Population dynamics

Population dynamics (or demography)

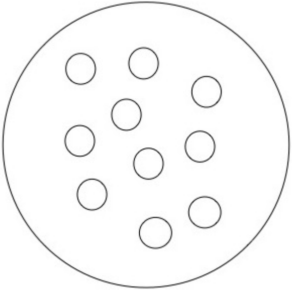
- This is the study of the change in the number of individuals in a population.

- It underlies evolutionary dynamics which is ultimately a population dynamic process (a multiplicative process) where entities reproduce differentially.

- Population dynamics is a good starting point to understand evolutionary dynamics.

The population

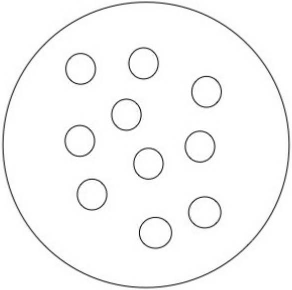
A population at a given point in time is a set of conspecific individuals.



We denote by n the total number of individuals in the population.

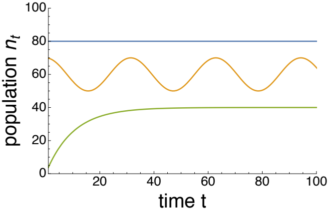
The population

The concepts of population dynamics we will study apply to any population. That is, any organism, human or otherwise.



The aim: describing population dynamics.

Question: how does the number n_t of individuals in a population depend on (demographic) time t?[1]



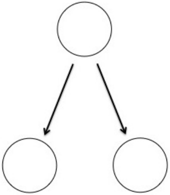
The x-axis represent time t and the y-axis represents population size n_t at time t. Different possible population size trajectories are displayed.

Aim: describing the main "laws" behind population dynamics, i.e., how population size varies as a function of time.

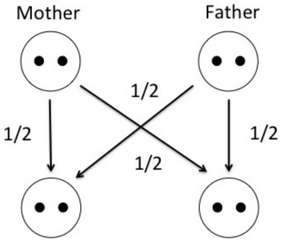
[1] A unit of (demographic) time depends on the situation at hand e.g., it could be one minute, a month, a year, etc. and we always consider discrete time in the course

Assumption 1: asexual reproduction

To introduce the main population dynamics concepts we focus on asexual reproduction[2], as this does not result in a loss of generality.



Asexual reproduction



Sexual reproduction (meiosis followed by syngamy)

[2] Asexual reproduction is the production of offspring with genetic material coming from a single parent, while sexual reproduction involves the joining of the genetic material of two parents.

Polymorphic populations

Usually populations are polymorphic.

Black morph of the beetle *Adalia bipunctata*

Red morph of the beetle *Adalia bipunctata*

Polymorphic populations

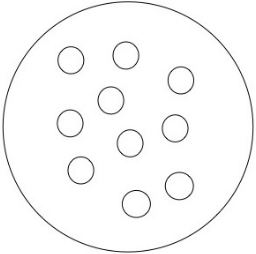
Usually populations are polymorphic.

Aborigine morph of the the hominin *Homo sapiens*

Spaniard morph of the hominin *Homo sapiens*

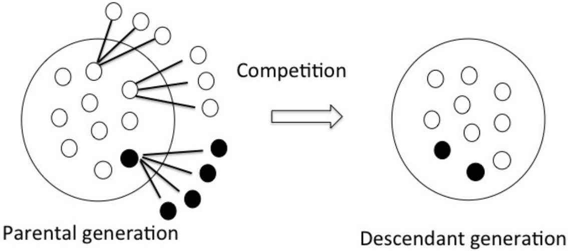
Assumption 2: we consider for now a monomorphic population

All individuals will be assumed to be the same (they are of the same type, they have the same genotypes and phenotypes). This is called a monomorphic population.



Fitness

The central quantity to study population dynamics is individual fitness.



Fitness is the expected number of successful descendants of an individual possibly including itself after a reproductive time step, going from a parental to a descendant (or offspring) generation

Fitness

We denote by w the fitness[3] of a typical (or focal) individual in the population. This consists of two terms

$$w = s + f_{\mathrm{e}}$$

- s is the survival probability the individual.
- f_{e} is the effective fecundity of the individual; namely, the expected successful number of offspring produced over one time step.

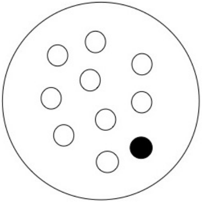
In most populations fecundity is much larger than effective fecundity, e.g., number of pollen grains or number of tadpoles produced is way larger than the number of them surviving.

[3] Fitness w is a real valued variable that is positive or zero ($w \in \mathbb{R}_+$). It should be thought as the expected (or average) number of offspring descending from an individual.

Fitness

The (expected) fitness of an individual is

$$w = s + f_{\mathrm{e}}$$



- Both s and f_{e} are often called vital rates.
- In general both s and f_{e} will depend on the population (e.g., behavior or phenotypes of all individuals in the population).

Population dynamics: general considerations

Given parental population size n_t, the number of individuals in the descendant generation (i.e., in the next demographic time period) is

$$n_{t+1} = w_t n_t$$

since the right-hand side counts the number of individuals in the population that all have fitness w_t at time t (monomorphic population), whereby $w_t n_t$ gives the total number of individuals in the descendant generation.

- The unit of demographic time we take is that between two typical reproductive events.[4]
- The above equation is an example of a dynamical system.

[4]For bacteria, the doubling time can be as short as 20 minutes so this can be taken as the length of a demographic period, for annual plants that reproduce once a year the unit of demographic time is one year. Human reproduce continuously so a relevant time interval is that between two census.

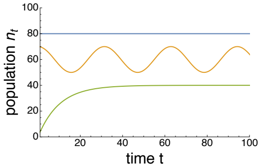
Population dynamics: the quintessential dynamical system

A dynamical system is a system that from a certain state develops into another state over the course of time. In population dynamics the state is population size. For any time point t, we write the system at the next time point as

$$n_{t+1} = g(n_t),$$

where the function g takes for input population size at time t and returns as an output the population size at the next time period.

Starting with the initial condition n_0, we can apply the function once to obtain state $n_1 = g(n_0)$, apply the function again to get the state, $n_2 = g(n_1) = g(g(n_0))$, and then the state $n_3 = g(n_2) = g(g(g(n_0)))$, and so on to determine all future states. We end up with a sequence of states, $n_0, n_1 =, n_2, n_3 \ldots$, called the trajectory of the dynamical system.



Population dynamics: general considerations

The equation for population dynamics is

$$n_{t+1} = \underbrace{w_t n_t}_{g(n_t)}$$

entails that:

- The population will grow in size ($n_{t+1} > n_t$) over one time period when the fitness is larger than one ($w_t > 1$).
- The population size will decline in size ($n_{t+1} < n_t$) when fitness is lower than one ($w_t < 1$).

We cannot say more without making more specific assumptions.

Density-independent growth

Assumption: $w_t = w$ is a constant for all time.

Hence, given some initial condition n_0, we have from

$$n_{t+1} = wn_t$$

that

$$\begin{aligned}
n_1 &= wn_0 \\
n_2 &= wn_1 = w(wn_0) = w^2 n_0 \\
n_3 &= wn_2 = w(wn_1) = ww(wn_0) = w^3 n_0 \\
&\dots
\end{aligned}$$

which implies

$$n_t = w^t n_0.$$

Density-independent growth

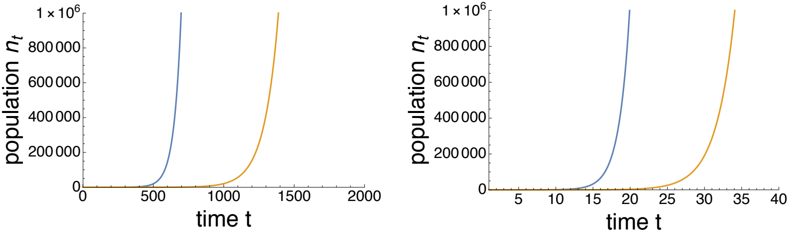
Under density-independent growth the number of individuals at time t given initial condition n_0 is

$$n_t = w^t n_0$$

- If $w = 1$, population size remains constant.
- If $w > 1$, population size grows. And it does so exponentially (or geometrically) fast.
- If $w < 1$, population size declines. And it does so exponentially fast.

Density-independent: time dynamics

Exponentially fast is lightening fast.

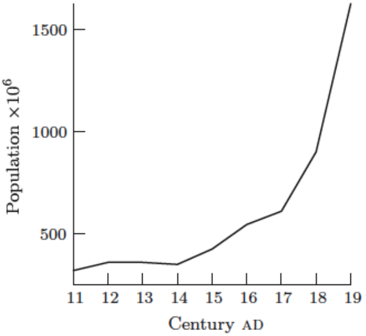


On the left panel, parameter values are $w = 1.02$ (blue) and $w = 1.01$ (yellow). On the right panel, they are $w = 2$ (blue) and $w = 1.5$ (yellow).

The bacteria *Escherichia coli* divides about every 20 minutes in the laboratory. Hence, $w = 2$ over such a demographic time period.

Density-independent growth in human population

The human population typically exhibited exponential growth over the last centuries.



Human population growth. The current expected fitness (per year) is approximatively $w = 1.011$.

Density-dependent growth

Real life: w is likely to dependent negatively on population size. Resources are limiting because individuals must share the same resource base, which is finite.

Density-dependent growth

Real life: w depends negatively on population size. Resources are limiting because individuals must share the same resource base.

Two fundamental resources for which individuals compete:

1. Competition for material resources (energy). Foraging success can further be affected by interference and aggression.
2. Competition for space (reproductive territories).

Density-dependent growth: Beverton-Holt model

Real life: fitness depends on population size and so we write it as $w(n)$.

One of the simplest form of (negative) density-depend competition for material resources is the Beverton-Holt model[5]

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

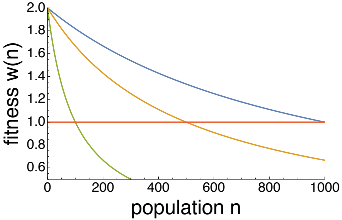
where $f \geq 0$ is the maximal fecundity (physiologically constrained) an individual can have in the absence of density-dependent competition (when resources are plentiful) and $\gamma \geq 0$ is a parameter tuning the importance of density-dependence.

[5] This model is of the form $w(n) = f_{\mathrm{e}}(n)$ with zero survival probability.

Beverton-Holt model: negative density-dependence

Fitness is decreasing with the number of individuals in the population.

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



Parameters values $f = 2$ and $\gamma = 0.01$ (green), $\gamma = 0.002$ (yellow), and $\gamma = 0.001$ (blue).

- The larger γ the stronger density-dependent competition and thus the reduction in fitness.
- Population size is thus a regulating variable of the population. Another regulating variable are microbes that kill.

Beverton-Holt model: justification

The model can be justified[6] by assuming that an individual has a limited time to catch and consume preys and that there is competition for preys.

- It takes time to search and handle preys. (time is also a limiting resource but for which individuals do not compete).
- The amount of prey available per individual is limited and likely to be proportional to $1/n$.

Then the density-dependence parameter γ will depend on various parameter describing catching, and handling preys and energy conversion efficiency into offspring.

[6] See the lecture notes for details

Change in population size

Let us now analyze population dynamic in the Beverton-Holt model. To do this it is useful to understand how population size changes over on demographic time period.

Given parental population size n_t, the change in population size over one time period is

$$\Delta n_t = n_{t+1} - n_t$$

- The symbol Δ is used to denote a difference and thus measures the change in population size over one demographic time period.

- This change Δn_t can be zero, positive, or negative.

Change in population size

To denote the change in population size, we will often use the simpler notation

$$\underbrace{\Delta n}_{\Delta n_t} = \underbrace{n'}_{n_{t+1}} - \underbrace{n}_{n_t}$$

to represent $\Delta n_t = n_{t+1} - n_t$ so that throughout the whole course a variable without any time index (e.g., n) is by default considered at some parental generation and a prime $'$ is used to denote that variable in the descendant generation (e.g., n'). You should thus think as n being population size at time t and n' as population size at $t + 1$.

Interesting points are equilibrium points where there is no change:

$$\Delta n = 0$$

An equilibrium point can be stable or unstable.

Change in population size

Since $n' = w(n)n$ and $\Delta n = n' - n$, we have that the change in population size is

$$\Delta n = w(n)n - n$$

which is equivalent to

$$\Delta n = (w(n) - 1)n$$

Hence

- If $w(n) > 1$, the change in population size Δn is positive ($\Delta n > 0$).
- If $w(n) < 1$, the change in population size Δn is positive ($\Delta n < 0$).

Beverton-Holt model: change in population size

For the Beverton-Holt model fitness is

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

and so the change $\Delta n = (w(n) - 1)n$ in population size is

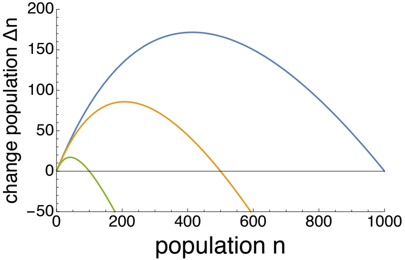
$$\Delta n = \left(\frac{f}{1 + \gamma n} - 1 \right) n$$

Note that the change in population size is a function of n.

Beverton-Holt model: change in population size

The change Δn in population size is

$$\Delta n = \left(\frac{f}{1 + \gamma n} - 1 \right) n$$

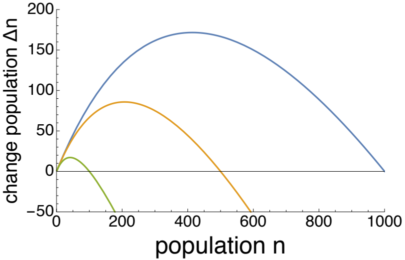


Parameters values $f = 2$ and $\gamma = 0.01$ (green), $\gamma = 0.002$ (yellow), and $\gamma = 0.001$ (blue).

Growth in population first increases, then reaches at maximum at intermediate population size and eventually vanishes.

Beverton-Holt model: equilibrium points

- No change when $\Delta n = 0$.
- This obtains when $n = 0$ and $n = 100$ (for $\gamma = 0.01$), $n = 500$ (for $\gamma = 0.002$), and $n = 1000$ (for $\gamma = 0.001$).
- These are the equilibrium points of the model.



Parameters values $f = 2$ and $\gamma = 0.01$ (green), $\gamma = 0.002$ (yellow), and $\gamma = 0.001$ (blue).

The point $n = 0$ is unstable and $n = 1000$ is stable.

Equilibrium point 1: on the boundary of the state space[7]

An equilibrium point, generally denoted n^*, satisfies

$$\Delta n^* = (w(n^*) - 1)\, n^* = 0$$

This thus characterizes a steady-state and is always satisfied by

$$n^* = 0$$

- This is the point were population is extinct and is often called the trivial equilibrium.
- This point is unstable if $f - 1 > 0$, since a single individual then produces more than one individual and the population grows in size.

[7] The state space is the the space of different values the system can take, here all values of population size (formally the set $\mathbb{R}_+$ of positive real numbers).

Equilibrium point 2: in the interior of the state space

An equilibrium point satisfying

$$\Delta n^* = (w(n^*) - 1)\, n^* = 0$$

is also satisfied when

$$w(n^*) = 1$$

- Here fitness is equal to one.
- This is the point were population size is positive and no longer changes.

Beverton-Holt model: equilibrium points

To obtain the non-trivial equilibrium for the Beverton-Holt model, we set

$$w(n^*) = \frac{f}{1 + \gamma n^*} = 1$$

and solve for n^*, which gives

$$n^* = \frac{f - 1}{\gamma}$$

Beverton-Holt model: carrying capacity

The equilibrium population size

$$n^* = \frac{f-1}{\gamma}$$

is the population carrying capacity.

- This is the population size the environment can sustain given all constraints on reproduction and survival.
- This depends on biotic and abiotic features.

Beverton-Holt model: time dynamics

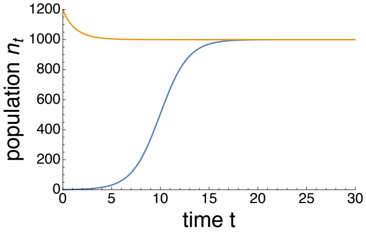
Iterating $n_{t+1} = w(n_t)n_t$, the Beverton-Holt model can be solved explicitly as a function of time. It dynamics displays the consequences of the features we just discussed.

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

where

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

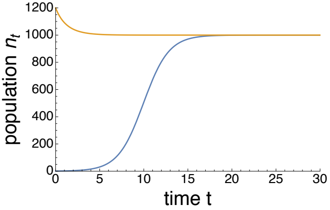
determines the initial conditions and depends on the parameters.



We have $f = 2$, $\gamma = 0.001$, and $n_0 = 1$ (blue) and $n_0 = 1200$ (yellow).

Because $1/f < 0$ as $f > 1$, we have that $(1/f)^t \to 0$ and so in the long run, as $t \to \infty$, the population converges to the carrying capacity ($\lim_{t\to\infty} n_t = (f-1)/\gamma$).

Beverton-Holt model: summary of the dynamics



We have $f = 2$, $\gamma = 0.001$, and $n_0 = 1$ (blue) and $n_0 = 1200$ (yellow).

- The point $n = 0$ is unstable if $f > 1$, the population then grows and growth is initially exponentially fast (Δn increases), since competition is weak.
- Eventually competition kicks in and reduces growth (Δn decreases). In the long run, the population converges to the carrying capacity $(f - 1)/\gamma$.
- Growth follows a sigmoid curve (S shaped).

Competition for space

Space is a fixed resource and determines the structure of many plant and sessile communities, but may also have affected human population who compete for water points, space to put a camp or a village.[8]

[8] Cro-Magnon man, our European forbearer, often used caves as shelters.

Competition for space

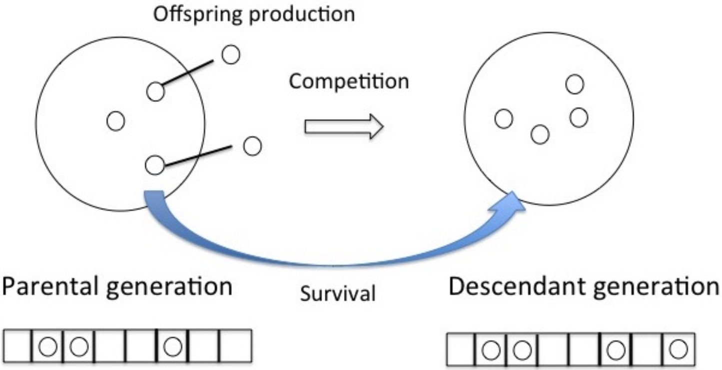
We consider a population with exactly $n_{\max}$ (breeding) sites and that the event in the life cycle[9] are as follows

1. Each of the n adults produces on average f offspring, which is assumed to be much smaller than the total number of breeding sites $n_{\max}$ ($f \ll n_{\max}$).
2. Each adult survives with probability s to the breeding season. Hence, a total number ns of adults survive.
3. Offspring compete at random for any of the $n_{\max}$ breeding sites but loose against surviving adults and so can effectively settle only on a fraction $(1 - ns/n_{\max})$ of sites.

[9] The life cycle is the sequence of life stages that an organism undergoes from birth to reproduction

Competition for space

The life cycle can be seen as follows



The total amount of space ("breeding sites" or boxes in the figure), $n_{\max}$, is fixed.

Competition for space: fitness

The fitness of an individual in this model is

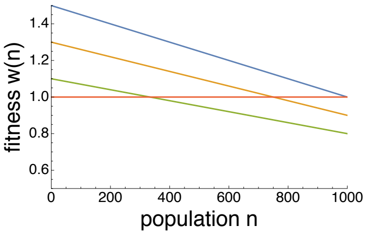
$$w(n) = s + \underbrace{\left(1 - \frac{sn}{n_{\max}}\right) f}_{\text{effective fecundity}}$$

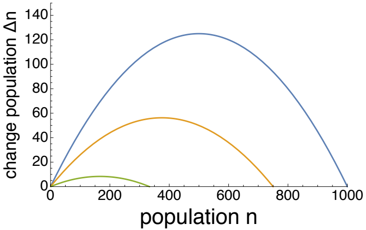
- Fitness is gained by survival and placing offspring in open breeding sites.
- $(1 - ns/n_{\max})$ should be thought as the fraction of open breeding sites (or habitats).
- $(1 - ns/n_{\max})f$ gives the expected number of surviving offspring to a focal adult (assuming $f \ll n_{\max}$).

This is sometimes called lottery competition.

Competition for space: negative density-dependence

As under competition for material resources, fitness $w(n)$ is negatively affected by density-dependence and the change in population size $\Delta n = (s + (1 - sn/n_{\max})\, f - 1)\, n$ is dome shaped.

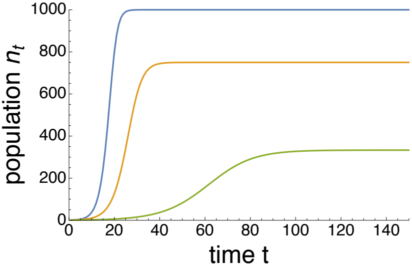




Parameter values in both figures are $n_{\max} = 1000$, $s = 0.5$; and $f = 1$ (blue), $f = 0.8$ (yellow), and $f = 0.6$ (green).

Competition for space: time dynamics

Iterating $n_{t+1} = w(n_t)n_t$, the number of individuals n_t as a function of time t is given by



Parameter values are $n_0 = 1$ (initial conditions), $n_{\max} = 1000$, $s = 0.5$; and $f = 1$ (blue), $f = 0.8$ (yellow), and $f = 0.6$ (green).

Population dynamic follows again a sigmoid curve. This is the same form as in the Beverton-Holt model.

Competition for space: equilibrium

An equilibrium requires $\Delta n^* = (w(n^*) - 1)n^* = 0$, whereby the equilibrium where $n^* > 0$ requires that

$$w(n^*) = 1$$

Using fitness for competition for space and solving for n^* gives the carrying capacity

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

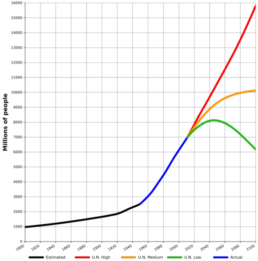
The carrying capacity increases with fecundity f and survival s.[10]

[10] The carrying capacity is stable if $f + s > 1$ and $f + s < 2$.

Human population dynamics

The human population has witness an impressive growth[11], in fact exponential growth, over the last thousands years.

- What will the future population dynamics look like?
- There is a tendency to a slow down.
- Fundamental question: what is the human carrying capacity?



Human population growth since 1800.

[11] For human population dynamics, the density dependent parameter γ is modified by economic growth and is likely to depend itself on population size.

Summary

- Fitness is the quantity that describes population dynamics.
- Fitness depends on survival and effective fecundity (the vital rates).
- Fitness is generally negative density-dependent since resources are limiting and competition occurs for material resources and space. This is an iron law of the natural world.
- Population growth follows a sigmoid curve in a finite world.

Exponential growth cannot go forever and growth must eventually equal zero (fitness equal one). This is true more generally for whatever quantity is growing and is dependent on a finite resource base.