# Lab 2: Density-dependence and more!

NRES 470/670

Spring 2022

In this lab we will have an opportunity to build more complex population models in InsightMaker. The most fundamental concept we cover in this lab is *density dependence*, but we will also look at concepts like *chaos* and *time delays*.

First let's do some math!

## Mathematics of Density-Dependent population regulation

Recall the basic population growth equation:

$\Delta N = (b - d) \cdot N_t \qquad \text{(Eq. 1)}$

Previously we considered $b$ and $d$ and $r$ to be constants.

Now we want them to be functions of abundance! In particular, as abundance goes up, $b$ goes down (becomes less favorable):

$b = b_{max} - a * N_t \qquad \text{(Eq. 2)}$

For the death rate $d$ we might expect it to go up as abundance goes up (becomes less favorable):

$d = d_{min} + c * N_t \qquad \text{(Eq. 3)}$

The above equations nicely illustrate the meaning of density dependence. That is, one or more vital rates are *dependent* on density!

**Q**: what do the $a$ and $c$ constants in the above equations really represent? You will have a chance to think more about this in the first exercise.

Okay, now we can substitute the above equations into **Eq. 1**:

$\Delta N = ((b_{max} - a * N_t) - (d_{min} + c * N_t)) \cdot N_t \qquad \text{(Eq. 4)}$

**Q**: what is the maximum rate of growth in this case?

Using some tricks of algebra (see the Gotelli book), we can simplify this to:

$\Delta N = r \cdot N_t \left[1 - \frac{a+c}{b-d} \cdot N_t\right] \qquad \text{(Eq. 5)}$

Which, if we define $\frac{b-d}{a+c}$ as a constant, $K$, we can re-write like this!

$\Delta N = r \cdot N_t \cdot \left(1 - \frac{N}{K}\right) \qquad \text{(Eq. 6)}$

This is called the **Logistic population growth equation**. This lab will give us an opportunity to get to know this equation and its implications for population ecology!

## Exercise 1: hypothetical mechanisms of density dependence

Please provide short answers to the following questions:

1a. Tell a plausible story about two (possibly hypothetical) wildlife populations, one of which experiences *lower survival* (higher mortality) as densities increase and another that experiences *lower reproduction*. In 2-3 sentences (for each of your two hypothetical populations), describe the mechanism(s) underlying the reduction in vital rates for your hypothetical populations. Be creative- we just want to give you a chance to think about the many possible mechanisms that could potentially regulate wild population in ecological systems. You can use real-world examples if you would rather- that is up to you.

1b. For *one of the above mechanisms*, draw (electronically-see below for an easy way to do this) two graphs to illustrate how this hypothetical mechanism might manifest at a population level:

i. Abundance (Y axis) over time (X axis). Initialize the abundance well below carrying capacity.

ii. Vital rate ($b$ or $d$) (Y axis) over abundance (X axis).

For each graph, provide a short (1-2 sentences) description of why you think your hypothetical D-D mechanism would result in this relationship!

NOTE: you can use a web app like "Web whiteboard" to quickly and easily make and save sketches! I encourage you to use this method, and to embed your sketches in your Top Hat answer.

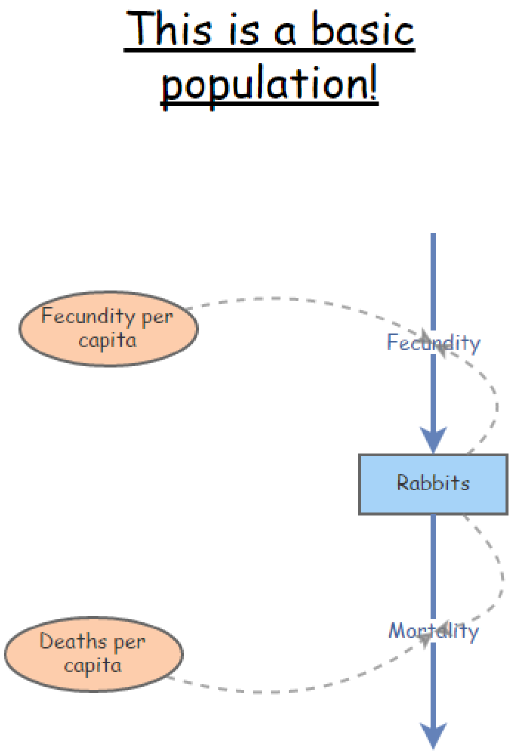
## Exercise 2: Determining Peruvian anchovy optimal harvest levels!

Let's use InsightMaker to create a logistic growth model based on the collapse of the Peruvian anchovy fisheries (pages 45-47 in Gotelli).

As you develop the logistic growth model for the Peruvian anchovy stock in InsightMaker, you might want to refer to the in-class example for the population regulation lecture.

**The Goal**: find the rate of harvest that maximizes the total harvest yield while maintaining a sustainable population!

1. In InsightMaker, open your basic exponential growth model (with explicit terms for birth and death rates, like you did in lab 1) and choose "Clone Insight" in the upper right corner to create a new copy that you can edit for this exercise. It should look something like this (see below; except for anchovies, not rabbits!). Note that it is not strictly necessary to have [Links] going from [Stocks] (e.g., *Population*) to connected [Flows] (e.g., *Total Births* and *Total Deaths*; InsightMaker assumes that flows may depend on the stocks they connect to). But it makes your models more visually explicit- now you know which parts of the system are interacting and what feedback mechanisms are occurring!)



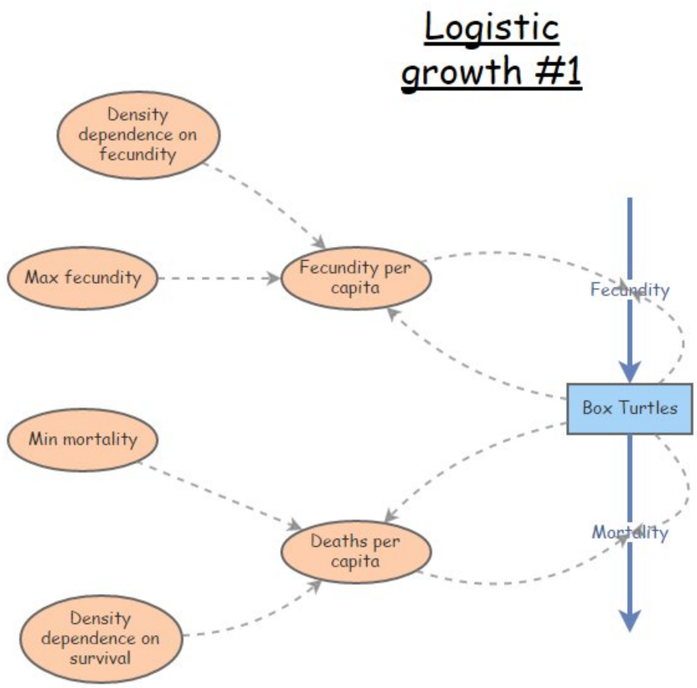

2. Now add the density-dependence components! Remember, the density-dependent birth and death rates in the logistic growth model can be expressed as the following:

$b = b_{max} - aN$, aka density-dependent birth rate = most favorable (maximum) birth rate - (strength of density dependence * N)

$d = d_{min} + cN$, aka density-dependent death rate = most favorable (minimum) death rate + (strength of density dependence * N)

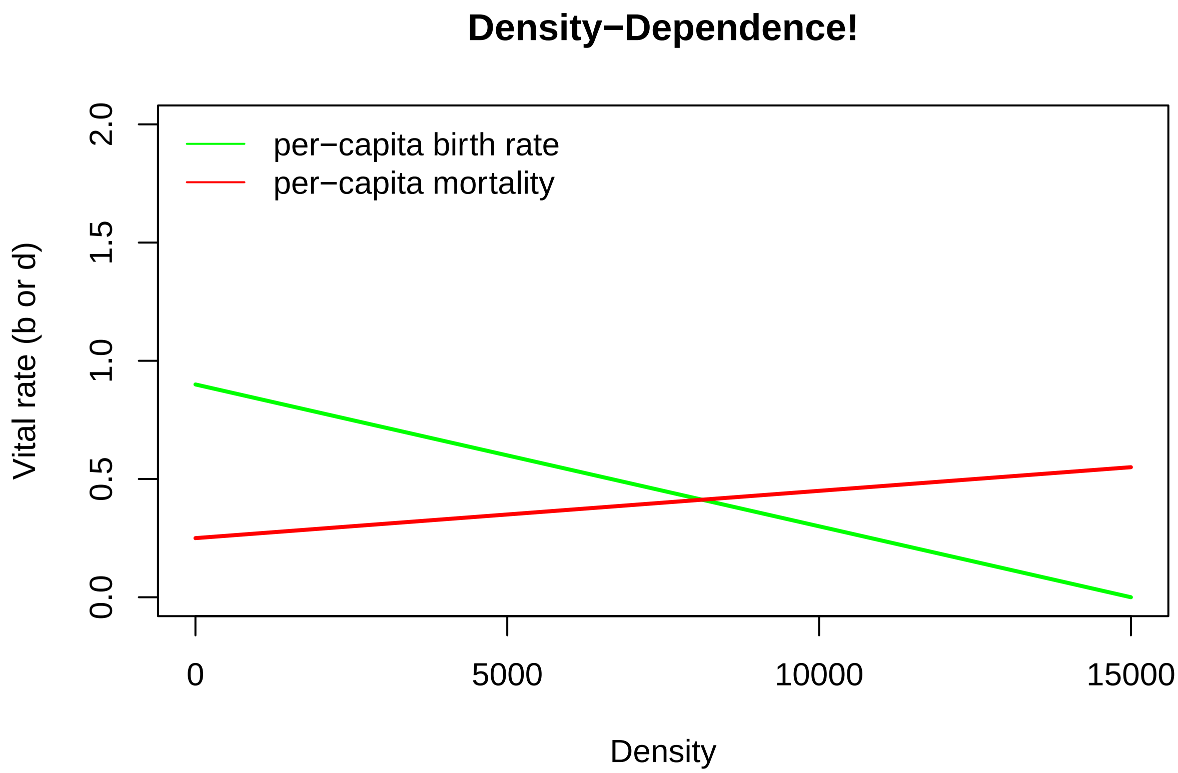
Rename your per-capita population vital rates: birth rate should be renamed *Max Birth Rate* (maximum birth rate) and death rate should be renamed *Min Death Rate* (minimum death rate).

The density-dependence terms $a$ and $c$ should be modeled in InsightMaker as [Variables] (Click on **Add Primitive** » **Add Variable**). Make sure the **Links** button is activated, and click and drag your mouse to create links from the new variables to the appropriate per-capita vital rates. Your final model should look something like this (except for anchovies, not box turtles!):




Here we visualize these relationships in R!

```
Density <- seq(0,15000,10)  # create a sequence of numbers from 0 to 15000, representing a range of pop

## CONSTANTS

b_max <- 0.9   # maximum reproduction (at low densities)
d_min <- 0.25  # minimum mortality (at low densities)

a <- 0.00006    # D-D terms
c <- 0.00002

b <- b_max - a*Density
d <- d_min + c*Density

K <- (b_max-d_min)/(a+c)   # compute carrying capacity

plot(Density,b,type="l",col="green",lwd=2,ylim=c(0,2),main="Density-Dependence!",xlim=c(0,15000),ylab="
points(Density,d,type="l",col="red",lwd=2)
legend("topleft",col=c("green","red"),lty=c(1,1),legend=c("per-capita birth rate","per-capita mortality
```




4. Next, you'll need to update the equations to calculate the per-capita birth and death rates. Click on the = sign in the corner of each variable, and enter the appropriate equations for the appropriate rates (see above):

5. Enter starting values for your variables. Let's use 5500 for the initial *Anchovy Population*, 0.85 for the *Ideal Birth Rate* (maximum birth rate), 0.00007 for *Density Dependence* for birth rate, 0.3 for *Ideal Death Rate*, and 0.00003 for *Density Dependence* for death rate.

6. Use the **Settings** button to change the **Simulation Length** to 24 and the timescale to "Months". Click **Simulate**. You may need to click **Configure** in order to clean up your plot to just show **Time** on the x-axis and **Anchovy Population** on the y-axis. Run the model to see if it is working. *Since the abundance is initialized at carrying capacity (K), abundance should not change over time.* Change the initial abundance to a small number (e.g., 10) temporarily to make sure that you see an "S-shaped" logistic growth curve. Once you have confirmed that you see S-shaped growth, return the initial population size to 5500.

7. Next, let's add an additional source of mortality (right now, we have natural baseline mortality (40% per year) and density-dependent effects). This new source of mortality is commercial fishing! This source of mortality should be a new [Flow Out] from the Anchovy population. For now, let's assume harvest is constant – that is, a constant number are harvested each year, regardless of the size of the population (no feedback!).

8. One last thing before we play around with harvest rates: in the properties menu for the anchovy stock, set the property **Allow Negatives** to "No" (the default is "Yes"). We don't want to harvest the population into negative numbers!!!

9. Finally, try to find the **maximum sustainable yield (MSY)** for this population. That is, find the *maximum harvest rate* that results in a sustainable (non-declining) population. To do this, try

different rates of harvest- I recommend using increments of 100 at first, then narrowing down to smaller increments. Otherwise you might be here a while!!

**QUESTIONS, Exercise 2:**

2a. What is the (approximate) maximum sustainable yield (MSY) for this population (i.e., the maximum number of individuals that can be harvested sustainably each month)? [HINT: you might want to increase the simulation length to make sure it's really sustainable!] [HINT: the answer is not one half of carrying capacity. However, when you harvest the population at its maximum sustainable rate, the new equilibrium population size will be half of carrying capacity!]

2b. Does the harvest process change the **carrying capacity** (total number of individuals that can be supported sustainably in this system) for the Peruvian anchovies? Explain your reasoning.

2c. Does the maximum number of individuals you can harvest each month (MSY) change if you reduce the initial population size to 1000 instead of 5500? If so, what is the new MSY?

2d. Does the equilibrium point from your answer for 2a (the equilibrium point for the anchovy system with harvest set to MSY) represent a **stable equilibrium**? That is, does the total anchovy abundance return to the same equilibrium condition even if you alter the initial anchovy abundance (i.e., try altering initial abundance by making it lower or higher and see what happens)? Why? Why not? Include one or more plots from InsightMaker to illustrate. [HINT: first set the initial abundance to the equilibrium abundance at MSY. Then try setting the initial abundance a little higher/lower and re-run the model. Does abundance return to the same equilibrium point – or to a new equilibrium?]

2e. If you were managing this Peruvian anchovy system, would you recommend that harvest limits be set at the MSY level you determined in part 2a? Why or why not? (More generally, is it sustainable to harvest a population at the maximum 'sustainable' rate?). Consider the fact that population vital rates (birth and death rates) in real systems exhibit *stochasticity* (random fluctuations) and that we never know population vital rates (e.g., the intrinsic rate of growth, birth and death rates, density dependence parameters) with complete certainty.

2f. Think back to your Wildlife Ecology and Management course. If you know $K$ and $r$ (intrinsic, or maximum, rate of growth for the population), how can you analytically solve for **Maximum Sustainable Yield** (maximum number of individuals that can be harvested sustainably)? Show your calculations. Does your analytical solution for MSY (maximum sustainable harvest rate) match the MSY you found by trial-and-error? (HINTS: use equation 6 as a starting point. Note that $r$ in this case is the difference between the maximum birth rate and the minimum death rate! Also, note that the population should have its highest growth potential at 1/2 of K [e.g., K/2]).

**NOTE**: remember to copy the URL for your Insight (saved as a Public Insight), insert the URL into Top Hat in the appropriate place. And don't make any more changes to this insight once you have submitted it (use a 'cloned' version if you want to keep making changes)!

## Exercise 3: basic logistic growth model

For this exercise we will set up a simpler model in InsightMaker- this time, we will replicate **Eq. 6** (above). We will sometimes refer to this as "basic logistic growth, r formulation" to distinguish this from basic logistic growth with explicit birth and death rates.

1. Starting from a blank canvas, add a [Stock] called *Population*. This population should be initialized at 10 individuals, and the *Allow Negatives* field in the properties window should be set to "No" (doesn't make sense to have negative numbers of individuals in the population). Set *Show Value Slider* to "Yes", and set the *Slider Min* to 0 and *Slider Max* to 1000 (with a slider step of 1).

2. Make a new [Flow] coming out of *Population*, called *Delta N*. In the properties window, set *Only Positive Rates* to "No". You should now see that the flow has an arrow on both ends. That is, this flow can either represent a [Flow In] or a [Flow Out]. It represents the change in *Population* each time step

(delta N!), which can either be positive or negative! [NOTE: the *tiny white triangle in one of the two arrow heads should be facing **out*** – this means that a positive value for the flow will mean an addition to the population and a negative flow will be a subtraction from the population]

3. Make a new [Variable] called *Max growth rate* (also known as $r_{max}$), and set it at 0.15. Make a link from *Max growth rate* to *Delta N*. Set *Show Value Slider* to "Yes", and set the *Slider Min* to 0 and *Slider Max* to 5.
4. Make a new [Variable] called *Carrying capacity* (also known as $K$), and set it at 650. Make a link from *Carrying Capacity* to *Delta N*.
5. Finally, open the equation editor for *Delta N* and type in the logistic growth equation (**Eq. 6**).
6. Run the simulation for 100 years (1-year time step) and make sure it behaves as expected- that is, it should exhibit logistic (S-shaped) growth and should level off at carrying capacity.

**QUESTIONS, Exercise 3:**

3a. Is carrying capacity a **stable equilibrium**? Explain your reasoning. [NOTE: you already addressed this in the 'population regulation' lecture page on Top Hat!] [HINT: remember, when testing if an equilibrium is stable or not, first initialize the population at the equilibrium point and verify that the population neither grows or declines. Next, 'perturb' the system by changing the initial abundance and run the model again to see if it returns to the equilibrium state!].

3b. Return the initial abundance to 10. Now start adjusting the value of *Max Growth Rate*. What do you notice as the maximum growth rate increases? Focus on the time series of population abundance over time. Can you identify different major changes in your 'abundance over time' plots as the growth rate increases from 1 to 5? You should be able to identify *at least* four unique patterns of population dynamics! Describe the patterns and the approximate thresholds at which change-overs occur from one pattern to the next. One of these patterns is known as **Chaos** (yes, that is the technical name)!! Can you figure out which pattern is known as chaos?? Provide *four plots* – one that illustrates each of the four unique patterns you identified.

**NOTE**: remember to copy the URL for your Insight, insert the URL in the appropriate place on Top Hat. And don't make any more changes to this insight once you have submitted it (clone it if you want to keep making changes)!

## Exercise 4: delayed density-dependence! [optional- not part of the 'official' lab]

What happens when the effects of resource competition are delayed? In this case, the effects of competition (reduction in fitness) will not manifest immediately- but will emerge later down the road!

Let's build on the previous model...

1. First, add a new [Variable] to the system, called *Delayed Abundance*, which will store an abundance value from a previous time step. Draw a new link from *Population* to *Delayed abundance* and from *Delayed abundance* to *Delta N* (you might need to curve your link arrow so it doesn't overlap with other objects on your canvas).
2. Add a new [Variable] to the system, called *Time Delay*. Set *Show Value Slider* to "Yes", and set the *Slider Min* to 0 and *Slider Max* to 5, and *Slider Step* to 1. Make a new link from *Time Delay* to *Delayed Abundance*
3. Open the equation window for *Delayed abundance*. This variable will store a previous value of *Abundance*, with the time delay set by *Time Delay*. To do this, use the following syntax (which you can access by clicking on "Delay" in the "Historical functions" menu within the equation editor):

```
Delay([Population], [Time delay], [Population])
```

The second "Population" in this function is there just to help the simulation get started (at time-step zero, there are no previous values of *Population*, so InsightMaker will use the initial value of "Population" instead).

4. Finally, modify the equation for *Delta N* so that *Delayed abundance* (not *Population*) is used in the density-dependent portion of the equation (1-N/K). Your equation should now look something like this:

```
[Population]*[Max growth rate]*(1-[Delayed abundance]/[Carrying Capacity])
```

**OPTIONAL QUESTIONS, Exercise 4: [NOTE: these are not part of the 'official' lab and do not count toward your Lab 2 grade]**

4a (optional). Run the model with different values for the time delay. How does the system behave with a time delay? Do you see any similarities with exercise 3?

4b (optional). Parasitoid wasps help to keep many lepidopteran populations in check. The wasps lay their eggs in caterpillars, and the caterpillars end up dying a horrific death as the wasp larva grows. Wasp parasitism on caterpillar populations often results in delayed density-dependence – which in turn results in oscillations in caterpillar populations. Can you think of why this might be the case? Explain your reasoning.

## Checklist for Lab 2 completion

Your lab answers and pertinent figures, tables and InsightMaker links (make sure they are public!) should be submitted in the Lab 2 quiz in Top Hat.

***Due Feb. 14 at midnight***

- Top Hat short answers
  - **Exercise 1**
    - *Short answer (1a.)*
    - *Short answer (1b.)*
  - **Exercise 2**
    - *Short answer (2a.)*
    - *Short answer (2b.)*
    - *Short answer (2c.)*
    - *Short answer (2d.)*
    - *Short answer (2e.)*
    - *Short answer (2f.)*
  - **Exercise 3**
    - *Short answer (3a.)*
    - *Short answer (3b.)*
- InsightMaker models
  - **Exercises 2,3 and 4**
    - Your models should show that you were able to create and specify your models correctly. This should be shared with your instructors in the appropriate place in the Top Hat quiz.