## Adding density-dependence in vital rates to a matrix model

This document describes the necessary steps for including density-dependence in a structured population model. For this tutorial, I assume that density-dependence has an effect on the underlying vital rates. The other option (not covered here) is to place a limit on the size of some classes. This document is also accompanied by worked R-examples (see below).

1. **Specify which demographic parameter(s) that are density-dependent, and further which stages in the matrix that are affected.**

For a structured population, it is possible for all stages to be dependent of some density, so for large matrices there are plenty of options where to include density-dependence. That is often unfortunate, since you need a lot of data for estimating density-dependence in a structured population. It is easier in an unstructured population, where only the growth rate of the population (or the underlying average birth and death rates) can be modeled as density-dependent. You’ll probably find that for your study species, there are uncertainties regarding density dependence. In some cases very little is known, and in some other (fortunate) cases density-dependence has been studied in at least some classes of the population. So you’ll probably have to rely on using general life-history theory and comparative studies that compares (similar) species. An educated guess is still better than not including density-dependence, if you think that it is operating… As usual, try different combinations of the strength of density-dependence, and which classes that are affected.

1. **Specify the shape of the density-dependence**

Density-dependence can be introduced in a multitude of ways, we have encountered for instance the Ricker-type and the Beverton-Holt model during the course (check handouts from the lecture on density-dependence!)

The Ricker function is:



The Beverton-Holt function is:



There are two important points here. First, which function that should be selected, and then you also have to decide the value of the parameter β that controls the strength of density-dependence. It is also necessary to know the value of the vital rate in the absence of density-dependence (Vital ratemax).

The Ricker function describes over-compensatory (or scramble competition), whereas the Beverton-Holt function describes compensatory (or contest competition). Review these concepts before you pick one of the functions. The Beverton-Holt function is usually used for territorial species where space is the limiting factor. The Ricker function is a better choice if the underlying process is resource depletion (such as oxygen depletion or competition among hatchlings for food).

Regarding the strength of the density-dependence, you’ll often find that β has not been estimated, and you then have to think of alternative strategies on how to proceed: is it to possible to compile data and estimate density-dependence, or is it necessary to rely on a combination of educated guesswork (maybe by using values estimated for another species) and trial and error? As always when data is limited (or non-existent), it is increasingly important to try different input values before you reach a final decision. This is even more important when you are working with non-linear functions such as the Ricker and Beverton-Holt models, since only a slight change in a parameter values can produce wildly different results. It is very important to plot the shape of the density dependence, and compare different values of β. β is usually a small number in the magnitude of 1/20 to 1/200.

1. **Plot the function so you know what it looks like, also plot the “recruitment curves”.**

This step shown is described in the R-script “Adding density-dependence to a matrix model.r”.

1. **Implement steps 1-3 in code.**

You have learnt to project an iterative equation by using for-loops. Adding density-dependence to your model requires some extra steps that have to be programmed *within* the for-loop. More specifically, the density-dependence effect has to be calculated at each step in the for-loop. The vital rate that is density dependent is hence called a dynamic rate, in contrast to non-varying rates that we refer to as static rates.

1. Sum the relevant density, i.e. which classes contributes to the density that each vital rate ”feels”. Are individuals in stage *i* only competing with other individuals in the same stage, or do they compete with individuals in other stages as well? It is extremely important to get this right! For instance, salmon eggs are only “competing” with other eggs, and not with salmon aged 1-5. The relevant density in this case would be the sum of all produced eggs (from all breeding stages) for calculation of the density-dependent survival rate. However, first year cormorants (birds) are likely to compete with birds of all other ages for food in winter, so here the relevant density is (most likely) the total population size.

Some important notes:

Let’s assume a pre-breeding census with three censused classes (1 year olds, 2 year olds and 2+ years), our model is further a female-only model where 2 year olds and 2+-individuals are reproductive. First, let’s assume that the density-dependent rate is juvenile survival. How should you calculate the density-dependent survival rate, if we assume that all individuals in the population compete over the same resource(s)? A common mistake (?) is to only summarize the number of individuals in the censused stages (three in this case), but such a procedure would ignore the 0-1 year-class segment of the populations, and hence the calculated value for the survival rate will be too high. In this case, you first have to calculate the total number of (female) offspring produced just after the census, and add this number to the sum of the number of individuals in the other classes.

If we assume the same basic structure for our model as above, but now let fecundities be density-dependent, we don’t have to take into account the 0-1 year class when calculating the fecundity rate (since individuals in this class are not yet born). Think of the timing of events. In a pre-breeding census, we assume that individuals are counted just before the census, and that the birth pulse follows immediately after the census. Mortality occurs only after the birth of new individuals, i.e. births occur before survival.

The situation is the opposite for a post-breeding census. Take our example with density-dependent juvenile survival, but now assume a post-breeding census. In this case, we census also the class 0-1 years old and we therefore know the total population size. It is not necessary to perform the extra step involving calculation of the total offspring production; we just take the sum of our stage vector **n**. However, if fecundities are density-dependent we must now calculate the number of individuals that have survived from our previous census and are “ready” to give birth just before our next census. The calculations of the density-dependent fecundities should be based on the sum of the number of individuals that have survived since our previous census (I assume here that is the density just before the birth pulse that determines reproductive output in this example, although you should be aware of that other biologically realistic hypotheses exists).

The key to get the model correct for both timing of census (pre- versus post-breeding) and inclusion of density-dependence is to understand when (in relation to the census) demographic events occur in time and which density that determines vital rates. You have to think very carefully about especially which density that the population “feels” – the notes above should not be considered as a general solution to a common problem, but rather as solutions to a particular situation. *When* density-dependence is manifested depends on the ecology of your study organism.

1. Calculate the new rate, dependent on the density calculated in step a, using the function from step 2.
2. Add the calculated, density-dependent vital rate to the correct position in the transition matrix **A**.
3. Perform the matrix multiplication, by multiplying the transition matrix **A** with the stage vector **n**.
4. Steps a-d are repeated for each time-step in the for-loop.

**Examples:**

This tutorial is accompanied by two R-scripts. Use particularly the first script as a blueprint for your own model:

**Adding density-dependence to a matrix model.r**

At the very top of this page, I have programmed the Ricker and Beverton-Holt functions. You can copy them and use them in your own code. What follow next is some graphs showing the general shape of the two functions, and then there are three examples. The first example has no density-dependence in it, and you should fully recognize how this model was set up. Example two adds density-dependence to first-year survival, and the third example displays how to add density-dependence in fecundity. These examples assume a pre-breeding census, and all density-dependent effects in the examples are of the Beverton-Holt form. The code is filled with comments, so hopefully you can use the examples to implement density-dependence in your model.

**Salmon\_density\_dependence.r**

This example shows the clear difference between over-compensatory and compensatory density-dependence. In other words, it displays that the Ricker (over-compensatory) and the Beverton-Holt (compensatory) models produces very different dynamics when fecundities are high. This should come as no surprise; we dealt with this in the beginning of the course (but for an unstructured population). I illustrated this in a lecture by showing you Robert May’s model for a discrete unstructured population. Remember that high growth rates can produce chaotic dynamics in discrete time.

The example deals with salmon, where egg survival has been found to be density-dependent (that is, dependent on only the total number of eggs produced by all spawning females). The models is a pre-breeding census with age classes 1-5. Female salmon can start to reproduce at ages 3 and reaches a maximum of 5 years in age. A female can only spawn once, and dies after the spawning event. Females aged 3-5 have an age-specific probability of spawning. This means that survival rates for ages 3-5 have to be adjusted for the age-specific probability of breeding, since a females dies right after spawning.

The code in this example is built by two for-loops, with the purpose of showing how population dynamics is increasingly different for the Ricker and Beverton-Holt function when fecundities increases (in this case, the initial fecundities are sequentially doubled for each run of the outer for-loop).