

# Introduction to Evolutionary Games

## Escuela de Bioestocástica

Kerlyns Martínez - Nicolás Rivera

# Evolutionary Operators

---

We will study basic building blocks of evolutionary dynamics: **Reproduction**, **Selection** and **Mutation**

We will study basic building blocks of evolutionary dynamics: **Reproduction**, **Selection** and **Mutation**

- ▶ they represent the fundamental and defining principles of biological systems

We will study basic building blocks of evolutionary dynamics: **Reproduction**, **Selection** and **Mutation**

- ▶ they represent the fundamental and defining principles of biological systems
  - ▶ **Reproduction**: allows a species to pass on its offspring

We will study basic building blocks of evolutionary dynamics: **Reproduction**, **Selection** and **Mutation**

- ▶ they represent the fundamental and defining principles of biological systems
  - ▶ **Reproduction**: allows a species to pass on its offspring
  - ▶ **Selection**: allows species to compete with each other, e.g. one reproduces faster than the other

We will study basic building blocks of evolutionary dynamics: **Reproduction**, **Selection** and **Mutation**

- ▶ they represent the fundamental and defining principles of biological systems
  - ▶ **Reproduction**: allows a species to pass on its offspring
  - ▶ **Selection**: allows species to compete with each other, e.g. one reproduces faster than the other
  - ▶ **mutation**: species 'transform' into other.

We will study basic building blocks of evolutionary dynamics: **Reproduction**, **Selection** and **Mutation**

- ▶ they represent the fundamental and defining principles of biological systems
  - ▶ **Reproduction**: allows a species to pass on its offspring
  - ▶ **Selection**: allows species to compete with each other, e.g. one reproduces faster than the other
  - ▶ **mutation**: species 'transform' into other.
- ▶ Combination of them allows us to create different evolutionary dynamics

## Reproduction

---

Let's imagine a single bacterial cell in a perfect environment containing all the nutrients required for it to survive, and reproduce.

- ▶ Suppose the bacteria divides into two every 20 minutes
- ▶ Then after 20 minutes we will have 2 bacteria
- ▶ after 40 we will have 4
- ▶ after 60 we will have 8
- ▶ in general, after  $20t$  minutes, we will have  $2^t$  bacteria



## Reproduction

---

Let's imagine a single bacterial cell in a perfect environment containing all the nutrients required for it to survive, and reproduce.

- ▶ Suppose the bacteria divides into two every 20 minutes
- ▶ Then after 20 minutes we will have 2 bacteria
- ▶ after 40 we will have 4
- ▶ after 60 we will have 8
- ▶ in general, after  $20t$  minutes, we will have  $2^t$  bacteria

Mathematically, we can denote by  $x_t$  the number of cells in the environment after  $20t$  minutes. Then we have the following [difference equation](#)

## Reproduction

Let's imagine a single bacterial cell in a perfect environment containing all the nutrients required for it to survive, and reproduce.

- ▶ Suppose the bacteria divides into two every 20 minutes
- ▶ Then after 20 minutes we will have 2 bacteria
- ▶ after 40 we will have 4
- ▶ after 60 we will have 8
- ▶ in general, after  $20t$  minutes, we will have  $2^t$  bacteria

Mathematically, we can denote by  $x_t$  the number of cells in the environment after  $20t$  minutes.

Then we have the following **difference equation**

**Difference equation for reproduction only**

$$x_{t+1} = 2x_t \quad t \in \{0, 1, 2, \dots, \}$$

## Reproduction

Let's imagine a single bacterial cell in a perfect environment containing all the nutrients required for it to survive, and reproduce.

- ▶ Suppose the bacteria divides into two every 20 minutes
- ▶ Then after 20 minutes we will have 2 bacteria
- ▶ after 40 we will have 4
- ▶ after 60 we will have 8
- ▶ in general, after  $20t$  minutes, we will have  $2^t$  bacteria

Mathematically, we can denote by  $x_t$  the number of cells in the environment after  $20t$  minutes.

Then we have the following **difference equation**

Difference equation for reproduction only

$$x_{t+1} = 2x_t \quad t \in \{0, 1, 2, \dots, \}$$

The solution for this difference equation is given by

Discrete-time exponential growth

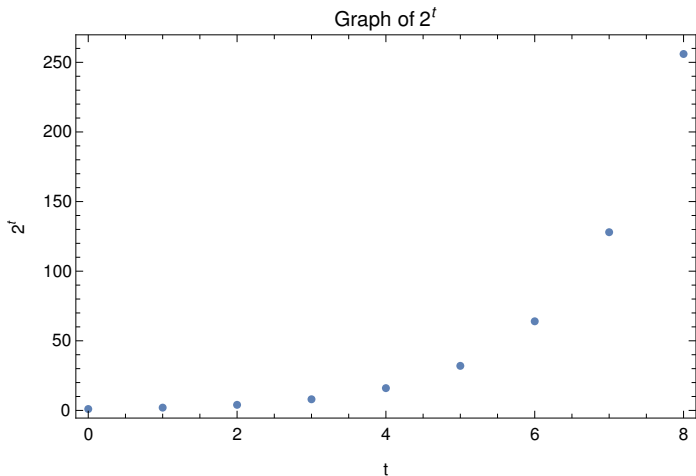
$$x_t = x_0 2^t \quad t \in \{0, 1, 2, \dots, \}$$

where  $x_0$  is the initial number of cells.

$$x_t = x_0 2^t \quad t \in \{0, 1, 2, \dots, \}$$

where  $x_0$  is the initial number of cells.

In our case  $x_0 = 1$  since we have one bacterium



This is the famous **exponential** growth.

# Reproduction

---

So far so good...

However, instead of thinking about reproduction over epochs, it is more convenient to think about reproduction rates.

There are many reasons

1. Solving [difference equations](#) is hard
2. Modelling with [difference equations](#) is hard
3. understanding [difference equations](#), without solving them, is hard

# Reproduction

---

So far so good...

However, instead of thinking about reproduction over epochs, it is more convenient to think about reproduction rates.

There are many reasons

1. Solving **difference equations** is hard
2. Modelling with **difference equations** is hard
3. understanding **difference equations**, without solving them, is hard

On the other hand, working with rates lead to **differential equations**. These has been used for many years in physical modelling, and we understand them much better than **difference equations** as they tend to be easier to solve and study.

In some sense, we want to do **classical mechanics** in biology, but instead of spheres and cars with mass, we have biological entities

## Reproduction in continuous time

---

Consider again our population of cells, but this time  $x(t)$  denotes the mechanisc of cells at time  $t$ , with  $t \in [0, \infty)$ .

- ▶ We consider **continuous** time  $t$

## Reproduction in continuous time

---

Consider again our population of cells, but this time  $x(t)$  denotes the mechanisc of cells at time  $t$ , with  $t \in [0, \infty)$ .

- ▶ We consider **continuous** time  $t$
- ▶  $t$  can be measure in seconds, minutes, hours, days, it doesn't matter, but we need to be clear about it in order to



## Reproduction in continuous time

---

Consider again our population of cells, but this time  $x(t)$  denotes the mechanisc of cells at time  $t$ , with  $t \in [0, \infty)$ .

- ▶ We consider **continuous** time  $t$
- ▶  $t$  can be measure in seconds, minutes, hours, days, it doesn't matter, but we need to be clear about it in order to **make sense of the numbers**
- ▶  $x(t)$  will also be **continuous**, meaning that it can take value 1.2 or  $\pi$ ,

## Reproduction in continuous time

---

Consider again our population of cells, but this time  $x(t)$  denotes the mechanisc of cells at time  $t$ , with  $t \in [0, \infty)$ .

- ▶ We consider **continuous** time  $t$
- ▶  $t$  can be measure in seconds, minutes, hours, days, it doesn't matter, but we need to be clear about it in order to **make sense of the numbers**
- ▶  $x(t)$  will also be **continuous**, meaning that it can take value 1.2 or  $\pi$ ,
- ▶ It is ok to think that  $x(t)$  is the number of cells, but probably it is more convenient to use a continuous measure, such as
  1. **weight (biomass)**
  2. **volume**

## A continuous-time model for Reproduction

---

- ▶ Let  $x(t)$  denotes the *number* of cells at time  $t$  for times  $t \in [0, \infty)$ .

## A continuous-time model for Reproduction

---

- ▶ Let  $x(t)$  denotes the *number* of cells at time  $t$  for times  $t \in [0, \infty)$ .
- ▶ and suppose that cells divide into two at *rate*  $r$

## A continuous-time model for Reproduction

---

- ▶ Let  $x(t)$  denotes the *number* of cells at time  $t$  for times  $t \in [0, \infty)$ .
- ▶ and suppose that cells divide into two at *rate*  $r$
- ▶ *rate* is the equivalent to velocity in classical mechanics

## A continuous-time model for Reproduction

- ▶ Let  $x(t)$  denotes the *number* of cells at time  $t$  for times  $t \in [0, \infty)$ .
- ▶ and suppose that cells divide into two at *rate*  $r$
- ▶ *rate* is the equivalent to velocity in classical mechanics
- ▶ Then, the dynamics satisfies

Differential Equation for reproduction only

$$\frac{d}{dt}x(t) = rx(t), \quad t > 0$$

which is usually written by

$$\dot{x}(t) = rx(t), \quad t > 0$$

or even shorter

$$\dot{x} = rX$$

## A continuous-time model for Reproduction

- ▶ Let  $x(t)$  denotes the *number* of cells at time  $t$  for times  $t \in [0, \infty)$ .
- ▶ and suppose that cells divide into two at *rate*  $r$
- ▶ *rate* is the equivalent to velocity in classical mechanics
- ▶ Then, the dynamics satisfies

Differential Equation for reproduction only

$$\frac{d}{dt}x(t) = rx(t), \quad t > 0$$

which is usually written by

$$\dot{x}(t) = rx(t), \quad t > 0$$

or even shorter

$$\dot{x} = rX$$

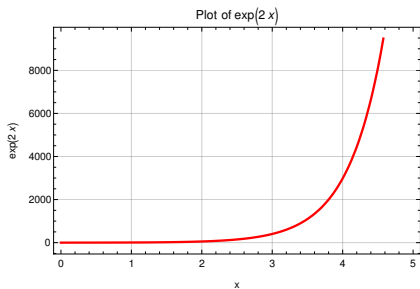
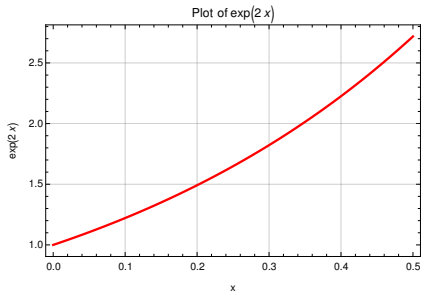
The solution of this differential equation is

Continuous-time exponential growth

$$x(t) = x_0 e^{rt}$$

## Continuous-time exponential growth

$$x(t) = x(0)e^{rt}$$



In the pictures we have  $x(0) = 1$  and  $r = 2$ .



# Reproduction and Death

---

- ▶ Let  $x(t)$  denotes the *abundance* of cells at time  $t$
- ▶ **Birth:** cells *divides* at rate  $r$
- ▶ **Death:** cells *die* at rate  $d$
- ▶ the dynamics satisfy the equation

# Reproduction and Death

---

- ▶ Let  $x(t)$  denotes the *abundance* of cells at time  $t$
- ▶ **Birth:** cells *divides* at rate  $r$
- ▶ **Death:** cells *die* at rate  $d$
- ▶ the dynamics satisfy the equation

$$\dot{x}(t) = (r - d)x(t) \quad t > 0,$$

## Reproduction and Death

- ▶ Let  $x(t)$  denotes the *abundance* of cells at time  $t$
- ▶ **Birth:** cells *divides* at rate  $r$
- ▶ **Death:** cells *die* at rate  $d$
- ▶ the dynamics satisfy the equation

$$\dot{x}(t) = (r - d)x(t) \quad t > 0,$$

which solution is given by

Simple birth-and-death equation

$$x(t) = x_0 e^{(r-d)t}$$

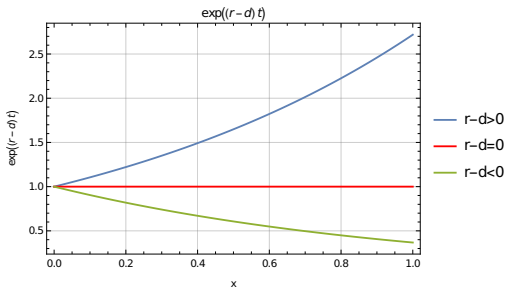
## A continuous-time model

Simple birth-and-death equation

$$x(t) = x_0 e^{(r-d)t}$$

Here we have three behaviours

1.  $r > d$ , then the population size grows to infinity
2.  $r < d$ , then the population size tends to 0
3.  $r = d$ , the population size remains fixed. Note, however, that a minimal change in  $r$  and  $d$  will change the behaviour of the dynamic.



## A continuous-time model: size-dependent effects

---

We can make our model a bit more complex

- ▶ **Birth:** cells **divides** at rate  $r$
- ▶ **Death:** cells **die** at rate  $x \cdot d$  when the **abundance** is  $x$

## A continuous-time model: size-dependent effects

We can make our model a bit more complex

- ▶ **Birth:** cells **divides** at rate  $r$
- ▶ **Death:** cells **die** at rate  $x \cdot d$  when the **abundance** is  $x$
- ▶ In this model the more cells we have, the faster they die: e.g. they are competing for nutrients, space, or just fight
- ▶ In this case, the dynamics satisfies the equation

$$\dot{x}(t) = (r - d \cdot x(t))x(t) \quad t > 0,$$

which is commonly written as

Logistic equation

$$\dot{x}(t) = rx(t)(1 - x(t)/K)$$

where  $K = r/d$ .

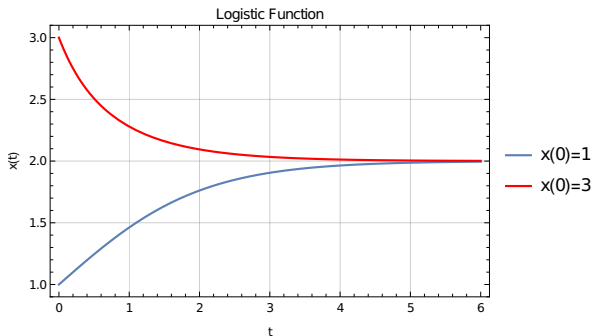
whose solution is

Logistic function

$$x(t) = \frac{Kx_0 e^{rt}}{K + x_0(e^{rt} - 1)}$$

## Logistic function

$$x(t) = \frac{Kx_0e^{rt}}{K + x_0(e^{rt} - 1)}$$



Example with  $K = 2$  and  $r = 1$

We have seen so far a few equations, but how do we come up with equations ourselves?



We have seen so far a few equations, but how do we come up with equations ourselves?

To write our own model, we need to be willing to

1. write equations that **roughly explain the situation**
2. make **concessions**

## Writing models

---

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

## Writing models

---

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years

## Writing models

---

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years
2.  $x(t)$  denotes the number of birds

## Writing models

---

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years
2.  $x(t)$  denotes the number of birds
3.  $x(0)$  is not given

## Writing models

---

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years
2.  $x(t)$  denotes the number of birds
3.  $x(0)$  is not given
4. we model  $\dot{x}$

## Writing models

---

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years
2.  $x(t)$  denotes the number of birds
3.  $x(0)$  is not given
4. we model  $\dot{x}$
5. reproduction add  $3x$  to the derivative

## Writing models

---

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years
2.  $x(t)$  denotes the number of birds
3.  $x(0)$  is not given
4. we model  $\dot{x}$
5. reproduction add  $3x$  to the derivative
6. the dead rate is 0.1 per year, so it adds  $-0.1x$  to the derivative



## Writing models

---

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years
2.  $x(t)$  denotes the number of birds
3.  $x(0)$  is not given
4. we model  $\dot{x}$
5. reproduction add  $3x$  to the derivative
6. the dead rate is 0.1 per year, so it adds  $-0.1x$  to the derivative
7. fights are a bit hard but the number of pairs is (roughly) $x^2/2$ ,

## Writing models

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years
2.  $x(t)$  denotes the number of birds
3.  $x(0)$  is not given
4. we model  $\dot{x}$
5. reproduction add  $3x$  to the derivative
6. the dead rate is 0.1 per year, so it adds  $-0.1x$  to the derivative
7. fights are a bit hard but the number of pairs is (roughly)  $x^2/2$ , the fighting rate is 4 per year, the average outcome of the fight is an average of  $\frac{3}{1000}$  dead birds. Therefore, due to fights we add the term  $-\frac{x^2}{2} \cdot 4 \cdot \frac{3}{1000}$

## Writing models

**Exercise:** Imagine a bird population on an isolated island. Birds reproduce at rate 3 per year, and they die at rate 1 every 10 years. Unfortunately, these Birds attack each other: in particular, each pairs of birds fight at rate 1 every three months. The outcome of the fight is that 0.1% of the time both die, 0.1% only one dies, and the rest of the time both survive.

1. We measure time in years
2.  $x(t)$  denotes the number of birds
3.  $x(0)$  is not given
4. we model  $\dot{x}$
5. reproduction add  $3x$  to the derivative
6. the dead rate is 0.1 per year, so it adds  $-0.1x$  to the derivative
7. fights are a bit hard but the number of pairs is (roughly)  $x^2/2$ , the fighting rate is 4 per year, the average outcome of the fight is an average of  $\frac{3}{1000}$  dead birds. Therefore, due to fights we add the term  $-\frac{x^2}{2} \cdot 4 \cdot \frac{3}{1000}$
8. Finally

$$\begin{aligned}\dot{x} &= 2.9x - \frac{6}{1000}x^2 = x(2.9 - 0.006x) \\ &= rx(1 - x/K)\end{aligned}$$

with  $r = 2.9$  and  $K = \frac{2.9}{0.006} \approx 483.333$ .

9. We recognise a logistic function, so for large times  $t$  we have a population of 483 birds, approximately.

Our logistic function with  $r = 2.9$  and  $K \approx 483.333$  looks like

