Chapter 3: Density dependence

\[ \frac{dN}{dt} = [bf(N) - dg(N)]N \]

Populations change by immigration, birth, and death processes, which could all depend on the density of the population itself.
Population density

\[\frac{dN}{dt} > 0\]
\[\frac{dN}{dt} < 0\]

Per capita birth or death rate

\[b\] birth rate
\[d\] death rate

steady state

\[\frac{dN}{dt} = [b - df(N)]N\]

\[F(N) = d + cN = df(N)\] \[\iff\] \[f(N) = 1 + N/k\]

\[\frac{dN}{dt} = [b - d\left(1 + \frac{N}{k}\right)]N\]

\[\bar{N} = k \frac{b - d}{d} = k(R_0 - 1)\]
Production or death rate

\[
\frac{dN}{dt} > 0 \\
\text{production rate}
\]

\[
\frac{dN}{dt} < 0 \\
\text{total death rate}
\]

steady state

Production or death rate

\[
\frac{dN}{dt} = s - d \left(1 + \frac{N}{k}\right)N
\]

\[
\bar{N} = \frac{-dk \pm \sqrt{dk(dk + 4s)}}{2d}
\]
\[
\frac{dN}{dt} = \left[ b f(N) - d \right] N
\]

\[
F(N) = b - cN = bf(N) \quad \leftrightarrow \quad f(N) = 1 - N/k
\]

\[
\frac{dN}{dt} = \left[ b \left( 1 - \frac{N}{k} \right) - d \right] N
\]

\[
\bar{N} = k \left( 1 - \frac{d}{b} \right) = k \left( 1 - \frac{1}{R_0} \right)
\]
Production or death rate

Production rate
\[ \frac{dN}{dt} > 0 \]

Total death rate
\[ \frac{dN}{dt} < 0 \]

Steady state

\[ \frac{dN}{dt} = s \left( 1 - \frac{N}{k} \right) - dN \]

\[ \bar{N} = \frac{sk}{dk + s} \]
Logistic growth: \[ \frac{dN}{dt} = rN(1 - N/K), \] with solution \[ N(t) = \frac{KN(0)}{N(0) + e^{-rt}(K - N(0))} \]
3.2 Logistic growth and our assumptions

Having derived a number of models for population growth we should start comparing them with existing models. The density-dependent models for replicating populations, Eq. (3.2) and Eq. (3.6), are both of the form

\[ \frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right), \]

where \( r \) and \( K \) are parameter combinations of the original birth and death rates, \( b \) and \( d \), and the density-dependence parameter \( k \) (see the exercises). Both models are therefore mathematically identical to the classical “logistic equation”:

\[ \frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right), \]

with solution

\[ N(t) = \frac{KN(0) + e^{rt} - 1}{K/N(0)} \]

(3.10)

with a natural rate of increase of \( r = \frac{b}{d} \), and a carrying capacity that is directly defined by the parameter \( K \) (these equations are identical because \( \frac{b}{d} = r \) and \( \frac{d}{K} = \frac{r}{K} \) in the logistic growth model). The behavior of the three models is therefore identical: starting from a small initial population the growth is first exponential, and will approaches zero when the population size approaches the carrying capacity (see Fig. 3.3). Starting from a large initial population, i.e., from \( N(0) > K \), the population size will decline until the carrying capacity is approached. Logistic growth is often employed to describe population growth in many biological disciplines (ranging from ecology, epidemiology, virology to cell biology), and by deriving Eq. (3.10) ourselves we have learned that it is indeed an excellent choice for populations having a linear density-dependence on their per capita birth and/or death rate. Eq. (3.10) is more

Generalized logistic growth:

\[ \frac{dN}{dt} = rN \left( 1 - \left( \frac{N}{K} \right)^m \right), \]

with

\[ N(t) = \frac{K}{1 - \left( [1 - \left( \frac{K}{N(0)} \right)^m \right)] e^{-rmt}}^{1/m} \]

(3.11)
Human logistic growth

Human population in Monroe Country, West Virginia
Figure 3.4: Populations with density-dependence either on the production (i.e., obeying Eq. (3.8); red lines), or on the death rate (i.e., obeying Eq. (3.4); blue lines). The horizontal black line in Panel (b) denotes the steady state level (i.e., the two panels are scaled differently). In Panels (b) we add noise sampled from a normal distribution with mean zero and 2.5% standard deviation to the population size $N(t)$ of both models at random selected time points. This figure was made with the model source.R.

The population size approaches the carrying capacity (see Fig. 3.3a). Starting from a large initial population, i.e., from $N(0) > K$, the population size will decline until the carrying capacity is approached. Logistic growth is often employed to describe population growth in many biological disciplines (ranging from ecology, epidemiology, virology to cell biology), and by deriving Eq. (3.10) ourselves we have learned that it is indeed an excellent choice for populations having a linear density-dependence on their per capita birth and/or death rate. Eq. (3.10) is more convenient than the models we derived ourselves because the carrying capacity is defined by just one of its parameters, but because Eq. (3.10) has no explicit death rate, we cannot define a life span, and hence the $R_0$ is not defined. One can easily extend Eq. (3.10) to allow for a non-linear density-dependence, e.g.,

$$\frac{dN}{dt} = s - d\left(1 + \frac{N}{K}\right)N,$$

where the meaning of $r$ and $K$ remain the same and $m$ can be used to define a concave or convex dependence of the per capita growth rate on the population density (Fig. 3.3c).

The two density-dependent models for populations that are maintained by a source, i.e., Eqs. (3.4) and (3.8), are mathematically not identical, and their steady states are defined by quite different parameter expressions. Thus, the effect of changing a parameter like the source, $s$, on the steady state of the population depends on our choice of which biological process depends (most strongly) on the population density. In Fig. 3.4 we depict the behavior of both models in the presence and absence of noise. The two models are given the same source and death rates, and the $k$ value of the model with density-dependent death is set to such a value that both models have the same steady state (see the R-script source.R). Thus, at low densities the two populations have the same initial growth rate, and at high densities they approach the same steady state (see Fig. 3.4a where the red line depicts the population with density-dependent production, and the blue curve is the population with density-dependent death). We observe that the population with density-dependent death approaches the steady state somewhat earlier than the population with density-dependent production. In the presence of noise, i.e., by frequently adding or removing a randomly drawn small value to $N$ (with 2.5% standard deviation), we observe that the (red) population with density-dependent production is somewhat more sensitive.
Density dependent birth

**Corn**

- Yield per plant (kg dry wt)
- Population density (plants/acre $\times 10^{-3}$)

**Salicornia**

- Number of seeds per plant
- Plant population density

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**Platan**

- Average number of seeds per reproducing individual
- Seeds planted per m²

**Song sparrow**

- Clutch size
- Density of females

**Grizzly bear**

- Young per female
- Cubes per female
- Number of adults

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[(a) Plantain](#)
[(b) Song sparrow](#)
[Grizzly bear](#)
Non-linear density dependence

\[
\begin{align*}
  f(x) &= \max(0, 1 - [x/k]^n) \\
  f(x) &= \min(1, [x/k]^n) \\
  f(x) &= \frac{x^n}{h^n + x^n} \\
  g(x) &= \frac{1}{1 + (x/h)^n} \\
  f(x) &= 1 - e^{-\ln[2]x/h} \\
  g(x) &= e^{-\ln[2]x/h}
\end{align*}
\]
For a replicating population with density dependent growth one would write
\[
\frac{dN}{dt} = (bf(N) - d)N
\]
functions
one would expect that competition only kicks in at high population densities. This is obviously not generally the case. Intuitively,
and to sketch how each of these processes should depend on the population size(s). Typically, it
Non-linear density dependence
Chapter 4

Because all functions in Eqs. (3.12–3.14) are dimensionless, and remain bounded between zero

For a replicating population with density dependent growth we can now generalize Eq. (3.5)

Each of the three models in Fig. 3.5 has a single non-trivial steady state (see Table 3.1), and

should probably remain close to its maximal value, as long as the population size is su

3.2a would speak in favor of using the linear

and use one of the several candidates from Eq. (3.12) or Eq. (3.14) to choose a decreasing density

Because the birth rate of Eq. (3.15). The intersects therefore correspond to steady states.

\[ f(N) = \frac{1}{1 + N/k}, \quad f(N) = \frac{1}{1 + [N/k]^2} \quad \text{and} \quad f(N) = e^{-\ln[2]N/k} \]
\[
\frac{dN}{dt} = (bf(N) - d)N
\]

\[f(N) = \frac{1}{1 + N/k}, \quad f(N) = \frac{1}{1 + [N/k]^2}\]

and

\[f(N) = e^{-\ln[2]N/k}\]

\[
\begin{array}{|c|c|c|c|c|c|}
\hline
\text{Function} & \text{\(f(0)\)} & \text{\(f(k)\)} & \text{\(f(\infty)\)} & \text{\(R_0\)} & \text{Carrying capacity} & \text{Eq.} \\
\hline
f(N) = \max(0, 1 - [N/k]^m) & 1 & 0 & 0 & b/d & \bar{N} = k^{m\sqrt{1 - 1/R_0}} & (3.12) \\
f(N) = 1/(1 + N/k) & 1 & 0.5 & 0 & b/d & \bar{N} = k(R_0 - 1) & (3.14) \\
f(N) = 1/([N/k]^2) & 1 & 0.5 & 0 & b/d & \bar{N} = k\sqrt{R_0 - 1} & (3.14) \\
f(N) = e^{-\ln[2]N/k} & 1 & 0.5 & 0 & b/d & \bar{N} = (k/\ln[2])\ln[R_0] & (3.14) \\
\hline
\end{array}
\]
One could use an increasing Hill-function to define a like a sigmoid function. In other words, finding a population with a sigmoid population growth instance, starting with a small population the population size plotted in time will always look these models is always the population density into a region where $d$ stable (see Fig. 3.5). The latter can be seen graphically because at the steady state, where competition kicks in, the sigmoid function of Eq. (3.14c) seems most realistic. Data maximal as long as the population size is su

Table 3.1: 

\[
\begin{array}{ccc}
N/(f) &=& 1 \\
2 &=& 0.5 \\
0 &=& 0 \\
\end{array}
\]

Figure 3.6: 

Density dependent death 

\[
\frac{dN}{dt} = [b - d - \delta f(N)]N \quad \frac{dN}{dt} = (b - d[1 + (N/k)^m])N
\]
Positive density dependence

\[
\frac{dN}{dt} = (bf(N)g(N) - d)N \quad \text{or} \quad \frac{dN}{dt} = (bg(N) - d[1 + (N/k)^m])N,
\]
Regression to the mean

```
n <- 100; data <- rnorm(n,1,0.1); hist(data)
N <- data[1:(n-1)]; r <- (data[2:n]-N)/N
plot(N,r,type="p")
lm(r~N,as.data.frame(cbind(N,r)))
```
Cell division takes time

Conventional ODE: \[ \frac{dN}{dt} = (p - d)N \]

Smith-Martin model (first ignoring death):

\[ \frac{dA(t)}{dt} = 2pA_{t-\Delta} - pA(t) \quad \text{and} \quad \frac{dB(t)}{dt} = pA(t) - pA_{t-\Delta} \]

Smith-Martin model with death:

\[ \frac{dA(t)}{dt} = 2pA_{t-\Delta}e^{-d\Delta} - (p+d)A(t) \quad \text{and} \quad \frac{dB(t)}{dt} = pA(t) - dB(t) - pA_{t-\Delta}e^{-d\Delta} \]
Time delays implemented as many small steps

Smith-Martin model with death:

\[
\frac{dA(t)}{dt} = 2pA_{t-\Delta}e^{-d\Delta} - (p+d)A(t) \quad \text{and} \quad \frac{dB(t)}{dt} = pA(t) - dB(t) - pA_{t-\Delta}e^{-d\Delta}
\]

Smooth the time delay by many \((n)\) small steps:

\[
\frac{dA}{dt} = \frac{2n}{\Delta} B_n - (p+d)A, \quad \frac{dB_1}{dt} = pA - \left(d + \frac{n}{\Delta}\right) B_1 \quad \text{and} \quad \frac{dB_i}{dt} = \frac{n}{\Delta} (B_{i-1} - B_i) - dB_i
\]