Introduction to Population Dynamics

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Abstract

Models for describing the dynamical behaviour of populations are reviewed, including the exponential growth model, the logistic growth model and its modifications, the Bass model as well as the Lotka-Volterra equations. How the models are related to each other is discussed, and the main concepts in studying the behaviour of the models are considered.

1 Introduction

Population dynamics studies the size and composition of populations as dynamic systems. Originating in the study of biological populations (see [3, Chapters 5 and 8]), models of population dynamics also have been applied, e.g, in describing techno-economic systems [9]. A good understanding of population dynamics is essential for interpreting survey data, predicting and managing future development (financial risk management, strategies for sustainable harvesting), as well as evaluating the effectiveness of past tactics.

The exponential growth model (or the Malthusian growth model after Malthus [5]) is often regarded as the first principle of population dynamics. In the exponential growth model, the growth rate of the quantity of interest is proportional to its current value, and the growth is unlimited. The simple logistic growth model, proposed by Verhulst [7], takes into account the amount of available resources. In the logistic model, the growth is limited by a carrying capacity. Both of these models consider only the population dynamics of a single species. The first model that takes into account interactions between different species was proposed independently by Lotka [4] (while studying autocatalytic chemical reactions) and Volterra [8] (while studying fish catches). The Lotka-Volterra equations, or the predator-prey model, describe the dynamics of a system in which two species interact, one as a predator and the other as a prey. Since publishing the original predator-prey model, refinements and generalizations of the Volterra-Lotka equations have been presented. Later, Bass [2] introduced a model that describes the adoption of new ideas or products in a population. For more thorough review of the history of mathematical population dynamics, see [1].

Starting from the exponential growth model, we review commonly used models for describing population dynamics. We discuss the relations of these models to each other, and consider the main concepts related to studying the behaviour of the models. The main sources in this presentation are [3, 6, 9].

2 Models for population dynamics

In this section, models for describing the time-dependent behaviour of populations are presented. We start from the models that describe the population dynamics of a single species or product, the exponential and logistic growth functions as well as the Bass model. By adding terms for interspecific competition in the exponential and simple logistic growth models, we end up with the Lotka-Volterra equations.

2.1 Exponential growth

The exponential growth model describes the dynamical behaviour of the size of a single species. Let us describe the size of the population with respect to time by a continuous function $f : \mathbb{R}_+ \to \mathbb{R}_+$.

Let the growth rate of f at time t be proportional to its current value $f(t)$:

$$\frac{df(t)}{dt} = bf(t). \tag{1}$$

By separation of variables, taking into account the initial value of f, the solution of (1) satisfies

$$\int_{f(0)}^{f(s)} \frac{dt}{t} = \int_0^s b dt. \tag{2}$$

Integrating the left hand side of (2) gives

$$\int_{f(0)}^{f(s)} \frac{1}{t} dt = \log(t)\Big|_{f(0)}^{f(s)} \tag{3}$$

$$= \log(f(s)) - \log(f(0)) \tag{4}$$

$$= \log\left(\frac{f(s)}{f(0)}\right). \tag{5}$$

Integrating the right hand side of (2) gives

$$\int_0^s b dt = bs. \tag{6}$$

Therefore, we obtain

$$\log\left(\frac{f(t)}{f(0)}\right) = bt \tag{7}$$

so that the solution of (1) is the exponential function

$$f(t) = f(0)e^{bt}. \tag{8}$$

When f satisfies (1) and $b > 0$, we talk about exponential growth. When the growth rate is negative, $b < 0$, we talk about exponential decay.

2.2 Simple logistic growth

The function (8) describes unbounded growth. However, when modelling a real-world phenomenon, the quantity of interest cannot usually grow exponentially forever but its growth will eventually be limited, e.g., by the lack of resources. This is when the logistic growth model steps in. The logistic growth model describes the quantity to grow first similarly to the exponential model but after a time the growth decays.

When modelled by the logistic growh, the quantity of interest is restricted by a certain level K, called the carrying capacity. This is obtained by adding a factor $1 - f/K$ into (1):

$$\frac{df(t)}{dt} = bf(t)\left(1 - \frac{f(t)}{K}\right). \tag{9}$$

The factor $1 - f(t)/K$ is close to one when $f(t) << K$ so that the growth of f is close to the exponential model. When f approaches

K, the factor $1 - f/K$ approaches zero so that the growth rate of f decays to zero.

As for the exponential growth, the solution of (9) can be obtained by separation of variables. The solution of (9) satisfies

$$\int_{f(0)}^{f(s)} \frac{dt}{t\big(1 - t/K\big)} = \int_0^s b dt. \tag{10}$$

Further, notice that the coefficient on the right hand side of (10) can be written as

$$\frac{1}{t\big(1 - t/K\big)} = \frac{1}{t} + \frac{1/K}{1 - t/K}. \tag{11}$$

Interating the second term on the right hand side of (11) gives

$$\begin{aligned}\int_{f(0)}^{f(s)} \frac{1/K}{1 - t/K} dt &= -\log(1 - t/K)\Big|_{f(0)}^{f(s)} &(12)\\ &= -\log\left(\frac{1 - f(s)/K}{1 - f(0)/K}\right). &(13)\end{aligned}$$

Therefore, integrating both sides of (10) yields to

$$\begin{aligned}bt &= \log\left(\frac{f(t)}{f(0)}\right) - \log\left(\frac{1 - f(t)/K}{1 - f(0)/K}\right) &(14)\\ &= \log\left(\frac{f(t)}{1 - f(t)/K}\frac{1 - f(0)/K}{f(0)}\right) &(15)\end{aligned}$$

or

$$e^{bt} = C\frac{f(t)}{1 - f(t)/K} \tag{16}$$

with

$$C = \frac{1 - f(0)/K}{f(0)}. \tag{17}$$

Now, $f(t)$ can be solved from (16) and reads as

$$\begin{aligned}f(t) &= \frac{e^{bt}}{C + e^{bt}/K} &(18)\\ &= \frac{K}{1 + KCe^{-bt}} &(19)\end{aligned}$$

or

$$f(t) = \frac{K}{1 + a\exp(-bt)}, \tag{20}$$

with

$$a = \frac{K}{f(0)} - 1. \tag{21}$$

We assume that

$$f(0) < K, \tag{22}$$

so that $a > 0$.

When $b > 0$, the function f is strictly increasing. For $b < 0$, the function f is strictly decreasing and we talk about reverse logistic growth. The logistic growth function ($b > 0$) has the limit

$$\lim_{t\to\infty} f(t) = \frac{K}{1 + a \cdot 0} = K. \tag{23}$$

The reverse logistic growth function ($b > 0$) approaches zero when $t \to \infty$.

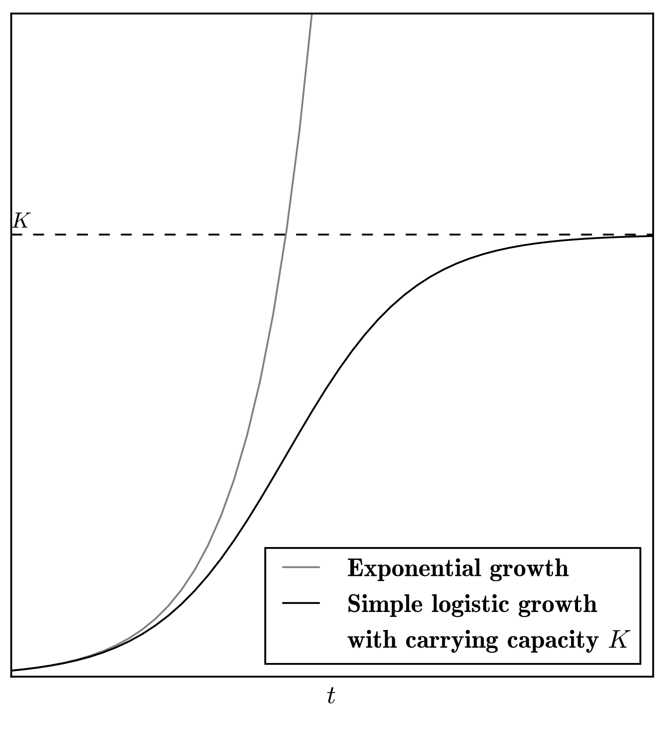


Figure 1: Exponential growth versus logistic growth.

2.3 Bi-logistic growth

The bi-logistic growth model is a sum of two separate logistic growth functions:

$$f(t) = f_1(t) + f_2(t) \tag{24}$$

where

$$f_1(t) = \frac{K_1}{1 + a_1 \exp(-b_1 t)}, \tag{25}$$

$$f_2(t) = \frac{K_2}{1 + a_2 \exp(-b_2 t)}. \tag{26}$$

See examples in Fig. 2 and 3. The model can be used to model the evolution of a single species with two growth phases (Fig. 2) but also two competitive species (Fig. 3). However, in the latter case, the interaction of the species is not taken into account.

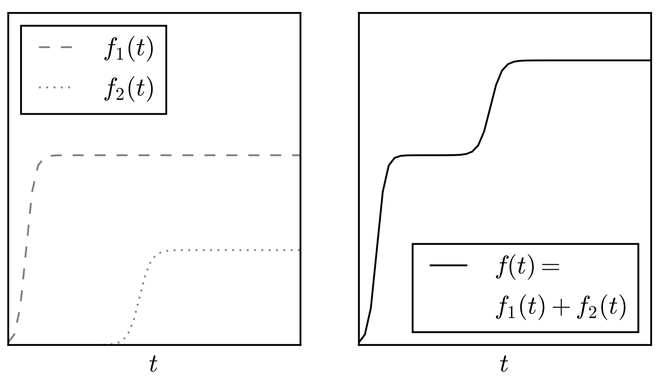


Figure 2: Bi-logistic model combines two simple logistic growth models.

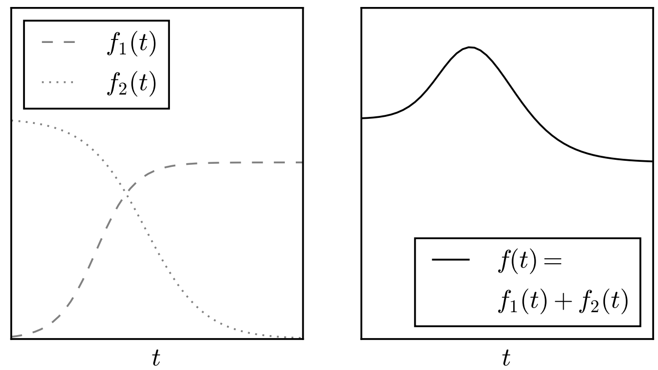


Figure 3: Bi-logistic model that combines logistic growth and decay models.

A generalization of the bi-logistic model, the multi-logistic model, naturally reads as

$$f(t) = \sum_{i=1}^{n} f_i(t) \tag{27}$$

where n is an integer and f_i, $i = 1, \ldots, n$ are simple logistic growth functions with carrying capacities K_i, growth rates b_i and coefficients a_i:

$$f_i(t) = \frac{K_i}{1 + a_i \exp(-b_i t)}. \tag{28}$$

2.4 Logistic growth within a dynamic carrying capacity

The conditions of the environment may change over time and influence the carrying capacity so that $K = K(t)$ and instead of the simple logistic growth (9) we have:

$$\frac{df(t)}{dt} = bf(t)\left(1 - \frac{f(t)}{K(t)}\right) \tag{29}$$

Of special interest here is the case in which K can also be described by the simple logistic growth model:

$$K(t) = \frac{K_K}{1 + a_K \exp(-b_K t)}, \tag{30}$$

where K_K is the ultimate carrying capacity.

The equation (29) can be written as

$$\frac{df(t)}{dt} = bf(t) - \frac{b}{K(t)} f^2(t). \tag{31}$$

This is a Bernoulli equation, and can be solved by substituting $v = 1/f$. This substitution gives

$$\frac{dv}{dt} + bv = \frac{b}{K(t)}, \tag{32}$$

which is a first order linear differential equation. The solution of (32) is given by

$$v(t) = e^{-bt}\left(v(0) + b\int_0^t \frac{e^{bs}}{K(s)} ds\right) \tag{33}$$

with the initial condition $v(0) = 1/f(0)$. From this it follows that the solution of (29)–(30) reads as

$$f(t) = K_K\left(1+\left(\frac{K_K}{f(0)}-1-\frac{b \cdot a_K}{b-b_K}\right)\exp(-bt)+\frac{b \cdot a_K}{b-b_K}\exp(-b_K t)\right)^{-1}, \tag{34}$$

where we assume that $b \neq b_K$. See an example in Fig. 4.

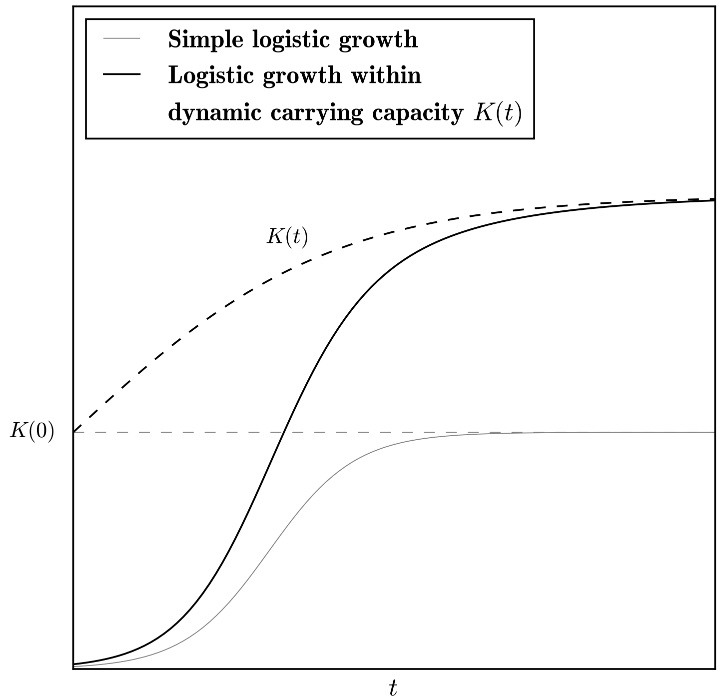


Figure 4: Logistic growth with constant vs. time-varying carrying capacity.

Example 2.1. The simple logistic growth function well describes the diffusion of refrigerators in Japan in the latter third of the twentieth century [9, Chapter 2].

In this time period, the diffusion of color TV sets can be described by a bi-logistic growth model. The first growth face is due to starting color TV broadcasting service in 1960. In 1973, color TV broadcasting became available in all TV programs, and second diffusion emerged.

An example of an innovative good that has diffused according to the logistic growth model within dynamic carrying capacity are cellular telephones. Continuous development of smaller an lighter handsets have made their diffusion process rather complicated. During 1993 to 2000, the logistic growth function within dynamic carrying capacity well describes their diffusion.

Among these innovative goods, cellular telephones have the highest

IT density. The diffusion of IT is different from that of manufacturing technology in that IT interacts with individuals and institutions, extending potential users with its newly acquired features and thus, altering the carrying capacity.

2.5 Bass model

The Bass model [2] describes the adoption of new ideas or products in a population. In the model, the adopters are classified as innovators (leaders) or as imitators (followers). Innovators are referred to as individuals who decide to adopt an innovation independently of the decisions of other individuals in a social system. Apart from innovators, imitators are influenced in the timing of adoption by the pressures of the social system. For this group, the pressure for adoption increases with the growth of the adoption process. For innovators, the opposite may be true. The Bass model aims at presenting a rationale how innovators and imitators interact.

According to the Bass model, for the number of adopters, f, it holds that

$$\frac{df(t)}{dt} = g_1(t) + g_2(t), \tag{35}$$

where

$$\begin{align} g_1(t) &= p\big(K - f(t)\big) \tag{36} \\ &= pK\left(1 - \frac{f(t)}{K}\right) \tag{37} \end{align}$$

is the number of adoptions by innovators and

$$g_2(t) = qf(t)\left(1 - \frac{f(t)}{K}\right) \tag{38}$$

is the number of adoptions by imitators. Above, p and q describe the degree of innovativeness and imitation among innovators and imitators, respectively. The speed and timing of adoption depends on these parameters. Combining (37)–(38), we have

$$\frac{df(t)}{dt} = \big(pK + qf(t)\big)\left(1 - \frac{f(t)}{K}\right). \tag{39}$$

Rewriting the equation (39) as

$$\frac{df(t)/dt}{K - f(t)} = p + \frac{q}{K}f(t) \tag{40}$$

we see that, according to the Bass model, the proportion of adopters at time t of those who have not yet adopted is equal to a linear function of previous adopters.

When $q = 0$, the equation (35) is similar to the exponential model (1) with an added constant. When $p = 0$, the equation (35) reduces to the simple logistic growth model (9).

Let us rewrite the equation (38) as

$$\frac{df(t)}{dt} = a + bf(t) - cf^2(t) \tag{41}$$

with

$$a = pK, \tag{42}$$
$$b = q - p, \tag{43}$$
$$c = -\frac{q}{K}. \tag{44}$$

The Bass diffusion is a Riccati equation with constant coefficients. To obtain the general solution to (41), let $\hat{f}$ be a known particular solution to it, and define

$$v(t) = f(t) - \hat{f}(t). \tag{45}$$

Then

$$\dot{f} = \dot{v} + \dot{\hat{f}} \tag{46}$$

with $\dot{x} = dx/dt$. Therefore, by (41),

$$\dot{v} + \dot{\hat{f}} = a + b(v + \hat{f}) + c(v + \hat{f})^2 \tag{47}$$
$$= a + bv + b\hat{f} + cv^2 + 2cv\hat{f} + c\hat{f}^2. \tag{48}$$

On the other hand, since $\hat{f}$ also satisfies (41),

$$\dot{v} + \dot{\hat{f}} = \dot{v} + a + b\hat{f} + c\hat{f}^2. \tag{49}$$

Combining (48) and (49) leads to

$$\dot{v} = (b + 2c\hat{f})v + cv^2, \tag{50}$$

which is again a Bernoulli equation. By substituting $u = v^{-1}$, the equation (50) becomes the first order linear differential equation

$$\dot{u} + (b + 2c\hat{f})u = -c. \tag{51}$$

The general solution of (51) reads as

$$u(t) = \exp\left(-bt - 2c\int \hat{f}(t)dt\right)\cdot$$
$$\cdot\left\{C - c\int \exp\left(bt + 2c\int \hat{f}(t)dt\right)dt\right\} \qquad (52)$$

with a constant C. From this, the general solution of f can be obtained.

Notice that the constant function $\hat{f}(t) = K$ satisfies (41). Moreover, assuming that

$$f(0) = 0, \qquad (53)$$

it holds

$$u(0) = -1/K. \qquad (54)$$

With the initial condition (53), by reversing the substitutions, we obtain

$$f(t) = \frac{K\left(1 - e^{-(p+q)t}\right)}{1 + \frac{q}{p}e^{-(p+q)t}}. \qquad (55)$$

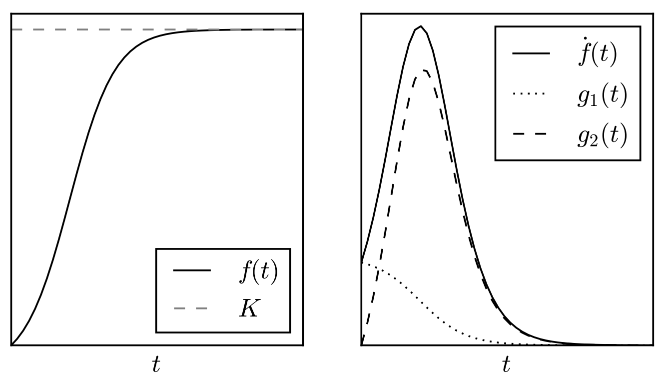


Figure 5: Bass model.

2.6 Bi-Bass model

Similarly as for the logistic growth, we may define a model that consists of two separate Bass models:

$$f(t) = f_1(t) + f_2(t), \qquad (56)$$

where

$$f_1(t) = \frac{K_1\big(1 - e^{-(p_1+q_1)t}\big)}{1 + \frac{q_1}{p_1}e^{-(p_1+q_1)t}} \quad \text{and} \tag{57}$$

$$f_2(t) = \frac{K_2\big(1 - e^{-(p_2+q_2)t}\big)}{1 + \frac{q_2}{p_2}e^{-(p_2+q_2)t}} \tag{58}$$

with K_i, p_i and q_i being the carrying capacity and the degrees of innovativeness and imitation for the model f_i.

2.7 Lotka-Volterra equations

Lotka-Volterra equations are a pair of first-order, non-linear differential equations

$$\frac{dx(t)}{dt} = b_1 x(t)\big(1 - c_1 y(t)\big), \tag{59}$$

$$\frac{dy(t)}{dt} = b_2 y(t)\big(c_2 x(t) - 1\big) \tag{60}$$

where b_1, b_2, c_1, $c_2 \in \mathbb{R}_+$. Such equations were originally used to describe a biological system consisting of a prey species x and a predator species y. Notice that, when $c_1 = 0$ or $c_2 = 0$ (meaning that y or x is not present, respectively), Eq. (59) and (60) reduce to exponential equations as in (1). In the absence of predators ($c_1 = 0$), the number of preys (x) increase exponentially. Similarly, when there are no preys ($c_2 = 0$), the number of predators (y) decrease exponentially. For simplicity, let us write (59)–(60) as

$$\dot{x} = x\big(a - by\big), \tag{61}$$

$$\dot{y} = y\big(dx - c\big) \tag{62}$$

with a, b, c, $d \in \mathbb{R}$.

In many applications, the solutions of (59)–(60) are sought in $\mathbb{R}^2_+$. Such solutions also are of interest here. Closed form solutions are usually difficult to find to this kind of systems, and therefore, numerical methods are often employed. For example, Matlab's *ode* functions are built for solving differential equations.

However, we can often gain some qualitative knowledge about the solutions. For this, we may be interested in states of the system which does not change. This means that

$$\frac{dx(t)}{dt} = 0, \tag{63}$$

$$\frac{dy(t)}{dt} = 0. \tag{64}$$

A point $(x(t), y(t))$ that satisfies (63)–(64) is called an *equilibrium.*

Consider the equilibria of (61)–(62). We notice that (61) is zero when $x = 0$ or $a - by = 0$, the latter being equivalent with $y = \overline{y}$ with

$$\overline{y} = \frac{a}{b}. \tag{65}$$

Similarly, (62) is zero when $y = 0$ or $x = \overline{x}$ with

$$\overline{x} = \frac{c}{d}. \tag{66}$$

In addition to how the solutions of (61)–(62) change in time, we are interested in how the quantities described by x and y change with respect to each other. Let $t \to (x(t), y(t))$ be a solution to (61)–(62) defined on an interval $I \subseteq \mathbb{R}_+$. Then the set of points

$$\mathcal{O} = \Big\{ (x(t), y(t)) : \ \ t \in I \Big\} \subset \mathbb{R}^2 \tag{67}$$

is called an orbit of (61)–(62). We may think of the solutions as points in the $x - y$ plane. An $x - y$ plane presenting the equilibrium points of the system and the behaviour of its orbits is called the *phase plane.*

Let us study the orbits of the Lotka-Volterra equations. First, we may write (61)–(62) as

$$\frac{1}{x}\dot{x} = a - by, \tag{68}$$

$$\frac{1}{y}\dot{y} = dx - c. \tag{69}$$

The solutions of (68)–(69) satisfy

$$\frac{1}{x}\dot{x}(dx - c) - \frac{1}{y}\dot{y}(a - by) = 0 \tag{70}$$

or

$$c\frac{1}{x}\dot{x} - d\dot{x} + a\frac{1}{y}\dot{y} - b\dot{y} = 0. \tag{71}$$

By noticing that

$$\frac{1}{x(t)}\dot{x}(t) = \frac{d}{dt}\log(x(t)), \tag{72}$$

we may write (71) as

$$\frac{d}{dt}(c\log(x) - dx + a\log(y) - by) = 0, \tag{73}$$

or

$$\frac{d}{dt}\big\{d(\overline{x}\log(x) - x) + b(\overline{y}\log(y) - y)\big\}. \tag{74}$$

By defining functions

$$H(x) = \overline{x}\log(x) - x, \tag{75}$$

$$G(y) = \overline{y}\log(y) - y \tag{76}$$

and

$$V(x,y) = dH(x) + bG(y), \tag{77}$$

Eqn. (74) can be written as

$$\frac{dV(x,y)}{dt} = 0. \tag{78}$$

When (x,y) is a solution of (61)–(62), it satisfies (78) so that the orbits of (61)–(62) can be found at the contours of V. The function V obtains its maximum at $(\overline{x},\overline{y})$. Therefore, the orbits of (61)–(62) are closed curves and the solutions are periodic with respect to time.

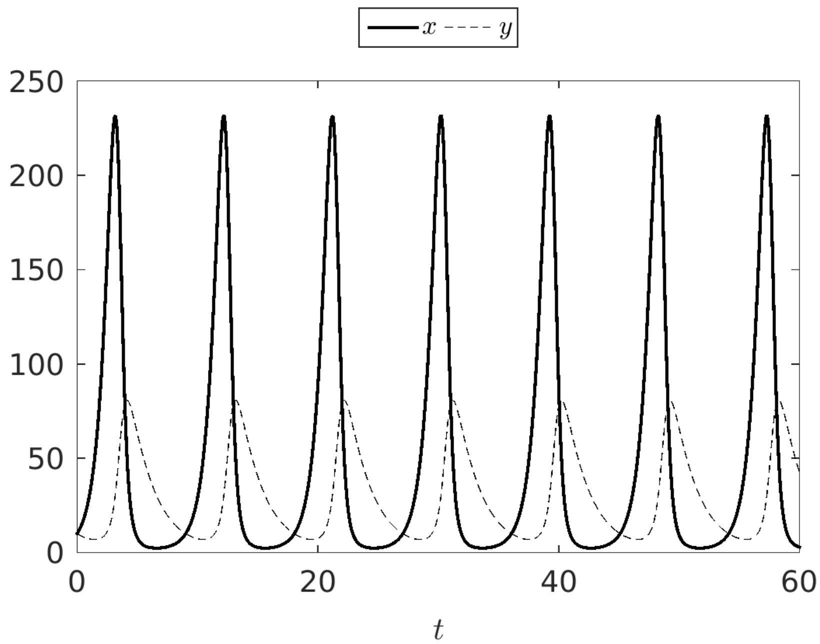


Figure 6: A solution with respect to time to the Lotka-Volterra equations with $a = 1.5$, $b = 0.05$, $c = 0.5$, $d = 0.01$ and $x(0) = y(0) = 10$. Simulated with Matlab's *ode45*.

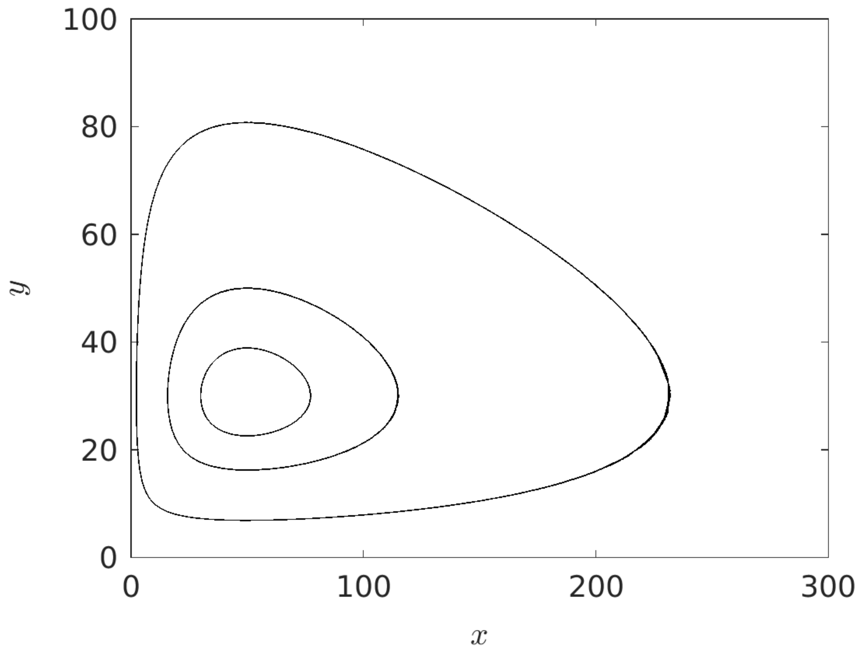


Figure 7: Orbits of the Lotka-Volterra equations with different initial conditions. Simulated with Matlab's *ode45*.

It turns out that $\overline{x}$ and $\overline{y}$ are the mean values of x and y on a period. Indeed, suppose that the period of an orbit is T. Thus, $x(T) = x(0)$, and from (61) it follows by integration that

$$\int_0^T \frac{d}{dt} \log x dt = \int_0^T (a - by) dt \tag{79}$$

i.e.

$$0 = \log x(T) - \log x(0) = aT - b \int_0^T y(t) dt. \tag{80}$$

Therefore,

$$\overline{y} = \frac{1}{T} \int_0^T y dt. \tag{81}$$

Similarly, one obtains

$$\overline{x} = \frac{1}{T} \int_0^T x dt. \tag{82}$$

In the Lotka-Volterra equations (59)–(60), the base population models are exponential. A similar system, but with a logistic population base model, is obtained by adding terms for intraspecific competition in (59)–(60):

$$\frac{dx(t)}{dt} = b_1 x(t)\big(1 - c_1 y(t) - \frac{x(t)}{K_1}\big), \tag{83}$$

$$\frac{dy(t)}{dt} = b_2 y(t)\big(c_2 x(t) - 1 - \frac{y(t)}{K_2}\big). \tag{84}$$

However, in the following, instead of (83)–(84) we study a system with slightly different coefficients.

2.8 Competitive Lotka-Volterra equations

The competitive Lotka-Volterra equations of two species read as

$$\frac{dx(t)}{dt} = b_1 x(t)\left(1 - \frac{x(t) + a_1 y(t)}{K_1}\right), \tag{85}$$

$$\frac{dy(t)}{dt} = b_2 y(t)\left(1 - \frac{y(t) + a_2 x(t)}{K_2}\right), \tag{86}$$

where b_1, b_2, a_1 and a_2 are positive real-valued constants. Above, b_1, b_2 are diffusion coefficients, a_1 and a_2 are interaction coefficients and K_1 and K_2 are the carrying capacities of f_1 and f_2. When x is stronger enough than y, we may approximate $a_1 \approx 0$ in (85) and the diffusion of x is described by the simple logistic growth model as in (9).

Let us study the equilibrium points of (85)–(86). The derivative of x is zero, when $x = 0$ or

$$y(t) = \frac{K_1}{a_1} - \frac{1}{a_1} x(t). \tag{87}$$

Similarly, $d(y(t))/dt = 0$ when $y = 0$ or

$$y(t) = K_2 - a_2 x(t). \tag{88}$$

Equations (87) and (88) define decreasing straight lines in $x - y$ coordinates. These lines are called the zero *isoclines* of x and y.

With the help of the zero isoclines we may study the behaviour of the orbits of (85)–(86). First, we notice that each of the zero isoclines divides $\mathbb{R}_+^2$ into two regions. When $(x(t), y(t))$ is below the isocline (87), $x(t)$ increases since

$$dx(t)/dt > 0. \tag{89}$$

Similarly, when $(x(t), y(t))$ is below the isocline (88),

$$dy(t)/dt > 0 \tag{90}$$

and therefore $y(t)$ increases. When $(x(t), y(t))$ is above (87) or (88), $x(t)$ or $y(t)$ decreases, respectively. See Fig. 8.

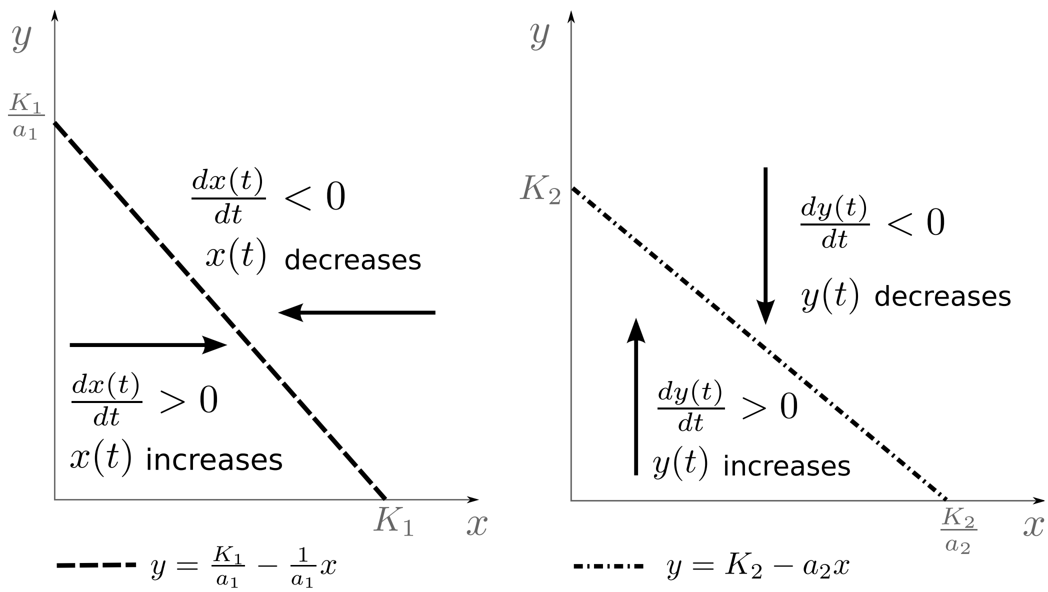


Figure 8: The zero isoclines and the behaviour of the solutions with respect to them. Adapted from [3, Figure 8.7].

How an orbit of (85)–(86) behaves depends on how the isoclines are located in $\mathbb{R}_+^2$ with respect to each other. Here we have four different scenarios. See Fig. 9. The figure in the upper left corner illustrates the scenario when the isocline of x is above the isocline of y. When a point $(x(t), y(t))$ is below both of the isoclines, both $x(t)$ and $y(t)$ increase. Similarly, when $(x(t), y(t))$ is above both of the isoclines, both $x(t)$ and $y(t)$ decrease. When $x(t)$ is below the isocline of x but $y(t)$ is above the isocline of y, $x(t)$ increases but $y(t)$ decreases and the orbit heads toward the point $(K_2/a_2, 0)$. In this scenario, species x outcompetes species y. The point $(K_2/a_2, 0)$ is a *stable equilibrium* of the system, i.e., when the system is near the equilibrium, it approaches it. In fact, in this scenario, the system approaches the equilibrium point regardless of its initial position.

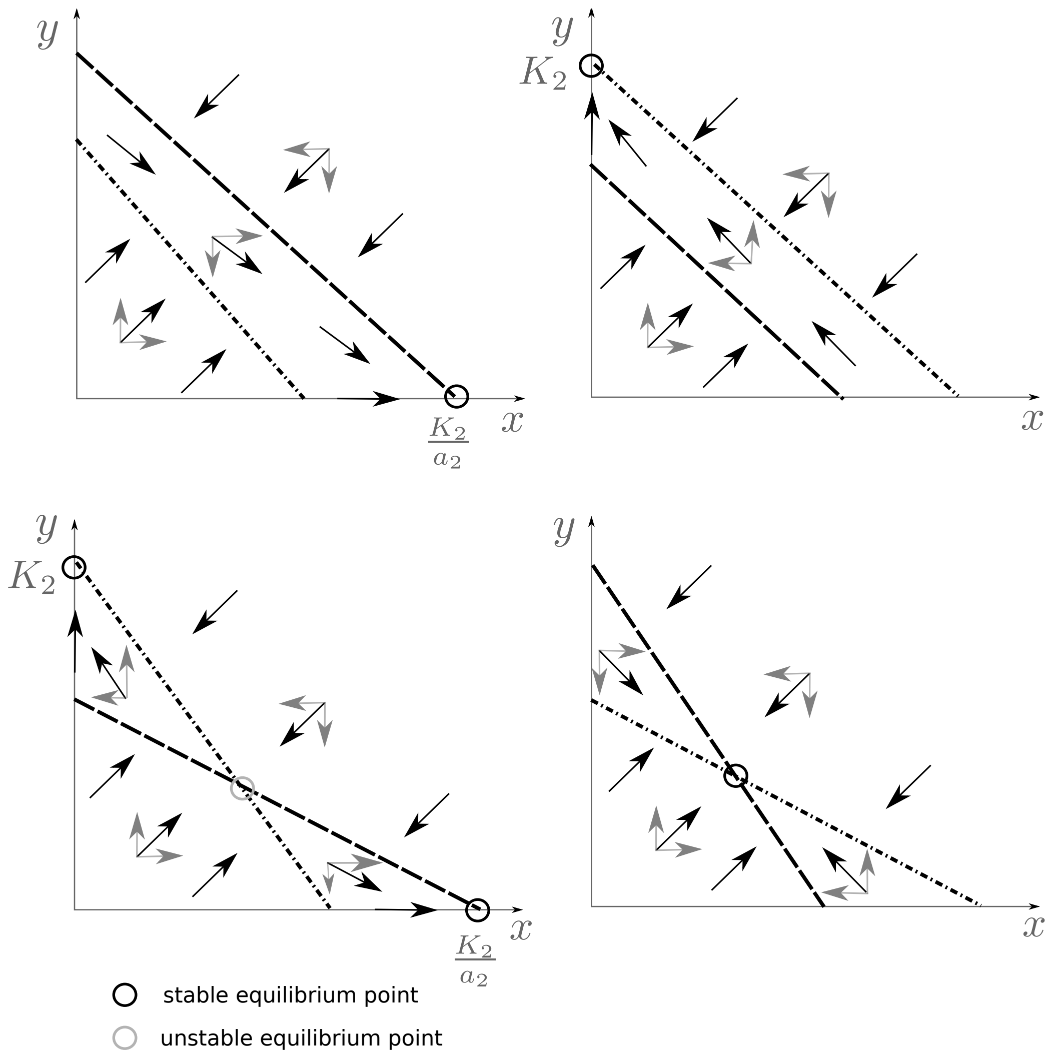
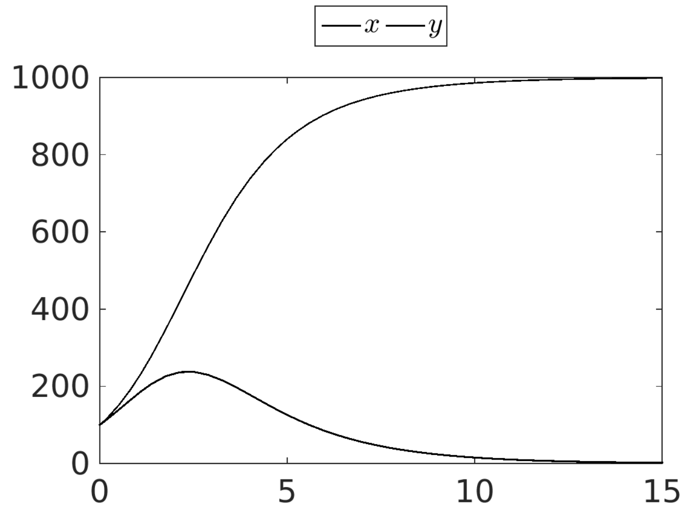
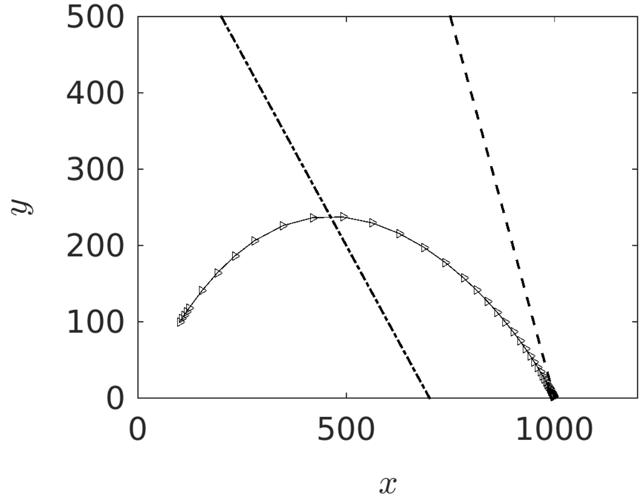


Figure 9: The behaviour of the orbits with respect to the two isoclines. Adapted from [3, Figure 8.9].



(a) A solution with respect to time.



(b) Isoclines and an orbit.

Figure 10: Competitive Lotka-Volterra equations with $K_1 = 1000$, $K_2 = 700$, $a_1 = 0.5$, $a_2 = 1$ and $x(0) = y(0) = 100$. The solutions are simulated with Matlab's *ode45*.

The orbit of (85)–(86) behaves similarly in the scenario illustrated in the figure on the upper right of Fig. 9. In this scenario, the isocline of y is above the isocline of x and the stable equilibrium point is $(0, K_2)$. Fig. 10 shows a simulated solution to (85)–(86) when the isocline of y is above the isocline of x.

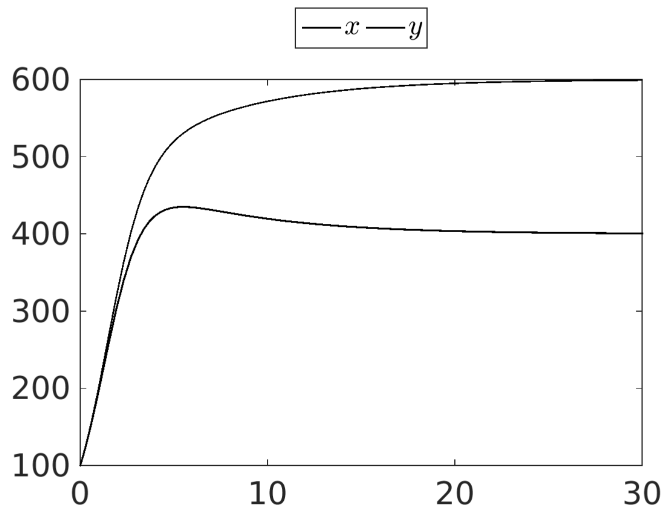
In the other two scenarios the isoclines cross each other. The scenario when the isocline of x crosses the y axis below the isocline of y is illustrated in the lower left corner of Fig. 9. As before, when a point is below or above both of the isoclines, both $x(t)$ and $y(t)$ increase or decrease, respectively. Similarly, when the point is above the isocline of x and below the isocline of y, $x(t)$ decreases and $y(t)$ increases, and the point $(0, K_2)$ is a stable equilibrium. Another stable equilibrium point is $(K_2/a_2, 0)$. The point where the isoclines cross each other is an equilibrium point that is *unstable*, i.e., a system near the equilibrium might move away from it.

The scenario when the isocline of x crosses the y axel above the isocline of y is illustrated in the lower right corner of Fig. 9. This differs from the scenario shown in the lower left corner in that when $(x(t), y(t))$ is between the isoclines, it moves towards the point where the isoclines cross. This point is a stable equilibirum point. Fig. 11 shows a numerical solution to (85)–(86) when the isoclines cross.

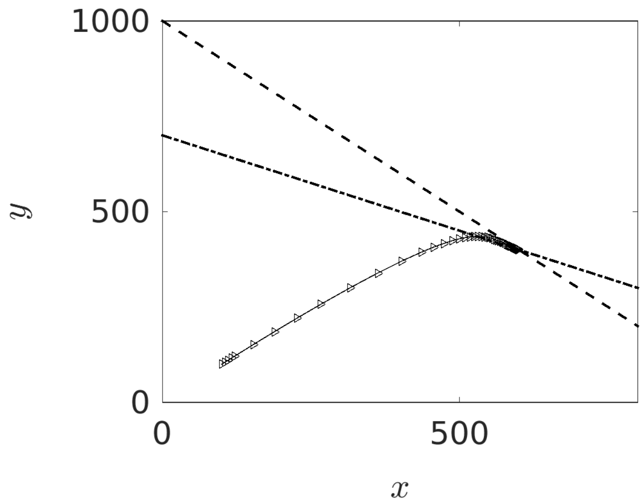
The Lotka-Volterra equations can be generalized for a system with n species by defining

$$\frac{dx_i(t)}{dt} = x_i(b_i + \sum_{j=1}^{n} a_{ij}x_j), \tag{91}$$

where x_i denotes the quantity of the ith species, b_i denotes its intrinsic growth rate and the matrix $A = (a_{ij})$ is the interaction matrix. For further reading on Lotka-Volterra equations, see [6, Chapter 11] and [9, Chapter 4].



(a) A solution with respect to time.



(b) Isoclines and an orbit.

Figure 11: Competitive Lotka-Volterra equations with $K_1 = 1000$, $K_2 = 700$, $a_1 = 1$, $a_2 = 0.5$ and $x(0) = y(0) = 100$.

Example 2.2. The diffusion process of TV sets in Japan can be described by the competitive Lotka-Volterra model. Television broadcasting started in Japan in 1953, followed by the color TV broadcasting in 1960 [9, Chapter 4]. Since 1960, the diffusion of color TV sets rapidly increased and exceeded that of monochrome TV sets around 1973 when color TV broadcasting became available in all TV programs.

After color TV broadcasting had started, people could watch color TV broadcasting by their monochrome TV sets as monochrome TV programs. Thus, people could choose either monochrome or color TV sets according to their preferences and, in this sense, color and monochrome TV broadcasting were competitive.

Also, the substitution from fixed to cellular telephones can be described by the competitive Lotka-Volterra equations. The number of subscribers of fixed telephones exhibited a rapid increase from the middle of the 1960s to the middle of the 1980s, but in the 1990s it first stagnated and then started to decrease in 1996. The development in the number of subscribers to fixed telephones in the 1990s can be explained by the emergence of cellular telephones, which developed their subscribers in the 1990s due to deregulations.

Cellular telephones are regarded as a complementery method to fixed telephones but also as a substitute for them. Thus, the relationship between fixed and cellular telephones can be considered as both complementery and substitute.

The competitive Lotka-Volterra equations also describe the subsitution from cellular telephones to mobile Internet access as well as the substitution from analog to digital TV broadcasting system.

3 Conclusions

Models for describing the dynamical behaviour of populations were reviewed. The exponential and logistic growth functions, the Bass model and the Lotka-Volterra equations as well as the relations of these models to each other were discussed. Main concepts related to studying the behaviour of the models were presented.

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