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Swiss. Federal Institute of Technology Zürich

𝔐athematical 𝔐odeling of 𝔓hysical 𝔖ystems

Population Dynamics II

- In this class, we shall analyze behavioral patterns of ecosystems, in which more than two species interact with each other.
- Such systems frequently exhibit *chaotic behavior*.
- Chaotic models shall be analyzed and discussed.

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Generalization of Ecological Models

- What happens when e.g. three species compete for the same food source? The previously used model then needs to be extended as follows:

$$\dot{x}_1 = a \cdot x_1 - b_{12} \cdot x_1 \cdot x_2 - b_{13} \cdot x_1 \cdot x_3 - b_{23} \cdot x_2 \cdot x_3$$
$$\dot{x}_2 = c \cdot x_2 - d_{12} \cdot x_1 \cdot x_2 - d_{13} \cdot x_1 \cdot x_3 - d_{23} \cdot x_2 \cdot x_3$$
$$\dot{x}_3 = e \cdot x_3 - f_{12} \cdot x_1 \cdot x_2 - f_{13} \cdot x_1 \cdot x_3 - f_{23} \cdot x_2 \cdot x_3$$

- There never show up terms such as:

$$-k \cdot x_1 \cdot x_2 \cdot x_3$$

as such a term would indicate that e.g. the competition between x_2 and x_3 disappears, when x_1 dies out.

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The Gilpin Model I

- *Michael Gilpin* analyzed the following three-species ecosystem model:

$$\dot{x}_1 = x_1 - 0.001 \cdot x_1^2 - 0.001 \cdot x_1 \cdot x_2 - 0.01 \cdot x_1 \cdot x_3$$
$$\dot{x}_2 = x_2 - 0.0015 \cdot x_1 \cdot x_2 - 0.001 \cdot x_2^2 - 0.001 \cdot x_2 \cdot x_3$$
$$\dot{x}_3 = -x_3 + 0.005 \cdot x_1 \cdot x_3 + 0.0005 \cdot x_2 \cdot x_3$$

- A single predator, x_3, feeds on two different species of prey, x_1 and x_2, both of which furthermore compete for the same food source, and suffer from crowding effects.
- The initial populations for all three species were arbitrarily set to *100 animals* each. We simulate over *5000 time units*.
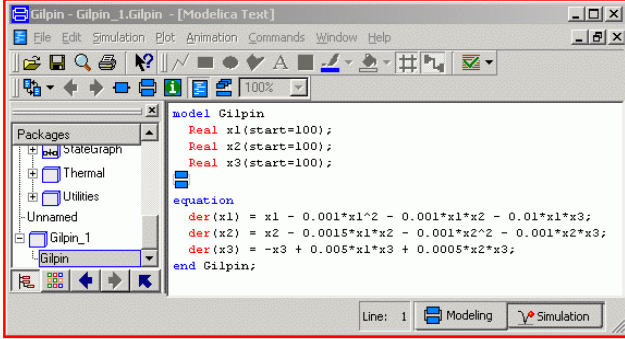
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The Gilpin Model II

- The model was coded in *Modelica*:


```
model Gilpin
  Real x1(start=100);
  Real x2(start=100);
  Real x3(start=100);

equation
  der(x1) = x1 - 0.001*x1^2 - 0.001*x1*x2 - 0.01*x1*x3;
  der(x2) = x2 - 0.0015*x1*x2 - 0.001*x2^2 - 0.001*x2*x3;
  der(x3) = -x3 + 0.005*x1*x3 + 0.0005*x2*x3;
end Gilpin;
```
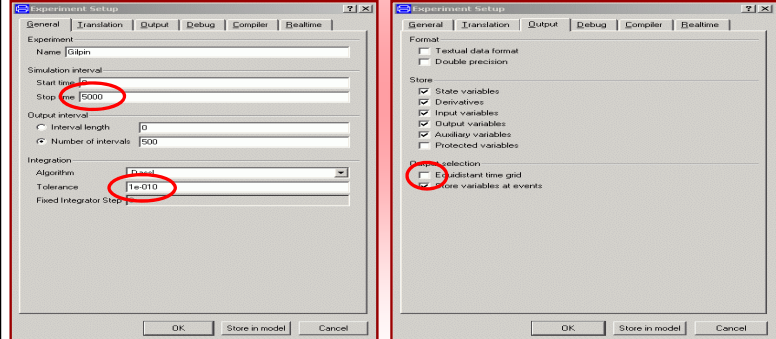
The Gilpin Model III

- We use simulation control as follows:
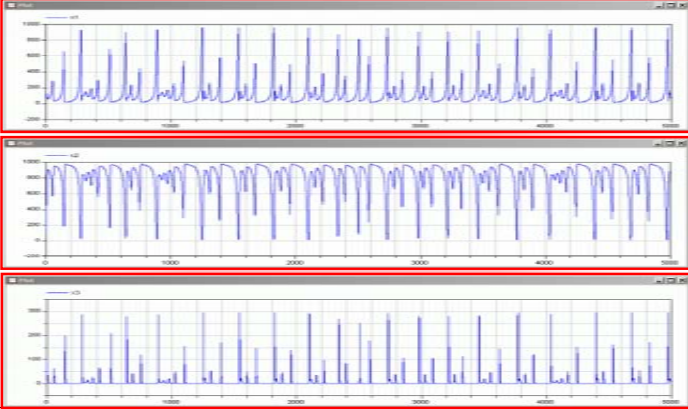
The Gilpin Model IV

The Gilpin Model V

- Most of the time, there are plenty of x_2 animals around.
- Once in a while, the predator (x_3) population explodes in a pattern similar to that of the *Lotka-Volterra model*.
- The predator then heavily decimates the x_2 population.
- The x_1 population is usually hampered by strong competition from the x_2 population for the common food source.
- Thus, when the x_2 population is decimated, the x_1 population can thrive for a short while.
- However, the x_2 population recovers quickly, depriving again the x_1 population of their food.

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The Gilpin Model VI

- Yet, the behavioral pattern of each cycle is slightly different from that of the previous one. This can be better seen in *phase portraits*.
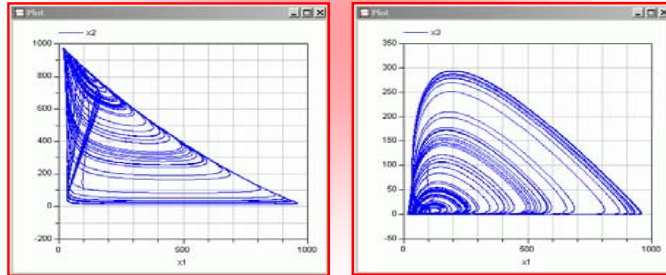
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The Gilpin Model VII

- In a *limit cycle*, the phase portrait would show a single orbit.
- The observed behavior is called *chaotic*. Each orbit is slightly different from the last. If the simulation were to proceed over an infinite time period, the orbits would cover an entire region of the phase plane.
- *Chaotic behavior* is caused here, because the two preys can coexist at different equilibrium levels, i.e., the predator can be fed equally well by eating animals of the x_1 kind as of the x_2 kind. One prey can substitute the other.
- In *continuous-time systems*, chaos can only exist in 3rd and *higher order systems*.

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The Discrete-Time Logistic Equation I

- In the case of *discrete-time systems*, chaos can already exist in 1st *order systems*.
- To study chaos in its purest form, we shall analyze the behavioral patterns of the *discrete-time logistic model*:

$$x_{k+1} = a \cdot x_k \cdot (1.0 - x_k)$$

- *a* is a parameter that shall be varied as part of the experiment.

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The Discrete-Time Logistic Equation II
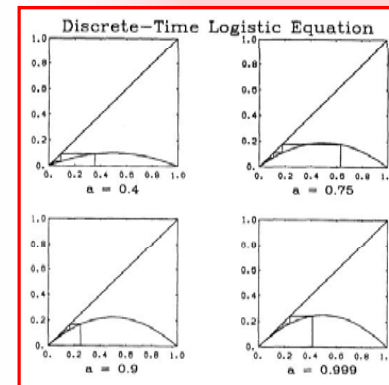
We find graphically the intersection(s) between the two functions:

$$y_1 = x$$
$$y_2 = a \cdot x \cdot (1.0 - x)$$

In the range $a \in [0.0, 1.0]$, there is only a single solution: $x = 0.0$.

As *a* approaches a value of $a = 1.0$, the two curves become more and more parallel. Consequently, it takes more and more iterations, before the *steady-state value* is reached.

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The Discrete-Time Logistic Equation III

In the range $a \in [1.0, 3.0]$, there are two intersections between the two functions.

However, only one of the two solutions is stable. There is still only one steady-state solution.

The iteration converges rapidly for intermediate values, but as a approaches either a value of $a = 1.0$ or alternatively a value of $a = 3.0$, the iteration converges more and more slowly.
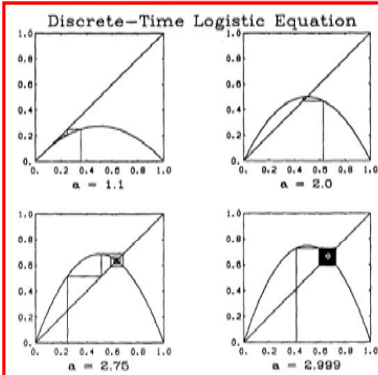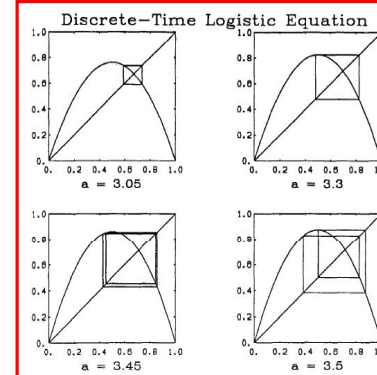
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The Discrete-Time Logistic Equation IV

In the range $a \in [3.0, 3.5]$, a limit cycle is observed.

For $a = 3.05$ and $a = 3.3$, the discrete limit cycle has a *period of 2*.

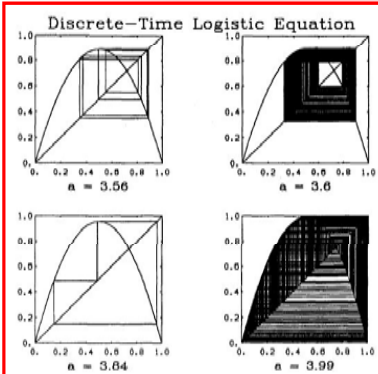For $a = 3.45$ and $a = 3.5$, the discrete limit cycle has a *period of 4*.

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The Discrete-Time Logistic Equation V

In the range $a \in [3.5, 4.0]$, the observed behavioral patterns become increasingly bizarre.

For $a = 3.56$, a discrete limit cycle with a *period of 8* is being observed.

For $a = 3.6$, the behavior is chaotic.

For $a = 3.84$, a discrete limit cycle with a *period of 3* is being observed.

For $a = 3.99$, the behavior is again chaotic.

For $a > 4.0$, the system is unstable.

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The Discrete-Time Logistic Equation VI

- We can plot the stable steady-state solutions as a function of the parameter a.
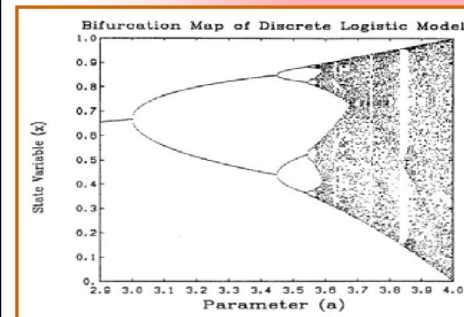
The dark region in the plot to the left is the *chaotic region*, yet, even within the chaotic region, there are a few *non-chaotic islands*, such as in the vicinity of $a = 3.84$.

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Bifurcations I

- How can the bifurcation points of the discrete-time logistic model be determined?
- A simple algorithm is presented below.
- We start with an assumption of a fixed steady state:

$$x_{k+1} = a \cdot x_k \cdot (1.0 - x_k) \equiv x_k \quad ; \quad k \to \infty$$

- We know that this assumption applies to the parameter range $a \in [1.0, 3.0]$.
- Thus we shall try to compute these two boundaries.

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Bifurcations II

- The equation has two solutions, $x_1 = 0.0$, and $x_2 = (a - 1.0)/a$.
- We know that the second solution, x_2, is stable.
- We move the stable solution to the origin using the transformation:

$$\xi_k = x_k - (a - 1.0)/a$$

- This generates the difference equation:

$$\xi_{k+1} = -a \cdot \xi_k^2 + (2.0 - a) \cdot \xi_k$$

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Bifurcations III

- We linearize this difference equation around the origin, and find:

$$\xi_{k+1} = (2.0 - a) \cdot \xi_k$$

- This difference equation is marginally stable for $a = 1.0$ and $a = 3.0$.
- We now proceed assuming a stable limit cycle with a discrete period of 2, thus:

$$x_{k+2} = a \cdot x_{k+1} \cdot (1.0 - x_{k+1}) \equiv x_k \quad ; \quad k \to \infty$$

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Bifurcations IV

- We evaluate this equation recursively, until x_{k+2} has become a function of x_k only.
- This leaves us with a 4th order polynomial in x_k.
- The previously found two solutions must also satisfy this new polynomial, i.e., we can divide by these two solutions, and again obtain a 2nd order polynomial in x_k.
- This new polynomial has again two solutions. One of them is $a = 3.0$, the other provides us with the next bifurcation point.

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The Gilpin Model VIII

- Let us now look once more at the Gilpin model. We shall treat the competition factor *k* as the parameter to be varied in the experiment:

$$\dot{x}_1 = x_1 - 0.001 \cdot x_1^2 - k \cdot 0.001 \cdot x_1 \cdot x_2 - 0.01 \cdot x_1 \cdot x_3$$
$$\dot{x}_2 = x_2 - k \cdot 0.0015 \cdot x_1 \cdot x_2 - 0.001 \cdot x_2^2 - 0.001 \cdot x_2 \cdot x_3$$
$$\dot{x}_3 = - x_3 + 0.005 \cdot x_1 \cdot x_3 + 0.0005 \cdot x_2 \cdot x_3$$

- The nominal value of *k* is *k = 1.0*.
- We shall vary *k* around its nominal value.
- We shall display only the x_1 population.

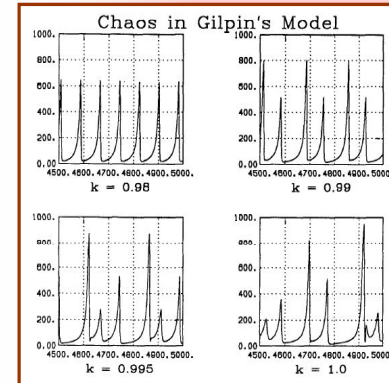# The Gilpin Model IX

For *k = 0.98*, we observe a limit cycle with peaks reaching each time the same level.

For *k = 0.99*, we observe a limit cycle where the peaks toggle between two discrete levels. Only looking at the peaks, we could say that we have a limit cycle with a discrete period of 2.

For *k = 0.995*, we have a limit cycle with a discrete period of 3.
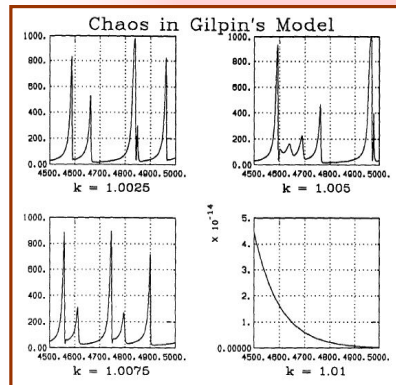
For *k = 1.0*, the behavior is chaotic.

The Gilpin Model X

For *k = 1.0025*, *k = 1.005*, and *k = 1.0075*, the behavior remains chaotic.

The behavior remains chaotic for values of *k < 1.0089*.

For *k > 1.0089*, such as *k = 1.01*, the x_1 population quickly dies out.

True Behavior or Numerical Artifact I?

- In the case of the *discrete-time logistic model*, we were able to analyze the observed behavior analytically, and verify that *chaos* indeed occurs.
- In the case of the *Gilpin model*, this is no longer as easy.
- The question thus needs to be raised, whether what we have observed is indeed the true behavior of the system, or whether we fell prey to a numerical artifact.

Slide 1

True Behavior or Numerical Artifact II?

- To this end, I propose to apply a *logarithmic transformation* on the Gilpin model:

$$y_i = \log(x_i)$$

- The *modified Gilpin model* presents itself as follows:

$$\dot{y}_1 = 1.0 - 0.001 \cdot \exp(y_1) - 0.001 \cdot \exp(y_2) - 0.01 \cdot \exp(y_3)$$
$$\dot{y}_2 = 1.0 - 0.0015 \cdot \exp(y_1) - 0.001 \cdot \exp(y_2) - 0.001 \cdot \exp(y_3)$$
$$\dot{y}_3 = -1.0 + 0.005 \cdot \exp(y_1) + 0.0005 \cdot \exp(y_2)$$

- The analytical results of the two models must be identical, yet their numerical properties are very different.
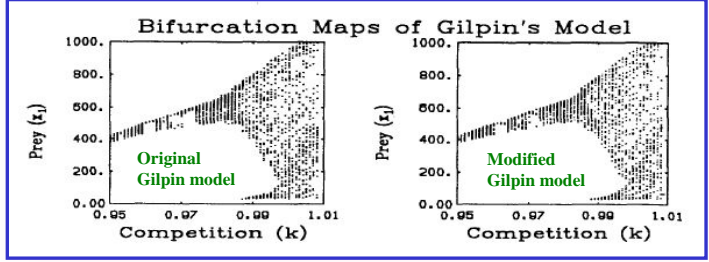
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Slide 2

True Behavior or Numerical Artifact III?

- We can now plot the *discrete bifurcation maps* of the two models. If they are the same, then chaos is indeed for real also in this model.

Bifurcation Maps of Gilpin's Model — Original Gilpin model / Modified Gilpin model. Prey (x_i) vs. Competition (k).

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Slide 3

Structural *vs.* Behavioral Complexity I

- We have seen that simple deterministic differential equations can lead to incredibly complex behavioral patterns in the solution space.

⇒ *The behavioral complexity of a system is generally much greater than its structural complexity.*

Structure	Behavior	Structure	Behavior
$\dot{x} = -a \cdot x$ $x(t = 0.0) = x_0$	$x(t) = \exp(-a \cdot t) \cdot x_0$	*Gilpin model*	*Population trajectories*
linear	*exponential*	*deterministic*	*chaotic*

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Slide 4

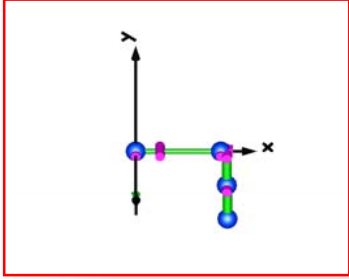### Structural *vs.* Behavioral Complexity II
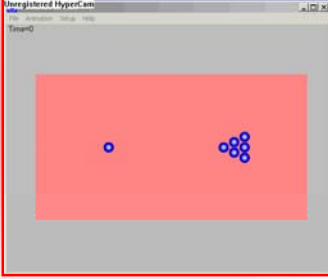
- Looking at the *Gilpin model*, we may reach the conclusion that *chaotic behavior* is the exception to the rule, that it occurs rarely, and is rather fragile.
- Nothing could be farther from the truth.
- As the structural complexity (the order of a differential equation model) increases, the *chaotic regions* grow larger and larger. In fact, they quickly dominate the overall system behavior.
- It is thus utterly surprising that no-one recognized *chaos* for what it is until the 1960s. Before then, chaotic behavior was always interpreted as a result of impurity.

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Chaos in Mechanical Systems

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Limits to Complexity

- We may thus ask ourselves, what limits complexity in our universe? How come that trees in unison grow leaves in the spring and shed them again in the fall? How come that we can still recognize structure at all among this maddening complexity that the laws of nature present us with?
- There are three mechanisms that limit complexity:
  - ❖ *Physical constraints:* When connecting two subsystems, the combined degrees of freedom are usually lower than the sum of the individual degrees of freedom.
  - ❖ *Control mechanisms:* Controllers in a system (abundant in nature) tend to restrict the possible modes of behavior of a system.
  - ❖ *Energy:* The laws of thermodynamics state that each system sheds as much energy as it can. This also limits complexity.

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The Forces of Creation I

- *Chaos* provides nature with a great mechanism for *constant innovation*.
- We are used to viewing *Murphy's law* as something negative: what can go wrong, will go wrong. However, Murphy's law can also be interpreted as something highly positive: *what can grow, eventually will grow*.
- *Chaos* is *the great innovator*. It brings any and every system constantly to the greatest degree of disorder that it can be in.
- *Chaos* is built into the very fabric of our universe. At the molecular level, the molecules move around like the balls on the pool table, in total chaos. This is what we measure as entropy. *Entropy is being maximized*.

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The Forces of Creation II

- Yet, chaos alone would leave us with a universe that is just an accumulation of random white noise. No structure would be retained.
- For structure to be preserved, we also need the opposite force, *the great organizer*, a force that fosters order, that sifts through the different possibilities, discards the bad ones, and only preserves those that look most promising.
- Three such mechanisms were outlined before. The most powerful among them: *Energy is being minimized*.

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Conclusions

- In the last two lectures, we have looked at predominantly inductive techniques for modeling population dynamics.
- Yet, these techniques have failed to e.g. provide us with a satisfactory model that could help us understand the mechanisms that lead to the oscillatory behavior of the *larch bud moth* (*zeiraphera diniana*).
- In the next lecture, we shall come up with an improved methodology to deal with these types of systems.

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References

- Cellier, F.E. (1991), *Continuous System Modeling*, Springer-Verlag, New York, Chapter 10.
- Gilpin, M.E. (1979), "Spiral chaos in a predator-prey model," *The American Naturalist*, **113**, pp. 306-308.

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