

# 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**

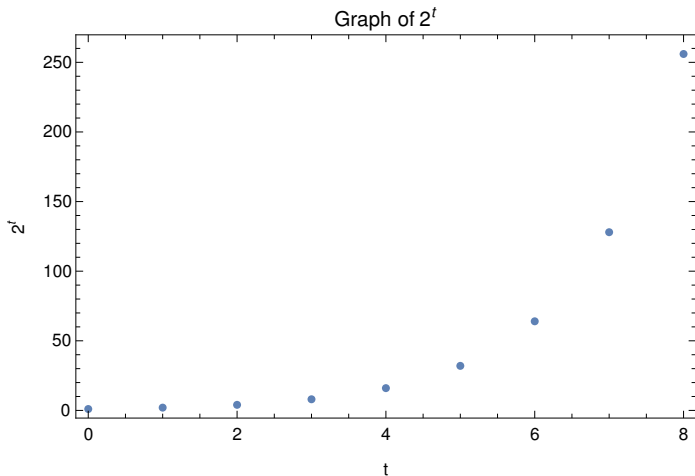
$$x_t = x_0 2^t \quad t \in \{0, 1, 2, \dots, \}$$

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  $t$

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



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  $\pi$ ,

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

$$\dot{x} = rx$$

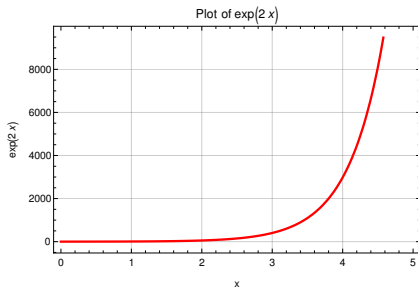
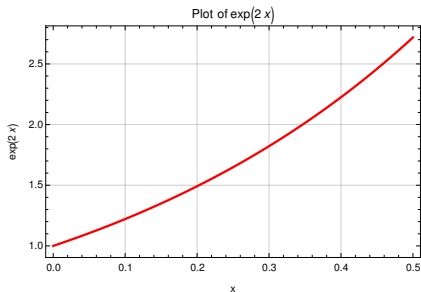
The solution of this differential equation is

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

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

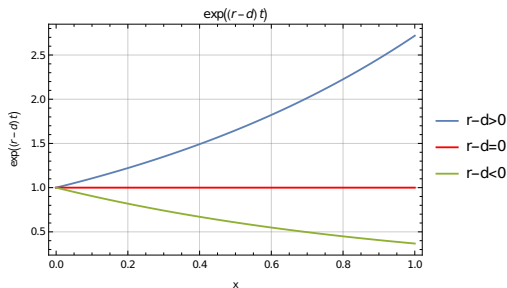
# A continuous-time model

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  $K = r/d$ .

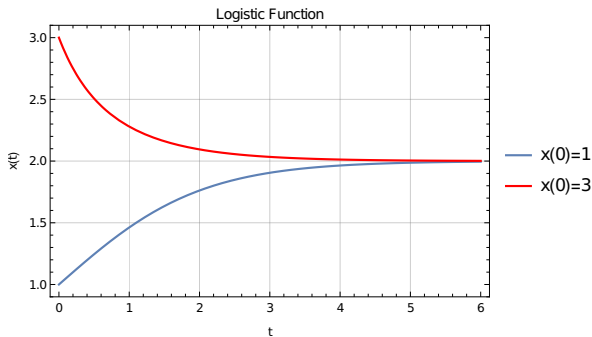
whose solution is

Logistic function

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

## Logistic function

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



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 773 birds, approximately.

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

