Population models in continuous time

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Introduction

In this chapter we will discuss some biological models that are defined by a scalar differential equation and discuss what we can learn about their solutions by only looking at the equation. This is because we usually have an equation that contains some parameters, and we want to see how the solution qualitatively changes when we change the parameter. We will start the discussion with something well-know, radioactive decay, in order to find out about the limits and assumptions of differential equation models in biology.

After having had a short discussion on modeling with differential equations in ecology we will turn to the problem of understanding the solution from the equation. Focus will be on examining equilibra and their stability and about how this information can help us produce a crude sketch of the solutions.

Radioactive decay

That Cesium-137 is radioactive with a half-life of 30.2 years, means that if we have a sample of $M$ g Cesium and let $\lambda = \ln 2/30.2$, then the function

$$u(t) = \text{amount Cesium (g) that has not decayed at time } t$$

follow the differential equation

$$u'(t) = \lambda u(t), \quad u(0) = M,$$

whose solution we know is

$$u(t) = Me^{-\lambda t}.$$

But is this actually true?

If we measure $u(t)$ in our sample with extreme sensitivity at all time points, we see that the function we observe is not a smooth exponential function. Instead it is a step function with small steps at irregular time points. Every time an atom decay, a fixed amount of Cesium disappear from the sample.

So the model cannot be fully accurate. But it is extremely useful and gives very accurate predictions. We need to understand why.

For this, we change our perspective a bit. Every Cesium atom remains a Cesium atom until it suddenly decays and no longer is a Cesium atom. We therefore introduce the stochastic variable

$$T = \text{time until the atom decay.}$$

The probability that it has not decayed at time $t$ is then given by the probability $P(T > t)$. As a function of $t$, $p(t) = P(T > t)$, this is called the survival function of $T$. About $T$ we make the following assumption: if the atom has not decayed at time $t$, the probability that it has decayed at time $t + h > t$ is approximately $\lambda h$. Or, more precisely, we assume

$$P(T <= t + h \mid T > t) = \lambda h + o(h),$$
where \( o(h) \) is a function such that \( o(h)/h \to 0 \) as \( h \to 0 \). Expressed in the survival function this can be written

\[
p(t + h) - p(t) = (P(T > t + h|T > t) - 1)p(t) = (-\lambda h - o(h))p(t).
\]

If we divide with \( h \) and let \( h \to 0 \), we see that

\[
p'(t) = -\lambda p(t), \quad p(0) = 1,
\]

for which the solution is \( p(t) = e^{-\lambda t} \). From probability theory we know that this means that \( 1/\lambda \) is the expected time to decay.

In other words: the differential equation is an equation for the survival function, which is a prediction of the observed fraction of atoms that has not decayed. So when we say that the number of atoms that has not decayed follow the differential equation, we actually talk about predictions and what happens on average.

It may be worth pointing out that the model implies that the relative decrease rate

\[
\lambda(t) = -\frac{p'(t)}{p(t)}
\]

is constant for radioactive decay. It is called the decay intensity.

There are other survival distributions that can be used.

**Example 1** A survival distribution much used to describe life expectancy in an insurance context is a distribution based on the following observation by Benjamin Gompertz 1825:

"... [assume] the average exhaustion of a man’s power to avoid death to be such that at the end of equal infinitely small intervals of time he lost equal portions of his remaining power to oppose destruction which he had at the commencement of these intervals."

This assumption lead to the differential equation

\[
\frac{d}{dt}(\lambda(t))^{-1} = -b\lambda(t)^{-1}
\]

which is equivalent to the simpler equation \( \lambda'(t) = b\lambda(t) \) and implies that \( \lambda(t) = \lambda e^{bt} \) and subsequently that

\[
p'(t) = -\lambda e^{bt}p(t).
\]

The solution to this equation is (since \( p(0) = 1 \))

\[
p(t) = e^{-\lambda(e^{bt}-1)/b}.
\]

**Models in ecology**

In light of the discussion in the previous section it should be meaningful to formulate models for animal populations as differential equations to be fulfilled by the function
$u(t)$ which is the expected number of animals at time $t$. Such a model typically start as a mass balance equation like

$$u'(t) = \text{production of animals} - \text{elimination of animals},$$

where the entities to the right have unit animal per time unit.

The simplest model of this kind is

$$u'(t) = ru(t) - du(t),$$

where $r$ measures how many new animals each animal produce per time unit, whereas $d$ is a corresponding death rate. As before we can interpret $1/d$ as the life expectancy of animals. This equation is rewritten as $u'(t) = \lambda u(t)$, $\lambda = r - d$, whose solution is $u(t) = e^{\lambda t} u(0)$. So, if $d > r$ the population dies out, whereas if $d < r$ it grows exponentially.

The latter can obviously not continue forever. At some point in time the resources will limit how large the population can be. We can model this in many ways; one is to say that the life expectancy decrease with an increasing population. Such a model can be written

$$u'(t) = ru(t) - (d + ku(t))u(t),$$

where $k$ is a constant. Here we assume $r > d$, so we can rewrite the rhs as

$$u(t)(r - d - ku(t)) = (r - d)u(t)(1 - \frac{ku(t)}{r - d}).$$

If we therefore introduce new constants $r = r - d$ and $K = (r - d)/k$ the differential equation can be written

$$u'(t) = ru(t)(1 - \frac{u(t)}{K}).$$

This model is called the logistic growth model.

An alternative, and perhaps more direct, derivation of the logistic equation is as follows. Start with $u'(t) = ru(t)$ where $r$ is the net growth rate and assume that $r$ depends on $u$ as a decreasing function. The simplest model for this is to assume that $r(u) = r(1 - u/K)$. Note that $r(K) = 0$, so when the population has reached size $K$ the births are balanced by the deaths. The number $K$ is called the carrying capacity of the environment w.r.t. the species in question.

Obviously there are many alternatives for the choice of rate function $r(u)$. If our animal is prey to some predators we can account for this by subtraction a term that describes the number of animals that fall prey to these predators. Starting with the logistic law, this gives us an equation

$$u'(t) = ru(t)(1 - \frac{u(t)}{K}) - P g(u(t)),$$

where $P$ is the number of predators and $g(u)$ describes how many prey a typical predator catches per unit time when the number of prey is $u$. 
What should such a function \( g(u) \) look like? Most predators can only eat so much, so we can expect \( g(u) \) to be an increasing function that is bounded from above. Moreover, \( g(0) = 0 \). A simple analytical expression for such a function is

\[
g(u) = \frac{au}{b + u}
\]

for positive constants \( a, b \).

Such a model is often useful when the predator is an invertebrate. For vertebrates we often use the expression

\[
g(u) = \frac{au^2}{b^2 + u^2}
\]

instead. The reason is that the graph of this function is sigmoidal, which means that there is relatively less interest in a particular prey when they are scarce. An intelligent animal do not seek a prey that is hard to find, if there are alternatives. This is illustrated below, where the predator is the deer mouse (\textit{Peromyscus leucopus}) which chooses to eat either a sawfly pupae (closed circles) or an alternative food (open circles). Note the sigmoidal nature for small densities of the sawfly pupae.

In such a case the dynamics of the prey population can be described by the differential equation

\[
(1) \quad u'(t) = ru(t)(1 - \frac{u(t)}{K}) - P\frac{au(t)^2}{b^2 + u(t)^2}.
\]

**Nondimensional equations**

Once we have found the differential equation, containing some unknown parameters, we want to understand how the solution changes, qualitatively (as opposed to quantitatively),
when we vary these parameters. After all the equation is at best a crude model of reality and is more a suggestion on what can happen, instead of an accurate prediction of what will happen.

The first step in such an analysis is to reduce the number of parameters by finding the combinations that are key to the understanding of the dynamics. This is done by making the equation nondimensional. To see what that means, consider the logistic law

$$u'(t) = ru(t)(1 - \frac{u(t)}{K}).$$

Assume $u$ measures the number of animals. We can then alternatively measure the amount of animals as a fraction of the carrying capacity $K$. Thus we introduce the function

$$y(t) = \frac{u(t)}{K}$$

which satisfies the equation

$$y'(t) = ry(t)(1 - y(t)).$$

Now we have one fewer parameter in the equation, and a function that does not depend on the actual units we measure in. If we want to compare model and reality we need an estimate of $K$. But not in order to understand the principles of the dynamics.

We can actually eliminate $r$ also from the equation. Its unit is 1/time, so $\tau = rt$ is an entity that measures time, but not in any particular clock unit. In order to introduce $\tau$ as our new time in the equation, write

$$y(t) = x(rt),$$

where $x$ is a function of $\tau$. Then $y'(t) = x'(rt)r$ and the equation for $x$ is

$$x'(\tau) = x(\tau)(1 - x(\tau)).$$

If we therefore know what the solution $x(\tau)$ looks like, we can derive the qualitative behaviour of $u(t) = Kx(rt)$ by changing the time scale and how we measure the number of animals.

**Remark** We traditionally want to denote time by $t$, so we use this variable for $\tau$ as well in the following discussion.

If we do the same substitution in the equation (1) we get

$$x'(t) = x(t)(1 - x(t)) - \frac{cx(t)^2}{d^2 + x(t)^2}, \text{ where } c = Pa/r, d = b/K$$

both are nondimensional constants. However, this is not the only way to make the equation nondimensional. Another way builds on the observation that $b$ and $u(t)$ have the same unit, so we introduce $y(t)$ by $u(t) = by(t)$. With the nondimensional time as above this gives us the nondimensional equation

$$x'(t) = x(t)(1 - \frac{x(t)}{Q}) - \frac{1}{R 1 + x(t)^2}, \text{ where } Q = K/b, \text{ and } R = r/aP.$$

This form has advantages when we want to see how the solution depends on the model parameters.
Qualitative analysis of differential equations

Next we want to see how can get some information about how the solutions to an equation
\[ y'(t) = f(y(t)) \]
looks like, without actually solving it (which might only be possible numerically, anyway).

A special kind of solutions are the equilibria, i.e. solutions \( y(t) = y_0 \) to the equation. We then must have that \( f(y_0) = 0 \) and, conversely, a zero of \( f \) defines an equilibrium solution.

If \( f \) is a \( C^1 \) function a start value \( y(t_0) = y_0 \) defines a unique solution to the equation. The graphs of two such solutions can therefore not intersect. In the regions between two equilibria the solutions must be strictly monotone. This simple information allows us to sketch the solutions as illustrated in the next example.

**Example 2** In order to sketch the solutions to the logistic growth model
\[ y' = ry(1 - \frac{y}{K}), \]
where \( r, K > 0 \), we note that it has its equilibria in \( y = 0 \) and \( y = K \). By looking at the sign of the function we get from this the following table

<table>
<thead>
<tr>
<th>( y )</th>
<th>0</th>
<th>( K )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( y'(t) )</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>( y(t) )</td>
<td>↘</td>
<td>↗</td>
</tr>
</tbody>
</table>

from which we can infer the qualitative behaviour of the solutions as shown in the graph to the right.

If \( y(0) < 0 \) we have that \( y(t) \to -\infty \) when \( t \) increases, whereas if \( y(0) > 0 \) we asymptotically approach \( y = K \). If \( 0 < y(0) < K \) the solution \( y(t) \) grows towards \( K \), whereas if \( y(0) > K \) the solution \( y(t) \) will decrease towards \( K \).

In this example we see that \( y = 0 \) is an unstable equilibria and \( y = K \) is an asymptotically stable equilibria, according to the following definition.

**Definition 1**

If an equilibria \( y_0 \) of a differential equation \( y' = f(y) \) has a neighborhood such that if \( y(0) \) is in this neighborhood, then \( y(t) \) stays close to \( y_0 \) forever, is said to be a *stable equilibria*. An equilibria \( y_0 \) that is not stable is said to be unstable. A stable equilibria is said to be asymptotically stable if there is a neighborhood of \( y_0 \) such that if \( y(0) \) is in it, we have that \( y(t) \to y_0 \) as \( t \to \infty \).

Whether an equilibria is stable or unstable is a local property, and should in general be
possible to derive from the derivative of $f$ in the point. To see how, we first note that when $y$ is close to $y_0$ we have

$$f(y) = f(y_0) + f'(y_0)(y - y_0) + \ldots = f'(y_0)(y - y_0) + \ldots$$

where $\ldots$ denotes terms that we will neglect because they are small. Approximately we therefore have

$$y'(t) = f'(y_0)(y(t) - y_0),$$

the solution of which takes the form

$$y(t) = y_0 + C \exp(f'(y_0)t).$$

It follows that the equilibria is asymptotically stable if $f'(y_0) < 0$, whereas it is unstable if $f'(y_0) > 0$. When $f'(y_0) = 0$ we cannot neglect the omitted terms, so we need a more careful analysis.

We close this section with two important observations.

The first is that we can go backwards in time, i.e. let $t \to -\infty$. It is the same as following $u(t) = y(-t)$ as $t \to \infty$, and $u(t)$ solves $u'(t) = -f(u(t))$. This equation has the same equilibria and the original one, with the difference that stable ones turn into unstable ones and vice versa.

Using this we can expand the graph in Example 2 to get the solutions also for negative $t$. This is done in the graph to the right.

The second observation is that we get the solution graph that passes through $(t_0, y_0)$ by solving the problem

$$y'(t) = f(y(t)), \quad y(t_0) = y_0.$$

Assume $y_1(t)$ is such that $y_1'(t) = f(y_1(t)), \quad y_1(0) = y_0$. Then the function $y_2(t) = y(t + t_0)$ is another solution to the same problem and, because of uniqueness, $y_2(t) = y_1(t)$. This means that $y(t) = y_1(t - t_0)$ and in order to get the graph of $y(t)$ we compute $y_1(t)$ and shift it sideways as illustrated in the graph below.
Exercises

Exercise 1 A species of wingless birds have since ancient time lived isolated on an island but was almost made extinct by a volcano eruption. After that, when there were only few birds, it was noted that the relative growth rate was 0.2 per month. The number of birds follows the logistic law and has stabilised on the level 1000. Recently humans brought cats to the island. Collectively they kill 32 birds every month, but the number of cats is held constant by the humans. On what level will the number of birds stabilize in the future?

Exercise 2 A pest has invaded an agricultural region. The number of pests \( N \) is assumed to follow the logistic law with relative growth rate 0.1/day when their numbers are small and the region can at most harbour 2500 individuals. In order to get to terms with the problem 120 predators are implanted into the region. For them there is plenty of alternative food and the reproduce on a much longer time scale, so we can assume their number is constant. Each predator eats

\[
\frac{N}{1000 + N}
\]

pests per day. Determine what will happen to the pests with time (the answer depends on how many they were when the predators were implanted).

Exercise 3 A larva have attacked a fruit farm and grow exponentially with a relative rate of 10% per day. To the farmers great pleasure the larvae are detected after some time by a group of 20 birds that start to eat them. If there are \( N \) thousand larvae, the birds eat

\[
\frac{400N^2}{400 + N^2}
\]

larvae per day (Note! not thousands.) Determine how much help these birds actually are to the farmers?

Exercise 4 Consider a fish population which, in the absence of human harvesting, follow a logistic growth model. What happens with this population with time in the following two cases:

a) Humans start to harvest the population with a rate proportional to the size of the fish population.

b) Humans harvest the fish population by extracting a fixt amount of fish (independent of the size of the fish population, assuming there is something to harvest).

(The latter is probably what happens with modern trawlers and fishing quotas, whereas the former describes what happens with more primitive fishing aids.)

Exercise 5 Redo the previous exercise, replacing the logistic law with the more general model

\[
N' = rN \frac{K - N}{K + \gamma N}.
\]

Does this change the conclusions?
**Exercise 6** (This exercise is an elaboration of Exercise 4.) Assume that the model in part a) of Exercise 4 is in equilibrium. Express the yield \( F \) as a function of the proportionality factor \( E \) and determine the \( E \) that maximizes \( F \). Show that the recovery time \( T_R(F) \) (which you need to figure out what it should mean) is given by

\[
\frac{T_R(F)}{T_R(0)} = \frac{2}{1 \pm \sqrt{1 - F/F_M}}.
\]

where \( F_M \) is the maximal yield.

If we plot this result we get the graph below.

Interpret this from a fishing perspective. What does \( A \) denote? What happens as we test our way towards finding the maximal yield?

Next consider the b)-part of Exercise 4 with \( F_0 \) denoting the amount of fish that is extracted. Show that now we have that

\[
\frac{T_R(F_0)}{T_R(0)} = \frac{1}{\sqrt{1 - F_0/F_M}}
\]

and that this approaches infinity as \( F_0 \to F_M \). In other words, if we test our way towards the maximal yield, we will eradicate the fish!

**Answers to exercises**

**Exercise 1** \( N' = 0.2N(1 - N/1000) - 32 \). Population will stabilize at 800 individuals.

**Exercise 2** \( N' = 0.1N(1 - N/2500) - 120 \cdot N/(1000 + N) \). If \( N(0) < 500 \) the pest will be eradicated, otherwise it will stabilize on level 1000.

**Exercise 3** a) \( N' = 0.1N - 8N^2/(400 + N^2) \).

b) If \( N(0) > 20(2 + \sqrt{3}) \) thousand the larvae will grow exponentially, if not they will stabilize on the level \( 20(2 - \sqrt{3}) \) thousand.
Exercise 4  a) Equation is \( N' = rN(1 - N/K) - EN = (1 - E)rN(1 - N/K') \), where \( K' = K(1 - E/r) \). As long as \( r > E \) the population will survive at the level \( K' \). If \( E > r \) the fish will go extinct.

b) Equation is \( N' = rN(1 - N/K) - E \). When we have two equilibria the population will settle on the higher level. As \( E \) is further increased solution will suddenly go to zero and the fish die out.

Exercise 5  No