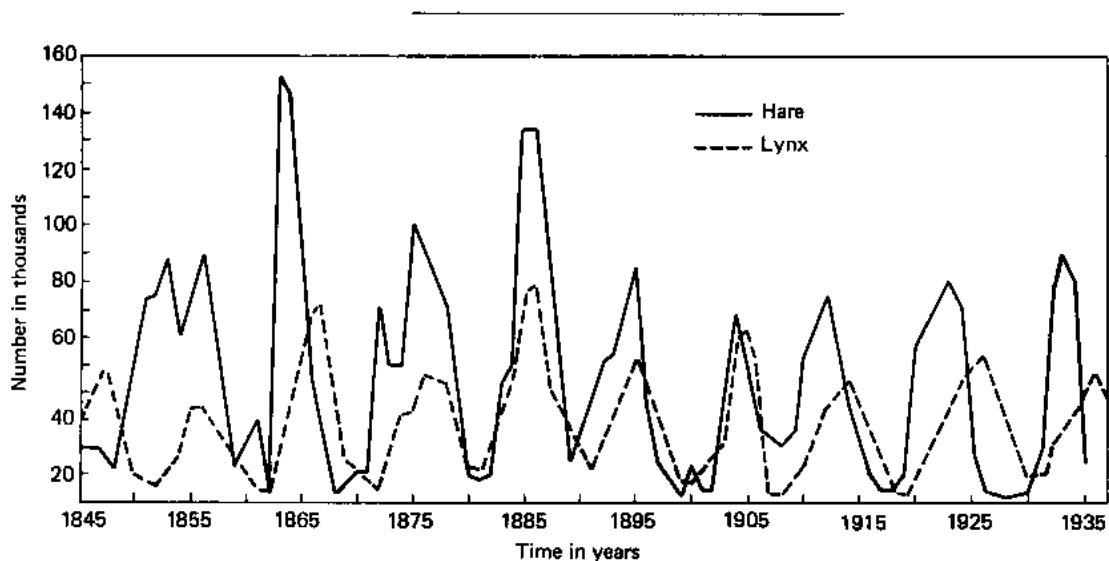


## EXERCISES IN POPULATION DYNAMICS AND EVOLUTIONARY DYNAMICS

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We will mainly investigate population/evolutionary dynamics *within* species in these exercises. Population dynamical phenomena comparable to the famous Lynx-Hare cycles occur just the same within species as in ecological systems of different strongly coupled species.



**Figure 9-3.** Changes in the abundance of the lynx and the snowshoe hare, as indicated by the number of pelts received by the Hudson's Bay Company. This is a classic case of cyclic oscillation in population density. (Redrawn from MacLulich 1937.)

### I. GROWTH AND DECLINE IN STRUCTURED POPULATIONS

Populations *grow*, *decline* or are approximately *stationary* over long time spans. Many population systems are *structured*, which means that individuals in them have differences in *individual state*, which affect their demography (*survival – reproduction – transitions between states*). In this group of exercises we investigate the effects of state on population dynamics.

Demographic parameters, for instance survival probabilities, can depend on many factors. In section I. we assume that they are constant, i.e., the only things that change in the population dynamics are the numbers or densities of individuals in different states. In Section II., this assumption is relaxed.

With constant demographic parameters, stationarity of populations is usually easily destroyed: If by luck, or intentionally, you would encounter a stationary population, then a small change in one of the parameters will make the population grow or decline. For that reason, we focus on *growth* and *decline* here.

We will use Microsoft Excel and the PopTools plug-in for Excel which can be downloaded from <http://www.cse.csiro.au/poptools/>. PopTools is freeware.

### I. A. Concepts - Intuition

Give examples of states in which individuals can be (give three sets of possible states).

Answer the following questions for your examples:

Is the set of possible states discrete or continuous?

What processes affect transitions between states?

In which states occurs reproduction and death?

### II. B. Example

We assume a clonal organism with a set of three discrete age classes: age one, age two, age-class three, which includes individuals of ages three and older.

The population dynamics is followed over discrete time steps. All demographic parameters apply to the cumulated events within one interval between two population censuses.

The demographic parameters we define are:

$P_0$  = survival from birth to age one [0.8]

$P_1$  = survival from age one to age two [0.6]

$P_2$  = survival from age two to age three [0.6]

$P_3$  = survival in age class three [0.4]

$F_1$  = number of offspring per time step for an individual in age class one [3]

$F_2$  = number of offspring per time step at age two [5]

$F_3$  = number of offspring per time step at age three [7]

$N_1(t)$  = number of individuals at age one at time  $t$  [10]

$N_2(t)$  = number of individuals at age two at time  $t$  [10]

$N_3(t)$  = number of individuals at age three at time  $t$  [10]

If you write the numbers of individuals at time  $t$  as  $N_1(t)$ ,  $N_2(t)$  and  $N_3(t)$ , then write the equations for the numbers of individuals one time step later, at time  $t + 1$ :

$$N_1(t + 1) =$$

$$N_2(t + 1) =$$

$$N_3(t + 1) =$$

Use the indicated values in [brackets] as parameter values and starting values of numbers of individuals at time  $t$  and calculate the numbers of individuals one time step later, at  $t + 1$ .

What is the total number of individuals after one interval?

We can write a growth factor of the total population size at time  $t$  as

$$\lambda(t) = \frac{\sum_{i=1}^3 N_i(t+1)}{\sum_{i=1}^3 N_i(t)}$$

What are the growth factors  $\lambda(t)$  and  $\lambda(t + 1)$  of the total population?

What changes to your calculations so far when all initial numbers of individuals are multiplied by ten?

What happens to the distribution of individuals over the three age classes at each time step (the percentages in each age class)?

Now you must choose an age class to invest in. You can multiply the initial number in one age class by ten. What choice makes the population after two generations largest?

Try to formulate few general conclusions on the effects of population structure on population growth.

*Note: So far, we studied numbers of intervals at discrete points in time. There are similar techniques for describing population dynamics at any point in time, and with continuous time change. These techniques often use ordinary differential equations (ODE's). All concepts we will encounter in models with discrete time steps have their counterpart in models with continuous time.*

### I. C. The Matrix Reloaded

Transition probabilities between states over a time interval can be written in tabular form with rows for states where you can go to and columns for states where you come from. Do this for the model in I. B., using the parameter values in brackets.

<i>Coming from age one</i>	<i>Coming from age two</i>	<i>Coming from age three</i>	
			<i>Going to age one</i>
			<i>Going to age two</i>
			<i>Going to age class three</i>

Such tabular forms are matrices (plural of matrix) in mathematical language, and appear in many applications.

There are specific ways of adding and multiplying matrices. Using the equations in section 1B, your knowledge, a book or the internet, figure out how matrix addition and multiplication work.

Every matrix with constant values in all cells has a so-called *eigensystem*. That is a collection of vectors and numbers which can be used to describe the behaviour of populations that have such a matrix which describes their demography. PopTools can be used to extract the eigensystem of a matrix quickly.

*Note: Maybe you still have to install PopTools into your excel program by hand. That goes as follows: Open Tools, Add-Ins, Browse; select the file "C:\Program Files\PopTools\poptools.xba.*

Type your demographic matrix into some cells of an excel spreadsheet.

[A handy way of doing this is making a list of parameter names and their values, and then link the values of the parameters (with "*=code for the cell location*") to the appropriate cells of the matrix.]

Make a list with initial numbers of individuals in the different ages. Use the values in I. B. to start with.

We will iterate the population dynamics for 20 generations. Use *PopTools-MatrixTools-Projection* for that.

Make an extra column with the total number of individuals at each time step.

Make an extra column with the ratio of total number of individuals at each time relative to the total at the previous census (this gives growth factors per time step).

Make an extra column with the ratio of individuals in the second age class to the number of individuals in the first age class, per time step again.

What do you observe?

Change the distribution of initial numbers of individuals over the age classes.

What do you observe?

Let's do something nifty. Apply the *PopTools-MatrixTools-Eigenanalysis* to the transition matrix.

What do the numbers that appear signify, where did you see them before?

Look up on the internet, in the library or in one of the available books:

*dominant eigenvalue:*

*asymptotic population growth rate:*

*stable age/state distribution:*

*reproductive value:*

### **I. D. Application - Right whales**

The Northern right whale (*Eubalaena glacialis*) is one of the rarest mammals in the world. Much effort is devoted to saving this species for future generations. Fujiwara and Caswell (2001) model the population dynamics of the Northern right whale, based on sighting data of photographed individuals. We will calculate asymptotic population growth rates for a model of Northern right whales published by Fujiwara and Caswell (2001). This paper is available as a *.pdf* document from the Leiden blackboard server, and also a news item by Peter Kareiva can be opened there.

Find the transition matrix for numbers of female whales in the Methods section of that paper. Figure one lists some of the parameter values you need to give values to the cells in the matrix. The equations in the Methods section can be used to calculate fecundity parameters  $F$ .

In the long-run, is the right whale population growing or declining? Calculate the asymptotic growth rate from the demographic transition matrix. Type your transition matrix into an Excel spreadsheet, and apply the *PopTools-MatrixTools-Basic Analysis*.

We calculated the asymptotic growth rate based on data for 1994, assuming that all parameters stayed identical after 1994. In the years after 1994, survival of mothers apparently went down. The Fujiwara and Caswell paper states that because of decreased survival of mothers, the asymptotic population growth rate went below one. This should mean that the population is expected to go extinct in the long run, based on survival estimates made after 1994. At which value of maternal survival does this growth rate become smaller than one?

Fujiwara, M. and H. Caswell (2001) Demography of the endangered North Atlantic right whale. *Nature* 414: 537-540.

## II. FEEDBACK AND POPULATION DYNAMICS

Usually, demographic parameters are not constant, but depend on environmental variables. These can be completely external, such as average temperature. Other variables are internal, which means that the changes in the size and composition of a population can change them. When a parameter depends on the total number of individuals in the population, then that is called *density-dependence*. One speaks of *frequency dependence* when also proportions or frequencies of different types of individuals in the population change the demography. Proportions of females and males often cause frequency dependence.

There are a large number of model examples in the lectures, where density- and frequency dependence matters.

In this lecture, we make use of available web tutorials and of a few demo's in the Populus package. This is freeware as well, available from <http://www.cbs.umn.edu/populus/>. We will also use PopTools again to study a model of *Tribolium* lab populations.

### II.A Intuition

Density- and frequency dependence produce *non-linearities* in the population dynamics. This means that equations such as in section I. B. are no longer linear in the numbers of individuals of the different classes/states. Some non-linear population models are quite famous, such as the logistic equation and the Ricker type of density dependence which is much used in fisheries.

A number of excellent tutorials on non-linear dynamics are available on the internet. A technique that I want you to pick up is called *cobwebbing*. You can learn it on the net as well. Cobwebbing is a simple graphical technique to figure out what the qualitative behaviour of a population dynamical model will be in the long run.

You can find stepwise instructions and a tutorial at

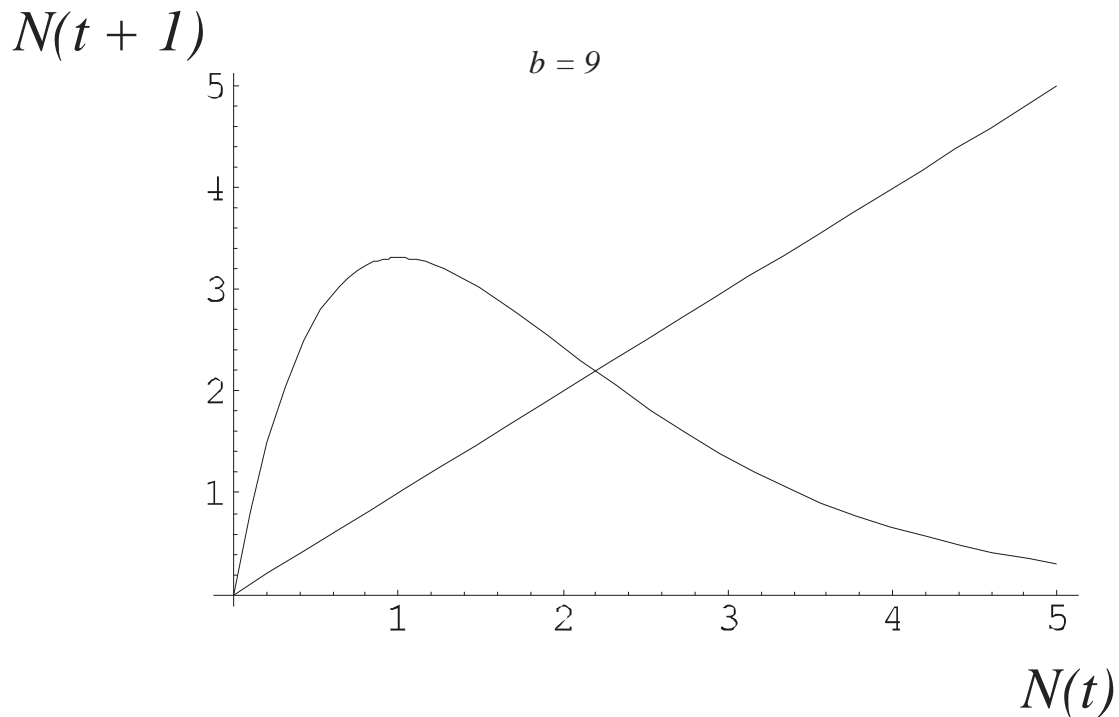
<http://www.public.iastate.edu/~kmoloney/Shared/cobweb.html>

or a Java-applet at the Non-Linear Lab:

<http://www.apmaths.uwo.ca/~bfraser/version1/iterated.html>

Try the tutorial and describe in a few steps how cobwebbing works.

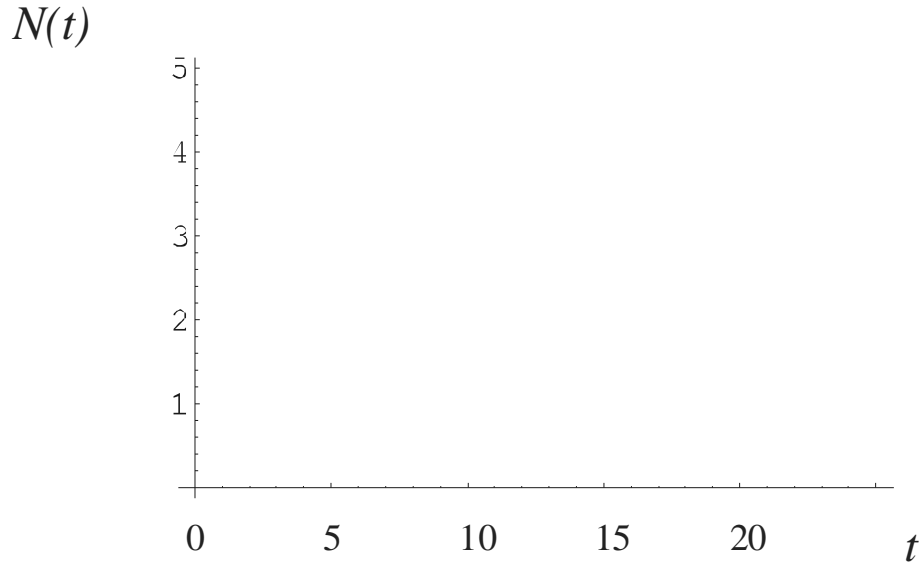
The following graph is from a model by Ricker with as update rule for the population dynamics  $N(t+1) = f[N(t)]$ , and  $f[N(t)] = bN(t)\exp[-N(t)]$ . The graph below gives  $N(t+1)$ , the number of individuals at time  $t+1$ , as a function of  $N(t)$ , for parameter value  $b = 9$ . Show your cobwebbing skills on this graph, starting from  $N(t) = 1$ .



How can you determine which values of  $N$  are *equilibria* of the population dynamics? Indicate the equilibria on the graph and whether they are *locally stable* or not.

What is the long-term dynamics like, starting from arbitrary  $N$ ? Is it a *stable equilibrium*, a *cycle*, or *chaos*?

Sketch the expected long-term dynamics on the following graph.



Try to figure out by using some simple cobwebbing graphs, under which local conditions on functions  $f$  an equilibrium  $N^*$  is locally stable or not.

There are some limitations to the cobwebbing technique. Give one example of a type of model where you cannot really use cobwebbing to follow the population dynamics.

## II.B. Model Examples in Populus

Start Populus 5.3 by clicking on the icon or start from the program menu. We will investigate models in the *Model, Multi-Species Dynamics, Discrete Predator-prey Models* group.

### THE NICHOLSON-BAILEY MODEL

*Components of predation.* The predator-prey model formulated by Nicholson (1933) and Nicholson and Bailey (1935) offers a basic starting point for comparison with more complex and realistic models of predator-prey interactions. The model is derived with two simplifying assumptions (1) *the number of encounters,  $N_e(t)$  between  $P(t)$  parasitoids or predators and  $N(t)$  hosts or prey is proportional to host density,  $N(t)$*  (implying a constant searching efficiency  $a$  and an unlimited appetite, or egg supply for parasitoids) and (2) *these encounters are randomly distributed among hosts.* This means that some hosts will be encountered more than once, so  $N_e(t)$  can be larger than  $N(t)$ . The number of hosts not parasitized is given by the zero term of the Poisson distribution,

$$P_0(t) = \exp[-N_e(t) / N(t)]$$

and the number of hosts actually parasitized (whether it be one or more times) is



$$N_e(t)(1 - \exp[-N_e(t) / N(t)])$$

The number of encounters between  $P(t)$  parasitoids and their hosts  $N(t)$  can be described by a linear relationship

$$N_e(t) = aN(t)P(t)$$

where parameter  $a$  is a proportionality constant called the *parasitoid's area of discovery*. It is a measure of searching efficiency, and can be thought of as the *proportion of all hosts that will be encountered by an individual parasitoid during its lifetime*.

The number of parasitized hosts can now be rewritten as

$$N(t)(1 - \exp[-aP(t)])$$

This expression implies parasitism will rise as a saturating function of  $aP(t)$  (with the number of parasitized hosts approaching  $N(t)$ ), because parasites encounter fewer and fewer *unparasitized* hosts as their number and searching efficiency increase. Nicholson called this relationship a competition curve.

The number of hosts remaining unattacked is

$$N(t)\exp[-aP(t)]$$

After rescaling the numbers/densities of parasitoids such that the conversion of parasitized hosts into numbers of parasitoids is by a factor one, the recursion equations defining host and parasitoid dynamics are

$$\begin{aligned} N(t+1) &= lN(t)\exp[-aP(t)] \\ P(t+1) &= N(t)(1 - \exp[-aP(t)]) \end{aligned}$$

where parameter  $l$  is the intrinsic geometric growth rate of the hosts.

Populus has the *Nicholson-Bailey* model on its menu. Select it. When the button *Model Type* is at *Density-Independent Prey*, then the equations are as above.

With two courses of Mathematical Biology behind you, can you still calculate the equilibria of the number of hosts and parasitoids by hand?

When are these equilibria stable, can you still figure that out? If not, and you're happy with few numerical results, then Populus can help. Below, we will take a simple approach and change parameter values until we observe changes in stability.

Populus produces two different outputs from the Nicholson-Bailey model, a time trajectory of the prey and parasitoid population sizes ( $N, P$  vs.  $t$ ) and a phase plane ( $P$  vs.  $N$ ). Try these out. The model's unstable oscillations usually increase until one or both parties are driven to extinction.

This model is directly analogous to the Lotka-Volterra predator-prey model, save for its formulation as a pair of difference equations. While the continuous Lotka-Volterra version produces a *neutrally stable limit cycle*, the Nicholson-Bailey model yields *diverging oscillations* when either population is perturbed away from equilibrium numbers.

*Density-dependent host growth rate.* Populations of hosts facing limited resources might have a density-dependent geometric growth rate. The introduction of such a host growth rate has a stabilizing influence on the Nicholson-Bailey dynamics. If you choose the *Density-Dependent Prey* option under *Model Type*, Populus substitutes a host recursion suggested by Beddington, Free, and Lawton (1975) which changes the rule for numbers of hosts as follows:

$$N(t+1) = \exp\left[r\left(1 - \frac{N(t)}{K}\right)\right]N(t) \exp[-aP(t)]$$

As  $N$  approaches  $K$ , the growth rate approaches 1.

The parasitoid recursion remains as above.

Hassell (1978; Figure 2.7) gives stability boundaries for this host-parasitoid model.

Comparison of the density-dependent and density-independent versions will show that density-dependent host growth is a strongly stabilizing factor, prolonging the oscillations or damping them to a steady-state equilibrium. Sometimes when the parasitoid goes extinct, host populations can reach extreme density and scaling of the graph obscures the oscillations.

Describe the dynamics of the two models. What are the conditions under which equilibria are stable and what are the factors (self-limitation in prey or host) that contribute to stability?

Make a grid of parameter values, and check for stability at each of these values.

*A Side Question:* What other models that you saw in lectures already, does Populus provide?

There are several packages that are specifically built to do *numerical bifurcation analysis* as you almost did by hand now. They are not extremely easy to use though, and you need a bit more knowledge in dynamical systems theory to use them efficiently. Some names to remember (assuming that you ever need to type them into a search engine) are *candys*, *auto* and *content*.

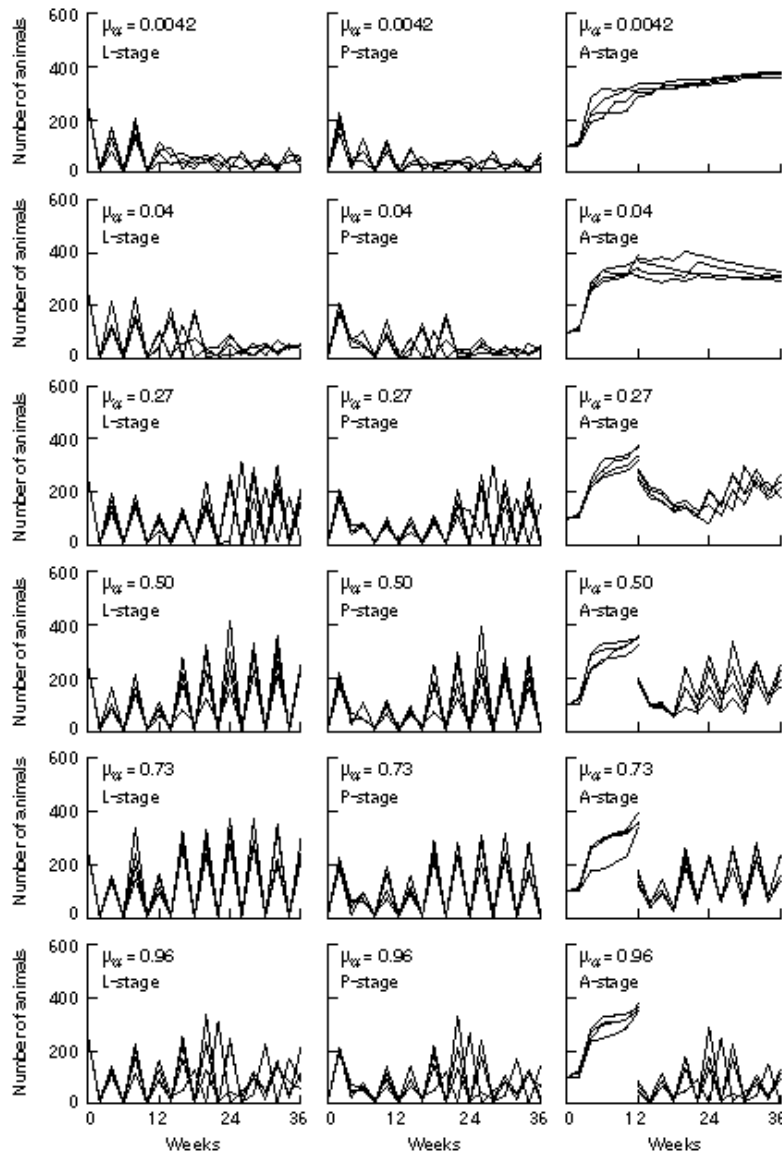
Hassell, M. P. 1978. *The Dynamics of Arthropod Predator-prey Systems*. Princeton University Press, Princeton, New Jersey, USA.

Nicholson, A. J. 1933. The balance of animal populations. *Journal of Animal Ecology* 2:131-178.

Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. *Proceedings of the Zoological Society of London Part 1*. 1935:551-598.

## II.C. *Tribolium* LPA – model

Non-linear population dynamics has made it to the lab. In the nineties, new sophisticated statistical modelling techniques have made it possible to fit different more or less complicated models to time series data and to compare their fit. This implies that it has become possible to test hypotheses on population dynamics on time series data. Much information on a number of lab experiments on population dynamics are to be found at: <http://caldera.calstatela.edu/nonlin/index.html>. These experiments use the red flour beetle *Tribolium castaneum* as a model species. The red flour beetle is a small cannibal, and it is this cannibalism that causes non-linearities.



The Figure above shows results from a population dynamical experiment (Dennis et al. 1997). The top row shows the population dynamics of a lab culture of *Tribolium*

*castaneum RR* strains. In the other rows, adult mortality was changed after twelve weeks of running the experiment (the sometimes abrupt change can be seen in the right column). Inspect the figure and describe the changes in the population dynamics.

We will simulate a popular *Tribolium*- based model.

The equations of this so-called LPA model ( $L(t)$  larvae,  $P(t)$  pupae,  $A(t)$  adults) are

$$L(t + 1) = bA(t) \exp[-c_{el}L(t) - c_{ea}A(t)]$$

$$P(t + 1) = L(t)(1 - \mu_l)$$

$$A(t + 1) = A(t)(1 - \mu_a) + P(t) \exp[-c_{pa}A(t)]$$

In here,  $b$  is the fecundity of adult beetles,  $\mu_l$  and  $\mu_a$  are probabilities of mortality of larvae and adults, respectively. The parameters  $c$  are caused by cannibalism, the subscripts stand for the eaten stage and the stage which is eating (for instance,  $ea$  are eggs  $e$  eaten by adults  $a$ ). When eggs are eaten, they don't make it to the larval stage.

Unfortunately, Populus doesn't handle user-defined functions which contain exponential functions (for reasons of not crashing the program too easily). Therefore we will investigate this model using PopTools.

Dennis et al. give parameter estimates of the LPA model for lab cultures of the *T. sp. RR* strain.

$$b = 7.87$$

$$\mu_l = 0.16$$

$$\mu_a = 0.0042$$

$$c_{el} = 0.014$$

$$c_{ea} = 0.011$$

$$c_{pa} = 0.0044$$

You can see that the value of adult mortality is given in the top row of the figure as well.

In experiments, Dennis and coworkers could change the population dynamics from stable equilibria to cycles by killing extra adults. We will simulate the effects of the experimental design in a Microsoft Excel spreadsheet, and PopTools is our helper. We will use *PopTools*, *Simulation Tools*, *Numerical Projection*. This is a general numerical simulation tool. It iterates a system which you have to give by formulae, and copies results to a new worksheet or a cell in the same worksheet. You can make graphs of the result.

Start with parameter values as above. Make a three cell column with starting values for Larvae, Pupae and Adults. Another column (of three cells) has to contain the equations that calculate numbers of individuals in the three stages at the next time step. You can

then use these as input for numerical projection with PopTools. Make a graph of number of larvae as a function of time, and do the same for pupae and adults.

Then change adult mortality to other values in the figure, which correspond to the experimental manipulations. What happens to the population dynamics in the long run? Does it correspond to what you see in the figure?

Compare your results with the example of section I. C on right whales. What did reducing adult (maternal) survival imply there, what are the consequences here? What causes the difference between the effects in the two models?

Dennis, B. et al. (1997) Transitions in population dynamics: equilibria to periodic cycles to aperiodic cycles. *J. anim. Ecol.* 66: 704-729.

### III. EVOLUTIONARY DYNAMICS

What is fitness?

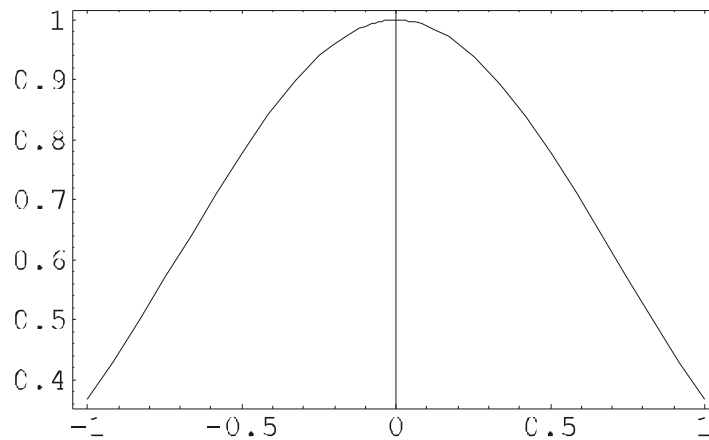
In population genetics, fitness usually is a function or a trait of genotypes, which you insert into a simple population dynamical model [see, for example, *Model, Natural Selection in Populus*]. Because many ecologists study pretty complicated ecologies and structured populations, there was a lack of a clear fitness concept for their systems. The traditional population genetic fitness was not capable of predicting the outcome of selective processes (Charlesworth 1993). In the late eighties and nineties an effort was made to arrive at more general fitness measure. General here means that for nearly any ecology, it should be possible to extract a useful fitness.

A handy measure appeared to be so-called "invasion fitness": *the long-term average growth rate of the number or population density of a mutant allele in a given stationary ecological environment that is affected by a resident population of one or several alleles or phenotypic strategies.*

In this section, we investigate graphical techniques to evaluate the long-term outcome of evolutionary dynamical processes. We will use invasion fitness to predict the outcome of long-term selection.

#### III.A. Changing Fitness Hills

##### *(Invasion) Fitness*



##### *(Mutant ) Trait Value $x$*

This figure gives fitnesses for individuals with a strategy that is represented by a scalar,  $x$ , which represents for instance  $\log(\text{body size})$  and which ranges between -1 and 1. In the population genetic approach to fitness, when fitness is a trait of individuals, you don't need to add "mutant" and "invasion". This becomes only important when fitness depends on the composition of the population.

What sort of change can you expect in the graph above when the population composition changes?

If the population consists of individuals all with trait value  $x^* = 0$ , which other strategies can invade and maybe take over the population?

If the population consists of individuals all with a trait value a little different from zero, can  $x^*$  invade such a population?

If you can start from an arbitrary trait value within  $[-1, 1]$  and mutations in  $x$  occur, which trait value do you expect to become fixed in the population after a very long time?

### III. B. Concepts

Instead of looking at population dynamics and numbers of individuals only, you can also study the *evolutionary dynamics* of populations, where mutations continually produce new variants that can invade and maybe take over the population.

Evolutionary dynamical systems have equilibria as well, which are trait values where (i) mutants with nearby trait values are selectively neutral. (ii) No new mutant appearing can invade.

These equilibria can be locally stable for the evolutionary dynamics, which means that they are reachable from nearby trait values, or not.

Usually, three aspects of a model are important in the study of evolutionary dynamics:

(1.) Which trait values of residents (usually indicated with an asterisk  $*$  added to the symbol for the trait) have *selective neutrality* with respect to similar strategies. Those are potential end points of the evolutionary dynamics. The question to be answered first is: *selective neutrality or not?*

(2.) Of those trait values in (1.), which strategies can be invaded by mutants similar to the resident? The question here is: *invasibility or not?*

(3.) Of those trait values in (1.), which ones can be reached from nearby strategies. That means, when the population has a trait value close to it already, can mutants invade that bring it even closer? The question here is: *convergence stability or not?*

Have you got anything to add to your effects of changing fitness landscapes in III. A.?

### III. C. Pairwise Invasibility Plot

We investigate a simple model of sex ratio evolution with a trait  $x$  that varies between zero and one. Mutant trait values  $x'$  are denoted by a prime to avoid confusion with the resident trait value  $x$ . There is a non-linear relationship between the trait and the proportion of male offspring it produces, described by a power law with parameter  $a$  and the proportion of female offspring it produces, described by a power law with parameter  $b$ .

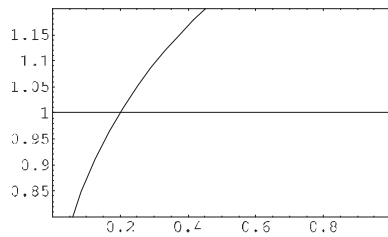
Invasion fitness equals

$$W(x', x) = \frac{1}{2} \frac{(x')^a}{(x)^a} + \frac{1}{2} \frac{(1-x')^b}{(1-x)^b}$$

The first term is the contribution of mutant individuals to the next generation via the male route, the second term the contribution via females. The next figures give invasion fitness functions for three values of  $x$ .

Resident Sex Ratio  $x = 0.2$

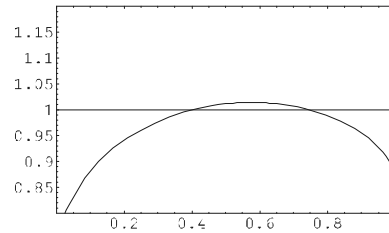
*Invasion Fitness*



*Mutant Sex Ratio  $x'$*

Resident Sex Ratio  $x = 0.4$

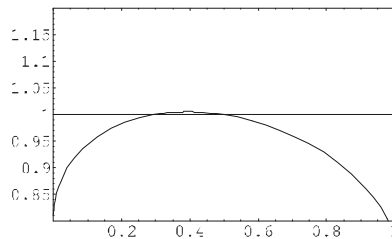
*Invasion Fitness*



*Mutant Sex Ratio  $x'$*

Resident Sex Ratio  $x = 0.5$

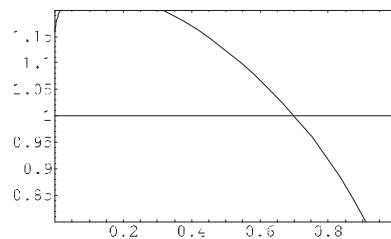
*Invasion Fitness*



*Mutant Sex Ratio  $x'$*

Resident Sex Ratio  $x = 0.7$

*Invasion Fitness*



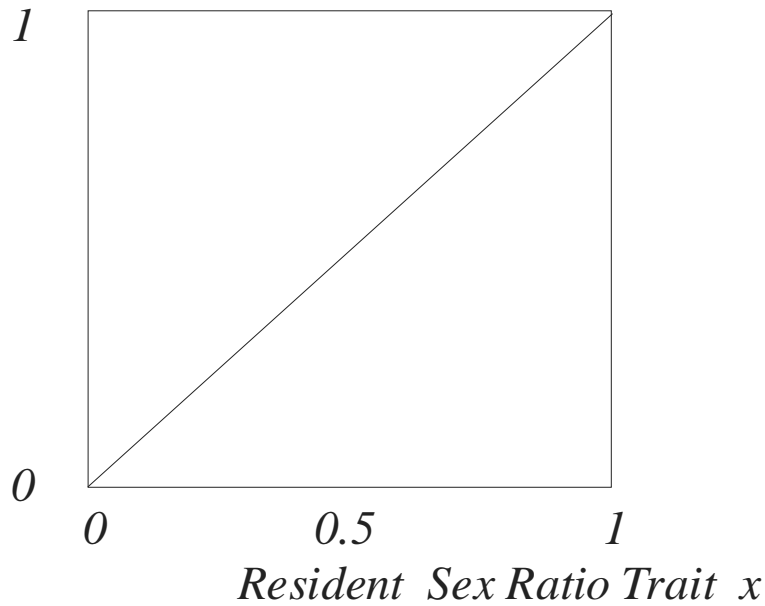
*Mutant Sex Ratio  $x'$*

What is the invasion fitness of mutants with a trait value equal to the resident trait value? Who can invade? Draw a black line under the  $x'$ -axis in the area where invasion fitness of mutants is smaller than the invasion fitness of a mutant that is equal to the resident. What might be an equilibrium sex ratio?

The main information of all these four plots can be summarized into a single plot of a specific type. It is called *Pairwise Invasibility Plot* (Matsuda 1985, Van Tienderen and de Jong 1986).



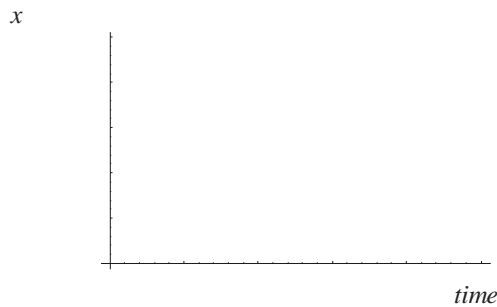
*Mutant Sex Ratio Trait  $x'$*



You will turn the plot above in a *PIP*. For each value of resident sex ratio in the panels above (i.e., 0.2, 0.4, 0.5, 0.7), draw a black vertical line segment that covers mutant sex ratios which are at a selective disadvantage. The diagonal line helps you a bit, it is the line where mutant and resident trait values are equal.

Try to interpolate what happens for other resident sex ratio trait values. Locally selectively neutral points appear as points where the sign pattern of invasion fitness changes across the diagonal (follow the diagonal with your finger if necessary). Which trait value  $x^*$  is selectively neutral in your plot? Is it invasible or not? Is it convergence stable or not?

Draw a sketch for the long-term evolution of the trait  $x$ , assuming that it starts at  $x = 0.1$ , and that all mutants which can invade, will go to fixation and become the new resident allele.



### III.D. Classification by Drawing

What are all possible combinations of invasibility and convergence stability at selectively neutral points?

Make PIP's for each combination and discuss the evolutionary pattern you expect. There's enough space on the bottom part of this page.

Charlesworth, B. (1993) *Evolution in Age-structured Populations*, 2nd Edition. Cambridge University Press.

Dieckmann, U. (1997) Can adaptive dynamics invade? *TREE* 12:128-131.