

# Homework 2: Density-dependent natural selection

---

## 1. The Beverton-Holt Equation

The logistic population growth model discussed in class is only one possible model of population growth. As we showed this model can have some illogical behaviour (chaos) and hence is not necessarily a good model for population dynamics in many systems. One common alternative model is the *Beverton-Holt Model* originally developed to describe the population dynamics of fish. One formulation of this model is as:

$$N(t+1) = N(t) + \lambda N(t) \frac{1}{1 + \alpha N(t)}$$

- A. What are the equilibria of this model and how does their stability depend on the model parameters?
- B. What are reasonable biological interpretations of the parameters  $\lambda$  and  $\alpha$ ?
- C. Consider the evolution of the parameter  $\alpha$  in a diploid population with a constant environment where the  $\alpha_{AA} = a$ ,  $\alpha_{Aa} = a(1-s)$  and  $\alpha_{aa} = a(1-2s)$ . Derive the selection coefficient for the  $A$  allele in this model. Is the  $A$  allele favoured or disfavoured?
- D. Derive the evolutionary equilibria of  $A$  allele using the model in part C. Is there any parameter conditions under which the population remains polymorphic?

---

## 2. Genotype-dependent survival

In class we assumed that all during hibernation a maximum number of  $N_0$  individuals survived hibernation and that survival was independent of genotype. Let's assume instead that neither  $r$  alleles nor  $K$  alleles survive well such that the probability of hibernation survival is greatest for the heterozygotes  $Aa$  and reduced for the  $AA$  and  $aa$  alleles. Such that the relative probabilities of accessing one of the limited number of hibernation spots  $S_x$  is:

$$S_{AA} = 1 - v \quad S_{Aa} = 1 \quad S_{aa} = 1 - v$$

- A. Draw a life cycle diagram for this model. Use the same order of events assumed in class.
- B. What are the recursion equations describing the evolutionary dynamics?
- C. Is there a polymorphic equilibrium to this model (don't worry about its stability)? If so, pick a value of  $v$ , how does the extent of polymorphism (as measured by heterozygosity  $H = 2p(1-p)$ ) compare with the model without genotype-dependent survival?
- D. Explain why your answer to C. makes sense biologically.

---

## 3. El Nino/La Nina Fluctuations

In class we focused on a model of environmental fluctuation that was motivated by hibernation but this is only one biological motivation. What if instead we are modelling the evolution of a population to El Niño/La Niña cycles? There are approximate two El Nino years followed by one La Nina year (with colder/wetter weather in Canada). To model this assume that in El Nino years the carrying capacity is multiplied by a factor  $(1 + \alpha)$  whereas in La Nina years it is multiplied by a factor  $(1 - \alpha)$  assuming  $\alpha > 0$ .

- A. Build an population dynamic model of El Nino/La Nina.
- B. What is the "effective carrying capacity" of the system?
- C. Using the result from class do you think there will be a polymorphic equilibrium for the  $r/K$  alleles? If so, do you think heterozygosity will increase or decrease with  $\alpha$  and why?