3506 Mathematical Ecology Notes

Based on the 2015 spring lectures by Dr S A Baigent

The Author(s) has made every effort to copy down all the content on the board during lectures. The Author(s) accepts no responsibility whatsoever for mistakes on the notes nor changes to the syllabus for the current year. The Author(s) highly recommends that the reader attends all lectures, making their own notes and to use this document as a reference only.

3506 (Mathematical Ecology)

Year: 2014–2015
Code: MATH3506
Level: Advanced
Value: Half unit (= 7.5 ECTS credits)
Term: 2
Structure: 3 hours lectures per week
Assessment: 100% examination
Normal Pre-requisites: MATH1401. Some basic knowledge of probability is essential, as covered in MATH1301 or the post-examination course on probability.
Lecturer: Dr SA Baigent

Course Description and Objectives

Mathematical models are used extensively in many areas of the Biological Sciences. This course aims to give a sample of the construction and mathematical analysis of such models in Population Ecology. The fundamental question to be addressed is: what natural (or human) factors control the abundance and distribution of the various populations of animals and plants that we see in Nature?

No special knowledge of Ecology is required or assumed. However, an interest in, and willingness to learn about, concepts and problems in this area are essential. Mathematical techniques used include calculus, mathematical methods and linear algebra, and those developed include the important qualitative technique of phase plane analysis which the course uses extensively.

This course is independent of MATHM505.

Recommended Texts

Ecology

(i) *Elements of Mathematical Biology*, Mark Kot, CUP 2001.

a bit advanced PhD level

(ii) *Evolutionary games and population dynamics*, Joseph Hofbauer and Karl Sigmund, CUP 2002.

pop. dynamics react.-diff. equations →

(iii) *Mathematical Biology*, J.D. Murray, Springer-Verlag Biomathematics Texts, 1989.

(iv) *A Primer in Ecology*, N.J. Gotelli, Sinaur Associates Inc.

written for biologist ↗

Detailed Syllabus

- Population models for a single species (discrete and continuous-time models). Constant and time-varying environments. Discrete-time population models; logistic map.
- Simple age-structured models. Stable age-structure. The Euler-Lotka demographic equation and its analysis using theory of non-negative matrices. Applications to the theory of life-history strategies.
- Basic phase plane and linear stability analysis. Two-species interactions: Competition, Cooperation and Predator-prey models. Holling's functional responses.
- Many-species interactions. General Lotka-Volterra models. Applications of Lyapunov functions.

Chapter 1

Elementary single species models

1 Some basic probability theory

We begin with some basic probability theory (i.e. stochastic processes) which will be useful in the development of the evolution equations modelling the change of populations with time. In what follows, think of typical events being an individual giving birth to an offspring, or an individual dying.

The following preposition is central to the interpretation of the population models. Essentially we are saying that the event E is exponentially distributed in time, but that the mean is time dependent.

Preposition 1 *For* δt *sufficiently small let* $p(t)\delta t + O(\delta t^2)$ *be the probability that an event* E *occurs in the infinitesimal time interval* $[t, t+\delta t)$*. Also assume that events in disjoint time intervals are independent. Then the probability that no event occurs in the interval* $[0,t)$ *is* $\exp(-\int_0^t p(s)\,ds)$.

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

$$\begin{aligned} P(t+\delta t) &= \text{prob[no event occurs in } [0,t)] \times \text{prob[no event occurs in } [t,t+\delta t)] \\ &= P(t) \times (1 - p(t)\delta t) + O(\delta t^2) \\ &= P(t) - p(t)P(t)\delta t + O(\delta t^2). \end{aligned}$$

Therefore

$$\frac{P(t+\delta t) - P(t)}{\delta t} = -p(t)P(t) + O(\delta t).$$

Taking the limit $\delta t \to 0$ gives $dP/dt = -p(t)P(t)$ which has solution $P(t) = \exp\left(-\int_0^t p(s)\,ds\right)P(0)$. But $P(0) =$ prob[no event has occurred at time t=0] $= 1$ and thus

$$P(t) = \exp\left(-\int_0^t p(s)\,ds\right). \tag{1.1}$$

□

Similarly, the probability that at least one event occurs in the interval $[0,t)$ is $1 - (\exp - \int_0^t p(s)\,ds)$.

Example: Birth-death models

In our application to population dynamics we could have $p(t) = b(t) =$ birth rate at time t. For a given (potential) parent at $t = 0$,

$$\begin{aligned} \text{prob[no descendants at time t]} &= \exp\left(-\int_0^t b(s)\,ds\right) \\ \text{prob[at least one descendant at time t]} &= 1 - \exp\left(-\int_0^t b(s)\,ds\right). \end{aligned}$$

Time to 1st event

We make the assumption (on how rapidly $p(t) \to 0$ as $t \to \infty$):

$$\text{Assumption:} \quad \lim_{t\to\infty}\left\{t \times \exp\left(-\int_0^t p(s)\,ds\right)\right\} = 0. \tag{1.2}$$

Probability that 1st event occurs in the interval $[t, t+\delta t)$ is $\exp\left(-\int_0^t p(s)\,ds\right) \times p(t)\delta t + O(\delta t^2)$. Note that

$$\begin{aligned} \int_0^\infty \exp\left(-\int_0^t p(s)\,ds\right) \times p(t)\,dt &= -\int_0^\infty \frac{d}{dt}\exp\left(-\int_0^t p(s)\,ds\right)\,dt \\ &= 1 - \lim_{t\to\infty}\exp\left(-\int_0^t p(s)\,ds\right) = 1, \end{aligned}$$

since (1.2) guarantees that the limit of the exponential term is zero. This shows that $\exp\left(-\int_0^t p(s)\,ds\right) \times p(t) \geq 0$ is a probability density function on $[0, \infty)$. If $0 \leq a < b < \infty$ then the probability that the first event occurs between $t = a$ and $t = b$ is

$$P(a,b) = \int_a^b \exp\left(-\int_0^t p(s)\,ds\right)\,p(t)\,dt.$$

The expected time to the first event is

$$\begin{aligned} \bar{T} &= \int_0^\infty t\exp\left(-\int_0^t p(s)\,ds\right)\,p(t)\,dt \\ &= -\int_0^\infty t\frac{d}{dt}\exp\left(-\int_0^t p(s)\,ds\right)\,dt \\ &= -\left\{\left[t\exp\left(-\int_0^t p(s)\right)\right]_0^\infty - \int_0^\infty \exp\left(-\int_0^t p(s)\,ds\right)\,dt\right\}. \end{aligned}$$

Using (1.2) to eliminate the first bracket and simplifying yields

$$\bar{T} = \int_0^\infty \exp\left(-\int_0^t p(s)\,ds\right)\,dt. \tag{1.3}$$

Example: Constant birth rate

$p(t) = \lambda$, a constant, then

$$\bar{T} = \int_0^\infty \exp\left(-\int_0^t \lambda\, ds\right) dt = \int_0^\infty e^{-\lambda t}\, dt = [-\frac{1}{\lambda} e^{-\lambda t}]_0^\infty = \frac{1}{\lambda}.$$

Example: Periodic birth rate

$p(t)$ periodic function of t: Take $a \in (0,1)$ and

$$p(t) = \begin{cases} \lambda & \text{if } kT \leq t < kT + aT, \\ 0 & \text{if } kT + aT \leq t < (k+1)T. \end{cases}$$

$$\begin{aligned} \int_0^{kT} p(t)\, dt &= \sum_{r=1}^{k} \int_{(r-1)T}^{rT} p(t)\, dt = \lambda \sum_{r=1}^{k} \int_{(r-1)T}^{rT} 1_{[0,a)}\, dt \\ &= \sum_{r=1}^{k} \lambda a T = k \lambda a T. \end{aligned}$$

Now define

$$\begin{aligned} \bar{T}_k &:= \int_0^{kT} \exp\left(-\int_0^t p(s)\, ds\right) dt \\ &= \sum_{r=1}^{k} \int_{(r-1)T}^{rT} \exp\left(-\int_0^t p(s)\, ds\right) dt \\ &= \sum_{r=1}^{k} \int_0^T \exp\left(-\int_0^{u+(r-1)T} p(s)\, ds\right) du \quad (\text{let } u = t-(r-1)T) \\ &= \sum_{r=1}^{k} \int_0^T \exp\left(-(r-1)\lambda a T - \int_0^u p(s)\, ds\right) du \\ &= \bar{t} \left(\sum_{r=1}^{k} e^{-(r-1)\lambda a T} \right) \text{ where } \bar{t} := \int_0^T \exp\left(-\int_0^u p(s)\, ds\right) du \\ &= \bar{t} \left(\frac{1 - e^{-k\lambda a T}}{1 - e^{-\lambda a T}} \right) \end{aligned}$$

Hence

$$\bar{T} = \lim_{k \to \infty} \bar{T}_k = \frac{\bar{t}}{1 - e^{-\lambda a T}} \tag{1.4}$$

Now for $\bar{t}$ we compute

$$\begin{aligned}
\bar{t} &= \int_0^{aT} \exp\left(-\int_0^u p(s)\,ds\right) du + \int_{aT}^{T} \exp\left(-\int_0^u p(s)\,ds\right) du \\
&= \int_0^{aT} e^{-\lambda u}\,du + \int_{aT}^{T} \exp(-\lambda a T)\,du \\
&= [-\frac{1}{\lambda}e^{-\lambda u}]_0^{aT} + (1-a)Te^{-\lambda aT} \\
&= \frac{1}{\lambda}[1-e^{-\lambda aT}] + (1-a)Te^{-\lambda aT} \qquad (1.5)
\end{aligned}$$

Substituting (1.5) into (1.4) yields:

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

Note that $\bar{T} \to 1/\lambda$ as $a \to 1$, and/or $T \to \infty$, both of which gives the constant event-rate $p(t) = \lambda$ of case 1 above.

1.1 Population Biology: basic notions

We start with some basic definitions:

Species A species is a set of organisms which are capable of interbreeding under natural conditions.

Population A population is a set of organisms of the same species occupying a particular place at a particular time (e.g. elephant population of India).

Population density The population density, N, is defined by

$$N = \frac{\text{number of individuals (of a certain subtype)}}{\text{Area occupied}}$$

Important: This makes N into a real number with range $[0,\infty)$, rather than an integer-valued variable. We will also assume that the changes in population are small in comparison to the total population, so that the population changes (in continuous time models) change continuously with time.

Population changes in time result from birth, death, immigration and emigration. For the most part we will ignore immigration and emigration - if these are important factors then the definition of the local population probably needs to be enlarged. Otherwise special models are needed to take them into account.

1.2 Population dynamics

We now develop linear evolution equations for populations where the only changes in population density are due to birth or death. To be most general we will allow the birth and death rates to be time dependent.

Later we will also let them be population density dependent (i.e. nonlinear), such as for the logistic equation.

We will assume that all members of the population are equal, so that for example we ignore variations in age, size, fecundity, and so on that are found in reality. Later we include some of these variations, but in order to do so we will need to keep the models very simple - linear even.

1 Simple birth models

Let $N(t)$ denote the (expected = mean) population density of a species at time t. We wish to derive equations for how this density changes with time due to the birth and death of individuals. For now, let us consider only birth, and let $b(t)$ be the **birth rate** at time t, i.e. (to first order in δt) $b(t)\delta t$ is the probability that an individual chosen at random from the population at time t will give birth to an offspring in the time interval $[t, t+\delta t)$. We let $p_k(t)$ denote the probability that at time t the population is k. In a time interval $[t, t+\delta t)$ there are two ways that $p_k(t)$ can change: the population can increase from $k-1$ to k with probability $(k-1)p_{k-1}b(t)\delta t$ or it can increase from k to $k+1$ with probability $kp_kb(t)\delta t$. Thus

$$p_k(t+\delta t) = p_k(t) + (k-1)p_{k-1}b(t)\delta t - kp_kb(t)\delta t + O(\delta t^2).$$

Hence

$$\frac{dp_k(t)}{dt} = \lim_{\delta t \to 0} \frac{p_k(t+\delta t) - p_k(t)}{\delta t} = b(t)((k-1)p_{k-1} - kp_k), \quad k = 2, \ldots.$$

For $k = 1$ we have $\dot{p}_1 = -b(t)p_1(t)$.

Now the mean population at time t is define by $N(t) = \sum_{k=0}^{\infty} kp_k(t)$. Thus multiplying the previous equation by k and summing gives

$$\begin{aligned}
\frac{dN}{dt} &= b(t)\left(\sum_{k=1}^{\infty} k(k-1)p_{k-1} - \sum_{k=0}^{\infty} k^2 p_k\right) \\
&= b(t)\left(\sum_{k'=0}^{\infty} (k'+1)k'p_{k'} - \sum_{k=0}^{\infty} k^2 p_k\right) \\
&= b(t)\sum_{k'=0}^{\infty} k'p_{k'} \\
&= b(t)N(t).
\end{aligned}$$

In lectures we generally use a dot over a variable to mean differentiation wrt t, e.g. $\dot{N} = \frac{dN}{dt}$. In this notation, we have, rearranging the last equation,

$$\frac{\dot{N}}{N} = b(t),$$

so that

$$[\log N(\tau)]_{t=0}^{t} = \int_0^t b(\tau)\,d\tau.$$

Hence with $N(0) = N_0 \geq 0$ we obtain

$$N(t) = \exp\left(\int_0^t b(\tau)\,d\tau\right) N_0.$$

This is the mean population size. Since the area occupied by the population is fixed, we may also interpret $N(t)$ to be the mean population density at time t.

2 Simple death models

This is very similar to the birth case, except now for a death rate of $d(t)$, the differential equation for the population density becomes

$$\frac{dN(t)}{dt} = -d(t)N(t), \qquad N(0) = N_0.$$

The solution of this IVP is

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

Recall that $\exp\left(-\int_0^t d(s)\,ds\right)$ is the probability that an individual does not die in the interval $[0.t)$, i.e. this is the **individual survival probability** to time t:

Probability of survival to time t

$$= \frac{N(t)}{N_0} = \exp\left(-\int_0^t d(s)\,ds\right).$$

Probability of dying in time $[0,t)$

$$= 1 - \exp\left(-\int_0^t d(s)\,ds\right).$$

3 Generations and Life Expectancy

Definition 1 *A* **generation** *is the expected time from the birth of an individual to the birth of its first offspring:*

$$T_{\text{gen}} = \bar{T}(\text{births}) = \int_0^\infty \exp\left(-\int_0^t b(s)\,ds\right) dt. \tag{1.6}$$

Definition 2 *The* **Life Expectancy** *is the expected time from birth of an individual to its death:*

$$T_{\text{surv}} = \bar{T}(\text{deaths}) = \int_0^\infty \exp\left(-\int_0^t d(s)\,ds\right) dt. \tag{1.7}$$

For a population to be **viable**, we expect that the individual survives long enough to produce offspring:

$$T_{\text{surv}} > T_{\text{gen}} \qquad \text{viability.} \tag{1.8}$$

In other words

$$\begin{aligned} T_{\text{surv}} - T_{\text{gen}} &= \int_0^\infty \exp\left(-\int_0^t d(s)\,ds\right) - \exp\left(-\int_0^t b(s)\,ds\right) dt \\ &= \int_0^\infty \exp\left(-\int_0^t d(s)\,ds\right)\left\{1 - \exp\left(-\int_0^t r(s)\,ds\right)\right\} dt. \end{aligned}$$

Here $r(s) = b(s) - d(s)$ is the **per capita net reproductive rate** at time t. Thus viability requires that $r(s) > 0$, for "most of the time".

4 Birth/Death Models

In the first example sheet, you will show that combining these two models to cater for both birth and death yields, for $r(s) = b(s) - d(s)$ the per capita net reproductive rate, the model

$$\frac{dN(t)}{dt} = r(t)N(t) \qquad N(0) = N_0. \tag{1.9}$$

The solution of this IVP is

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

Population explosion

This is when $N(t) \to \infty$ as $t \to \infty$. A sufficient condition for this is that $r(t) \geq r_0 > 0$ for all $t \geq t_0$ and some $t_0 \geq 0$, since then

$$\int_0^t r(s)\,ds \to \infty, \;\; t \to \infty.$$

Population collapse

This is when $N(t) \to 0$ as $t \to \infty$. A sufficient condition for this is that $r(t) \leq -r_1 < 0$ for all $t \geq t_1$ and some $t_1 \geq 0$, since then

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

Stable Population

Here $|N(t) - N^*(t)| \to 0$ as $t \to \infty$, for any $N(0) = N_0 > 0$. Here $N^*(t)$ is a "stable" population trajectory. For example, when $r(t) \to 0$ as $t \to \infty$, such that $\int_0^\infty |r(s)|\,ds < \infty$ then $N(t) \to N^*$ as $t \to \infty$, where $N^*(t) = N_0 \exp\left(\int_0^\infty r(s)\,ds\right) < \infty$.

Example: Seasonality: Periodic populations

Suppose that the net reproductive rate $r(s)$ is a periodic function with period T (=one year). We let

$$R := \frac{1}{T}\int_0^T r(s)\,ds = \text{mean reproductive rate over period } T \tag{1.10}$$

Note that, by periodicity of r,

$$\int_{(m-1)T}^{mT} r(s)\,ds = \int_0^T r(s)\,ds = RT.$$

Thus

$$\int_0^{kT} r(s)\,ds = kRT.$$

Now write $t = kT + s$ where $0 \leq s < T$. Then

$$\begin{aligned} N(kT+s) &= \exp\left(\int_0^{kT} r(t)\,dt + \int_{kT}^{kT+s} r(u)\,du\right) N_0 \\ &= e^{kRT} \exp\left(\int_0^{s} r(u)\,du\right) N_0 \\ &= e^{kRT} N(s). \end{aligned}$$

i.e.

$$N(kT+s) = e^{kRT} N(s), \qquad k \geq 0, 0 \leq s < T. \tag{1.11}$$

It follows that $N(t)$ is periodic in t if and only if $R = 0$, i.e. if and only if the average net reproduction rate over a season is zero. Furthermore,

1. If $R > 0$, the $N(t) \to \infty$ as $t \to \infty$: Population explosion,
2. If $R < 0$, the $N(t) \to 0$ as $t \to \infty$: Population collapse.

Chapter 2

Single species, density dependent models

So far we have assumed that net reproductive rate $r(t)$ depends only on external time (e.g. seasonal changes, aging in a cohort, etc). This is valid, for example, when the birth and death rates are heavily influenced by climatic factors, and there is no competition between individuals for important resources (e.g. food, sunlight, space, breeding sites, etc.) If, however, these resources are limited then the more competitors that there are for them, the lower is the expected amount of resources that the average individual obtains. If successful reproduction within the lifetime of an individual depends on the capture of sufficient resources (as it always does in nature) then we may expect that the birth and death rates of the average individual to be influenced by the number of competitors; i.e. a dependence on the density $N(t)$

$$\begin{aligned} b &= \beta(t,N) \\ d &= \delta(t,N). \end{aligned}$$

The expected *qualitative* influences are: (for fixed t)

1. $\beta(t,N)$ decreases as N increases, i.e. $\frac{\partial\beta}{\partial N} < 0$ - more time is spent in searching for food and/or other resources leading to lower fecundity (= ability to produce offspring) and/or higher infant mortality;
2. $\delta(t,N)$ increases a N increases, i.e. $\frac{\partial\delta}{\partial N} > 0$ - lowered life expectancy - greater probability of dying of starvation, or from injuries sustained in competitive fights - greater susceptibility to disease and/or predation due to poorer physiological condition.

We write

$$r = \rho(t,N), \qquad \rho(t,N) = \beta(t,N) - \delta(t,N).$$

with

$$\frac{\partial\rho}{\partial N} = \frac{\partial\beta}{\partial N} - \frac{\partial\delta}{\partial N} < 0.$$

Thus the per capita net growth rate ρ decreases as the density N increases.

Our fundamental equation for population growth thus becomes:

$$\frac{1}{N}\frac{dN}{dt} = \rho(t,N) = \text{per capita net reproductive rate.} \tag{2.1}$$

Suppose now that $N_{\max}$ is the "standing room density" of the population. We expand ρ in the Taylor series:

$$\rho(t,N) = \rho_0(t) + \rho_1(t)\left(\frac{N}{N_{\max}}\right) + \rho_2(t)\left(\frac{N}{N_{\max}}\right)^2 + \cdots$$

Since in all real situations $N(t) \ll N_{\max}$ we can neglect quadratic terms in $N(t)/N_{\max} \ll 1$ and higher to obtain the linear approximation

$$\rho(t,N) = \rho_0(t) + \rho_1(t)\left(\frac{N}{N_{\max}}\right).$$

Since $\frac{\partial\rho}{\partial N} < 0$, we require that $\rho_1(t) < 0$. Let us thus write

$$\rho(t,N) = \rho(t)\left(1 - \frac{N}{K(t)}\right), \tag{2.2}$$

where $\rho(t) = \rho_0(t)$ and $K(t) = -N_{\max}\rho_0(t)/\rho_1(t)$. Here

$\rho(t)$ = **intrinsic growth rate** at time t

$K(t)$ = **environmental carrying capacity** at time t

Substituting (2.2) into (2.1) we obtain the form:

$$\frac{dN}{dt} = \rho(t)N\left(1 - \frac{N}{K(t)}\right). \quad \underline{\text{Time dependent Logistic equation.}} \tag{2.3}$$

For constant $\rho(t), K(t)$ in (2.3), we obtain the **Logistic equation** as a special case:

$$\frac{dN}{dt} = \rho N\left(1 - \frac{N}{K}\right). \tag{2.4}$$

Solution of the time-dependent logistic equation

It is not difficult to integrate (2.3) as follows.

Write $M(t) = N(t)\exp(-\int_0^t \rho(s)\,ds)$. Then $M_0 = M(0) = N(0) = N_0$, and

$$\begin{aligned}
\frac{dM}{dt} &= \left[\frac{dN}{dt} - \rho(t)N(t)\right]\exp(-\int_0^t \rho(s)\,ds) \\
&= \left[\rho(t)N\left(1 - \frac{N}{K(t)}\right) - \rho(t)N(t)\right]\exp(-\int_0^t \rho(s)\,ds) \\
&= -H(t)M(t)^2 \qquad \text{where } H(t) = \frac{\rho(t)}{K(t)}\exp\left(\int_0^t \rho(s)\,ds\right).
\end{aligned}$$

Thus $dM/M^2 = -H(t)dt$ and integrating yields

$$M(t) = \frac{1}{\left\{\frac{1}{M_0} + \int_0^t H(u)\,du\right\}} = \frac{M_0}{1 + M_0 \int_0^t H(u)\,du}.$$

Finally, in terms of N we have

$$\begin{aligned} N(t) &= \frac{N_0 \exp\left(\int_0^t \rho(s)\,ds\right)}{1 + N_0 \int_0^t H(u)\,du}, \\ H(u) &= \frac{\rho(u)}{K(u)} \exp\left(\int_0^u \rho(s)\,ds\right). \end{aligned} \tag{2.5}$$

Example: The Logistic Equation

When $\rho(t) = \rho$ and $K(t) = K$ we have the Logistic equation

$$\frac{dN}{dt} = \rho N \left(1 - \frac{N}{K}\right). \tag{2.6}$$

Now

$$\int_0^t \rho(s)\,ds = \rho t, \ \ H(u) = \frac{\rho}{K} e^{\rho u}, \ \ \int_0^t H(u)\,du = \frac{\rho}{K} \int_0^t e^{\rho u}\,du = \frac{1}{K}(e^{\rho t} - 1).$$

Hence, from (7.1),

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

giving

$$N(t) = \frac{N_0}{\frac{N_0}{K} + (1 - \frac{N_0}{K})e^{-\rho t}}. \tag{2.7}$$

With this explicit expression for the density, it is easy to see that $N(t) \to K$ as $t \to \infty$ for all N_0. Solutions are plotted in Figure 2.1.

Example:

Constant K, time-dependent $\rho(t)$.
We have

$$\frac{dN}{dt} = \rho(t) N \left(1 - \frac{N}{K}\right),$$

which we may rewrite as

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

Rescale time by setting $d\tau = \rho(t)dt$, i.e. $\tau = \int_0^t \rho(u)\,du$. Then we have

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

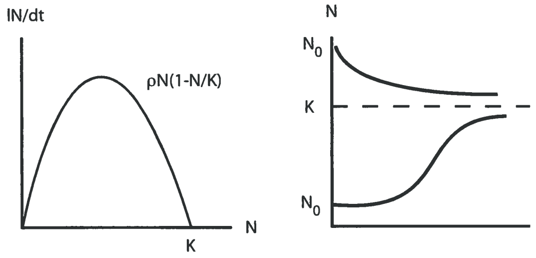

Figure 2.1: Solutions to the logistic equation (2.6)

By the Logistic equation for constant ρ, K this has solution

$$N(\tau) = \frac{N_0}{\frac{N_0}{K} + (1 - \frac{N_0}{K})e^{-\tau}} = \frac{N_0}{\frac{N_0}{K} + (1 - \frac{N_0}{K})\exp\left(-\int_0^t \rho(u)\,du\right)}.$$

If $\rho(t)$ is periodic with period T, then decomposing $t = kT + s$ as usual with $s \in [0, T)$ we get

$$\int_0^t \rho(u)\,du = \int_0^{kT} \rho(u)\,du + \int_{kT}^{kT+s} \rho(u)\,du = kR + \int_0^s \rho(u)\,du,$$

where $R = \int_0^T \rho(u)\,du$. Hence

$$N(kT + s) = \frac{N_0}{\frac{N_0}{K} + (1 - \frac{N_0}{K})e^{-kR}\exp\left(-\int_0^s \rho(u)\,du\right)}.$$

Hence if $R > 0$, $N(t) \to K$ as $t \to \infty$. If $R < 0$ then $N(t) \to 0$ as $t \to \infty$. Finally if $R = 0$ then $N(kT + T + s) = N(kT + s)$, so that $N(t + T) = N(t)$ and so the population is periodic.

Example: Periodic environment

Suppose that $\rho(t)=\rho$ (a constant) and $K(t)$ is a periodic function of period T. Then

$$H(t)=\frac{\rho}{K(t)}e^{\rho t}$$

and

$$\begin{aligned}\int_0^t H(u)\,du &= \rho\int_0^t \frac{e^{\rho u}}{K(u)}\,du \qquad \text{write } t=kT+s && (2.8)\\ &= \rho\sum_{r=1}^{k}\int_{(r-1)T}^{rT}\frac{e^{\rho u}}{K(u)}\,du+\rho\int_{kT}^{kT+s}\frac{e^{\rho u}}{K(u)}\,du && (2.9)\end{aligned}$$

Now let $v=u-(r-1)T$ so that

$$\int_{(r-1)T}^{rT}\frac{e^{\rho u}}{K(u)}\,du=\int_0^T\frac{1}{K(v)}e^{\rho(r-1)T}e^{\rho v}\,dv=e^{\rho(r-1)T}\kappa \text{ where } \kappa=\int_0^T\rho\frac{e^{\rho v}}{K(v)}\,dv=\int_0^T H(v)\,dv.$$

Thus

$$\begin{aligned}\int_0^t H(u)\,du &= \kappa\sum_{r=1}^{k}e^{\rho(r-1)T}+\rho e^{\rho kT}\int_0^s\frac{e^{\rho u}}{K(u)}\,du\\ &= \kappa\sum_{j=1}^{k-1}(e^{\rho T})^j+\rho(e^{\rho T})^k\int_0^s\frac{e^{\rho u}}{K(u)}\,du\\ &= \kappa\left[\frac{1-e^{\rho kT}}{1-e^{\rho T}}\right]+e^{\rho kT}\int_0^s H(u)\,du,\ \ 0\le s<T.\end{aligned}$$

Also

$$\exp\int_0^t\rho\,ds=e^{\rho kT}e^{\rho s}.$$

It now follows from (7.1) that

$$N(kT+s)=\frac{N_0e^{\rho kT}e^{\rho s}}{1+N_0\left(\kappa\left[\frac{1-e^{\rho kT}}{1-e^{\rho T}}\right]+e^{\rho kT}\int_0^s H(u)\,du\right)} \qquad (2.10)$$

Let $k\to\infty$; then

$$\begin{aligned}\lim_{k\to\infty}N(kT+s) &= N_\infty(s)\\ &= \lim_{k\to\infty}\frac{N_0e^{\rho kT}e^{\rho s}}{1+N_0\left(\kappa\left[\frac{1-e^{\rho kT}}{1-e^{\rho T}}\right]+e^{\rho kT}\int_0^s H(u)\,du\right)}\\ &= \frac{e^{\rho s}}{[\kappa/(e^{\rho T}-1)]+\int_0^s H(u)\,du} \qquad 0\le s<T.\end{aligned}$$

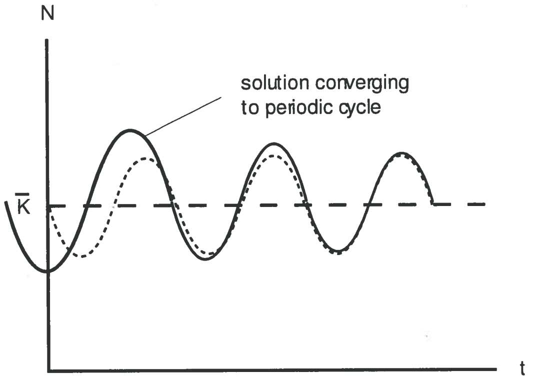

Figure 2.2: Solution for the periodic carrying capacity logistic model

This gives a well-defined periodic function independent of the initial population N_0:

$$\begin{aligned}
N_\infty(s) &= \frac{e^{\rho s}}{[\kappa/(e^{\rho T}-1)] + \int_0^s H(u)\,du} \\
N_\infty(T+s) &= \frac{e^{\rho(T+s)}}{[\kappa/(e^{\rho T}-1)] + \int_0^{T+s} H(u)\,du} \\
&= \frac{e^{\rho(T+s)}}{[\kappa/(e^{\rho T}-1)] + \kappa + \int_T^{T+s} H(u)\,du} \\
&= \frac{e^{\rho(T+s)}}{[\kappa e^{\rho T}/(e^{\rho T}-1)] + \int_0^s H(u+T)\,du} \\
&= \frac{e^{\rho(T+s)}}{[\kappa e^{\rho T}/(e^{\rho T}-1)] + \int_0^s \frac{\rho e^{\rho u} e^{\rho T}}{K(u)}\,du} \\
&= \frac{e^{\rho(T+s)}}{[\kappa e^{\rho T}/(e^{\rho T}-1)] + e^{\rho T}\int_0^s H(u)\,du} = N_\infty(s).
\end{aligned}$$

We therefore have a bounded, periodic, asymptotically stable cycle as a long time solution (see Figure 2.2) which oscillates symmetrically around the average carrying capacity $\bar{K} = \int_0^T K(t)\,dt$.

2.1 Stability Analysis of 1st order odes in 1 dimension

We consider

$$\dot{N} = f(N), \quad N(0) = N_0, \; t \geq 0. \tag{2.11}$$

where $f : \mathbb{R}_+ \to \mathbb{R}$ is smooth.

A steady state of (6.9) is a point N^* such that $f(N^*) = 0$. If $N(t_0) = N^*$ then $N(t) = N^*$ for all $t \geq t_0$ by the uniqueness theorem for solutions to odes. Graphically steady states can be identified by plotting the function f; the steady states are where the function crosses the horizontal axis.

1 Linear Stability Analysis

The idea is to see what happens to solutions starting nearby the steady state: $N(t)$ where $N(0) = N^* + \varepsilon$ for ε small. We write $N(t) = N^* + n(t)$ for the solution satisfying $N(0) = N^* + \varepsilon$ so that $n(0) = \varepsilon$. By Taylor's theorem:

$$N^* \dot{+} n = f(N^* + n) = f(N^*) + f'(N^*)n + f''(N^*)n^2/2! + \cdots$$

To first order in n, using that $f(N^*) = 0$, we obtain, provided $f'(N^*) \neq 0$,

$$\dot{n} = f'(N^*)n.$$

For times t for which small $n(t)$ is small this linear equation captures the same behaviour as the full non-linear equation when n is small, namely

$$n(t) = \exp(f'(N^*)t)\varepsilon.$$

$$\begin{aligned} f'(N^*) > 0 &\quad \Rightarrow \quad \text{solution grows, i.e. is unstable} \\ f'(N^*) < 0 &\quad \Rightarrow \quad \text{solution decays, i.e. is stable} \end{aligned}$$

Thus if $f'(N^*) > 0$ the steady state is called unstable. If $f'(N^*) < 0$ the steady state is called locally stable. If $f'(N^*) = 0$ points are called neutrally stable; then the local stability is determined by

$$\dot{n} = \frac{1}{2} f''(N^*)n^2.$$

The result of perturbing from a neutrally stable steady state depends upon which direction the perturbation goes. For example, if $f''(N^*) > 0$ then a perturbation $N^* - \varepsilon$ is stable in the sense that the solution returns to N^*. A perturbation $N^* + \varepsilon$ continues to grow to the nearest larger steady state.

2.2 Graphical analysis of $\dot{x} = f(x)$

Consider, for $f : \mathbb{R}_+ \to \mathbb{R}$ continuously differentiable

$$\dot{x} = f(x), \;\; x(0) \in \mathbb{R}.$$

By plotting f the complete qualitative behaviour of (6.9) can be examined. As mentioned above the steady states are the zeroes of f and the gradient alternates in sign between them (if it does not vanish), so that the steady states are ...stable, unstable, stable, unstable..., etc.

Exercise What happens if the curve touches the $x-$axis?

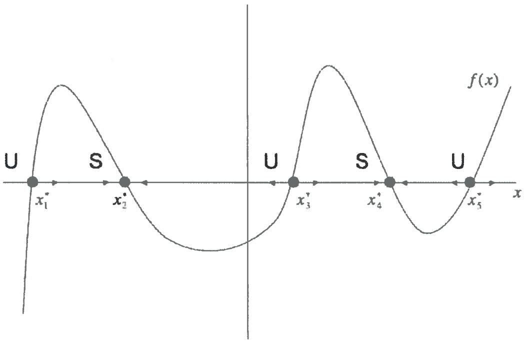

Figure 2.3: Graphical treatment of $\dot{x} = f(x)$, $x \in \mathbb{R}$

Example: Logistic Equation revisited

We may use this technique understand solutions to the Logistic equation. In Figure **??** we see that for $N(0) < K/2$, $N(t)$ must pass through $K/2$ where the slope of $\dot{N}$ (as a function of N) vanishes. This is a point where $\frac{d^2N}{dt^2} = \frac{d}{dt}\dot{N} = \frac{d}{dt}F(N) = F'(N)\dot{N} = F'(N)F(N)$ vanishes. Hence for the $N(t)$ plot on the left, the solution curve has a point of inflexion that occurs where the curve crosses the line at $K/2$. Notice that for any $N(0) > 0$ then $N(t) \to K$ as $t \to \infty$.

Example: Population hit by famine

In a population model, the population density is N, and the per capita birth and death rates are $\beta(N)$ and δ respectively where

$$\beta(N) = \frac{rN}{K + N^2}, \quad \delta(N) = d,$$

where $r, d, K > 0$ are constants.

1. Write down the differential equation for the population growth.

2. Show that there is a unique locally asymptotically steady state population when $\mu := \frac{r}{d\sqrt{K}} < \mu^*$ for some μ^* which you should find. Find and classify the stability of all the steady states of the model when $\mu > \mu^*$.

3. Suppose that initially that $\mu = 3\mu^*/2$ and the population is steady and at its maximum stable size. The population then experiences a severe and sustained famine during which the per capita death rate doubles. After a long period the famine lifts and food resources are restored. Explain what happens to the population during this sequence of events.

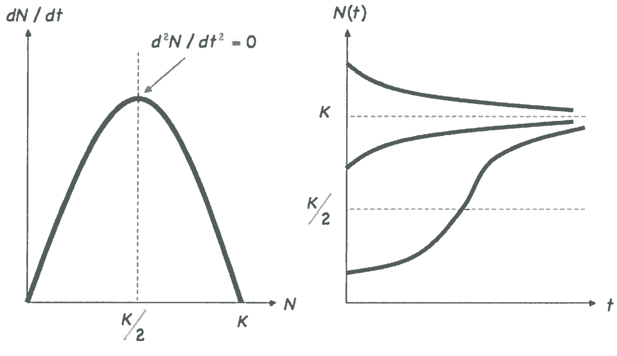

Figure 2.4: Graphical treatment of Logistic equation

Solution:

We have $\dot{N} = N(\beta(N) - \delta(N)) = N\left(\frac{rN}{K+N^2} - d\right)$. The steady states satisfy $N = 0$ and $\frac{rN}{K+N^2} - d = 0$. In the latter case $N_\pm = \frac{r}{2d} \pm \frac{r}{2d}\left(\frac{r^2}{d^2} - 4K\right)^{1/2} = \frac{r}{2D}\left(1 \pm \left(1 - \frac{4}{\mu^2}\right)^{1/2}\right)$. So if $\mu > \mu^* = 2$ we have two non-zero steady states, and for $\mu < 2$ we have no non-zero steady states. From the figure we see that $N = 0$ is unconditionally stable and that N_- is unstable and N_+ is stable (all locally). Now for the famine situation: If initially $\mu = 3\mu^*/2$, so that $\mu > \mu^* = 2$, then the information in the question tells us that the system is settled in the locally stable steady state N_+. Now if d doubles then $\mu = \frac{r}{d\sqrt{K}}$ halves to $\mu = 3\mu^*/4 < \mu^*$ and the two non-zero steady states disappear, leaving the single steady state at $N = 0$. Since in this case $N = 0$ attracts all initial $N > 0$, the population dies out (we are told this happens in a long period). After the famine has lifted, and the food restored, the two non-zero steady states reappear, but the population stays at zero, since the middle steady state is unstable. (NB: Even if the population does no completely die out before the food is restored, the population cannot recover since it remains trapped in the "domain of attraction" of $N = 0$).

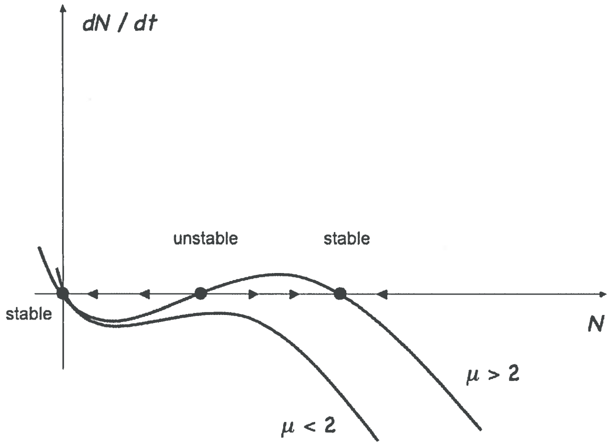

Figure 2.5: Steady states and stability for $\dot{N} = N\left(\frac{rN}{K+N^2} - d\right)$

Chapter 3

Two species models

In this chapter we will study two species N_1 and N_2 occupying the same habitat and interacting, e.g. competing for resources, predation, symbiosis, etc. The general form of the models we will consider is

$$\begin{aligned} \frac{dN_1}{dt} &= F_1(t, N_1, N_2) \\ \frac{dN_2}{dt} &= F_2(t, N_1, N_2). \end{aligned} \tag{3.1}$$

The model (3.1) is a coupled pair of ordinary differential equations, which given initial data $N_1(0) - N_{10}, N_2(0) = N_{20}$ and reasonable assumptions on the regularity of F_1 and F_2 have a unique solution for all $t \geq 0$.

In many cases, F_1, F_2 will not depend explicitly on time, i.e. $F_1 = F_1(N_1, N_2)$ and $F_2 = F_2(N_1, N_2)$. Such systems are called **autonomous**. Thus the vector field (F_1, F_2) giving the velocity of a point (N_1, N_2) is fixed in time. To study such systems we can construct the **phase plane**, i.e. a picture of the solution trajectories mapped out by points $(N_1(t), N_2(t))$ as t varies over $(-\infty, +\infty)$. In particular we identify the steady state populations:

Definition 3 *The steady states of the system (3.1) are the solutions of* $dN_1/dt = 0 = dN_2/dt$*:*

$$\begin{aligned} F_1(N_1, N_2) &= 0 \\ F_2(N_1, N_2) &= 0. \end{aligned} \tag{3.2}$$

The lines upon which trajectories are horizontal or vertical have special names:

Definition 4 *We call* $F_1(N_1, N_2) = 0$ *and* $F_2(N_1, N_2) = 0$ *the* **nullclines** *of (3.1), i.e. they are the curves upon which either* $dN_1/dt = 0$ *or* $dN_2/dt = 0$.

The points where the nullclines (but not different branches of the same nullcline) cross are precisely the steady states. Each phase plane sketch includes the nullcllines, the steady states, and a collection of trajectories that start in varies parts of the plane. The individual trajectories are solutions of

$$\frac{dN_1}{dN_2} = \frac{F_1(N_1,N_2)}{F_2(N_1,N_2)}, \quad N_1(0) = N_{10}, N_2(0) = N_{20}. \tag{3.3}$$

In some cases the complete picture of the solutions of (3.1) can be established just by considering the nullclines, steady states and how the sign of dN_1/dN_2 changes as we go between regions demarked by nullclines. In some cases, however, this level of detail is insufficient, and we must study more carefully how (3.1) behaves near a steady state by considering its linearised form about that steady state.

1 Rules aiding construction of the phase plane

We list the following set of rules that help with the construction of the phase plane of the system (3.1):

1. trajectories cross vertically the nullcline

   $$F_1(N_1,N_2) = 0$$

   since here $dN_1/dt = 0$;

2. trajectories cross horizontally the nullcline

   $$F_2(N_1,N_2) = 0$$

   since here $dN_2/dt = 0$;

3. in regions enclosed by nullclines dN_1/dN_2 has constant sign, i.e. trajectories are either rising or falling;

4. trajectories can only go flat or vertical across nullclines;

5. steady states are where any branches of nullclines $F_1(N_1,N_2) = 0$ and $F_2(N_1,N_2) = 0$ cross.

In some cases further analysis (linear stability analysis of (3.1)) is required to further characterise the detailed behaviour near a steady state, such as, for example, to distinguish between simple non-oscillatory behaviour (e.g. tending directly to a steady state) or oscillatory behaviour (spiralling in to the steady state).

Example: Construction of the phase plane I

Suppose we are given

$$\begin{aligned} dN_1/dt &= F_1(N_1,N_2) = N_2 \\ dN_2/dt &= F_2(N_1,N_2) = -N_1. \end{aligned}$$

This is not a particularly realistic 2 species population model (it is, in fact, a model for a simple harmonic oscillator), but it serves as a simple example of how the phase plane can be reconstructed. The nullclines are

$$N_2 = 0,\ N_1 = 0,$$

i.e. the two axes of the plane. The nullclines cross at the unique steady state $(0,0)$. One may put a series of arrows at various points in the plane that point in the direction of (F_1, F_2) at those points. On $N_1 = 0$ where $\dot{N}_2 = 0$ these arrows point horizontally to the left when $N_2 > 0$ and horizontally to the right when $N_2 < 0$. Similarly on $N_2 = 0$ where $\dot{N}_1 = 0$ the arrows point vertically upwards when $N_1 > 0$ and vertically downwards when $N_1 < 0$. In the interior of the first quadrant $\dot{N}_1 < 0, \dot{N}_2 > 0$ so that the trajectory is moving upwards to the left, and so on. Notice that there is not enough information to know whether the actual trajectories spiral inwards, outwards or otherwise. However, for this simple example, the trajectories satisfy

$$\frac{dN_1}{dN_2} = -\frac{N_2}{N_1},$$

which is a separable ode and can be integrated immediately to yield

$$N_1(t)^2 + N_2(t)^2 = \text{ constant } = N_{10}^2 + N_{20}^2.$$

The solution trajectories are therefore all circles centred on the origin. The origin is neutrally stable, also known as a **centre**.

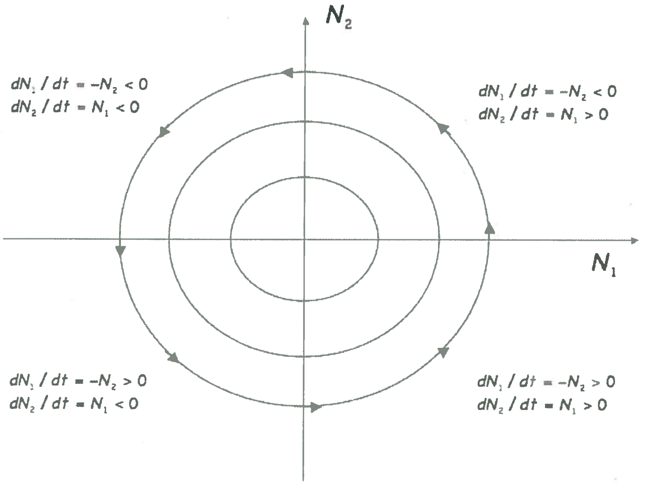

Figure 3.1: The phase plane for $dN_1/dt = -N_2$, $dN_2/dt = N_1$. The inequalities in each quadrant are for the interior of each quadrant, and indicate how N_1 and N_2 are changing along an orbit. Note that without knowing that $N_1^2 + N_2^2$ is conserved, we would not know that the orbits are circles - there is nothing in the sign of the velocities that guarantees that the orbits are not spirals.

2 Behaviour on the boundary of the first quadrant

The kind of ode population models considered in this course are part of a larger class of systems called *Kolmogorov systems*. Such systems take the form $\dot{x}_i = x_i f_i(x_1, \ldots, x_n)$ for $i = 1, \ldots, n$ where n is the number of species and the smooth functions f_i describe the per capita growth rate for the ith species. One of the key properties of such systems is that if at some time t^* we have $x_i(t^*) = 0$ for $i \in J$ (where $J \subset \{1, 2, \ldots, n\}$ is some nonempty set) then $x_i(t) = 0$ for all t and $i \in J$. In our planar models this means that trajectories starting on the axes stay on the axes, and interior trajectories cannot reach the axes in finite time. Hence to find what happens to a trajectory starting at $x_1 = 0$ we simply solve

$$\dot{x}_2 = x_2 f_2(0, x_2), \;\; x_2(0) \;\; \text{given},$$

which is a ode in one variable, as for the single species models of the first 2 chapters. Hence drawing the trajectories on each axes in the phase plane is a relatively simple task for planar Kolmogorov systems.

Example: The Lotka-Volterra competition equations

Recall the Logistic equation for a single speces:

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

Here ρ is the linear birth rate, and K the carrying capacity. For two species N_1, N_2 living in the same habitat, but not interacting, we simply have

$$\begin{aligned} \frac{dN_1}{dt} &= \rho_1 N_1 \left(1 - \frac{N_1}{K_1}\right) \\ \frac{dN_2}{dt} &= \rho_2 N_2 \left(1 - \frac{N_2}{K_2}\right). \end{aligned}$$

The competition in these equations intraspecific (i.e. between the same species). When the species compete with each other (for nesting sites, food, etc.), the interspecific competition is detrimental to both specie's per capita growth rates. The simplest model is to say that the per capital growth rates decrease linearly with the density of the other species. The competition equations then become

$$\begin{aligned} \frac{dN_1}{dt} &= \rho_1 N_1 \left(1 - \frac{N_1}{K_1} - \frac{c_1}{\rho_1} N_2\right) \\ \frac{dN_2}{dt} &= \rho_2 N_2 \left(1 - \frac{N_2}{K_2} - \frac{c_2}{\rho_2} N_1\right), \end{aligned} \tag{3.4}$$

where $c_1, c_2 > 0$ measure the strength of the interspecific competition. To ease calculations, we first set $u_i = N_i / K_i$ for $i = 1, 2$ and $a_{12} = c_1 K_2 / \rho_1$, $a_{21} = c_2 K_1 / \rho_2$. We also introduce a dimensionless time $\tau = \rho_1 t$ and set $\rho = \rho_2/\rho_1$. This gives the simpler set of equations (fewer parameters)

$$\begin{aligned}\frac{du_1}{d\tau} &= u_1(1-u_1-a_{12}u_2)\\ \frac{du_2}{d\tau} &= \rho u_2(1-u_2-a_{21}u_1).\end{aligned}\tag{3.5}$$

Our first step is to locate the nullclines: These are

$$u_1 = 0 \quad \text{and} \quad 1-u_1-a_{12}u_2 = 0 \tag{3.6}$$

$$u_2 = 0 \quad \text{and} \quad 1-u_2-a_{21}u_1 = 0. \tag{3.7}$$

Hence steady states occur at points

$$(u_1^*, u_2^*) = (0,0),\ (1,0),\ (0,1), P = \left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right).$$

This last steady state is only feasible (non-negative populations!) when either[1]

1. $a_{12} > 1$ and $a_{21} > 1$, since then also $1-a_{12}a_{21} < 0$; OR
2. $a_{12} < 1$ and $a_{21} < 1$, since then also $1-a_{12}a_{21} > 0$;

Hence we have either 3 or 4 steady states. As we indicate in Figure 3.2 there are 4 cases to consider:

Case I $a_{12} < 1$ and $a_{21} < 1$;
Case II $a_{12} > 1$ and $a_{21} > 1$;
Case III $a_{12} < 1$ and $a_{21} > 1$;
Case IV $a_{12} > 1$ and $a_{21} < 1$.

Now let us determine what happens on the axes. Suppose first that initially $u_2 = 0$, so that the evolution is on the u_1 axis. We find $u_1(t)$ by solving the first equaton in (3.5) with $u_2 = 0$:

$$\dot{u}_1 = u_1(1-u_1).$$

This is just the Logistic equation with $\rho = 1, K = 1$. Provided $u_1(0) > 0$ we have $u_1(t) \to 1$ as $t \to \infty$. Similarly we find when $u_1(0) = 0$ then $\dot{u}_2 = \rho u_2(1-u_2)$ and hence $u_2(t) \to 1$ as $t \to \infty$ if $u_2(0) > 0$ (see Figure 3.3).

Let us consider the case I in detail (see figure 3.4). We have already dealt with the boundary behaviour. Consider an interior trajectory $A1$. It starts (as drawn, at least) in region $R1$ that lies below both nullclines $1-u_1-a_{12}u_2 = 0$ and $1-u_2-a_{21}u_1 = 0$ so that here $\dot{u}_1 > 0, \dot{u}_2 > 0$ and the trajectory therefore advances in the direction shown. This trajectory has positive gradient provided that it does not cross a nullcline. In fact, all trajectories in $R1$ have positive gradient. Following $A1$ we see that it cannot turn back on itself, and so must cross the nullcline where $\dot{u}_1 = 0$, whereby its gradient becomes negative since then, in $R3$ we

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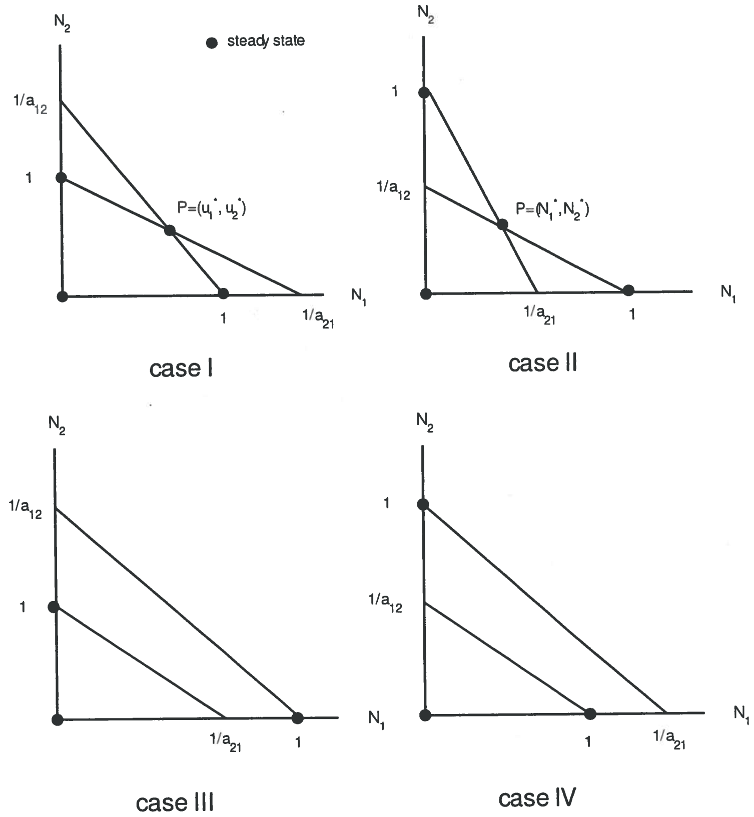
[1] For simplicity here we do not consider the cases where $a_{12} = 1$ and/or $a_{21} = 1$.



case I

case II

case III

case IV

Figure 3.2: The possible nullcline crossings for the Lokta-Volterra model (3.4)

have $\dot{u}_1 < 0, \dot{u}_2 > 0$. The trajectory thus goes vertical across $\dot{u}_1 = 0$ and continues upwards to the left. It cannot leave $R3$, since to re-enter $R1$ is needs to cross it vertically and thus must go horizontal first, and it cannot enter $R2$ since trajectories cross the boundary between $R2$ and $R3$ downwards. Hence $A1$ ends at the interior steady state. A similar argument works for $A2$. In $R3$ the trajectories are above the nullclines $1 - u_1 - a_{12}u_2 = 0$ and $1 - u_2 - a_{21}u_1 = 0$ so that here $\dot{u}_1 < 0, \dot{u}_2 < 0$. $A2$ enters from $R2$ into $R3$ where it is then trapped and must end at the interior steady state. After some practice, it is possible to draw the trajectory directions by noting their directions on the nearby boundary. We can thus construct sketches for the phase planes in each of these 4 cases:

Case I $a_{12} < 1$ and $a_{21} < 1$;
The steady state P attracts all interior trajectories. The remaining 3 steady states are unstable.

Case II $a_{12} > 1$ and $a_{21} > 1$;
The steady state P is unstable. The steady state $(0,0)$ is unstable, and both $(1,0)$ and $(0,1)$ are stable. A separatrix splits the phase plane into two regions; above the seperatrix interior trajectories go to the steady state $(1,0)$ and below they go to the steady state $(0,1)$

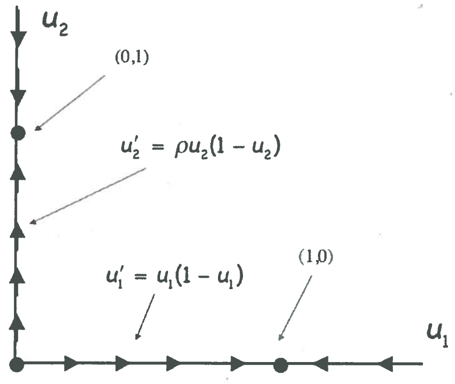


Figure 3.3: The trajectories on the boundary for the phase plane of the Lokta-Volterra model (3.4). These trajectories stay on the axes and tend to the normalised carrying capacities if the initial population is not at the origin.

Case III $a_{12} < 1$ and $a_{21} > 1$;
There is no steady state P. The steady states $(0,0)$ and $(0,1)$ are unstable, but $(1,0)$ is stable and interior trajectories go to this steady state.

Case IV $a_{12} > 1$ and $a_{21} < 1$
There is no steady state P. The steady states $(0,0)$ and $(1,0)$ are unstable, but $(0,1)$ is stable and interior trajectories go to this steady state.

Considering all these possibilities, we see that whatever the parameter values, the population always tends (globally, i.e. whatever the initial populations are) to a finite steady state. In particular there can be no population explosion or total extinction, nor oscillations.

Ecological considerations

In terms of the ecology, we understand the 4 cases as follows:

Case I $a_{12} < 1$ and $a_{21} < 1$;
If the interspecific competition is not too strong the two populations can coexist stably, but at lower populations than their respective carrying capacities. Thus although the species may coexist, the price that they pay for competing with each other is that they do not reach the population density that they would have achieved (i.e. their carrying capacity) with the other species absent;

Case II $a_{12} > 1$ and $a_{21} > 1$;
Interspecific competition is aggressive and ultimately one population wins, while the other is driven to extinction. The winner depends upon which has the starting advantage;

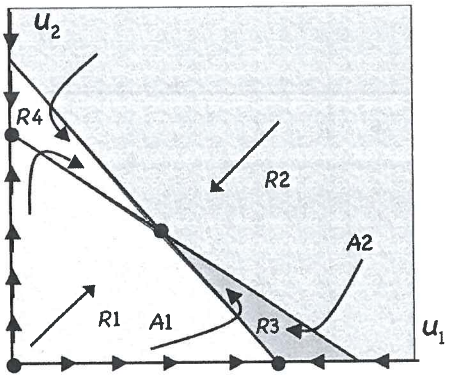


Figure 3.4: Building the phase plane for case I of the competition model (3.4). The (non-zero) null-clines divide the first quadrant into 4 regions $R1-R4$. In each region, the trajectories are curves where the gradient has constant sign. The direction so trajectories can be determined by continuation from the boundaries.

Case III, IV $a_{12} < 1$ and $a_{21} > 1$ or $a_{12} > 1$ and $a_{21} < 1$;
Interspecific competition of one species dominates the other and, since the stable node in each case is globally stable, the species with the strongest competition always drives the other to extinction.

3 Predator-Prey systems

In 1926 Volterra came up with a model to describe the evolution of predator and prey fish populations in the Adriatic. Let $N(t)$ denote the prey population and $P(t)$ the predators. He assumed that

1. in the absence of predators the per capita prey growth rate was constant, but fell of linearly as a function of predator population when predation was present;
2. in the absence of prey the per capita growth rate of the predator was contsant (and -ve), and increased linearly with the prey population when prey was present.

Thus

$$\begin{aligned} \frac{1}{N}\frac{dN}{dt} &= a - bP \\ \frac{1}{P}\frac{dP}{dt} &= cN - d \end{aligned} \tag{3.8}$$

where $a, b, c, d > 0$ are constants. It turns out that this model has an explicit integration. We find that

$$\frac{(-d+cN)}{N}\frac{dN}{dt} - \frac{(a-bP)}{P}\frac{dP}{dt} = 0,$$

or

$$\frac{d}{dt}\{cN + bP - d\log N - a\log P\} = 0.$$

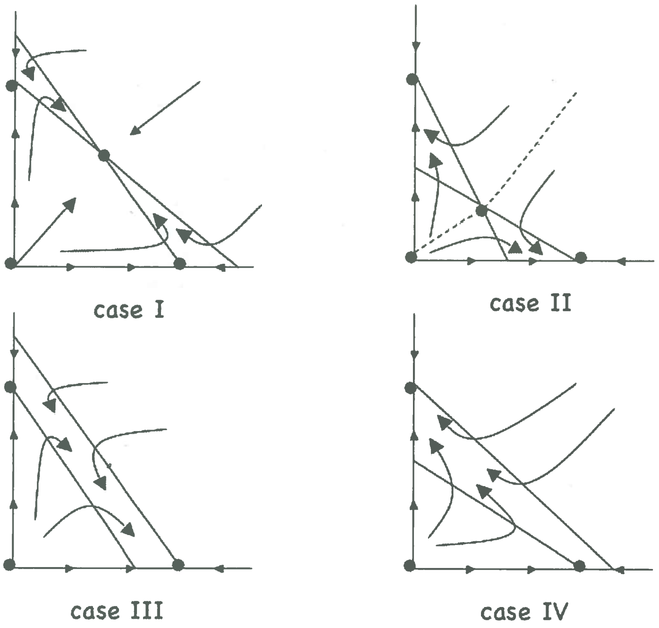


Figure 3.5: The 4 topologically distinct phase planes for the Lokta-Volterra model (3.4)

If we set

$$H(N,P) = cN + bP - d\log N - a\log P,$$

then all trajectories $(N(t),P(t))$ evolve so that $H(N(t),P(t)) = H(N(0),P(0)) =$ constant , i.e they are the projections of the the level curves of H. Now we claim that H is a concave function. Note that

$$H_{NN} = d/N^2,\ H_{PP} = a/P^2,\ H_{NP} = H_{PN} = 0,$$

so that $H_{NN}H_{PP} - H_{NP}^2 = ad/(NP)^2 > 0$ and $H_{NN} > 0, H_{PP} > 0$, and hence H is convex. It is strictly convex for $NP > 0$. The minimum of H occurs where $\nabla H = 0$, i.e. where

$$c - \frac{d}{N} = 0 = b - \frac{a}{P} \Rightarrow (N,P) = \left(\frac{d}{c}, \frac{a}{b}\right).$$

Notice that this corresponds to the unique steady state of the system (3.8). Since H is strictly convex with a unique minimum in the positive quadrant, every trajectory must be a closed curve. Thus the orbits are a one-parameter (the value of H) set of closed curves starting at the steady state.

The Lokta-Volterra equations are actually canonically Hamiltonian (in appropriate coordinates) and so are not structurally stable. This means that a small change in the model will not typically lead to another Hamiltonian system, nor one where the phase plane is topologically equivalent. In general we will end up

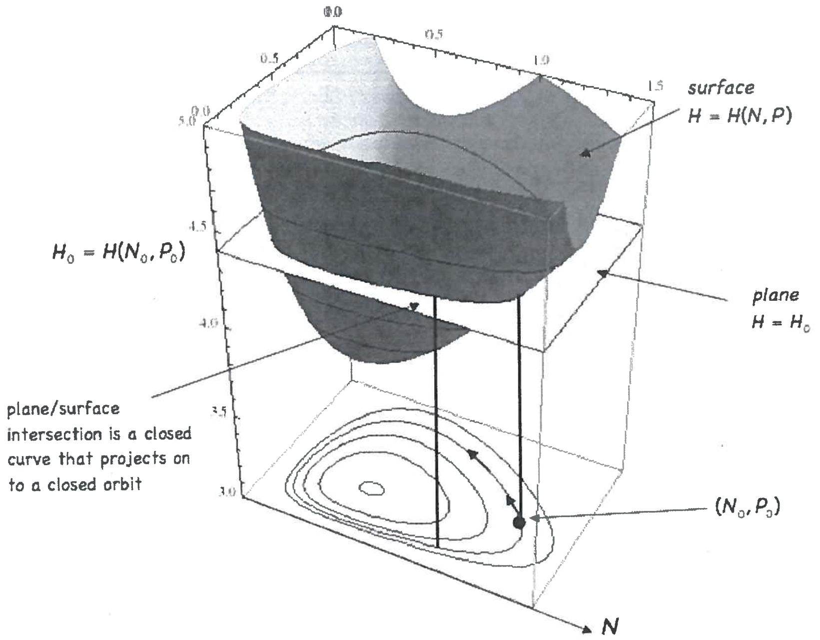


Figure 3.6: Orbits for the classic predator-prey model. The orbits are the level sets of H, i.e. each orbit is a projection of the intersection of a plane $H = H_0$ with the surface $H = H(N,P)$. NB: This figure, and many of the figures in the notes were produced using the CurvesGraphics Mathematica package by Gianluca Gorni, Department of Mathematics and Computer Science, University of Udine, Italy.

with a dissipative system. For a biological system life is the constant struggle against increasing entropy where irreversible processes play an important role. In this light, a Hamiltonian system cannot model a 'living' system. There are several points of criticism worth noting for the Volterra-Lokta model:

1. There is no possibility of either population being driven to extinction;

2. Changing the birth and death rates does nothing but change the period of the oscillation - i.e. noone can dominate;

3. For certain ecological conditions (fitness of species, etc.) one would expect one species to win regardless of initial conditions, but this does not happen.

We will now take a digression into *Linear stability analysis* for pairs of autonomous ODEs.

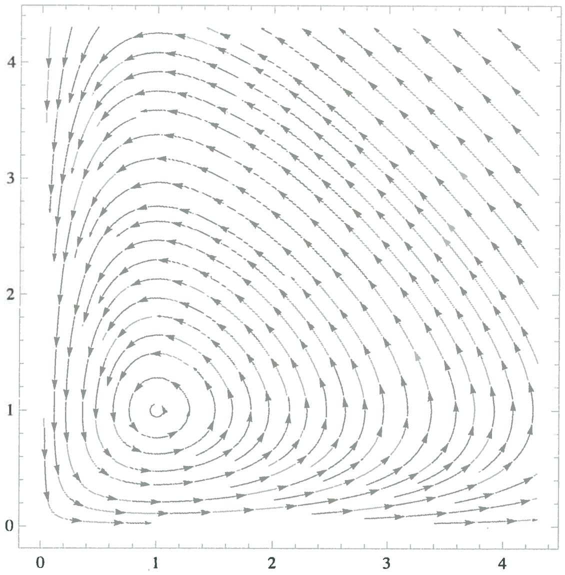


Figure 3.7: Nested periodic orbits for the classic predator-prey model. Boundary trajectories are not shown. All interior trajectories a periodic and enclose the unique interior steady state at $(1,1)$.

3.1 Digression: Linear stability analysis of planar odes

In many of the models we meet in the course, we will need to study the behaviour of trajectories close to steady states for the system

$$\begin{aligned} \frac{dx}{dt} &= f(x,y) \\ \frac{dy}{dt} &= g(x,y). \end{aligned} \tag{3.9}$$

We assume that $P = (a,b)$ is a steady state of (3.9). Thus

$$f(a,b) = 0 = g(a,b). \tag{3.10}$$

Consider the evolution of a trajectory close to P, and write $x(t) = a + X(t)$ and $y(t) = b + Y(t)$. We may expand in (3.9) using the Taylor expansion:

$$\begin{aligned} \frac{dX}{dt} &= f(a,b) + f_x(a,b)X + f_y(a,b)Y + \cdots \\ \frac{dY}{dt} &= g(a,b) + g_x(a,b)X + g_y(a,b)Y + \cdots . \end{aligned}$$

Using (3.10), this becomes

$$\begin{aligned}\frac{dX}{dt} &= f_x(a,b)X + f_y(a,b)Y + \cdots \\ \frac{dY}{dt} &= g_x(a,b)X + g_y(a,b)Y + \cdots .\end{aligned}$$

Close to P, $|X(t)|, |Y(t)| \ll 1$ this system is well-approximated by the linearised version obtained by neglecting second order terms in X, Y:

$$\begin{aligned}\frac{dX}{dt} &= f_x(a,b)X + f_y(a,b)Y \\ \frac{dY}{dt} &= g_x(a,b)X + g_y(a,b)Y.\end{aligned} \tag{3.11}$$

Notice that since we are neglecting higher order than linear terms, the linear approximation will only potentially give a good indication of the full nonlinear system while $X(t), Y(t)$ remain small.

Now let $\mathbf{X}(t) = (X(t), Y(t))^T$ and

$$M = \begin{pmatrix} f_x(a,b) & f_y(a,b) \\ g_x(a,b) & g_y(a,b) \end{pmatrix}.$$

Then (6.12) can be rewritten in matrix form:

$$\frac{d\mathbf{X}(t)}{dt} = M\mathbf{X}(t). \tag{3.12}$$

This has steady state $(0,0)$ (which corresponds to $(x,y) = (a,b)$). For a trajectory of the linearised system (3.12) starting at $\mathbf{X}(0) = \mathbf{X}_0$,

$$\mathbf{X}(t) = \exp(Mt)\mathbf{X}_0.$$

If M has two distinct eigenvalues λ_1, λ_2 with corresponding eigenvectors $\mathbf{v}_1, \mathbf{v}_2$ then

$$\mathbf{X}(t) = \alpha e^{\lambda_1 t}\mathbf{v}_1 + \beta e^{\lambda_2 t}\mathbf{v}_2, \tag{3.13}$$

where α, β are defined by the decomposition $\mathbf{X}_0 = \alpha\mathbf{v}_1 + \beta\mathbf{v}_2$ (using linear independence of $\mathbf{v}_1, \mathbf{v}_2$). When the two eigenvalues are equal (and therefore real) we have

$$\mathbf{X}(t) = e^{\lambda t}(\mathbf{X}_0 + ct\mathbf{v}) \tag{3.14}$$

for some real c (which may be zero).

To find the (local) stability of the steady state (a,b) we examine the dynamics of (3.12) which has solution (3.13). If (a,b) is stable then for small $\mathbf{X}_0$, the solution $\mathbf{X}(t)$ will eventually decay to the origin $(0,0)$ and this happens, according to (3.13), when both eigenvalues have negative real parts.

Let us list the various possibilities for behaviour near a steady state

1. $\lambda_1 \neq \lambda_2 \in \mathbb{R}$
   (a) $\lambda_1 < \lambda_2 < 0$ - stable node.

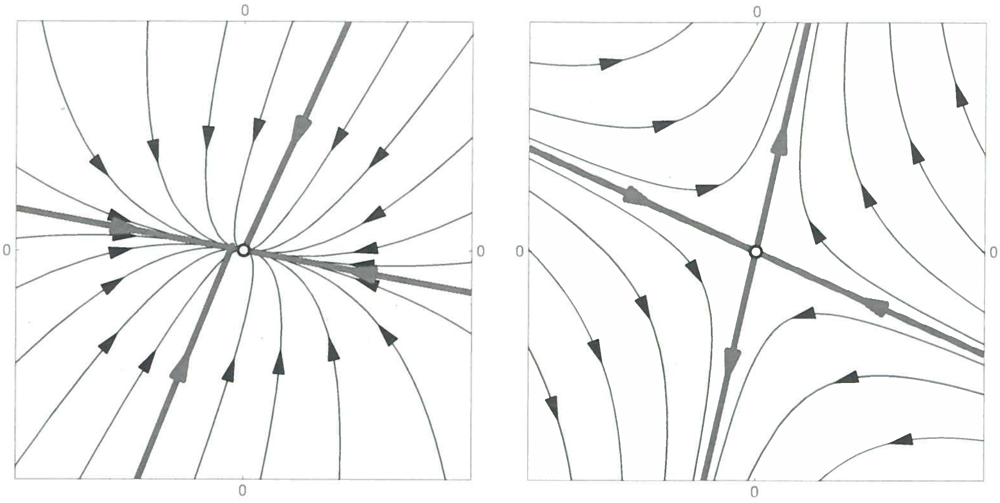


Figure 3.8: Linear stability for real eigenvalues: (i) $\lambda_1, \lambda_2 < 0$ (stable node) and (ii) $\lambda_1\lambda_2 < 0$ (saddle). The thick (red) lines are in the direction of the eigenvectors.

(b) $\lambda_1 > \lambda_2 > 0$ - unstable node.

(c) $\lambda_1\lambda_2 < 0$ - saddle (unstable)

(The reader may wish to ask themselves what happens when $\lambda_1\lambda_2 = 0$)

2. Complex eigenvalues
Then $\lambda_1 = \mu + iw, \lambda_2 = \mu - iw$ and

$$\mathbf{X}(t) = \Re\{e^{\mu t}(\alpha \mathbf{v}_1 e^{iwt} + \beta \mathbf{v}_2 e^{-iwt})\}$$

Hence we have spirals. If $\mu < 0$ the trajectories go to the steady state (stable spiral), for $\mu > 0$ they leave (unstable spiral). When $\mu = 0$ the linearised system gives concentric ellipses (but caution: we need to consider the nonlinear terms to get true picture as this linear system is not structurally stable).

3. $\lambda_1 = \lambda_2$ Now the Jordan form of M is

$$\begin{pmatrix} a & 0 \\ b & a \end{pmatrix}.$$

There are two cases:

(a) $b = 0$
Then we have what is known as a ‘star’ - all trajectories approach the origin along straight lines (all lines through origin are eigenvectors) when $a < 0$, and leave origin when $a > 0$.

(b) $b \neq 0$

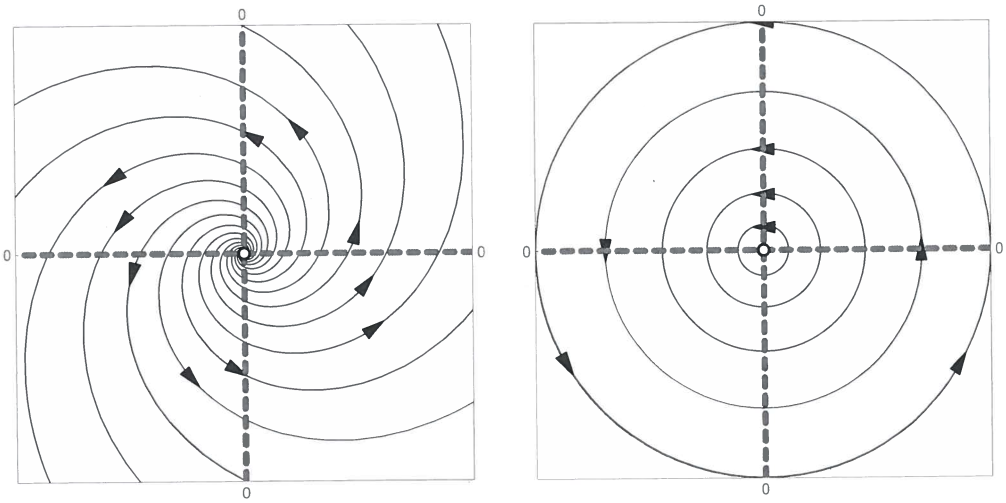


Figure 3.9: Linear stability for complex eigenvalues: (i) $\lambda = \mu \pm iw, \mu > 0$ (unstable spiral) and (ii) $\lambda = \pm iw$ (centre).

> Then there is only one linearly independent eignevector and we have behaviour as shown in Figure 4.12).

The following lemma is very useful when determining the nature of eigenvalues. Recall that the trace of a matrix is the sum of its diagonal elements.

Lemma 1 *Let M be a 2×2 matrix with eigenvalues λ_1, λ_2. Then*

$$\lambda_1 + \lambda_2 = \text{Trace}\, M, \tag{3.15}$$

$$\lambda_1 \lambda_2 = \det M. \tag{3.16}$$

Proof: Let $M = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$. Then the characteristic equation for the eigenvalues λ reads $\det(M - \lambda I) = 0$ which becomes

$$\lambda^2 - (a+d)\lambda + (ad - bc) = 0,$$

or equivalently

$$\lambda^2 - \text{Trace}\, M\lambda + \det M = 0.$$

On the other hand, if $\lambda^2 - \text{Trace}\, M\lambda + \det M$ has roots λ_1, λ_2 then $\lambda^2 - \text{Trace}\, M\lambda + \det M = (\lambda - \lambda_1)(\lambda - \lambda_2)$. Multiplying out the last product and comparing coefficients in λ gives the desired formulae.

Corollary 1 *Let $S = (a,b)$ be a steady state of some planar ode and M the 2×2 real stability matrix at (a,b).*

1. *If $\det M < 0$ then M has eigenvalues of opposite sign and S is a saddle;*

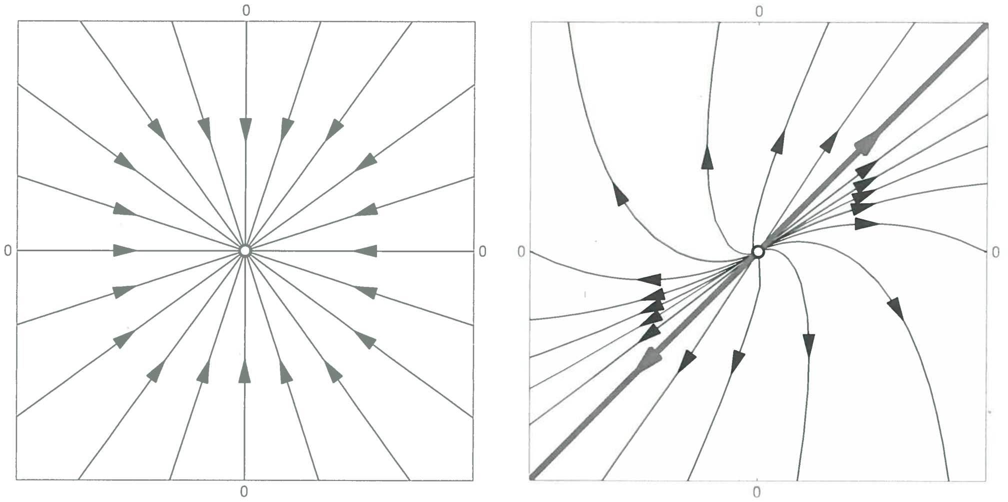


Figure 3.10: Linear stability for equal eigenvalues: (i) Jordan form $\begin{pmatrix} a & 0 \\ 0 & a \end{pmatrix}$ and (ii) Jordan form $\begin{pmatrix} a & 0 \\ b & a \end{pmatrix}$ $(b \neq 0)$.

2. *If* $\det M > 0$ *and Trace* $M < 0$ *then the real parts of the eigenvalues of* M *are negative and* S *is locally stable.*

3. *If* $\det M > 0$ *and Trace* $M > 0$ *then the real parts of the eigenvalues of* M *are positive and* S *is unstable.*

4. *If* $\det M > 0$ *and* $(\text{Trace } M)^2 \geq 4 \det M$ *then* S *is a node and if* $(\text{Trace } M)^2 < 4 \det M$ *then* S *is a spiral.*

1 Linear stability analysis of the LV competition model

We will now demonstrate how the above linear stability analysis works with the competition model:

$$\begin{aligned} \frac{du_1}{d\tau} &= f(u_1,u_2) = u_1(1-u_1-a_{12}u_2) \\ \frac{du_2}{d\tau} &= g(u_1,u_2) = \rho u_2(1-u_2-a_{21}u_1) \end{aligned} \tag{3.17}$$

The first thing we have to do is compute the matrix

$$M = \begin{pmatrix} f_{u_1} & f_{u_2} \\ g_{u_1} & g_{u_2} \end{pmatrix}.$$

We find that at the point (u_1,u_2) that

$$M_{(u_1,u_2)} = \begin{pmatrix} 1-u_1-a_{12}u_2-u_1 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1-u_2-a_{21}u_1)-\rho u_2 \end{pmatrix}. \tag{3.18}$$

There are always the 3 steady states $(0,0)$, $(1,0)$ and $(0,1)$. There may be a fourth and interior steady state.

1. $(u_1,u_2)=(0,0)$. Here
$$M_{(0,0)}=\begin{pmatrix}1 & 0\\ 0 & \rho\end{pmatrix}.$$
Since the eigenvalues of a triangular matrix are its diagonal elements, we see that the eigenvalues of the linear stability matrix at the origin are $1,\rho$. Since these are both positive we conclude that $(0,0)$ is an unstable node.

2. $(u_1,u_2)=(1,0)$. Here
$$M_{(1,0)}=\begin{pmatrix}-1 & -a_{12}\\ 0 & \rho(1-a_{21})\end{pmatrix}.$$
Thus the eigenvalues are $-1,\rho(1-a_{21})$ and hence $(1,0)$ is a stable node if $a_{21}>1$ and a saddle if $a_{21}<1$.

3. $(u_1,u_2)=(0,1)$. Here
$$M_{(0,1)}=\begin{pmatrix}1-a_{12} & 0\\ -\rho a_{21} & -\rho\end{pmatrix}.$$
Thus the eigenvalues are $1-a_{21},-\rho$ and hence $(0,1)$ is a stable node if $a_{12}>1$ and a saddle if $a_{12}<1$.

Finally, when the interior steady state (u_1^*,u_2^*) exists, so that $a_{12},a_{21}>1$ or $a_{12},a_{21}<1$, we obtain
$$M_{(u_1^*,u_2^*)}=\begin{pmatrix}(1-u_1^*-a_{12}u_2^*)-u_1^* & -a_{12}u_1^*\\ -\rho a_{21}u_2^* & \rho(1-u_2^*-a_{21}u_1^*)-\rho u_2^*\end{pmatrix}.$$
Now since (u_1^*,u_2^*) is an interior steady state $1-u_1^*-a_{12}u_2^*=0=1-u_2^*-a_{21}u_1^*$ and hence the bracketed expressions in the last matrix vanish and we have
$$M_{(u_1^*,u_2^*)}=\begin{pmatrix}-u_1^* & -a_{12}u_1^*\\ -\rho a_{21}u_2^* & -\rho u_2^*\end{pmatrix}. \tag{3.19}$$
Notice that we left M in the form (3.18) in order to obtain the simple form of the stability matrix at the the interior steady state in (3.19). In order to determine the nature of the eigenvalues of $M_{(u_1^*,u_2^*)}$ we use Corollary 1. We see that Trace $M=-u_1^*-\rho u_2^*<0$ and $\det M=\rho u_1^*u_2^*(1-a_{12}a_{21})$. Hence if $a_{12}<1,a_{21}<1$ then S is locally stable (we do not bother to distinguish between a focus and a spiral), and if $a_{12}>1,a_{21}>1$ then S is a saddle.

These calculations can be checked by referring back to the phase plane plots in Figure 3.5.

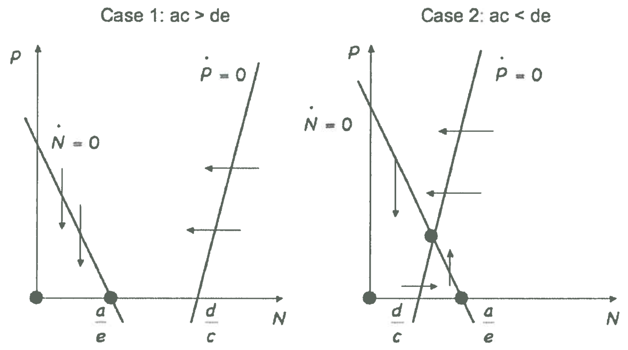


Figure 3.11: The possible nullcline crossings for the predator-prey Lokta-Volterra model with intraspecific competition (Equations (3.20), (3.21)).

Example: Predator-Prey with intraspecific competition

Now we consider the classic Predator-Prey model with additional interactions, namely intraspecific competition.

$$\begin{aligned} \dot{N} &= N(a-eN-bP) &= F(N,P) \qquad (3.20)\\ \dot{P} &= P(-d-fP+cN) &= G(N,P). \qquad (3.21) \end{aligned}$$

Thus we have the original predator-prey model with the intraspecific competition terms $-eN^2$ and $-fP^2$ added. Recall that in the original model $e=0, f=0$ and we obtain a continuum of periodic orbits around the interior steady state. What happens when $e>0, f>0$?

Let us consider the nullclines. These are solutions to:

$$\dot{N}=0: \quad N=0 \text{ or } a-eN-bP=0,$$

$$\dot{P}=0: \quad P=0 \text{ or } -d+cN-fP=0.$$

The two possible cases are plotted in Figure 3.11. In case 1, there are only two steady states $(0,0)$ and $(a/e,0)$, but when $ac>de$ there is a third non-zero steady state, say (N^*,P^*).

On the boundary $P=0$ we have $\dot{N}=N(a-eN)$ so the trajectories tend to $N=a/e$ if $N(0)\neq 0$. On $N=0$, we have $\dot{P}=-P(d+fP)\leq 0$ with equality if and only if $P=0$, so that trajectories tend to $P=0$.

In case 1, it is possible to fill in the trajectories to complete the phase space plot. However, in case 2, while it is clear that the trajectories near the non-zero steady state cycle around the steady state, it is not obvious whether these trajectories are closed paths or spirals (or something else?). To complete the phase plots we need to determine the correct behaviour of the trajectories near to steady states, i.e. perform the linear stability analysis.

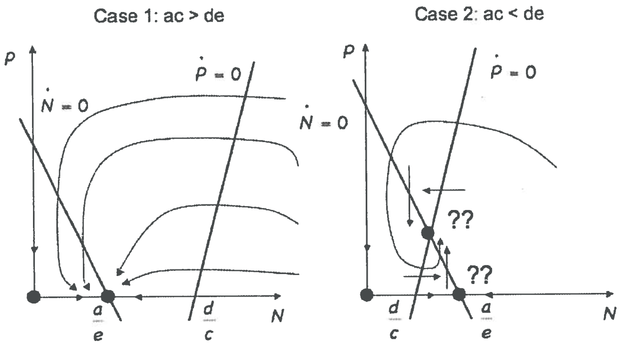


Figure 3.12: The possible phase space plots for the predator-prey Lokta-Volterra model with intraspecific competition (Equations (3.20), (3.21)).

For the stability matrix we obtain

$$M = \begin{pmatrix} F_N & F_P \\ G_N & G_P \end{pmatrix} = \begin{pmatrix} (a-eN-bP)-eN & -bN \\ cP & (-d-fP+cN)-fP \end{pmatrix}.$$

Hence at $(0,0)$ we have

$$M_{(0,0)} = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix},$$

so that the eigenvalues $a, -d$ are of opposite sign showing that the origin is a saddle. At $(a/e, 0)$ we have

$$M_{(a/e,0)} = \begin{pmatrix} -a & -ba/e \\ 0 & -d+ca/e \end{pmatrix},$$

The eigenvalues of $M_{(a/e,0)}$ are thus $-a<0$ and $-d+ca/e$. In the case $ca<de$, so that there is no interior steady state, $(a/e,0)$ is a stable node, whereas when $ca>de$, so that the interior steady state exists, $(a/e,0)$ is a saddle.

Finally when $ca > de$ we consider the linear stability of (N^*, P^*). We have

$$M_{(N^*,P^*)} = \begin{pmatrix} -eN^* & -bN^* \\ cP^* & -fP^* \end{pmatrix},$$

Trace $M_{(N^*,P^*)} = -eN^* - fP^* < 0$ and $\det M_{(N^*,P^*)} = N^*P^*(ef + bc) > 0$, so that the eigenvalues of $M_{(N^*,P^*)}$ have negative real parts. Hence when it exists (N^*, P^*) is locally stable.

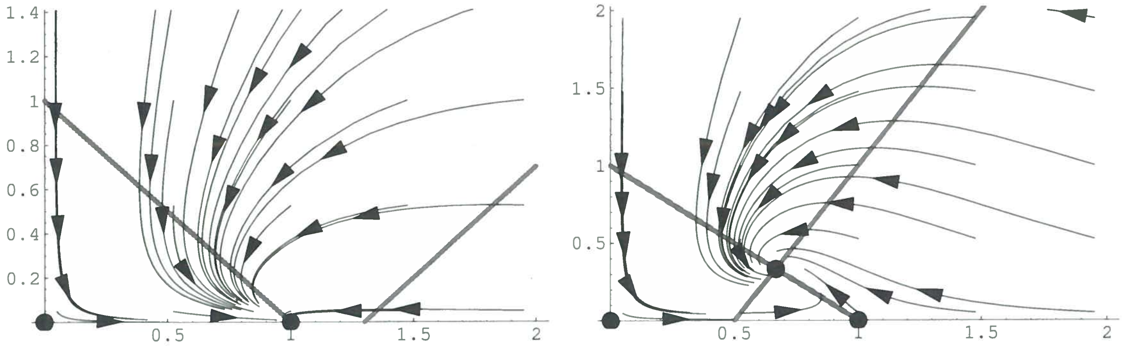


Figure 3.13: Phase space plots for the predator-prey Lokta-Volterra model with intraspecific competition (Equations (3.20), (3.21)). Left $ca < de$ where there are just two steady states, right $ca > de$ where the interior steady state now exists and is locally stable with a spiral.

MATH3506 Mathematical Ecology Problem Sheet 1

NB: Coursework does not count towards the exam - it is up to you whether you do it!

1. Find the expected time to the first event when $p(t) = \lambda t$, $\lambda > 0$. Is this longer or shorter than the corresponding time for $p(t) = \lambda$?

   [Recall that $\int_0^\infty e^{-u^2}\,du = \frac{\sqrt{\pi}}{2}$].

2. Suppose that the birth-rate, $b(t) = e^{-\lambda t}$, for some $\lambda > 0$. That is, the average fecundity (ability to produce offspring) of a typical individual is declining exponentially over time.

   Show that there is a non-zero residual probability that an individual from such a population will *never* give birth, even if it lives forever. What is the probability that an individual will give birth sometime?

   Given that individuals from this population does give birth sometime, what is the probability that no such event happens in the interval $[0, t)$, conditional on this assumption?

   [Recall that, if A and B are events with probabilities $P(A)$ and $P(B)$, and $P(A|B)$ is the conditional probability of A given B, then $P(A \cap B) = P(A|B)P(B)$, where $A \cap B$ is the event A *and* B.]

3. In lectures we derived a differential equation for the mean population $N(t)$ for a model where the birth rate was $b(t)$ (i.e. the probability that an individual gives birth in $[t, t + \delta t)$ is $b(t)\delta t$ to first order in δt (small)). For the model we derived, find explicit expressions for $p_k(t)$, the probability that the population is size k at time t.

4. Let the death rate be $d(t)$, so that the net intrinsic growth rate (per individual) is $r(t) = b(t) - d(t)$. Using $p_k(t)$ to denote the probability that the population is size k at time t, derive a new set of differential equation for $p_k(t)$ for each $k = 0, 1, \ldots$. Hence show that the mean $N(t) = \sum_{k=0}^\infty k p_k(t)$ is given by $N(t) = \exp\left(\int_0^t r(s)\,ds\right) N(0)$.

5. When $r(t) = e^{-\lambda t}$, so that the net intrinsic growth rate goes to zero as $t \to \infty$, what happens to the mean population size in the long run?

(Last updated October 8, 2012)

MATH3506 Problem Sheet 2

NB: Coursework does not count towards the exam - it is up to you whether you do it!

1. Find $N(t)$, the solution to the time-dependent equation

$$\frac{dN}{dt} = A\cos(\omega t)\, N \left(1 - \frac{N}{K}\right), \quad (K > 0, \text{a constant}).$$

   What can you say about $N(t)$ as $t \to \infty$? What are the maximum and minimum populations?

2. A population with continuous generations has constant per capita death-rate $d(N) = \delta > 0$, but density dependent per capita birth-rate, $b = \beta(N)$, where

$$\beta(N) = \frac{rN}{K + N^2}.$$

   Plot the function β as a function of $N > 0$. Observe that the associated net-reproductive rate $\rho(N)$ does *not* satisfy the assumption made in the lectures that $\rho'(N) < 0$. Why might you nevertheless regard these conditions as biologically reasonable? [Think about how very small populations might be distributed in their territory, and what consequences this might have for their breeding success.]

   Study the dynamics of this population, i.e. according to $\frac{dN}{dt} = N(\beta(N) - \delta)$. Find the possible steady states and their stability for different values of r, δ, K, and make an ecological interpretation of your results.

3. The dynamics of 2 species in a closed habitat is given by the system

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} + b_{12}\frac{N_2}{K_2}\right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} + b_{21}\frac{N_1}{K_1}\right) \end{aligned}$$

   where $b_{12} \geq 0$ and $b_{21} \geq 0$. What kind of interactive behaviour is implied by the model? Scale the equations appropriately and plot the phase plane for $b_{12}b_{21} > 1$ and $b_{12}b_{21} < 1$. Comment on your results in an ecological context.

(Last updated October 19, 2010.)

CENTRE MAY NOT BE A CENTRE

We consider

$$\begin{aligned} \dot{x} &= \mu x - y - x(x^2+y^2) \\ \dot{y} &= x + \mu y - y(x^2+y^2). \end{aligned} \tag{1}$$

By multiplying the first equation by x and the second by y we obtain

$$\begin{aligned} x\dot{x} &= \mu x^2 - xy - x^2(x^2+y^2) \\ y\dot{y} &= yx + \mu y^2 - y^2(x^2+y^2). \end{aligned}$$

Adding we get

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

But $x\dot{x} + y\dot{y} = \frac{1}{2}\frac{d}{dt}(x^2+y^2)$, so setting $r = \sqrt{x^2+y^2}$ and simplifying, we obtain $\dot{r} = \mu r - r^3$. By using $\tan\theta = y/x$ we also find that $\dot{\theta} = 1$. The set $r = 1$ i.e. $\{(x,y) : x^2+y^2 = \sqrt{\mu}\}$, i.e. a circle radius $\sqrt{\mu}$, is invariant (i.e trajectories on the circle stay on the circle). Also $(x,y) = (0,0)$ is the unique steady state, since where $\dot{x} = 0 = \dot{y}$ we have $\mu(x^2+y^2) - (x^2+y^2)^2 = r(\mu - r^2) = 0$ which can only happen if $r = 0$ or $r = \sqrt{\mu}$. $r = \sqrt{\mu}$ is a circle and clearly not a steady state (it is not a point!), which leaves $r = 0$ as the only possibility. Hence $(0,0)$ is the unique steady state. It is not difficult to see that any trajectory is either the unique steady state $(0,0)$, the unit circle, or a spiral that tends towards the circle radius $\sqrt{\mu}$.

On the other hand, if we do the linear stability analysis at the steady state, we get for the linear system

$$\dot{X} = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix} X = MX. \tag{2}$$

The matrix M has eigenvalues $\lambda = \mu \pm i$. When $\mu = 0$ the eigenvalues both have zero real part and the linear stability analysis predicts a centre (concentric circles around the steady state in this example). However, the above analysis, which solves the full nonlinear equations shows, setting $\mu = 0$, that $\dot{r} = -r^3$, so that there is now no invariant circle and trajectories just spiral into the origin.

Hence the linear stability analysis does not provide the correct prediction of the behaviour of (1) close the the steady state. The linear stability analysis has been done correctly, it is just that whenever the real part of one or more of the eigenvalues of M vanishes the linear stability analysis cannot be used - it is not reliable. It *may* give the correct answer (e.g. as for the predator-prey model $\dot{N} = N(a - bP), \dot{P} = P(-d + cN)$), but *not always.* The problem is that when the real parts of an eigenvalue vanishes, the nonlinear higher order terms which have been thrown away in constructing the linear system cannot be thrown away - they play an import role in determining the trajectories.

On the other hand if the real parts of all eigenvalues are nonzero then it will correctly predict the trajectories close to a steady state.

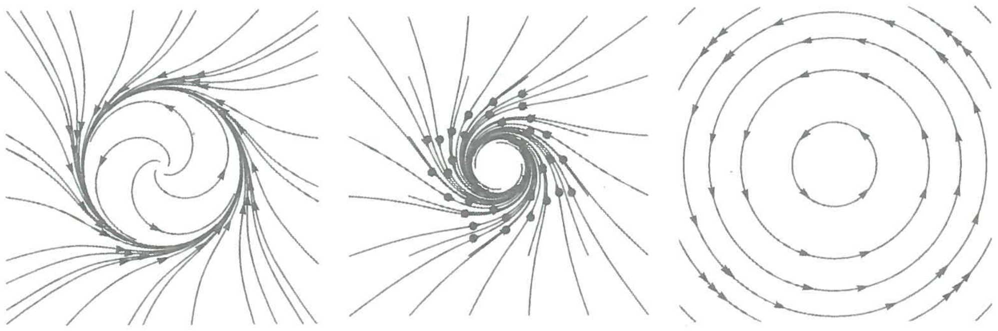


FIGURE 1. From left to right: $\mu > 0$ (spirals onto circle), $\mu = 0$ (spirals to origin) for the full system (1), $\mu = 0$ for the linear system (2).

Mathematical Ecology MATH3506 13/1/15
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Basic Outline Aim is to build and analyse a series of mathematical models of population growth, with some realism traded with complexity

Types of models

1) Continuous time models r.o.c of population is a function which depends on various things

$$\dot{\underline{N}} = \underline{F}(\underline{N}, \underline{\lambda})$$

Here $\underline{N} = (N_1, \dots, N_n)$ n = # species

N_i is a real number representing population density = $\frac{\text{no. of indiv.}}{\text{area}}$

$\underline{\lambda}$ is a vector of parameters
e.g. birth rates, death rates, amount of food etc.

2) Discrete time models
Here one time ~~limit~~ unit is typically a generation
Non-overlapping generations ⟹ parents are all dead before children offspring give birth

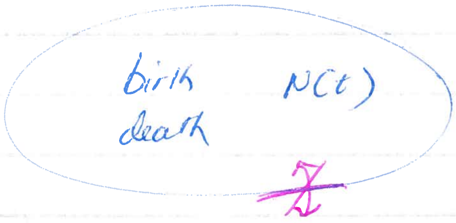
$$\underline{N}_{t+1} = \underline{f}(\underline{N}_t)$$ just an iteration - can be v. complicated
e.g. logistic map
may exhibit chaos

3) Age-structured models where we split population in to distinct age groups (i.e. more fertile at young, stronger when older)

4) Predator-prey competition, cooperation - flowers + bees
(2 populations)

5) General Lotka - Volterra models - v. powerful if right

1 Single species; continuous time



No immigration
No emigration
Closed system

Ignore movement in to or out of the habitat of the population
Looking for $\underline{\dot{N}} = F(N, \underline{\lambda})$ $N \in \mathbb{R}$
$\underline{\lambda} \in \mathbb{R}^n$

Some probability

Proposition For $\delta t > 0$ small let $p(t)\,\delta t + O(\delta t^2)$ be the probability that an event E occurs in the time interval $[t, t+\delta t)$, and assume that events in disjoint time intervals are independent

Then

$P(t)$ = prob that NO event occurs in $[0, t)$
is $\exp\left(-\int_0^t p(s)\, ds\right)$

Derive equation for $P(t)$:

$P(t+\delta t)$ = prob no event in $[0, t+\delta t)$
then no event occurs in $[0, t)$ OR $[t, t+\delta)$

since indep.

$P(t+\delta t)$ = (prob no event in $[0, t)$) ×
(prob no event in $[t, t+\delta t)$)

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

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

Therefore $\dfrac{P(t+\delta t) - P(t)}{\delta t} = -p(t)P(t) + O(\delta t)$

Take the limit $\delta t \to 0$

$$\underline{P'(t) = -p(t)P(t)}$$

Initial condition $P(0) = 1$ since no event happens in $[0,t)$ as $t \to 0$

$$\frac{P'(t)}{P(t)} = -p(t), \quad \left[\log P(t)\right]_0^t = -\int_0^t p(s)\, ds$$

$$\log P(t) - \underbrace{\log 1}_{=0} = -\int_0^t p(s)\, ds$$

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

To apply we will use $p(t) = b(t)$ = birth rate

So then

$P(t) = \exp\left(-\int_0^t b(s)\, ds\right)$ is probability that randomly chosen individual has not given birth in $[0,t)$

Expected time to 1st event (e.g. expected time to 1st offspring)

Assume

$$t \times \exp\left(-\int_0^t p(s)\, ds\right) \to 0 \quad \text{as} \quad t \to \infty$$

Have to make this assumption for integration by parts

Prob that 1st event happens in $[t, t+\delta t)$ is

$$\exp\left(-\int_0^t p(s)ds\right) \times \left(p(t)\delta t + O(\delta t^2)\right)$$

$$= \exp\left(-\int_0^t p(s)\,ds\right) + p(t)\,\delta t + O(\delta t^2)$$

Integrate

$$\int_0^\infty \left[\exp\left(-\int_0^t p(s)\,ds\right) \times p(t)\right] dt$$

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

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

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

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

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

$$= 1 - \lim_{T\to\infty} \exp\left(-\int_0^t p(s)\,ds\right) = 1$$

since if $t \times \exp\left(-\int_0^t p(s)\,ds\right) \to 0$ as $t \to \infty$

then certainly $\exp\left(-\int_0^t p(s)\,ds\right) \to 0$ as $t \to \infty$

Hence $\exp\left(-\int_0^t p(s)\,ds\right) p(t)$ is probability density function for ~~first~~ time to 1st event

Hence expected time to 1st event is

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

~~$= \int_0^\infty t \times \left(- \frac{d}{dt} \exp\left(\right.\right.$~~

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

= [illegible]

$$= \underbrace{\cancel{\left[-t\exp\left(-\int_0^t p(s)\,ds\right)\right]_0^\infty}}_{=0} + \int_0^\infty \exp\left(-\int_0^t p(s)\,ds\right)dt$$

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

16/01/15

Expected time to 1st event $\bar{T} = \int_0^\infty \exp\left(-\int_0^u p(s)\,ds\right) du$

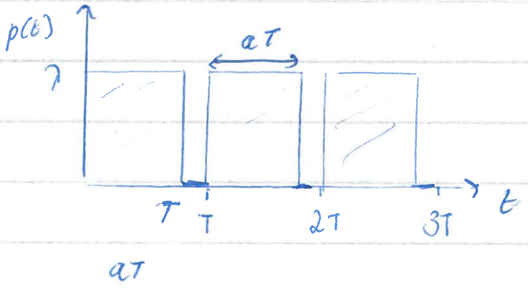
Example $p(t) = \lambda$ a constant

$\int_0^u p(s)\,ds = \lambda u$

$\Longrightarrow \quad \bar{T} = \int_0^\infty \exp(-\lambda u)\,du = \left[\frac{1}{\lambda} e^{-\lambda u}\right]_\infty^0 = \frac{1}{\lambda}$

what we expected

Example $p(t)$ periodic in t, period T



(r−1) of these areas

$\bar{T}$? Look at $\int_0^{kT} \exp\left(-\int_0^u p(s)\,ds\right) du = \bar{T}_k$

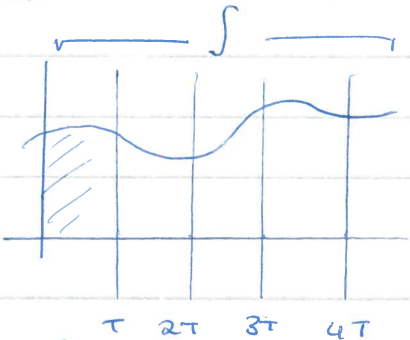
$\bar{T} = \lim_{k\to\infty} \bar{T}_k$

First note that

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

Let $v = u - (r-1)T$ then

$\bar{T}_k = \sum_{k=1}^{k} \int_0^T \exp\left(-\int_0^{v+(r-1)T} p(s)\,ds\right) dv$



$\int_0^{v+(r-1)T} p(s)\,ds = \int_0^{(r-1)T} p(s)\,ds + \int_{(r-1)T}^{v+(r-1)T} p(s)\,ds$

$= \cancel{\int_0^v p(s)\,ds}$

$= \underset{\substack{\uparrow \\ \text{just area}}}{(r-1)\lambda a T} + \int_{(r-1)T}^{(r-1)T+v} p(s)\,ds$

Let $w = s - (r-1)T$

$$\int_0^{v+(r-1)T} p(s)\,ds = (r-1)\lambda a T + \int_0^{v} p(w+(r-1)T)\,dw$$

But by periodicity of p, $p(w+(r-1)T) = p(w)$

$$\Longrightarrow \int_0^{v+(r-1)T} p(s)\,ds = (r-1)\lambda a T + \int_0^{v} p(w)\,dw$$

Hence $$\bar{T}_k = \sum_{r=1}^{k} \int_0^T \exp\left(-(r-1)\lambda a T - \int_0^v p(w)\,dw\right)$$

$$= \sum_{r=1}^{k} \int_0^T \left(\exp(-(r-1)\lambda a T)\exp\left(-\int_0^v p(w)\,dw\right)\right)dv$$

Hence $$\bar{T}_k = \sum_{r=1}^{k} \underline{e^{-\lambda a T(r-1)}} \int_0^T \exp\left(-\int_0^v p(w)\,dw\right)dv$$

Write $$\bar{t} = \int_0^T \exp\left(-\int_0^v p(w)\,dw\right)dv$$

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

Let $k \to \infty$

$$\bar{T} = \lim_{k\to\infty} \bar{T}_k = \frac{\bar{t}}{1-e^{-\lambda a T}}$$

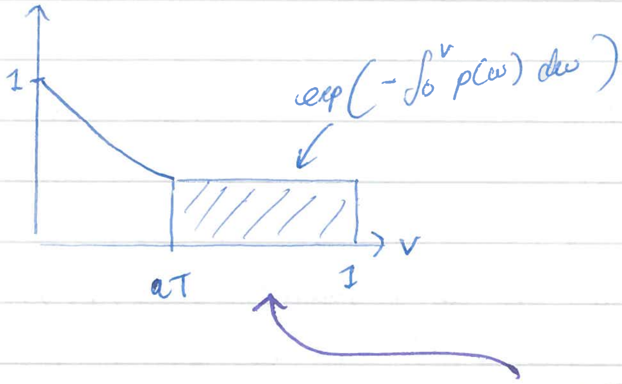
Here

$$\bar{t} = \int_0^T \exp\left(-\int_0^v p(w)\,dw\right)dv$$

$$= \int_0^{aT} \exp\left(-\int_0^v p(w)\,dw\right)dv + \int_{aT}^{T} \exp\left(-\int_0^v p(w)\,dw\right)dv$$

We are exploiting the fact that p is piecewise constant

$$= \int_0^{at} e^{-\lambda v}\,dv \xleftarrow{\;p \text{ is just const}\;} + \underbrace{\int_{aT}^{T} \exp\left(-\int_0^v p(w)\,dw\right)dv}_{\text{consider}}$$



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

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

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

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

To check: as $a \to 1$ we get $\frac{1}{\lambda}$

This agrees with taking $a \to 1$ since $\bar{T} \to \frac{1}{\lambda}$ as in $p(s) = \lambda$ case

Recall that we derived $P(t) = \exp\left(-\int_0^t p(s)\,ds\right)$

after time t,

This is the probability that a given individual chosen at random has ~~not given birth~~ no offspring (we assume asexual reproduction so we do not ~~have~~ need to ~~deal~~ distinguish between males + females)

could be strawberries

Simple birth model

Assume as before that prob. of producing offspring in $[t, t+\delta t)$ is $b(t)\delta t + O(\delta t^2)$ (here $b(t)$ is birth rate)

Consider a population of reproducing individuals, which has size k (integer) at time t with probability $p_k(t)$

Then $N(t)$ = expected population size at time t is

$$\sum_{k=0}^{\infty} k p_k(t) = N(t)$$

Suppose at time t the population is size k

Then at time $t+\delta t$, provided δt is chosen so small that at most one offspring is produced, there are 2 possible outcomes: either there are no offspring with probability $1 - k\,\delta t\, b(t)$, or the population can increase by 1 with probability $\underset{(k-1)}{\cancel{(k)}}\delta t\, b(t)$ ← increases from k-1 to k

Hence $$p_k(t+\delta t) = p_k(t)\left(1 - k b(t)\delta t + O(\delta t^2)\right) + p_{k-1}(t)\cdot\left((k-1)\delta t\, b(t) + O(\delta t^2)\right)$$

$$\frac{p_k(t+\delta t) - p_k(t)}{\delta t} = -k b(t) p_k(t) + (k-1) b(t) p_{k-1}(t) + O(\delta t$$

$$\frac{dp_k}{dt} = -k b(t) p_k(t) + (k-1) b(t) p_{k-1}(t) \qquad k = 2, \ldots$$

$$\frac{dp_1}{dt} = -b(t) p_1 \qquad k = 1$$

So we have eq^n for how probabilities change

Then $\frac{dN}{dt} = \frac{d}{dt} \sum_{k=0}^{\infty} k p_k(t) = \sum_{k=0}^{\infty} k \dot{p}_k(t)$ $\qquad \circ = \frac{d}{dt}$

$$= \overset{b(t)}{\cancel{b(t)}} \left(\sum_{k=0}^{\infty} k((k-1)p_{k-1}(t)) - \sum_{k=0}^{\infty} k^2 p_k(t) \right)$$

$$= b(t) \left(\sum_{k'=0}^{\infty} (k'+1)k' p_{k'} - \sum_{k=0}^{\infty} k^2 p_k(t) \right)$$

$$= b(t) \left(\sum_{k'=0}^{\infty} k' p_{k'}(t) \right) = b(t) N(t)$$

Expected pop. size $\dot{N} = b(t) N$

assuming you know it

$N(t) = \exp\left(\int_0^t b(s)\, ds \right) N_0$ where N_0 is the initial population

If we treat death rather than birth $p(t) = d(t)$

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

If both birth & death processes are included we obtain

$$N(t) = \exp\left(\int_0^t r(s)\, ds \right) N_0 \quad \text{where } r(s) = b(s) - d(s)$$

Definition 1 A generation is the expected time from the birth of a randomly chosen individual to the birth of their 1st offspring

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

Definition The life expectancy is the expected time of a randomly chosen individual to die from when they were born

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

For viability of the population we need that

$$\bar{T}_{surv} > \bar{T}_{gen}$$

$$\bar{T}_{surv} - \bar{T}_{gen} = \int_0^\infty \exp\left(-\int_0^t d(s)\,ds\right)dt - \int_0^\infty \exp\left(-\int_0^t b(s)\,ds\right)dt$$

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

$$\left(r(s) = b(s) - d(s)\right)$$

For $\bar{T}_{surv} > \bar{T}_{gen}$ we need

$$\exp\left(-\int_0^t r(s)\,ds\right) < 1$$

for enough of the time

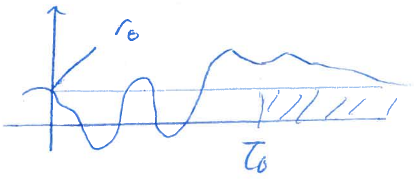
and for this expression to hold we need $r(s) > 0$ for enough of the time t difficult to be more exact/precise

Examples Suppose $r(t) \geq r_0 > 0$ for all $t \geq t_0 \geq 0$

Population explosion

Then $\int_0^t r(s)\,ds \to \infty$ as $t \to \infty$

and $N(t) \to \infty$ as a result



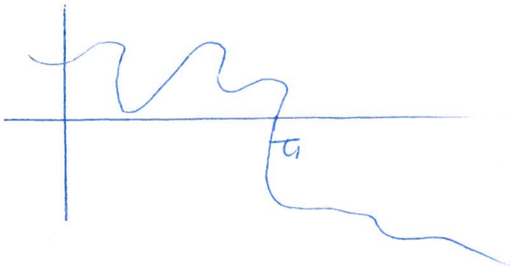
$$N(t) = \exp\left(\int_0^t r(s)\,ds\right)N_0 \to \infty$$

Extinction

$r(s) \leq -r_1 < 0, \quad t \geq t_1 \geq 0$

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

$$N(t) \to 0$$



Now suppose $r(t)$ is periodic, period T

Define $\frac{1}{T}\int_0^T r(s)\,ds = R$

= mean birth rate over T

Then consider $N(t)$ where $t = kT + s$ where k integer

$s \in [0, T)$

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

By solution $N(t) = \exp\left(\int_0^t r(u)\,du\right) N_0$

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

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

$$= \exp\left(k\int_0^T r(u)\,du + \int_0^s r(w+kT)\,dw\right) N_0$$

$\omega = u - kT$

$$= \exp\left(kT\frac{1}{T}\int_0^T r(u)\,du + \int_0^s r(\omega)\,d\omega\right)$$

$$= \exp\left(kRT + \int_0^s r(\omega)\,d\omega\right) N_0$$

$$= e^{kRT}\exp\left(\int_0^s r(\omega)\,d\omega\right) N_0 = e^{kRT} N(s)$$

$N(kT+s) = e^{kRT} N(s) \qquad s \in [0, T)$

<u>Hence</u> if $R < 0$ then $e^{kTR} \to 0$ as $k \to \infty$

i.e. $N(t) \to 0$ $t \to \infty$

This says that if on average the birth rate < death rate (so $R < 0$) then the population goes extinct

(and if you reverse sign of R get pop. explosion

When $R>0$, $e^{kRT} \to \infty$ and $N(t) \to \infty$ as $t \to \infty$
When $R=0$ (on average birth rate = death rate)
Then $N(kT+s) = N(s)$ for any integer k
and in particular $k=1$, so $N(t)$ is periodic, period T

Models too naive to capture finiteness of our populations
ATM all linear, going to add in nonlinear elements

These models make limited practical sense; they predict population is unbounded in some cases
Thus we need to consider new models where the finiteness of food, space, suitable resting sites, etc.
We expect the number of offspring produced per individual to decrease as the total population increases because more individuals are competing for resources, so each individual gets fewer resources which leads to lower fecundity (ability to produce viable offspring)

So far we have considered

$$\dot{N} = r(t)N$$

We call $\frac{\dot{N}}{N}$ = per capita growth rate

In the new model we want $\frac{\dot{N}}{N}$ to decrease as $N \uparrow$

We take as our ~~no~~ second model $\frac{\dot{N}}{N} = f(t, N)$

We want $\frac{\partial}{\partial N} f(t, N) < 0$ to reflect frequency dependence
i.e. dependence of f on N

We assume model has some large maximum population $N_{max} >> 0$

Expand $f(t,N) = f_0(t) + f_1(t)\dfrac{N}{N_{max}} + f_2(t)\left(\dfrac{N}{N_{max}}\right)^2 + \dots$

Truncate, to get

$$f(t,N) = f_0(t) + f_1(t)\frac{N}{N_{max}}$$

So the model reads

$$\dot{N}(t) = N(t)\left(f_0(t) + f_1(t)\frac{N(t)}{N_{max}}\right)$$

$$= f_0(t)N(t)\left(1 + \frac{f_1(t)}{f_0(t)}\frac{N(t)}{N_{max}}\right) \qquad f_0(t) > 0$$

define $K(t)$ by $\dfrac{-1}{K(t)} = \dfrac{f_1(t)}{f_0(t)N_{max}}$, $\rho(t) = f_0(t)$

$$\Longrightarrow \quad \dot{N}(t) = \rho(t)N(t)\left(1 - \frac{N(t)}{K(t)}\right)$$

Since $\dfrac{\partial f(t,N)}{\partial N} = \dfrac{\partial}{\partial N}\left(f_0(t) + \dfrac{f_1(t)N}{N_{max}} + \dots\right) < 0$

So need $f_1(t) < 0$ $\qquad$ ($\rho(t) > 0$ previous board)

Hence $\dot{N}(t) = \rho(t)N(t)\left(1 - \dfrac{N(t)}{K(t)}\right)$

= Time dependent logistic equation

$\rho(t)$ = per capita net linear reproductive rate
$K(t)$ = carrying capacity

20/01/15

$$\frac{dN}{dt} = \rho(t) N \left(1 - \frac{N}{K(t)}\right)$$ Time-dependent logistic model

Introduce $M(t) = N(t) \exp\left(-\int_0^t \rho(s)\, ds\right)$

$$\frac{dM}{dt} = \frac{dN}{dt} \exp\left(-\int_0^t \rho(s)\, ds\right) + N(t) \left\{-\rho(t) \exp\left(-\int_0^t \rho(s)\, ds\right)\right\}$$

$$= \exp\left(-\int_0^t \rho(s)\, ds\right)\left(\frac{dN}{dt} - \rho(t) N(t)\right)$$

$$= \exp\left(-\int_0^t \rho(s)\, ds\right)\left(\rho(t) N(t) - \frac{\rho(t)}{K(t)} N(t)^2 - \rho(t) N(t)\right)$$

$$= \exp\left(-\int_0^t \rho(s)\, ds\right)\left(-\frac{\rho(t)}{K(t)} M(t)^2 \exp\left(2\int_0^t \rho(s)\, ds\right)\right)$$

$$= -\frac{\rho(t)}{K(t)} \exp\left(\int_0^t \rho(s)\, ds\right) \cdot M(t)^2$$

Let $H(t) = \frac{\rho(t)}{K(t)} \exp\left(\int_0^t \rho(s)\, ds\right) \Rightarrow \frac{dM}{dt} = -H(t) M^2$

$t=0 \quad M=M_0$

$$\int_{M_0}^{M} \frac{dM}{M^2} = -\int_0^t H(s)\, ds$$

$$\left[-\frac{1}{M}\right]_{M_0}^{M} = -\int_0^t H(s)\, ds$$

$$\frac{1}{M_0} - \frac{1}{M} = -\int_0^t H(s)\, ds$$

$$M(t) = \frac{M_0}{1 + M_0 \int_0^t H(s)\, ds}$$

But now $M(t) = N(t) \exp\left(-\int_0^t \rho(s)\, ds\right)$

$$\Longrightarrow M(0) = N(0) = N_0$$

$$\Longrightarrow \quad N(t) = \frac{N_0 \exp\left(\int_0^t \rho(s)\, ds\right)}{1 + N_0 \int_0^t H(s)\, ds}$$

Here $H(s) = \frac{\rho(s)}{k(s)} \exp\left(\int_0^s \rho(u)\, du\right)$

Example Choose $\rho(t) = \rho$, $k(t) = k$ positive constants

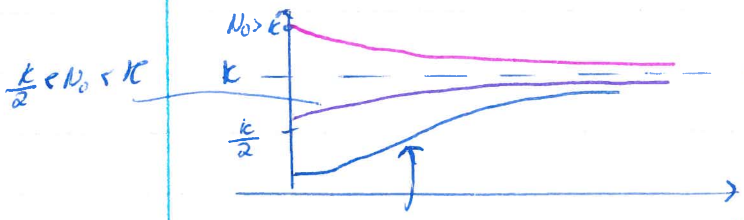
$H(s) = \frac{\rho}{k} e^{\rho s} \longrightarrow \int_0^t H(s)\, ds = \frac{\rho}{k} \int_0^t e^{\rho s} ds = \frac{1}{k}(e^{\rho t} - 1)$

$\exp\left(\int_0^t \rho(s)\, ds\right) = e^{\rho t}$

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

$$N(t) = \frac{N_0}{\frac{N_0}{k} + e^{-\rho t}\left(1 - \frac{N_0}{k}\right)}$$

We have as $t \to \infty$ $N(t) \to k$ provided $N_0 > 0$



$\leftarrow$ k is always the limiting population density if $N_0 > 0$

point of inflexion for $N_0 \in \left(0, \frac{k}{2}\right)$

Time-independent logistic equation $\dot{N} = \rho N\left(1 - \frac{N}{k}\right)$

Now suppose the intrinsic growth rate $\rho(t)$ is no longer constant

$$\frac{dN}{dt} = \rho(t) N\left(1 - \frac{N}{k}\right)$$

(k constant)

$\rho(t) > 0 \quad \forall t$

redefining infinitessimal time

$$\frac{dN}{\rho(t)\,dt} = N\left(1-\frac{N}{K}\right)$$

Let $d\tau = \rho(t)\,dt$ i.e. $\tau = \int_0^t \rho(s)\,ds$

$$\Longrightarrow \frac{dN}{d\tau} = N\left(1-\frac{N}{K}\right)$$

Now set $\rho = 1$ in the time independent logistic model

$$N(\tau) = \frac{N_0}{\frac{N_0}{K} + \left(1-\frac{N_0}{K}\right)e^{-\tau}}$$

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

Suppose $\rho(T+t) = \rho(t)$

i.e. ρ periodic period T

We need $\int_0^t \rho(\sigma)\,d\sigma$?

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

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

$v = u - kT$

$$= k\int_0^T \rho(u)\,du + \int_0^s \rho(v + kT)\,dv$$

$$= k\int_0^T \rho(u)\,du + \int_0^s \rho(v)\,dv$$

$$= kR + \int_0^s \rho(v)\,dv \quad \text{where } R = \int_0^T \rho(u)\,du$$

different in notes - have $\frac{1}{T}$ since this is mean

Hence $$N(t) = \frac{N_0}{\frac{N_0}{K} + \left(1-\frac{N_0}{K}\right)\exp\left(-kR - \int_0^s \rho(v)\,dv\right)}$$

$$= \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{-kR} \cdot \exp\left(-\int_0^s \rho(v)\, dv\right)}$$

i.e. $$N(kT+s) = \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) e^{-kR} \cdot \exp\left(-\int_0^s \rho(u)\, du\right)}$$

Define $N_\infty(s) = \lim_{k \to \infty} N(kT+s)$

If $R > 0$ $\quad N_\infty(s) = \overset{\swarrow\text{ constant function}}{K} \quad \forall s$

$R < 0 \quad N_\infty(s) \to 0 \quad \forall s$ extinction

$R = 0$ $$N_\infty(s) = \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) \exp\left(-\int_0^s \rho(u)\, du\right)}$$

$$N_\infty(s) = \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) \exp\left(-\int_0^s \rho(u)\, du\right)}$$

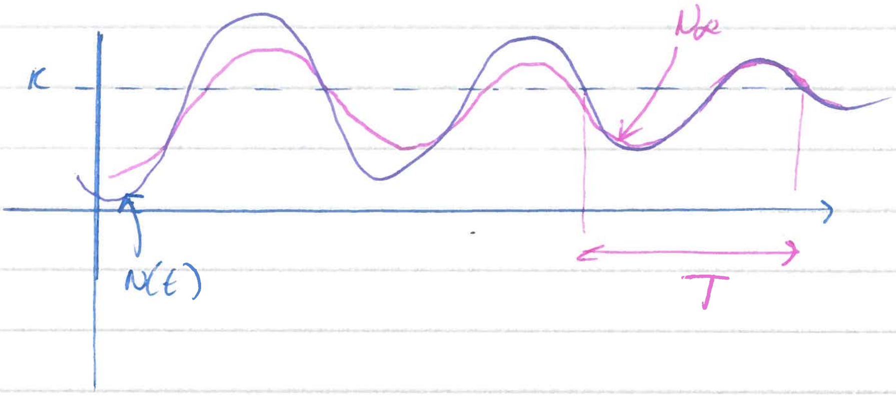
$$N_\infty(T+s) = \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) \exp\left(-\int_0^T \rho(u)\, du - \int_T^{T+s} \rho(u)\, du\right)}$$

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

$$= \frac{N_0}{\frac{N_0}{K} + \left(1 - \frac{N_0}{K}\right) \exp\left(-\int_0^s \rho(u)\, du\right)}$$

$= N_\infty(s)$ since $R = 0$

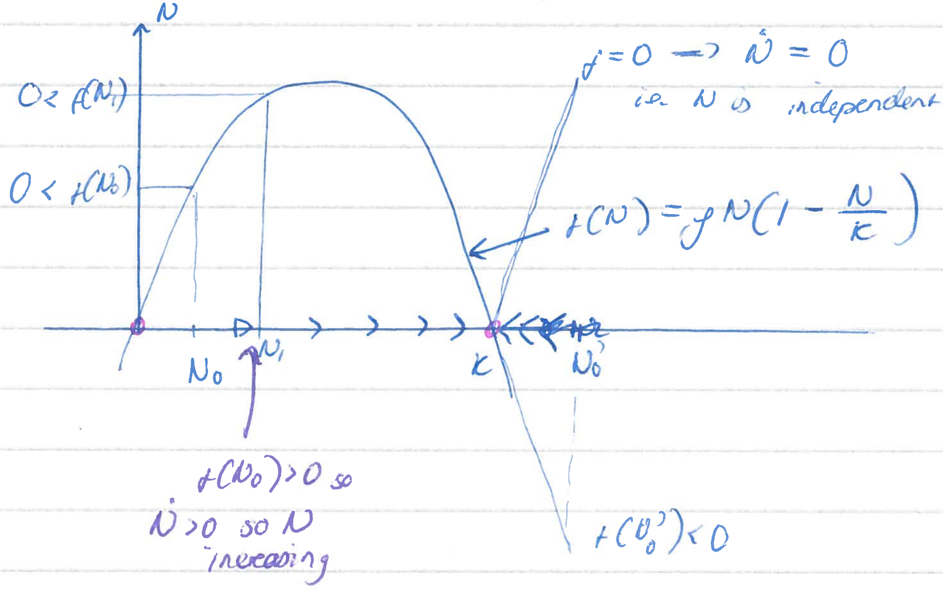
Hence $N_\infty(T+s) = N_\infty(s)$; N_∞ is periodic period T



Analysis of 1st order ODEs in one dependent variable

Consider $f : [0, \infty) \longrightarrow \mathbb{R}$
and $\dot{N} = f(N)$ e.g. $f(N) = \rho N \left(1 - \frac{N}{K}\right)$
↑ no explicit time dependence

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



$N = K$ is steady state or an equilibrium
preferred since implies balance
implies all dead

This shows that if $N_0 > 0$, $N(t) \to K$ as $t \to \infty$

e.g. $f(N) = \dfrac{e^{-N^2} \cos N}{\log(N^2+1)}$

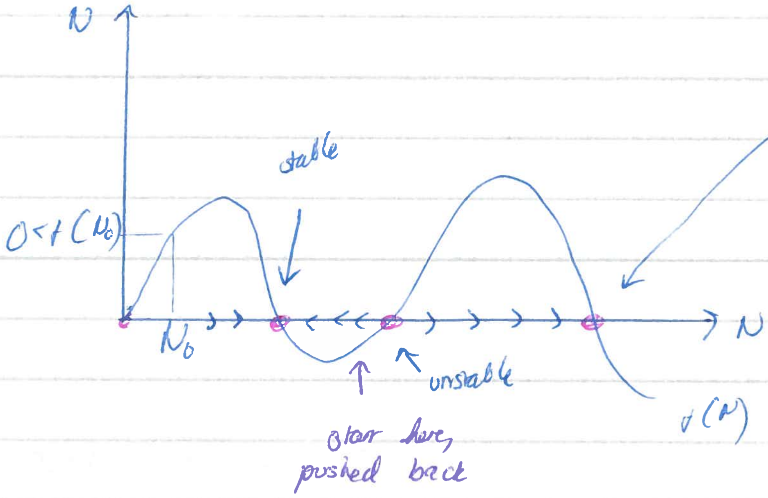
23/01/15

Stability analysis of 1st order ODE's in one variable

Consider the ODE $\dot{N} = f(N)$ $N(0) = N_0$ $f: \mathbb{R} \rightarrow \mathbb{R}$

assume f continuously differentiable

This is an autonomous ODE



$f(N) = 0$

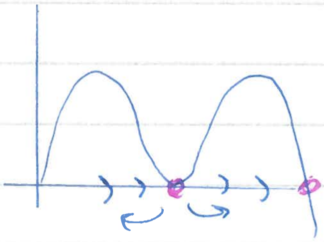
The points where $f(N) = 0$ are called steady states

For a stable* steady state, a small perturbation dies out & the system returns to that steady state

Small because large perturbations from a stable steady state may go close to a second stable steady state

If a steady state is unstable otherwise

[



Still steady state but just touching axes so more complicated!

i.e. perturb right then shoots off left. then returns

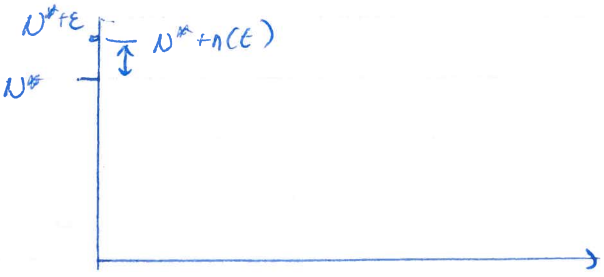
]

The gradient of the graph of f at a steady state indicates whether that steady state is stable or unstable

Let us suppose N^* is a steady state of $\dot{N} = f(N)$ ie. $f(N^*) = 0$

* Here strictly speaking we say 'asymptotically' stable.
ie. some stable states don't return to steady state but also don't go far

We will consider a perturbation at $t=0$ to the point $N^* + \varepsilon$ $\quad |\varepsilon| << 1$



Here $\dot{N} = f(N)$ measures distance

write $N(t) = N^* + n(t)$

$n(t)$ is the perturbation

If stable $n(t) \to 0$ as $t \to \infty$

$N(t) = N^* + n(t)$ is the solution to $*$ with initial condition $n(0) = \varepsilon$

$N(0) = N^* + \varepsilon$

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

$$\frac{dN^*}{dt} = 0, \qquad \frac{dn}{dt} = f(N^* + n)$$

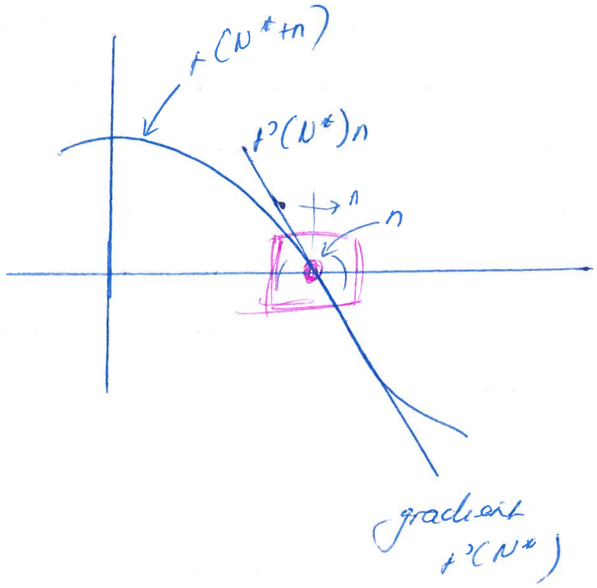
=0 since steady state

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

$$= 0 + f'(N^*)n + O(n^2) \qquad \boxed{**}$$

If n remains small for say $t \in [0, T)$ then when $f'(N^*) \neq 0$ $\boxed{**}$ is faithfully represented by the linear system

$$\dot{n} = f'(N^*)n \qquad Ⓐ$$



Solve to obtain

$$n(t) = \exp(f'(N^*)t)\, n(0)$$
$$= \exp(f'(N^*)t)\, \varepsilon$$

Provided $f'(N^*) < 0$, $n(t)$ initially decreases & in fact, for $f'(N^*) < 0$ approx Ⓐ remains valid and $n(t) \to 0$ $t \to \infty$

If $f'(N^*) > 0$ $n(t)$ grows – which immediately tells us N^* is unstable

In fact $n(t)$ will continue to grow & eventually the validity of the approx. breaks down.

Example Logistic equation

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

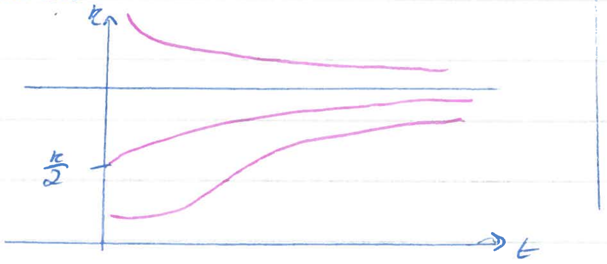
Steady states $N^* = 0$ and $N^* = K$

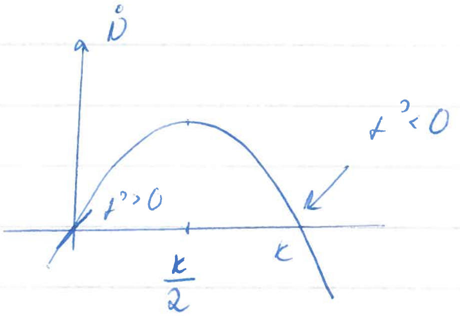
$$f'(N) = \rho\left(1 - \frac{2N}{K}\right)$$

So $f'(0) = \rho > 0$ $N^* = 0$ is unstable

$f'(K) = -\rho < 0$ $= K$ is stable

Recall:





There is a point t^* where $\ddot{N} = 0$

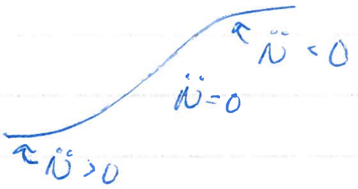
$\dot{N}(t) = f(N(t))$

$\ddot{N}(t) = f'(N(t)) \cdot \dot{N}(t)$

$$= f'(N(t))f(N(t))$$

But $f(N(t)) > 0$ if $0 < N(t) < K$

If $N(0) \in (0, \frac{k}{2})$ then $N(t)$ increases & passes through $\frac{k}{2}$ where $\ddot{N}$ changes sign



<u>Example</u> $\dot{N} = \frac{rN^2}{K+N^2} - dN$ $\quad r, k > 0$

density dependent growth

mortality

Steady states: $\frac{rN^2}{K+N^2} = dN \Rightarrow N^* = 0$ or $\frac{rN}{K+N^2} = d$

$$dN^2 - rN + dk = 0$$

$$N_\pm^* = \frac{r}{2d} \pm \frac{\sqrt{r^2 - 4d^2k}}{2d}$$

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

If $\mu < 2$ $N_\pm$ are complex

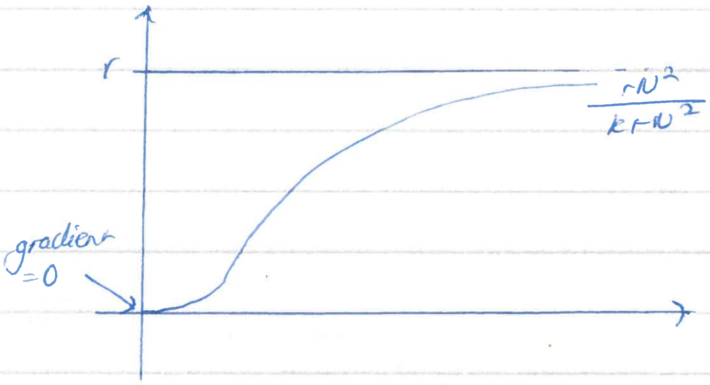
$\mu \geq 2$ there are 2 real roots. Since $0 < r^2 - 4d^2K < r^2$,

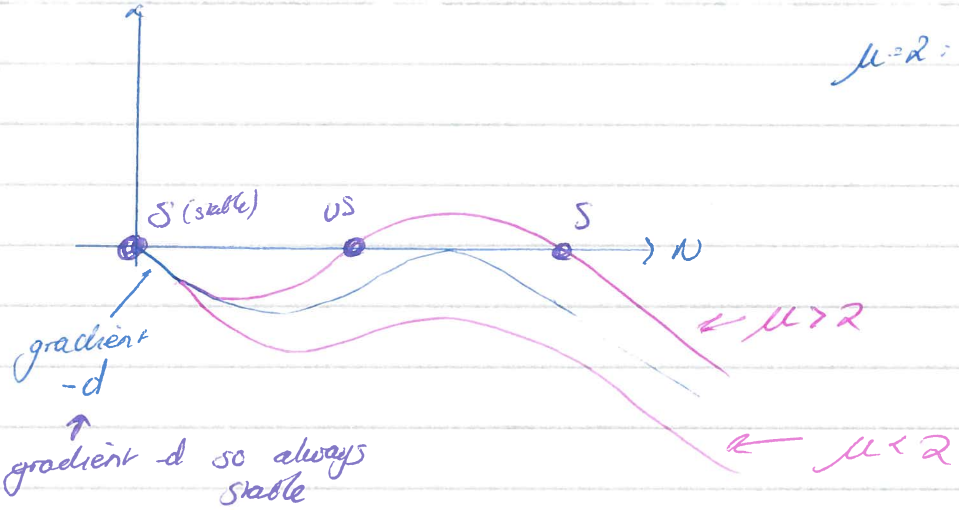
$N^*_\pm$ are both ~~positive non negative~~ positive

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

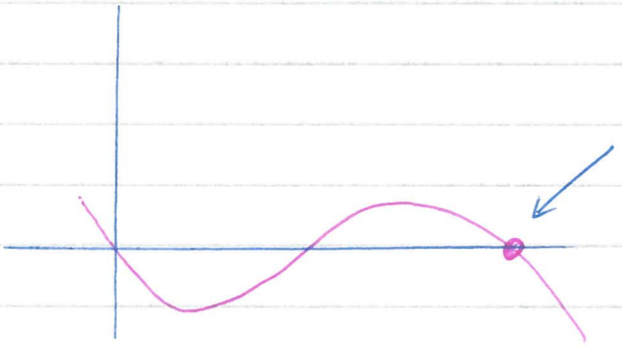
$\frac{rN^2}{K+N^2} \approx rN^2$ for N small

$\to r$ as $N \to \infty$





$\mu = 2$: get double root

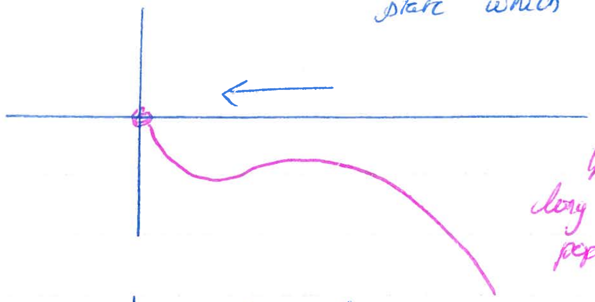


N_1^* stable steady state

$\mu = \frac{r}{d\sqrt{K}} = 3 > 2$

Consider what happens when community is hit by a famine so the death rate doubles

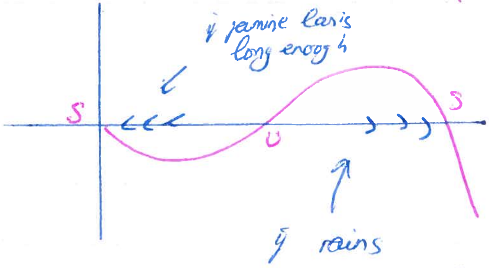
For $\mu < 2$ 0 is the origin steady state which is stable



μ goes from 3 to $\frac{3}{2}$ since d doubles

when famine lifts death rate halves

$\Longrightarrow \mu$ back to 3



Two species continuous time models

$\frac{\text{population}}{\text{area}}$ → assumed large

Let $N_i(t)$ be the population density of species i in the habitat

real number since density so not integer

$$\underbrace{\frac{dN_1}{dt} = f_1(N_1) \qquad \frac{dN_2}{dt} = f_2(N_2)}_{\text{species interact}}$$

$$\boxed{\begin{aligned} \frac{dN_1}{dt} &= f_1(N_1, N_2) \\ \frac{dN_2}{dt} &= f_2(N_1, N_2) \end{aligned}} \qquad \text{ODE 1}$$

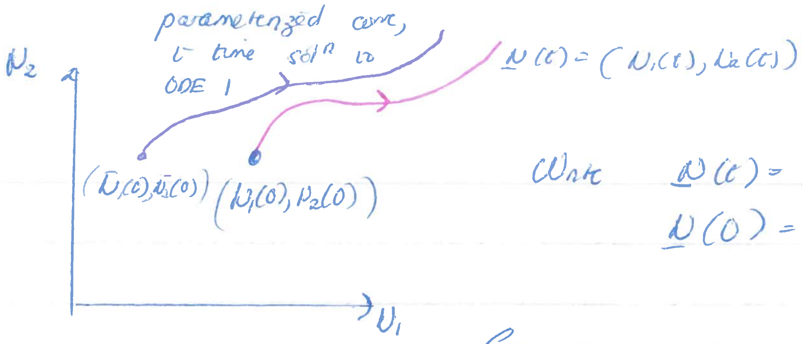
i) Given even simple functions f_1, f_2 explicit solutions $N_1(t) =$ $N_2(t) =$ is virtually unheard of. When f_1, f_2 are linear, you can solve explicitly

So we rely almost exclusively on qualitative analysis - the phase plane

2) ODE 1 has no explicit time dependence, & are referred to as 'autonomous'

~~Solutions to~~

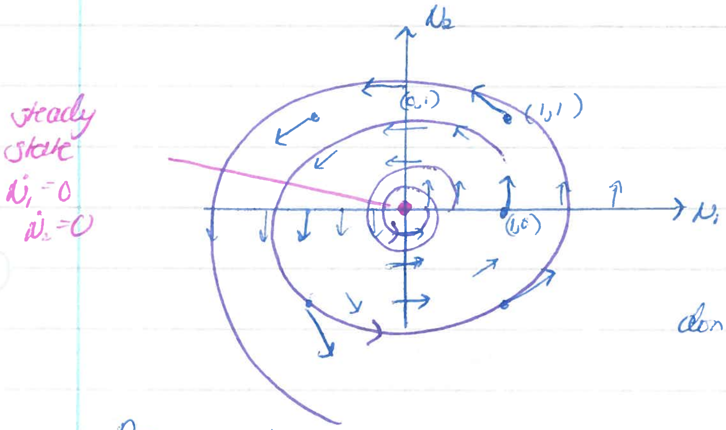
Solutions to ODE 1 depend upon the initial data $N_1(0)$, $N_2(0)$



Write $\underline{N}(t) = (N_1(t), N_2(t))$
$\underline{N}(0) = (N_1(0), N_2(0))$

Can use computer to plot entire time evolution

Example $\dot{N}_1 = -N_2, \quad \dot{N}_2 = N_1$ (not a population model)



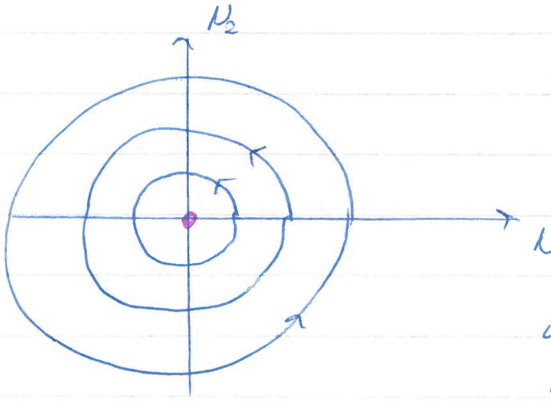
$\dot{\underline{N}} = (\dot{N}_1, \dot{N}_2)$
$= (-1, 1)$

don't know yet whether curve goes in or out

Draw enough tangent vectors to see where curve ends up

$$\frac{d}{dt}(N_1^2 + N_2^2) = N_1(-N_2) + N_2 N_1 = 0$$

$\Longrightarrow$ along ~~the~~ a solution $N_1^2(t) + N_2^2(t) = \text{constant}$
$= N_1(0)^2 + N_2(0)^2$



Phase plot (for simple harmonic oscillator)

Non generic - a slightly different differential equation would give us spirals

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Consider a model for competition between 2 species

Logistic model: $\dfrac{dN_1}{dt} = \rho_1 N_1 \left(1 - \dfrac{N_1}{K_1}\right) - c_1 N_1 N_2$

$$\frac{dN_2}{dt} = \rho_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - c_2 N_1 N_2$$

In terms of per capita growth rates

$$\frac{1}{N_1}\frac{dN_1}{dt} = \rho_1\left(1-\frac{N_1}{K_1}\right) - c_1 N_2$$

linearly decreasing in N_2

The term $c_1 N_1 N_2$ models competition between the two species

In general $c_1 \neq c_2$; the effect of N_1 on N_2 is not equal to the effect of N_2 on N_1

$$\frac{dN_1}{dt} = \rho_1 N_1 - \underset{\uparrow}{\frac{\rho_1 N_1^2}{K_1}} - \underbrace{c_1 N_1 N_2} \qquad Ⓑ$$

intraspecific competition (between same species)

interspecific competition ← between different species

Rewrite Ⓑ as

$$\frac{dN_1}{dt} = \rho_1 N_1\left(1-\frac{N_1}{K_1} - \frac{c_1}{\rho_1}N_2\right)$$

$$\frac{dN_2}{dt} = \rho_2 N_2\left(1-\frac{N_2}{K_2} - \frac{c_2}{\rho_2}N_1\right)$$

This is the basic 2-species competition model

demand: start w/ +ve population, stay with +ve

also that population is bounded

We have six parameters

By scaling parameters we can reduce to 3 parameters

Let $u_1 = \frac{N_1}{K_1}$, $u_2 = \frac{N_2}{K_2}$ ← scaled by carrying capacity

$N_1 = K_1 u_1$, $N_2 = K_2 u_2$

$$\Rightarrow \frac{d}{dt}(K_1 u_1) = \rho_1 K_1 u_1\left(1 - u_1 - \frac{c_1}{\rho_1}K_2 u_2\right)$$

$$\frac{du_1}{dt} = \rho_1 u_1 \left(1 - u_1 - \frac{c_1}{\rho_1} K_2 u_2\right)$$

$$\frac{du_2}{dt} = \rho_2 u_2 \left(1 - u_2 - \frac{c_2}{\rho_2} K_1 u_1\right)$$

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

$$\frac{du_1}{dt} = \rho_1 u_1 (1 - u_1 - \alpha_{12} u_2)$$

$$\frac{du_2}{dt} = \rho_2 u_2 (1 - u_2 - \alpha_{21} u_1)$$

Now set $\tau = \rho_1 t$ ← rescaling time

$$\frac{du_1}{dt} = \frac{du_1}{d\tau}\frac{d\tau}{dt} = \rho_1 \frac{du_1}{d\tau}$$

$$\Rightarrow \boxed{\frac{du_1}{d\tau} = u_1 (1 - u_1 - \alpha_{12} u_2)}$$

$$\frac{du_2}{\rho_1 dt} = \frac{\rho_2}{\rho_1} u_2 (1 - u_2 - \alpha_{21} u_1)$$

$$\boxed{\frac{du_2}{d\tau} = r u_2 (1 - u_2 - \alpha_{21} u_1)} \qquad r = \frac{\rho_2}{\rho_1}$$

$$\boxed{\begin{aligned} \dot{u}_1 &= u_1 (1 - u_1 - \alpha_{12} u_2) \\ \dot{u}_2 &= r u_2 (1 - u_2 - \alpha_{21} u_1) \end{aligned}}$$

Nullclines The curves (which may have several branches) where $\dot{N}_1 = 0$ are called nullclines

$\dot{N}_2 = 0$ also defines nullclines (either - not both)

The nullclines are important because as trajectories cross them they are either vertical or horizontal ↗

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

↑ not changing in horizontal direction

first thing you do is draw nullclines

Competition model

27/01/15

$\dot{u}_1 = u_1(1 - u_1 - \alpha_{12} u_2) = f_1(u_1, u_2)$

$\dot{u}_2 = r u_2 (1 - u_2 - \alpha_{21} u_1) = f_2(u_1, u_2)$

Analysis of model

Steady states: where $f_1 = 0 = f_2$

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

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

If $u_1 = 0$ then from 2nd line either $u_2 = 0$ or $1 - u_2 - \alpha_{21} u_1 = 0$

$\Rightarrow$ $u_1 = 0$ either $u_2 = 0$ or $u_2 = 1$

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

If $u_2 = 0$ then either $u_1 = 0$, $u_1 = 1$

$\Rightarrow$ $(1,0)$ is also a steady state

If $1 - u_1 - \alpha_{12} u_2 = 0$
$1 - u_2 - \alpha_{21} u_1 = 0$
$\Rightarrow \begin{pmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$

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

↑ in class he wrote $1 - \alpha_{21}$ here - I think that is wrong

$u_1 = \dfrac{1 - \alpha_{12}}{1 - \alpha_{12}\alpha_{21}}$ ~~$u_2 = \dfrac{1 - \alpha_{21}}{(1 - \alpha_{12}\alpha_{21})}$~~

$u_2 = \dfrac{1 - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}}$

Need $\dfrac{1 - \alpha_{12}}{1 - \alpha_{12}\alpha_{21}} > 0$ and $\dfrac{1 - \alpha_{21}}{1 - \alpha_{12}\alpha_{21}} > 0$

If $\alpha_{12} < 1$ then need denominator $1 - \alpha_{12}\alpha_{21} > 0$

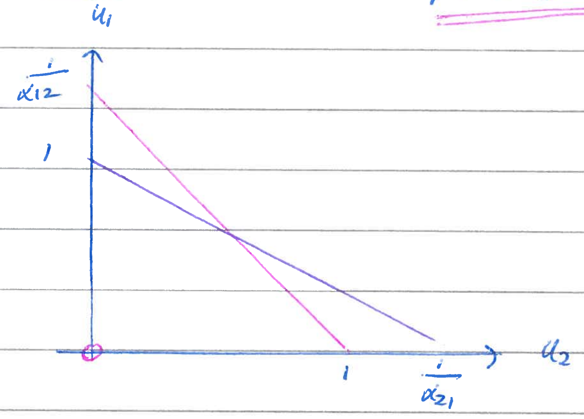
$\Rightarrow$ need numerator $1 - \alpha_{21} > 0$ i.e. $\alpha_{21} < 1$

If $\alpha_{12} > 1$ then need $1 - \alpha_{12}\alpha_{21} < 0 \implies$ need $\alpha_{21} > 1$

$\implies$ positive steady state exists if $\alpha_{12}, \alpha_{21} < 1$

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

Nullclines These are $f_1(u_1, u_2) = 0$ and $f_2(u_1, u_2) = 0$



← I think axes should be swapped over

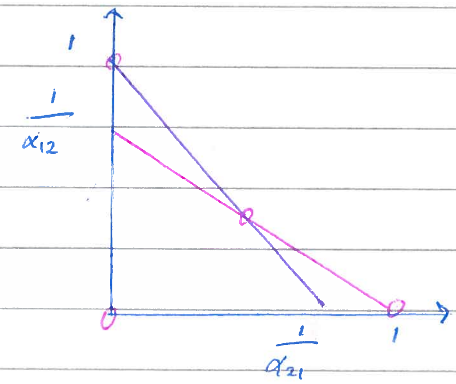
$f_1 = 0 \implies u_1(1 - u_1 - \alpha_{12}u_2) = 0$

i.e. $u_1 = 0$ or $1 - u_1 - \alpha_{12}u_2 = 0$

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

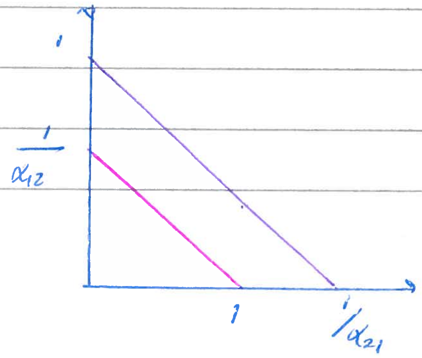
$f_2 = 0 \implies u_2(1 - u_2 - \alpha_{21}u_1) = 0$

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



Steady states are where graphs of f_1, f_2 cross

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

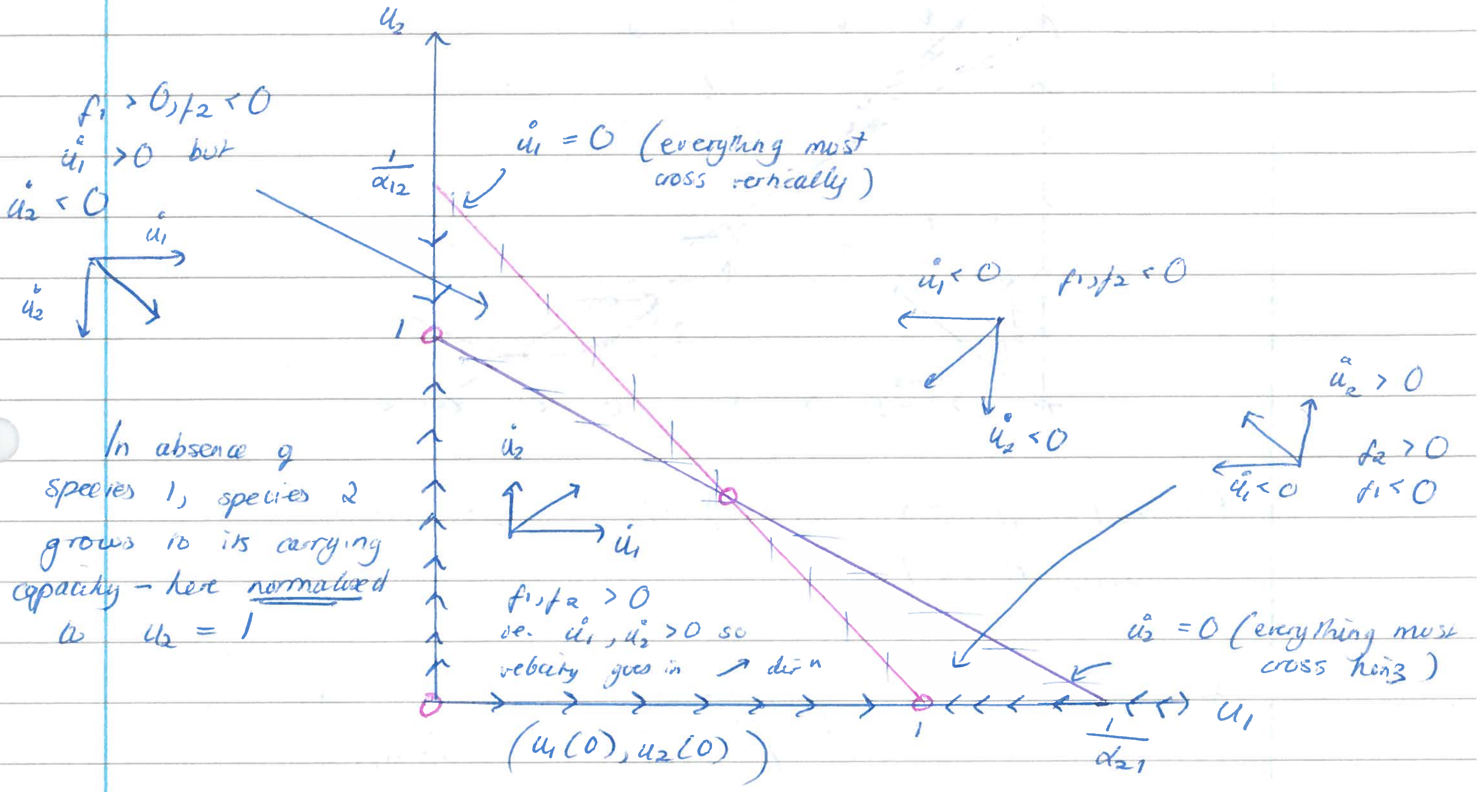


First look at boundary orbits:

If $u_2(0) = 0$, $u_1(0) > 0$

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

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



In absence of species 1, species 2 grows to its carrying capacity – here normalised to $u_2 = 1$

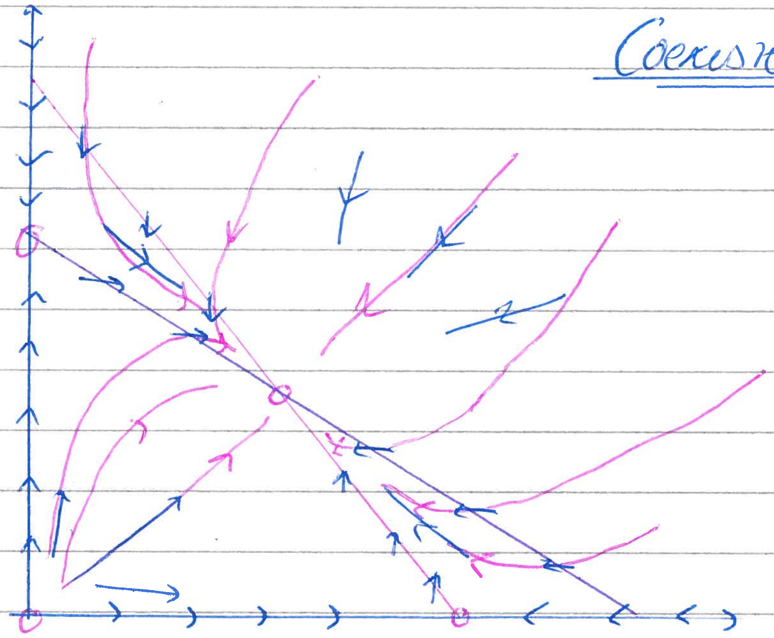
Note that $u_2(t) = 0$ $\forall t$ satisfies $*$ if $u_2(0) = 0$

$\Longrightarrow$ $u_2(t) = 0$ is the solution

$\Longrightarrow$ $\dot{u}_1 = u_1(1 - u_1)$

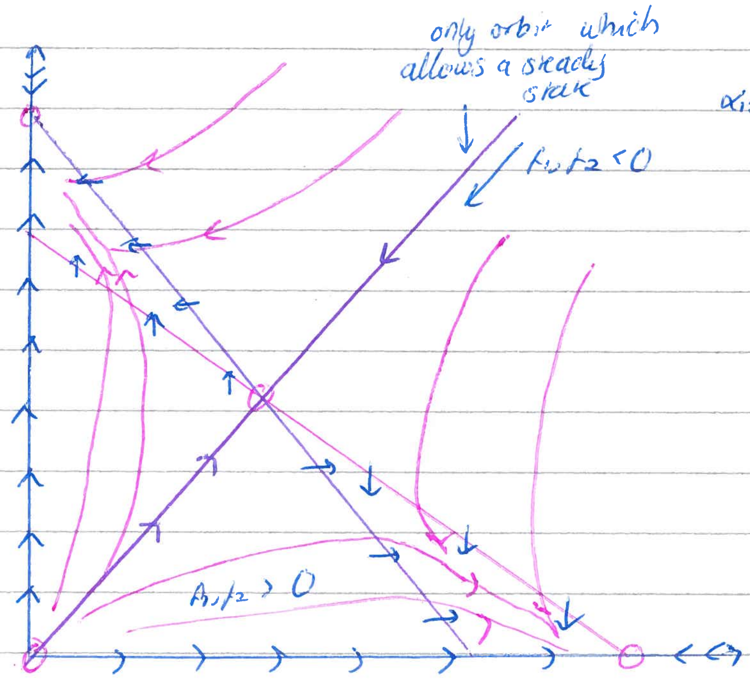
Solution is same as for $\dot{N} = \rho N(1 - N/K)$ with $\rho = 1$, $K = 1$

Coexistence



Provided $u_1(0), u_2(0) > 0$ then when $\alpha_{12}, K_{21} < 1$

then $\underline{u}(t) \to \left(\frac{1-\alpha_{12}}{1-\alpha_{12}\alpha_{21}} , \frac{1-\alpha_{21}}{1-\alpha_{12}\alpha_{21}} \right)$



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

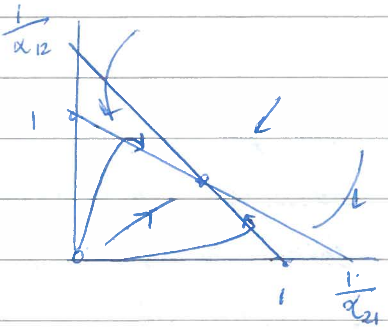
Here <u>"winner takes all"</u> i.e. one species goes extinct and the other reaches carrying capacity

Who prevails depends on initial conditions

$\dot{u}_1 = u_1(1 - u_1 - \alpha_{12}u_2)$ 30/01/15

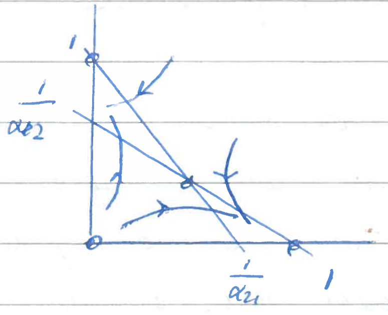
$\dot{u}_2 = ru_2(1 - u_2 - \alpha_{21}u_1)$

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

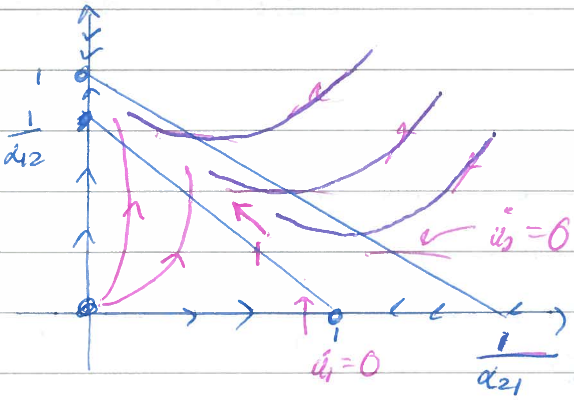


Coexistence

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



Winner takes all (depends on starting position)



$\alpha_{12} > 1 \quad \alpha_{21} < 0$

(doesn't depend upon starting position)

↳ $u_2(0) > 0$

$u_1(t) \to 0$

$u_2(t) \to 1$

Other one v. similar just swapped over

4 outcomes

1) $\alpha_{12}, \alpha_{21} < 1$ competition is weak, stable coexistence

2) $\alpha_{12}, \alpha_{21} > 1$ Both strongly competing. One species drives a extinction, other reaches carrying capacity
Who wins depends on the initial population densities

3) $\alpha_{12} > 1, \alpha_{21} < 1$ or vice versa
Here the stronger competitor will win and reach carrying capacity

(NB) α_{21} measures the effect of species 1 on species 2
$\alpha_{12} > 1, \alpha_{21} < 1$ means 2 is stronger

Lotka - Volterra model (predator - prey model)

P = predator density, N = prey density

Make some simple assumptions about the per capita growth rates $\frac{\dot{N}}{N}$, $\frac{\dot{P}}{P}$

1. In the absence of predator $P=0$, the per capita growth is linear and decreasing with N (intraspecific competition)
When there are predators present then the per capita growth rate of N decreases linearly with P

$$\frac{1}{N}\frac{dN}{dt} = a - bP - eN \qquad a,b,e > 0 \text{ are constants}$$

2. In the absence of prey $(N=0)$ the per capita growth of predator P is linearly decreasing in P; and if there is no ~~predator~~ prey and no predator the per-capita growth is a constant $-d < 0$
When there is prey $N > 0$ the per capita growth of P is linearly increasing with N

$$\frac{1}{P}\frac{dP}{dt} = -d + \underset{\substack{\uparrow \\ \text{prey consumption}}}{cN} - fP \qquad d,c,f > 0$$

Gives rise to:

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

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

-d because without food, for small P, we want P to go extinct

Consider case where $e, f = 0$ (no intraspecific competition)

$$dN/dt = \dot{N} = N(a - bP)$$

$$dP/dt = \dot{P} = P(-d + cN)$$

$\Longrightarrow$ along solution ~~cure~~ curve $NP \neq 0$

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

$$\int -\frac{d}{N} + c \; dN = \int \frac{a}{P} - b \; dP$$

$-d\log N + cN = a\log P - bP + \text{constant}$

$-d\log N(t) + cN(t) - a\log P(t) + bP(t)$ is constant along solution curve

Introduce $H(N, P) = cN + bP - d\log N - a\log P$

$$H(N(t), P(t)) = H(N(0), P(0)) \quad \forall t$$

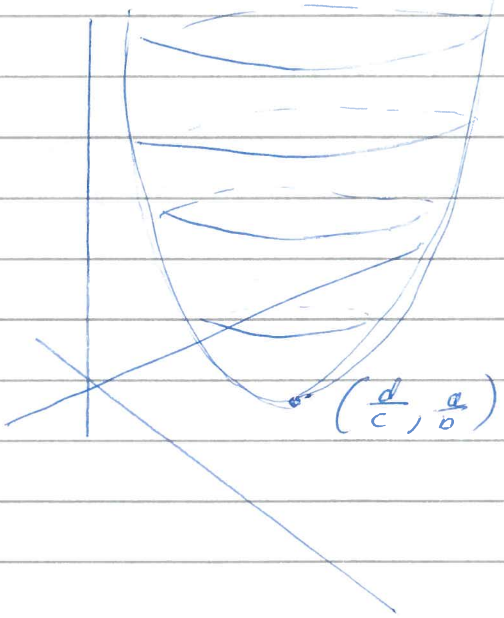
Hence (generally) solutions lie on curves given by

$H(N, P) = \text{constant}$

It turns out that all solutions are periodic orbits

If drew phase plane would see spirals - wouldn't know if they join up

Consider graph of H



$H = cN + bP - d\log N - a\log P$

$$\nabla H = \left(c - \frac{d}{N}, \; b - \frac{a}{P}\right)$$

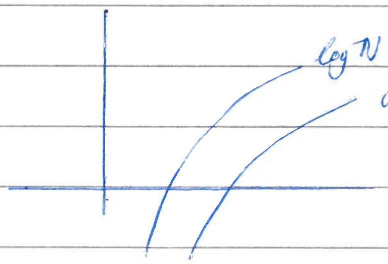
Hence H has a turning point at $(N, P) = \left(\frac{d}{c}, \frac{a}{b}\right)$ and there are no others

$H_{NN} = \frac{d}{N^2} > 0$; $H_{PP} = \frac{a}{P^2} > 0$ $\quad H_{NP} = 0$

$= \left(\frac{d}{c}, \frac{a}{b}\right)$ is a minimum of H

If we fix $P=P^*$ in H;

$$H(N, P^*) = cN + bP^* - d\log N - a\log P^*$$



$d\log N$ concave $\Rightarrow -d\log N$ convex

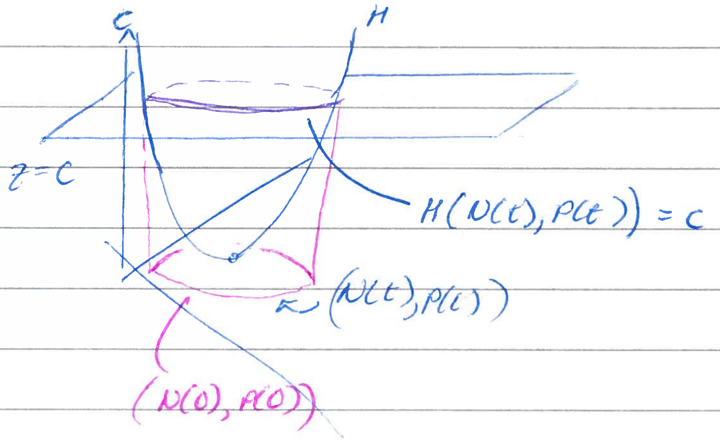
$\Rightarrow cN - d\log N$ is convex

Since H is the sum of convex functions, H is convex

except: e^{-x} convex but goes to 0

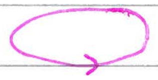
here we do go back up

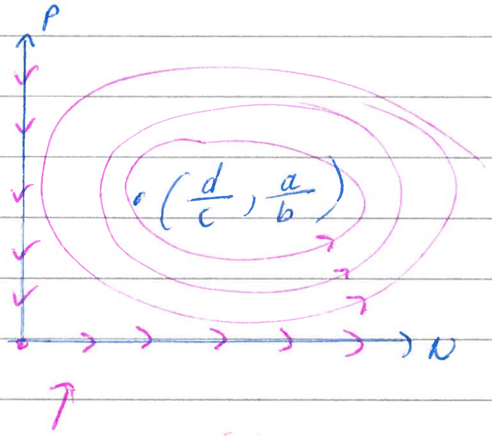
Take a horizontal slice through graph of H & the intersection is a closed curve



H must be const along sol^n curve so this is sol^n curve

Then $(N(t), P(t))$ is the solution curve





$$\dot N = N(a-bP) = 0$$
$$\dot P = P(-d+cN) = 0$$

we know circles anticlockwise since if no predator, prey increases

Is this a realistic model? (No)

1) There is unbounded growth for prey in absence of predator
2) There are no conditions $N(0), P(0) > 0$ such that one is made extinct
3) If the base model and slightly perturb it with additional ecologically motivated terms, the periodic orbits would be destroyed and 'typically' all orbits would approach a steady state

- structurally unstable

Linear stability analysis of planar ODEs

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

Assume there is an isolated steady state at $(0,0)$

If the steady state is at (x^*, y^*) then substitute

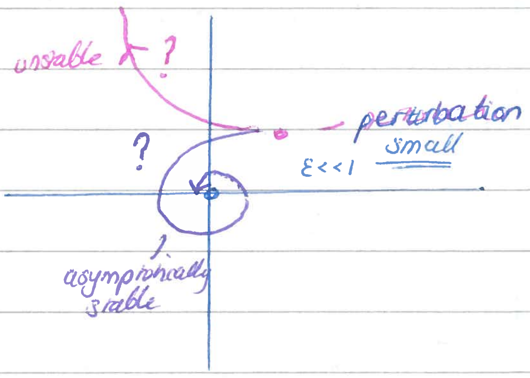
$$X = x - x^*, \qquad Y = y - y^*$$

$$\dot{X} = f(X + x^*, Y + y^*) = F(X, Y)$$
$$\dot{Y} = g(X + x^*, Y + y^*) = G(X, Y)$$

where $F(0,0) = 0 = G(0,0)$

As in $\circledast$ we have chosen $(0,0)$ as a steady state

$f(0,0) = 0 = g(0,0)$

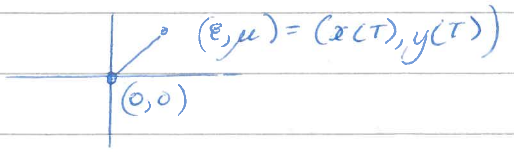


At $t = 0$, $x(0) = 0$, $y(0) = 0$,

at some time T perturb

to $x(T) = \varepsilon$ $y(T) = \mu$

where $\varepsilon^2 + \mu^2 \ll 1$



~~Then $x(t) = X(t)$~~

If $|x(T), y(T)| = \sqrt{\varepsilon^2 + \mu^2} << 1$ then for some time $[T, T+\tau)$ it remains close to origin

During this time a Taylor expansion can be used

$$f(x(t), y(t)) = f(0,0) + x(t)\frac{\partial f}{\partial x}(0,0) + y(t)\frac{\partial f}{\partial y}(0,0)$$

$$+ \text{H.O.T} \quad (\text{higher order terms})$$

$$g(x(t), y(t)) = g(0,0) + x(t)\frac{\partial g}{\partial x}(0,0) + y(t)\frac{\partial g}{\partial y}(0,0) + HOT$$

So $\dot{x}(t) = f(x(t), y(t))$

$$= \underbrace{f(0,0)}_{=0} + x(t)\frac{\partial f}{\partial x}(0,0) + y(t)\frac{\partial f}{\partial y}(0,0) + HOTs$$

$$\dot{x}(t) = x(t)\frac{\partial f}{\partial x}(0,0) + y(t)\frac{\partial f}{\partial y}(0,0) + HOTs$$

$$\dot{y}(t) = x(t)\frac{\partial g}{\partial x}(0,0) + y(t)\frac{\partial g}{\partial y}(0,0) + HOTs \leftarrow$$

particularly small in comparison w/ linear terms

Provided that a certain non-degeneracy condition is satisfied (see later)

the phase plane near $(0,0)$ looks qualitatively the same for the full system

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

and the linear system $\dot{x} = \frac{\partial f}{\partial x}(0,0)\,x + \frac{\partial f}{\partial y}(0,0)\,y$

$$\dot{y} = \frac{\partial g}{\partial x}(0,0)\,x + \frac{\partial g}{\partial y}(0,0)\,y$$

This approximation is valid while $(x,y)(t)$ remains small

If it grows the $(0,0)$ is unstable,

if $\underset{\uparrow}{(x,y)}(t) \to 0$ then $(0,0)$ is stable

perturbation

Set $M = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}_{(0,0)}$ ie. evaluated at origin

$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = M\begin{pmatrix} x \\ y \end{pmatrix}$ initial condition $x(0) = \varepsilon$, $y(0) = \mu$

i) Solution is $\begin{pmatrix} x \\ y \end{pmatrix}(t) = \exp(Mt)\begin{pmatrix} \varepsilon \\ \mu \end{pmatrix}$

where $\exp(A) = I + A + \frac{A^2}{2!} + \frac{A^3}{3!} + \dots$
A a square matrix

$\begin{pmatrix} x \\ y \end{pmatrix}(t) = \left(I + Mt + \frac{M^2t^2}{2!} + \frac{M^3t^3}{3!} + \dots\right)\begin{pmatrix} \varepsilon \\ \mu \end{pmatrix}$ ← checking to see if satisfies

$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix}(t) = \left(0 + \frac{M}{\cancel{1!}} + \frac{M^2t}{1!} + \frac{M^3t^2}{2!} + \dots\right)\begin{pmatrix} \varepsilon \\ \mu \end{pmatrix}$

$= M\left(I + \frac{Mt}{1!} + \frac{M^2t^2}{2!} + \dots\right)\begin{pmatrix} \varepsilon \\ \mu \end{pmatrix}$

$= M\begin{pmatrix} x \\ y \end{pmatrix}(t)$ so satisfies equation

When eigenvalues of M are distinct, $\lambda_1 \neq \lambda_2$ then

$\begin{pmatrix} x \\ y \end{pmatrix}(t) = \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} e^{\lambda_1 t} + \begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix} e^{\lambda_2 t}$

where $\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix}$, $\begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix}$

can be determined by initial conditions

For more simplicity we can write

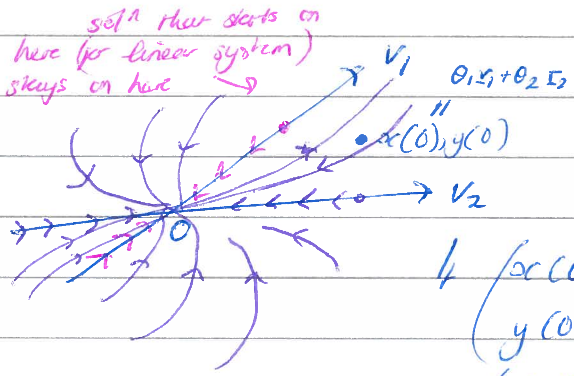
$\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} = a\underline{v_1}$ $\begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix} = d\underline{v_2}$

where $\underline{v_1}, \underline{v_2}$ are eigenvectors corresponding to λ_1, λ_2

$$\begin{pmatrix} x \\ y \end{pmatrix}(t) = ae^{\lambda_1 t}\underline{v_1} + be^{\lambda_2 t}\underline{v_2}$$

Since $\underline{v_1}, \underline{v_2}$ are lin independent, a, b can be found from the $(x(0), y(0))$.

Consider $\lambda_1, \lambda_2 < 0$ and $\lambda_1 < \lambda_2$



Suppose initially $(x(0), y(0))$ is such that $b = 0$

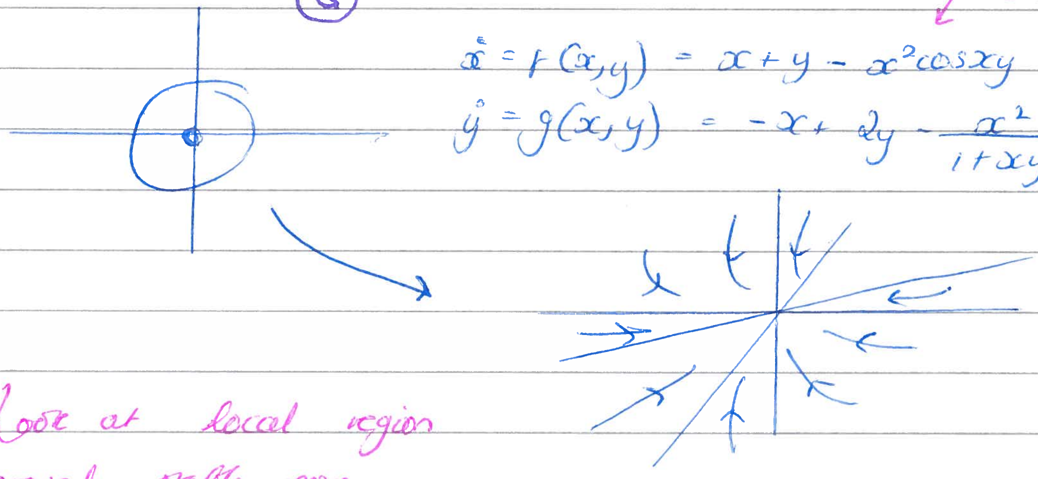
$$\Rightarrow \begin{pmatrix} x(0) \\ y(0) \end{pmatrix} = a\underline{v_1}$$

If $\begin{pmatrix} x(0) \\ y(0) \end{pmatrix}$ lies on the eigenvector $\underline{v_1}$ then $\begin{pmatrix} x(t) \\ y(t) \end{pmatrix}$ lies on the eigenvector $\underline{v_1}$ for all t

$$\underset{\substack{\uparrow \\ \text{decays faster} \\ \text{since } \lambda_1 < \lambda_2}}{ae^{\lambda_1 t}}\underline{v_1} + be^{\lambda_2 t}\underline{v_2} \qquad \lambda_1 < \lambda_2$$

could have horrible system

$$\dot{x} = f(x,y) = x + y - x^2\cos xy + x^3 y$$
$$\dot{y} = g(x,y) = -x + 2y - \frac{x^2}{1+xy}$$



Look at local region around stable point

If $\lambda_1, \lambda_2 > 0$ direction of arrows just changes SAME PICTURE

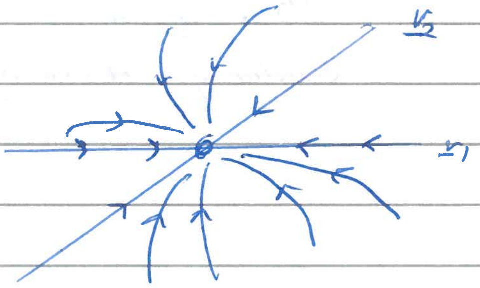
03/02/15

$$\begin{pmatrix} X \\ Y \end{pmatrix} = M \begin{pmatrix} x \\ y \end{pmatrix} \qquad M = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}_{\underline{0}}$$

Let M have eigenvalues λ_1, λ_2

If $\lambda_1 \neq \lambda_2$ $\quad \underline{\underline{x}(t) = a\underline{v}_1 e^{\lambda_1 t} + b\underline{v}_2 e^{\lambda_2 t}}$

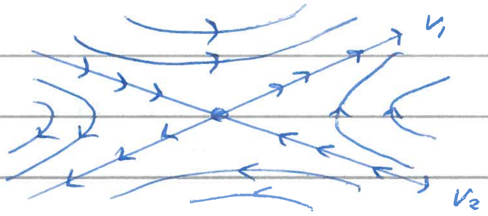
i) Case $\lambda_1, \lambda_2 < 0$ Stable node



Unstable node $\lambda_1, \lambda_2 > 0$

- same, but with arrows reversed

$\lambda_1 > 0, \ \lambda_2 < 0$



Saddle point
(unstable)

λ_1, λ_2 complex   Must occur in conjugate pairs

$$\left.\begin{aligned} \lambda_1 &= \sigma + i\omega \\ \lambda_2 &= \sigma - i\omega \end{aligned}\right\} \ \omega \neq 0$$

$$\underline{x}(t) = \mathrm{Re}\left(a\underline{v}_1 e^{\lambda_1 t} + b\underline{v}_2 e^{\lambda_2 t}\right)$$

$$= \mathrm{Re}\left(a\underline{v}_1 e^{\sigma t} e^{i\omega t} + b\underline{v}_2 e^{\sigma t - i\omega t}\right)$$

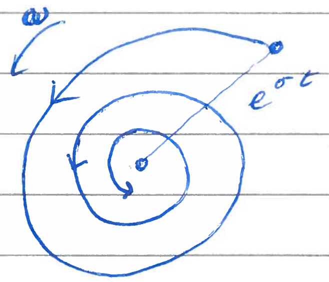
$$= \underset{\substack{\uparrow \\ \text{magnification}}}{e^{\sigma t}} Re\big(a\underline{v}_1 \underbrace{e^{i\omega t} + b\underline{v}_2}_{\text{periodic}} e^{-i\omega t}\big)$$

If $\sigma < 0$ $e^{\sigma t} \downarrow 0$ as $t \to \infty$

> 0 $e^{\sigma t} \uparrow$ $t \to \infty$

$= 0$ $e^{\sigma t} = 1$ (get oscillation)

Case $\sigma < 0$

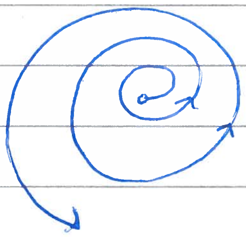


Stable spiral

oscillating, decreasing radius

Case $\sigma > 0$

Unstable spiral



Case $\sigma = 0$

Centre

This is the prediction from the linearisation of the nonlinear system $\dot{\underline{x}} = f(\underline{x})$

But the theory of replacing the nonlinear system with its ~~linearisation~~ linearisation does not work when an eigenvalue has zero real part.

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

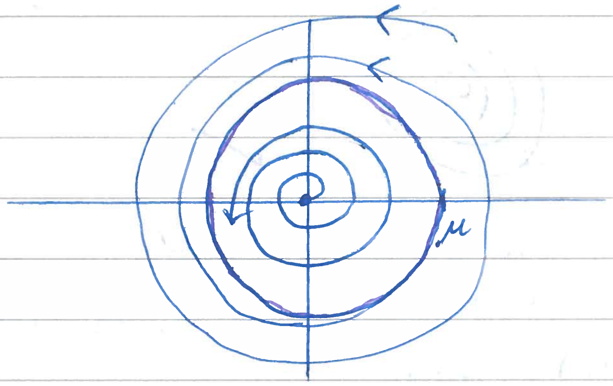
$$x\dot{x} + y\dot{y} = \left(\mu x^2 - xy - x^2\sqrt{x^2+y^2}\right) + \left(xy + \mu y^2\right) - y^2\sqrt{x^2+y^2}$$
$$= \mu(x^2+y^2) - (x^2+y^2)\sqrt{x^2+y^2}$$

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

$R^2 = x^2+y^2$ $\qquad$ $\tan\theta = y/x$

$$\frac{d}{dt}\left(\frac{1}{2}R^2\right) = \mu R^2 - R^3$$

$$R\dot{R} = \mu R^2 - R^3 \Longrightarrow \dot{R} = \mu R - R^2 = R(\mu - R)$$



Inside: unstable
Outside: stable

Let's find the linear stability of $\underline{0} = (0,0)$

$\dot{x} = \mu x - y$ $\qquad$ linearised system
$\dot{y} = x + \mu y$

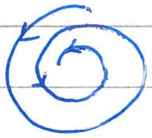
$$\frac{d}{dt}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} \Longrightarrow M = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix}$$

$$\det(M - \lambda I) = \det\begin{pmatrix} \mu-\lambda & -1 \\ 1 & \mu-\lambda \end{pmatrix}$$
$$= (\mu-\lambda)^2 + 1$$
$$= 0$$

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

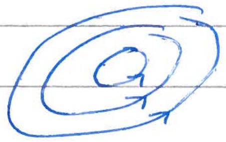
$\lambda = \mu \mp i$

If $\mu \neq 0$ this predicts a spiral



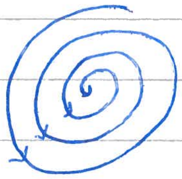
as shown in our system

If $\mu = 0$, linear system predicts a centre



✗ so cannot use linear system when $\mu = 0$

But when $\mu = 0$ $\mathring{R} = -R^2$



✓

Lemma If $M = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$ and M has eigenvalues λ_1, λ_2 then

$$\lambda_1 + \lambda_2 = \text{trace}(M) = a + d$$
$$\lambda_1 \lambda_2 = \det(M) = ad - bc$$

Proof

$$\det(M - \lambda I) = \left| \begin{pmatrix} a-\lambda & b \\ c & d-\lambda \end{pmatrix} \right|$$

$$= ad - (a+d)\lambda + \lambda^2 - bc$$
$$= \lambda^2 - (a+d)\lambda + ad - bc$$
$$= \lambda^2 - \text{trace}(M)\lambda + \det M$$

But if λ_1, λ_2 are roots

$$\det(M - \lambda I) = (\lambda - \lambda_1)(\lambda - \lambda_2) = \lambda^2 - (\lambda_1 + \lambda_2)\lambda + \lambda_1 \lambda_2$$

$\Longrightarrow$ $\text{trace } M = \lambda_1 + \lambda_2$

$\det M = \lambda_1 \lambda_2$

I like Hummus
and carrot sticks
– Mhari

Hence if $\det M < 0$, $\lambda_1, \lambda_2 \in \mathbb{R}$ and opposite sign

$\det M = 0$ one eigenvalue is 0

$\det M > 0$ $\begin{cases} \lambda_1, \lambda_2 \text{ are real and same sign} \\ \text{or } \lambda_1 = \bar{\lambda}_2, \text{ if complex} \end{cases}$

When $\det M > 0$ and λ_1, λ_2 are real. Then if

$\text{trace } M > 0$ then $\lambda_1, \lambda_2 > 0$

< 0 $\lambda_1, \lambda_2 < 0$

If $\lambda_1 = \bar{\lambda}_2$ then $Re(\lambda_1) = Re(\lambda_2)$ and

$\text{trace } M = 2 Re \lambda_1$

$\Longrightarrow$ $\text{trace } M > 0$ λ_1 has +ve real part

< 0 λ_1 has −ve real part

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

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

Jacobian

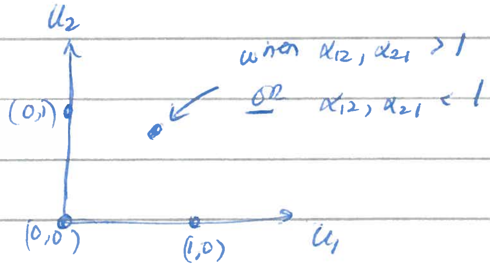
$$M = \begin{pmatrix} 1 - u_1 - \alpha_{12} u_2 + u_1(-1) & -\alpha_{12} u_1 \\ -\alpha_{21} r u_2 & r(1 - u_2 - \alpha_{21} u_1) - r u_2 \end{pmatrix}$$

$M_{(0,0)} = \begin{pmatrix} 1 & 0 \\ 0 & r \end{pmatrix}$ has eigenvalues $\underline{\lambda_1 = 1, \lambda_2 = r}$

$\Longrightarrow$ $(0,0)$ is an unstable node

since eigenvalues both positive

Recall



$$M_{(1,0)} = \begin{pmatrix} -1 & -\alpha_{12} \\ 0 & r(1-\alpha_{21}) \end{pmatrix} \Longrightarrow \begin{array}{l} \lambda_1 = -1 < 0 \\ \lambda_2 = r(1-\alpha_{21}) \end{array}$$

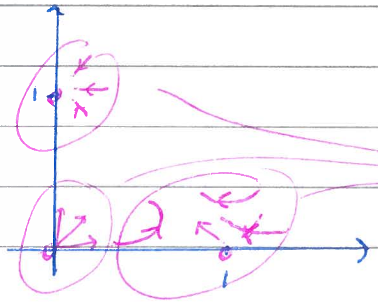
If $\alpha_{21} > 1$, $\lambda_2 < 0 \Longrightarrow$ stable node

$\alpha_{21} < 1$, $\lambda_2 > 0 \Longrightarrow$ saddle

$$M_{(0,1)} = \begin{pmatrix} 1-\alpha_{12} & 0 \\ -\alpha_{21} r & -r \end{pmatrix} \Longrightarrow \begin{array}{l} \lambda_1 = 1-\alpha_{12} \\ \lambda_2 = -r < 0 \end{array}$$

If $\alpha_{12} > 1$ stable node

$\alpha_{12} < 1$ saddle



$\alpha_{12} > 1$

$\alpha_{21} < 1$

obtained from linearisation

will explain in detail next lecture

06/02/15

$$\dot{u}_1 = u_1(1 - u_1 - \alpha_{12}u_2)$$
$$\dot{u}_2 = ru_2(1 - u_2 - \alpha_{21}u_1)$$

$$J = \begin{pmatrix} (1-u_1-\alpha_{12}u_2)-u_1 & -\alpha_{12}u_2 \\ -r\alpha_{21}u_1 & r(1-u_2-\alpha_{21}u_1)-ru_2 \end{pmatrix}$$

Linear stability

$(0,0)$ was unstable node

$(1,0)$ $\quad M_{(1,0)} = \begin{pmatrix} -1 & 0 \\ -r\alpha_{21} & r(1-\alpha_{21}) \end{pmatrix}$

~~α_{21}~~ [illegible] $\alpha_{21} > 1$ stable node

$\alpha_{21} < 1$ saddle

$(0,1)$ $\quad \alpha_{12} > 1$ stable node

$\alpha_{12} < 1$ saddle

The last steady state is the interior point

$$(u_1^*, u_2^*) = \left(\frac{1-\alpha_{12}}{1-\alpha_{12}\alpha_{21}}, \frac{1-\alpha_{21}}{1-\alpha_{12}\alpha_{21}}\right)$$

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

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

(u_1^*, u_2^*) comes from solving

$$\left.\begin{aligned} 1 - u_1^* - \alpha_{12}u_2^* &= 0 \\ 1 - u_2^* - \alpha_{21}u_1^* &= 0 \end{aligned}\right\} A$$

Then $$M = \begin{pmatrix} \overset{=0}{\cancel{(1-u_1^*-\alpha_{12}u_2^*)}}-u_1^* & -\alpha_{12}u_2^* \\ -r\alpha_{21}u_1^* & r\underset{=0}{\cancel{(1-u_2^*-\alpha_{21}u_1^*)}}-ru_2^* \end{pmatrix}$$

didn't simplify Jacobian for this purpose

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

$\lambda_1 + \lambda_2 = \text{trace } M$

$\lambda_1 \lambda_2 = \det M$

$u_1^*, u_2^* > 0$

$\text{trace } M(u_1^*, u_2^*) = -u_1^* - r u_2^* < 0 \Rightarrow \lambda_1 + \lambda_2 < 0$

$\det M(u_1^*, u_2^*) = r u_1^* u_2^* - r\alpha_{12}\alpha_{21} u_1^* u_2^* = r u_1^* u_2^* (1 - \alpha_{12}\alpha_{21})$

If $\alpha_{12}, \alpha_{21} > 1$, $\alpha_{12}\alpha_{21} > 1 \Rightarrow \det M(u_1^*, u_2^*) < 0$

$\Rightarrow$ ~~$\lambda_1, \lambda_2 < 0 \Rightarrow$~~

$\Rightarrow \lambda_1 \lambda_2 < 0 \Rightarrow \lambda_1, \lambda_2$ real + opposite sign

$\Rightarrow$ saddle

If $\alpha_{12}, \alpha_{21} < 1$ then $\det M(u_1^*, u_2^*) > 0 \Rightarrow$ either complex conjugates OR both eigenvalues real + same sign

But also we know $\lambda_1 + \lambda_2 < 0$

$\Rightarrow \text{Re}(\lambda_1, \lambda_2) < 0 \Rightarrow$ stable

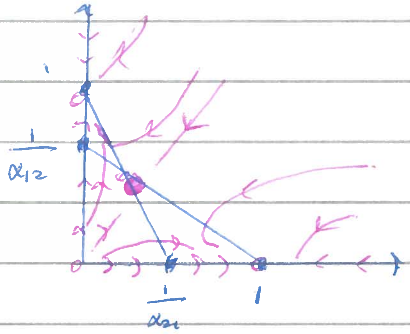
Since $\lambda^2 - \text{trace } M \lambda + \det M = 0$

λ are real if $(\text{trace } M)^2 \geq 4 \det M$

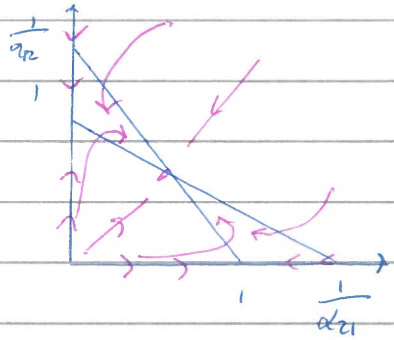
can be bit messy under exam conditions

(In exam he will want to know stable or unstable
is it a saddle)

complex if $(\text{trace } M)^2 < 4 \det M$



This is our saddle

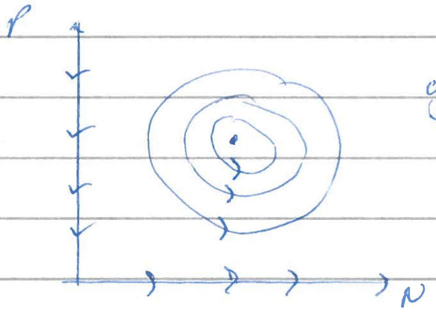


$\alpha_{12}, \alpha_{21} < 1$

Predator - Prey

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

Have done case where $f = 0$ and $c = 0$



cycle around

When $f, e > 0$ we have added intraspecific competition

Nullclines

$N = 0$ or $a - eN - bP = 0$

and $P = 0$ or $-d + cN - fP = 0$

If $N = 0$ then $P = 0$ or $P = \cancel{-d/f} < 0$ (negative population)

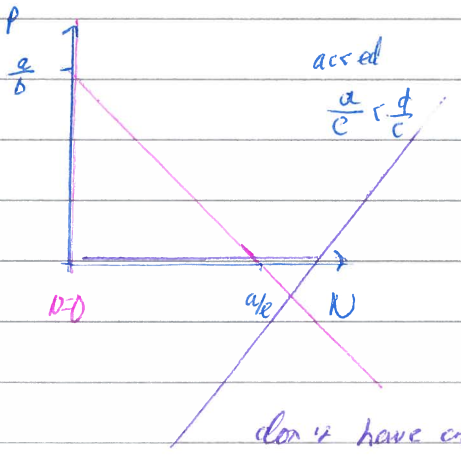
If $P = 0$ then $a - eN - bP = 0 \Rightarrow N = \frac{a}{e}$

For an interior steady state $a - eN - bP = 0$

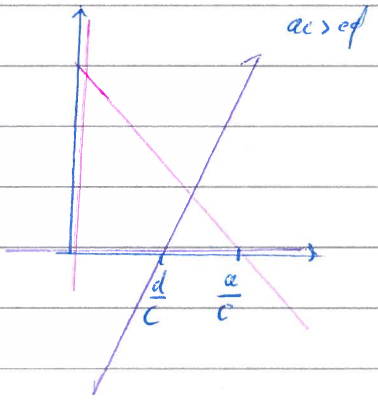
$-d + cN - fP = 0$

$$\begin{pmatrix} e & b \\ c & -f \end{pmatrix}\begin{pmatrix} N \\ P \end{pmatrix} = \begin{pmatrix} a \\ d \end{pmatrix} \Rightarrow \begin{pmatrix} N \\ P \end{pmatrix} = \frac{1}{-ef-bc}\begin{pmatrix} -f & -b \\ -c & e \end{pmatrix}\begin{pmatrix} a \\ d \end{pmatrix}$$

$$\begin{matrix} N \\ P \end{matrix} = \frac{1}{ef+bc}\begin{pmatrix} fa+bd \\ ca-ed \end{pmatrix}$$ but need $ac > ed$ for this to exist



don't have crossing which is relevant



Let $F(N,P) = N(a - eN - bP)$

$G(N,P) = P(-d + cN - fP)$

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

Steady state $(0,0)$ $\left(\frac{a}{e}, 0\right)$

and (N^*, P^*) when $ac > ed$

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

$\Rightarrow$ saddle at 0

$$M_{(\frac{a}{e},0)} = \begin{pmatrix} -a & -\frac{ba}{e} \\ 0 & \frac{ca}{e} - d \end{pmatrix}$$

$\lambda_1 = -a < 0, \quad \lambda_2 = \frac{1}{e}(ca - de) < 0$ if $ac < de$ i.e. when there is no interior

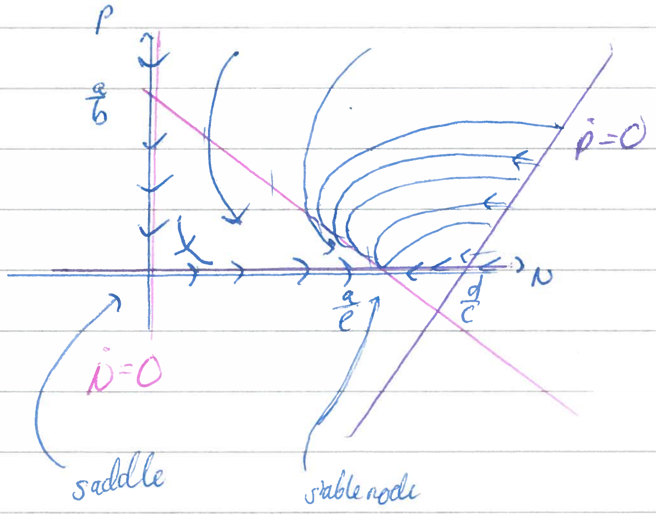
> 0 if $ac > de$ when there is a steady state

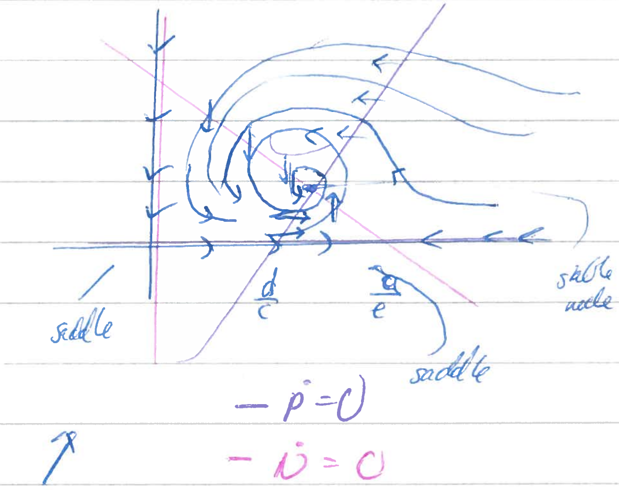
$$M_{(N^*,P^*)} = \begin{pmatrix} -eN^* & -bN^* \\ cP^* & -fP^* \end{pmatrix}$$

$\Longrightarrow \det M = N^* P^* (ef + bc) > 0$ so don't have saddle

$\operatorname{trace} M = -eN^* - fP^* < 0$

$\Longrightarrow$ stable





↗

know this is stable so expect a spiral

Predator - Prey models

N = prey

P = predator

per capita growth rate → $\frac{\dot N}{N} = F(N,P)$ $\qquad \frac{\dot P}{P} = G(N,P)$

$\dot N = NF(N,P)$ ← makes sense since if no pop. at beginning ⟹ always no population

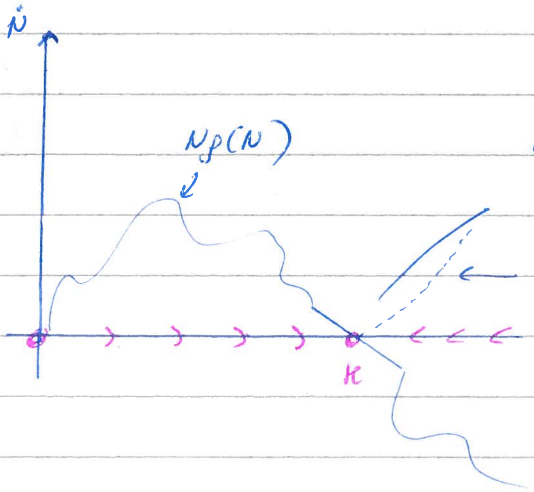
In absence of predator $(P=0)$ we would like the feature that provided $N(0)>0$, $\exists$ K such that $N(t) \to K$
(i.e. always tend to a carrying capacity $K>0$)

When $P=0$ $\quad \dot N = Nf(N)$ some f

For K to be a steady state, need $f(K)=0$ since then $\dot N = 0$ at $N=K$

Since we want all $N(t) \to K$ we do not want any other non-zero steady states

We also want K to be stable i.e. for $N=K+\varepsilon$ $(\varepsilon>0)$ we want $\dot N = (K+\varepsilon)f(N+\varepsilon) < 0$ and for $N = K-\varepsilon$ $\quad \dot N = (N-\varepsilon)f(N-\varepsilon) > 0$



want $\frac{d}{dN} Nf(N)\Big|_{N=K} < 0$

← want to avoid this (zero gradient)

Need $Nf(N)$ increasing at $N=0$

$$\frac{d}{dN}\left(Nf(N)\right) = Nf'(N) + f(N)\Big|_{N=0} = f(0) > 0$$

For k to be stable need,

$$\frac{d}{dN}(N f(N))\Big|_{N=k} < 0$$

$$f(K) + K f'(K) < 0$$

$$\Longrightarrow f'(K) < 0 \quad \text{since } f(K) = 0$$

$$\frac{\dot{N}}{N} = f(N) - \phi(N, P)$$

↑ non negative function which represents predation

What can we say about ϕ?

If there's no predator $P=0$, there's no predation

$$\phi(N, 0) = 0 \quad \forall N \geq 0$$

Rate of increase in 'predation'

If $P \uparrow$ then the net reproduction rate of growth of N will decrease i.e. predation ϕ will increase

$$\frac{\partial \phi}{\partial P}(N, P) > 0$$

For $\frac{\partial \phi}{\partial N}$ we note that as $N \uparrow$ the chances that any individual is consumed decreases (safety in numbers)

$$\frac{\partial \phi}{\partial N}(N, P) < 0$$

Now for P: $\frac{\dot{P}}{P} = \sigma(N) - \mu$ $\quad \sigma(N) \geq 0$

$\mu > 0$ constant

As density $N \uparrow$ we expect increased consumption of prey to increase the per-capita growth of the predator

When $N=0$, no consumption $\Longrightarrow \sigma(0)=0$

If $N=0$, $\sigma(0)=0 \Longrightarrow \dot{P} = -\mu P \Longrightarrow P(t) = e^{-\mu t}P(0)$
$\longrightarrow 0$

$\longrightarrow$ extinction of predator

$\frac{\dot{N}}{N} = f(N) - \phi(N,P) \qquad \dot{P} = P(\sigma(N) - \mu)$

Check for steady states

$N(f(N) - \phi(N,P)) = 0 \qquad P(\sigma(N) - \mu) = 0$

If $N=0$ then $P=0$ is the only possibility

If $P=0$ $\quad N(f(N) - \phi(N,0)) = 0$

$\Longrightarrow N(f(N)) = 0 \Longrightarrow N = K$

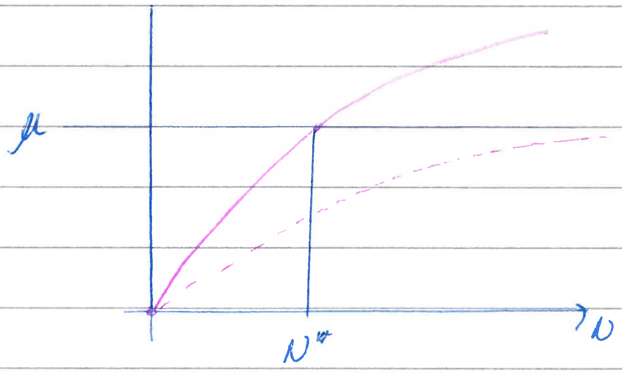
$\Longrightarrow (K, 0)$

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

$f(N^*) = \phi(N^*, P^*)$ ①

$\sigma(N^*) = \mu$ ②

From ②



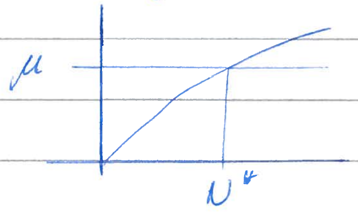
$\sigma'(N) > 0 \Longrightarrow$

σ is increasing

Either $\exists$ unique N^* where $\sigma(N^*) = \mu$

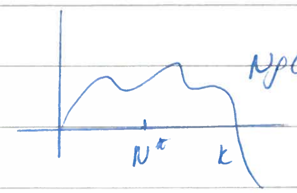
OR there is no interior steady state

$\sigma(N^*) = \mu \Longrightarrow N^* = \sigma^{-1}(\mu)$



If $\exists\ N^*$ with $\sigma(N^*) = \mu$ then we need to find a P such that $\rho(N^*) = \phi(N^*, P)$

We know that for $P > 0$, $\varphi(N^*, P) > 0 \implies$ necessarily $\rho(N^*) > 0$
$\implies N^* < K$

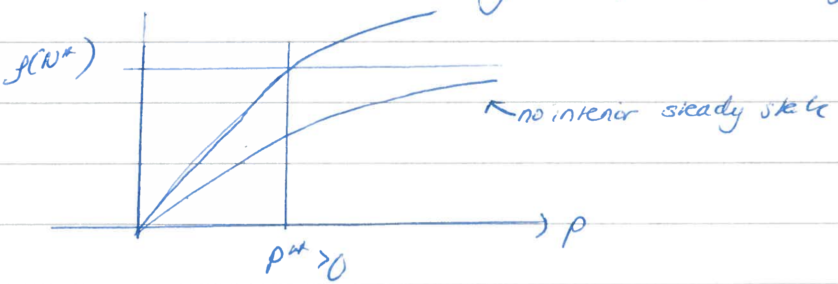


and if $N^* < K$
$\underline{\sigma^{-1}(\mu) < K}$

An interior steady state will not exist unless $\sigma^{-1}(\mu) < K$ (i.e. $\sigma(K) > \mu$)

Thus when $\sigma^{-1}(\mu) < K$ we seek P s.t. $\rho(N^*) = \phi(N^*, P)$

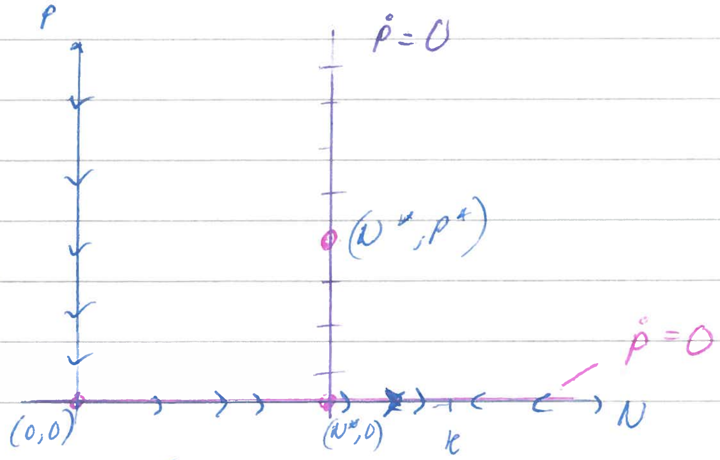
Since $\frac{\partial \phi}{\partial P} > 0$



So if ϕ passes above $\rho(N^*)$ there is a unique P^* such that $\rho(N^*) = \phi(N^*, P^*)$

$\implies$ solve for P function of N

$\sigma(N) = \phi(N, P)$ ← other nullcline



no prey $\implies$ predator goes extinct

$N^* = \sigma^{-1}(\mu)$

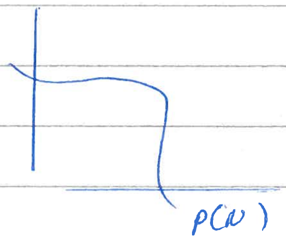
no predator
$N \to$ carrying capacity

Assume that when $\sigma(N) = \phi(N, P)$ we can solve to get

$P = P(N)$ $\qquad \sigma(N) = \phi(N, P(N))$

Differentiate $\qquad \sigma'(N) = \frac{\partial \phi}{\partial N}(N, P(N)) + \frac{\partial \phi}{\partial P}(N, P(N)) \frac{dP}{dN}(N)$

$$\frac{dP}{dN} = \frac{\overset{>0}{\sigma'(N)} - \frac{\partial \phi}{\partial N}(N, P(N))}{\frac{\partial \phi}{\partial P}(N, P(N))} \boxed{>0}$$



Try $N = K$ $\boxed{>0}$

$$\frac{dP}{dN}(K) = \frac{\sigma'(K) - \frac{\partial \phi}{\partial N}(K, 0)}{\frac{\partial \phi}{\partial P}(K, 0)} \boxed{>0}$$

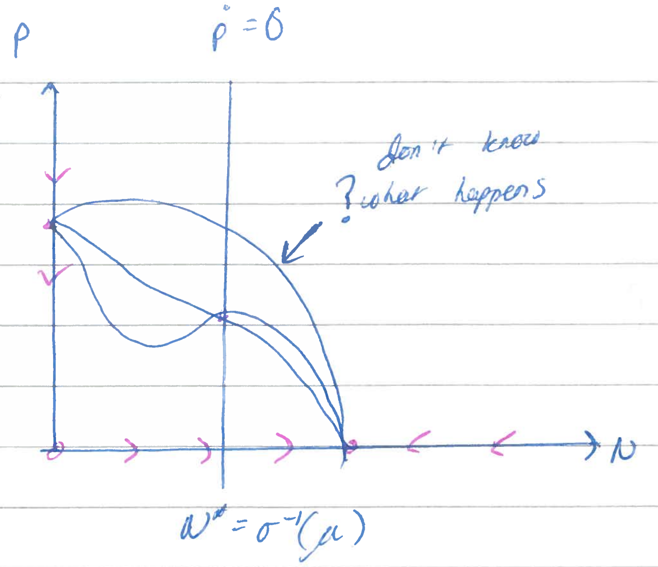
$$= \frac{dP/dt}{dN/dt}$$

$N^*, 0$ between $(N^*, 0)$ and K $\qquad \mathring{N} > 0$

$\mathring{P} = P(\sigma(N) - \mu) > 0$

Will come back to this

10/02/15



Nullcline $\dot{N} = 0$ if $N = 0$

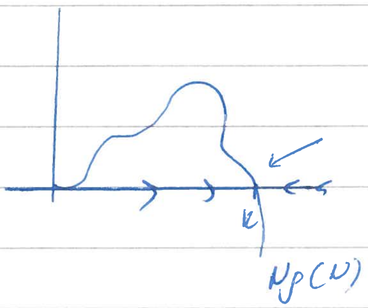
or $\rho(N) = \varphi(N, P)$

↑ was σ in last lecture i.e. wrong

$$\rho'(N) = \frac{\partial\varphi}{\partial N}(N, P) + \frac{\partial\varphi}{\partial P} \cdot P'(N)$$

$$P'(N) = \frac{\rho'(N) - \frac{\partial\varphi}{\partial N}(N, P(N))}{\frac{\partial\varphi}{\partial P}(N, P(N))}$$

$\frac{\partial\varphi}{\partial P} > 0$, $\frac{\partial\varphi}{\partial N} < 0$ and for $\rho'(N)$



$\dot{N} = N\rho(N)$ in absence of predator

We wanted $\rho'(K) < 0$ for stable

$=0$ since $P = 0$

$$P'(K) = \frac{(<0) - \cancel{\frac{\partial\varphi}{\partial N}(K, 0)}}{(>0)}$$

$P(K) = 0$

System at carrying capacity - it is steady

< 0

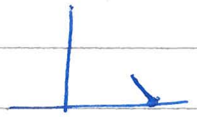
When $N = 0$, $0 < \rho(0) = \varphi(0, P(0))$

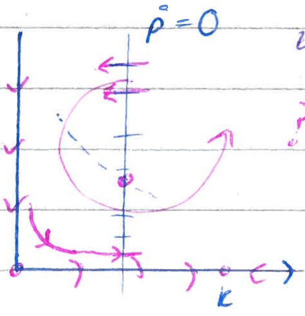
$\Rightarrow \varphi(0, P(0)) > 0$, $\varphi(0, 0) = 0$

$\Rightarrow P(0) > 0$

Nullcline crosses $N=0$ with $P(0) > 0$

Nullcline at $N=K$ has $P'(K) < 0$





$N^* = \sigma^{-1}(\mu)$

change of sign since above line in middle

$$\dot{N} = N(\rho(N) - \varphi(N, P)) = F$$
$$\dot{P} = P(\sigma(N) - \mu) = G$$

$$M = \begin{pmatrix} \frac{\partial F}{\partial N} & \frac{\partial F}{\partial P} \\ \frac{\partial G}{\partial N} & \frac{\partial G}{\partial P} \end{pmatrix} = \begin{pmatrix} \rho(N) - \phi(N,P) + N(\rho'(N) - \frac{\partial \varphi}{\partial N}) & -N\frac{\partial \varphi}{\partial P} \\ P\sigma'(N) & \sigma(N) - \mu \end{pmatrix}$$

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

$\rho(0) > 0$
$-\mu < 0$ $\implies$ $(0,0)$ is a <u>saddle</u>

$$M_{(K,0)} = \begin{pmatrix} 0 - \phi(K,0) + K(\rho'(K) - \frac{\partial \varphi}{\partial N}(K,0)) & -K\frac{\partial \varphi}{\partial P}(K,0) \\ 0 & \sigma(K) - \mu \end{pmatrix}$$

$$= \begin{pmatrix} K\rho'(K) & -K\frac{\partial \varphi}{\partial P}(K,0) \\ 0 & \sigma(K) - \mu \end{pmatrix}$$

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

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

For an interior steady state $\sigma(K) > \mu$ and in this case $(K, 0)$ is a saddle

If $\sigma(K) < \mu$ then $\lambda_1, \lambda_2 < 0 \implies (K, 0)$ is stable node

$$M_{(N^*,P^*)} = \begin{pmatrix} 0 + N^*\left(f'(N^*) - \frac{\partial \varphi}{\partial N}(N^*, P^*)\right) & -N^* \frac{\partial \varphi}{\partial P}(N^*, P^*) \\ P^* \sigma'(N^*) & 0 \end{pmatrix}$$

$$\text{trace } M_{(N^*,P^*)} = \lambda_1 + \lambda_2 = N^*\left(f'(N^*) - \frac{\partial \varphi}{\partial N}(N^*, P^*)\right)$$

$$\det M_{(N^*,P^*)} = \lambda_1 \lambda_2 = N^* P^* \sigma'(N^*) \frac{\partial \varphi}{\partial P}(N^*, P^*) > 0$$

$\implies$ cannot have a saddle at (N^*, P^*)

Comes down to the trace

$\lambda_1 + \lambda_2 = 2\,\mathrm{Re}(\lambda_1 + \lambda_2)$

$\implies$ if $\lambda_1 \lambda_2$ real, $\det > 0 \implies$ must be same sign

If trace $M > 0 \implies \lambda_1, \lambda_2 > 0 \implies$ unstable

$< 0 \implies$ " < 0 stable node

If λ complex, $\lambda_1 = \overline{\lambda_2}$ $\quad \lambda_1 + \lambda_2 = 2(\mathrm{Re}\,\lambda_1)$

$\implies$ if trace $M < 0$ (N^*, P^*) stable spiral

> 0 (N^*, P^*) unstable spiral

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

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

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

Set $x = R\cos\theta$ $\quad y = R\sin\theta$ $\qquad R^2 = x^2+y^2$

$\frac{d}{dt}\left(\frac{1}{2}R^2\right) = \mu R^2 - R^4$ $\qquad 2R\dot{R} = 2x\dot{x} + 2y\dot{y}$

$\Longrightarrow \dot{R} = \mu R - R^3$

$\frac{y}{x} = \tan\theta$ $\qquad \frac{\dot{y}}{x} - \frac{\dot{x}y}{x^2} = \sec^2\theta\,\dot{\theta}$

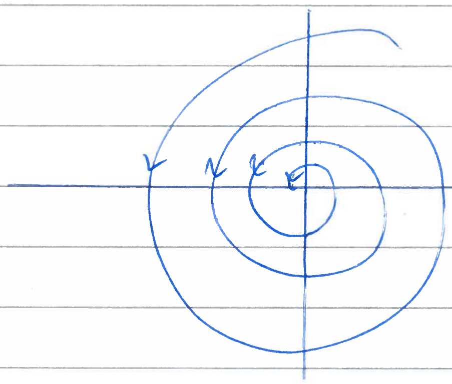
$x\dot{y} - \dot{x}y = x^2\left(1 + \frac{y^2}{x^2}\right)\dot{\theta}$

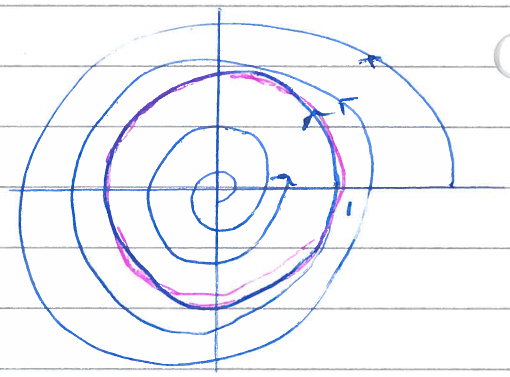
$x^2 + \mu xy - xyR^2 - (\mu xy - y^2 - xyR^2) = R^2\dot{\theta}$

$R^2 = R^2\dot{\theta} \Longrightarrow \dot{\theta} = 1$

$\Longrightarrow$ in polars H becomes $\dot{R} = R(\mu - R^2)$ $\quad \dot{\theta} = 1$

$\mu = 0$, $\dot{R} = -R^3$ $\qquad \mu = 1$ $\quad \dot{R} = R(1-R^2)$





$\dot{R} > 0$ if $R < 1$

$\dot{R} < 0$ if $R > 1$

○ is periodic orbit

periodic orbit trapped between the two

This formation of a periodic orbit following a change of stability of a steady state around which the periodic orbit winds; this is called a HOPF Bifurcation

Hopf Bifurcation Theorem

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

$(x, y) \in \Omega \subset \mathbb{R}^2 \qquad (\Omega \text{ open})$

$\mu \in (-\varepsilon, \varepsilon)$ for some $\varepsilon > 0$

Let $\underline{x}_\mu = (x_\mu, y_\mu)$ be a steady state for each $\mu \in (-\varepsilon, \varepsilon)$

Suppose that $M = \begin{pmatrix} f_x & f_y \\ g_x & g_y \end{pmatrix}$ at $\underline{x}_\mu$ has eigenvalues $\lambda = \sigma(\mu) \pm i\omega(\mu)$

such that $\sigma(\mu) < 0$ if $\mu \in (-\varepsilon, 0)$

$\sigma(\mu) > 0 \qquad \mu \in (0, \varepsilon)$ and $\sigma(0) = 0$

but $\omega(0) \neq 0$

Suppose also that the following technical conditions hold

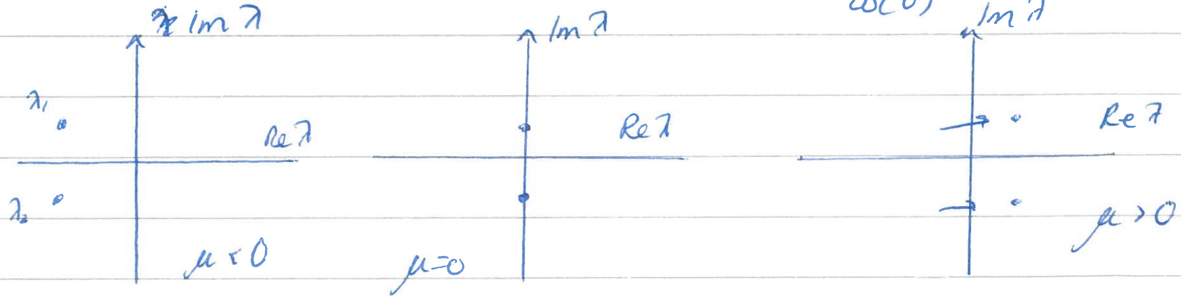
i) f, g analytic in x, y, μ

ii) $\frac{d\sigma}{d\mu}(0) > 0$

iii) $\underline{x}_0$ is asymptotically stable

don't need to check in an exam

Then for sufficiently small $\mu > 0$ the unstable steady state $\underline{x}_\mu$ is surrounded by a periodic orbit (which is stable) and whose ~~period~~ amplitude typically depends on μ, and whose period is approximately $\frac{2\pi}{\omega(0)}$



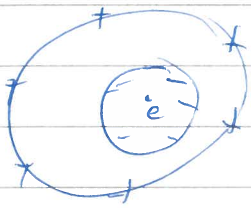
+ve real parts
lost stability

Bifurcation at
$\mu = 0$

6) ∞ from self energy of point charge so can exclude it

may
In ⑦ will get log ∞

Exam: significant amount of bookwork
can repeat bookwork - will get 60%



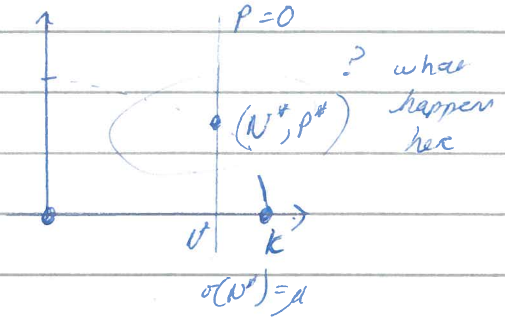
-ve charges induced
on inside
+ve on outside

13/02/15

Predator Prey Models

$\dot{N} = N(\rho(N) - \phi(N,P))$ ← predation term

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



Stability matrix

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

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

$\text{trace } M^* = \lambda_1 + \lambda_2 = N^*\boxed{(\rho'(N^*) - \phi_N(N^*,P^*))}$

If trace $M^* > 0 \Rightarrow$ unstable

$< 0 \Rightarrow$ stable

i.e. stability of (N^*,P^*) changes precisely where trace $M^* = 0$

Nullcline $\dot{N} = 0$, $N \neq 0$ $\rho(N) = \phi(N, P(N))$

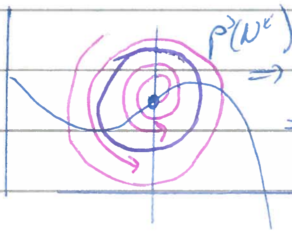
$\rho'(N) = \phi_N + P'(N)\phi_P$

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

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

observe similarity to above

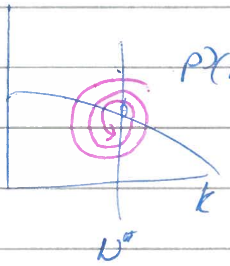
Hence $\text{sgn trace } M_{(N^*,P^*)} = \text{sgn}(P'(N^*))$



$P'(N^*) > 0$

$\Rightarrow \lambda_1 + \lambda_2 > 0$

$\Rightarrow$ unstable



$P'(N^*) < 0$

$\Rightarrow \lambda_1 + \lambda_2 < 0$

$\Rightarrow$ stable

1

Hence for a Hopf Bifurcation we look for the gradient of the nullcline $N \to P(N)$ to vary from negative to positive

Holling Functional Responses I - III

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

$$\omega = \frac{N\phi(N,P)}{P}$$

= expected density of prey consumed per unit time per predator

= feeding rate

Holling type I

$\omega = \gamma N$; i.e. feeding rate grows linearly (unbounded) with N

with $\sigma = \frac{\sigma N}{\gamma P} \phi(N,P)$ Ps cancel so this is a function of N

increases linearly unbounded

$$\Longrightarrow \quad \dot{N} = N(\rho(N) - \gamma P)$$
$$\dot{P} = P\left(\frac{\sigma}{\gamma}N - \mu\right)$$

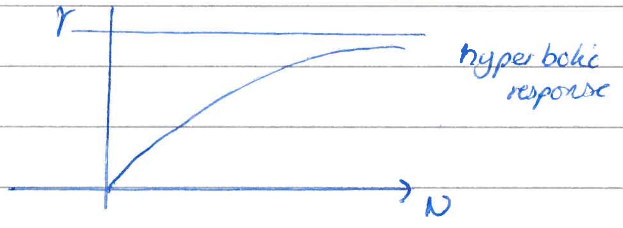
$\rho(N) = 1 - \frac{N}{K}$

$\Rightarrow$ predator prey equations we've met previously

Holling type II

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

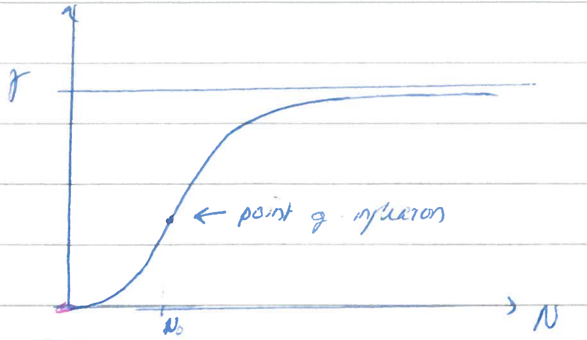
γ = max feeding rate



Here there's a max feeding rate which agrees with the fact that a predator has to catch, consume prey & so the max feeding rate cannot increase indefinitely - it has to saturate at γ

Holling type III

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



γ = max feeding rate

Point of inflexion N_0 below which the prey can successfully take refuge

Holling type II (in detail)

~~$\dot{N} = N$~~

$$\dot{N} = \rho N\left(1-\frac{N}{K}\right) - \frac{\gamma N P}{A+N} \qquad \gamma, A > 0$$

logistic growth   predation type II

$$\dot{P} = P\left(\frac{\sigma N}{A+N} - \mu\right) \qquad \sigma, \mu > 0$$

Steady states $$N\left(\rho\left(1-\frac{N}{K}\right) - \frac{\gamma P}{A+N}\right) = 0$$

$$P\left(\frac{\sigma N}{A+N} - \mu\right) = 0$$

↳ $N=0$, $P=0$

$P=0$ $\quad N\left(\rho\left(1-\frac{N}{K}\right)\right) = 0 \Rightarrow N=K$

For interior steady state $\frac{\sigma N}{A+N} = \mu$ and $P = \frac{\rho}{\gamma}(A+N)\left(1-\frac{N}{K}\right)$

$\Rightarrow \sigma N = \mu A + \mu N$

$$N = \frac{\mu A}{\sigma - \mu}$$

$\Rightarrow$ > 0 $\Rightarrow$ require $\sigma > \mu$

But for $P > 0$ need $N < K$

For $N < K \implies \frac{\mu A}{\sigma - \mu} < K \implies \underline{\mu A < K(\sigma - \mu)}$

also required for interior steady state (N^*, P^*)

Summarize $(0,0)$, $(K,0)$ and (N^*, P^*) if $\underline{\sigma > \mu}$ and $\mu A < K(\sigma - \mu)$

This is embedded in this

Stability matrix

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

$$M_{(0,0)} = \begin{pmatrix} \rho & 0 \\ \cancel{\frac{\sigma}{A}}\ 0 & -\mu \end{pmatrix} \implies \begin{array}{l} \lambda_1 = \rho > 0 \\ \lambda_2 = -\mu < 0 \end{array}$$

$\implies (0,0)$ is a saddle

$$M_{(K,0)} = \begin{pmatrix} -\rho & \frac{-\gamma K}{A+K} \\ 0 & \frac{\sigma K}{A+K} - \mu \end{pmatrix} \implies \begin{array}{l} \lambda_1 = -\rho < 0 \\ \lambda_2 = \frac{\sigma K}{A+K} - \mu \end{array}$$

$$\lambda_2 = \frac{\sigma K}{A+K} - \mu$$

Looking at $\mu A < K(\sigma - \mu) \implies \mu(A+K) < K\sigma$

$$\implies \mu < \frac{K\sigma}{A+K}$$

If $\exists$ interior steady state, then $\mu < \frac{K\sigma}{A+K}$

$\implies \lambda_2 > 0$

and so $\lambda_1 = -\rho < 0$, $\lambda_2 > 0 \implies \underline{\text{saddle}}$ at $(K,0)$

If there's no interior steady state $\left(\mu > \frac{k\sigma}{A+k}\right)$

then $\lambda_2 < 0$ & hence $\lambda_1 < 0,\ \lambda_2 < 0 \Longrightarrow (k,0)$ is a stable node.

Interior steady state $\quad A\mu < k(\sigma - \mu)$

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

should be A rather than N^* →

For (N^*, P^*)

$$\text{trace } M_{(N^*,P^*)} = -\frac{\rho N^*}{k} + \frac{\rho N^* P^*}{(A+N^*)^2} = \lambda_1 + \lambda_2$$

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

$\Longrightarrow$ not saddle

But $\lambda_1 + \lambda_2 = N^*\left(\frac{\rho P^*}{(A+N^*)^2} - \frac{\rho}{k}\right)$

Use that from

$\dot{N} = 0 \qquad N\left(\rho\left(1 - \frac{N}{k}\right) - \frac{\rho P}{A+N}\right) = 0$

$\Longrightarrow (N^*, P^*)$ has $\rho\left(1 - \frac{N^*}{k}\right) = \frac{\rho P^*}{A+N^*}$

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

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

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

$$= \frac{s N^*}{(A+N^*)K} (K - A - 2N^*) \qquad = \lambda_1 + \lambda_2$$

If $A > K$ $\quad \lambda_1 + \lambda_2 < 0$ and then (N^*, P^*) is always stable

But if $K > A$ a Hopf Bifurcation is now possible

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

So $\lambda_1 + \lambda_2 = \left(K - A - \frac{2\mu A}{\sigma - \mu} \right)$

Suppose $K > A$, let $\delta = \sigma(K-A) - \mu(K+A)$

Fix σ, K, A and vary μ (death rate of predator)

For $\delta > 0$ $\quad (N^*, P^*)$ is unstable

$\delta < 0$ $\quad$ stable

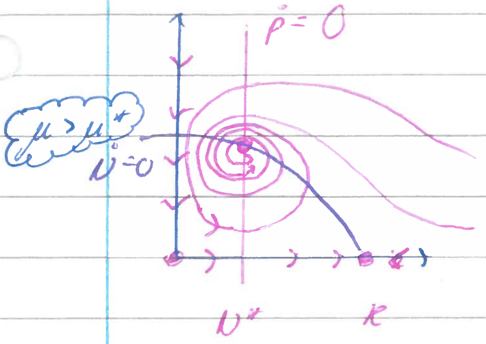
Change μ so that δ changes from <0 to >0

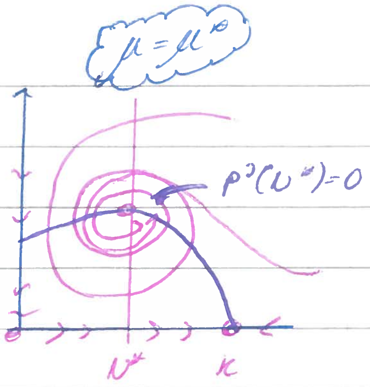
Start with $\mu > \frac{\sigma(K-A)}{K+A} \Rightarrow \delta < 0 \Rightarrow (N^*, P^*)$ stable

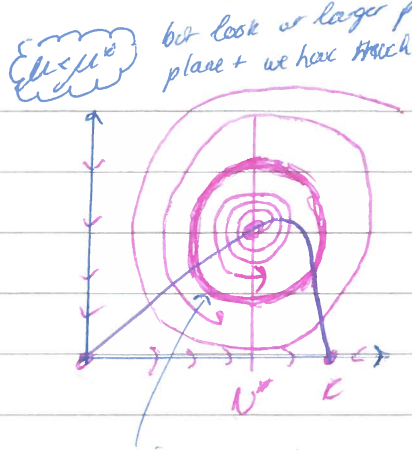
reduce μ through $\mu^* = \frac{\sigma(K-A)}{A+K}$ to $\mu < \frac{\sigma(K-A)}{K+A}$

Then the steady state (N^*, P^*) goes unstable as μ passes through μ^* $(\delta = 0)$

And so we get a Hopf Bifurcation (assuming technical points 1-3 can be verified)







unstable inside but look at larger phase plane + we have much the same

attracting periodic orbit appears

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

↑ parabola

μ gets smaller, circle gradually grows

Holling Type III

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

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

Steady states $(0,0)$ $(K,0)$ and (N^*, P^*) satisfying

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

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

$$\Longrightarrow \quad \sigma N^2 = \mu A^2 + \mu N^2$$

$$N^* = \left(\frac{\mu}{\sigma-\mu}\right)^{1/2} A \qquad \text{when} \quad \sigma > \mu$$

and $\quad P^* = \rho/_{N^*\gamma}\,(A^2+N^{*2})\left(1-\frac{N^*}{K}\right)$

so again need $N^* < K$

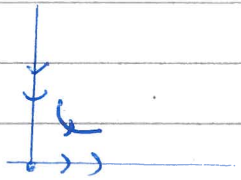
i.e. $\quad \frac{\mu}{\sigma-\mu} A^2 < K^2 \Longrightarrow A\sqrt{\mu} < (\sqrt{\sigma-\mu})K$

Stability matrix

$$M = \begin{pmatrix} \rho\left(1-\frac{N}{K}\right) - \rho\frac{N}{K} - \frac{2\gamma PN}{A^2+N^2} - \frac{2\gamma N^3 P}{(A^2+N^2)^2} & \frac{-\gamma N^2}{A^2+N^2} \\ \frac{2\sigma PA^2 N}{(A^2+N^2)^2} & \frac{\sigma N^2}{A^2+N^2} - \mu \end{pmatrix}$$

typo in online notes - should be N here

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



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

So $\lambda_1 = -\rho < 0$, $\lambda_2 = \frac{\sigma K^2}{A^2+K^2} - \mu$

We have $A^2\mu < K^2(\sigma - \mu)$

$(A^2+K^2)\mu < K^2\sigma$

$\mu < \frac{K^2\sigma}{A^2+K^2}$

So $\lambda_2 > 0$ if (N^*, P^*) exists

$\Longrightarrow$ saddle

If no interior steady state exists so that $\mu > \frac{K^2\sigma}{A^2+K^2}$

then $\lambda_1 < 0$ $\lambda_2 < 0$

$\Longrightarrow$ stable node

Interior steady state (case $A\sqrt{\mu} < \sqrt{\sigma-\mu}\, K$)

used eqn then defines steady state

$$M_E = \begin{pmatrix} -\frac{\rho N}{K} - \frac{\gamma NP}{A^2+N^2} + \frac{2\gamma N^3 P}{(A^2+N^2)^2} & \frac{-\gamma N^2}{A^2+N^2} \\ \frac{2\sigma PA^2N}{(A^2+N^2)^2} & 0 \end{pmatrix}$$

$$\lambda_1 + \lambda_2 - \text{trace } N^* = -\frac{\rho N}{\kappa} - \frac{\gamma N P}{A^2+N^2} + \frac{2\gamma N^3 P}{(A^2+N^2)^2}$$

$$\lambda_1 \lambda_2 = \det N^* = \frac{2\sigma \gamma A N^3 P}{(A^2+N^2)^2} > 0$$

So we cannot have a saddle at N^*, P^*

Let's look at where

$$\alpha := -\frac{\rho N}{\kappa} - \frac{\gamma N P}{A^2+N^2} + \frac{2\gamma P N^2}{(A^2+N^2)^2}$$

$$\alpha = -\frac{\rho N^*}{\kappa} - \underset{\substack{\uparrow \\ \text{using nullcline} \\ \text{condition once}}}{\rho\left(1 - \frac{N^*}{\kappa}\right)} + \frac{2\gamma N^* P^*}{A^2+N^{*2}} \frac{N^{*2}}{A^2+N^{*2}}$$

$$= -\frac{\rho N^*}{\kappa} - \rho\left(1 - \frac{N^*}{\kappa}\right) + 2\rho\left(1 - \frac{N^*}{\kappa}\right)\frac{N^{*2}}{A^2+N^{*2}}$$

$$= -\rho + 2\rho\left(1 - \frac{N^*}{\kappa}\right)\frac{\mu}{\sigma}$$

$$= \rho\left(\frac{2\mu}{\sigma} - 1 - \frac{2\mu A}{\sigma k}\sqrt{\frac{\mu}{\sigma-\mu}}\right)$$

If $2\mu < \sigma$, $\alpha < 0 \implies$ no Hopf Bifurcation can occur

$\implies$ periodic orbit only if $2\mu > \sigma$

You are possibly missing some notes here!

24/02/15
27/02/15

Single species discrete time models

We consider populations that undergo reproduction at discrete times (e.g. seasonally) and are non-overlapping (e.g. the generations do not overlap as the parents all die before the offspring reach sexual maturity

Let N_t = population density at generation t
So $N_{t+1} = f(N_t)$ non-overlapping discrete time

Here $f : \mathbb{R} \rightarrow \mathbb{R}$

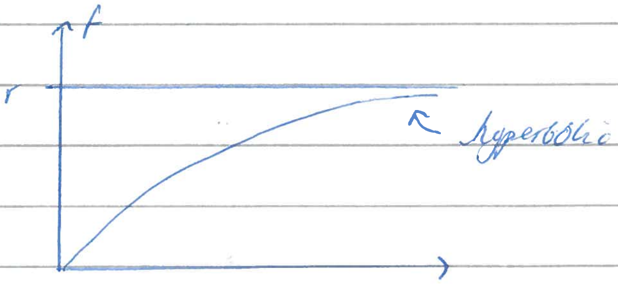
Simplest model: Number in generation $t+1$ is proportional to number in generation t
i.e. $N_{t+1} = r N_t$

$\Longrightarrow$ $N_t = N_0 r^t$ for $t = 0, 1, 2, 3, \dots$
and N_0 = population at $t = 0$

If $r > 1$, $N_t \longrightarrow \infty$
$r < 1$, $N_t \longrightarrow 0$
$r = 1$, $N_t = N_0$ $\forall$ $t = 1, 2, \dots$

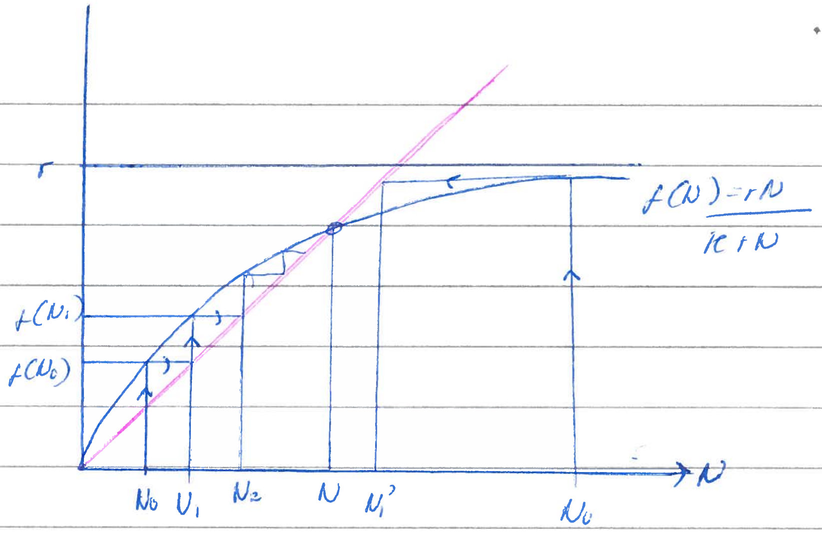
To avoid $N_t \rightarrow \infty$ we require density dependent growth

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



$N_{t+1} = f(N_t)$ so if $f(N_t) < N_t$ N is decreasing
$f(N_t) > N_t$ increasing
$f(N_t) = N_t$ then $N_{t+1} = N_t$
$\forall$ $k = 1, 2, \dots$

Cobweb map:



This construction shows that if $N_0 > 0$, $N_t \to N^*$ as $t \to \infty$

To find steady states; these are points N^* where $f(N^*) = N^*$

$\longrightarrow$ they are fixed points of the map f

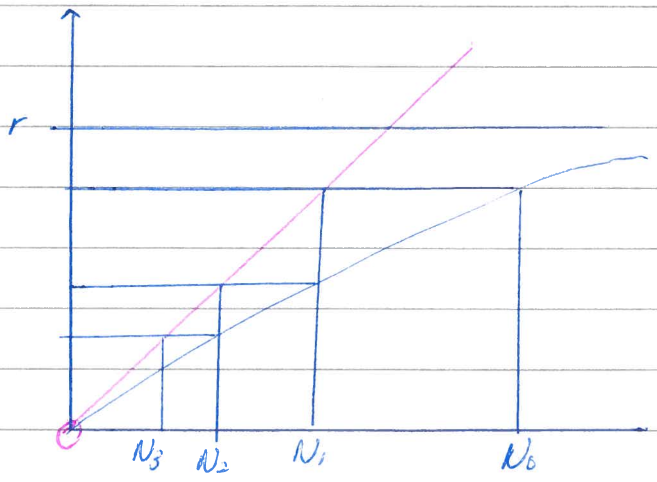
For Verhulst map:

$$N = \frac{rN}{K+N} \Rightarrow N\left(1 - \frac{r}{K+N}\right) = 0$$

$\Longrightarrow$ either $N^* = 0$ or $N^* = r - K$

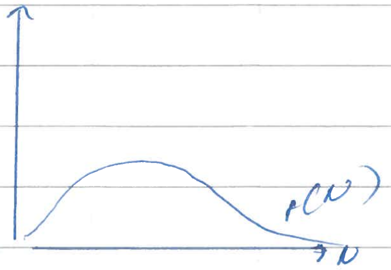
If $r < K$ the origin is the only steady state

If $r > K$ $\exists$ 2 steady states



Here $N_t \to 0$ as $t \to \infty$

$$N_t = \frac{rN_t}{1+N_t^2} = f(N_t)$$



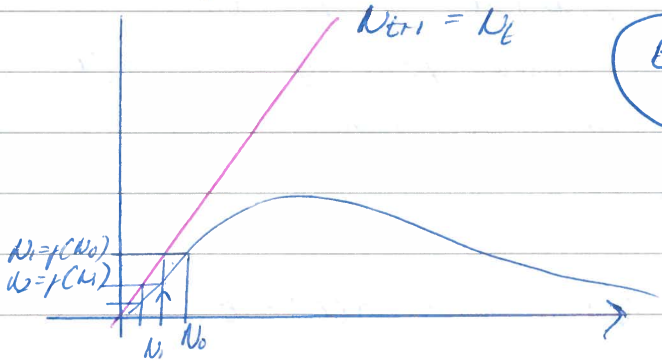
Steady states: $\frac{rN}{1+N^2} = N$:

$$\Longrightarrow N\left(1 - \frac{r}{1+N^2}\right) = 0$$

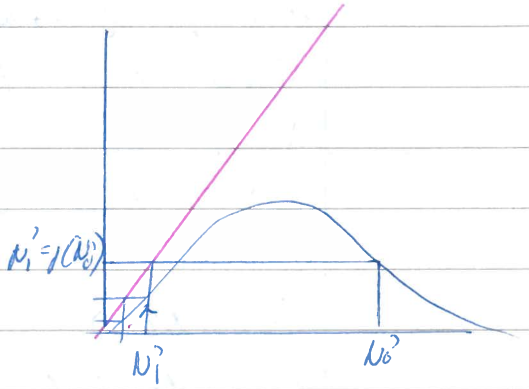
So $N^* = 0$ or $N^* = \sqrt{r-1}$ (provided $r > 1$)

27/02/15

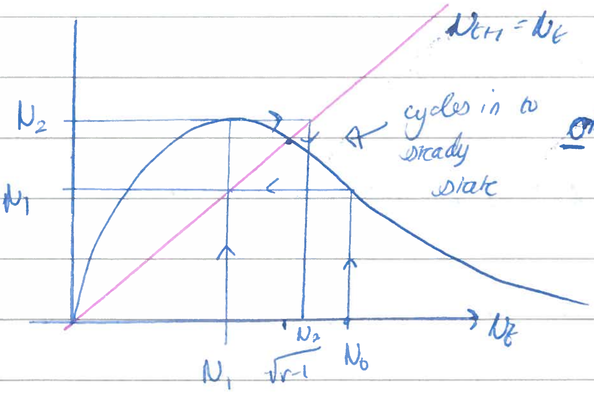
$N = f(N) = \frac{rN}{1+N^2} \Longrightarrow N = 0$ or $N = \sqrt{r-1}$ when $r > 1$.



Both $r<1$

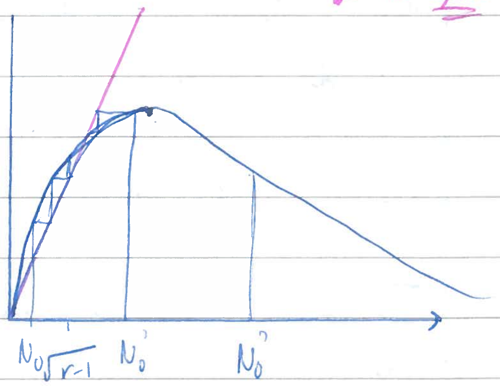


here peak
f is after line



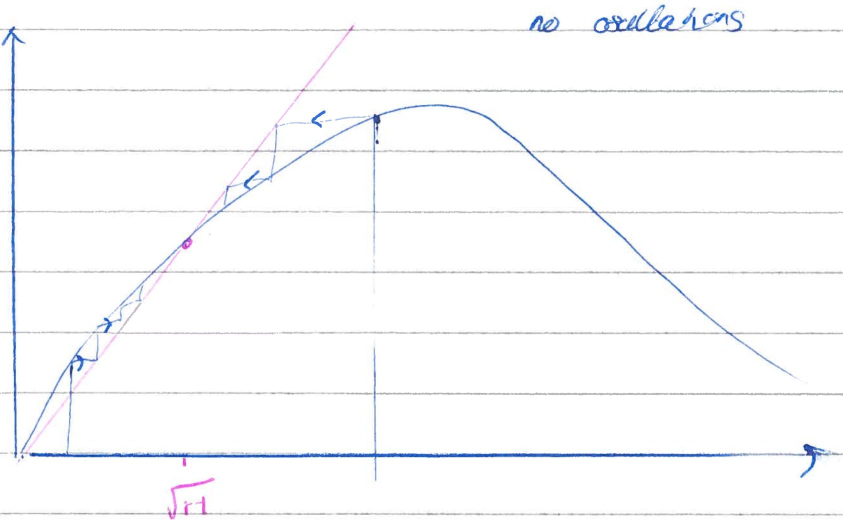
cycles in to steady state

OR



↑
this is because gradient at $\sqrt{r-1}$ is $-ve$

Last one exaggerated



no oscillations

Linear stability (of maps)

Map $f: \mathbb{R} \rightarrow \mathbb{R}$ $f(N) > 0$ if $N > 0$

Suppose that N^* is a fixed point of f $f(N^*) = N^*$

Suppose we consider a small perturbation $|\varepsilon| << 1$ from N^*. What happens?

Let $N(t) = N^* + n(t)$ where $n(0) = \varepsilon$

Let $N_t = N^* + n_t$ where $n_0 = \varepsilon$

Then $N_{t+1} = f(N_t)$

$N^* + n_{t+1} = f(N^* + n_t)$

Taylors: $N^* + n_{t+1} = f(N^*) + f'(N^*)n_t + O(n_t^2)$

This should be a good approximation for n_t if i) $f'(n_t) \neq 0$ and n_t is small

N^* is a fixed point of f: $f(N^*) = N^*$

So ignoring terms of order n_t^2 and higher, when n_t is small

$$n_{t+1} = f'(N^*)n_t$$

gives a good linear approximation to the evolving perturbation n_t

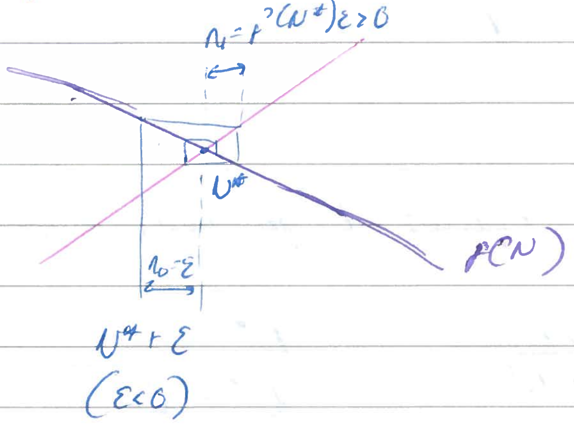
$$n_t = (f'(N^*))^t n_0 = (f'(N^*))^t \varepsilon$$

~~$N_{t+1} = \frac{rN_t}{1+N_t^2}$~~

~~$f(N) = \frac{rN}{4+N^2}$~~

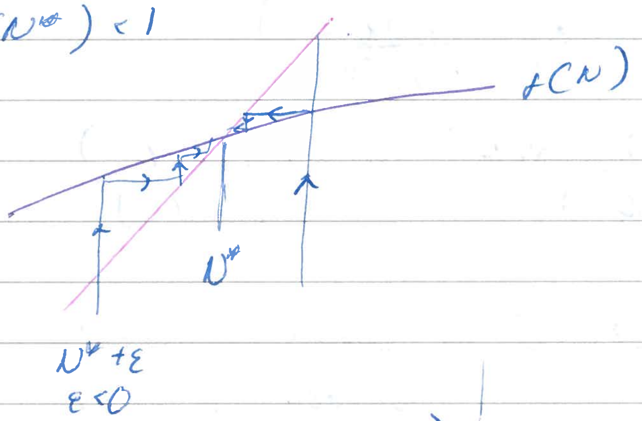
If $0 < |f'(N^*)| < 1$ then $n_t \to 0$ as $t \to \infty$ so this is (linear) stability

If $-1 < f'(N^*) < 0$ then $n_t \to 0$ but oscillates in sign



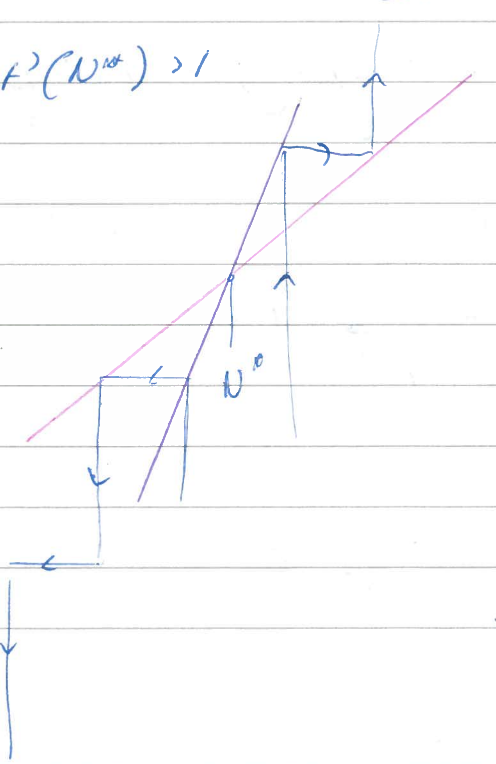
stable with oscillations

$0 < f'(N^*) < 1$



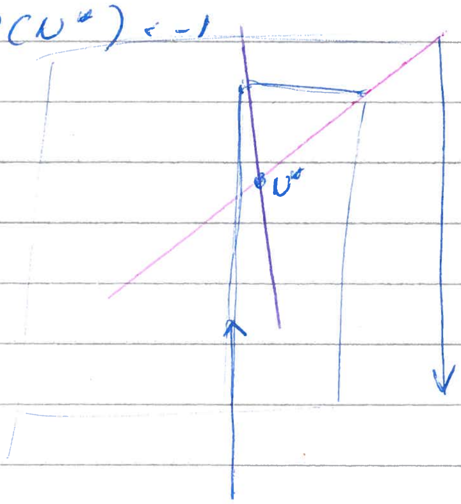
monotonically stable

Case $f'(N^*) > 1$



unstable (monotonic growth)

$f'(N^*) < -1$



unstable with oscillations

We ignore case when modulus = 1 for now, it is complicated

Example $f(N) = \frac{rN}{1+N^2}$ $\qquad N^* = 0$

$N^* = \sqrt{r-1}$ if $r > 1$

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

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

$f'(0) = r \Rightarrow 0$ is stable if $r < 1$

unstable if $r > 1$

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

When $r>1$: $f'(N^*) = \frac{r(1-N^{*2})}{(1+N^{*2})^2} = \frac{r(1-N^{*2})}{r^2}$

$$= \frac{r}{r^2}(1-r+1) = \frac{1}{r}(2-r) = \frac{2}{r} - 1$$

For stability we need $-1 < \frac{2}{r} - 1 < 1$

$0 < \frac{2}{r} < 2 \Rightarrow r > 1$

i.e. N^* is stable wherever it exists

If ~~we had $-1 = \frac{2}{r} - 1 \Rightarrow \frac{2}{r} = 0$ which is nonsense~~

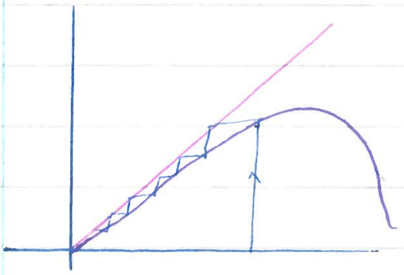
~~$\Rightarrow f'(N^*) > -1$~~

a) ~~$f(x) = O(g(x))$ as $x \to \infty$ / $x \to 0$ if we can find fixed constants K, X s.t. $|f| < K|g|$ / $|f| > K|g|$ for $x > X$~~

b) ~~$f(x) = o(g(x))$ as $x \to \infty$ / $x \to 0$ means $|f/g| \to 0$ as $x \to \infty$ / $x \to 0$~~

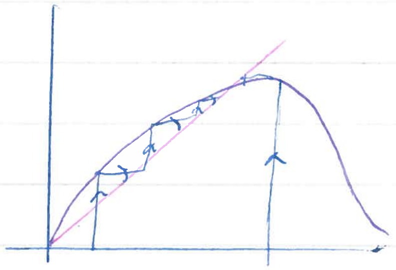
$0 = \frac{2}{r} - 1 \Rightarrow \frac{2}{r} = 1 \Rightarrow$ when $r = 2$ $f'(N^*) = 0$

$\Rightarrow$ if $r > 2$ then $f'(N^*) < 0$

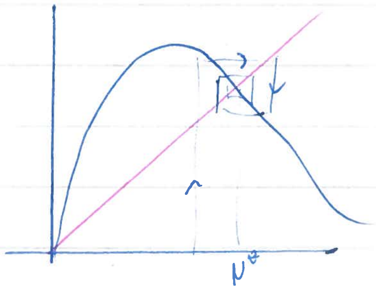


$r < 1$

origin $N^* = 0$ is stable (globally)



$1 < r < 2$



$r > 2$

$f(N) = N\exp\left(r\left(1-\frac{N}{K}\right)\right)$

$N_{t+1} = N_t \exp\left(r\left(1-\frac{N_t}{K}\right)\right)$ Set $u_t = \frac{N_t}{K}$

$U_{t+1} = u_t \exp(r(1-u_t))$

<u>Steady states</u>

$u = u\exp(r(1-u))$, $u^* = 0$ or $u^* = 1$
always exist unconditionally

$f(u) = u\exp(r(1-u))$

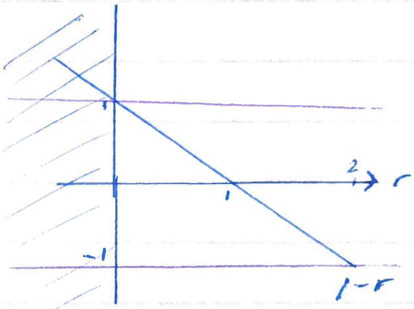
$f'(u) = \exp(r(1-u)) + u(-r)\exp(r(1-u))$

$= (1-ru)\exp(r(1-u))$

$f'(0) = e^r > 1$ since $r > 0$

$\longrightarrow$ $u^* = 0$ is unstable

$f'(u^*) = f'(1) = 1-r$

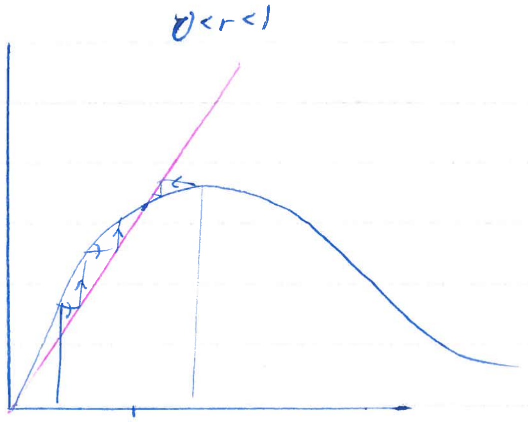


For $0 < r < 2$, $f'(1) \in (-1, 1)$

$\Longrightarrow$ stable

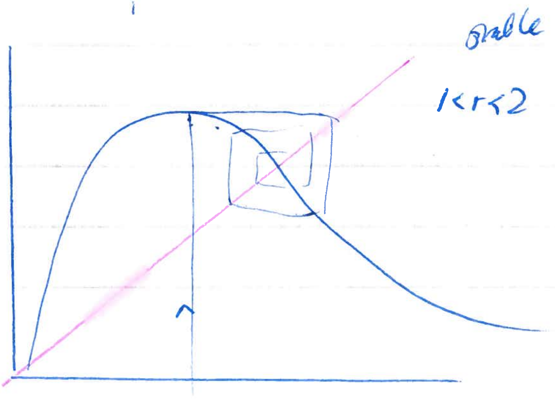
For $r > 2$ $u^* = 1$ is unstable with oscillations

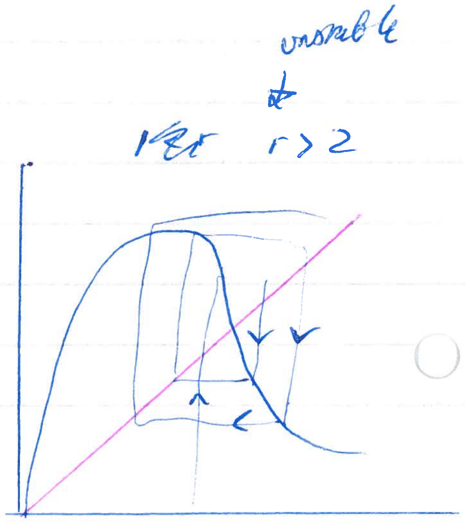
$(f'(1) < -1)$



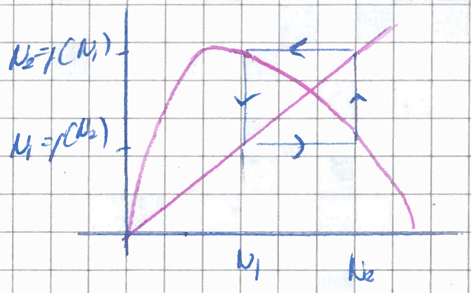
$f(u) = ue^{r(1-u)}$

$f'(u) = (1-ru)e^{r(1-u)}$





Cycles Cycle is discrete version of periodic orbit
2-cycle is of the form $\{N_1, N_2)$ when $f(N_1)=N_2$, $f(N_2)=N_1$
generates: N_1, N_2, N_1, N_2



For a 3-cycle $\{N_1, N_2, N_3\}$ $N_2 = f(N_1)$
$N_3 = f(N_2)$
$N_1 = f(N_3)$

... and so on

How to find 2-cycles

$$N_1 = f(N_2), \quad N_2 = f(N_1)$$

$$f(N_1) = f(f(N_2)) = N_2$$

$$f(f(N_1)) = N_1$$

Let $f^2 = f \circ f$ map composition
$f^k = f \circ f \circ \dots \circ f$ k composition of f

If $\{N_1, N_2\}$ is a 2-cycle then N_1, N_2 are fixed points of f^2

Does it mean that if $f^2(N) = N$ then $N \in \{N_1, N_2\}$

No! Every fixed point of f is also a fixed point of f^2, but is not part of a 2-cycle

So to find a 2-cycle $\{N_1, N_2\}$ we require solutions to $f^2(N) = N$ but $f(N) \neq N$

Example $f(N) = \dfrac{rN}{1+N^3} \Longrightarrow N^* = 0$ and $N^* = (r-1)^{1/3}$ if $r>1$

Find $f \circ f$

$$f(f(N)) = \frac{r f(N)}{1+(f(N))^3} = \frac{r\left(\frac{rN}{1+N^3}\right)}{1+\left(\frac{rN}{1+N^3}\right)^3} \qquad (A)$$

Fixed points of f^2

$$N = f^2(N) = \frac{r^2N/(1+N^3)}{1+r^3N^3/(1+N^3)^3}$$

Remove the steady state $N^* = 0$

$$\implies 1 = \frac{r^2 / 1+N^3}{1+ r^3N^3 / (1+N^3)^3} \qquad \text{Substitute } x = 1+N^3$$

$$1 = \frac{r^2/x}{1+\frac{r^3(x-1)}{x^3}} = \frac{r^2x^2}{x^3+r^3(x-1)}$$

$-3-2r+r^2$
$(r+1)(r-3)$

$$\implies x^3 - r^2x^2 + r^3x - r^3 = 0$$

Steady states $N^* = (r-1)^{1/3} \implies N^{*3}+1 = r$ $\qquad x = 1+N^3$

When $x = r$ $\qquad r^3 - r^4 + r^4 - r^3 = 0$

$$(x-r)(x^2 + \alpha x + r^2) = 0$$

Compare coeff. $\qquad -rx^2 + \alpha x^2 = -r^2x^2$

$$\alpha = -r^2 + r = r(1-r)$$

$$(x-r)(x^2 + r(1-r)x + r^2) = 0$$

$x = r$ or $x_\pm = -\frac{1}{2}r(1-r) \pm \frac{1}{2}\sqrt{r^2(1-r)^2 - 4r^2}$

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

$$= -\frac{1}{2}r(1-r) \pm \frac{r}{2}\left((r-5)(r-3)\right)^{1/2}$$ ⟵ this is wrong

Fixed points of f^2 are $x_\pm$ or in terms of N

$N^3+1 = x$

$$\implies N_\pm = (x_\pm - 1)^{1/3}$$

Hence we need $x_\pm > 1$ for a cycle $N_1 = (x_+ - 1)^{1/3}$
$N_2 = (x_- - 1)^{1/3}$

How do we find $x_\pm$ qualitatively

$x_\pm$ satisfies $x^2 + r(1-r)x + r^2 = 0$

So $\quad x^2 + r^2 = r(r-1)x$

So $\quad x_\pm r(r-1) > r^2$ when $r > 1$

$$x_\pm > \frac{r}{r-1} > 1 \quad \text{for } r > 1$$

Hence $N_\pm > 0$

Thus $f^2(N_\pm) = N_\pm$

Eliminated steady states so $f(N_\pm) \neq N_\pm$

Last point is that we need $(r-3)(r-5) > 0$

$(r-1)^2 > 4 \qquad 5 > r > 3$

If ~~[illegible]~~ $r > 3$ then ∃ a 2-cycle

This is wrong since he did factorisation wrong

Logistic Map

$N_{t+1} = rN_t\left(1 - \frac{N_t}{K}\right)$ where $K = \frac{1}{b}$

$= rN_t(1 - bN_t)$ this set of chaos theory

Set $u_t = \frac{N_t}{K}$

$u_{t+1} = ru_t(1-u_t)$

Steady states $u = ru(1-u)$ $\quad u = 0$ or $u = 1 - \frac{1}{r}$

$f(u) = ru(1-u)$, $\quad f'(a) = r(1-2u)$

$u^* = 0 \quad f'(0) = r$ So for $0 < r < 1$ this is stable

Stable for $r \in (0,1)$

and there are no other steady states when $r \in (0,1]$

If $r > 1$ there's a 2nd steady state and $u^* = 0$ is unstable

$f'\left(1 - \frac{1}{r}\right) = r - 2r\left(1 - \frac{1}{r}\right) = -r + 2 = 2 - r$

and $1 - \frac{1}{r}$ is stable for $r \in (1,3)$

Logistic map

03/03/15

$u_{t+1} = f(u_t)$ $f(u) = ru(1-u)$

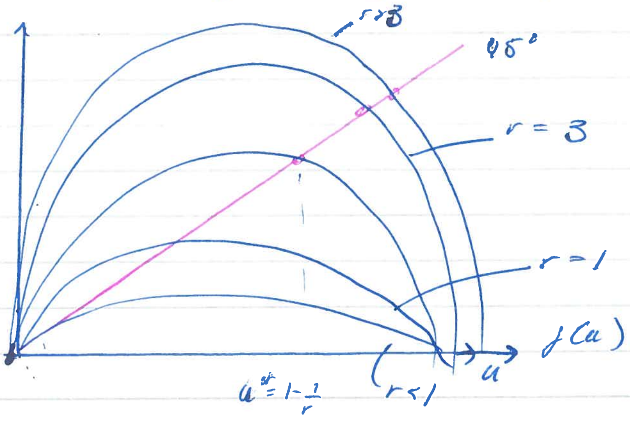
Steady states $u^* = 0$ and $u^* = 1 - \frac{1}{r}$

$f'(u) = r(1-2u)$

$f'(0) = r$ stable if $r < 1$

$f'(1-\frac{1}{r}) = 2 - r \implies$ stable if $0 < r < 3$ ~~exists~~

↑ exists for $r > 1$



What happens at r=3?

At $r=3$, $u^* = 1 - \frac{1}{r} = \frac{2}{3}$, u^* becomes unstable

Since for $2 < r < 3$ $-1 < f'(1-\frac{1}{r}) < 0$

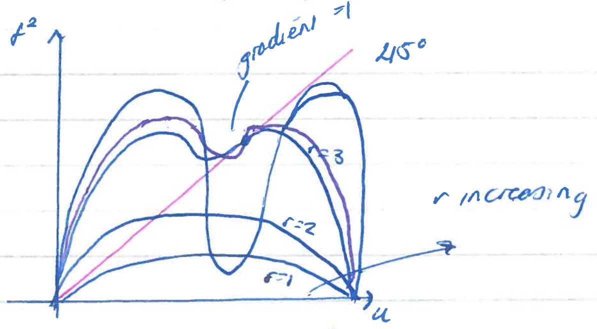
$\implies u^* = 1 - \frac{1}{r}$ is stable with oscillations

$r > 3$ $f'(1-\frac{1}{r}) < -1 \implies u^* = 1 - \frac{1}{r}$ is unstable with oscillations

$r = 3$ $f'(1-\frac{1}{r}) = -1$

Is there a 2-cycle at r=3?

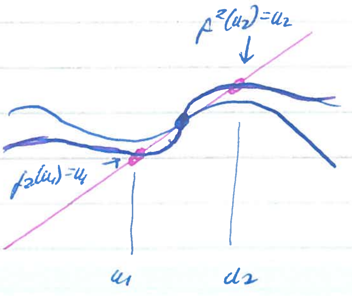
Look at $f^2 = f \circ f$



$$f^2 = rf(u)(1-f(u))$$
$$= r^2u(1-u)(1-ru(1-u))$$
$$= r^2u(1-u)(1-ru+ru^2)$$

— show r slightly bigger than r=3, two points that it crosses

enlarged



Distinct values for u_1, u_2 so get cycle.

$r^2u(1-u)(1-ru+r^{\cancel{2}}u^2) = u$ for fixed point u

$u\,(r^2(1-u)(1-ru+r^{\cancel{2}}u^2)-1) = 0$

$\uparrow$

$u=0$ is fixed point

$\Longrightarrow \quad r^2(1-u)(1-ru+r^{\cancel{2}}u^2) = 1$

Know that $u = 1-\frac{1}{r}$ is a fixed point

$\Longrightarrow \left(u-1+\frac{1}{r}\right)$ divides $r^2(1-u)(1-ru+r^{\cancel{2}}u^2) - 1$

$$\frac{1}{u}\left(f^2(u)-1\right) = -\left(u-1+\frac{1}{r}\right)\left(1+r-(r+r^2)u+r^2u^2\right) = 0$$

$\Longrightarrow u$ satisfies $r^2u^2 - r(1+r)u + 1+r = 0$ $\quad *$

$u = \frac{N}{K} > 0$ so we need both roots of $*$ to be positive

$$u^2 - \frac{1}{r}(1+r)u + \frac{1}{r^2}(1+r) = 0$$

If u_1, u_2 are roots then $\left.\begin{aligned}\frac{1}{r}(1+r) &= u_1+u_2 \\ \frac{1}{r^2}(1+r) &= u_1u_2\end{aligned}\right\} \Rightarrow$ must be +ve

We also check that real: $B^2 \geqslant 4AC$

$$\left(\frac{1}{r}(r+1)\right)^2 \geqslant 4\frac{1}{r^2}(1+r)$$

$$\underline{r \geqslant 3}$$

For $r \geqslant 3$ the roots u_1, u_2 are real and positive since (β)

Hence as r passes through 3 the 2-cycle $\{u_1, u_2\}$ appears and simultaneously $u^* = 1-\frac{1}{r}$ becomes unstable

As r increases from ~~-~~ $r=3$ eventually / $r = 1+\sqrt{6}$ the 2-cycle becomes unstable, and stable 4-cycle appears

i.e. $\{v_1, v_2, v_3, v_4\}$ such that $v_{i+1} = f(v_i)$ $\quad i = 1,2,3,4$

where $v_5 = v_1$

Hence for $0<r<1$ $\quad$ 0 is unique stable fixed point

$1<r<3$ $\quad$ 0 is unstable, $u^* = 1-\frac{1}{r}$ is stable

$r = 3$ 2-cycle appears, which is stable
$r = \sqrt{6} + 1$ 2-cycle becomes unstable, stable 4 cycle appears
$r = ?$ 4 cycle becomes unstable, 8 cycle appears

So as r increases, cycles of periods $2, 2^2, 2^3, 2^4 \dots$ etc. appear
and as 2^{k+1} appears, 2^k becomes unstable
The values of r for which the next cycle appears get closer together, and at $r = r_c \simeq 3.57$ all powers of 2 cycles appear
At around $r = 3.6786$ the first odd period cycle appears
Eventually at 3.8248 a 3-cycle appears

At r_c chaos appears and orbits are indistinguishable from "NOISE" even though the system is deterministic

time series for u_t looks like a random signal

Introduced because of historical significance

Take home message: this is a deterministic (even simple $f(u) = ru(1-u)$) model with some parameter value which appears to give and random signal
Thus if data from the field e.g. populations of insects, buffalos etc. over time appears to be random it still may come from a deterministic model.

Take a look on web at random behaviour that comes from logistic map

Age - Structured Models

Idea is to split population in to classes where the individuals in each class have the same fitness / fecundity
= ability to produce viable offspring, survival probability, age of sexual maturity ...)

Requires linear algebr

Age structured models

06/03/15

We divide the population in to classes. To start with the classes will indicate the age of individuals within the class. Let N_k be the # of individuals of age $k \geq 0$. N_0 is the # of newborns. We will assume no individual can live past age n. Hence we may describe the state of the population by

$$N(t) = (N_1(t), \dots, N_n(t)) \quad \text{at time } t$$

The age units are equal to the time units

Let b_k = expected # of new offspring to individual age $k \geq 1$

p_0 = probability of surviving from birth $(k=0)$ to age 1 $(k=1)$

p_k = probability of surviving from age k to $k+1$

(so $p_n = 0$, since no one lives to age $n+1$)

Consider age class $k \geq 1$. Then:

expected # age $k+1$ at time $t+1$ is fraction of those that survive from age k at time t

$$N_{k+1}(t+1) = p_k N_k(t) \qquad (n \geq k \geq 1)$$

For new borns:

$N_1(t+1)$ = expected # newborns at t that survive to age 1

$= p_0 N_0(t)$

But $N_0(t)$ = expected # offspring from all classes

$= \sum_{k=1}^{n} b_k N_k(t)$

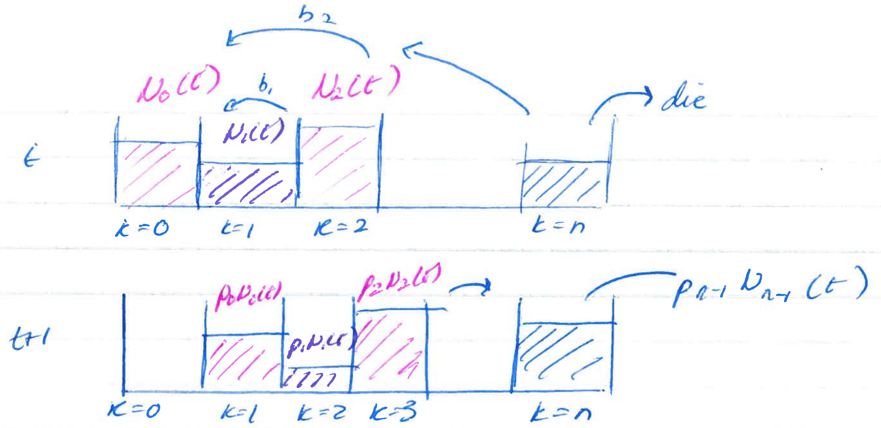
$$\Longrightarrow N_1(t) = p_0 \sum_{k=1}^{n} b_k N_k(t) = \sum_{k=1}^{n} f_k N_k(t)$$

where $f_k = p_0 b_k$ = expected # of offspring from age k that survive to age 1

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \\ \vdots \\ N_n(t+1) \end{pmatrix} = \begin{pmatrix} f_1 & f_2 & \cdots & & f_n \\ p_1 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & & & \vdots \\ \vdots & 0 & \ddots & & \\ & & \ddots & 0 & \\ 0 & \cdots & 0 & p_{n-1} & 0 \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \\ \vdots \\ N_n(t) \end{pmatrix}$$

The matrix L is called the Leslie-Matrix

$$N(t+1) = L\, N(t)$$



$N(t+1) = L N(t)$ $\qquad N \in \mathbb{R}^n$

$N(t) = L^t N(0)$

How $N(t)$ changes is governed by the eigenvalues & eigenvectors of the Leslie matrix L

Eigenvalues of matrix L

1) There is no zero eigenvalue $\qquad \det L = f_n p_1 p_2 \dots p_n > 0$

$\implies \underbrace{\lambda_1 \lambda_2 \dots \lambda_n}_{= \det L} \neq 0$

2) Let λ be an eigenvalue of L and $\underline{v}$ be an associated eigenvector $\underline{v} \neq 0$

$$\begin{pmatrix} f_1 & f_2 & \dots & f_n \\ p_1 & 0 & \dots & \\ 0 & p_2 & \dots & \\ \vdots & & & \\ 0 & 0 & \dots p_{n-1} & 0 \end{pmatrix} \begin{pmatrix} v_1 \\ v_2 \\ \vdots \\ v_n \end{pmatrix} = \lambda \begin{pmatrix} v_1 \\ v_2 \\ \vdots \\ v_n \end{pmatrix}$$

$= \sum_{i=1}^{n} f_i v_i = \lambda v_1$ $\qquad$ 1st equation

2nd equation: $p_1 v_1 = \lambda v_2$

3rd equation $p_2 v_2 = \lambda v_3$

$\vdots$

n^{th} equation $p_{n-1} v_{n-1} = \lambda v_n$

If $v_1 = 0$ then all $v_i = 0 \implies v = 0$ - not allowed since $\underline{v} = 0$ eigenvectors per n

Hence we may choose $v_1 = 1$

$\implies v_2 = p_1/\lambda$

$\implies v_3 = p_2/\lambda \; v_2 = \frac{p_1 p_2}{\lambda^2}$

$\vdots$

$v_n = \frac{p_1 p_2 \dots p_{n-1}}{\lambda^{n-1}}$

Now from first equation:

$$\lambda = \lambda v_1 = \sum_{k=1}^{n} f_i v_i = \sum_{k=1}^{n} \frac{f_k p_1 p_2 \cdots p_{k-1}}{\lambda^{k-1}}$$

$$\sum_{k=1}^{n} \frac{f_k p_1 \cdots p_{k-1}}{\lambda^{k}} = 1 \qquad f_k = p_0 \cdot b_k$$

Now use $p_0 p_1 \cdots p_{k-1} = l_k$ $\quad k = 1, 2, \ldots, n-1$

$$\sum_{k=1}^{n} \frac{p_0 b_k p_1 \cdots p_{k-1}}{\lambda^{k}} = 1$$

$$\implies \sum_{k=1}^{n} \frac{b_k l_k}{\lambda^k} = 1$$

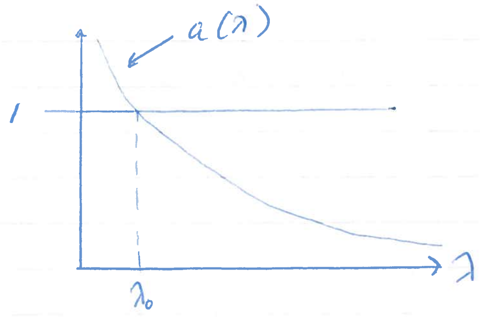
Euler-Lotka Equation (for the eigenvalues λ)

Lemma: L has a unique positive eigenvalue

Let $a(\lambda) = \sum_{k=1}^{n} \frac{b_k l_k}{\lambda^k}$ $\qquad l_k > 0$ but some b_k's may be zero $\implies$ at least one product $b_k l_k > 0$

The function a is strictly decreasing

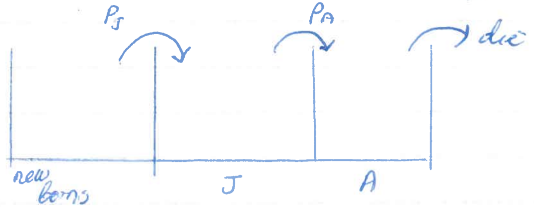
$$\lim_{\lambda \to 0^+} a(\lambda) = +\infty \quad \text{and} \quad \lim_{\lambda \to \infty} a(\lambda) = 0$$



Corollary Any eigenvector $\underline{v}$ of L with eigenvalue λ_0 has $v_i > 0$ $\quad i = 1, 2, \ldots, n$ $\quad$ (since $v_k = \frac{1}{\lambda_0^k} p_1 \cdots p_{k-1} > 0$

This says that if $N(t) = \underline{v}_0$ then $N(t+1) = L\underline{v}_0 = \lambda_0 \underline{v}_0$ i.e. the population 'distribution' stays the same, but the population of each age class grows by a factor of λ_0

Example Consider two age classes. Adults A and Juveniles J



b_J = juvenile birth rate $= 0$
p_J = juvenile prob of surviving to adult
b_A = adult birth rate, $b_A > 0$
p_A = survival rate from juveniles to adults
in notes p_A = adult survival prob.
p_J = juvenile survival prob

$J(t+1) = p_J b_A A(t)$ $\quad\quad$ $A(t+1) = p_A J(t)$

$$\Longrightarrow \quad L = \begin{pmatrix} 0 & p_J b_A \\ p_A & 0 \end{pmatrix} \quad\quad \begin{pmatrix} J \\ A \end{pmatrix} = N$$

Eigenvalues $\quad \left| \begin{pmatrix} -\lambda & p_J b_A \\ p_A & -\lambda \end{pmatrix} \right| = 0 \quad\quad \lambda^2 - p_A p_J b_A = 0$

$$\Longrightarrow \lambda = \pm \sqrt{p_A p_J b_A}$$

$$\Longrightarrow \lambda_0 = + \sqrt{p_J p_A b_A}$$

Assume that L has distinct eigenvalues & so has a complete set of eigenvectors $\{ v_0, v_1, \dots, v_{n-1} \}$
Hence any population $\underline{N}$ can be written as

$$\underline{N} = \sum_{k=0}^{n-1} \alpha_k \underline{v}_k \quad \text{for some } \alpha_k$$

Thus if $\underline{N}(0) = \sum_{k=0}^{n-1} \alpha_k \underline{v}_k$

then $\underline{N}(1) = L(\underline{N}(0)) = L\left(\sum_{k=0}^{n-1} \alpha_k \underline{v}_k\right) = \sum_{k=0}^{n-1} \alpha_k \lambda_k \underline{v}_k$

$$\underline{N}(2) = L(\underline{N}(1)) = \sum_{k=0}^{n-1} \alpha_k \lambda_k^2 \underline{v}_k$$

$$\vdots$$

$$\underline{N}(t) = \sum_{k=0}^{n-1} \alpha_k \lambda_k^t \underline{v}_k$$

Assume that $\lambda_0 > 0$ is such that $\lambda_0 > |\lambda|$ for all eigenvalues of L $(\neq$ ← check notes, didn't get this last bit

Then $\underline{N}(t) = \sum_{k=0}^{n-1} \alpha_k \lambda_k^t \underline{v}_k = \lambda_0^t \sum_{k=0}^{n-1} \alpha_k \left(\frac{\lambda_k}{\lambda_0}\right)^t \underline{v}_k$

Since $\left| \frac{\lambda_k}{\lambda_0} \right| < 1$, as $t \to \infty$ the contribution from $\left(\frac{\lambda_k}{\lambda_0}\right)^t v_k \to 0$

and hence if $\alpha_0 \neq 0$, $\underline{N}(t) \sim \lambda_0^t \alpha_0 \underline{v}_0$ for t large

Hence for t large $\underline{N}(t+1) = \lambda_0 \underline{N}(t)$

λ_0 is often referred to as the mean fitness of the population

$\lambda_0 < 1 \Rightarrow \underline{N}(t) \to \underline{0}$ extinction
$\lambda_0 > 1 \Rightarrow \underline{N}(t)$ grows unboundedly
$\lambda_0 = 1 \Rightarrow \underline{N}(t)$ is at equilibrium

Instead of working with $\underline{N}(t)$ we often work with $\underline{X}(t) = (x_1(t), \dots, x_n(t))$ population distribution

where $$x_k(t) = \frac{N_k(t)}{\sum_{i=1}^{n} N_i(t)}$$

By construction $\sum_{k=1}^{n} x_k(t) = 1 \quad \forall t$

For large t $$\underline{N}(t+1) \sim \lambda_0 \underline{N}(t)$$
$$N_k(t+1) \sim \lambda_0 N_k(t)$$

$$\Longrightarrow \sum_{k=1}^{n} N_k(t+1) \sim \lambda_0 \sum_{k=1}^{n} N_k(t)$$

$$\Longrightarrow x_k(t+1) = \frac{N_k(t+1)}{\sum_{j=1}^{n} N_j(t+1)} = \frac{\lambda_0 N_k(t)}{\lambda_0 \sum_{k=1}^{n} N_k(t)} = x_k(t)$$

So for $t \to \infty$ we get $\underline{X}_t \longrightarrow \underline{X}^*$ where $X^* = \frac{\underline{v}_0}{\sum_{k=1}^{n} (\underline{v}_0)_k}$

<u>Example</u> $$L = \begin{pmatrix} 0 & \overset{\swarrow p_J b_A ?}{p_J p_A} \\ p_A & 0 \end{pmatrix} \Longrightarrow \lambda_0 = +\sqrt{p_J p_A b_A}$$

$$J(t+1) = p_J b_A A(t)$$
$$A(t+1) = p_A J(t)$$

$$X(t) = X_J(t) = \frac{J(t)}{A(t) + J(t)}$$

$$X(t+1) = \frac{J(t+1)}{J(t+1) + A(t+1)} = \frac{p_J b_A A(t)}{p_J b_A A(t) + p_A J(t)}$$

$$X(t+1) = \frac{p_J b_A A(t)/N(t)}{p_J b_A \frac{A(t)}{N(t)} + p_A \frac{J(t)}{N(t)}} \qquad N = A + J$$

$$= \frac{p_J b_A (1 - X(t))}{p_J b_A (1 - X(t)) + p_A X(t)}$$

Write as $X(t+1) = F(X(t))$ where $F(x) = \frac{1 - X}{1 - X + \alpha X}$

where $\alpha = \frac{p_A}{p_J b_A}$

Look for steady states $F(x) = x$

$$\Longrightarrow \frac{1-x}{1-x+\alpha x} = x \Longrightarrow 1-x = x(1-x+\alpha x) = x - x^2 + \alpha x^2$$

$$Q(x) = (1-\alpha)x^2 - 2x + 1 = 0$$
$$(x-1)^2 - \alpha x^2 = 0$$

$$\Longrightarrow x = (1 \pm \sqrt{\alpha})^{-1}$$

Only $x = \frac{1}{1+\sqrt{\alpha}}$ is in $[0,1]$

Stability $F'(x) = \frac{-\alpha}{(1-x+\alpha x)^2}$

$$F'\left(\frac{1}{1+\sqrt{\alpha}}\right) = -1$$

indeterminate linear stability ~~analysis~~ analysis

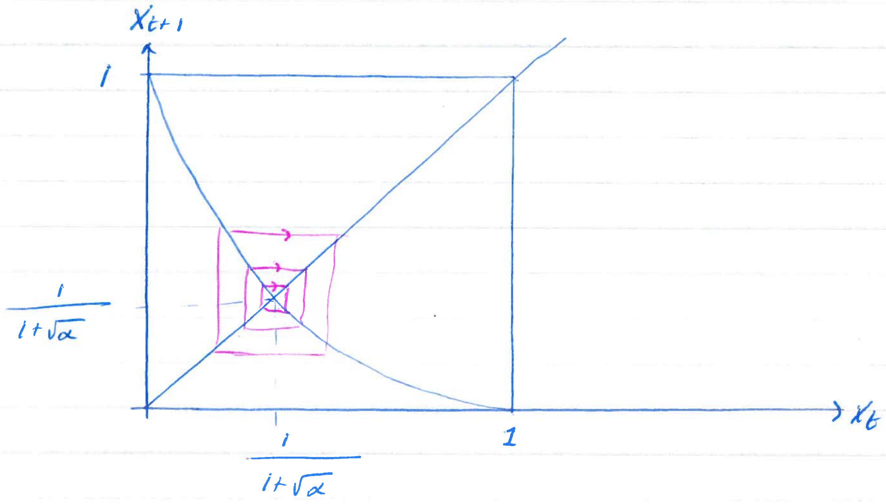
$$F(F(x)) = \frac{1 - \left(\frac{1-x}{1-x+\alpha x}\right)}{1 - (\alpha-1)\left(\frac{1-x}{1-x+\alpha x}\right)} = \frac{1-x+\alpha x - 1 + x}{1-x+\alpha x + \alpha - \alpha x - 1 + x}$$

$$= \frac{\alpha x}{\alpha} = x$$

$$\underline{F(F(x))}$$
$$\parallel$$
$$\frac{1-x}{1-x+\alpha x}$$

$$\longrightarrow F(F(x)) = x \quad \text{ie.} \quad F^2(x) = x \quad \forall x \in [0,1]$$

$\Longrightarrow$ every orbit is a 2-cycle



Now we want some conditions that ensure that $\lambda_0 > |\lambda|$ for all eigenvalues λ of $L \neq \lambda_0$, since then we know that $\underline{X}_t \longrightarrow \dfrac{\underline{v}_0}{|\underline{v}_0|}$,

- **Recall** Given $m, n \in \mathbb{Z}_+$, the $GCD(m,n)$ - the greatest common divisor is the largest integer k such that k divides m and k divides n

$GCD(\{1, 2, 5\}) = 1$
$GCD(\{4, 16, 8\}) = 4$
$GCD(\{2, 1, 8\}) = 1$ etc.

- **Definition** Let $\Omega(L) = \{k \in \{1, 2, \ldots, n\}$ such that $p_k > 0\}$
$:= \{k \in \{1, 2, \ldots, n\}$ such that $b_k > 0\}$

Examples

$$L = \begin{pmatrix} 0 & 0.5 & 0 & 5 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 2 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 2 & 0 \end{pmatrix} \qquad \Omega(L) = \{2, 4\}$$

$$L = \begin{pmatrix} 0 & 0 & 0.2 \\ 1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \qquad \Omega(L) = \{3\}$$

We define L to be aperiodic if $GCD(\Omega(L)) = 1$

Theorem: if L is aperiodic then $\lambda_0 > |\lambda|$ for any eigenvalue of L not equal to λ_0

10/03/15

Theorem If L is an aperiodic Leslie matrix and λ is any eigenvalue of L other than the unique positive eigenvalue λ_0 then $|\lambda| < \lambda_0$

Proof Split in to two cases $(i)\ \lambda < 0$ $(ii)\ \lambda \in \mathbb{C}$

i) Let $\mu = -\lambda > 0$. ~~Set $a(x) = \sum_{k=1}$~~

Set $a(x) = \sum_{k=1}^{n} \frac{l_k b_k}{x^k}$

An eigenvalue satisfies the Euler Lotka equation

$$a(\lambda) = 1$$

$$a(\lambda) = a(-\mu) = \sum_{k \text{ even}} \frac{l_k b_k}{(-\mu)^k} + \sum_{k \text{ odd}} \frac{l_k b_k}{(-\mu)^k}$$

$$= \sum_{k \text{ even}} \frac{l_k b_k}{\mu^k} - \sum_{k \text{ odd}} \frac{l_k b_k}{\mu^k}$$

Now suppose that ~~for each k odd such that $b_k > 0$~~ $b_k = 0$ for all odd k

since contains even numbers

Then $\Omega = \{k : b_k > 0\}$ has a $GCD(\Omega) \geq 2$, but since L is aperiodic this is a contradiction (so my assumption ~~that~~ was wrong) so that there exists an odd k such that $b_k > 0$

Hence $\sum_{k \text{ even}} \frac{l_k b_k}{\mu^k} > 0$

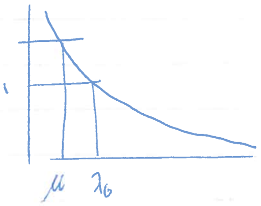
evens + odds

and hence

$$1 = a(\lambda) = a(-\mu) < \sum_{k \text{ even}} \frac{b_k l_k}{\mu^k} < \sum_{k=1}^{n} \frac{b_k l_k}{\mu^k} = a(\mu)$$

and hence $a(\mu) > 1$

But since $a(\lambda_0) = 1$ & a is strictly decreasing we must have $\mu < \lambda_0$ i.e. $|\lambda| < \lambda_0$



Now for (ii) let $\lambda = re^{i\theta}$ so for $a(\lambda) = 1$

$$\sum_{k=1}^{n} b_k l_k (re^{-i\theta})^k = 1$$

$$\Rightarrow \sum_{k=1}^{n} b_k l_k r^k \cos k\theta = 1$$

$$\sum_{k=1}^{n} b_k l_k r^k \sin k\theta = 0$$

equating real & imaginary parts

Let us suppose that $\cos k\theta = 1$ for all $k \in \Omega(L)$ i.e. all k such that $b_k > 0$
Then $\exists$ integers n_i such that $\Omega = \{ k_i ; i = 1, \dots, |\Omega| \}$

$$k_i \theta = 2\pi n_i \qquad i = 1, 2, \dots, |\Omega|$$

Since L is aperiodic $GCD\{\Omega\} = 1$ and hence $\exists$ integers α_i such that
$$\sum_{i=1}^{|\Omega|} \alpha_i k_i = 1$$

Hence $\theta = \sum_{i=1}^{n} \alpha_i k_i \theta = \sum_{i=1}^{n} \alpha_i 2\pi n_i = 2\pi a$ where $a \in \mathbb{Z}$

$\Rightarrow$ θ is a multiple of 2π
$\Rightarrow$ $re^{i\theta}$ is real & positive $\Rightarrow$ $re^{i\theta} = \lambda_0$

Hence we have $\cos k\theta < 1$ for some $k \in \Omega(L)$

$$1 = G(\lambda) = Re(G(\lambda)) = \sum_{k=1}^{\infty} b_k l_k r^{-k} \cos k\theta$$
$$< \sum_{k=1}^{\infty} b_k l_k r^{-k} \quad \text{since } \cos k\theta < 1 \text{ for at least one } k$$
$$= G(r)$$

since G is decreasing, $r < \lambda_0$

$$\Longrightarrow \underline{\underline{|\lambda| = r < \lambda_0}}$$

Example Let m be age of sexual maturity
Population of juveniles J and adults A

$$p_k = \begin{cases} p_J & k < m \\ p_A & k \geq m \end{cases} \qquad l_k = \begin{cases} p_J^{k} & k < m \\ p_J^{m} p_A^{k-m} & k \geq m \end{cases}$$

$$b_k = \begin{cases} 0 & k < m \\ b > 0 & k \geq m \end{cases}$$

Euler Lotka equation $\displaystyle\sum_{k=1}^{n} \frac{b_k l_k}{\lambda^k} = 1$

$$\Rightarrow \sum_{k=m}^{n} \frac{b_k \ell_k}{\lambda^k} = 1$$

$$\Rightarrow b\rho_J^m \sum_{k=m}^{n} \rho_A^{-m+k} \frac{1}{\lambda^k} = 1$$

$$b\rho_A^{-m} \rho_J^m \sum_{k=m}^{n} \left(\frac{\rho_A}{\lambda}\right)^k = 1$$

$$b\rho_A^{-m} \rho_J^m \left(\frac{\rho_A}{\lambda}\right)^m \sum_{r=0}^{n-m} \left(\frac{\rho_A}{\lambda}\right)^r = 1$$

$$b\left(\frac{\rho_J}{\lambda}\right)^m \left(\frac{\left(\frac{\rho_A}{\lambda}\right)^{n-m+1} - 1}{\frac{\rho_A}{\lambda} - 1}\right) = 1$$

$$b\frac{\rho_J^m}{\lambda^m}\left(\left(\frac{\rho_A}{\lambda}\right)^{n-m+1} - 1\right) = \frac{\rho_A}{\lambda} - 1$$ could solve for λ

Take an approximation $n = \infty$; then for $\lambda > \rho_A$ we get the sum

$$-b\frac{\rho_J^m}{\lambda^m} = \frac{\rho_A}{\lambda} - 1$$

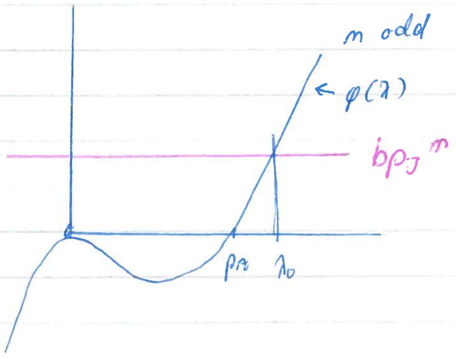
$$-b\rho_J^m = \lambda^{m-1}\rho_A - \lambda^m$$

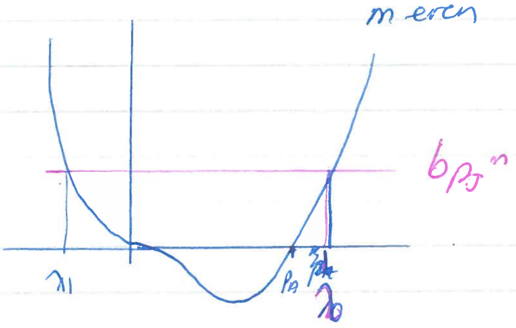
$$\Rightarrow \underline{\lambda^m - \rho_A\lambda^{m-1} - b\rho_J^m = 0}$$

Hence λ satisfies $\lambda^m - \rho_A\lambda^{m-1} = b\rho_J^m$

Hence $\varphi(\lambda) = \lambda^{m-1}(\lambda - \rho_A) = b\rho_J^m$

Sketch $\varphi(\lambda)$





We see that there is a unique positive root $\lambda_0 > \rho_A$

For m odd, there are no other real roots λ

m even, there ~~are~~ is also a negative eigenvalue λ_1

$$\lambda_0^{m-1}(\lambda_0 - \rho_A) = b\rho_J^m$$

$$\Rightarrow \lambda_0 = \rho_A + \frac{b\rho_J^m}{\lambda_0^m} > \lambda_0$$

Take $m=3$ $\qquad L =$

$$L = \begin{pmatrix} 0 & 0 & bp_J & bp_J & \cdots \\ p_J & 0 & 0 & 0 & \cdots \\ 0 & p_J & 0 & 0 & \cdots \\ 0 & 0 & p_A & 0 & \cdots \\ 0 & 0 & 0 & p_A & \cdots \end{pmatrix}$$

Euler Lotka becomes $\lambda^3 - p_A \lambda^2 = p_J^3 b$

Suppose $p_A = \frac{1}{4}$, $p_J = \frac{1}{2}$, $b = \frac{1}{2}$

$$\longrightarrow \lambda^3 - \frac{1}{4}\lambda^2 - \frac{1}{16} = 0$$

By inspection $\lambda = \frac{1}{2}$ is a root and then $\lambda_{\pm} = -\frac{1}{8} \pm \frac{\sqrt{7}}{8} i$

Need modulus to see if L is aperiodic

$$\left|-\frac{1}{8} \pm i\frac{\sqrt{7}}{8}\right| = \frac{1}{8}\left|-1 + i\sqrt{7}\right| = \frac{1}{8}(1+7)^{1/2} = \frac{1}{\sqrt{8}} = \frac{1}{2\sqrt{2}} < \frac{1}{2} = \lambda_0$$

✓

For the long term age distribution we need $\underline{v_0}$, an eigenvector associated with $\lambda_0 = \frac{1}{2}$

Need to solve
$$\begin{pmatrix} 0 & 0 & \frac{1}{4} & \frac{1}{4} & \cdots \\ \frac{1}{2} & 0 & 0 & 0 & \cdots \\ 0 & \frac{1}{2} & 0 & 0 & \cdots \\ 0 & 0 & \frac{1}{4} & 0 & \cdots \\ 0 & 0 & 0 & \frac{1}{4} & \cdots \end{pmatrix} \begin{pmatrix} v_0 \\ v^1 \\ v^2 \\ \vdots \end{pmatrix} = \frac{1}{2}\begin{pmatrix} v^0 \\ v^1 \\ v^2 \\ \vdots \end{pmatrix}$$

$$\Rightarrow \frac{1}{4}v^2 + \frac{1}{4}v^3 + \cdots = \frac{1}{2}v^0 \qquad v^0 = \alpha \text{ say}$$

$$\frac{1}{2}v^0 = \frac{1}{2}v^1, \quad \frac{1}{2}v^1 = \frac{1}{2}v^2, \quad \frac{1}{4}v^2 = \frac{1}{2}v^3$$

$$\Rightarrow \quad 1 = \sum v^i = \alpha(1+1+1) + \alpha\left(\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \cdots\right) \qquad v^i = \alpha \text{ for } i = 0,1,2; \quad = \frac{\alpha}{2^{i-4}} \quad i = 3,4$$

$$= 3\alpha + \alpha\frac{1}{2}\left(\frac{1}{1-\frac{1}{2}}\right) \longleftarrow \text{geometric series}$$

$$= (3+1)\alpha \Rightarrow \alpha = 4$$

$$\Rightarrow \text{distribution is } \frac{1}{4}\left(1, 1, 1, \frac{1}{2}, \frac{1}{4}, \frac{1}{8}, \cdots\right)$$

Optimal Life History Strategies 13/03/15

For individual 2 chief concerns: (i) fecundity (ability to produce viable offspring)
(ii) survival

There's a tradeoff between devoting resources between fecundity & survival
What is the best tradeoff to maximise fitness, and these maximal fitness species will be selected for by Natural Selection
Note that fitness of an individual can be taken to be the unique positive eigenvalue of the Leslie matrix L, since in the long term the distribution X^* will be will be proportional to the eigenvector v_0 associated with λ_0 & so the population grows at rate λ_0 when t is large. So the larger λ_0 is the fitter the individuals since the fitness is λ_0
We want to model the action of Natural Selection on phenotypes of the population; e.g. height, body weight, speed of flight, beak size etc.

Let $\sigma = (\sigma_1, \sigma_2, \dots, \sigma_n)$ be values of phenotypic parameters. The eigenvalue λ_0 will be a function of σ: $\lambda_0 = \lambda_0(\sigma)$
Natural selection (over evolutionary time scale) will act to select values of σ for which the fitness $\lambda_0(\sigma)$ has a local maximum
~~∇(λ0~~ $\nabla \lambda_0(\sigma) = 0$
and the matrix of 2nd derivatives

$$\left(\left(\frac{\partial^2 \lambda_0}{\partial \sigma_i \partial \sigma_j}\right)\right) = H$$

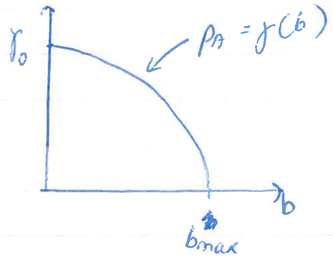
is negative definite at the optimal σ_i

From the Leslie matrix approach we obtain an Euler Lotka equation for the eigenvalues λ

Example Life History Strategies (b, p's etc.)

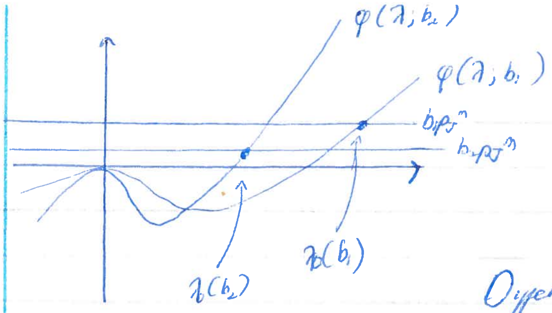
$$p_k = \begin{cases} p_J & k < m \quad \text{sexual maturity} \\ p_A & k \geq m \end{cases} \qquad b_k = \begin{cases} 0 & k < m \\ b > 0 & k \geq m \end{cases}$$

This gave the E-L eqn:
$\lambda^m - p_A \lambda^{m-1} = b p_J^m$ λ_0 will be a function of $\sigma = (p_A, p_J, b)$
Fix p_J, and we'll let p_A be a function b, i.e. as I vary fecundity, it will affect ability to survive from one year to the next



This reflects the tradeoff in the allocation of finite resources to producing offspring and survival at adult stage

So $\lambda_0 = \lambda_0(b)$ now
$\varphi(\lambda; b) = \lambda^m - \gamma(b)\lambda^{m-1} = b p_J^m$



We want to find b^* such that $\lambda_0(b)$ is maximised at $b = b^*$

$$\lambda_0(b)^m - \gamma(b)\lambda_0(b)^{m-1} = b\rho_J^m$$

Differentiate wrt b:

$$m\lambda_0(b)^{m-1}\frac{d\lambda_0}{db} - \gamma'(b)\lambda_0(b)^{m-1} - \gamma(b)(m-1)\lambda_0(b)^{m-1}\frac{d\lambda_0}{db} = \rho_J^n$$

When $b = b^*$; $\frac{d\lambda_0}{db}(b^*) = 0 \Rightarrow -\gamma'(b^*)\lambda_0(b^*)^{m-1} = \rho_J^n \Rightarrow \lambda_0(b^*) = \left(\frac{\rho_J^n}{-\gamma'(b^*)}\right)^{\frac{1}{m-1}}$

This makes sense because $\gamma'(b) < 0$ since the probability of survival $p_A = \gamma(b)$ decreases as more resources are devoted to producing offspring

Since $\lambda_0(b^*)$ is an eigenvalue, it satisfies the E-L equation

$$\lambda_0^m - \gamma(b^*)\lambda_0^{m-1} = b^*\rho_J^m$$

$$\left(\frac{\rho_J^n}{-\gamma'(b^*)}\right)^{\frac{m}{m-1}} - \gamma(b^*)\left(\frac{\rho_J^m}{-\gamma'(b^*)}\right) = b^*\rho_J^m \Rightarrow \text{determines } b^*$$

$$\left(\frac{\rho_J^m}{-\gamma'(b^*)}\right)^m = \left(b^*\rho_J^m + \gamma(b^*)\frac{\rho_J^m}{-\gamma'(b^*)}\right)^{m-1}$$

$$\rho_J^m = -\gamma'(b^*)\left(\gamma(b^*) - b^*\gamma'(b^*)\right)^{m-1} \qquad *$$

Before introducing a specific γ, we note:

$\lambda^n - \gamma(b)\lambda^{m-1} = b\rho_J^m \qquad \left(m\lambda^{m-1} - (m-1)\gamma\lambda^{m-2}\right)\frac{d\lambda}{db} - \gamma'(b)\lambda^{m-1} = \rho_J^m$

To check for a max λ_0

$$\frac{d}{d\lambda}\left(m\lambda^{m-1} - (m-1)\gamma\lambda^{m-2}\right)\frac{d\lambda}{db} + \left(m\lambda^{m-1} - (m-1)\gamma\lambda^{m-2}\right)\frac{d^2\lambda}{db^2} - \gamma''(b)\lambda^{m-1} - \gamma'(b)(m-1)\frac{d\lambda}{db} = 0$$

At b^* $\frac{d\lambda}{db}(b^*) = 0$

$$\left(m\lambda^{m-1} - \gamma(m-1)\lambda^{m-2}\right)\frac{d^2\lambda}{db^2}(b^*) = \gamma''(b^*)\lambda^{m-1}$$

$$\Longrightarrow \frac{d^2\lambda}{db^2} = \frac{\gamma''(b^*)\lambda^{m-1}}{m\lambda^{m-1} - \gamma(b^*)(m-1)\lambda^{m-2}}$$

For a max λ_0 we need $\frac{d^2\lambda}{db^2}(b^*) < 0$

Find sign of denominator: $\lambda^m - \gamma(b^*)\lambda^{m-1} = b^*\rho_J^m > 0$

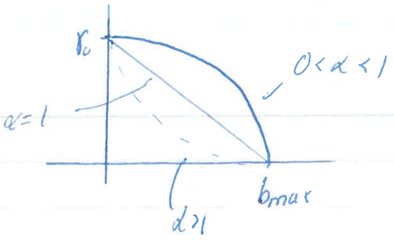
$\lambda^{m-1}(\lambda - \gamma(b^*)) > 0$

Hence $\lambda > \gamma(b^*)$

$$\Longrightarrow m\lambda^{m-1} - \gamma(b^*)\lambda^{m-2}(m-1) = m\lambda^{m-2}(\lambda - \gamma(b^*)) + \gamma(b^*)\lambda^{m-2} > 0$$

Hence if $\gamma''(b) < 0$, λ is maximised at b^* (if b^* exists)

For example



$$\gamma(b) = \gamma_0\left(1-\frac{b}{b_{max}}\right)^{\alpha}$$

$\alpha>0,\ b_{max}>0,\ \gamma_0>0$

$$\gamma'(b) = -\frac{\alpha\gamma_0}{b_{max}}\left(1-\frac{b}{b_{max}}\right)^{\alpha-1} \qquad \gamma''(b) = \frac{\alpha(\alpha-1)}{b_{max}^2}\left(1-\frac{b}{b_{max}}\right)^{\alpha-2}$$

from $*$ $\rightarrow$
$$p_J^m = \frac{\alpha\gamma_0}{b_{max}}\left(1-\frac{b}{b_{max}}\right)^{\alpha-1}\left(\gamma_0\left(1-\frac{b}{b_{max}}\right)^{\alpha}+\frac{b\alpha}{b_{max}}\left(1-\frac{b}{b_{max}}\right)^{\alpha-1}\right)^{m-1}$$

$$= \frac{\alpha\gamma_0}{b_{max}}\left(1-\frac{b}{b_{max}}\right)^{m(\alpha-1)}\left(\gamma_0\frac{b\alpha}{b_{max}}+\gamma_0\left(1-\frac{b}{b_{max}}\right)\right)^{m-1}$$

$$1+(\alpha\mp1)\frac{b}{b_{max}} = \left(\frac{b_{max}}{\alpha\gamma_0^{\,m}}\left(1-\frac{b}{b_{max}}\right)^{m(1-\alpha)}\right)^{\frac{1}{m-1}} p_J^{\,m/m-1}$$

$$L(b) = 1+(\alpha-1)\frac{b}{b_{max}} = \left(\frac{b_{max}}{\alpha}\left(\frac{p_J}{\gamma_0}\right)^m\right)^{\frac{1}{m-1}}\left(1-\frac{b}{b_{max}}\right)^{\frac{m}{m-1}(1-\alpha)} = N(b)$$

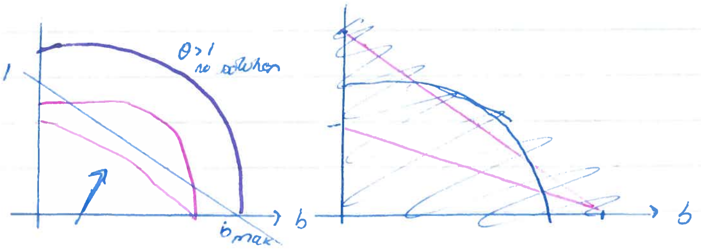
$\frac{m}{m-1}(1-\alpha)=1$ when $\alpha=\frac{1}{m}$

Then $\left(1-\frac{b}{b_{max}}\right)^{\frac{m(1-\alpha)}{m-1}}$ concave if $\alpha>\frac{1}{m}$ and convex otherwise

i) Case (i) $m>\frac{1}{\alpha}$, $\alpha<1$

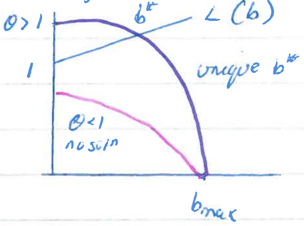
$(1-\alpha)\frac{b}{b_{max}}=1 \qquad \frac{b}{~~b_{max}~~}=\frac{b_{max}}{1-\alpha}$

$$\theta = \left(\frac{b_{max}}{\alpha}\left(\frac{p_J}{\gamma_0}\right)^m\right)^{\frac{1}{m-1}}$$

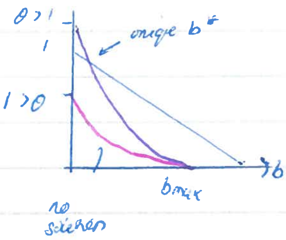


$\theta<1$, no or 2 solutions

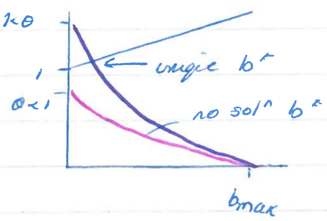
ii) $m>\frac{1}{\alpha}$, $\alpha>1$



iii) $m<\frac{1}{\alpha}$ $\alpha<1$



iv) $m<\frac{1}{\alpha}$ $\alpha>1$



$\exists$ either no max, or 1 or 2 possible turning points & one will be a max

<u>Example</u> Look at birth rate $b=\beta(m)$

$\varphi(\lambda,m) = \lambda^m - p_A\lambda^{m-1} - \beta(m)p_J^{\,m} = 0 \qquad (p_J, p_A \text{ constants})$

$F(m) = \varphi(\lambda(m),m) \qquad \frac{dF}{dm} = \frac{\partial\varphi}{\partial\lambda}\frac{d\lambda}{dm} + \frac{\partial\varphi}{\partial m} = \left(m\lambda^{m-1} - \varphi_A(m-1)\lambda^{m-2}\right)\frac{d\lambda}{dm} + \frac{\partial\varphi}{\partial m}$

Hence an optimal $m=m^*$ satisfies $\frac{\partial\varphi}{\partial m}(m^*)=0$

$$\boxed{\begin{aligned}\text{Recall: } \frac{d}{dm}x^m &= \frac{d}{dm}\left(e^{\log x}\right)^m = \frac{d}{dm}e^{m\log x}\\ &= \log x\, e^{m\log x} = \log x\,(x^m)\end{aligned}}$$

$$\frac{\partial\varphi}{\partial m} = \frac{\partial}{\partial m}\left(\lambda^m - p_A\lambda^{m-1} - \beta(m)p_J^{\,m}\right) = (\log\lambda)\lambda^m - p_A(\log\lambda)\lambda^{m-1} - \beta'(m)p_J^{\,m} - \beta(m)\log p_J\, p_J^{\,m} = 0$$

$\log\lambda\,(\lambda^m - p_A\lambda^{m-1} = \beta'(m)p_J^{\,m} + \beta(m)\log p_J\, p_J^{\,m}$

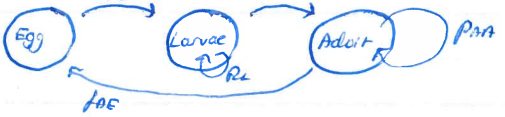
$\lambda^m - p_A\lambda^{m-1} = \beta(m)p_J^{\,m} \longleftarrow$ from above $\varphi(\lambda,m)$)

$$\log \lambda (B(m)\cancel{p_J^m}) = B'(m)\cancel{p_J^m} + B(m)\log p_J^{m} \cancel{p_J^m}$$

$$\lambda = \exp\left(\log p_J + \frac{B'(m)}{B(m)}\right) = p_J \exp\left(\frac{B'(m)}{B(m)}\right)$$

This then goes in to the E-L equation to find m^*

More general 'age' structure models We now replace ages with 'stage' of development

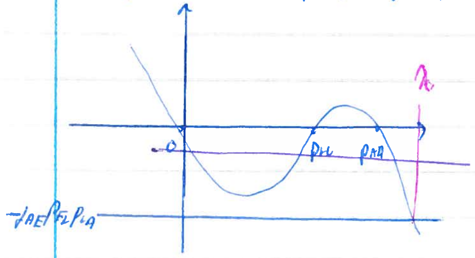


Let $\underline{N}(t) = (E(t), L(t), A(t))$; $E(t+1) = f_{AE}A(t)$; $L(t+1) = p_{EL}E(t) + p_{LL}L(t)$;
$A(t+1) = p_{LA}L(t) + p_{AA}A(t)$ $\underline{N}(t+1) = \mathcal{L}\underline{N}(t)$; $\underline{N}(t) = \mathcal{L}^t \underline{N}(0)$

$$\mathcal{L} = \begin{pmatrix} 0 & 0 & f_{AE} \\ p_{EL} & p_{LL} & 0 \\ 0 & p_{LA} & p_{AA} \end{pmatrix}$$ = leslie matrix + diagonal terms

Again we look for eigenvalues of $\mathcal{L}$ $\begin{vmatrix} -\lambda & 0 & f_{AE} \\ p_{EL} & p_{LL}-\lambda & 0 \\ 0 & p_{LA} & p_{AA}-\lambda \end{vmatrix} = -\lambda(p_{LL}-\lambda)(p_{AA}-\lambda) + f_{AE}p_{EL}p_{LA} = 0$

Let $\varphi(\lambda) = -\lambda(\lambda - p_{LL})(\lambda - p_{AA}) = 0$ at $\lambda = 0, p_{LL}, p_{AA}$; Assume for the plot $p_{AA} > p_{LL}$



not nec. unique - could be - line, always one $> p_{AA}$

We see $\exists$ a ~~unique~~ eigenvalue $\lambda_0 > p_{AA}$

(or more generally $\lambda_0 > \max\{p_{AA}, p_{LL}\}$)

It is easy to show that $\underline{v}_0$ here is positive by solving $\mathcal{L}\underline{v}_0 = \lambda_0 \underline{v}_0$ where $\lambda_0 > \max\{p_{AA}, p_{LL}\}$

Do this at home

General Population Models

17/03/15

Consider a species in a closed habitat. Let density of species k be N_k. The idea is to choose the simplest realistic per capita growth rate possible: i.e. linear

Per capita growth of species k is $\frac{1}{N_k}\frac{dN_k}{dt} = r_k + \sum_{i=1}^{n} a_{ki} N_i$

Here r_k = intrinsic growth rate of species k, which can be 0 or +ve or -ve

The numbers $a_{ki} \in \mathbb{R}$ & can be 0, +ve or -ve ; a_{ki} measures the effect of species i on the per capita growth rate of species k : $\frac{\partial}{\partial N_i}\left(\frac{1}{N_k}\frac{dN_k}{dt}\right) = a_{ki}$

If $a_{ki} > 0$, the per capita growth of species k is promoted by species i

$a_{ki} < 0$ ―――― " ―――― impeded ―― " ――

$a_{ki} = 0$ species i does not affect the growth of species k

The matrix $A = ((a_{ki}))$ is not usually symmetric : effect of species i on k is not equal to that of k on i. For example for predator prey models

prey → $\frac{1}{N}\dot{N} = a - bN - cP$ predator ↓ $\frac{1}{P}\dot{P} = -d + eN - fP$ $a, b, c, d, e, f > 0$

effect of predator on prey: $\frac{\partial}{\partial P}\left(\frac{1}{N}\dot{N}\right) = -c < 0$

prey on predator : $\frac{\partial}{\partial N}\left(\frac{1}{P}\dot{P}\right) = e > 0$

Predator prey has $a_{ik}a_{ki} < 0$

The matrix A is called the interaction matrix. Thus the model is specified by n^2 interactions a_{ik} and n intrinsic growth rates

The system $\dot{N}_k = N_k\left(r_k + \sum_{i=1}^{n} a_{ki} N_i\right)$ can be written as $\dot{N}_k = N_k\left(r_k + \overset{k\text{th component of row vector } AN}{\overset{\downarrow}{(AN)_k}}\right)$

$$\frac{\partial}{\partial N_i}\left(\frac{\dot{N}_k}{N_k}\right) = \frac{\partial}{\partial N_i}\left(r_k + (AN)_k\right) = \frac{\partial}{\partial N_i}\left(r_k + \sum a_{ki} N_i\right) = a_{ki}$$

j on i, a_{ij}	i on j, a_{ji}	interaction type
< 0	< 0	interspecific competition
> 0	> 0	mutualism = cooperation
< 0	> 0	predator j, prey i
> 0	0	harmless parasite i, host j

Competition model $\dot{N}_1 = N_1(r_1 - b_{11}N_1 - b_{12}N_2)$ $\dot{N}_2 = N_2(r_2 - b_{21}N_1 - b_{22}N_2)$ i.e. $b_{ij} = -a_{ij}$ for interaction matrix

$\frac{\partial}{\partial N_2}(\dot{N}_1/N_1) = -b_{21} < 0$ $\frac{\partial}{\partial N_1}(\dot{N}_2/N_2) = -b_{12} < 0$

Steady states of $\dot{N}_k = N_k(r_k + (AN)_k)$. For n species there could be a large number of steady states. For a steady we need either $N_k = 0$ or $r_k + (AN)_k = 0$

e.g. for the competition model, there were at least 2, and maximum of 3 steady states

With 3 species N_1, N_2, N_3

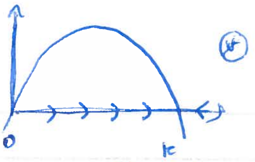
$$\left.\begin{aligned} \dot{N}_1 &= N_1(r_1 + a_{11}N_1 + a_{12}N_2 + a_{13}N_3) \\ \dot{N}_2 &= N_2(r_2 + a_{21}N_1 + a_{22}N_2 + a_{23}N_3) \\ \dot{N}_3 &= N_3(r_3 + a_{31}N_1 + a_{32}N_2 + a_{33}N_3) \end{aligned}\right\} \quad \text{Here } r_k > 0$$

Suppose $N_3 = 0 \Rightarrow$ solve planar system for N_1, N_2 & there are at least 2, possibly 3

& can do this for $N_2 = 0$ and $N_1 = 0$ ...

For an interior steady state we need to solve $r_k + (AN)_k = 0 \Rightarrow N = -A^{-1}r$; has to be positive which depends on choice of r and A

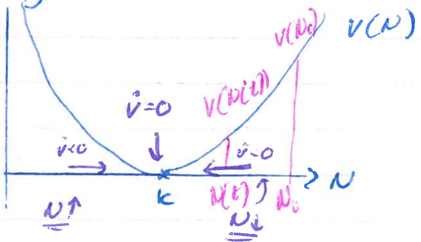
$N = -A^{-1}r > 0$ are the coexistence states which are of major interest to conservation biologists



$\dot{N} = rN(1 - \frac{N}{k})$ logistic model
2 steady states: $N=0$, $N=k$
We can do this graphically ⊕ or analytically $N(t) = \dfrac{N_0 e^{-rt}}{\frac{N_0}{k} + 1 - \frac{N_0}{k} e^{-rt}}$ ← something like this, check notes
There is a 3rd method:

Here we know that k is globally stable i.e. start anywhere $\neq 0$ - end up at k

$V(N) = N - ~~k~~ k \log\frac{N}{k} - k$; when $N=k$ $V(k) = k - k\log 1 - k = 0$
$V'(N) = 1 - k/N$, $V''(N) = k/N^2 > 0$
$= 0 \iff N = k$



Given solution $N(t)$ $\frac{d}{dt}V(N(t)) = V'(N(t))\dot{N}$
$= (1 - \frac{k}{N})(rN(1 - \frac{N}{k}))$
$= r(N-k)(\frac{k-N}{k}) = -\frac{r}{k}(N-k)^2 \leq 0$ with equality $\iff N = k$
$\dot{V} < 0$ means $V(N(t))$ is decreasing with t ; V decreases along a solution $N(t)$ drawn in purple ; conclusion: always end up at k
Since V is always decreasing $N(t) \to k$ which is the minimum of V
This is the most powerful method because it translates to higher dimensions
Analog here for higher dimensions would be a bowl.

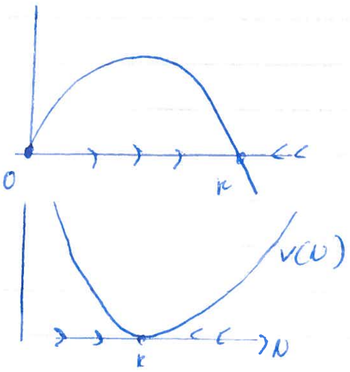
Previously considered 3 methods 20/03/15

$\dot{N} = rN(1 - \frac{N}{k}) = f(N)$

method 1 $\Rightarrow N(t) = \dfrac{N_0}{\frac{N_0}{k} + (1 - \frac{N_0}{k})e^{-rt}}$

$\Rightarrow$

$V(N) = N - k\log(\frac{N}{k}) - k$
$\dot{V}(N) = -k(k-N)^2 \leq 0$



← method 2

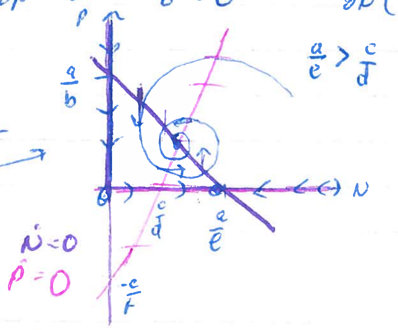
← method 3

Can only hope for explicit sol^ns when have one species
Method 3 is the only method (other than phase plane/portrait) for more than 1 species

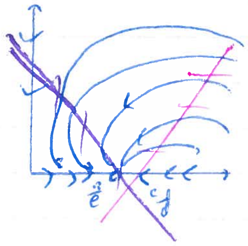
<u>2nd example</u> $\dot{N} = N(a - eN - bP)$ $\dot{P} = P(-c + dN - fP)$ $a, b, c, d, e, f > 0$
~~interspecific comp~~ ~~interspecific competition~~ ← intraspecific competition

$\frac{\partial}{\partial P}\frac{\dot{N}}{N} = -b < 0$ $\frac{\partial}{\partial N}(\frac{\dot{P}}{P}) = d > 0 \Rightarrow$ N prey, P predator

because predator dies out →



$\frac{a}{e} > \frac{c}{d}$



$\frac{a}{e} < \frac{c}{d}$

$\dot{N} = 0$, $N \neq 0$, $a - eN - bP = 0$, ~~if~~ $=0$
$\dot{P} = 0$, $P \neq 0$, $-fP + dN - c = 0$, $P = \dfrac{dN - c}{f} = -\dfrac{c}{f}$ $N = 0$

The aim is to show <u>analytically</u> that when $\frac{a}{e} > \frac{c}{d}$ and $N(0) > 0$, $P(0) > 0$ then $(N(t), P(t)) \longrightarrow (N^*, P^*)$ the interior equilibrium

<u>Define</u> $V(N,P) = d(N - N^*\log\frac{N}{N^*} - N^*) + b(P - P^*\log\frac{P}{P^*} - P^*)$

$p^* \log \frac{p}{p^*} \to p^* \frac{\frac{1}{p^*}}{\frac{p}{p^*}}$

Sketch the graph of V: $\nabla V(N,P) = \left(d\left(1-\frac{N^*}{N}\right), b\left(1-\frac{P^*}{P}\right)\right)$

$\nabla V = 0 \iff$ $N = N^*$ and $P = P^*$

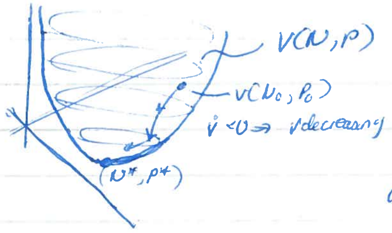
$\log N, \log P$ are concave $\Rightarrow$ $-N^* \log \frac{N}{N^*}$, $-P^* \log P/_{P^*}$ are convex

bP and dN are also convex (and concave - they are linear) $\Rightarrow$ the sum that constructs V is thus a sum of convex functions

$\Rightarrow V(N,P)$ is convex ; note also $V(N,P) \to +\infty$ as $N \to 0$ and/or $P \to 0$

Finally, N increases faster than $\log N$: $\frac{N}{\log N} \to \infty$ as $N \to \infty$

Constructed V s.t. $V(N^*, P^*) = 0$



By showing $\dot{V} < 0$ in the 1st quadrant

$\Rightarrow V(N(t), P(t)) \downarrow \Rightarrow V \to 0$ at $N = N^*$, $P = P^*$

$$\frac{d}{dt} V(N(t), P(t)) = \frac{d}{dt}\left(d\left(N(t) - N^* - N^* \log \frac{N(t)}{N}\right) + b\left(P - P^* \log \frac{P}{P^*} - P^*\right)\right)$$

Remember this trick

$$= d\dot{N} - d\frac{N^*\dot{N}}{N} + b\dot{P} - b\frac{P^*\dot{P}}{P} = \frac{d\dot{N}}{N}(N - N^*) + \frac{b\dot{P}}{P}(P - P^*)$$

$= d(a - eN - bP)(N - N^*) + b(-c + dN - fP)(P - P^*)$

The interior steady state satisfies $a - eN^* - bP^* = 0$, $-c + dN^* - fP^* = 0$

Thus $a - eN - bP = a - eN - bP - (a - eN^* - bP^*)$

$= e(-N + N^*) + b(-P + P^*) = -e(N - N^*) - b(P - P^*)$

$-c + dN - fP = -c + dN - fP - (-c + dN^* - fP^*)$

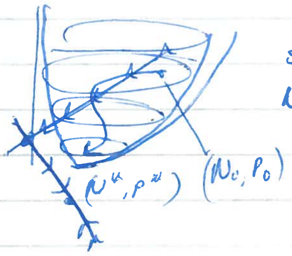
$= d(N - N^*) - f(P - P^*)$

$\dot{V} = d(N - N^*)(-e(N - N^*) - b(P - P^*)) + b(P - P^*)(d(N - N^*) - f(P - P^*))$

$X = N - N^*$, $Y = P - P^* \Rightarrow \dot{V} = dX(-eX - bY) + bY(dX - fY)$

$\dot{V} = -edX^2 - bdXY + bdYX - bfY^2 = -edX^2 - bfY^2 \leq 0$

with equality $\iff X = 0, Y = 0$; $N = N^*$, $P = P^*$



so start at a point + you will move down to N^*, P^*

NB if N_0 and/or $P_0 = 0$ this does not work - points on the boundaries stay on those boundaries

Hence conclude (theorem to be stated) that if (N_0, P_0) is interior, $N(t) \to N^*$, $P(t) \to P^*$ as $t \to \infty$

We had to say $\frac{a}{e} > \frac{c}{d}$ because otherwise $\nexists$ an interior steady state

We give (Chap 9) the Lyapunov theorem

smooth

Theorem Let $U \subseteq \mathbb{R}^n$ be an open set, and $f: U \to \mathbb{R}^n$ a continuously differentiable on U. Suppose $\exists$ $x_0 \in U$ such that $f(x_0) = 0$ (i.e. x_0 is a steady state)

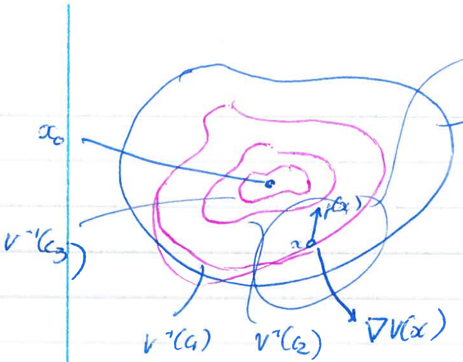
Suppose further that there's a scalar-valued function $V: U \to \mathbb{R}$ such that $V(x) > V(x_0)$ if $x \in U \setminus \{x_0\}$ ~~Then if $\dot{V} \geq \nabla f$~~

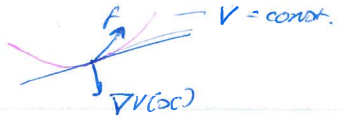
Then if $\dot{V} = \nabla V \cdot f < 0$ for $x \in U \setminus \{x_0\}$ then for $x(0) \in U$

$x(t) \to x_0$ as $t \to \infty$

scalar value function which is minimised at steady state

Most important model in dynamical systems





$U \subseteq \mathbb{R}^n$

vector field $f : U \to \mathbb{R}^n$

scalar function $V : U \to \mathbb{R}$

$V^{-1}(c) = \{x \in U : V(x) = c\}$

$c_1 > c_2 > c_3 \dots$

Told $\nabla V \cdot f < 0 \implies$ point on a pink curve has to move inside that curve

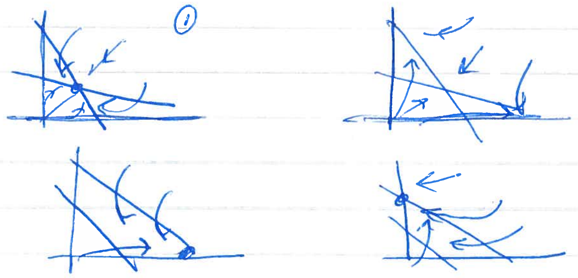
This theorem does not say how to find a Lyapunov function V

Unless V is some physical (e.g. energy, entropy etc.) it can be v. difficult to find it.

$\dot{x} = f(x) \implies x(t)$ ← vector field

<u>Competition model revisited</u>

$$\dot{x} = x(a - ex - by)$$
$$\dot{y} = y(c - dx - fy)$$



Going to prove/show ① rigorously

Interior steady state: $a - ex - by = 0$ $c - dx - fy = 0$

$$\begin{pmatrix} x \\ y \end{pmatrix} = \frac{1}{ef - bd}\begin{pmatrix} f & -b \\ -d & e \end{pmatrix}\begin{pmatrix} a \\ c \end{pmatrix} \qquad \begin{pmatrix} e & b \\ d & f \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} a \\ e \end{pmatrix}$$

$$= \left(\frac{fa - bc}{ef - bd}, \frac{ce - ad}{ef - bd} \right)$$

This is feasible if either (i) $ef > bd$ then $fa > bc$ and $ce > da$

$\frac{f}{b} > \frac{c}{a} > \frac{d}{e}$ $\frac{d}{e} < \frac{c}{a}$

ii) $\frac{f}{b} < \frac{c}{a} < \frac{d}{e}$

Above $\implies$ $x^* = \dfrac{fa - bc}{ef - bd} > 0$ $y^* = \dfrac{ce - ad}{ef - bd} > 0$

$$V(x,y) = d\left(x - x^* - x^* \log \frac{x}{x^*}\right) + b\left(y - y^* - y^* \log \frac{y}{y^*}\right)$$

$$\dot{V} = d\left(\dot{x} - \frac{\dot{x} x^*}{x}\right) + b\left(\dot{y} - \frac{\dot{y} y^*}{y}\right)$$

$$= \frac{\dot{x}}{x} d(x - x^*) + \frac{\dot{y}}{y} b(y - y^*) = (a - ex - by) d(x - x^*) + (c - dx - fy) b(y - y^*)$$

$$\frac{\dot{x}}{x} = a - ex - by = a - ex - by - (a - ex^* - by^*) = -e(x - x^*) - b(y - y^*)$$

$$\frac{\dot{y}}{y} = c - dx - fy = -d(x - x^*) - f(y - y^*)$$

$$\dot{V} = d(x - x^*)(-e(x - x^*) - b(y - y^*)) + b(-d(x - x^*) - f(y - y^*))(y - y^*)$$

Set $X = x - x^*$, $Y = y - y^*$

$\dot{V} = dX(-eX - bY) + bY(-dX - fY) = -edX^2 - bfY^2 - 2bdXY$

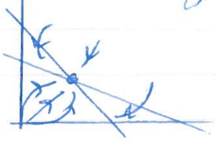
$q(X,Y) = -edX^2 - bfY^2 - 2bdXY$

Need to show ≤ 0 $\forall\ x,y$. This is < 0 if $q = 0$ has only complex roots $B^2 < 4AC$; $(-2bd)^2 < 4(-ed)(-bf)$

$(2bd)^2 - 4edbf = 4bd(bd - ef)$ and for an interior (x^*, y^*) to exist is
< 0 if $\longrightarrow$ $\frac{f}{b} > \frac{a}{c} > \frac{d}{e} \Rightarrow ef > bd$

When $bd - ef < 0$ $\dot{V} \leq 0$ with equality iff $x = x^*, y = y^*$

Hence to apply Lyapunov's theorem, choose $U = \{(x,y) \in \mathbb{R}^2, x > 0, y > 0\}$
$f = (x(a - ex - by), y(c - dx - fy))$ $x_0 = (x^*, y^*)$ and V = same V given
$\Rightarrow$ if $bd < ef$ $x(0) = (x_0, y_0)$ with $x_0 > 0$, $y_0 > 0$ then
$x(t) \longrightarrow (x^*, y^*)$ as $t \to \infty$



Theorem For the Lotka-Volterra system

$$\dot{x}_i = x_i(r_i + (Ax)_i) \qquad i = 1, 2, \ldots, n$$

Assume that there exists a unique interior steady state x^*
Then if $\exists\ \gamma_i > 0$ $i = 1, 2, \ldots, n$ such that

$$M = \begin{pmatrix} \gamma_1 & & 0 \\ & \gamma_2 & \\ 0 & & \ddots\ \gamma_n \end{pmatrix} A + A^T \begin{pmatrix} \gamma_1 & & \\ & \gamma_2 & 0 \\ 0 & & \ddots\ \gamma_n \end{pmatrix} < 0$$

(negative definite matrix; i.e. all eigenvalues of M are negative)
$\equiv \underline{u}^T M \underline{u} < 0$ $\forall\ \underline{x} \neq \underline{0}$

then for any $\underline{x}(0)$ with each $x_i(0) > 0$, $\underline{x}(t) \longrightarrow \underline{x}^*$ as $t \to \infty$

Proof Let $V(\underline{x}) = \sum_{i=1}^{n} \gamma_i \left(x_i - x_i^* - x_i^* \log \frac{x_i}{x_i^*}\right)$

$$\dot{V} = \nabla V(x) \cdot \dot{x} = \sum_{i=1}^{n} \gamma_i \left(1 - \frac{x_i^*}{x_i}\right) \cdot \dot{x}_i = \sum_{i=1}^{n} \gamma_i \frac{\dot{x}_i}{x_i}(x_i - x_i^*)$$

$\frac{\dot{x}_i}{x_i} = r_i + (Ax)_i = -(Ax^*)_i + (Ax)_i = (A(x - x^*))_i$ and $-Ax^* = r$

$$\dot{V} = \sum_{i=1}^{n} \gamma_i (A(x - x^*))_i (x_i - x_i^*)$$

$$= \sum_{i,j=1}^{n} \gamma_i a_{ij} (x_i - x_i^*)(x_j - x_j^*)$$

$$= (\underline{x} - \underline{x}^*)^T \begin{pmatrix} \gamma_1 & & \\ & \ddots & \\ & & \gamma_n \end{pmatrix} A(\underline{x} - \underline{x}^*)$$

$$= \frac{1}{2}(\underline{x} - \underline{x}^*)^T \left[\begin{pmatrix} \gamma_1 & 0 \\ 0 & \gamma_n \end{pmatrix} A + A^T \begin{pmatrix} \gamma_1 & \\ & \gamma_n \end{pmatrix}\right](\underline{x} - \underline{x}^*)$$

$\underline{u}^T B \underline{u} = (\underline{u}^T B \underline{u})^T = \underline{u}^T B^T \underline{u}$

$\underline{u}^T B \underline{u} = \frac{1}{2}(\underline{u}^T B \underline{u} + \underline{u}^T B^T \underline{u})$

$\underline{u}^T B \underline{u} = \frac{1}{2} \underline{u}^T (B + B^T) \underline{u}$

If can find $\gamma_i > 0$ such that

$$\begin{pmatrix} \gamma_1 & & 0 \\ & \ddots & \\ 0 & & \gamma_n \end{pmatrix} A + A^T \begin{pmatrix} \gamma_1 & & 0 \\ & \ddots & \\ 0 & & \gamma_n \end{pmatrix} < 0$$

then $\dot{V} \leq 0$

with equality iff $x = x^*$, $y = y^*$

Theorem Lotka-Volterra system $\dot{x}_i = x_i(r_i + (Ax)_i)$ $i=1,2,\dots,n$ 24/03/15

Suppose there is a positive steady state $p = -A^{-1}r$ $(p_i > 0 \quad i=1,2,\dots,n)$

Let D be the diagonal matrix $\begin{pmatrix} \gamma_1 & \ddots & 0 \\ 0 & & \gamma_n \end{pmatrix}$ with $\gamma_i > 0$ $i=1,2,\dots,n$

Then if $\gamma_i > 0$ can be found such that $DA + A^TD$ is negative definite

Then for each $x(0)$ with $x_i(0) > 0$, the solution $x(t) \to p$ as $t \to \infty$

May-Leonard system 3 species competing

$\dot{x} = x(1-x-\alpha y - \beta z)$; $\dot{y} = y(1-y-\beta x - \alpha z)$; $\dot{z} = z(1-z-\alpha x - \beta y)$

$\alpha, \beta > 0$; $\frac{\partial}{\partial y}\left(\frac{\dot{x}}{x}\right) = -\alpha < 0 \implies$ competition ; similarly for other species

Here $A = -\begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix}$ and $r = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$

Consider $D = \begin{pmatrix} \gamma_1 & 0 & 0 \\ 0 & \gamma_2 & 0 \\ 0 & 0 & \gamma_3 \end{pmatrix}$ $\gamma_i > 0$ $i = 1,2,3$

Take $\gamma_1 = 1$, $\gamma_2 = a > 0$, $\gamma_3 = b > 0$

$M = DA + A^TD = \begin{pmatrix} 1 & 0 & 0 \\ 0 & a & 0 \\ 0 & 0 & b \end{pmatrix}\begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix} + \begin{pmatrix} 1 & \beta & \alpha \\ \alpha & 1 & \beta \\ \beta & \alpha & 1 \end{pmatrix}\begin{pmatrix} 1 & 0 & 0 \\ 0 & a & 0 \\ 0 & 0 & b \end{pmatrix}$

Find a, b such that M is negative definite. Guess $a = b = 1$

$M = -\begin{pmatrix} 2 & \alpha+\beta & \alpha+\beta \\ \alpha+\beta & 2 & \alpha+\beta \\ \alpha+\beta & \alpha+\beta & 2 \end{pmatrix} = \begin{pmatrix} -2 & -\theta & -\theta \\ -\theta & -2 & -\theta \\ -\theta & -\theta & -2 \end{pmatrix}$ $\theta = \alpha + \beta$

$r1 - r2$

Characteristic equation for M

$\det(M - \lambda I) = \det\begin{pmatrix} -2-\lambda & -\theta & -\theta \\ -\theta & -2-\lambda & -\theta \\ -\theta & -\theta & -2-\lambda \end{pmatrix} = \det\begin{pmatrix} \theta-2-\lambda & 2+\lambda-\theta & 0 \\ -\theta & -2-\lambda & -\theta \\ -\theta & -\theta & -2-\lambda \end{pmatrix}$

$c2 + c1$

$= \det\begin{pmatrix} \theta-2-\lambda & 0 \; \cancel{\theta} & 0 \\ -\theta & -2-\lambda+\theta & -\theta \\ -\theta & -2\theta & -2-\lambda \end{pmatrix} = (\theta-2-\lambda)[(2+\lambda)(2+\lambda+\theta) - 2\theta^2]$

$= (\theta-2-\lambda)[4 + 2\lambda + 2\theta + 2\lambda + \underset{+\lambda\theta}{\lambda^2} - 2\theta^2)$

$= (\theta-2-\lambda)(\lambda^2 + \lambda(4+\theta) + 4 + 2\theta - 2\theta^2)$

$= (\theta-2-\lambda)(\lambda+2-\theta)(\lambda+2(1+\theta))$

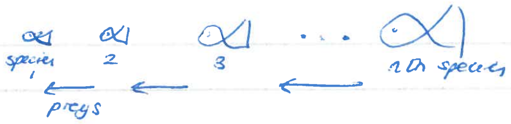
$\implies \lambda = \theta - 2$ $\theta = \alpha + \beta$

$-2(1+\theta)$

If $\theta = \alpha+\beta < 2 \implies \lambda = \theta - 2 < 0$, $\lambda = -2(1+\alpha+\beta) < 0$

$\implies$ stability for $\alpha + \beta < 2$

Food chain



1st species: $\frac{\dot{x}_1}{x_1} = \underset{\substack{\uparrow \\ \text{intrinsic} \\ \text{growth}}}{r_1} - \underset{\substack{\uparrow \\ \text{intraspecific} \\ \text{competition i.e.} \\ \text{crowding}}}{a_{11}x_1} - \underset{\substack{\uparrow \\ \text{predation of} \\ \text{species 1 on 2}}}{a_{12}x_2}$

minus since if no species 1, 2 will die out

Species 2 $\frac{\dot{x}_2}{x_2} = -r_2 + \underset{\substack{\uparrow \\ \text{consumption} \\ \text{of 1}}}{a_{21}x_1} - \underset{\substack{\uparrow \\ \text{intraspecific} \\ \text{competition}}}{a_{22}x_2} - \underset{\substack{\uparrow \\ \text{predation of} \\ \text{3 on 2}}}{a_{23}x_3}$

$\frac{\dot{x}_j}{x_j} = -r_j + a_{j\,j-1}x_{j-1} - a_{j\,j}x_j - a_{j\,j+1}x_{j+1}$ $j = 2,\dots,n-1$

nothing else since
no predator further up

$$\frac{\dot{x}_n}{x_n} = -r_n + a_{n,n-1}x_{n-1} - a_{nn}x_n$$

Let $a_{1,0} = 0$, $a_{n,n+1} = 0$

$$\Longrightarrow \frac{\dot{x}_j}{x_j} = -r_j + a_{j,j-1}x_{j-1} - a_{j,j}x_j - a_{j,j+1}x_{j+1} \qquad j = 1, 2, \dots, n$$
$$= \omega_j$$

$$V(x) = \sum_{i=1}^{n} \gamma_i \left(x_i - p_i - p_i \log \frac{x_i}{p_i}\right)$$ where p is the assumed interior equilibrium

$$\dot{V} = \sum_{i=1}^{n} \gamma_i (x_i - p_i)\frac{\dot{x}_i}{x_i} = \sum_{i=1}^{n} \gamma_i (x_i - p_i)\omega_i$$

But $\omega_j(p) = 0 \quad \forall j$ since p is interior steady state

$$\Longrightarrow \dot{V} = \sum_{i=1}^{n} \gamma_i (x_i - p_i)(\omega_i(x) - \omega_i(p))$$
$$= \sum_{i=1}^{n} \gamma_i(x_i - p_i)\left(a_{i,i-1}(x_{i-1} - p_{i-1}) - a_{ii}(x_i - p_i) - a_{i,i+1}(x_{i+1} - p_{i+1})\right)$$
$$= -\sum_{i=1}^{n} \gamma_i a_{ii}(x_i - p_i)^2 + \sum_{i=1}^{n} \gamma_i \left(a_{i,i-1}(x_{i-1} - p_{i-1}) - a_{i,i+1}(x_{i+1} \cancel{+} - p_{i+1})\right)\cdot(x_i - p_i)$$
$$= -\sum_{i=1}^{n} \gamma_i a_{ii}(x_i - p_i)^2 + \sum_{i=1}^{n} (x_i - p_i)(x_{i+1} - p_{i+1})\left[-\gamma_i a_{i,i+1} + \gamma_{i+1} a_{i+1,i}\right]$$ ← just some manipulation

$$\gamma_1 = 1, \quad \gamma_{i+1} = \frac{\gamma_i a_{i,i+1}}{a_{i+1,i}}$$ ← need to double check

$i = 1, 2, \dots, n \Longrightarrow$ square brackets vanishes

$$\dot{V} = -\sum_{i=1}^{n} \gamma_i a_{ii}(x_i - p_i)^2$$

So if $a_{ii} > 0 \ \forall i$, since $\gamma_i > 0$ then $\dot{V} \le 0$ with equality iff $x_i = p_i$ all i

By Lyapunov thm, $x(t) \longrightarrow p$ if $x_i(0) > 0$

A negative definite matrix is a Hermitian matrix all of whose eigenvalues are negative. A square matrix is called Hermitian if it is self adjoint. A Hermitian matrix $A = (a_{ij})$ is defined as one for which

$$A = A^H \qquad \text{i.e.} \qquad a_{ij} = \bar{a}_{ji}$$

where A^H is the conjugate transpose

$b_1, b_2, a_{12}, \alpha_{21}, r_1, r_2, k_1, k_2 > 0$

Phase plane analysis 27/03/15

$\dot{N}_1 = N_1 r_1 \left(1 - \frac{N_1}{K_1} - \frac{b_1 N_1}{1+\alpha_{12} N_2}\right)$ $\dot{N}_2 = r_2 N_2 \left(1 - \frac{N_2}{K_2} - \frac{b_2 N_2}{1+\alpha_{21} N_1}\right)$

If $\alpha_{12} = 0$ and $\alpha_{21} = 0$ we get a decoupling in to 2 decoupled logistic growth models

Set $u_1 = \frac{N_1}{K_1}$, $u_2 = \frac{N_2}{K_2}$ to get $\dot{u}_1 = r u_1 \left(1 - u_1 - \frac{b_1 K_1 u_1}{1+\alpha_{12} K_2 u_2}\right)$

$\frac{du_1}{dt} = u_1 \left(1 - u_1 - \frac{\gamma_1 u_1}{1+\theta_2 u_2}\right)$ here $\gamma_1 = b_1 k_1$, $\theta = \alpha_{12} k_2$

Let $\tau = r_1 t$ $\frac{du_1}{d\tau} = u\left(1 - u_1 - \frac{\gamma_1 u_1}{1+\theta_2 u_2}\right)$

similarly $\frac{du_2}{d\tau} = \rho u_2 \left(1 - u_2 - \frac{\gamma_2 u_2}{1+\theta_1 u_1}\right)$ $\rho = \frac{r_2}{r_1}$

Set $x = u_1$, $y = u_2$ $\Rightarrow$ $\dot{x} = x\left(1 - x - \frac{\gamma_1 x}{1+\theta_2 y}\right)$ $\dot{y} = y\left(1 - y - \frac{\gamma_2 y}{1+\theta_1 x}\right)$

Steady states $x = 0$; $y = \frac{1}{1+\gamma_2}$ $y = 0$; $x = \frac{1}{1+\gamma_1}$

For interior steady states $1 - x = \frac{\gamma_1 y}{1+\theta_2 y}$ $1 - y = \frac{\gamma_2 y}{1+\theta_1 x}$

$y_1(x) = \frac{x(\gamma_1+1)-1}{\theta_2(1-x)}$ $y_2(x) = \frac{1+\theta_1 x}{1+\gamma_2+\theta_1}$

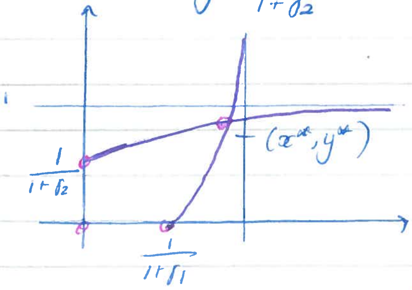
$\dot{x} = 0$ $\dot{y} = 0$

Consider y_1 $y_1 = \frac{(1+\gamma_1)x - 1}{\theta_2(1-x)}$ $\Rightarrow$ $y_1''(x) = \frac{+2\gamma_1}{\theta_2(x-1)^2} < 0$ y_1 is concave

when $y = 0$ $x = \frac{1}{1+\gamma_1}$ and as $x \to 1$ from left $y \uparrow \infty$

Consider y_2 $y_2 = \frac{1+\theta_1 x}{1+\gamma_2+\theta_1 x}$ $\Rightarrow$ $y_2''(x) = \frac{-2\theta_1^2\gamma_2}{(1+\gamma_2+\theta_1 x)^2} < 0$ $\Rightarrow$ y_2 is concave

when $x = 0$ $y = \frac{1}{1+\gamma_2}$ As $x \to \infty$ $y_2(x) \to 1$



$\frac{1}{1+\gamma_1} < x^* < 1$ $\frac{1}{1+\gamma_2} < y^* < 1$

When $\underset{x=0}{y=0} \Rightarrow x^* = x(1 - x - \gamma_1 x) \Rightarrow x \to \frac{1}{1+\gamma_1}$ $y \to \frac{1}{1+\gamma_2}$

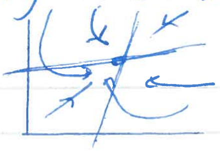
Hence both species at (x^*, y^*) are at greater values than their carrying capacities $\Rightarrow$ species are cooperating

$\frac{\dot{x}}{x} = \left(1 - x - \frac{\gamma_1 x}{1+\theta_2 y}\right)$ $\frac{\dot{y}}{y} = 1 - y - \frac{\gamma_2 y}{1+\theta_1 x}$

$\frac{\partial}{\partial y}\left(\frac{\dot{x}}{x}\right) = \frac{\theta_2 \gamma_1 x}{(1+\theta_2 y)^2} > 0$ $\frac{\partial}{\partial x}\left(\frac{\dot{y}}{y}\right) = \frac{\gamma_2 \theta_1 y}{(1+\theta_1 x)^2} > 0$ $\Rightarrow$ cooperation

The corresponding Lotka-Volterra cooperation $\frac{\dot{x}}{x} = 1 - x + \underline{\alpha y}$ $\frac{\dot{y}}{y} = 1 - y + \underline{\beta x}$ $\alpha, \beta > 0$

$-\frac{\gamma_1 x}{1+\theta_2 y}$



Stability

$f(x,y) = x\left(1 - x - \frac{\gamma_1 x}{1+\theta_2 y}\right)$

$g(x,y) = y\left(1 - y - \frac{\gamma_2}{1+\theta x}\right)$

$$J = \begin{pmatrix} f_x & f_y \\ g_x & g_y \end{pmatrix} = \begin{pmatrix} \left(1-x-\frac{\gamma_1 x}{1+\theta_2 y}\right)+x\left(-1-\frac{\gamma_1}{1+\theta_2 y}\right) & \frac{\theta_2\gamma_1 x^2}{(1+\theta_2 y)^2} \\ \frac{\rho\,\theta_1\gamma_2 y^2}{(1+\theta_1 x)^2} & \rho\left(1-y-\frac{\gamma_2 y}{1+\theta_1 x}\right)+\rho y\left(-1-\frac{\gamma_2}{1+\theta_1 x}\right) \end{pmatrix}$$

$J\left(\frac{1}{1+\gamma_1}, 0\right) = \begin{pmatrix} -1 & * \\ 0 & \rho \end{pmatrix}$ ← not going to bother w/ top since we already have triangular matrix

$\Rightarrow$ eigenvalues $-1, \rho > 0 \Rightarrow$ saddle

$J\left(0, \frac{1}{1+\gamma_2}\right) = \begin{pmatrix} 1 & 0 \\ * & -\rho \end{pmatrix} \Rightarrow$ eigenvalues $1, -\rho < 0 \Rightarrow$ saddle (opposite sign)

Let (x^*, y^*) be interior steady state

$$J(x^*,y^*) = \begin{pmatrix} -x^*\left(1+\frac{\gamma_1}{1+\theta_2 y^*}\right) & \frac{\theta_2\gamma_1 x^{*2}}{(1+\theta_2 y^*)^2} \\ \frac{\rho\theta_1\gamma_2 y^{*2}}{(1+\theta_1 x^*)^2} & -\rho y^*\left(1+\frac{\gamma_2}{1+\theta_1 x^*}\right) \end{pmatrix}$$

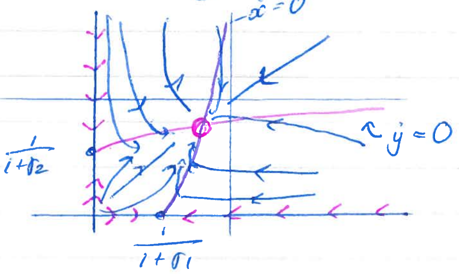
We immediately see $\operatorname{tr} J_{(x^*,y^*)} < 0$

$$\det J_{(x^*,y^*)} = \rho x^* y^*\left(1+\frac{\gamma_1}{1+\theta_2 y^*}\right)\left(1+\frac{\gamma_2}{1+\theta_1 x^*}\right) - \frac{\rho\theta_1\gamma_2\theta_2\gamma_1(x^*y^*)^2}{(1+\theta_1 x^*)^2(1+\theta_2 y^*)^2}$$

$$= \frac{\rho x^* y^*\left((1+\theta_2 y^*)^2+\gamma_1(1+\theta_2 y^*)\right)\left((1+\theta_1 x^*)^2+\gamma_2(1+\theta_1 x^*)\right) - \rho\theta_1\theta_2\gamma_1\gamma_2(x^*y^*)^2}{(1+\theta_1 y^*)^2(1+\theta_1 x^*)^2}$$

> 0 since pink bits exactly balance

$\longrightarrow (x^*, y^*)$ is stable

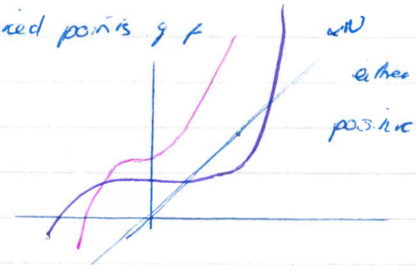


<u>Discrete time</u> $N_{t+1} = f(N_t)$ Steady states ≡ fixed points of f

$|f'(N^*)| < 1 \Rightarrow$ stable

$f(N) = \frac{\alpha N^2}{1+\beta N^3}$ Clearly $N^* = 0$ is a steady state

<u>else</u> $\alpha N = 1 + \beta N^3$



αN either 2 or 0 positive roots

Consider a double root ⟶

$1 + \beta N^3 - \alpha N = 0$

$3\beta N^2 - \alpha = 0 \Rightarrow N^2 = \frac{\alpha}{3\beta} \Rightarrow 1 + N(\beta N^2 - \alpha) = 0 \Rightarrow 1 + N\left(\frac{\alpha}{3} - \alpha\right) = 0$

$\Rightarrow N = \frac{3}{2\alpha}$ $\quad 1 = \frac{2}{3}N\alpha$

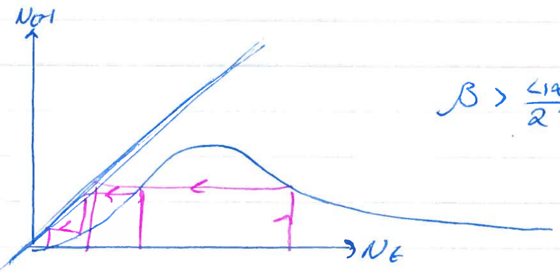
$\Rightarrow 3\beta\left(\frac{9}{4\alpha^2}\right) = \alpha \Rightarrow \beta = 4\alpha^3/27$

2 N exist when $\beta < \frac{4\alpha^3}{27}$

Want to plot cobweb map

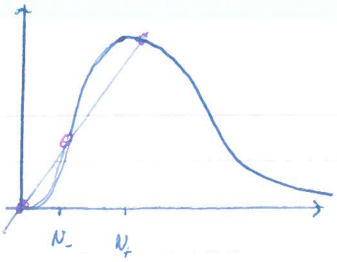
$f(N) = \frac{\alpha N^2}{1+\beta N^3}$

$N^* = 0$ is globally stable



$\beta > \frac{4\alpha^3}{27}$

Case $\beta < \frac{4\alpha^3}{27}$



We know $f'(N_-) > 1$ by construction - could not have anything else

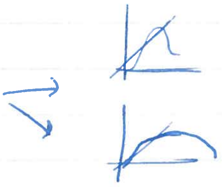
$f(N) = \frac{\alpha N^2}{1+\beta N^3}$, $f'(N) = \frac{2\alpha N}{1+\beta N^3} - \frac{\alpha N^2 3\beta N^2}{(1+\beta N^3)^2} = \frac{2\alpha N(1+\beta N^3) - 3\alpha\beta N^4}{(1+\beta N^3)^2} = \frac{2\alpha N \cdot \alpha\beta N^4}{(1+\beta N^3)^2}$

$= \frac{\alpha N(2-\beta N^3)}{(1+\beta N^3)^2}$

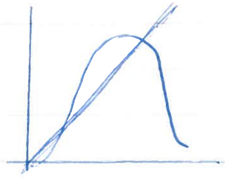
We know $1+\beta N_\pm^3 = \alpha N_\pm$ $\quad f'(N_\pm) = \alpha N_\pm\left(2-(\alpha N_\pm - 1)\right) / (\alpha N_\pm)^2$

$f'(N_\pm) = \frac{3-\alpha N_\pm}{\alpha N_\pm} = \frac{3}{\alpha N_\pm} - 1$

Is it negative?
// needn't be

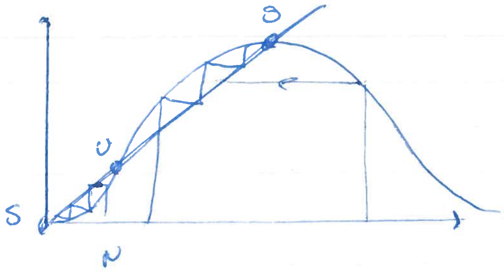


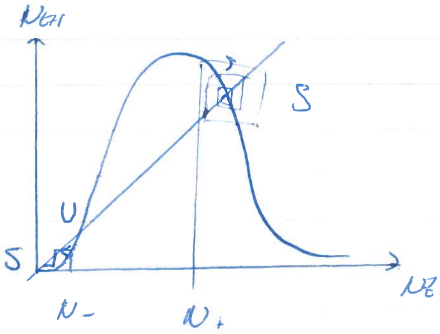
$f'(N_\pm) > -1$



$f'(N_\pm) < 1$

To complete picture





$\dot{N} = \rho N\left(1-\frac{N}{K}\right) - \frac{\gamma NP}{A+N}$ $\quad$ N = prey, P = predator

logistic growth

Holling Type II

Will consider dynamics of prey + have predator pop fixed

Consider P = constant

Let $u = \frac{N}{K}$ ← always scale by dividing population by carrying capacity, if available

$\dot{u} = \rho u(1-u) - \frac{\gamma uP}{A+KN}$ $\quad \frac{du}{\rho dt} = u(1-u) - \frac{\gamma P/\rho\, u}{A+Ku}$

$\frac{du}{\rho dt} = u(1-u) - \frac{\gamma P}{\rho K}\frac{u}{\frac{A}{K}+u}$ $\quad$ Let $\alpha = \frac{\gamma P}{\rho K}$, $\beta = \frac{A}{K}$ $\quad \tau = \rho t$

$\frac{du}{d\tau} = u(1-u) - \frac{\alpha u}{\beta+u}$

Steady states: $u=0$ or $1-u = \frac{\alpha}{\beta+u}$

$\Longrightarrow \beta+u-\beta u-u^2 = \alpha \Rightarrow u^2+(\beta-1)u+\alpha-\beta = 0$

$u_\pm = \frac{1-\beta}{2} \pm \frac{1}{2}\sqrt{(\beta-1)^2-4(\alpha-\beta)}$

If $\beta > \alpha$, $u_+ > 0$, $u_- < 0 \Rightarrow$ If $\beta > \alpha$, $\exists$ unique positive steady state

If $\beta < \alpha$, then first we need real u

$(\beta-1)^2 > 4\alpha - 4\beta \rightarrow (\beta+1)^2 > 4\alpha \Rightarrow \beta+1 > 2\sqrt{\alpha}$

Need $u_+, u_- > 0 \Rightarrow$ need $\beta < 1$

$\Rightarrow \quad 1 > \beta > 2\sqrt{\alpha} - 1 \iff$ 2 positive roots

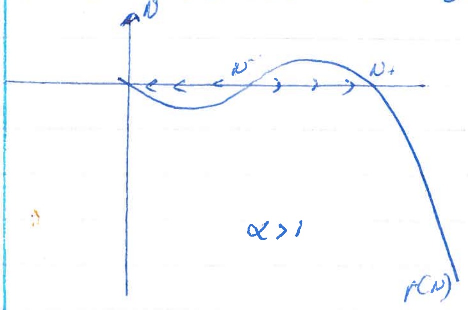
$f(u)$ here is wrong, obviously

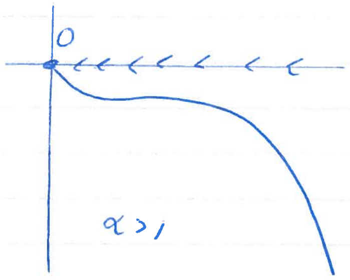
NB ; $\alpha = \beta$ we get $0, 0$ and $1 - \beta > 0$ when $\beta < 1$

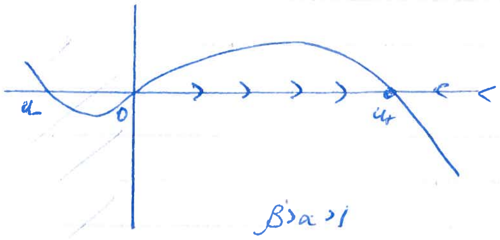
$f(u) = u(1-u) - \frac{\alpha u}{1+\beta u} \qquad f'(u) = 1 - 2u - \frac{\alpha}{1+\beta u} + \frac{\alpha \beta u}{(1+\beta u)^2}$

$f'(0) = 1 - \alpha$; if $\alpha > 1$ $f'(0) < 0$

In this case we cannot have $\beta < 1$ and $\beta > \alpha$







-ve root irrelevant.

<u>Exam</u>

2011 - there is <u>another</u> topic SIR - don't worry about this

Harder questions

UNIVERSITY COLLEGE LONDON

EXAMINATION FOR INTERNAL STUDENTS

MODULE CODE : **MATH3506**

ASSESSMENT PATTERN : **MATH3506A**

MODULE NAME : **Mathematical Ecology**

DATE : **13-May-15**

TIME : **14:30**

TIME ALLOWED : **2 Hours 0 Minutes**

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All questions may be attempted but only marks obtained on the best **four** *solutions will count.*
The use of an electronic calculator is **not** *permitted in this examination.*

1. Two interacting species with densities x, y are modelled by the system

$$\begin{aligned} \frac{dx}{dt} &= x(a - bx - cy) \\ \frac{dy}{dt} &= y(-d + ex) \end{aligned} \qquad (1)$$

where $a, b, c, d, e > 0$ are constants.

   (a) Briefly discuss the model, identifying carefully the type of species-species interactions involved. What are the carrying capacities for the two species?

   (b) Find all steady states of the system (1) and determine whether they are locally stable or unstable.

   (c) Carefully sketch the phase plane for the system (1) when $ae > bd$.

   (d) Sketch $x(t)$ as a function of t when $x(0) = a/c$ and $y(0) = d/e$ when $ae > bd$.

2. Suppose that the probability that an individual gives birth in a time interval $[t, t+\delta t)$ is $b(t)\delta t + O((\delta t)^2)$, where $b(t) > 0$. Let $P(t)$ be the probability that a given individual does not give birth in $[0, t)$.

   (a) By considering $\frac{1}{\delta t}(P(t + \delta t) - P(t))$, or otherwise, show that

$$P(t) = \exp\left(-\int_0^t b(s)\, ds\right).$$

   (b) Show that, provided $tP(t) \to 0$ as $t \to \infty$, the expected time to the first birth is

$$\bar{T} = \int_0^\infty P(t)\, dt.$$

   Now suppose that the birth rate is $b(t) = te^{-\lambda t}$ $(\lambda > 0)$ and that each individual's life expectancy is so long that they effectively live forever.

   (c) Find an expression for the expected number of offspring born to an individual after time t. Hence derive a differential equation for the expected population size $N(t)$ at time t given that $N(0) = N_0 > 0$. What happens to the expected population size as $t \to \infty$?

3. (a) A population is modelled by the differential equation

$$\frac{dN}{dt} = \rho(t) N \left(1 - \frac{N}{K(t)}\right), \quad N(0) = N_0, \tag{2}$$

where $N_0 > 0$ is constant and $\rho(t), K(t) > 0$ are functions of t. By considering $M(t) = N(t)\, e^{-\int_0^t \rho(s)\, ds}$, or otherwise, show that (2) has the solution

$$N(t) = \frac{N_0 e^{\int_0^t \rho(s)\, ds}}{1 + N_0 G(t)}, \qquad \text{where } G(t) = \int_0^t \frac{\rho(u)}{K(u)} e^{\int_0^u \rho(\tau)\, d\tau}\, du.$$

(b) Find all fixed points and their stability for the discrete-time system $N_{t+1} = \dfrac{2N_t^2}{1 + N_t^3}$. Sketch the cobweb map. You should take care to indicate the stability of each fixed point and you should indicate all types of solution behaviour.

4. A food chain of 3 species is modelled so that species i has density x_i $(i = 1, 2, 3)$ and the resulting equations are

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(r_1 - a_{11}x_1 - a_{12}x_2) \\ \frac{dx_2}{dt} &= x_2(-r_2 + a_{21}x_1 - a_{22}x_2 - a_{23}x_3) \\ \frac{dx_3}{dt} &= x_3(-r_3 + a_{32}x_2 - a_{33}x_3) \end{aligned} \tag{3}$$

where $r_i > 0$ for $i = 1, 2, 3$ and each $a_{ij} > 0$ for indices i, j where it is defined.

(a) Give a brief explanation of the model.

(b) State Lyapunov's theorem for asymptotically stable steady states.

(c) Show that the function $\phi(x) = x - r\log(x/r)$ has a unique minimiser and find it.

(d) Assuming that the system (3) has a unique interior steady state $x^* = (x_1^*, x_2^*, x_3^*)$, and by considering a function V of the form

$$V(x) = \sum_{i=1}^{3} \gamma_i \left\{ x_i - x_i^* - x_i^* \log\left(\frac{x_i}{x_i^*}\right)\right\},$$

for suitable $\gamma_i > 0$ $(i = 1, 2, 3)$, show that if the populations $x_i(0) > 0$ for $i = 1, 2, 3$ then the solution of (3) tends to the interior steady state x^* as t tends to infinity.

5. In an age-structured population there are n age classes where n is large. The population density of age k at time t is denoted by $N_k(t)$ and $\mathbf{N}(t) = (N_1(t), \dots, N_n(t))^T$. The expected number of new offspring of an individual at age k is b_k $(k \geqslant 1)$ and the probability that an individual aged $k \geqslant 0$ (with $k = 0$ the newborns) survives to age $k+1$ is p_k. No individual can survive past age n.

   (a) Show that $\mathbf{N}(t+1) = L\mathbf{N}(t)$ for $t = 0, 1, 2, \dots$ where L is the $n \times n$ Leslie matrix which you should find.

   (b) Show that the non-zero eigenvalues λ of L satisfy the Euler-Lotka equation.

$$\sum_{r=1}^{n} \frac{b_r \ell_r}{\lambda^r} = 1,$$

   where $\ell_k = \Pi_{i=0}^{k-1} p_i$ for $1 \leqslant k \leqslant n$. Give an interpretation of each ℓ_k.

   (c) Show that the Euler-Lotka equation has a unique positive root λ_0.

   (d) The life history of a species is such that individuals reach sexual maturity at $k = 3$ units of age and their birth rate b_k equals $1/2$ for $k \geqslant 3$. They have a survival probability $p_k = 1/2$ for $0 \leqslant k < 3$ and $p_k = 1/4$ for $k \geqslant 3$. Their maximum age is n where n is very large. Taking $n = \infty$ as an approximation, and given that the eigenvalue of the Leslie matrix of maximum modulus is $\frac{1}{2}$, find the long-term age distribution of the population.

END OF PAPER