Nonlinear dynamics and chaos

Purpose: To use simulations to investigate how simple population dynamics models can have complicated dynamics.

Assessment: 10 points for each of questions 1-10. 100 points total.

Introduction: Discrete modeling of population abundances can take many forms. We have previously encountered the simple population model that, when the population growth rate (*r*) is positive, results in exponential growth (Figure 1):

$$N_{t+1} = N_t e^{r}$$

where *N* is population abundance at time *t* and *r* is the population growth rate. However, uncontrolled growth is rare and populations are often limited in their growth by their environment.

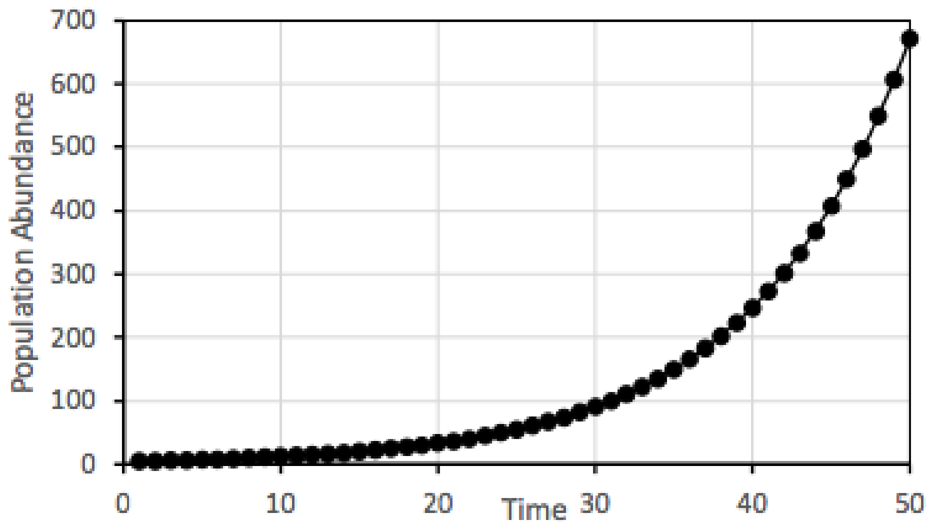

Figure 1. Simple population model showing exponential positive growth over time.

A more realistic model to use is the Ricker Model (1954). Dr. Bill Ricker was a Canadian quantitative fisheries biologist who contributed to how we study fisheries populations today. This model continues to be used to analyze time-series data of density-dependent populations, (e.g. Myers et al. 1999). The Ricker Model is what we call a discrete time density-dependent model:

$$N_{t+1} = N_t e^{r(1-\frac{N_t}{K})}$$

This equation models the population abundance (*N*) at time $t + 1$ as a function of population abundance (*N*) at time t, the intrinsic growth rate (*r*), and the carrying capacity (*K*).

Exercise 1. Similarly to Figure 1, plot a simulation of the Ricker Model over 100 years using a scatterplot. Start with a population size (*N*) of 5 individuals and parameters *r* = 0.1 and *K* = 1000. Make sure to connect the dots in your plot with lines.

Hint:

#Parameters

- r<-0.1
- K<-1000

#Timescale of simulation

- T<-101

#Vector to store abundance in

- N<-numeric(T)

#Initial Conditions

- N[1]<-5

#Simulation

```
for(t in 2:T){
    N[t]=N[t-1]*exp(r*(1-(N[t-1]/K)))
}
```

#Plot results

```
TT<-seq(1,T)
plot(TT,N,xlab="Time(years)", ylab="Abundance(N)",type="o")
```

Exercise 2. Plot a simulation where the initial population size is 200. Make an additional plot with the simulation from Exercise 1 with the new simulation from Exercise 2. Notice that both simulations converge on the same number. This is the equilibrium abundance and is equal to *K*.

Hint:

- The code for this exercise is very similar to the code that you used in Exercise 1

Exercise 3. Let's investigate the influence of environmental stochasticity. Suppose the population is exposed to a random environmental perturbation each year such that:

$$N_{t+1} = N_t e^{r\left(1-\frac{N_t}{K}\right)+\epsilon_t}$$

where e_t is a normal random variable with mean zero and standard deviation equal to 0.4. For this model, in each year there is a random variable that is drawn which affects the survival of that cohort. Simulate the model for 100 years with initial population size 5. To simulate e_t in R, use the function ‘rlnorm.’

Exercise 4. Simulate and plot the model in Exercise 3 several (5) times and observe how the dynamics change from simulation to simulation. How do the plots compare to the deterministic (i.e. no randomness) model in Exercise 1? Does adding environmental stochasticity have a large effect on population abundance?

Exercise 5. Let’s re-examine the deterministic model in Exercise 1, but this time, plot the results of a simulation for each of the following values of *r*: 0.5, 1, 1.5, 1.9, 2, 2.2, 2.5, 2.6, 2.7, 2.8, 2.9. Describe how the dynamics change as you increase *r*.

Hint:

- The code for this exercise is very similar to the code you used in Exercise 1. You only need to change the value of the r parameter for each simulation.

Exercise 6. Redo the simulation in Exercise 5 where $r = 2.9$ and compare the dynamics using a scatterplot between initial population sizes of 5 and 5.1. Do it again when $r = 0.3$. Notice that a small change in initial conditions has on the subsequent dynamics. At high values of *r* there is a high sensitivity to initial conditions.

Hint:

- The code for this exercise is very similar to the code you used in Exercise 5. You only need to change the value of the *r* parameter for each simulation.

Exercise 7. At high values of *r*, in Exercises 5 and 6, what you observed was chaos. The chaotic fluctuations in abundance looked like random fluctuations similar to Exercise 3 but notice that the model in Exercise 5 has no random component to it whatsoever. Sensitivity to initial conditions in Exercise 6 is a hallmark characteristic of chaos. These have been big issues in ecology and other scientific fields – when presented with a plot like in Exercise 3 or in Exercise 5 (with $r = 2.9$) are the data random? Or are there simple rules that have no randomness at all that determine the fluctuations? There are no easy answers. Furthermore, if chaotic dynamics are common then the sensitivity to initial conditions means our ability to predict is very poor – that is partly why long range weather forecasting is so bad!

Exercise 8. The previous exercises all assumed constant growth models across a population. However, in reality, population growth models may need to be stage-structured, such as between adults and juveniles, to account for differing growth dynamics. For example, in some cases, there may be increased numbers of immature or juvenile individuals relative to adults, causing an overall larger population size. This is called overcompensation and can occur in nature for many different reasons, for example, as a result of a pathogen outbreak in European Perch (Perca fluviatilis; Ohlberger et al. 2011) or as a result of harvest of Smallmouth Bass (Micropterus dolomieu; Zipkin et al. 2008).

For this exercise, let's assume that juveniles (*J*) and adults (*A*) follow differing growth models with juveniles showing overcompensation:

$$J_t = A_{t-1}e^{f}$$

$$A_t = J_{t-1}e^{-aJ_{t-1}} + sA_{t-1}$$

where *J* is the juvenile population abundance, *A* is the adult population abundance, *f*=12 is fecundity rate, *a*=5 is the density dependent survival rate, and *s*=0.85 is the annual adult survival rate. Simulate both models for 2000 years with initial population sizes of 100 for juveniles and 120 for adults. Plot the simulations for years 500 – 2000 on separate scatterplots. Make sure to alter your axes to ensure readability. What do you conclude from the individual scatterplots?

Hint:

#Parameters

- f<-12
- a<-5
- s<-0.85

#Timescale of simulation

- T<-2000

#Vectors for each stage

- J<-numeric(T); A<-numeric(T)

#Initial conditions

- J[1]<-100; A[1]<-120

#Simulation

- for(t in 2:T){

```
     J[t]<-A[t-1]*exp(f)
    A[t]<-(J[t-1]*exp(-a*J[t-1]))+s*A[t-1]

}
```

Exercise 9. Now, let's build the attractor in state-space and relate the dynamics in state space to those in the time series. To build a state space, put the juvenile abundance on the x-axis and the adult abundance on the y-axis and plot the Juvenile-Adult data pairs on the graph for years 500 to 2000. Again, make sure to adjust your axes to provide the best visualization. How do the individual time series look in comparison to the state space?

Exercise 10. To make a little bit more sense of the juvenile-adult state space, let's compare it with a null model created from random normal variables. This depicts the situation where juvenile and adult growth rates are random. Create two vectors in R, one consisting of 1500 random variables with a mean of 100 and a standard deviation of 10, and the other vector consisting of 1500 random variables with a mean of 120 and a standard deviation of 10. To do this, use the 'rlnorm' function in R and specify the mean, standard deviation and number of random variables that you need to generate. Create your null model state space. What does it look like? How does this compare with the state space from Exercise 10?

Exercise 11. Based on your null model, what conclusions can you draw from your realized juvenile-adult state space? Explain. Also, how do your conclusions relate to your expectations when you first looked at the individual time series of juveniles and adults?

Exercise 12. Optional: At some point this semester, watch the movie "Run Lola Run." It is about chaos. Note how the story line changes dramatically based on small differences in her initial flight down the stairs – that is sensitivity to initial conditions.

Literature Cited

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Ohlberger, J., Langangen, Ø., Edeline, E., Claessen, D., Winfield, I.J., Stenseth, N.C., and Vøllestad, L.A. 2011. Stage-specific biomass overcompensation by juveniles in response to increased adult mortality in a wild fish population. Ecology **92**(12):2175–2182.

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Zipkin, E.F., Sullivan, P.J., Cooch, E.G., Kraft, C.E., Shuter, B.J., and Weidel, B.C. 2008. Overcompensatory response of a smallmouth bass (Micropterus dolomieu) population to harvest: release from competition? Canadian Journal of Fisheries and Aquatic Sciences 6**5**:2279–2292.