

## Chapter 2

# Population dynamics

*A finite world can support only a finite population; therefore, population growth must eventually equal zero.*      Garrett Hardin

### 2.1 Introduction

Evolution is ultimately a population dynamic process, hence we will study how populations change over time. A **population** at a given point in time is a set of conspecific individuals (individuals of the same species). Each individual in a population can be characterized by its genotype (and thus phenotype), which determines how the individual acts and reacts to its environment throughout its entire lifespan. Both the number of individuals and the frequency of genotypes (and thus phenotypes) will change over time as a result of various forces. The change in population size is usually studied in **demography** and **ecology**, while the change in the composition of types is the focus of **population genetics**. But the two processes generally interact leading to eco-evolutionary feedback. Hence, to obtain an understanding of evolution requires to understand the forces changing both the number of individuals and their types as time passes by.

A good place to start our analysis of evolutionary forces is to focus only on understanding how population size changes over time: this is the study of **population dynamics** addressed in this chapter. We will analyze changes in population size assuming that individuals are asexual, since all the main ideas can be introduced using this simple case. We make the assumption that time is discrete, such that a unit of **demographic time** could represent any time interval relevant to the species under study (being a day, a month, a year, etc...). We then denote by  $n_t$  the number of individuals in a **parental generation** at time  $t = 0, 1, 2, 3, \dots$ . Our aim is to evaluate the number of individuals  $n_{t+1}$  in the next demographic time period  $t + 1$ ; that is, in a **descendant generation**. The change in the number of

individuals over a demographic time period is expressed as

$$\Delta n_t = n_{t+1} - n_t, \quad (2.1)$$

where the symbol  $\Delta$  is the forward difference operator. We thus view the population as a **discrete dynamical system** (see Appendix 1 for a dynamical system refresher). For simplicity of presentation, the change in population size will often be denoted

$$\Delta n = n' - n, \quad (2.2)$$

without any explicit time index. Thus, throughout these lecture notes and the course's slides, a variable without any time index (e.g.,  $n$ ) is by default considered at some **parental generation**  $t$ , and we use a prime  $'$  to denote that variable (e.g.,  $n'$ ) in the next time period; namely the **descendant generation** at  $t + 1$ .

## 2.2 Fitness

We will first consider deterministic population dynamics (chance or stochastic effects will be discussed in a later chapter) so that population size  $n$  is real valued and either positive or zero ( $n \in \mathbb{R}_+$ ). To describe how the number of individuals deterministically changes over time, we introduce the **fitness** of a representative or focal individual in the population. Fitness, denoted  $w$ , is defined as the expected number of individuals “produced” over one demographic time period by the focal individual, possibly including self when it survives. It is thus also a real valued variable that can only be positive or equal to zero ( $w \in \mathbb{R}_+$ ). We have that

$$w = s + f_e, \quad (2.3)$$

where  $s$  is the **survival probability** over a demographic period, while  $f_e$  is the **effective fecundity**, i.e., the expected number of offspring produced by an individual that survive to the next demographic time period. Survival and fecundity are collectively referred to as **vital rates**.

While in general different individuals can have different fitnesses, we assume in this chapter that each individual in the population has exactly the same fitness  $w$ . We call this a **monomorphic** population. In such a population, all individuals have the same phenotype and thus have equal survival and reproductive capabilities, meaning equal fitness.

When each and every individual in the population has the same fitness  $w$ , then the number of individuals in the descendant generation given parental population size  $n$  is

$$n' = wn, \quad (2.4)$$

since the right-hand side counts the number of individuals in the parental population that all have fitness  $w$ , thereby giving a total number  $wn$  of individuals in the descendant generation.

Substituting eq. (2.4) into eq. (2.2), then using eq. (2.3), we see that the change in population size over one demographic time period is

$$\Delta n = (w - 1)n = \left( \underbrace{f_e}_{\text{birth}} - \underbrace{(1 - s)}_{\text{death}} \right) n. \quad (2.5)$$

This shows that population size will grow over one time period ( $\Delta n > 0$ ) when fitness is larger than one ( $w > 1$ ) and will decline ( $\Delta n < 0$ ) if fitness is lower than one ( $w < 1$ ). In other words, population size increases if the per capita number of successful births,  $f_e$ , exceeds the per capita probability of death,  $1 - s$ .

## 2.3 Modes of population dynamics

### 2.3.1 Density-independent growth

When material resources available to each individual are unlimited in a monomorphic population, neither survival nor effective fecundity will be affected by population number. Then, the fitness of each individual will be completely independent of population size  $n$  and, therefore,  $w$  is a constant for all time, say  $w = 1.5$  or  $w = 4$ . The equation  $n' = wn$  (eq. 2.4) then says that in each time period, population size is multiplied by a constant factor, which results in **density-independent** population dynamics with far reaching consequences, as will be next demonstrated.

If we now explicitly introduce the time index  $t$  (hence population dynamics is described by  $n_{t+1} = wn_t$ ), and population size takes the initial value  $n_0$  at time  $t = 0$ , then its values in subsequent time periods is

$$\begin{aligned} n_1 &= wn_0 \\ n_2 &= wn_1 = wwn_0 = w^2n_0 \\ n_3 &= wn_2 = wwn_1 = wwnn_0 = w^3n_0 \\ n_4 &= wn_3 = wwn_2 = wwnn_1 = wwnn_0 = w^4n_0 \\ &\dots \end{aligned} \quad (2.6)$$

This implies that, in general, we have

$$n_t = w^t n_0,$$

which shows that population size changes at an **exponential rate** (or geometric rate). If  $w < 1$ , the population decreases and goes extinct asymptotically at an exponential rate. By contrast, if  $w > 1$  population size grows at an exponential rate, which is marked by an explosive population growth.

### 2.3.2 Density-dependent growth

Natural populations cannot maintain infinite exponential growth and fitness must ultimately depend on the number of individuals. Several factors can produce a negative feedback between population size and fitness, and they can all be summarized by the two following broad categories of factors:

- **Competition for material resources.** This is a consequence of the fact that available material resources per individual decreases as the number of individuals increases.

- **Competition for space.** This is a consequence of the fact that available space per individual decrease as the number of individual increases.

Hence, owing to one of these two factors population size will eventually be regulated by **density-dependent competition**.

#### Competition for material resources

One of the simplest form of density-dependent competition is given by the so-called Beverton-Holt model of **intraspecific competition** (competition between individuals from the same species) with fitness taking the form

$$w(n) = \frac{f}{1 + \gamma n}, \quad (2.7)$$

where fitness  $w(n)$  is now written as a function of  $n$  since it depends explicitly on population size. Here,  $f \geq 0$  is the maximum fecundity that an individual can have in the absence of density-dependent competition. The denominator  $1 + \gamma n$  captures the effect of density-dependence where  $\gamma \geq 0$  is a parameter tuning its strength. As  $\gamma$  increases given a fixed  $n$ , the term  $1 + \gamma n$  increases, which thus decreases fitness. Likewise, for a fixed  $\gamma$ , an increase in  $n$  decreases fitness and this decrease can be very rapid. One way to justify the functional form of density-dependent competition displayed in eq. (2.7) is to assume that the fecundity of individuals is limited by time to process material resources (e.g., killing preys, digesting them, making new cells), and that these resources come in finite amount so that individuals in the population compete for them (see Appendix 2).

With density-dependent fitness, the number of individuals in the descendant generation and the change in population size are, respectively, given by

$$n' = w(n)n \quad (2.8)$$

and

$$\Delta n = (w(n) - 1)n. \quad (2.9)$$

From this, we can further evaluate the population **equilibria**, which are the values of  $n$ , usually denoted  $n^*$ , such that there is no longer any population change:  $\Delta n = 0$  (see also

Appendix 1 for a refresher on the notation of equilibrium). Then, the population is in a steady-state; that is, in an equilibrium state. We can see from eq. (2.9) that there are two types of equilibria. First, one in which population size is extinct,  $n^* = 0$ , and which is called the **trivial equilibrium**. Any other equilibrium satisfies

$$w(n^*) = 1, \quad (2.10)$$

which means that for any individual in the parental generation, a single individual reaches adulthood in the descendant generation. This is the usual equilibrium to which a population will converge in the long run, and such an equilibrium can be found by solving eq. (2.10) for  $n$ . At this point, the population growth rate is zero.

For the Beverton-Holt model the trivial equilibrium is **unstable** if maximal fecundity exceeds one ( $f > 1$ ), which means that the population will grow if each individual produces more than at least one individual. The population will then converge towards the equilibrium

$$n^* = \frac{f - 1}{\gamma} \quad (2.11)$$

(obtained by substituting eq. (2.7) into eq. (2.10) and solving for  $n^*$ ). This is called the population **carrying capacity**, which is the maximum population size that the environment can sustain and is **stable** if  $f > 1$ .

The explicit time dependent solution to the Beverton-Holt model must satisfy  $n_{t+1} = w(n_t)$  (not that we have now re-introduced time index) and using iterations like in eq. (2.6) (see Appendix 3), we find that

$$n_t = \frac{f - 1}{\gamma + k \left(\frac{1}{f}\right)^t}, \quad (2.12)$$

where

$$k = \frac{\gamma}{n_0} \left[ \frac{f - 1}{\gamma} - n_0 \right] \quad (2.13)$$

characterizes growth behavior depending on whether the initial population size  $n_0$  is larger or smaller than the carrying capacity. If  $k > 0$ , then population size is initially below carrying capacity and will grow towards it (if  $f > 1$ ) following a sigmoid curve (Fig. 2.1). If  $k < 0$ , the initial population size is above the carrying capacity and will then return to it. Note that if we let  $t \rightarrow \infty$  in eq. (2.12) for  $f > 1$ , we recover eq. (2.11), as we should.

As can be seen from Fig. (2.1), when population size is initially low, growth is exponential. The change in population size,  $\Delta n$ , over a demographic time step thus increases like in the absence of density-competition at first. As population size increases, the effect of density-dependent competition eventually kicks in. Then, the change in population size decreases giving rise to an *S*-shaped **sigmoidal growth**. Hence, the change in population size,  $\Delta n$ , as a function of  $n$  is a dome-shaped curve (see lecture slides), first increasing, then decreasing and eventually hitting the point where no change occurs at the value of population size where the fitness is one ( $w = 1$ ), i.e., at the carrying capacity  $n^*$ .

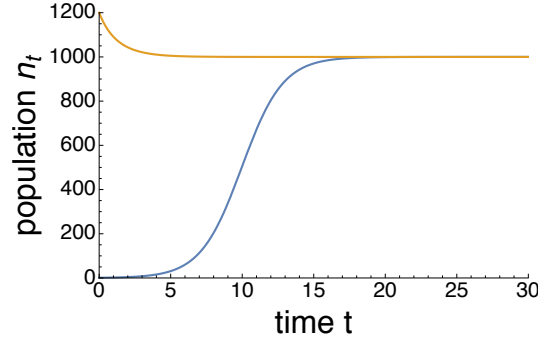


Figure 2.1: Time dynamics of population size  $n_t$  for the Beverton-Holt model (fitness given by eq. 2.7) with  $n_0 = 1$  (blue) and  $n_0 = 1200$  (yellow), while  $f = 2$ , and  $\gamma = 0.001$ .

### Competition for space

We now turn to a model of competition for space. We assume that there is a fixed number  $n_{\max}$  of habitable sites in the population for which individuals compete. We consider that in the population the individuals follow a **life-cycle**, which describes the changes and events an organism undergoes during its lifespan. The following events occur in cyclic order. (1) Each of the  $n$  adult produces a number  $f$  of offspring. This number is assumed to be much lower than the total number of sites ( $f \ll n_{\max}$ ). (2) Each adult survives with probability  $s$  to the next period. (3) Offspring compete at random for any of the  $n_{\max}$  breeding sites but loose against surviving adults. This is an example of an **iterparous** life-cycle where individuals can reproduce multiple times. Note that there is a staggering diversity of other life-cycles in natural populations, among which **semelparous** life-cycles where individuals reproduce only once.

From the life-cycle assumptions, the fitness of an individual is

$$w(n) = s + \left(1 - \frac{sn}{n_{\max}}\right) f, \quad (2.14)$$

which is the sum of the survival of an individual and its effective fecundity. The expression for effective fecundity can be understood as follows. On average  $sn$  adults survive, which constitutes a fraction  $sn/n_{\max}$  of population space. This means that  $1 - sn/n_{\max}$  is the fraction of open space in the population when there are  $n$  adult individuals, and it gives the probability that an offspring will succeed and settle in a site. Effective fecundity is the sum of this probability over each offspring. This holds as long as  $f$  is much lower than the total number of sites ( $f \ll n_{\max}$ ), and space is filled up gently by offspring production.

The effect of density-dependent competition is measured under competition for space by  $1 - sn/n_{\max}$ . As under the Beverton-Holt model for material resource competition, the

fitness of an individual thus decreases as population size increases, the decrease being here linear. Let us substitute eq. (2.14) into the first term of eq. (2.9) and solve (numerically) for the number of individuals  $n_t$  at time  $t$ . We then find that the growth of the number of individuals follows a sigmoid curve (Fig. 2.2), exactly as in the Beverton-Holt model. This stems again from the fact that growth is exponential when there are initially few individuals, because  $sn/n_{\max}$  is close to zero. Eventually, density-dependence comes into effect and decreases the change in population size,  $\Delta n$ , to the point where it is zero and fitness is equal to one ( $w(n^*) = 1$ ). Solving this for  $n$  by using eq. (2.14) we find that the equilibrium population size is

$$n^* = n_{\max} \left( \frac{f + s - 1}{fs} \right). \quad (2.15)$$

This equilibrium increases with fecundity (Fig. 2.2), which results in more sites becoming occupied per unit time and thus larger overall population size.

Finally, we note that the qualitative population dynamics features displayed in Fig. 2.1 and Fig. 2.2 are general to density-dependent growth models, and not specific to particular situations.

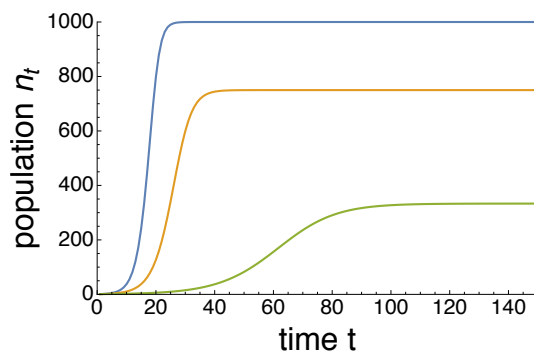


Figure 2.2: Time dynamics of population size  $n_t$  under competition for space (fitness given by eq. 2.14) with parameter values  $n_0 = 1$  (initial conditions),  $n_{\max} = 1000$ ,  $s = 0.5$ ; and  $f = 1$  (blue),  $f = 0.8$  (yellow), and  $f = 0.6$  (green).

## 2.4 Appendix

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**Appendix 1.** Here, we briefly recall the notion of a dynamical system. This is a system that from a certain **state** develops into another state over the course of time. Examples of a state include the amount of petrol in an oil field, the GDP of a country, the number of fish in a lake, or, as we will later often encounter, the frequency of an allele in a population. We can denote by  $x_t$  the state of the system at time  $t = 0, 1, 2$ , (an example of  $x_t$  is population size  $n_t$ ). Then, for any time point  $t$ , we write the system at the next time point as

$$x_{t+1} = f(x_t), \quad (2.16)$$

where the function  $f$  takes for input the state of the system at time  $t$  and returns as an output the state of the system at the next time period. The function  $f$  thus determines the dynamics of the system (when the state of the system is population size  $x_t = n_t$  the function is  $f(n_t) = w(n_t)n_t$ , i.e., eq. 2.8). Therefore, starting with the initial condition  $x_0$ , we can apply the function once to obtain state  $x_1 = f(x_0)$ , apply the function again to get the state,  $x_2 = f(x_1)$ , and so on to determine all future states. We end up with a sequence of states,  $x_0, x_1, x_2, x_3, \dots$ , called the **trajectory** of the dynamical system. Of special interest is what happens with the system after a long period of time (say as  $t \rightarrow \infty$ ), namely, the **asymptotic** properties of the system. The simplest kind of behavior, and the only one we encounter in this course, is that the system concentrates on an equilibrium point, or fixed point. An **equilibrium** is a point that is asymptotically time invariant so that we can set  $\lim_{t \rightarrow \infty} x_t = \lim_{t \rightarrow \infty} x_{t+1} = x^*$ . Thus, we deduce from eq. (2.16) that an equilibrium point satisfies

$$x^* = f(x^*), \quad (2.17)$$

where this equation can have several solutions (there can be multiple equilibrium points). It is also natural to ask whether for any such equilibrium a change in the state of the system will result in the return of the system towards the equilibrium. When this happens, we say the equilibrium is **stable**, since nearby trajectories converge to it. When the system does not return to the equilibrium it is called **unstable**.

Equation (2.16) for the iteration of the dynamical system can also be regarded as a difference equation

$$\Delta x_t = x_{t+1} - x_t = f(x_t) - x_t, \quad (2.18)$$

which allows to evaluate the sequence of change of states of the system  $\Delta x_0, \Delta x_1, \Delta x_2, \dots$ . More specifically, this allows to determine whether  $\Delta x_t$  is positive (so that  $x_t$  grows at  $t$ ) or negative (so that  $x_t$  shrinks at  $t$ ) at any time point, a perspective that is useful in evolutionary dynamics. At an equilibrium point, there is no change in the system and thus

$$\Delta x^* = f(x^*) - x^* = 0, \quad (2.19)$$

which is only another way of writing eq. (2.17).

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**Appendix 2.** We here provide a justification for the Beverton-Holt model (eq. 2.7) based on behavioral considerations. Suppose  $r_e$  is the amount of resources an individual consumer can find per unit time searching. The consumer may have difficulties handling the resource once found; it needs to be approached, killed, and digested. This takes time and we denote by  $T_h$  the time used to handle a unit of resource (e.g., killing, eating, digesting). Since for each unit of time spent searching,  $r_e$  resource items are found, the handling time per unit searching time is therefore  $r_e T_h$ , and the time needed to *discover and handle*  $r_e$  units of resource is  $1 + r_e T_h$ . Hence, the resource uptake  $c$  (consumption) per unit time is

$$c = \frac{r_e}{1 + r_e T_h}, \quad (2.20)$$

which is a so-called Holling type two *functional response*. If individuals compete for resources in a monomorphic population (i.e., all have equal strength and anything else), then the total amount of resources in the environment should be shared equally between all individuals and a plausible assumption for this is that the amount of resources obtained by a single individual is inversely proportional to the total number  $n$  of individuals in competition. Hence, we can write  $r_e = \alpha/n$  for some parameter  $\alpha > 0$  that takes into account resources abundance, discovery rate of the resource or any other feature affecting resource extraction. Substituting  $r_e = \alpha/n$  into eq. 2.20 and letting fitness in the Beverton-Holt model (eq. 2.7) be proportional to consumed resources, we have

$$w(n) = \varphi c = \varphi \frac{\alpha/n}{1 + (\alpha/n)T_h} = \frac{\varphi}{\frac{n}{\alpha} + T_h} = \frac{\varphi/T_h}{\frac{n}{\alpha T_h} + 1} \quad (2.21)$$

where  $\varphi$  is the conversion factor of consumed resources into offspring number. The third equality is obtained by multiplying both the numerator and the denominator by  $n/\alpha$  (which means the whole expression is multiplied by 1), and the fourth equality is obtained by multiplying both the numerator and the denominator by  $1/T_h$ . The last term in eq. 2.21 shows that eq. 2.21 defines a Beverton-Holt model with  $f = \varphi/T_h$  and  $\gamma = 1/(\alpha T_h)$ .

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**Appendix 3.** We here prove eq. (2.12). If population size takes the initial value  $n_0$  at time  $t = 0$ , its value in subsequent time periods in the Beverton-Holt model is given by iterating  $n_{t+1} = w(n_t)n_t$  with  $w(n_t) = f/(1 + \gamma n_t)$  such that

$$\begin{aligned} n_1 &= \frac{f n_0}{1 + \gamma n_0} = \frac{n_0}{\frac{1}{f} + \frac{1}{f} \gamma n_0} \\ n_2 &= \frac{f^2 n_0}{1 + (1 + f) \gamma n_0} = \frac{n_0}{\frac{1}{f^2} + (\frac{1}{f^2} + \frac{1}{f}) \gamma n_0} \\ n_3 &= \frac{f^3 n_0}{1 + (1 + f + f^2) \gamma n_0} = \frac{n_0}{\frac{1}{f^3} + (\frac{1}{f^3} + \frac{1}{f^2} + \frac{1}{f}) \gamma n_0} \\ &\dots, \end{aligned} \quad (2.22)$$

which implies that, in general, we have

$$n_t = \frac{n_0}{\left(\frac{1}{f}\right)^t + \left(\left(\frac{1}{f}\right)^t + \dots + \frac{1}{f}\right) \gamma n_0} = \frac{n_0}{\left(\frac{1}{f}\right)^t + \left(\left(\frac{1}{f}\right)^t - 1\right) \frac{\gamma n_0}{1-f}}, \quad (2.23)$$

where the second equality follows from the property of geometric series:  $\sum_{i=1}^t 1/x^i = ((1/x^t) - 1)/(1 - x)$ . Rearranging the last equation produces eq. (2.12).

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