\rho < 0$, $\lambda_2 = \dfrac{\sigma K}{A+K} - \mu < 0$ $\sigma K < \mu(A+K)$

$= \mu A + K\mu$

$(\sigma-\mu)K < \mu A$ if $\dfrac{\mu A}{\sigma-\mu} < 0$

and (N^*, P^*) does not exist

$\Rightarrow$ stable node

> 0 if $0 < \dfrac{\mu A}{\sigma-\mu} < K$ ie (N^*, P^*) exists

$\Rightarrow$ saddle.

When $0 < \dfrac{\mu A}{\sigma-\mu} < K$

$$M(N^*, P^*) = \begin{pmatrix} N^*\left(\dfrac{-\rho}{K} + \dfrac{\gamma P^*}{(A+N^*)^2}\right) & -\dfrac{\gamma N^*}{A+N^*} \\ \dfrac{P^* A\sigma}{(A+N^*)^2} & 0 \end{pmatrix}$$

$$\text{trace } M = \lambda_1 + \lambda_2 = N^*\left(-\frac{\rho}{K} + \frac{\gamma P^*}{(A+N^*)^2}\right)$$

$$\det M = \lambda_1\lambda_2 = \frac{\gamma N^* P^* A\sigma}{(A+N^*)^3} > 0$$

$N^* = \dfrac{\mu A}{\sigma-\mu}$

$\dot{N} = N\rho(1 - N/K) - \dfrac{\gamma NP}{A+P} \Rightarrow \rho(1 - N^*/K) = \dfrac{\gamma P^*}{A+N^*}$

$$\lambda_1 + \lambda_2 = N^*\left(-\frac{\rho}{K} + \frac{1}{A+N^*} \cdot \frac{\gamma P^*}{A+N^*}\right)$$

$$= N^*\left(-\frac{\rho}{K} + \frac{1}{A+N^*}\rho\left(1 - \frac{N^*}{K}\right)\right)$$

$$= \frac{\rho N^*}{K}\left(-1 + \frac{1}{A+N^*}(K-N^*)\right)$$

$$= \frac{\rho N^*}{K(A+N^*)}(-A-N^*+K-N^*)$$

$$= \frac{\rho N^*}{K(A+N^*)}(K-A-2N^*)$$

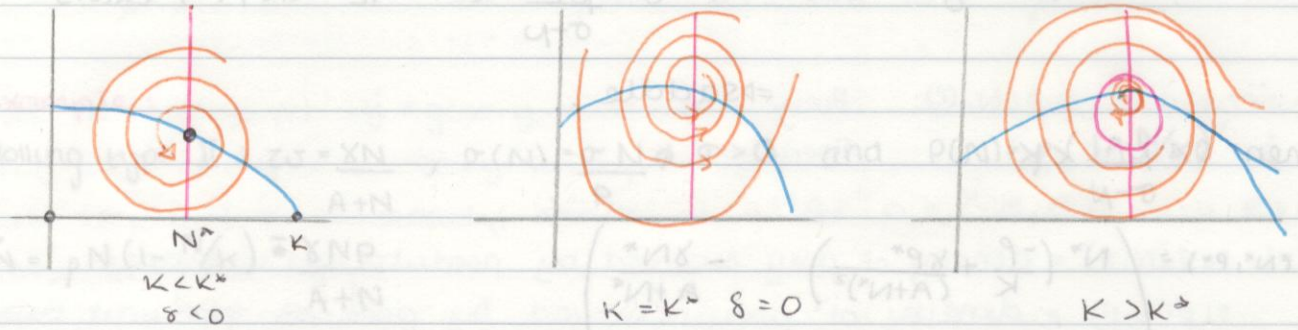
$$= \frac{\rho N^*}{K(A+N^*)}\left(K-A-\frac{2\mu A}{\sigma-\mu}\right)$$

Let $\delta = K - A - \dfrac{2\mu A}{\sigma-\mu}$ $(\sigma > \mu)$

If $K<A$ then $\delta<0$ always $\Rightarrow$ trace cannot ~~be~~ change sign $\Rightarrow \lambda_1, \lambda_2$ have negative real parts $\Rightarrow (N^*, P^*)$ stable.

But if $K>A$ a change of sign in δ is possible

eg by increasing K from $K < A + \dfrac{2\mu A}{\sigma - \mu}$ through this critical value and above, δ moves from <0, through 0 and then >0



Holling Type III

Feeding rate $\omega = \dfrac{\gamma N^2}{A+N^2}$

$$\dot{N} = \rho N(1 - N/K) - \frac{\gamma N^2 P}{A^2+N^2}$$

$$\dot{P} = P\left(\frac{\sigma N^2}{A^2+N^2} - \mu\right)$$

Steady ~~pon~~ states:

$(0,0)$, $(K,0)$

For an interior steady state (N^*, P^*)

$$\rho(1-N/K) - \frac{\gamma NP}{A^2+N^2} = 0$$

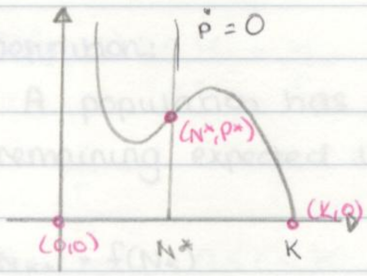
$$\frac{\sigma N^2}{A^2+N^2} = \mu \longrightarrow \sigma N^2 = \mu A^2 + \mu N^2$$

$$N^* = A\sqrt{\frac{\mu}{\sigma-\mu}} \quad \text{provided } \sigma > \mu$$

For P^* we solve

$$P^* = \frac{\rho}{\gamma N^*}(1 - N^*/K)(A^2+N^2) > 0 \text{ if } N^* < K$$

and $N^* < K$ we need $A\sqrt{\dfrac{\mu}{\sigma-\mu}} < K \quad (\sigma > \mu)$ *



Case $A\sqrt{\frac{\mu}{\sigma-\mu}} < K$ Nullclines: $\frac{\sigma N^2}{A^2+N^2} = \mu$

$\dot{P} = \frac{\rho}{\gamma N}(1-N/K)(A^2+N^2)$

Stability: $f(N,P) = N\left(\rho\left(1-\frac{N}{K}\right) - \frac{\gamma N P}{A^2+N^2}\right)$

$g(N,P) = P\left(\frac{\sigma N^2}{A^2+N^2} - \mu\right)$

$$\frac{\partial f}{\partial N} = \left(\rho\left(1-\frac{N}{K}\right) - \frac{\gamma NP}{A^2+N^2}\right) + N\left(-\frac{\rho}{K} - \gamma P \frac{\partial}{\partial N}\left(\frac{N}{A^2+N^2}\right)\right)$$

$$= \left(\rho\left(1-\frac{N}{K}\right) - \frac{\gamma NP}{A^2+N^2}\right) + N\left(-\frac{\rho}{K} - \frac{\gamma P}{A^2+N^2} + \frac{2\gamma P N^2}{(A^2+N^2)^2}\right)$$

$$\frac{\partial f}{\partial P} = \frac{-\gamma N^2}{A^2+N^2}$$

$$\frac{\partial g}{\partial N} = P\cdot\sigma \frac{\partial}{\partial N}\left(\frac{N^2}{A^2+N^2}\right) = \sigma P \frac{\partial}{\partial N}\left(1 - \frac{A^2}{A^2+N^2}\right) = \frac{\sigma P A^2 2N}{(A^2+N^2)^2}$$

$$\frac{\partial g}{\partial P} = \frac{\sigma N^2}{A^2+N^2} - \mu$$

At $(0,0)$

$M_{(0,0)} = \begin{pmatrix} \rho & 0 \\ 0 & -\mu \end{pmatrix} \Rightarrow \lambda_1 = \rho > 0 \quad \lambda_2 = -\mu < 0$

opposite signs $\Rightarrow$ saddle point

$M_{(K,0)} = \begin{pmatrix} -\rho & -\gamma K^2/A^2+K^2 \\ 0 & \sigma K^2/A^2+K^2 - \mu \end{pmatrix}$

Eigenvalues are $-\rho < 0$ and $\frac{\sigma K^2}{A^2+K^2} - \mu$

[* $\Rightarrow$ $A^2\frac{\mu}{\sigma-\mu} < K^2$ $\quad A^2\mu < \sigma K^2 - \mu K^2 \Rightarrow (A^2+K^2)\mu < \sigma K^2$

If this holds $\exists$ interior steady state.]

$\frac{\sigma K^2}{A^2+K^2} - \mu > 0$ if $A\sqrt{\frac{\mu}{\sigma-\mu}} < K$ ie if (N^*, P^*) exists - saddle

Otherwise $\frac{\sigma K^2}{A^2+K^2} < \mu \Rightarrow$ stable node.

At (N^*,P^*) $M_{(N^*,P^*)} = \begin{pmatrix} N^*\left(-\frac{\rho}{K} - \frac{\gamma P^*}{A^2+N^{*2}} + \frac{2\gamma N^{*2}P^*}{(A^2+N^{*2})^2}\right) & \frac{-\gamma N^{*2}}{A^2+N^{*2}} \\ \frac{2\sigma A^2 N^* P^*}{(A^2+N^{*2})^2} & 0 \end{pmatrix}$

$\det M_{(N^*,P^*)} = \dfrac{2\gamma\sigma A^2 N^{*3} P^*}{(A^2+N^{*2})^3} > 0$

$\text{trace}\, M_{(N^*,P^*)} = N^*\left(-\dfrac{\rho}{K} - \dfrac{\gamma P^*}{A^2+N^{*2}} + \dfrac{2\gamma N^{*2} P^*}{(A^2+N^{*2})^2}\right)$

$f = \rho N\left(1-\dfrac{N}{K}\right) - \dfrac{\gamma N^2 P}{A^2+N^2}$ $\qquad g = P\left(\dfrac{\sigma N^2}{A^2+N^2} - \mu\right)$

Where $N = N^*$, $P = P^*$ from $f = 0$ $\quad \rho\left(1-\dfrac{N^*}{K}\right) = \dfrac{\gamma N^* P}{A^2+N^2}$ $\quad \alpha$

Hence ~~using~~ trace $M_{(N^*,P^*)} = -\dfrac{\rho N^*}{K} - \rho\left(1-\dfrac{N^*}{K}\right) + 2\left(\dfrac{\gamma N^* P^*}{A^2+N^{*2}}\right)\left(\dfrac{N^{*2}}{A^2+N^{*2}}\right)$

using α

$= \rho + 2\rho\left(1-\dfrac{N^*}{K}\right)\left(\dfrac{\mu}{\sigma}\right) = \rho\left[-1+\dfrac{2\mu}{\sigma} - \dfrac{2N^*}{K}\dfrac{\mu}{\sigma}\right]$

$\left[\sigma N^{*2} = \mu(A^2+N^{*2}) \Rightarrow N^{*2}/A^2+N^{*2} = \mu/\sigma \quad \text{from } g = 0\right]$.

Trace $M_{(N^*,P^*)}$ $\quad \lambda_1+\lambda_2 = \rho\left(-1+\dfrac{2\mu}{\sigma} - \dfrac{2\mu A}{\sigma K}\sqrt{\dfrac{\mu}{\sigma-\mu}}\right)$

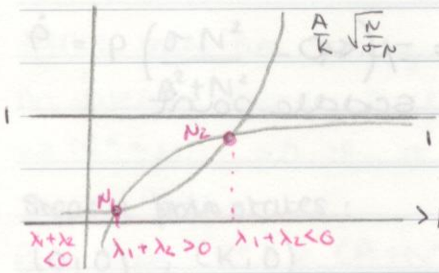
and we already know $\lambda_1\lambda_2 > 0$

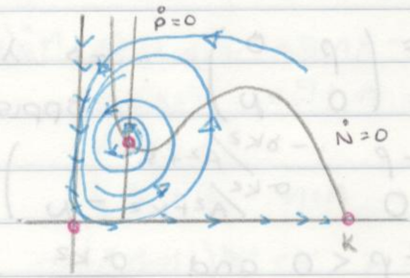
if $\dfrac{2\mu}{\sigma} < 1$ then trace $M_{(N^*,P^*)} = \lambda_1+\lambda_2 < 0 \Rightarrow$ always stable.

In this case $\lambda_1+\lambda_2$ can change sign from being -ve to +ve as μ changes

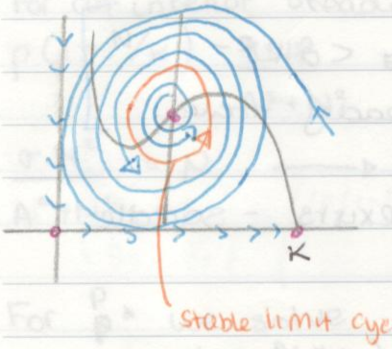
Start with μ such that $\lambda_1+\lambda_2 < 0$ and increase μ

Consider the plot $-\sigma/2\mu + 1$ against $A/K\sqrt{\mu/\sigma-\mu}$



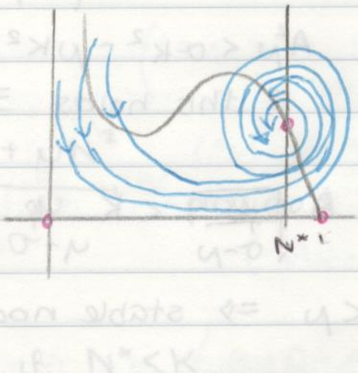


$\mu < \mu_1$



$\mu_1 < \mu < \mu_2$

stable limit cycle



$\mu > \mu_2$

limit cycle disappears

(N^*, P^*) locally stable

Definition:

A population has discrete (non-over lapping) generations if the remaining expected lifespan of a sexually mature individual $\leq$ 1 generation.

$N_{k+1} = f(N_k)$

k interger

N is not an interger.

Example: Malthus.

$N_{k+1} = \lambda N_k$, N_0 given, λ const ≥ 0

$N_k = N_0 \lambda^k$

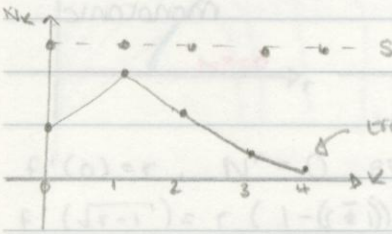
$|N_k| \to \infty$ if $\lambda > 1$

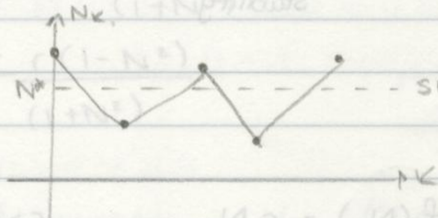
$N_k \to 0$ if $0 < \lambda < 1$.

General $f(N)$

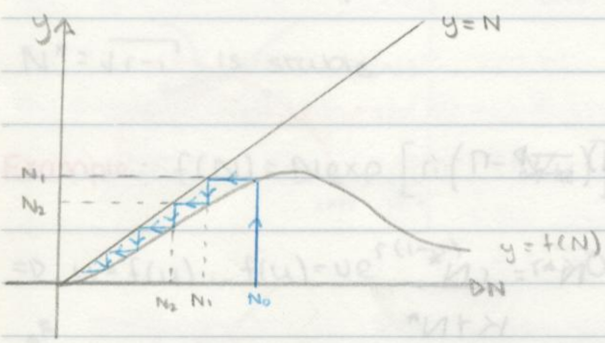
Qualitative analysis

Stationary points, $N_k = N^*$ are $N^* = f(N^*)$ $(N_{k+1} = f(N_k))$





Cobwep map for $N_{k+1} = f(N)$



2 lines $y = f(N)$, $y = N$

Start from N_0 $N_1 = f(N_0)$ . . .

Local Stability of SP.

$N^* = f(N^*)$ at SP

Let $N_0 = N^* + n_0$ small

Then $N_k = N^* + n_k$

$N_{k+1} = f(N_k)$

$N^* + n_{k+1} = f(N^* + n_k)$

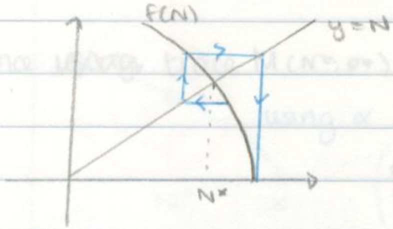
$f(N^* + n_k) = f(N^*) + n_k f'(N^*) + O(n_k^2)$

$N^* + n_{k+1} = f(N^*) + n_k f'(N^*)$

$n_{k+1} = \lambda n_k \quad \lambda = f'(N^*)$

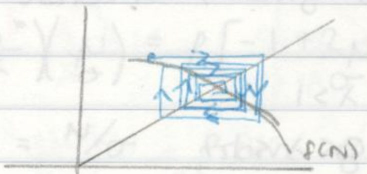
$\Rightarrow n_k = n_0 \lambda^k$

If $\lambda < -1$, $|n_k| \rightarrow \infty$ oscillates.



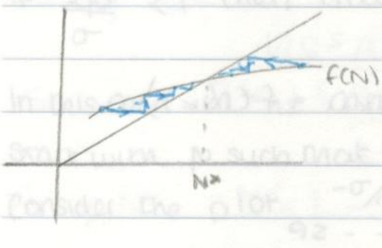
unstable

If $-1 < \lambda < 0$, $n_k \rightarrow 0$ oscillates.



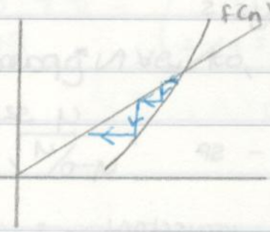
Stable stationary point.

If $0 < \lambda < 1$, $n_k \rightarrow 0$



monotonic stability

If $\lambda > 1$.



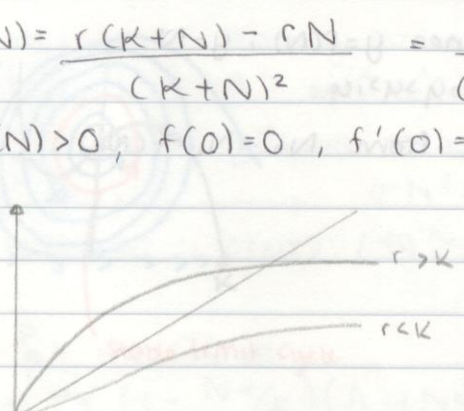
unstable monotonic.

Example: $N_{k+1} = f(N_k) = \dfrac{r N_k}{K + N_k}$ $\quad r > 0, \quad K > 0.$

$f(N) = \dfrac{rN}{K+N}$

$f'(N) = \dfrac{r(K+N) - rN}{(K+N)^2} = \dfrac{rK}{(K+N)^2}$

$f'(N) > 0, \; f(0) = 0, \; f'(0) = r/K \quad f(N) \xrightarrow[N \to \infty]{} r$



SP $N^* = \dfrac{rN^*}{K+N^*}$

$\Rightarrow N^* = 0$ or $N^* = r - K$

$N^* \geq 0 \Rightarrow r \geq K$

Stability: $f'(0) = r/K < 1$ if $r < K$ (stable)

> 1 if $r > K$ (unstable.

$$f'(r-K) = \frac{rK}{r^2} = \frac{K}{r}$$

$\therefore \frac{K}{r} < 1$ when $r > K \Rightarrow$ stable when it exists.

Summary: $0 < r < K$ - $N^* = 0$ single stable stationary point
$r > K$ - $N^* = 0$ unstable
$N^* = r - K$ stable.

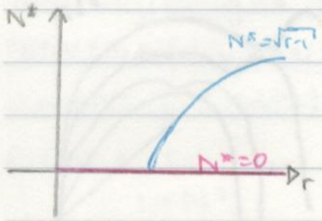
Example: $N_{k+1} = \frac{rN_k}{1+N_k^2}$

$$f(N) = \frac{rN}{1+N^2}$$

Stationary point $N^* = \frac{rN^*}{1+N^*}$

$N^* = 0$ or $1 + N^{*2} = r$, $N^* = \sqrt{r-1}$ exists if $r \geq 1$.

Bifurcation diagram is graph of $N^*(r)$



$$f'(N) = \frac{r(1+N^2) - 2rN^2}{(1+N^2)^2}$$
$$= \frac{r(1-N^2)}{(1+N^2)}$$

$f'(0) = r$, $N^* = 0$ stable for $r < 1$

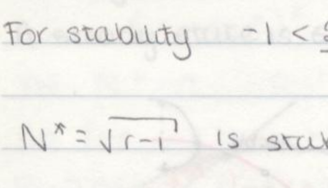
$$f'(\sqrt{r-1}) = \frac{r(1-(r-1))}{r^2} = \frac{2-r}{r}$$

For stability $-1 < \frac{2-r}{r} < 1 \Rightarrow \begin{cases} 2-r < r & r > 1 \\ -r < 2-r & \text{always true} \end{cases}$

$N^* = \sqrt{r-1}$ is stable

Example: $f(N) = N\exp\left[r\left(1 - N/K\right)\right]$ $u = N/K$.

$\Rightarrow u = f(u)$, $f(u) = ue^{r(1-u)}$ $r > 0$



Stationary points:
$u = ue^{r(1-u)}$
$u^* = 0$ or $u^* = 1$
$f'(u) = e^{r(1-u)} + u(-r)e^{r(1-u)}$
$= e^{r(1-u)}[1 - ru]$.

Stability: $f'(0) = e^r > 1$ unstable

$f'(1) = 1 - r$

$\Rightarrow u^* = 1$ is stable when

i) $0 < r < 1$ - monotonic

ii) $1 < r < 2$ - oscillatory.

iii) unstable (oscillates) when $r > 2$.

Example: With Harvesting

$$f(N) = \frac{bN}{1+N^2} - HN. \qquad b > 1, \ H > 0.$$

$$f'(N) = \frac{b(1-N^2)}{(1+N^2)^2} - H$$

$N^* = 0$, $f'(0) = b - H$

Must have $b \geq H$

Stable if $|b - H| < 1$

Other stationary point $N^* = f(N^*)$

$$\frac{b}{1+N^{*2}} - H = 1$$

$$1 + N^{*2} = \frac{b}{1+H}$$

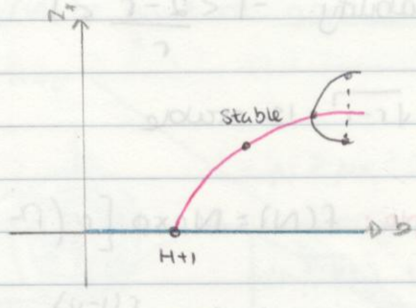
$$N^* = \sqrt{\frac{b-H-1}{1+H}}$$

$$f'(N^*) = \frac{b(1-N^{*2})}{(1+N^{*2})^2} - H = \frac{2(1+H)^2 - b(1+2H)}{b}$$

$N^* = 0$ stable if $b - H < 1$, $b < H+1$

If $b > H+1$, $N^* = 0$ is unstable.

$N^* = \sqrt{\frac{b-(H+1)}{H+1}}$ appears at $b \geq H+1$



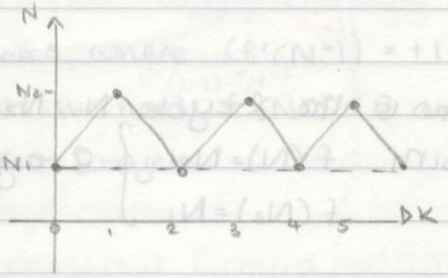
Stability: $f'(N^*) = -1$ at $b = \frac{(H+1)^2}{H}$

and $f'(N^*) < -1$ when $b > \frac{(H+1)^2}{H}$

$N^* = \sqrt{\frac{b-(H+1)}{H+1}}$ is stable when $H+1 < b < \frac{(H+1)^2}{H}$.

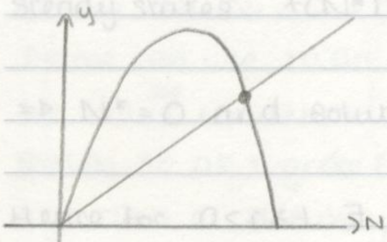
2-cycle solution of $N_{k+1} = f(N_k)$ with $N_1 = f(N_2)$, $N_2 = f(N_1)$

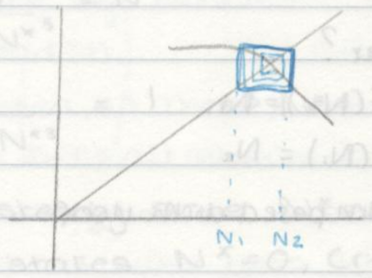
Trajectory:

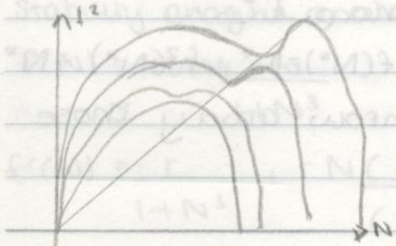


Consider composition $f^2 = f(f(N))$

$\boxed{\text{2-cycle is stationary point of } f^2}$ (which is not a stationary point of $f(N)$)

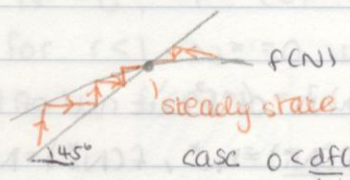


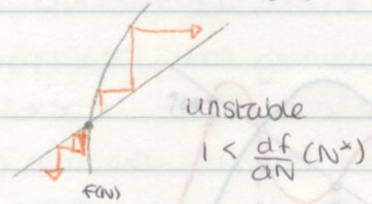


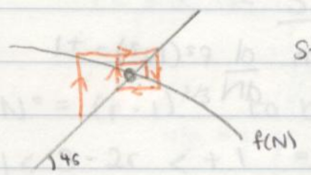


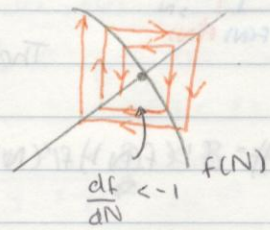
Steady states are fixed points of f: ie N^* such that $f(N^*) = N^*$

A steady state is stable if $\left|\frac{df}{dN}(N^*)\right| < 1$ and unstable if $\left|\frac{df}{dN}(N^*)\right| > 1$



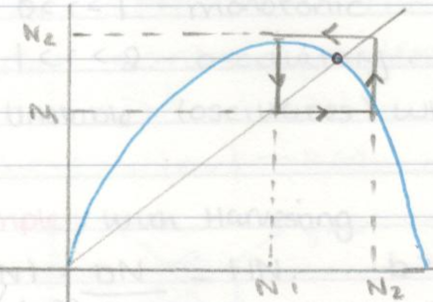






Case $\left|\frac{df}{dN}(N^*)\right| = 1$ is more tricky. If $\frac{df}{dN}(N^*) = -1$ then a periodic orbit can occur.

Here we mean 2-cycle.



Here is the 2-cycle $N_1, N_2, N_1, N_2, \ldots$

with $\left.\begin{array}{l} f(N_1) = N_2 \\ f(N_2) = N_1 \end{array}\right\}$ 2-cycle.

When do 2-cycles appear?

$f(N_1) = N_2 \qquad f(f(N_1)) = f(N_2) = N_1$

$\qquad\qquad\qquad f(f(N_2)) = f(N_1) = N_2$

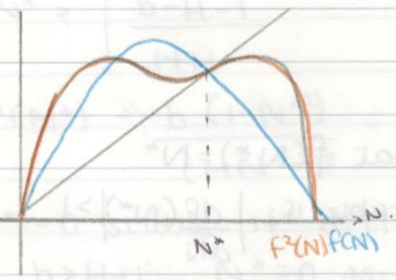
Use f^2 to mean $f \circ f$ = f composed with itself.

$f^2(N_1) = N_1, \quad f^2(N_2) = N_2$

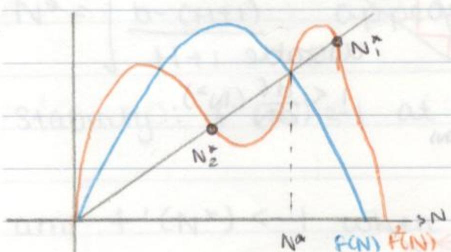
Which says that N_1 and N_2 are fixed points of the map f^2.

The fixed points of f^2 include the fixed points of f: if $f(N^*) = N^*$, $f^2(N^*) = N^*$.

To find a 2-cycle we solve $f^2(N) = N$ for N and throw away those solutions N^* such that $f(N^*) = N^*$.



Here f^2 has a single fixed point N^*, which is a steady state: $f(N^*) = N^*$ (and $\therefore f^2(N^*) = N^*$)



N_1^* and N_2^* are fixed points of f^2 but not of f.

These points satisfy $f(N_1^*) = N_2^*$, $f(N_2^*) = N_1^*$

ie the 2-cycle is

$N_1^*, N_2^*, N_1^*, N_2^*, \ldots$

The 2-cycle appears when $\frac{d}{dN} f^2(N^*) = +1$

$$\frac{d}{dN} f^2(N) = \frac{d}{dN}\left(f(f(N))\right) = f'(f(N))\,f'(N)$$

$$\frac{d}{dN} f^2(N^*) = \cancel{d}\, f'(f(N^*))\,f'(N^*)$$

But $f(N^*) = N^*$

$\Rightarrow \frac{d}{dN} f^2(N^*) = (f'(N^*))^2 = +1$

So cycle appears where $(f'(N^*)) = +1$

For ~~oscuanonts~~ oscillations we need $f'(N^*) < 0$ and hence $f'(N^*) = -1$ at the appearence of a 2-cycle.

Example:

$N_{t+1} = \frac{rN_t}{1+N_t^3} = f(N_t) \quad r > 0$

Steady states $f(N^*) = N^* \quad \frac{rN^*}{1+N^{*3}} = N^*$

$\Rightarrow N^* = 0$ and solution to $\frac{r}{1+N^{*3}} = 1 \Rightarrow N^* = (r-1)^{1/3}$ for $r>1$

Hence for $0 < r \le 1$ $\exists$ unique steady state $N^* = 0$

$r > 1$ 2 steady states $N^* = 0, (r-1)^{1/3}$

Stability ~~anagna~~ analysis.

$f(N) = \frac{rN}{1+N^3}$

$f'(N) = \frac{r}{1+N^3} + rN\frac{(-3N^2)}{(1+N^3)^2}$

$= \frac{r(1+N^3) - 3rN^3}{(1+N^3)^2}$

$= \frac{r(1-2N^3)}{(1+N^3)^2}$

At $N^* = 0$, $f'(0) = r$

So for $r < 1$ $N^* = 0$ is stable

For $r > 1$, $f'(N^*) = f'((r-1)^{1/3})$

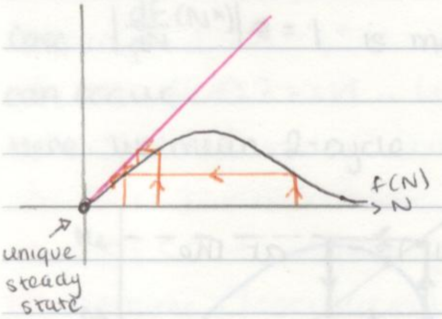
$= \frac{r(1-2(r-1))}{r^2}$

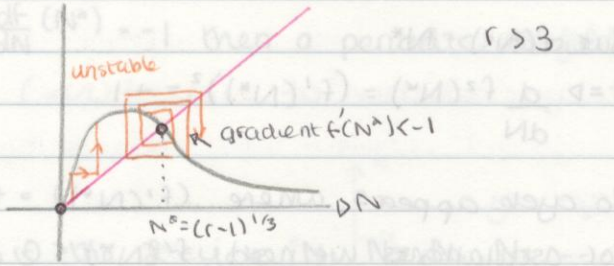
$= \frac{3-2r}{r}$

For $N^* = (r-1)^{1/3}$ to be stable we need

$-1 < \frac{3-2r}{r} < +1 \Rightarrow -1 < \frac{3}{r} - 2 < +1 \Rightarrow 1 < \frac{3}{r} < 3 \Rightarrow 1 < r < 3$

For $r > 3$, we find $f'((r-1)^{1/3}) < -1 \Rightarrow N^*$ unstable.





What happens at $r=3$?

See if there are any fixed points of f^2

Solve $f^2(N) = N$

$$\frac{r f(N)}{1+f(N)^3} = N$$

$$\frac{r\left(\frac{rN}{1+N^3}\right)}{1+\left(\frac{rN}{1+N^3}\right)^3} = N$$

One solution is $N=0$ remove it. (already steady state)

$$\frac{\frac{r^2N}{1+N^3}}{1+\frac{r^3N^3}{(1+N^3)^3}} = 1 \qquad \text{Substitute } x = 1+N^3 \Rightarrow \frac{\frac{r^2}{x}}{1+\frac{r^3(x-1)}{x^3}} = 1$$

$$\Rightarrow \frac{r^2x^3}{x^3+r^3(x-1)} = 1$$

$\Rightarrow x^3 - r^2x^2 + r^3(x-1) = 0$

Now recall $N^* = (r-1)^{1/3}$ is a steady state

$\Rightarrow N^{*3}+1 = r$ ie $x^* = r$

$r^3 - r^2r^2 + r^3(r-1) = 0$

$(x-r)(x^2+(r-r^2)x+r^2) = 0$

So the remaining roots $x_\pm$ are roots of $x^2+(r-r^2)x+r^2=0$

$\Rightarrow N_\pm = (x_\pm - 1)^{1/3}$ $\quad (x = 1+N^3)$

The N_+ and N_- are the two points of the 2-cycle:

$f(N_+) = N_-$ and $f(N_-) = N_+$

Still need to check that $N_+, N_- > 0$, ie that $x_+ > 1$ and $x_- > 1$

We use that x_+, x_- satisfy $x_\pm^2 + (r-r^2)x_\pm + r^2 = 0$

$(r^2-r)x_\pm = x_\pm^2 + r^2 \geq r^2$

$\Rightarrow$ If $r^2 > r$ $(r>1)$ $x_\pm > \frac{r^2}{r^2-r} = \frac{1}{1-1/r} > 1$ if $r>1$.

So if $r>3$ then $N_\pm$ exists and $N_+, N_-, N_+, N_-, \ldots$

If $f = \frac{\text{poly}}{\text{poly}}$ (ie rational function) you can sometimes find roots of f^2 explicitly and hence cycles.

Simple Age Structured Models

So far all models have assumed identical indaviduals (in each species)

But in reality
- fecundity
- survival propability
- competivity

etc vary with age.

The idea of this model is to divide the total population of one species into age classes

Here age is one unit (could be 1 year, 1 month, 1 season etc).

We suppose there are n age classes

N_k = number of indaviduals in class k.

Classes $N_1, N_2, \ldots, N_n$ are the age classes

No one can live to an age beyond n.

We will use t to denote time chosen so that 1 time unit = 1 age unit.

~~So~~ So as t goes from T to $T+1$, all ~~mem~~ members move to next age class or ~~die~~ they die.

At each time step, an indavidual either gets 1 unit older or dies.

Need to bring offspring into the model.

At each time step offspring are produced and are put in the zero age class N_0.

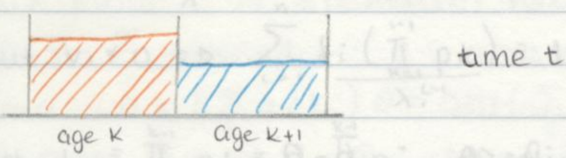
Suppose that:

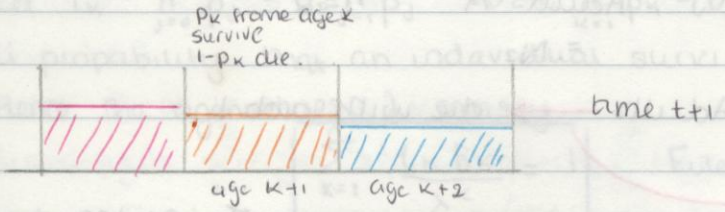
p_0 = fraction of offspring that survive to age 1

p_k = fraction surviving from age k to age $k+1$

b_k = expected # offspring produced by an indavidual of age k.

Let $N_k(t)$ = # of indaviduals age k at time t.





$N_{k+1}(t+1)$ = fraction of surviving from age k at t
$= p_k N_k(t)$

for $k = 1, 2, \ldots, n-1$

We need an equation for $N_1(t+1)$ = number of newborns that survive ~~age~~ to age 1

Number of offspring produced at time t is $\sum_{k=1}^{n} b_k N_k(t)$

These offspring at t survive to t+1 and age 1 with probability p_0

$\Rightarrow N_1(t+1) = p_0\left(\sum_{k=1}^{n} b_k N_k(t)\right)$.

Let $f_k = p_0 \cdot b_k \Rightarrow N_1(t+1) = \sum_{k=1}^{n} f_k N_k(t)$

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \\ \vdots \\ N_n(t+1) \end{pmatrix} = \underbrace{\begin{pmatrix} f_1 & f_2 & \cdots & \cdots & f_n \\ p_1 & 0 & \cdots & \cdots & 0 \\ 0 & p_2 & 0 & \cdots & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & \cdots & \cdots & p_{n-1} & 0 \end{pmatrix}}_{L} \begin{pmatrix} N_1(t) \\ N_2(t) \\ \vdots \\ N_n(t) \end{pmatrix}$$

L is called the Leslie matrix

$\underline{N}(t+1) = L\underline{N}(t)$ A

From A start with $\underline{N}(0)^T = (N_1(0), \ldots, N_n(0))$

$\underline{N}(1) = L\underline{N}(0)$

$\underline{N}(2) = L\underline{N}(1) = L^2\underline{N}(0)$

$\underline{N}(t) = L^t\underline{N}(0) \quad t = 1, 2, \ldots$

want to say something qualitative about $\underline{N}(t)$, so we need to know something about eigenvalues of L.

If L is diagonalisable, ie $\exists P$ such that $PLP^{-1} = D$ diagonal

$$= \begin{pmatrix} \lambda_1 & & 0 \\ & \ddots & \\ 0 & & \lambda_n \end{pmatrix}$$

$D^k = (PLP^{-1})^k = PL^kP^{-1}$

$\Rightarrow L^k = P^{-1}D^kP = P^{-1}\begin{pmatrix} \lambda_1^k & & 0 \\ & \ddots & \\ 0 & & \lambda_n^k \end{pmatrix} P$

Hence if L is diagonalisable

$\underline{N}(t) = P^{-1}\begin{pmatrix} \lambda_1^t & & 0 \\ & \ddots & \\ 0 & & \lambda_n^t \end{pmatrix} P\underline{N}(0)$

Example: 2 age classes Juveniles J $= N_1$, Adults A $= N_2$ $\quad n = 2$

$$\text{Newborns} \xrightarrow[\text{survive}]{p_0} \text{Juveniles} \xrightarrow[\text{survive}]{p_1} \text{Adults} \longrightarrow \text{die with prob } 1$$

Newborns: die $1-p_0$; Juveniles: die $1-p_1$

b_A = expected number of offspring from an adult.

Juveniles do not produce offspring.

$A(t+1) = p_1 J(t) \quad J(t+1) = p_0(b_A A(t))$

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & p_0 b_A \\ p_1 & 0 \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

The leslie matrix here is $L = \begin{pmatrix} 0 & p_0 b_A \\ p_1 & 0 \end{pmatrix}$

~~Find eigenvalues of L~~ Done differently in notes, both good ways

~~An eigen~~vector ~~$\underline{v}^T = (v_1, \dots, v_n)$ of L with eigenvalue λ_1 is a non-zero~~ is a non-zero solution of $L\underline{v} = \lambda \underline{v}$

Finding eigenvalues of L

An ~~eigenvalue~~ eigenvector of $\underline{v}^T = (v_1, \dots, v_n)$ of L with eigenvalue λ, is a non-zero solution of $L\underline{v} = \lambda \underline{v}$

$$\begin{pmatrix} f_1 & f_2 & \cdots & \cdots & f_n \\ p_1 & 0 & \cdots & \cdots & 0 \\ 0 & p_2 & & & \vdots \\ \vdots & & \ddots & & \vdots \\ 0 & \cdots & 0 & p_{n-1} & 0 \end{pmatrix} \begin{pmatrix} v_1 \\ v_2 \\ \vdots \\ v_n \end{pmatrix} = \lambda \begin{pmatrix} v_1 \\ v_2 \\ \vdots \\ v_n \end{pmatrix}$$

$$\sum_{i=1}^{n} f_i v_i = \lambda v_1$$

$$p_1 v_1 = \lambda v_2$$

$$\vdots$$

$$p_i v_i = \lambda v_{i+1}$$

$$\vdots$$

$$p_{n-1} v_{n-1} = \lambda v_n$$

Suppose $v_1 \neq 0$ $\quad v_2 = \frac{p_1 v_1}{\lambda}$, $v_3 = \frac{p_2 v_2}{\lambda^2} = \frac{p_1 p_2 v_1}{\lambda^2}$ $\dots$ $v_{i+1} = \frac{p_i v_i}{\lambda} = \frac{p_1 p_2 \dots p_i v_1}{\lambda^i}$

Hence $\sum_{i=1}^{n} f_i v_i = f_1 v_1 + f_2 \frac{p_1 v_1}{\lambda} + f_3 \frac{p_1 p_2 v_1}{\lambda_2} + \dots + f_n \frac{p_1 \dots p_{n-1} v_1}{\lambda^{n-1}} = \lambda v_1$

$$\Rightarrow \left(\sum_{i=1}^{n} \frac{f_i \left(\prod_{k=1}^{i-1} p_k \right)}{\lambda^{i-1}} - \lambda \right) v_1 = 0$$

But $v_1 \neq 0 \Leftrightarrow \sum_{i=1}^{n} \frac{f_i \left(\prod_{k=1}^{i-1} p_k \right)}{\lambda^i} = 1$

Let $l_k = \prod_{j=0}^{k-1} p_j = p_0 \prod_{j=1}^{k-1} p_j \Rightarrow f_i \prod_{k=1}^{i-1} p_k = b_i p_0 \prod_{k=1}^{i-1} p_k = b_i l_i$

l_i propability that an individual survives from birth to age i

Hence the eigenvalues λ satisfy

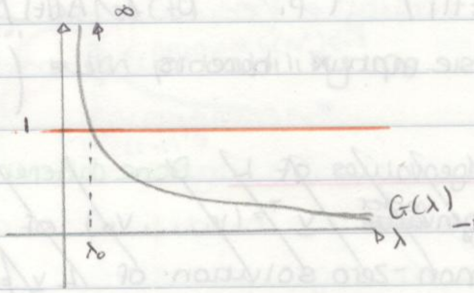
$$\boxed{\sum_{k=1}^{n} \frac{l_k b_k}{\lambda^k} = 1} \quad \text{Euler - Lotka equation}$$

(If $v_1 = 0$, move to v_2 etc).

Existence of eigenvalues

Look for a positive eigenvalue λ_0

Define $G(\lambda) = \sum_{k=1}^{n} \frac{b_k l_k}{\lambda^k}$



Since $b_k l_k \geq 0$ and some $b_k l_k > 0$ the function $G(\lambda)$ is strictly decreasing for $\lambda > 0$

From figure or IVT $\exists$ solution $\lambda_0 > 0$ such that $G(\lambda_0) = 1$ and is unique since $G(\lambda)$ strictly decreasing.

Hence there can only be one positive real eigenvalue of L.

All other eigenvalues must be <0 or complex ($\lambda = 0$ is obviously not an eigenvalue)

Periodicity of L.

~~Recall that for m,n integers~~

Definition:

A Leslie matrix is <u>aperiodic</u> if $GCD(\{k \mid b_k > 0\}) = 1$ (ow L is periodic)

$$L = \begin{pmatrix} p_0 b_1 & p_0 b_2 & p_0 b_3 & \cdots & p_0 b_n \\ p_1 & & & & \\ & \ddots & & & \\ & & \ddots & & \end{pmatrix}$$

if $b_2 > 0$, $b_n > 0$

$\{1, n\} \subseteq \{k \mid b_k > 0\}$.

eg.

$$L = \begin{pmatrix} p_0 & 0.3p_0 & 2p_0 & 1.2p_0 \\ p_1 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 \\ 0 & 0 & p_3 & 0 \end{pmatrix}$$

$\{k \mid b_k > 0\} = \{1, 2, 3, 4\}$

$GCD(\{1, 2, 3, 4\}) = 1$

$\Rightarrow L$ ~~APA~~ aperiodic.

$$L = \begin{pmatrix} 0 & 0.9p_0 & 0 & 7p_0 \\ p_1 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 \\ 0 & 0 & p_3 & 0 \end{pmatrix}$$

$\{k \mid b_k > 0\} = \{2, 4\}$

$\Rightarrow$ ~~GDV~~ $GCD = 2$

$\Rightarrow$ periodic

Theorem:

If the Leslie matrix L is aperiodic and λ_0 is the unique positive eigenvalue of L and λ is any other (real or complex) eigenvalues of L then $\lambda_0 > |\lambda|$

Proof: λ is real $\Rightarrow \lambda < 0 \Rightarrow \lambda = -\mu, \mu > 0$

$$G(\lambda) = \sum_{k=1}^{n} \frac{b_k l_k}{\lambda_k}$$

$$G(\lambda) = G(-\mu) = \sum_{k=1}^{n} \frac{b_k l_k}{(-\mu)^k}$$

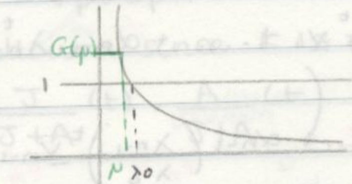
$$= \sum_{k \text{ even}} \frac{b_k l_k}{\mu^k} - \sum_{k \text{ odd}} \frac{b_k l_k}{\mu^k}$$

Suppose $b_k = 0$ for all odd $k \Rightarrow$ GCD ≥ 2

$\Rightarrow$ at least one $b_k > 0$ for k odd

Hence $\underset{1}{\underset{\shortparallel}{G(\lambda)}} = G(-\mu) < \sum_{\text{even } k} \frac{b_k l_k}{\mu^k} < \sum_{k} \frac{b_k l_k}{\mu^k} = G(\mu)$

$\Rightarrow G(\mu) \geq 1$



Since G is decreasing

$\mu < \lambda_0$

$\Rightarrow |\lambda| < \lambda_0$

Case $\lambda \in \mathbb{C}$. Let ~~$\lambda = Re$~~ $\lambda = Re^{i\theta}$

Recall Euler Lotka equation for the eigenvalues is $G(\lambda) = \sum_{k=1}^{\infty} \frac{b_k l_k}{\lambda^k} = 1$

(can use ∞ in sum since $l_k = 0$ for $k \geq$ age limit).

$$G(Re^{i\theta}) = \sum_{k=1}^{\infty} \frac{b_k l_k}{R^k} e^{ik\theta} = 1$$

Equate real and imaginary parts $\sum_{k=1}^{\infty} \frac{b_k l_k}{R^k} \cos k\theta = 1$

$$\sum_{k=1}^{\infty} \frac{b_k l_k}{R^k} \sin k\theta = 0$$

Now suppose that for each k such that $b_k > 0$, we have $\cos k\theta = 1$

$\Rightarrow k_i \theta = 2\pi n_i$ where k_i enumerates the k st $\cos k\theta = 1$

But since L is aperiodic, the GCD of the k_i's is 1, so $\exists$ intergers

α_i st $\sum_i \alpha_i k_i = 1$

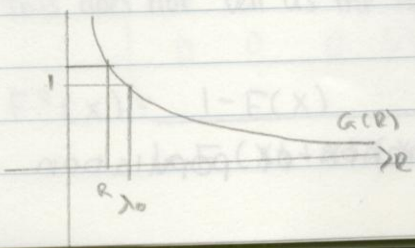
Hence $\theta = (\sum_i \alpha_i k_i)\theta = 2\pi (\sum_i n_i \alpha_i)$ = interger multiple of 2π

So that $\lambda = Re^{i\theta} \in \mathbb{R} \Rightarrow$ contradiction since we have done $\lambda > 0$ and $\lambda < 0$

Hence $\exists$ at least one k_i such that $\cos k_i\theta < 1$

$$1 = G(\lambda) = \sum_{k=1}^{\infty} \frac{1}{R^k} b_k l_k \cos k\theta < \sum_{k=1}^{\infty} \frac{1}{R^k} b_k l_k = G(R)$$

So $G(R) > 1 \Rightarrow R < \lambda_0 \Rightarrow |\lambda| < \lambda_0$



Suppose that L is aperiodic. Suppose $\underline{N}(0)^T = (N_1(0), \ldots, N_n(0))$ is given

Then $\underline{N}(1) = L\underline{N}(0)$ ..... $\underline{N}(t) = L^t N(0)$

Suppose that the eigenvalues of L are complete

ie form a basis for $\mathbb{R}^n$ (eg if eigenvalues are distinct).

Then $N(0) = \sum_{j=0}^{n-1} \alpha_j \underline{v}_j$ where $\underline{v}_0$ will be an eigenvector associated with $\lambda_0 > 0$

The α_j are unique for each $\underline{N}(0)$.

$$N(1) = L\underline{N}(0) = L\left(\sum_{j=0}^{n-1} \alpha_j \underline{v}_j\right) = \sum_{j=0}^{n-1} \alpha_j L\underline{v}_j = \sum_{j=0}^{n-1} \alpha_j \lambda_j \underline{v}_j$$

By induction $\underline{N}(t) = \sum_{j=0}^{n-1} \alpha_j \lambda_j^t \underline{v}_j$

$$= \alpha_0 \lambda_0^t \underline{v}_0 + \alpha_1 \lambda_1^t \underline{v}_1 + \ldots + \alpha_{n-1} \lambda_{n-1}^t \underline{v}_{n-1}$$

Assume $\alpha_0 \neq 0$

$$\underline{N}(t) = \lambda_0^t \left(\alpha_0 \underline{v}_0 + \alpha_1 \left(\frac{\lambda_1}{\lambda_0}\right)^t \underline{v}_1 + \ldots + \alpha_{n-1}\left(\frac{\lambda_{n-1}}{\lambda_0}\right)^t \underline{v}_{n-1}\right)$$

By aperiodicity $|\lambda_j| < \lambda_0$ for $j = 1, \ldots, n-1$

So $\left|\frac{\lambda_j}{\lambda_0}\right|^t \to 0$ as $t \to \infty$

Hence as $t \to \infty$ the term $\lambda_0^t \alpha_0 \underline{v}_0$ will dominate the terms $\underline{N}(t)$

For large t, $\underline{N}(t) \sim \lambda_0^t \alpha_0 \underline{v}_0$

$$\underline{N}(t+1) \sim \lambda_0^{t+1} \alpha_0 \underline{v}_0 = \lambda_0 \underline{N}(t)$$

So for t large each age class grows by a factor of λ_0.

λ_0 is ~~con~~ sometimes called the fitness of the population

If $\lambda_0 > 1$ then $N_k(t)$ grows since λ_0^t grows.

$\lambda_0 < 1$ $N_k(t) \to 0$.

To capture the age structure we look at the fraction $X_k(t)$ of the population in class k at time t:

$$X_k(t) = \frac{N_k(t)}{\sum_{r=1}^{n} N_r(t)}$$

Since $\underline{N}(t) \sim \lambda_0^t \alpha_0 \underline{v}_0$ $\quad \underline{v}_0^T = (v_{01}, v_{02}, \ldots, v_{0n})$

$$X_k(t) \sim \frac{\lambda_0^t \alpha_0 v_{0k}}{\lambda^t \alpha_0 \sum_{r=1}^{n} v_{0r}} = \frac{v_{0k}}{\sum_{r=1}^{n} v_{0r}} \quad \text{for } t \text{ large}$$

This tells us from the eigenvector $\underline{v}_0$ what is the fraction of population in age class K for t large.

Example: A=adults, J= juveniles.

Same model as befor

$$\begin{tikzcd} \text{new born} \arrow[r, "p_J"] & J \arrow[r, "p_A"] & A \arrow[r] \arrow[ll, bend left, "b"] & \text{die} \end{tikzcd}$$

$J(t+1) = p_J\, b A(t)$
$A(t+1) = p_A\, J(t)$
$\Rightarrow L = \begin{pmatrix} 0 & p_J b \\ p_A & 0 \end{pmatrix}$ is not aperiodic

Eigenvalues: $\begin{vmatrix} -\lambda & p_J b \\ p_K & -\lambda \end{vmatrix} = \lambda^2 - p_J b p_A = 0$

$\Rightarrow$ has eigenvalues $\pm\sqrt{p_J b p_A} = \lambda_1, \lambda_2$

(Note $|\lambda_1| = |\lambda_2|$ is allowed since L is not aperiodic)

We have $\underline{X}(t) = \left(\frac{J}{J+A}(t), \frac{A}{J+A}(t)\right)$

Let $x(t) = \frac{J(t)}{J(t)+A(t)}$ so that the other fraction is just $1 - x(t)$

$x(t+1) = \frac{J(t+1)}{J(t+1)+A(t+1)}$

$J(t+1) + A(t+1) = p_J b + p_A J(t)$
$\qquad = (A(t)+J(t))\left[p_J b(1-x(t)) + p_A x(t)\right]$

Hence $x(t+1) = \frac{p_J b A(t)}{(A(t)+J(t))\left[p_J b(1-x(t)) + p_A x(t)\right]}$

$x(t+1) = \frac{p_J b(1-x(t))}{p_J b(1-x(t)) + p_A x(t)} = F(x(t))$

Find steady states $F(x) = x$

$x = \frac{p_J b(1-x)}{p_J b(1-x) + p_A x} = \frac{1-x}{1-x+\alpha x}$ where $\alpha = \frac{p_A}{p_J b}$

Solutions are $x_\pm = \frac{1}{1 \pm \sqrt{\alpha}}$ of which $\frac{1}{1+\sqrt{\alpha}}$ is only root in $[0,1]$
(x is a fraction)

Stability: $F'(x) = \frac{-\alpha}{[1-x+\alpha x]^2} < 0$

$F'(x_+) = \frac{-\alpha}{\left(1 - {(\alpha-1)}/{(\sqrt{\alpha}+1)}\right)^2} = \frac{-\alpha}{\left(1 + (\sqrt{\alpha}-1)\right)^2} = -1$

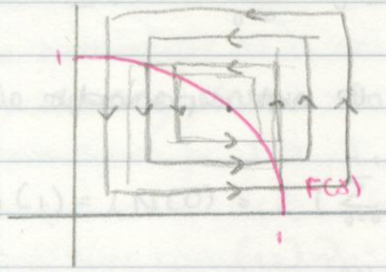
This does not tell us the local stability of $\frac{1}{1+\sqrt{\alpha}}$

$F^2(x) = \frac{1 - F(x)}{1 - F(x) + \alpha F(x)}$

$$= \frac{1 - \frac{1-x}{1-x+\alpha x}}{1 + (\alpha - 1)\left(\frac{1-x}{1-x+\alpha x}\right)} = \frac{1 - x + \alpha x - 1 + x}{1 - x + \alpha x + (\alpha-1)(1-x)} = \frac{\alpha x}{\alpha(1-x) + \alpha x} = x$$

ie $F^2(x) = x$.

All orbits are 2 cycles



Example:

$$\text{Newborns} \xrightarrow{p_J} \text{Age } 1 \xrightarrow{p_J} \underbrace{\cdots \xrightarrow{p_J} m-1}_{\text{juveniles}} \xrightarrow{p_J} \underbrace{\overset{\text{sexual maturity}}{\text{Age } m} \xrightarrow{p_A} m+1 \xrightarrow{p_A} \cdots}_{\text{adults}}$$

Survival probability is

$$p_k = \begin{cases} p_J & k < m \\ p_A & k \geq m \end{cases}$$

Birth rates

$$b_k = \begin{cases} 0 & k < m \\ b & k \geq m \end{cases}$$

We impose no age limit.

Euler-Lotka equation $\displaystyle\sum_{k=1}^{\infty} \frac{1}{\lambda^k} b_k l_k = 1$

$$\Rightarrow \sum_{k=m}^{\infty} \frac{1}{\lambda^k} b l_k = 1$$

We have $l_k = \begin{cases} p_J^k & k < m \\ p_J^m p_A^{k-m} & \text{for } k \geq m \end{cases}$

$$\Rightarrow \sum_{k=m}^{\infty} \frac{1}{\lambda^k} b\left(p_J^m p_A^{k-m}\right) = 1$$

$$1 = b\left(\frac{p_J}{p_A}\right)^m \sum_{k=m}^{\infty} \frac{1}{\lambda^k} p_A^k = b\left(\frac{p_J}{p_A}\right)^m \cdot \left(\frac{p_m}{\lambda}\right)^m \sum_{k=0}^{\infty} \left(\frac{p_A}{\lambda}\right)^k$$

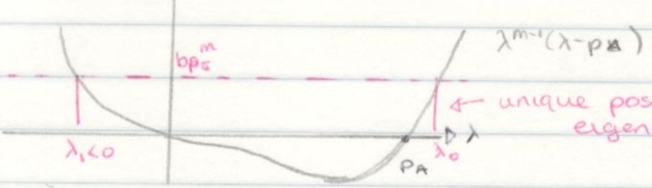
Provided $\lambda > p_A$ we have:

$$1 = b\left(\frac{p_J}{p_A}\right)^m \left(\frac{p_A}{\lambda}\right)^m \frac{1}{1 - p_A/\lambda}$$

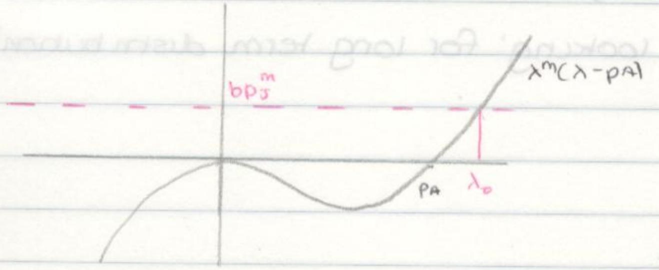
$$\lambda^m - p_A \lambda^{m-1} = b p_J^m$$

What are the eigenvalues?

Plot $\lambda^m - p_A \lambda^{m-1} = \lambda^{m-1}(\lambda - p_A)$



$m > 2$ (integer)



$n > 1$ (odd)

Notice that $\lambda_0 > p_A$ as was required for convergence of series

Take $m = 3$ and $p_A = \frac{1}{4}$ $b = \frac{1}{2} = p_J$

EL becomes $\lambda^3 - \frac{1}{4}\lambda^2 = \frac{1}{2} \cdot \frac{1}{8} = \frac{1}{16}$

By inspection $\lambda = \frac{1}{2}$ is a root and also $\lambda_\pm = -\frac{1}{8} \pm i\frac{\sqrt{7}}{8}$

(check $|\lambda_\pm| < \frac{1}{2} = \lambda_0$)

Suppose $\underline{v}_0^T = (v^1, v^2, \dots,)$ is an eigenvector associated with $\lambda_0 (= \frac{1}{2})$

$$L = \begin{pmatrix} 0 & 0 & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & \cdots \\ \frac{1}{2} & 0 & 0 & 0 & 0 & \cdots \\ 0 & \frac{1}{2} & 0 & 0 & 0 & \cdots \\ 0 & 0 & \frac{1}{4} & 0 & 0 & \cdots \\ 0 & 0 & 0 & \frac{1}{4} & 0 & \cdots \\ \vdots & \vdots & \vdots & & & \end{pmatrix}$$

So $\underline{v}_0$ satisfies

$L\underline{v}_0 = \lambda_0 \underline{v}_0$

$$\begin{pmatrix} 0 & 0 & \frac{1}{4} & \frac{1}{4} & \frac{1}{4} & \cdots \\ \frac{1}{2} & 0 & 0 & 0 & 0 & \cdots \\ 0 & \frac{1}{2} & 0 & 0 & 0 & \cdots \\ 0 & 0 & \frac{1}{4} & 0 & 0 & \cdots \\ 0 & 0 & 0 & \frac{1}{4} & 0 & \cdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \end{pmatrix} \begin{pmatrix} v^1 \\ v^2 \\ v^3 \\ \vdots \\ \vdots \\ \vdots \end{pmatrix} = \frac{1}{2} \begin{pmatrix} v^1 \\ v^2 \\ v^3 \\ \vdots \\ \vdots \\ \vdots \end{pmatrix}$$

Ignore first row $\frac{1}{2}v^1 = \frac{1}{2}v^2$

$$\frac{1}{2}v^2 = \frac{1}{2}v^3$$
$$\frac{1}{4}v^3 = \frac{1}{2}v^4$$
$$\frac{1}{4}v^4 = \frac{1}{2}v^5$$

Choose $v^1 = \alpha \Rightarrow v^1 = v^2 = v^3 = \alpha$

$v^4 = \frac{1}{2}\alpha, \ v^5 = (\frac{1}{2})^2\alpha \dots$

$\Rightarrow \underline{v}_0 = (\alpha, \alpha, \alpha, \frac{1}{2}\alpha, \frac{1}{4}\alpha, \frac{1}{8}\alpha, \dots)$

Since we want $\sum_k v_{0k} = 1$ (we are looking for long term distribution)

$\alpha + \alpha + \alpha + \frac{1}{2}\alpha + \frac{1}{4}\alpha + \frac{1}{8}\alpha + \dots = 1$

$\alpha(3 + \frac{1}{2}(1 + \frac{1}{2} + \frac{1}{2^2} + \dots)) = 1$

$\alpha(3 + \frac{1}{2}(\frac{1}{1 - 1/2})) = \alpha(3+1) \Rightarrow \alpha = 1/4$

Life History Strategies

λ_0 measures the growth of the population from one age step to the next as time gets large, ie measures # offspring produced each age unit. Because higher λ_0 means that an individual will be more likely to propogate its genes onwards, λ_0 is traditionally called <u>fitness</u>. With the action of natural selection, over evolutionary timescales we expect the population to ~~grow~~ develop maximum fitness.

How is λ_0 maximised?

Because energy reserves for an individual are ~~maximised~~ finite they cannot simultaneously maximise fecundity and survival probabilities. There has to be a trade off.

Suppose that fitness λ_0 depends ~~on~~ upon a number of <u>phenotypis</u> parameters (ie observeable characteristics that follow from genes)

eg. size, colour, maximum speed, facundity etc.

Let these parameters be $\underline{\sigma}^T = (\sigma_1, \dots, \sigma_s)$

So now $\lambda_0 = \lambda_0(\underline{\sigma})$

For maximum fitness need $\nabla\lambda_0(\underline{\sigma}^*) = \underline{0}$ (turning point)

matrix $\left(\frac{\partial^2 \lambda_0}{\partial\sigma_i \partial\sigma_j}\right) = H$ is positive definite.