Algebraic and Discrete Methods in Biology

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Difference Equations

Introduction

For we will always have as 5 is to 8 so is 8 to 13, practically, and as 8 is to 13, so is 13 to 21 almost.

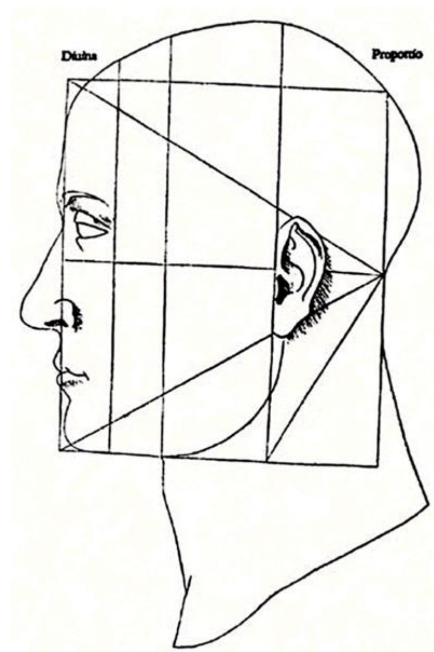
I think that the seminal faculty is developed in a way analogous to this proportion which perpetuates itself, and so in the flower is displayed a pentagonal standard, so to speak. I let pass all other considerations which might be adduced by the most delightful study to establish this truth.

J. Kepler, Sterna seu de nive sexangule, 1611

Introduction

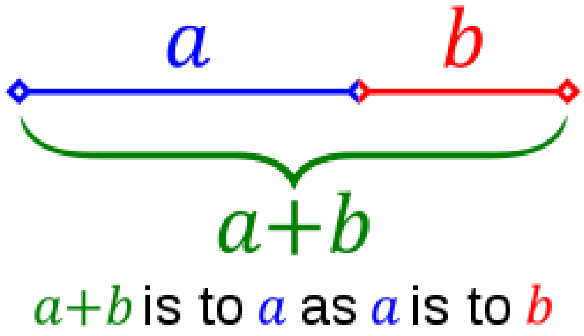
- The early Greeks were fascinated by numbers and believed them to hold magical properties.

- Proportions:



Introduction

- Golden mean:



- Two quantities *a* and *b* are said to be in the *golden ratio φ* if: $$\frac{a+b}{a} = \frac{a}{b} = \varphi \,.$$

- $$\varphi = \frac{1+\sqrt{5}}{2} \approx 1.6180339887\ldots$$

Introduction

- Leonardo of Pisa – Fibonacci (1175-1250) proposed a problem whose solution is the series:

  0, 1, 1, 2, 3, 5, 8, 13, 21, …

- By definition, the first two Fibonacci numbers are 0 and 1, and each remaining number is the sum of the previous two.

Fibonacci Numbers

- Kepler observed that successive elements of the Fibonacci sequence satisfy the following recursive relation:

$$F_n = F_{n-1} + F_{n-2}$$

Fibonacci Numbers

- Kepler also observed that the ratio of consecutive Fibonacci numbers converges.
- He wrote that "as 5 is to 8 so is 8 to 13, practically, and as 8 is to 13, so is 13 to 21 almost", and concluded that the limit approaches the golden ratio φ

$$\lim_{n\to\infty} \frac{F(n+1)}{F(n)} = \varphi$$

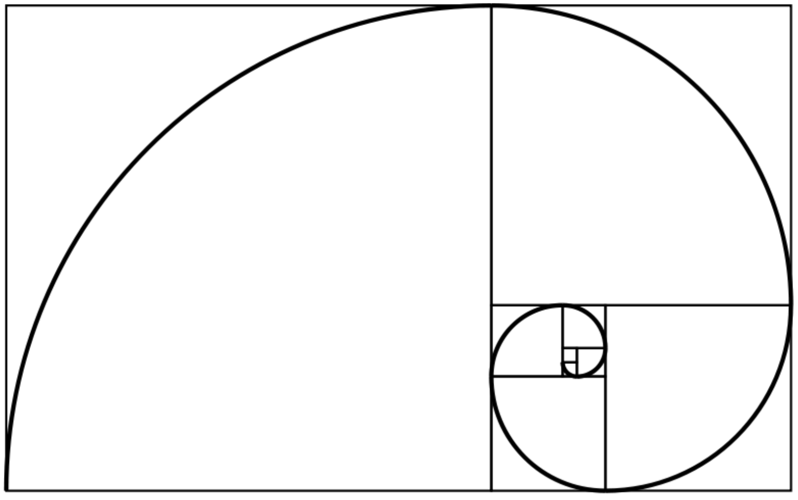
Fibonacci Numbers

- Like every sequence defined by linear recurrence, the Fibonacci numbers have a closed-form solution.

$$F(n) = \frac{\varphi^n - (1-\varphi)^n}{\sqrt{5}} = \frac{\varphi^n - (-1/\varphi)^n}{\sqrt{5}}$$

Fibonacci Numbers

- A Fibonacci spiral created by drawing arcs connecting the opposite corners of squares in the Fibonacci tiling:



Fibonacci Numbers

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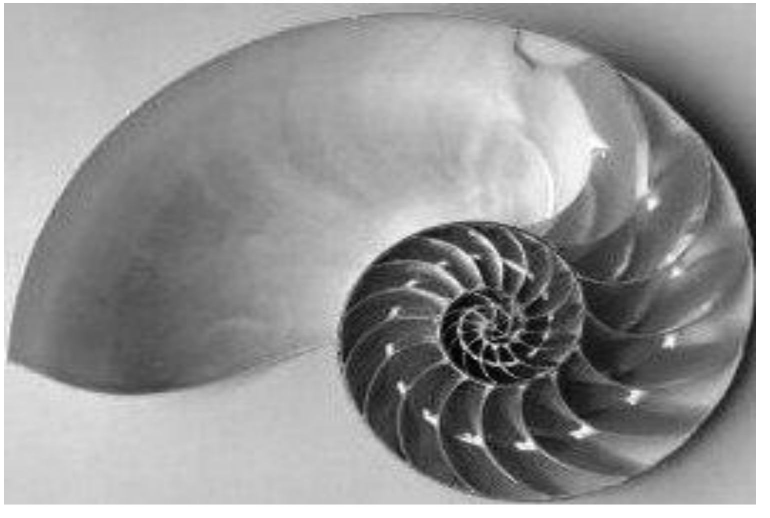


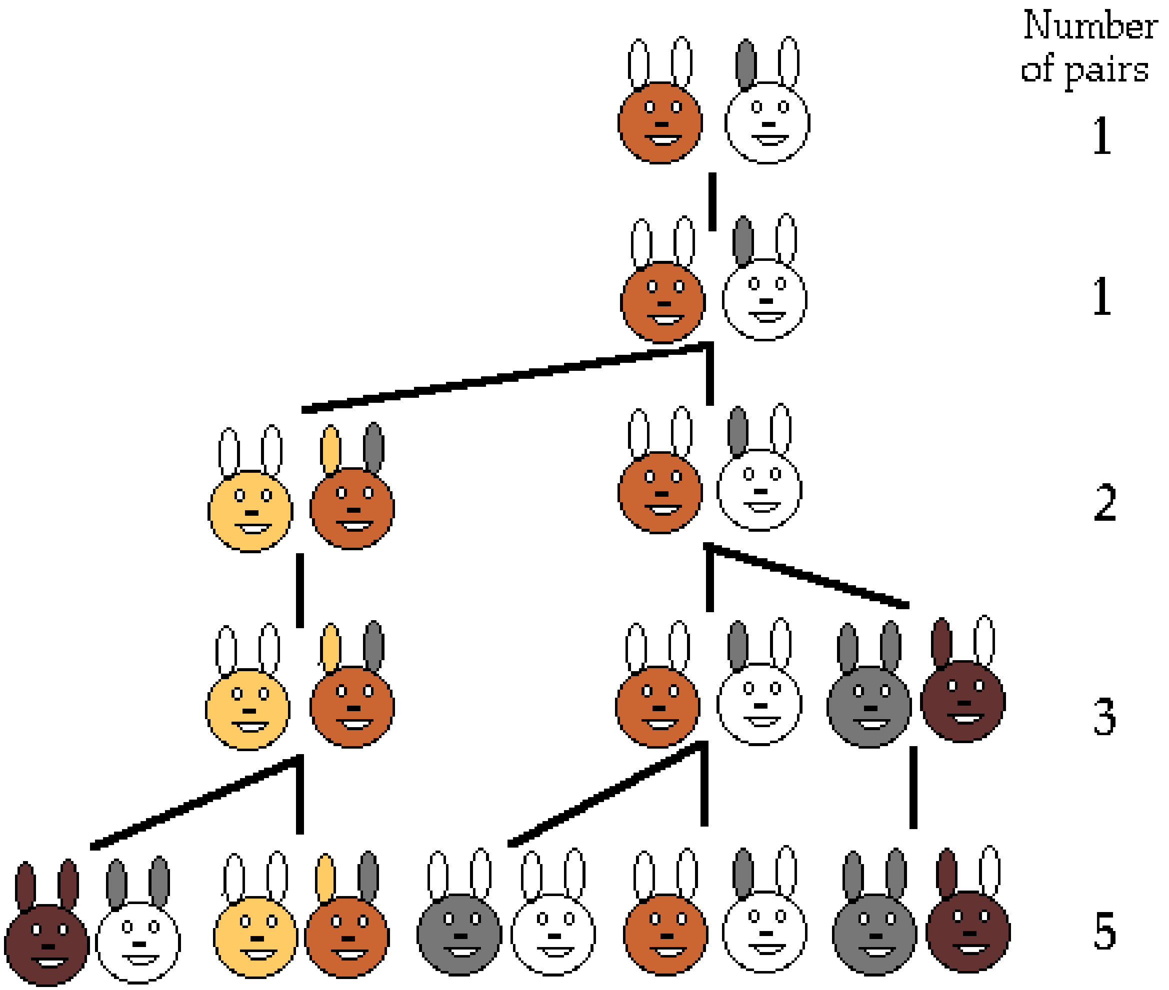
Fibonacci Numbers

- Fibonacci stumbled onto the esoteric realm of the golden mean through a question related to the growth of rabbits.
- It was the question of how fast rabbits could breed under ideal circumstances that Fibonacci originally investigated in 1202.

Fibonacci Numbers

- Suppose a newborn pair of rabbits, one male and one female, is put in the wild.
- The rabbits mate at the age of one month and at the end of its second month a female can produce another pair of rabbits.
- Suppose that the rabbits never die and that each female always produces one new pair, with one male and one female, every month from the second month on.
- How many pairs will there be in one year?

Fibonacci Numbers



Fibonacci Numbers

- Equations defined by a recursive relation are commonly called *difference equations*.

$$F_n = F_{n-1} + F_{n-2}$$

Bio Models: Cell division

- Suppose a population of cells divides synchronously, with each member producing a daughter cells.
- Define the number of cells in each generation with:

$$M_1, M_2, \ldots, M_n$$

- The following equation relates successive generations:

$$M_{n+1} = a\,M_n$$

Bio Models: Cell division

- Suppose that initially there are M_0 cells.
- How big will the population be after n generations?
- The following equation relates successive generations:

$$M_{n+1} = a\, M_n$$

- Applying recursively the definition:

$$M_{n+1} = a\,(a\, M_{n-1}) = a\,(a\,(a\, M_{n-2})) = a^{n+1} M_0$$

Bio Models: Cell division

- For the *n*-th generation we obtain:

$$M_n = a^n M_0$$

- The magnitude of *a* will determine if the population grows or not.

$|a| > 1$: M_n increases over the generations

$|a| < 1$: M_n decreases

$|a| = 1$: M_n is constant

Bio Models: Insect population

- Insects have several stages in their life cycle from progeny to maturity.
- Customary to use singe generation as the basic unit of time.
- Different stages are described by several difference equations.
- The system is then transformed into a single difference equation combining all the basic parameters.

Bio Models: Poplar gall aphid

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- Poplar gall aphid: Adult female aphids produce galls on the leaves. All the progeny of a single aphid are contained in one gall. Some fraction of these will emerge and survive to adulthood.

- We ignore (for the moment) the environmental conditions.

Bio Models: Poplar gall aphid

- Given:

a_n – n. of adult female aphids in the *n*-th generation

p_n – n. of progeny in the *n*-th generation.

m – fractional mortality of the young aphids.

f – n. of progeny per female aphid.

r – ratio of female aphids to total adult aphids.

Bio Models: Poplar gall aphid

- Each female produces *f* progeny:

$$p_{n+1} = f \cdot a_n$$

p_{n+1} – no. of progeny in the *n+1*-st generation.

f – no. of offspring per female aphid.

a_n – n. of adult female aphids in the *n*-th gen.

Bio Models: Poplar gall aphid

- From these p_{n+1} the fraction $1-m$ will survive to adulthood, yielding a proportion of r females:

$$a_{n+1} = r\,(1-m)\,p_{n+1}$$

p_{n+1} – no. of progeny in the $n+1$-st generation.

f – no. of offspring per female aphid.

a_{n+1} – n. of adult female aphids in the $n+1$-st gen.

m – fractional mortality of the young aphids.

r – ratio of female aphids to total adult aphids.

Bio Models: Poplar gall aphid

- Combing the equations:

$$p_{n+1} = f \,.\, a_n$$

.

$$a_{n+1} = r\,(1 - m)\, p_{n+1}$$

- We obtain:

$$a_{n+1} = f \,.\, r\,(1 - m)\, a_n$$

Bio Models: Poplar gall aphid

- When f, r and m are constants:

$$a_{n+1} = f \, . \, r \, (1 - m) \, a_n$$

- transforms into:

$$a_n = (f \, . \, r \, (1 - m))^n \, a_0$$

where a_0 is the initial number of adult females.

Conclusions

- Biological phenomena are modeled by difference equations.

- Difference equations are easy to compute:

$$a_{n+1} = f(a_n)$$

corresponds to the program:

$$a(n) = \textbf{ if } n=0 \textbf{ then } a_0 \textbf{ else } f(a(n-1))$$