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Courseware «Stability»

A. Fischlin and M. Ulrich

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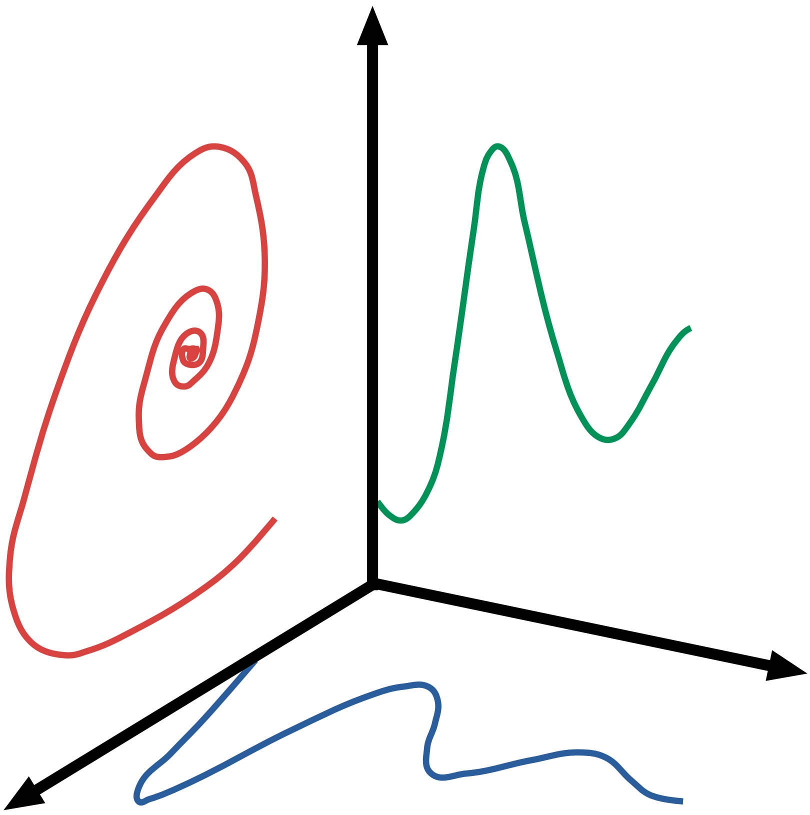

ETH zürich

Department of Environmental Systems Science
Institute of Biogeochemistry and Pollutant Dynamics
Environmental Physics`

Adresse der Autoren / Address of the authors:

Prof. Dr. Andreas Fischlin, Terrestrial Systems Ecology, Environmental Physics, Institute of Biogeochemistry and Pollutant Dynamics,, Department of Environmental Systems Science, ETH Zurich, Universitätsstrasse 16, CH-8092 Zurich
SWITZERLAND

e-mail: andreas.fischlin@env.ethz.ch
www.sysecol.ethz.ch

Dr. Markus Ulrich, UCS Ulrich Creative Simulations GmbH, Herracherweg 93, 8610 Uster
SWITZERLAND

e-mail: markus.ulrich@ucs.ch
www.ucs.ch

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Das zugehörige Unterrichtsprogramm ist erhältlich bei / The related learning program is available at:

www.sysecol.ethz.ch/education/courseware/courseware-downloads.html#stability

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Courseware "Stability"

A. Fischlin ‡ and M. Ulrich €

‡ Department of Systems Ecology/ITÖ - Dept. of Environmental Sciences ETH Zurich, ETH-Zentrum, CH-8092 Zurich

€ Eidg. Institute for Water Supply, Wastewater Treatment and Water Protection (EAWAG), 8600 Dübendorf

1. Introduction

The courseware "Stability" comes with this text and a learning program that allows students to get familiar with the fundamental concept of stability, in particular the stability of ecological systems.

1.1 Theme and purpose of the courseware

The concept of stability plays an important role in the field of ecology, especially population ecology, as many living systems are said to have the ability to self-regulate. The purpose of this introduction to "Stability" is to provide a precise understanding of the term stability and the associated system properties. Following features of the learning program serve this purpose: The behavior of three different predator-prey models, each with different stability properties, can be simulated. All boundary conditions of the simulation can be selected or changed by the user interactively, via menu commands, at any time. In particular, each model system can be exposed to perturbations of selectable magnitude in order to be able to investigate the stability behavior not only in the case of initial value variation, but also under continuous perturbations. The output of the system behavior (simulation results) is done graphically in a tailorable special three-dimensional representation on the screen. That flexible representation helps to understand the model behavior in time and state space.

All three predator-prey models have a steady state, i.e. a singular equilibrium point. From model to model, this equilibrium differs in its stability properties: asymptotic stability, neutral stability, and unstable singularity. Based on the simulations that can be carried out with the three given model systems, the student will now experimentally investigate the stability behavior of these systems. For this purpose, the initial values of the state vector or the extent and frequency of the perturbations can be varied (the models are fixed, i.e. model parameters in particular cannot be changed). In order to be able to detect possible influences of numerical integration and distinguish them from actual stability properties of the mathematical model, the program "Stability" allows the use of different numerical integration methods. Hereby the importance of the accuracy and efficiency of different integration algorithms can also be clearly demonstrated.

1.2 Learning objective

Recognize the different stability properties of simple model predator-prey systems. In particular, the terms asymptotically stable, neutrally stable and unstable equilibrium should become clear and well understood. The three types of stability properties are then also to be assigned to each of the three mathematical models given by the corresponding system equations.

1.3 System requirements (hardware and software)

The program has been programmed in Modula-2 (MacMETH version 2.6), based on the "Dialog Machine" © (version 1.1), and runs on any Apple Macintosh ® with a main memory of at least 512 KByte RAM (random access memory). [1] An external floppy drive is not required. The program is available as a stand-alone application ("double-clickable") and does not require any other special software in addition to the system software (standard character sets) that is by default available on every Macintosh. A printer (ImageWriter I or II or LaserWriter) is advantageous in order to be able to record certain simulation runs on paper. However, the learning objective can also be achieved easily without printing of any simulation outputs.

2. Theory

2.1 On Stability and Stability analysis

There exist different definitions of the term stability. Of particular interest are the stability properties of equilibrium positions of nonlinear, time-invariant systems, i.e. systems of the form: $\underline{x}(k+1) = \underline{f}(\underline{x}(k))$ or $d\underline{x}(t)/dt = \underline{f}(\underline{x}(t))$. For example, the stability of the equilibrium position $\underline{x}°$ according to Lyapunov for the listed class of systems can be defined as follows: Given the domain $G(\underline{x}°, R)$ in the state space. In its center is the equilibrium position $\underline{x}°$. G includes all system states with the Euclidean distance ∂ of $\underline{x}°$, so that $\partial \leq R$. For second-order systems an illustrative, geometric interpretation of this concept is shown in Fig. 1: In this special case, the state space corresponds to the drawing plane.

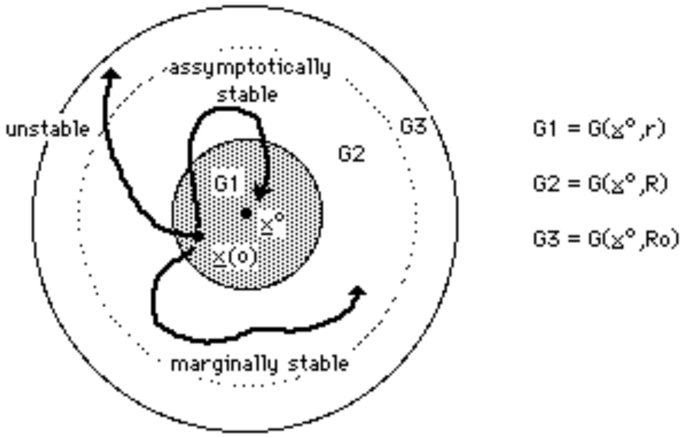

Fig. 1: Geometric illustration of various stability concepts for the special case of a second-order system with an equilibrium (steady state) point $\underline{x}°$: Case a) $\underline{x}°$ is asymptotically stable as all trajectories lead back to the equilibrium $\underline{x}°$; Case b) $\underline{x}°$ is neutrally stable (marginally stable) as trajectories no longer lead back to the equilibrium $\underline{x}°$, although trajectories stay within the limited finite domain G2= $G(\underline{x}°, R)$; Case c) $\underline{x}°$ is unstable as trajectories lead completely away from the equilibrium $\underline{x}°$ and end outside any finite definable domain. For both cases a) and b) $\underline{x}°$ is called Lyapunov stable.

An equilibrium point **$\underline{x}°$ is Lyapunov stable** if the following conditions are satisfied by the system behavior: There is at least one $R_o > 0$ such that for every $R < R_o$ there is an r between 0 and R, so that all subsequent system states $\underline{x}(k)$ or $\underline{x}(t)$ remain within the region $G(\underline{x}°, R)$, even if the initial state $\underline{x}(0)$ remains within $G(\underline{x}°, r)$. To put it less formally: If the initial state $\underline{x}(0)$ is close to a stable equilibrium point $\underline{x}°$, then subsequent system states remain close to $\underline{x}°$. **$\underline{x}°$ is asymptotically stable** if there is also an *R*, so that whenever $\underline{x}(0)$ lies within $G(\underline{x}°, R)$, the state $\underline{x}(k)$ or $\underline{x}(t)$ strives with increasing time k (or t) towards the equilibrium point $\underline{x}°$. **$\underline{x}°$ is unstable** if it is not stable according to Lyapunov, i.e. there is an initial state $\underline{x}(0)$ within the region $G(\underline{x}°, r)$ so that at least one subsequent system state $\underline{x}(k)$ or $\underline{x}(t)$ with $k > 0$ or $t > 0$ outside the region $G(\underline{x}°, R)$ $(0 > r > R)$. Asymptotically stable always implies stable according to Lyapunov, but not the other way around. An asymptotically stable equilibrium point is called a **stable spiral point** or **spiral sink**. It is surrounded by trajectories, all of which lead asymptotically back to it, similar to a spiral or vortex. An unstable equilibrium point is called an **unstable spiral point** or **spiral source**. It is surrounded by trajectories that no longer lead back to the equilibrium, but only away from it. There exist also equilibrium points which are unstable and stable at the same time, e.g. a saddle point. Finally, **Neutrally or**

[1] The learning program still runs on modern systems using an emulator. Available at www.sysecol.ethz.ch

marginally stable is the marginal case between asymptotically stable and unstable. Such an equilibrium point is still Ljapunov stable, as once perturbed, the surrounding trajectories stay nearby the equilibrium point but do never return to it nor go further and further away from it as would be the case for an unstable equilibrium point. Thus $\underline{x}°$ is neutrally stable if and only if $\underline{x}°$ is stable according to Ljupunov, but not asymptotically stable. In the case of a second-order system the trajectories typically form so-called **limit cycles** enclosing the equilibrium point.
In the stability analysis of a given model system, the most expedient way to proceed is to first **identify any equilibrium points** that may exist. An equilibrium corresponds to a system state, i.e. point $\underline{x}°$, in which the system no longer shows any changes, i.e. no changes in any of its state variables. Such a point is thus also called a stationary solution, a steady state, or a fixed point of the system. This means for discrete time systems that the differences of the difference equations given in canonical form or for the continuous time systems that the derivatives of the differential equations given in canonical form are all equal to zero at such a point. Mathematical transformations can then be used to derive for each individual state variable the function that fulfils that condition. The intersections of all these functions represent equilibrium positions of the entire system, i.e. equilibrium points. For example, the positive differential equation system given here in canonical form (ordinary differential equations)

$$dx_1/dt \;=\; a\,x_1 - b\,x_1^2 - c\,x_1x_2$$
$$dx_2/dt \;=\; c'\,x_1x_2 \;-\; d\,x_2$$

where a>0, b>0, c>0, c'>0, d>0 and $\underline{x}$>0 (system positive)

contains two equilibrium points, which can be derived as follows: $dx_1/dt = 0$ results in $x_1 = 0$ (trivial solution, entire ordinate) and $0 = a - b\,x_1 - c\,x_2$ (non-trivial second solution). The latter can be formulated as $x_2 = -b/c\,x_1 + a/c$, which represents in the two-dimensional state space x_2 vs. x_1 a straight line with a negative slope -b/c and the intercept a/c (Fig. 2). Along that line x_1 does not change. From $dx_2/dt = 0$ ==> $x_2 = 0$ (trivial solution, entire abscissa) and $0 = c'\,x_1x_2 - d\,x_2$ (non-trivial second solution). The latter can be formulated as $x_1 = d/c'$, which represents in the two-dimensional state space x_2 vs. x_1 a vertical straight line starting from point [d/c',0] (Fig. 2). Along that line x_2 does not change. The intersections of all these equilibrium functions correspond to the sought equilibrium positions: The trivial solution is a fixed point at the origin [0,0] and the non-trivial equilibrium position is the fixed point $\underline{x}°$ = [d/c', a/c - bd/cc'], i.e. the point where the two lines cross (Fig. 2).

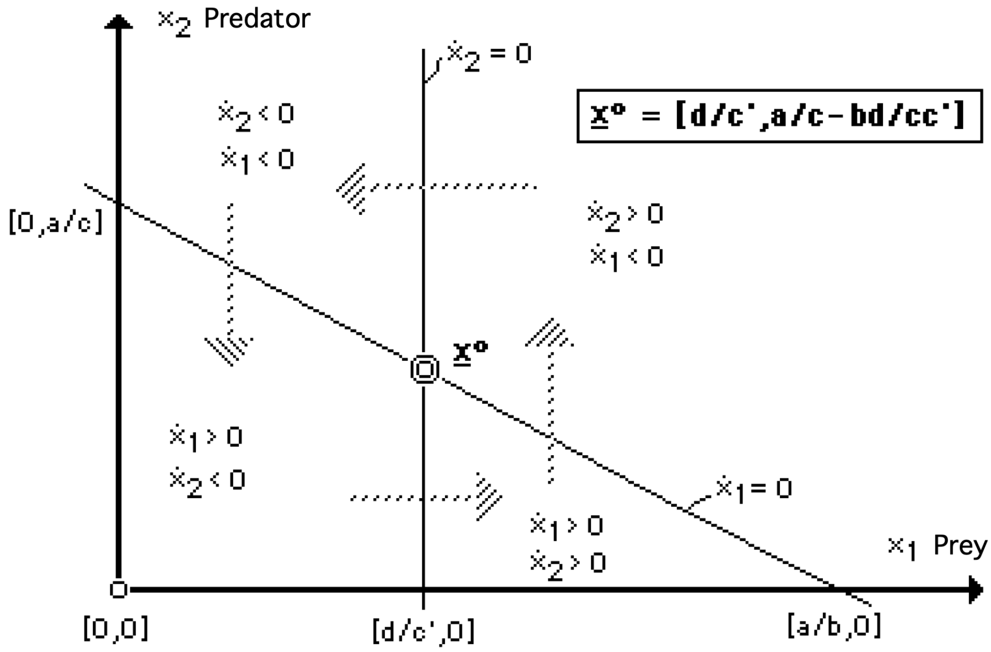

Fig. 2: Equilibrium positions or fixed points in the state space of a nonlinear differential equation system of the second order (Lotka-Volterra predator-prey model).

In a second step, investigate the **properties of the derivatives** dx_1/dt or dx_2/dt in state space **near the found equilibrium functions** (Fig. 2, $\dot{x}_1 = dx_1/dt = 0$ or $\dot{x}_2 = dx_2/dt = 0$). This can be done, for example, by adding or subtracting an arbitrarily small number h from the independent state variable in the determined equilibrium functions $dx_1/dt = 0$ or $dx_2/dt = 0$. For example, substituting x_2 in dx_1/dt by $x_2 + h = -b/c\,x_1 + a/c + h$ yields: $dx_1/dt = -cx_1h < 0$ for any $h > 0$ und $dx_1/dt > 0$ for any $h < 0$. Analogously, substituting x_1 by $x_1 + h = d/c' + h$ in dx_2/dt, results in: $dx_2/dt = hc'x_2 > 0$ for any $h > 0$ and $dx_2/dt < 0$ for any $h < 0$. Fig. 2 shows the four emerging regions ($\dot{x}_1<0$ AND $\dot{x}_2<0$; $\dot{x}_1>0$ AND $\dot{x}_2<0$; $\dot{x}_1>0$ AND $\dot{x}_2>0$; $\dot{x}_1<0$ AND $\dot{x}_2>0$) around the non-trivial fixed point $\underline{x}°$ listed with the corresponding properties of the two derivatives $dx_1/dt = \dot{x}_1$ and $dx_2/dt = \dot{x}_2$ respectively. This information now allows to make a first estimate of which directions the trajectories follow in the state space (Fig. 2, gray arrows).

In a third step, the **stability properties of the determined equilibrium points are investigated**. A powerful method to examine these properties in detail is the **first method of Lyapunov**. Here, the nonlinear system is linearized at the equilibrium points in order to investigate the stability properties of the linear system instead of the nonlinear system. In most cases, this approach allows to draw valid conclusions about the stability properties of the equilibrium points of the nonlinear system. Liapunov's first method proceeds as follows: First, the so-called Jacobi matrix J is determined at the equilibrium position $\underline{x}°$ for the nth-order system, which is given in the form $\underline{x}(k+1) = \underline{f}(\underline{x}(k))$ or $\underline{dx}(t)/dt = \underline{f}(\underline{x}(t))$. This is accomplished by partially differentiating each function of the function vector $\underline{f}$ with respect to the state variables. Any remaining state variables are replaced by the specific values of the stationary solution, i.e. the equilibrium point $\underline{x}°$.

$$J = \begin{pmatrix} \partial f_1/\partial x_1 & \partial f_1/\partial x_2 & \dots & \partial f_1/\partial x_n \\ \partial f_2/\partial x_1 & \partial f_2/\partial x_2 & \dots & \partial f_2/\partial x_n \\ \partial f_3/\partial x_1 & \partial f_3/\partial x_2 & \dots & \partial f_3/\partial x_n \\ \dots & & & \\ \partial f_n/\partial x_1 & \partial f_n/\partial x_2 & \dots & \partial f_n/\partial x_n \end{pmatrix}$$

The result is a matrix, which can be interpreted as the system matrix of the linearized system at the equilibrium point $\underline{x}°$. It determines the dynamics of sufficiently small deviations $\underline{\varepsilon}$ of the system state from the equilibrium position (first term of a Taylor series expansion):

$$\underline{x}(k) \approx \underline{x}° + \underline{\varepsilon}(k) \qquad \text{or.} \qquad \underline{x}(t) \approx \underline{x}° + \underline{\varepsilon}(t)$$

This relationship shows that the stability properties of the following linear system can be used to determine the stability properties of the nonlinear system at the equilibrium point and its vicinity:

$$\underline{\varepsilon}(k+1) = J\,\underline{\varepsilon}(k) \qquad \text{or.} \qquad \underline{d\varepsilon}(t)/dt = J\,\underline{\varepsilon}(t)$$

From linear system theory we know that in the discrete time case, all eigenvalues of the Jacobian matrix J at the position $\underline{x}°$ must have an absolute value < 1 or, in the continuous time case, all eigenvalues must have a negative real part in order for $\underline{x}°$ to be asymptotically stable. If, in the discrete time case, at least one eigenvalue of the Jacobi matrix J has an absolute value > 1, or in the continuous time case at least one eigenvalue has a positive real part, then $\underline{x}°$ is unstable. Note, in case of complex eigenvalues the imaginary part is always bounded in its magnitude and can therefore never decide over the question whether $\underline{x}°$ is stable or unstable. It indicates rather whether we have oscillatory behavior of the system near the fixed point. Finally, in marginal cases, i.e. the absolute value of an eigenvalue is 1 or the real part of an eigenvalue is 0, then it is no longer possible to draw firm conclusions from the properties of the linearized system to those of the nonlinear system. Then additional terms than just the first of the Taylor series expansion may have to be included in the analysis and this reminds us of the fact that in the case of a non-linear system, the vicinity within which $\underline{x}°$ can be considered stable, is generally limited. To determine the size of that vicinity, i.e. the stability range $G(\underline{x}°,R)$ surrounding the equilibrium point $\underline{x}°$ (Fig. 1), further steps need to be taken, steps we do not introduce here as this would go beyond the scope of this courseware. Nevertheless, in general it is safe to say that the stability properties of the linearized system apply at the equilibrium point $\underline{x}°$ itself and in the very immediate vicinity of that point.

2.2 Ecological Examples

To date the stability behaviour of entire ecological systems has been studied in detail only in a few cases. In this context the rather spectacular study of Embree (1966) in Nova Scotia, Canada offers interesting insights. To control the winter moth *Operophtera brumata* L, which caused severe damage to eastern Canadian orchards, the parasitic wasps of the species *Cyzenis albicans* and *Agrypon flaveolatum* were introduced. After an initial transient phase during which the pest population started to collapse, these parasitoids managed to keep the pest densities at low, no damage causing levels, levels which were maintained thereafter for at least two decades (Fig. 3). In other words, after the initial disturbance due to the parasitoids, the trajectory gradually settled down to a new equilibrium position. The phase portrait of this system shows similarities to a spiral where trajectories lead towards a centre.

Interesting investigations have also been carried out for a number of laboratory systems. For example, the extremely interesting study by Luckinbill (1973), is the very first evidence for the periodic population cycles long previously predicted by Lotka (1925) and Volterra (1926) (Fig. 4). The periodic solutions seem to lie on almost closed trajectories or limit cycles. The phase portrait resembles that of a so-called vortex, but one where the trajectories do not get gradually closer to the centre, but surround it forever in a circular motion.

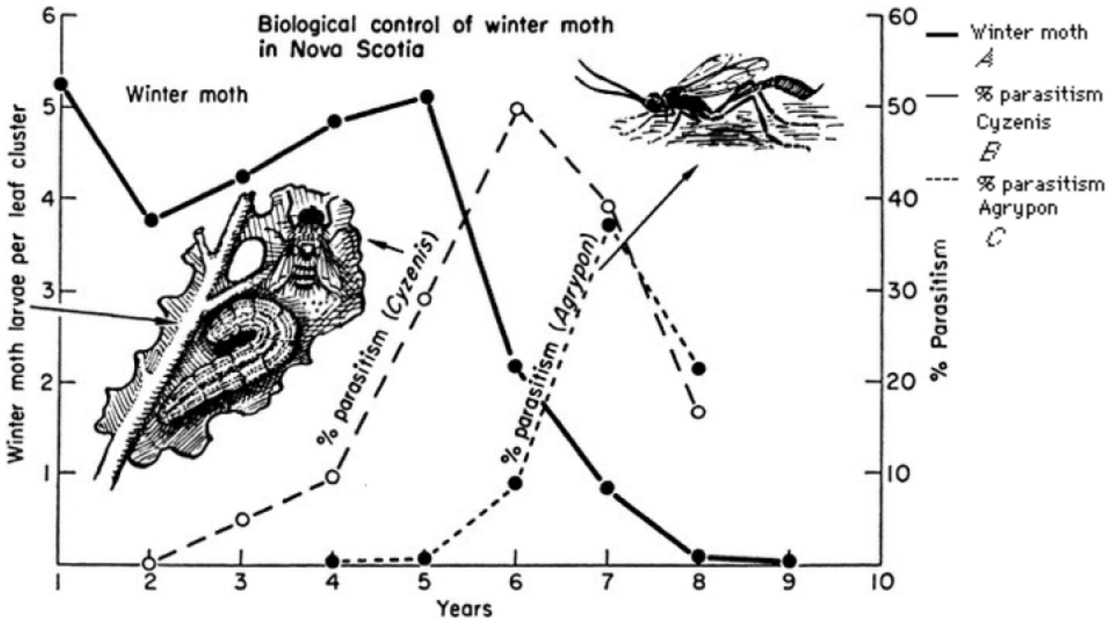

Fig. 3: Behaviour of the winter moth *Operophtera brumata* , a pest which caused damage to the orchards of Nova Scotia, Canada, at the beginning of this century, and its parasitoids *Cyzenis albicans* and *Agrypon flaveolatum*. Since the introduction of the parasitoids, presence first time verified in 1954, the pest population has remained at the shown low values thereafter for decades (according to Varley et al., 1973).

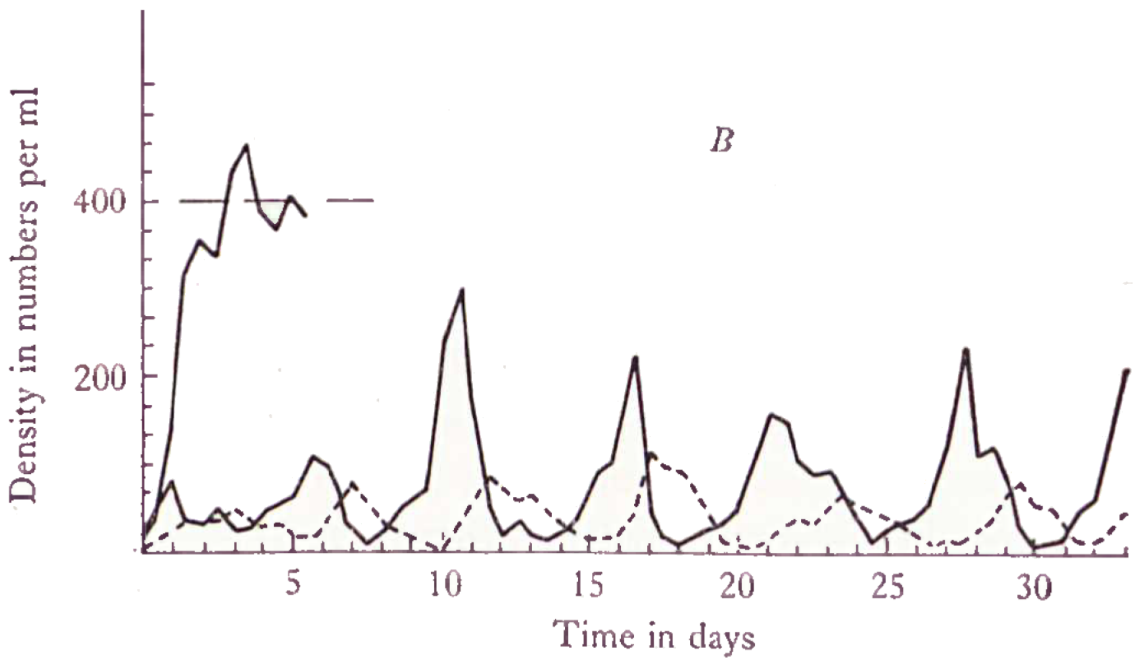

Fig. 4: Behaviour of a ciliate predator-prey system in the laboratory. The prey species is the ciliate *Paramecium aurelia* (——) the predator *Didinium nasutum* (------). This cyclic behaviour was only achieved after adding movement-inhibiting methylcellulose to the medium in which the ciliates live (according to Luckinbill, 1973).

Thirdly, unstable behaviour has also been found: Here the classical modelling approaches of Nicholson and Bailey (1935) and the experiment by Burnett (1958) (Fig. 5) have become quite famous. They show that host-parasitoid fluctuations can lead to mutual amplification of those fluctuations until collapse.

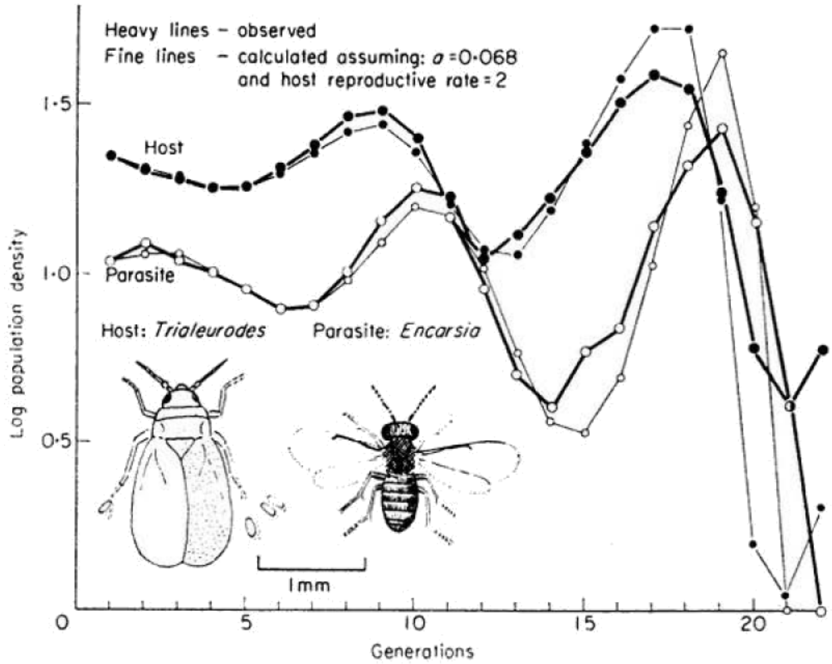

Fig. 5: Behaviour of the host and parasitoid populations, the whitefly *Trialeurodes vaporariorum* and its chalcid parasitoid *Encarsia formosa* during 22 generations (according to Varley et al., 1973).

2.3 Further Reading and References

General, further reading on the stability of systems:

[1] Lecture notes, stability
[2] LUENBERGER, Ch. 9.2, 9.3 pp. 320-324
[3] LUENBERGER, Ch. 10.3 pp.370-374
[4] LUENBERGER, Ch. 5.9 pp. 154-159

Special, cited literature:

BURNETT, A.A. 1958. *Effects of natural temperatures on oviposition of various numbers of an insect parasite (Hymenoptera, Chalcididae, Tenthredinidae).* Ann. ent. Soc. Am. **49**:55-59.

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LOTKA, A.J. 1925. *Elements of physical biology.* Baltimore: Williams and Wilkins.

LUCKINBILL, L.S. 1973. *Coexistence in laboratory popualtions of Paramecium aurelia and its predator Didinium nasutum.* Ecology **54**: 1320-1327.

LUENBERGER, D.G. 1979. *Introduction to dynamic systems - Theory, models, and applications.* New York op. cit., John Wiley & Sons, 446pp.

NICHOLSON, A.J. & BAILEY, V.A. 1935. *The balance of animal populations.* Proc. Zool. Soc. Lond. **3**: 551-598.

SMITH, M.J. 1974. *Models in ecology.* Cambridge, Cambridge University Press, 146pp.

VARLEY, G.C., GRADWELL, G.R. & HASSELL, M.P. 1973. *Insect population ecology.* Oxford, Blackwell Scientific Publications, 2nd ed., 212pp.

VOLTERRA, V. 1926. *Variazione e fluttuazioni del numero d'individui in specie animali conviventi.* Mem. Accad. Nazionale Lincei (ser. 6) **2**: 31-113.

3. Program description

The program "Stability" is used for the interactive numerical simulation of three different model systems each having different stability properties. Simulation results are shown in graphs that the user can taylor to her needs freely, experiencing the system behavior from many different perspectives. At the core is a 3-dimensional view onto the temporal evolution of the state space predator vs. prey. The user can intervene in the processes anytime and alter views while observing the dynamics, the strength of interactive simulations.

All program activities can be called up via menus. The program works with a non-movable window of constant size showing by default three axes: One shows the population size of the prey, one that of the predator and the third represents time. The result is a 3-dimensional view onto the dynamics of the currently selected model system. The axes of the coordinate system can be moved, their scales changed, or the axis can be set to overlap, allowing to obtain also a 2-dimensional view. In addition, there are dialog windows that can be opened via the corresponding menu commands. They allow to control what is happening, e.g. to enter simulation parameters such as maximum time for the simulation, frequency of perturbations, and many other parameters and settings.

Three predator-prey models (simulation models 1, 2, and 3) are available in the program. For each the initial values of the state vector can be varied, and the system can be exposed to stochastic, normally distributed perturbations simulating natural disturbances. The 3-dimensional coordinate system can be adjusted with the interactive coordinate system editor (CS-editor). Moreover, some simulation parameters can be edited freely, including the numerical integration method. A little help window is also available from within the learning program.

At any point in time the learning program is in one of following three main states (Fig. 6):

- **Idle**, i.e. waiting for a user input
- **Simulating**
- **Editing** some settings, e.g. the coordinate system

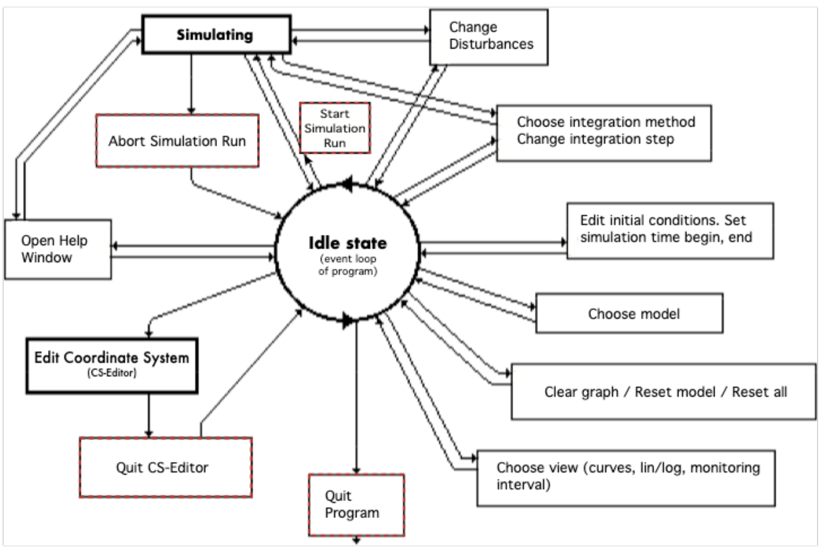


Fig. 6: State transition diagram of learning program "Stability". Shown are the possible program states with the related user actions and the arrows representing the possible transitions between states. The most important states are shown with a thicker frame.

Initially the program is in the idle state and does nothing. It just waits for the user to choose a menu command or press a keyboard shortcut. To launch a simulation with the current settings the user chooses the menu command “Simulation → Start Simulation (Run)” or the keyboard shortcut ⌘^R. The program starts to numerically solve the model from the current initial state and remains in the "Simulating" state until it reaches the end of the simulation time or the user aborts the simulation run (kills it, e.g. with ⌘^K). The program then resumes the idle state. During editing of some settings, e.g. the coordinate system is edited (⌘^E), the program is in an editing state that needs to be completed (OK button) or exited (⌘^T) to resume the idle state or continue the interrupted simulation run (Fig. 6).

A simulation run is defined by various parameters. Among them are the initial values for predators and prey (⌘^A), the end time for simulations, time step, and the numerical integration method. All these settings can be changed freely. It is also possible to choose between deterministic and stochastic (explicit inclusion of random events) simulations. Stochastic simulations add normally distributed perturbations that alter the state vector. The frequency of such disturbances and their magnitude in percentage of the current state can be chosen (deterministic simulation means a disturbance probability of zero). If a particular disturbance should result in negative values for the prey or predator population, a zero value is automatically used instead as in reality exist no negative populations. The simulated disturbances, which can increase or decrease populations can be interpreted to represent the influence of weather modifying reproduction or mortality or any other impacts on the system from the outside, the so-called natural disturbances such as fire or trampling by large mammals.

The output values that are calculated during a simulation run (time, number of predators and prey) are by default displayed in a three-dimensional coordinate system that can be freely edited. A total of four different curves can be displayed: Prey vs. Time, Predator vs. Time, Predator vs. Prey (State Space) and the three-dimensional curve Prey vs. Predator vs. Time (by default off). The display can be changed freely using the coordinate system editor. Since this program is mainly intended to convey qualitative relationships (stability properties), a tabular representation of the computed numerical values has been omitted.

4. Operating Instructions

4.1 Tutorial

After starting the program, the screen presents itself as follows: At the top is the menu bar, with the "Apple" to the very left and the program menus. Below that appears the working window with an empty three-dimensional coordinate system showing the prey, the predator and the time axis sparsely labelled with some scale value to avoid a cluttered view, yet giving you an idea about the current scale of each axis.

Start a first simulation with all default settings by choosing the menu command “**Simulation → Start Simulation (Run)**”. Alternatively use the keyboard shortcut **⌘^R** (for **R**un). As the simulation progresses the program shows you now the three curves prey and predator vs. time, and predator vs. prey (state space).

Then make the second model active by choosing the menu command “**Models → Model 2**” and run another simulation with keyboard shortcut ⌘^R. In the same graph, you can now compare the behavior of the two models. They show quite contrasting stability properties.

Activate now the editor of the coordinate system by choosing menu command “**Graph → Edit Coordinates (CS Editor)**” or press keyboard shortcut **⌘^E**. You can choose a new display by clicking on the end points of the axes, the origin or one of the scale points and moving them on the screen while keeping the mouse button pressed down. Release the mouse button at the desired position. For example move in this manner the point near the label 10 on the time axis and move it along the time axis towards you, i.e. to the right and release the mouse button once the point has crossed roughly the middle of the time axis. Then exit the CS-Editor with menu command “**CS-Editor → Terminate CS-editing**“ or press **⌘^T**. Note, the simulation results previously computed are now redrawn and you have now zoomed into the graph by having a closer view near the origin.

Understand also that you can move the point near the number label of an axis beyond the small tick marks shown at both ends of the axis. This alters the scale of the entire axis and increases or decreases the scale by a power of ten. Try it out by moving the point near label 10 on the time axis towards the origin until the point is between origin and the tick mark. Note, the label of the time axis jumps to the value 100. Note, if you try to move a point outside the allowed range, the move is ignored and the coordinate system remains unchanged. If the point disappears keep the mouse pressed until the point is reshown. Legal areas are those where the point is shown. To see now simulation results for that lengthened time axis you need to set a longer end time by choosing menu command “Simulation → End time…”. Set the value to 200, click button OK and run the simulation with **⌘^R**. To gain a closer view of the state space predator vs. prey press **⌘^E** to edit the coordinate system once more. Grab and move the end of the prey axis X until it is horizontal. Then grab and move the origin towards the right bottom corner of the screen. Exit the CS-editor **⌘^T** to see the curves in the state space better. Perhaps also select Model 2 (see above) and run a simulation **⌘^R**. In any case, familiarize yourself with the way the CS-editor works by trying out the learned commands some more to obtain other views, e.g. prey and predator vs. time.

To continue working, reset the program by choosing menu command “**Control → Reset all**”. Perform the two simulation runs again as described at the begin, i.e. a run for Model 1 and a second run for Model 2.

Now, let's say you want to examine the trajectories in state space (predator vs. prey) of the first two models in the traditional X-Y view in more detail. Use the CS-editor **⌘^E** to define the desired view: Once in the CS-editor click on the end point of the time axis t and move this point until the time axis t points approximately to the bottom left. Then move the end point of the prey’s axis X to the right until it is horizontal, i.e. it becomes an abscissa, and forms a right angle to the vertical predator's axis Y. Remember, if you try to move a point outside the allowed range, the dragged point disappears and if the mouse is then released, the move is ignored and the coordinate system remains unchanged. Finally move the origin to the lower left corner. The display should now look something like a simple, two-dimensional graph with the horizontal X-axis (prey) going from the left origin to the right and the vertical Y-axis (predator) going from the origin vertically upwards. After exiting the CS-editor **⌘^T**, the state curves of both simulation runs are redrawn. Adjust the scale of the prey axis X by **⌘^E** and moving the point near label 1.0E4 slightly to the right until the trajectories make good use of the shown state space.

Change the initial values, i.e. the initial state of the system, for the current model 2 by choosing menu command “**Simulation → Initial Values…**” or press **⌘^A**. E.g. enter 10’000 for the prey and 900 for the predator, click button OK and run another simulation **⌘^R**. What changes?

The program allows also to perform stochastic simulations. The states, i.e. either prey and/or predator, are stochastically altered due to random, normally distributed disturbances. Clear the graph with menu command “**Graph → Clear graph**” or press **⌘^B**, select Model 1 (“**Models → Model 1**”) and run a simulation **⌘^R** with the set parameters as a reference. Then choose menu command “**Simulation → Perturbations…**” and enter the following values: Enter for “Probability of perturbation during an integration step” value 1.0, for “Coefficient of variation of the perturbation (in %)” value 3.0. Note, the coefficient of variation is the standard deviation of the perturbation expressed in % of the current value of the state variable. And the probability of perturbation during an integration step is the probability for such a change actually to happen. Click button OK and start a new, now stochastic simulation **⌘^R**. What do you notice? You may wish to adjust the scaling with the CS-editor **⌘^E**, by moving the scale label point of the X-axis (prey) slightly to the right, press **⌘^T** and repeat, perhaps also for the ordinate, until the view satisfies you. Press **⌘^R** to run another simulation. Note, repeating the simulation yields nothing new and gives always the same results. To change that and obtain always new stochastic simulations you need disable the resetting of the random number generator before every run. Choose menu command “Simulation → Perturbations…” and **uncheck “Reset random number generator before every run”**. Run now many simulations. What do you see? Perhaps compare that with simulations where the “Probability of perturbation during an integration step” is smaller, e.g. 0.25. Clear the graph by **⌘^B** as you prefer. You should now have a good idea about the basic features of the learning program. Enjoy!

4.2 Menu Commands

<u>Control</u>

Help... (⌘^H)**:** Displays a window with a brief description of the program's most important features.

Reset all: Resets the program to its initial state. Exactly the same conditions are created as immediately after the start of the program.

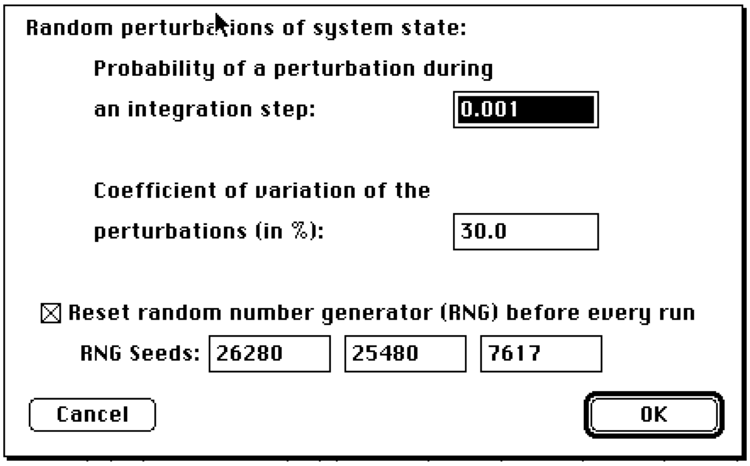
Quit (⌘^Q)**:** Exit the program.

<u>Simulation</u>

Initial values... (⌘^A)**:** The initial values of the state variables (number of predators and prey) for the currently selected model can be set with the help of an input form.

End time...: Enter the end time for the simulation runs.

Perturbations...: The program "Stability" allows simulations to be carried out deterministically or stochastically, whereby in the case of stochastic simulation a normally distributed disturbance value is added or subtracted from the state vector (number of predators and prey).



The frequency and magnitude of the disturbances can be controlled via two parameters:

The first parameter “Probability of perturbation during an integration step” represents the probability that an element of the state vector will be perturbed during an integration step. If it is set to zero, the simulation is carried out undisturbed, i.e. deterministically, with probability 1 all elements of the state vector are disturbed during each integration step.

The second parameter “Coefficient of variation of the perturbation (in %)” determines the coefficient of variation, i.e. the standard deviation of the change (disturbance) as a percentage of the current value of the altered state variable. A value of e.g. 10% means that the standard deviation of the random change amounts to 10% of the current value of the altered state variable. In other words, 67% of all disturbances cause a deviation from the current value of the state variable in the range of ± 10% (as for a normally distributed random variable about 67% of all values fall into the interval "mean value ± standard deviation").

Note, you can edit these two parameters also in the middle of a simulation.

By default the used pseudorandom number generator is reset at the beginning of each simulation to the same state it was at the launch of the learning program. This resetting causes all calculations to be carried out with identical pseudorandom numbers (allows for precise repetition of a stochastic simulation, which may be useful if you wish to merely simulate longer or with another integration method). If you uncheck the option “Reset random number generator before every run” new pseudo-random numbers are generated during repeated simulations with the same parameters, producing a more realistic stochastic behavior.

The random number generator uses the three shown seeds at the begin of every simulation. To fully reproduce the results of any stochastic simulation, you need to write out those three seeds at the end of the run of interest. Reentering those three seeds and checking the option “Reset random number generator before every run” allows you then to reproduce precisely any stochastic simulation run results. This is particularly relevant when relaunching the learning program. Note, the pseudorandom number generator is always initialised with real-time dependent values, i.e. it is “randomized” during the launch of the learning program.

Start simulation (Run) (⌘^R)**:** Starts a simulation run with all current settings and parameters. The graph is continuously updated during the simulation.

Stop simulation (Kill) (⌘^K)**:** Aborts or kills the currently running simulation.

Graph

Representation parameters...: The following parameters can be edited:

Curves to be displayed (any combination):

Prey vs. Time, Predator vs. Time, State Space, Prey vs. Predator vs. Time. Check or uncheck any of the curves as needed.

Output Interval: Interval for graphical output in time units.

ATTENTION: *Only a maximum of 250 points per curve per simulation run drawn can be saved. All points computed are always drawn, but points exceeding former limit will no longer be redrawn during the next automatic redrawing (e.g. after exiting the CS-editor).*

Representation of predator and prey axis:

Linear or logarithmic scale.

NOTE: In the logarithmic representation, the axis scaling is done in units of the natural logarithm, i.e. an axis scaling of 10, for example, means that the value exp(10)=22'026.47 is listed here.

Clear graph (⌘^B)**:** Clear all curves, i.e. make the current graph blank.

Edit coordinates (CS-Editor) (⌘^E)**:** Enters the Coordinate System Editor (CS-editor) mode. This allows to change the position of the axes, their scales, and move the origin. In the CS-editor mode you see little circles representing points that can be clicked and dragged with the mouse to a new position on the screen. Releasing the mouse button sets that point to a new position. However, this is possible only within certain legal ranges. The circle disappears under the mouse when leaving the legal range. Keep the mouse pressed and search for the legal range. For scale changing stay close to the axis, for all other points stay within the borders of the graph. ATTENTION: *In the CS-editor mode you can only edit display settings and issue no other commands. Find in the temporarily shown additional menu "CS-Editor" the command "Terminate CS-editing" to exit the CS-editor.*

Models

Model 1: Select simulation model 1. All subsequent simulations are carried out with the selected model. The selection of the currently valid model is indicated by a check mark next to the menu command.

Model 2: Select simulation model 2. Ditto.

Model 3: Select simulation model 3. Ditto.

Reset Model: Resets the initial values of the selected model to the predefined default values, the same ones assigned at initial program start. No other settings or parameters are affected.

Integration:

Euler-Cauchy Method: This activates for the numerical integration the Euler-Cauchy integration method (Runge-Kutta of the first order). All subsequent simulation is carried out using that method, which applies even when altered in the middle of an ongoing simulation run. A check mark on the left shows the currently active integration method.

Heun Method: Activates numerical integration method Heun (Runge-Kutta of the second order). Ditto.

Runge-Kutta 4th Order: Activates numerical integration Runge-Kutta fourth-order with a fixed step length. Ditto.

Discrete time: Activates numerical solving of discrete time models (automatically selected when selecting model 3). It cannot be changed by the user as this depends on the type of model to be simulated. It merely serves to notify the user.

Step length...: Enter the size of the integration step in time units as used for all subsequent numerical integration. It can be changed in the middle of a simulation run.

CS-Editor (temporary menu):

Terminate CS-editing (⌘^T)**:** This menu command appears only while editing the coordinate system. This menu command is the only way to exit the CS-editor mode. ATTENTION: *To enter the CS-editor mode use command "Edit coordinates (CS-Editor) (⌘^E)" under menu "Graph".*

<u>Print (no menu command):</u>

On legacy Mac systems press ⌘^Shift^3 (all at once):[2] Creates a file named "Screen #" (# means a single digit). This file can be printed with a drawing program (e.g. MacDraw or SuperPaint®) on a matrix or laser printer or inserted into a documentation. Such a functionality may not be available on modern Mac systems when running the learning program Stability in an emulator. Use then the host computer's screen capturing functionality to the same end.

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[2] This option is only available on black-and-white screens, or on color screens set to black-and-white mode (set the number of screen colors to 2 in the control device *Monitors* in the Desk Control *panel*).

5. Exercise

a) Familiarize yourself with following terms: equilibrium position or equilibrium point, stability, stable according to Lyapunov, asymptotically stable, neutrally stable or marginally stable, and unstable.

b) There are three real systems, as discussed in section 2.2:

System **A** - Winter moth in Nova Scotia
System **B** – Ciliate predator-prey laboratory system
System **C** - Biological control of whitefly by parasitoids

In addition, the following three mathematical model systems are given:

Model **X**

$$dx_1/dt = a\, x_1(t) - b\, x_1(t)\, x_2(t)$$
$$dx_2/dt = c\, x_1(t)\, x_2(t) - d\, x_2(t)$$

Model **Y**

$$x_1(k+1) = x_1(k)\, r\, e^{-a\, x_2(k)}$$
$$x_2(k+1) = x_1(k)\, r\, (1-e^{-a\, x_2(k)})$$
where $r = 2.0$; $a = 0.68$

Model **Z**

$$dx_1(t)/dt = a\, x_1(t) - b\, x_1(t)^2 - c\, x_1(t)\, x_2(t)$$
$$dx_2(t)/dt = d\, x_1(t)\, x_2(t) - e\, x_2(t)$$

Finally, the "Stability" learning program contains three different simulation models, each corresponds to one of the above listed systems and mathematical models, respectively:

Simulation Model **1**
Simulation Model **2**
Simulation Model **3**

The goal of this exercise step is to assign to each system (**A**, **B**, **C**) the corresponding mathematical model (**X**, **Y**, **Z**) as well as the corresponding simulation models (**1**, **2**, **3**). To accomplish this, use the "Stability" learning program.

c) Determine the equilibrium points of the three mathematical models **X**, **Y** and **Z**. Can you make statements about their stability properties? (Note: Try to follow the approach as described for the example in section 2.1).

ANNEX I (Worksheet):

It may help to write your findings into the following table:

Results (Courseware Stability)		Date: Name:
Observed behavior of the real System		
Model	Description of temporal behavior	Steady state(s)
A		
B		
C		

Investigation of the mathematical model		
Model	Steady state(s)	Stability properties
X		
Y		
Z		

Investigation of the simulation model			
Modell	Description of temporal behavior	Steady state(s)	Phase portrait
1			
2			
3			

Matching models und systems (Conclusions)		
Simulation model (1..3)	Mathematical model (X..Z)	Reale system (A..C)
1		
2		
3		

ANNEX II (Solutions):

Exercise a):

The real systems A, B and C, their temporal behaviour and the stability properties of the equilibrium positions are roughly described in Chapter 2 «Theory» under Section 2.2 «Ecological Examples». The student should therefore be encouraged to read that section carefully. She should then be able to compile the relevant information on the summary result sheet (Annex I). The result could be similar to this:

System A (winter moth *O. brumata*, Fig. 3): Fluctuations with initially large amplitude (transient behavior) that subside and seem to converge towards a point-like equilibrium position. Seems asymptotically stable and dynamics resemble a spiral sink.

It is known from the literature that the pest density has remained relatively constant at a low population level for at least two decades, indicating a new steady state. In particular, the parasitoid *C. albicans* is held responsible for this fact. However, recent works (Myers, 1986) have cast some doubt on this interpretation.

System B (ciliates in the laboratory: prey *P. aurelia*, predator *D. nasutum*, Fig. 4): fluctuations with constant amplitude, periodic population cycles (almost closed trajectories). Dynamics similar to limit cycles. At least Lyapunov stable, but then neutral stability cannot be excluded, the unrealistic the latter may be.

System C (white fly *T. vaporariorum* and Calcid *E. formosa* (*Hym*., *Calcididae*), Fig. 5): Fluctuations with increasing amplitude. Unstable and leading sooner or later to the extinction of the species, which may be advantageous in the case of pest control.

Exercise b):

Following describes possible observations and results when conducting simulation experiments using the learning program “Stability”:

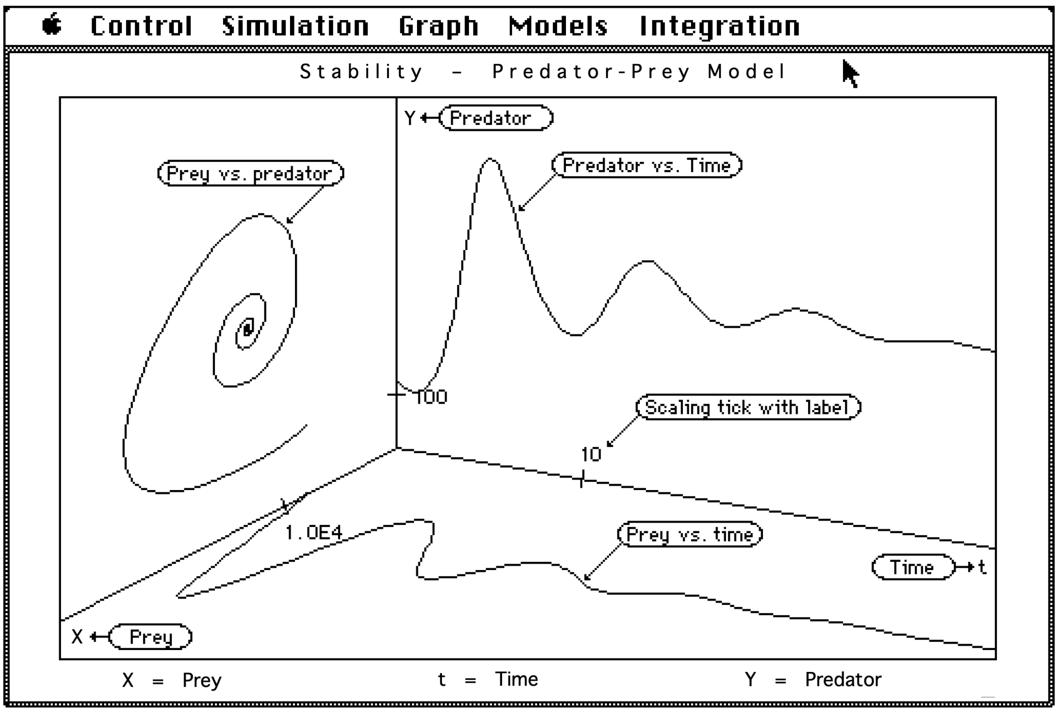

Fig. 7: Typical working screen of the stability learning program. The simulation with the model 1 is shown (only default values were used). The prey density (B), the predator density (R) vs. the time (t) as well as a state space representation (R vs B) are represented. With the coordinate system editor, the display (see figures below) or the scaling of the respective axes can be changed as desired.

The simulation models were built using the three mathematical models X, Y and Z. The differential equation systems are solved as initial value problems by numerical integration with either a simple one-step method (Euler-Cauchy), a Heun (Runge-Kutta 2nd order), or a Runge-Kutta method 4th order (fixed step length).

To investigate stability properties it is advantageous to pay particular attention to the state-space representations and to construct phase portraits (see Fig. 8).

On the behavior of the three simulation models:

Simulation Model 1: All trajectories (e.g. generated by changing the initial values) lead to an equilibrium position. Damped oscillations result. Spiral sink. Model Z, (a>be/d) (Fig. 8 - Lotka-Volterra asymptotically stable with self-inhibition of the prey (Term $-bx_1(t)^2$) in dx_1/dt equation).

Simulation Model 2: Periodic, undamped oscillations result, i.e. limit cycles enclosing the stationary solution in their middle. Changing initial values is likely to produce another more or less closed trajectory. Model X (Fig. 8 - Lotka-Volterra neutrally stable).

Note, closed trajectories are computed only when using a higher-order integration method such as the method Heun and the step size is sufficiently small. For Model 2 the default method is Heun and the default step length 0.05. This combination gives acceptable results. Experimenting with other combinations, e.g. the here unsuitable integration method Euler (combined with the default step length), shows trajectories that are no longer closed. The simulation model 2 starts to deviate strongly from the underlying mathematical model X. The behavior of the simulation model starts to resemble the behavior of the mathematical model Z. Thus, the simulated stability properties can be easily misinterpreted. Note, the underlying mathematical model X is not unstable, but only neutrally stable (cf. next section). The latter makes it of course sensitive to all perturbations, including numerical errors. An important lesson to be learned here is that simulation models may easily deviate from the underlying mathematical model and need to be carefully investigated before jumping to conclusions. This is critical in particular when simulation is the prevalent means of study, e.g. due to the difficulty of a mathematical analysis, which may not always be as straightforward as this is the case for the three mathematical models presented here. In the case of continuous time systems the robustness of simulation results need to be at least tested empirically, e.g. by simply changing the numerical integration method. Simulation software, that does not allow for that, including programmed models with a fixed built in solving algorithm, should therefore be avoided. If not possible, then results have at least to be tested for their robustness otherwise with utmost care.

Simulation Model 3: The default initial values are close to the equilibrium point. As a result of the instability of this solution, the trajectories run away from it very quickly. The behavior of this system is obviously unstable and corresponds to Model Y, Nicholson-Bailey model for host-parasitoid relationship. Note, with the reproduction parameter r = 2 and as the area of discovery a=0.68, the non-trivial fixed point is [1.019334, 1.019334]. With initial values precisely set to that value, the trajectories form the expected straight line. However, already a small deviation, e.g. with the initial values [1.019, 1.019], the oscillations start to show an increasing amplitude already after about 25 time steps.[3] This makes the instability of this non-trivial equilibrium point very obvious.

Remark: In nature ecological systems are subject to frequent perturbations, a situation in which the stability properties matter greatly. Therefore a general lesson is to be learned by the student of ecology: **The validity of an ecological model must not be based only on considerations of temporal behavior, but must also consider the stability properties, notably those revealed while be exposed to frequent perturbations**. This insight can be illustrated by means of the learning program easily with following two observations:

First observation: A stochastic simulation with simulation model 1 shows almost periodic cycles even with only small perturbations (4%) (Fig. 9). Merely due to stochastic perturbations pseudo-regular cycles resembling somewhat limit cycles may arise, despite the fact that the system has just an asymptotically stable fixed point. The impression that the system behavior tends towards a periodicity, that does actually not exist, may mislead the researcher unless the stability properties of the system are carefully

[3] Note, the learning program contains a bug and fails to properly label the time axis. Shown values are too large and need to be divided by a factor of 2.62 to get a correct label value for the current scaling of the time axis.

studied.

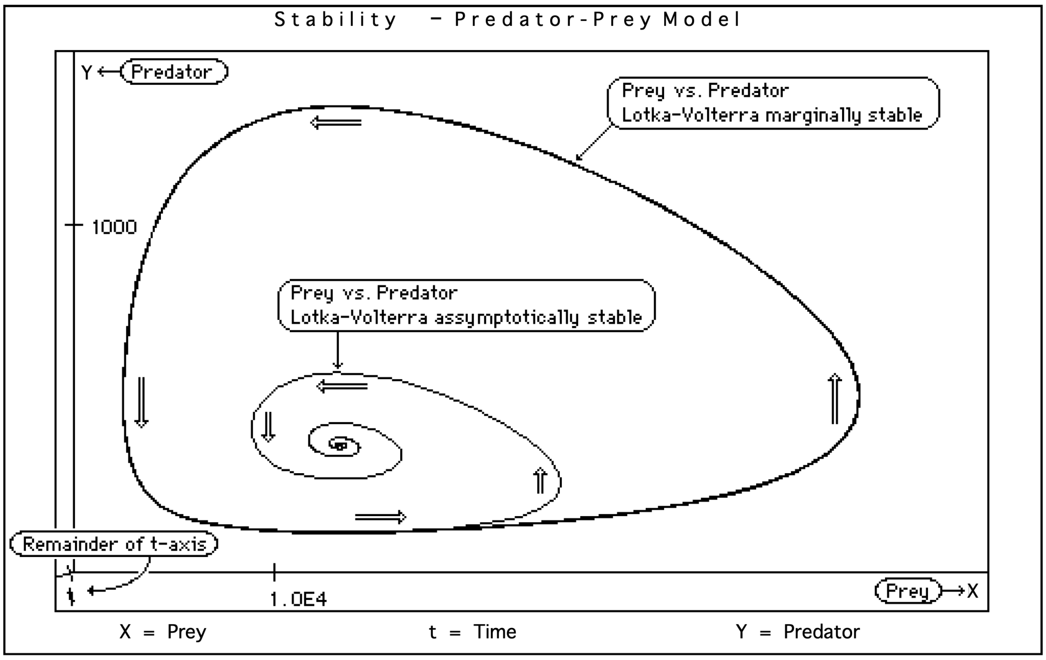

Fig. 8: State-space representation of the trajectories of two predator prey models. This graph has been created with the help of the stability learning program. Simulation model 1 generated the trajectory forming a spiral that leads to the stationary solution in the centre. Simulation model 2 generated the large egg-like, closed trajectory (All calculations were performed with the default settings, i.e. default initial values, integration method, integration step. Only the view was changed to focus on the state space by using the coordinate system editor.).

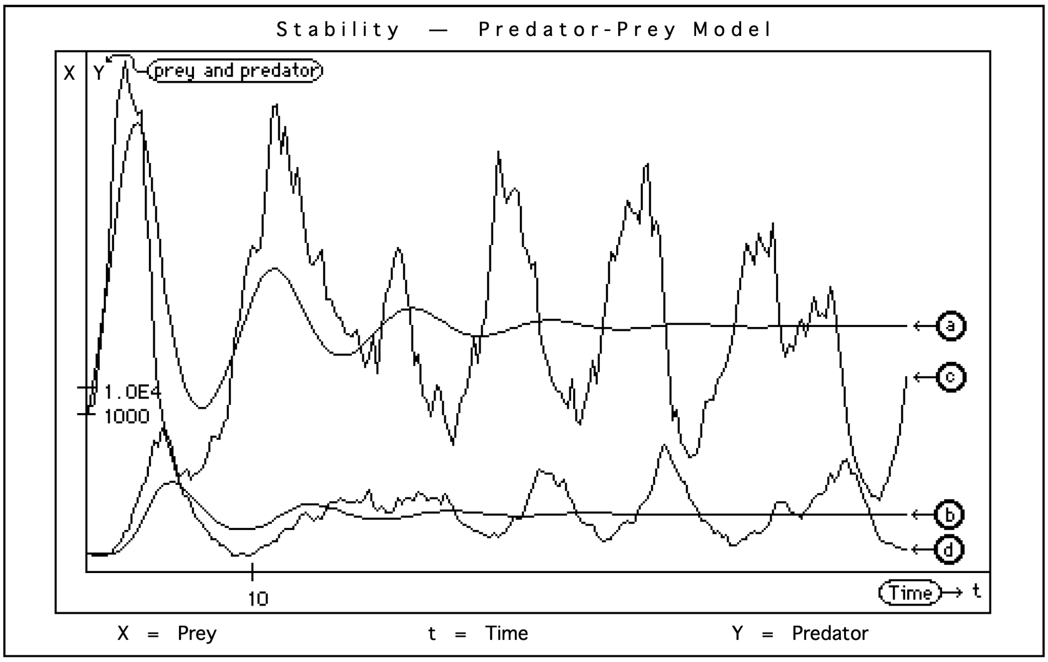

Fig. 9: Prey (curves a,c) and predator (b,d) population curves vs. time, once without (a,b) and once with (c,d) perturbations. This graph has been created with the help of the learning program "Stability". The simulation model 1 (Lotka-Volterra model Z with self-inhibition of the prey) has an asymptotically stable stationary solution showing damped oscillations. Without perturbations (curves a and b) we obtain a deterministic simulation results, with perturbations a stochastic simulation. (The perturbations occurred at each integration step with probability p=1.0 and with a magnitude of 4.0% (coefficient of variation) by which the current values of the state variables were altered. All other settings were kept at default values. Only the view was changed to focus on the population changes over time by using the coordinate system editor.)

Second observation: A deterministic simulation with simulation model 2 gives the impression of regular predictable cycles (Fig. 10). Only exposing that simulation model to perturbations shows how little such model behavior has in common with the regular cycles one can observe in several population systems in nature where perturbations are prevalent. Simulations with a miniscule perturbation probability of 0.001 but a change of 30% (coefficient of variation) show how single small perturbations cause the system to start cycling in a different manner forever until the next rare perturbation occurs (Fig. 11).

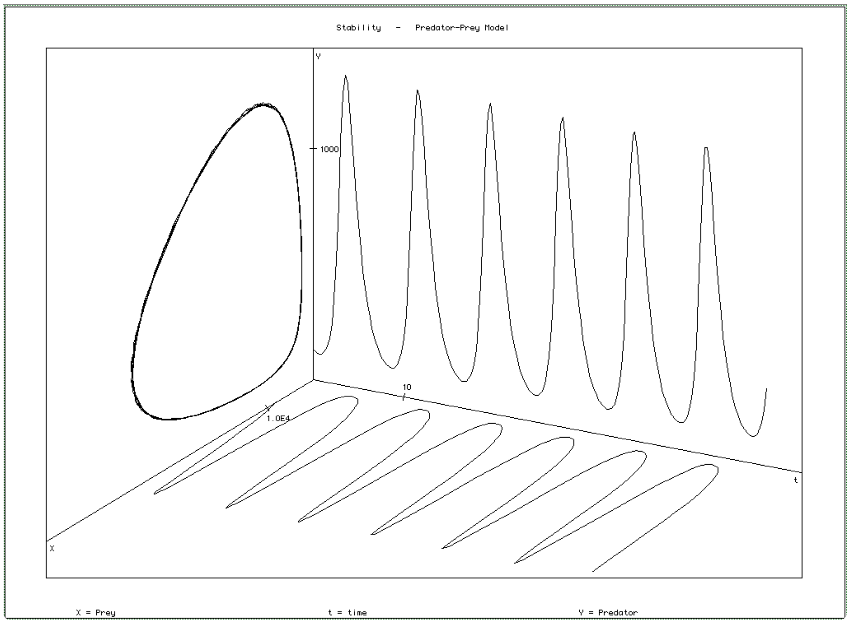

Fig. 10: Behavior of simulation model 2 with default settings. Regular limit cycles result.

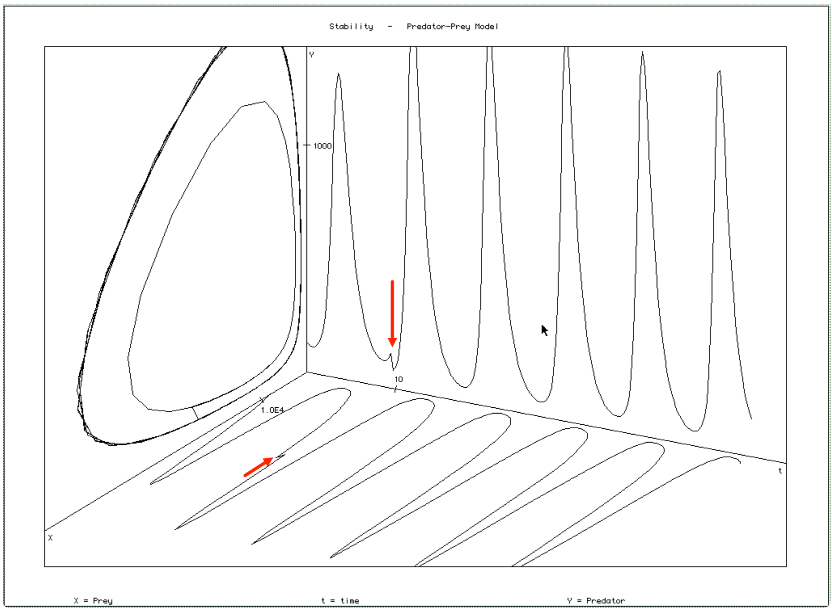

Fig. 11: Behavior of simulation model 2 exposed to a rare perturbation (probability of occurrence p=0.001) with a coefficient of variation of 30%. That perturbation reduces both populations to some small random extent. It takes place shortly after the begin of the 2nd cycle for the predator (vertical red arrow) and in the middle of the build-up of the 2nd cycle for the prey (slanted red arrow). At this point the model dynamics change drastically to another cycle with a larger amplitude and bigger cycle length, despite the small change in population sizes. The new cycle would occur forever until perturbed again (note, no other perturbation occurred in the run shown). The precise simulation results shown here can be reproduced by setting the three seeds of the random number generator to 26280, 25480, and 7617 (output interval = 0.1).

In general holds, without studying the stability properties of a system, modellers must not jump to conclusions with respect to model acceptance based merely on a fit of observational data to particular simulated trajectories. An example of such practice is the regular, nevertheless obviously incorrect mentioning of the neutrally stable Lotka-Volterra model (simulation Model 2) in the context of some cyclic population dynamics illustrate impressively the relevance of this argument. Given its neutral stability and the fact that population cycles such as the famous hare lynx cycles, are in reality permanently disturbed, yet do not show amplitude changes at each perturbation. The latter should be the case if the model would correctly describe the famous hare-lynx cycles.

Exercise c):

The equilibrium positions of the three systems all comprise the trivial solution $\underline{x}^{\circ\prime}$, i.e. the origin [0,0], and the non-trivial equilibrium position $\underline{x}^{\circ\prime\prime}$. Following the first method of Lyapunov (Chapter 2 «Theory», Section 2.1 «On Stability and Stability analysis») we obtain for each mathematical model following solutions:

Model **X**

$dx_1/dt = a\, x_1(t) - b\, x_1(t)\, x_2(t) = 0 \qquad \Rightarrow \qquad x_2 = a/b$

$dx_2/dt = c\, x_1(t)\, x_2(t) - d\, x_2(t) = 0 \qquad \Rightarrow \qquad x_1 = d/c$

The trivial, first stationary solution lies in the origin $\underline{x}^{\circ\prime} = [0,0]$. It makes ecological sense, since any growth or decline of a population requires the presence of some individuals (population density > 0). In absence of any, nothing happens and the system is in an equilibrium. The non-trivial, second stationary solution $\underline{x}^{\circ\prime\prime}$ is

$$\boxed{\underline{x}^{\circ\prime\prime} = [\, d/c \, , \, a/b \,]}$$

(similar to Fig. 2, but dx_1/dt corresponds to a horizontal straight line)

The Jacobimatrix

$$J = \begin{pmatrix} \partial f_1/\partial x_1 & \partial f_1/\partial x_2 \\ \partial f_2/\partial x_1 & \partial f_2/\partial x_2 \end{pmatrix} = \begin{pmatrix} a - b\, x_2(t) & -b\, x_1(t) \\ c\, x_2(t) & c\, x_1(t) - d \end{pmatrix}$$

at the position [0,0] (trivial, stationary solution)

$$J' = \begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix}$$

and at the point $\underline{x}^{\circ\prime\prime}$ (non-trivial stationary solution)

$$J'' = \begin{pmatrix} 0 & -bd/c \\ ca/b & 0 \end{pmatrix}$$

The characteristic polynomial derived from matrix J'

$$\det[J' - \lambda I] = \begin{vmatrix} a-\lambda & 0 \\ 0 & -d-\lambda \end{vmatrix} = (a - \lambda)(-d - \lambda) = 0$$

$\lambda_1 = a$
$\lambda_2 = -d$

Ecologically meaningful are only populations with an intrinsic growth rate a>0. Similarly meaningful is only d>0 or the predator would not be a predator. For a>0, we have always the positive eigenvalue $\lambda_1 > 0$. One positive eigenvalue suffices to make the system unstable. Therefore, the **trivial, stationary solution [0,0] is unstable**.

For the second, non-trivial stationary solution $\underline{x}°''$ given matrix J'' we obtain the characteristic polynomial

$$\det[J'' - \lambda I] = \begin{vmatrix} -\lambda & -bd/c \\ ca/b & -\lambda \end{vmatrix} = (-\lambda)(-\lambda) + d\,a = 0$$

or the quadratic equation

$$\lambda^2 + a\,d = 0$$
$$\lambda_{1/2} = \pm\sqrt{-ad}$$

A predator-prey relationship requires that a>0 and d>0, i.e. the discriminant is always negative. Therefore, these ecological assumptions result always in conjugate, complex eigenvalues $\lambda_{1/2} = \pm\sqrt{ad}\,i$ with a non-existent real part. Therefore the **non-trivial stationary solution $\underline{x}°''$ is neutrally stable** and due the imaginary part of the eigenvalues we have to expect some **oscillations**. Note that while this solution is not asymptotically stable, it is still Lyapunov stable.

Since the trivial solution [0,0] is unstable and the non-rivial solution $\underline{x}°''$ is neutrally stable, a system behavior with periodic, undamped – but not “exploding” – oscillations is to be expected, i.e. neutrally stable limit cycles (closed trajectories) that enclose the stationary solution $\underline{x}°''$.

Model **Y**

$x_1(k+1) = x_1(k)\, r\, e^{-a\, x_2(k)}$ ⇒ $x_2 = \ln r / a$

$x_2(k+1) = x_1(k)\, r\, (1-e^{-a\, x_2(k)})$ ⇒ $x_1 = \ln r / [a(r-1)]$ [4]

The trivial, first stationary solution lies in the origin $\underline{x}°' = [0,0]$. The non-trivial, second stationary solution $\underline{x}°''$ is

$$\boxed{\underline{x}°'' = [\,\ln r / \{a(r-1)\}\,,\ \ln r / a\,]}$$

The Jacobimatrix

$$J = \begin{pmatrix} \partial f_1/\partial x_1 & \partial f_1/\partial x_2 \\ \partial f_2/\partial x_1 & \partial f_2/\partial x_2 \end{pmatrix} = \begin{pmatrix} r\, e^{-a\, x_2(k)} & -\, x_1(k)\, a\, r\, e^{-a\, x_2(k)} \\ r\,(1-e^{-a\, x_2(k)}) & x_1(k)\, a\, r\, e^{-a\, x_2(k)} \end{pmatrix}$$

at the position [0,0] (trivial, stationary solution)

$$J' = \begin{pmatrix} r & 0 \\ 0 & 0 \end{pmatrix}$$

and at the point $\underline{x}°''$ (non-trivial stationary solution)

$$J'' = \begin{pmatrix} 1 & -\ln r/(r-1) \\ r-1 & \ln r/(r-1) \end{pmatrix}$$

The characteristic polynomial according to matrix J'

$$\det[J' - \lambda I] = \begin{vmatrix} r-\lambda & 0 \\ 0 & -\lambda \end{vmatrix} = (r-\lambda)(-\lambda) = 0$$

[4] To obtain this value substitute in the 2nd difference equation for $x_2(k)$ the before found equilibrium value ln r/a

$\lambda_1 = r$
$\lambda_2 = 0$

As this is a discrete time system, ecologically meaningful are only host and parasitoid populations with a reproductive rate of r>1. For r>1, there is always an eigenvalue with the absolute value of $|\lambda| > 1$. Therefore, the **trivial, stationary solution [0,0] is unstable**.

For the second, non-trivial stationary solution given matrix J" we obtain the characteristic polynomial

$$\det[J'' - \lambda I] = \begin{vmatrix} 1-\lambda & -\ln r/(r-1) \\ r-1 & \ln r/(r-1)-\lambda \end{vmatrix} = (1-\lambda)(\ln r/(r-1) - \lambda) + \ln r = 0$$

or the quadratic equation

$$\lambda^2 - (1 + \ln r/(r-1))\lambda + r \ln r/(r-1) = 0$$
$$\lambda_{1/2} = 1/2\,[1 + \ln r/(r-1)] \pm \sqrt{1/4[1 + \ln r/(r-1)]^2 - r \ln r/(r-1)}$$

For r > 1 – the only ecologically meaningful assumption – the discriminant becomes negative, the eigenvalues become complex and oscillations arise. The discriminant becomes negative for following reasons: The first term of the Taylor series expansion of exp(r-1) is 1 + r – 1 = r, which means that r < exp(r-1) or ln(r) < (r-1) so that the term ln(r)/(r-1) < 1. Adding 1 to a term smaller than 1 gives a sum smaller than 2, squared a value smaller than 4 resulting in the first term of the discriminant $1/4[1 + \ln r/(r-1)]^2$ being always < 1. Similarly, the first term of the Taylor series expansion of ln(r) is (r-1)/r, which means that the absolute value of the second term of the discriminant r ln(r)/(r-1) is always > 1. Thus the sum of the two terms of the discriminant is always < 0.

As this is a discrete time system, we need the absolute value of the resulting conjugate complex eigenvalues $\lambda_{1/2}$. It can be derived as this

$$\lambda_{1/2} = 1/2\,[1 + \ln r/(r-1)] \pm i\,\sqrt{-\{1/4[1 + \ln r/(r-1)]^2 - r \ln r/(r-1)\}}$$
$$\lambda_{1/2} = 1/2\,[1 + \ln r/(r-1)] \pm i\,\sqrt{-1/4[1 + \ln r/(r-1)]^2 + r \ln r/(r-1)}$$
$$|\lambda_{1/2}| = \pm\sqrt{\{1/2[1 + \ln r/(r-1)]\}^2 + \{\sqrt{-1/4[1 + \ln r/(r-1)]^2 + r \ln r/(r-1)}\ \}^2}$$
$$|\lambda_{1/2}| = \left|\ \sqrt{r \ln r/(r-1)}\ \right|$$

This means we get for r>1 always $|\lambda_{1/2}| > 1$. Therefore, the **non-trivial, stationary solution x°" is unstable**. Remember, the absolute value of a complex number is defined as the length of the vector from the origin to the point given by the real and imaginary part of the number in the complex plane. Above derivation then simply used the Pythagoras theorem to get the absolute value of the complex eigenvalues. In general holds for any discrete time system, asymptotic stability results only if the vectors associated with complex eigenvalues lie fully within the unit circle and any non-complex eigenvalues are negative. If any vector ends outside the unit circle or any non-complex eigenvalue is positive, instability results.

Since both existing stationary solutions are unstable, the entire system also exhibits unstable behavior. The trajectories all lead away from both stationary solutions x°' as well as x°".

Model **Z**

$dx_1(t)/dt = a\,x_1(t) - b\,x_1(t)^2 - c\,x_1(t)\,x_2(t) = 0 \quad \Rightarrow \quad x_2 = a/c - b/c\,x_1$
$dx_2(t)/dt = d\,x_1(t)\,x_2(t) - e\,x_2(t) = 0 \quad \Rightarrow \quad x_1 = e/d$

The trivial first stationary solution is x°' = [0,0] and the non-trivial second stationary solution is x°"

x°" = [e/d , a/c - be/cd] (see also Fig. 2)

The Jacobimatrix

$$J = \begin{pmatrix} \partial f_1/\partial x_1 & \partial f_1/\partial x_2 \\ \partial f_2/\partial x_1 & \partial f_2/\partial x_2 \end{pmatrix} = \begin{pmatrix} a - 2b\, x_1(t) - c\, x_2(t) & - c\, x_1(t) \\ dx_2(t) & dx_1(t) - e \end{pmatrix}$$

at the position [0,0] (trivial, stationary solution)

$$J' = \begin{pmatrix} a & 0 \\ 0 & -e \end{pmatrix}$$

and at the point $\underline{x}°''$ (non-trivial stationary solution)

$$J'' = \begin{pmatrix} -be/d & - ce/d \\ (ad - be)/c & 0 \end{pmatrix}$$

The characteristic polynomial given matrix J'

$$\det[J' - \lambda I] = \begin{vmatrix} a-\lambda & 0 \\ 0 & -e-\lambda \end{vmatrix} = (a - \lambda)(-e - \lambda) = 0$$

$$\lambda_1 = a$$
$$\lambda_2 = -e$$

Ecologically meaningful are only populations with an intrinsic growth rate >0. For a>0, there is always at least one positive eigenvalue $\lambda_1 > 0$. Therefore, the **trivial, stationary solution [0,0] is unstable**.

For the second, non-trivial stationary solution $\underline{x}°''$ given matrix J'' we obtain the characteristic polynomial

$$\det[J'' - \lambda I] = \begin{vmatrix} -be/d - \lambda & - ce/d \\ (ad - be)/c & -\lambda \end{vmatrix} = (-be/d - \lambda)(-\lambda) + e(a-be/d) = 0$$

or the quadratic equation

$$\lambda^2 + be/d\lambda + e(a - be/d) = 0$$

$$\lambda_{1/2} = - be/2d \pm \sqrt{(be/2d)^2 - e(a - be/d)}$$

A predator-prey relationship requires that all parameters a>0, b>0, c>0, d>0, and e>0. Under these conditions, the values of the parameters can still form different relationships, which need to be distinguished. Following three cases α, β, and γ, matter with respect to the stability properties of $\underline{x}°''$. In case α we have a=be/d, i.e. the second term of the discriminant disappears and the value of the root becomes exactly be/2d. This results in following eigenvalues

$$\lambda_1 = 0 \qquad a = be/d \qquad (\alpha)$$
$$\lambda_2 = -be/d$$

$\lambda_1 = 0$ indicates **neutral stability of $\underline{x}°''$** and closed trajectories surrounding the stationary solution $\underline{x}°''$ are to be expected.

For the other two cases, the value of the root term becomes either greater or less than be/2d.

In case (β) holds a<be/d, which can be ecologically interpretated that the carrying capacity of the ecosystem (K = a/b) for the prey is lower than the ratio between the death and growth rate of the predator (e/d), i.e. K = a/b < e/d. In this case the second, term of the discriminant becomes positive and causes the amount of the root value to become larger than be/2d. This results in one real, positive eigenvalue, so for this case the solution **$\underline{x}°''$ becomes unstable**

$\sqrt{(be/2d)^2 - e(a - be/d)}$ > be/2d   a < be/d   (β)

$\lambda_1 = -be/2d + \sqrt{(be/2d)^2 - e(a - be/d)} > 0$

$\lambda_2 = -be/2d - \sqrt{(be/2d)^2 - e(a - be/d)} < 0$

In the third case (γ) holds a > be/d, which can be ecologically interpretated that the carrying capacity of the ecosystem (K = a/b) for the prey is higher than the ratio between the death and growth rate of the predator (e/d), i.e. K = a/b > e/d. In this case the second term of the discriminant becomes negative and causes the root value to become always smaller than be/2d. This means that only eigenvalues with negative real parts can result

$\sqrt{(be/2d)^2 - e(a - be/d)}$ < be/2d   a > be/d   (γ)

$\lambda_{1/2} = -be/2d \pm \sqrt{(be/2d)^2 - e(a - be/d)} < 0$

In case (γ), the solution **x°" is therefore asymptotically stable**. Due to the imaginary parts oscillations result. Thus a system behavior with damped oscillations around an asymptotically stable equilibrium x°", i.e. a spiral sink, is to be expected.

The non-trivial, stationary solution x°" is thus neutrally stable in the case a=be/d (α), unstable in the case a<be/d (β), and asymptotically stable in the case a>be/d (γ). We can expect that evolution would select against case (β) and that case (α) would be rare and evolution would also select against it as the slightest deviation towards case (β) results in the same fate as all cases (β). It can therefore be expected that natural variation would select a safety margin so that case (γ) is unlikely to become case (α), let alone (β). This means we can expect in nature to find mostly case (γ) for the model Z. Since the trivial solution [0,0] is unstable and the non-trivial solution x°" is asymptotically stable, such a parameter constellation always results in an overall system behavior resembling damped oscillations where the trajectories lead back towards a spiral sink, i.e. the stationary solution, in the event of ongoing disturbances or deviating initial conditions, e.g. resulting from human interventions.

Summary of solutions including model assignments:

Simu-lation Model	Mathe-matical Model	Real System	Model Name	Equilibrium points (fixed points, steady states)	
				trivial [0,0]	non-trivial
1	Z	A	Lotka-Volterra with self-inhibition of prey	unstable $\lambda_1 > 0, \lambda_2 < 0$	asymptotically stable $\mathcal{Re}(\lambda_{1/2}) < 0$ [5]
2	X	B	Lotka-Volterra without self-inhibition of prey	unstable $\lambda_1 > 0, \lambda_2 < 0$	neutrally stable $\mathcal{Re}(\lambda_{1/2}) = 0$
3	Y	C	Nicholson-Bailey host parasitoid	unstable $\lambda_1 > 0, \lambda_2 = 0$	unstable $\lvert\lambda_{1/2}\rvert > 1$

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[5] $\mathcal{Re}(x)$ denotes the real part of x and for model Z we consider only the ecologically more likely case (γ)

Teaching Experiences

The courseware «Stability» was used for the first time in the summer semester of 1986 and since then in the winter semester at the ETHZ as part of the lecture "Systems Analysis" by A. Fischlin. This lecture counted for the final diploma at Department VII of Agriculture (Systems Analysis: Topic Agricultural Economics (5th Semester); Animal Production (7th Semester) and Plant Production (7th Semester) plus Department X of Natural Sciences (Ecological Systems Analysis: Topic Biology (5th Semester); Ecology and Systematics (5^{th} Semester). Since the winter semester 1988/89, the lecture has been a compulsory course at Department XB1 (Environmental Natural Sciences) in the 3rd semester forming part of the exam for the 2nd intermediate diploma (2. Vordiplom).

The students worked with the program during two supervised practice sessions and then solved the task in further independent work. The students each wrote a small report in which they describe their finding and handed it in the following week. The tasks were satisfactorily solved by the majority.

Later the courseware «Stability» was also used for many years in the course “Systems Ecology” by A. Fischlin and H. Lischke as offered for the master degree at the department of Environmental Systems Science of ETH Zurich.

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