Mathematical Techniques in Evolution and Ecology

General solutions and transformations – One-variable models (part II)

Based on Chapter 6 in Otto and Day (2007)

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Outline

Goals

- To describe methods for obtaining general solutions for models with one variable
- To describe transformation methods for simplifying models

Concepts

- Transformation
- Affine models
- Brute force iteration
- Separation of variables

Nonlinear models in discrete time

- There is **no general recipe for solving nonlinear models in discrete time**, even when there is only one variable. Yet, that does not mean that a general solution cannot be found in certain cases.

- In practice, one must **try a number of different tranformations** to see if any of them works. Of course, this is also a **matter of experience**.

- While the logistic model and the *diploid* model of natural selection do not have a general solution, the *haploid* model of natural selection does. It is a good example of how the dynamics can be simplified using the appropriate tranformation.

Example: Haploid model of natural selection

We recall the discrete-time recursion equation

$$p(t+1) = \frac{W_A\, p(t)}{W_A\, p(t) + W_a\, q(t)},$$

(1)

and the corresponding equilibria $\hat{p}_1 = 0$ and $\hat{p}_2 = 1$. We can try a number of different approaches:

- **Brute-force iteration** will produce a general solution, but it is cumbersome. Let us discuss a number of tranformations instead.

- **Distance to the equilibrium:** Note that Eq. (5) *is* already expressed as a distance from equilibrium $\hat{p}_1 = 0$! We could express it as a distance from equilibrium $\hat{p}_2 = 1$, i.e. as $q(t) = 1 - p(t)$, but this obviously results in an equation analogous to Eq. (5) due to symmetry.

- **Distance between $p(t)$ and $q(t)$:** Recalling the symmetry of the model ($p(t) + q(t) = 1$), it is a good idea to try a transformation that *maintains this symmetry*. The difference $d(t) = p(t) - q(t)$ does so. After some algebra, a recursion for $d(t)$ can be found, but it is even more complicated than Eq. (5):

$$d(t+1) = \frac{W_A - W_a + W_A\, d(t) + W_a\, d(t)}{W_A + W_a + W_A\, d(t) - W_a\, d(t)}. \tag{2}$$

- **Ratio of $p(t)$ and $q(t)$:** Another tranformation that maintains symmetry is the ratio, $f(t) = p(t)/q(t)$, which turns out to have a particularly nice recursion equation:

$$f(t+1) = \frac{p(t+1)}{q(t+1)} = \frac{\frac{W_A\, p(t)}{W_A\, p(t) + W_a\, q(t)}}{\frac{W_a\, q(t)}{W_A\, p(t) + W_a\, q(t)}} = \frac{W_A\, p(t)}{W_a\, q(t)} = \frac{W_A}{W_a}\, f(t). \tag{3}$$

The recursion in Eq. (7) has the general solution

$$f(t) = \left(\frac{W_A}{W_a}\right)^t f(0). \tag{4}$$

To transform this back to the original variable $p(t)$, we solve $f(t) = p(t)/q(t) = p(t)/(1-p(t))$ for $p(t)$, which yields $p(t) = f(t)/(1-f(t))$. Therefore,

$$p(t) = \frac{f(t)}{1-f(t)} = \frac{\left(\frac{W_A}{W_a}\right)^t f(0)}{1-\left(\frac{W_A}{W_a}\right)^t f(0)} = \frac{\left(\frac{W_A}{W_a}\right)^t \frac{p(0)}{q(0)}}{1-\left(\frac{W_A}{W_a}\right)^t \frac{p(0)}{q(0)}}$$

$$= \frac{W_A{}^t p(0)}{W_A{}^t p(0) - W_a{}^t q(0)} = \frac{W_A{}^t p(0)}{W_A{}^t p(0) - W_a{}^t(1-p(0))}.$$

(5)

Equation (7) provides us with an additional insight: *selection alters the ratio of allele frequencies by the ratio of their fitnesses*, i.e. the ratio of allele frequencies undergoes **exponential growth** ($W_A > W_a$) **or decline** ($W_A < W_a$) over time.

We can even take this a step further and ask what happens when fitnesses depend on time, i.e. when $W_A = W_A(t)$ and $W_a = W_a(t)$. Equation (7) suggests that

$$f(t) = \prod_{i=0}^{t-1} \frac{W_A(i)}{W_a(i)} f(0) = \frac{\prod_{i=0}^{t-1} W_A(i)}{\prod_{i=0}^{t-1} W_a(i)} f(0). \tag{6}$$

At this point, we recall the definition of the geometric mean,

$$\overline{x}_g = \sqrt[n]{\prod_{i=0}^{n-1} x_i} \ . \tag{7}$$

If all the x_i are positive, then the geometric mean is smaller or equal to the arithmetic mean.

Therefore, Eq. (10) can be written as

$$f(t) = \frac{(\overline{W}_{A,g})^t}{(\overline{W}_{a,g})^t} f(0) = \left(\frac{\overline{W}_{A,g}}{\overline{W}_{a,g}}\right)^t f(0), \tag{8}$$

where $\overline{W}_{A,g}$ and $\overline{W}_{a,g}$ are the geometric mean fitnesses over time of alleles A and a, respectively.

Equation (12) tells us that allele A spreads over time if $\overline{W}_{A,g} > \overline{W}_{a,g}$, and vice versa.

Cannings (1971, *J. Genet.* 60:255–259) demonstrated this result in more general terms. He also pointed out that **an allele with less fitness variability over time tends to have a higher geometric fitness** and is thus selectively **favoured over alleles with the same arithmetic mean fitness but greater temporal variability** in fitness.

Linear models in continuous time

Similar to linear models in discrete time, those in continuous time come in two main forms of differential equations:

$$\frac{d\,n(t)}{d\,t} = r\,n(t), \tag{9}$$

and an *affine* form:

$$\frac{d\,n(t)}{d\,t} = r\,n(t) + m. \tag{10}$$

Equation (9) implies that changes in the systems arise from processes that occur to each individual independently, causing a constant *per capita rate of change* (e.g. due to births, deaths, emigration, selection,...). In contrast, Eq. (10) also allows for an *increase or decrease* of the dynamic variable that is *independent of the value of the variable*.
Both Eqs. (9) and (10) can be solved using a method called *separation of variables* (see below).

Separation of variables: A technique for solving differential equations that are some function of the *dependent* variable, i.e. $f(n(t))$, multiplied by some other function of the *independent* variable, i.e. $g(t)$. The method is described in **Recipe 6.2** below.

Recipe 6.2: Solving differential equations using a separation of variables

Differential equations that can be written as

$$\frac{d\,n(t)}{d\,t} = f(n(t))\,g(t) \tag{11}$$

can be solved as follows:

- (1) Rewrite the differential equation as

$$\frac{1}{f(n)}\,d\,n = g(t)\,d\,t \tag{12}$$

- (2) Take the indefinite integral of both sides, $\int(1/f(n))\,d\,n = \int g(t)\,d\,t$. Integrate the left-hand side w.r.t. the dependent variable n and the right-hand side w.r.t. the independent variable t. Importantly, add a constant of integration (e.g. c) on one side!

- (3) Attempt to solve the resulting equation for n.

- (4) Use an initial condition (e.g. at time $t = 0$, there are $n(0)$ individuals) to determine the constant of integration c.

Remark: Although n is a function of t, we sometimes simplify the notation by omitting this dependence, writing $f(n)$ instead of $f(n(t))$, for instance. We have done so in Eq. (12) above.

Exercise

- (a) Use a separation of variables (Recipe 6.2) to solve Eqs. (9) and (10).

- (b) Compare the solution to Eq. (9) – which essentially is the continuous-time version of the exponential growth model – to the explicit solution for the discrete-time version of the exponential growth model, $n(t) = R^t n(0)$. Recall that the reproductive factor R in discrete time is equal to one plus the intrinsic per capita growth rate r in continuous time, i.e. $R = 1 + r$. For a given r, does a population in continuous or discrete time grow faster?

In[3]:= **expGrowthContVsDisrTimePlot**

Out[3]=

$n_0 = 1000$

$r_0 = -0.1$
$r_0 = 0.1$
$r_0 = 0.2$

Population size $n(t)$

Time t
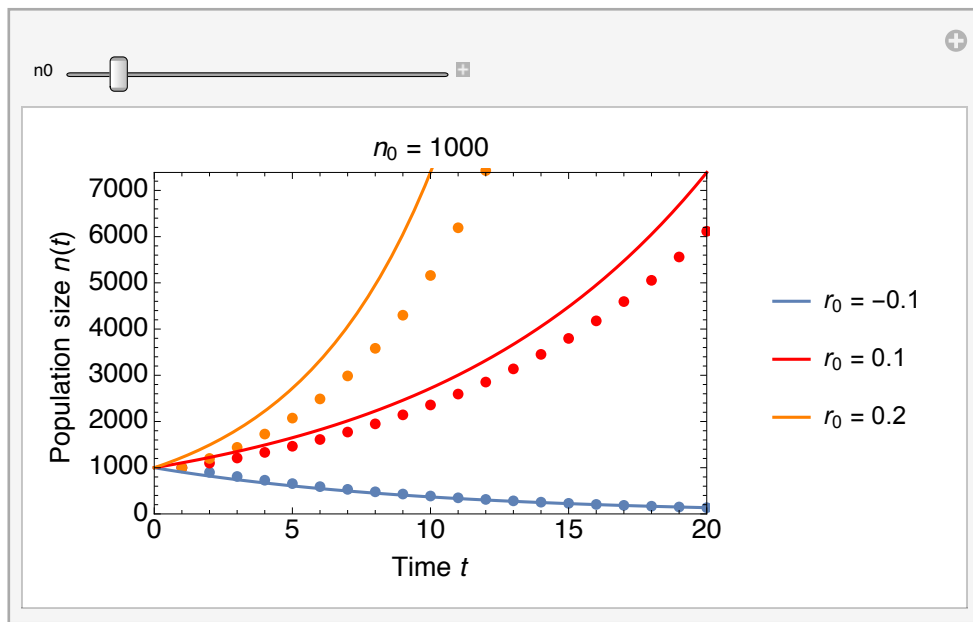
As we just saw in the Exercise above, the exponential growth model with a constant inflow or out-flow can be solved using the method of separation of variables. Alternatively, we can tranform the equation into the form of Eq. (9) to obtain a linear differential equation without a constant term, the solution of which we know. To do so, we use **Recipe 6.3**.

Recipe 6.3: Solving a linear continuous-time model with a constant term

Affine linear differential equations of the form

$$\frac{d n(t)}{dt} = \rho \, n(t) + c \tag{13}$$

can be solved as follows:

- (1) Solve for the equilibrium $\hat{n}$. Here, $\hat{n} = -c/\rho$.

- (2) Define a new variable δ as the distance from the equilibrium, $\delta(t) = n(t) - \hat{n}$. Reversing this equation implies $n(t) = \delta(t) + \hat{n}$.

- (3) Using the definitions from steps (1) and (2), set up a differential equation for $\delta = \delta(t)$, which turns out to be independent of the constant c:

$$\frac{d\delta}{dt} = \frac{d(n - \hat{n})}{dt} = \frac{dn}{dt} - \frac{d\hat{n}}{dt} = \rho \, n + c =$$

$$\rho(\delta - \hat{n}) + c = \rho\left(\delta - \left(-\frac{c}{\rho}\right)\right) + c = \rho \, \delta \tag{14}$$

- (4) From before (solving Eq. 9), we know that the general solution to Eq. (14) is $\delta(t) = e^{\rho t} \delta(0)$.

- (5) The general solution for the original variable is found by replacing δ in Eq. (14) with $n - \hat{n}$, and simplifying to get

$$
\begin{aligned}
n(t) - \hat{n} &= e^{\rho t}\left(n(0) - \hat{n}\right) \\
\Rightarrow n(t) &= e^{\rho t} n(0) + \left(1 - e^{\rho t}\right) \hat{n}
\end{aligned}
\tag{15}
$$

Remark: It is a good idea to check your result by differentiating it w.r.t. to t and comparing it to the differential equation from which you started.

Nonlinear models in continuous time

Most differential equations arising in biology are nonlinear functions of the variable(s) of interest. As long as they can be written in the form

$$\frac{dn}{dt} = f(n)\,g(t) \tag{16}$$

they can still be solved using a separation of variables as described in **Recipe 6.2** above.

We have seen two examples of differential equations of the appropriate form:

1. The logistic model of growth

$$\frac{dn}{dt} = r\,n\left(1 - \frac{n}{K}\right); \tag{17}$$

2. The haploid model of natural selection

$$\frac{dp}{dt} = s\,p(1 - p). \tag{18}$$

Although these models look different at first, they are closely related: The model of haploid selection represents a special case of the logistic model, where $p = n$, $s = r$, and $K = 1$. Therefore, if we find a solution to Eq. (17), we obtain the solution to Eq. (18) for free.

Exercise

Use Recipe 6.2 (separation of variables) to solve Eq. (17). From this, derive the solution to Eq. (18).

As a hint, notice that a fraction of the form

$$\frac{1}{(a_1 + b_1\, x)\,(a_2 + b_2\, x)} \tag{19}$$

can be written as

$$\frac{A}{(a_1 + b_1\, x)} + \frac{B}{(a_2 + b_2\, x)}, \tag{20}$$

where

$$A = -\frac{b_1}{(a_1\, b_2 - a_2\, b_1)},$$

$$B = \frac{b_2}{(a_1\, b_2 - a_2\, b_1)}.$$

This is a form of the "partial fractions" rule (Rule A1.9 in OD2007).

Remarks

A separation of variables applied to nonlinear differential equations is not guaranteed to yield a solution.

- The integrals produced in step (2) of Recipe 6.2 might be impossible to evaluate.

- Even if the integrals in step (2) of Recipe 6.2 can be obtained explicitly, they can yield an equation for the variable n that cannot be explicitly solved.

On the other hand, just because a differential equation cannot be written in the form $dn/dt = f(n) g(t)$ does not mean that it cannot be solved. Entire books are devoted to methods for solving various types of differential equations.

Box 6.2 in OD2007 provides solutions to other forms of differential equations that are commonly encountered in biology.

Initialisation cells

```mathematica
In[4]:= expGrowthContVsDisrTimePlot := Manipulate[
        rList = {-0.1, 0.1, 0.2};
        tMax = 20;
        Show[
          {
            ListPlot[Table[(1 + rList[[1]])^t n0, {t, 0, tMax, 1}],
              PlotRange → {{0, tMax}, {0, e^(rList[[2]] tMax) n0}}],
            ListPlot[Table[(1 + rList[[2]])^t n0, {t, 0, tMax, 1}], PlotStyle → Red],
            ListPlot[Table[(1 + rList[[3]])^t n0, {t, 0, tMax, 1}], PlotStyle → Orange],
            Plot[{e^(rList[[1]] t) n0}, {t, 0, tMax},
              PlotLegends → {"r0 = " <> ToString[rList[[1]]]}],
            Plot[{e^(rList[[2]] t) n0}, {t, 0, tMax}, PlotStyle → Red,
              PlotLegends → {"r0 = " <> ToString[rList[[2]]]}],
            Plot[{e^(rList[[3]] t) n0}, {t, 0, tMax}, PlotStyle → Orange,
              PlotLegends → {"r0 = " <> ToString[rList[[3]]]}]
          },
          Frame → True,
          FrameLabel →
            {{"Population size n(t)", ""}, {"Time t", "n0 = " <> ToString[n0]}},
          LabelStyle → Directive[FontFamily → "Helvetica", FontSize → 14]
        ]
        ,
        {{n0, 1000}, 1, 10 000}
      ]
```