

Calculating Biological Quantities

CSCI 2897

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2021¹, Lecture 6

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Last time on CSCI 2897..

- ✓ 1. **Finding the analytical solution to exponential growth.**
- ✓ 2. **Separation of variables (general)**
- ✓ 3. **Separability**
- ✓ 4. **Finding the analytical solution to logistic growth**
- ✓ 5. **Analysis of the solution.**

Lecture 6 Plan

1. Haploid model of natural selection

The need for models of natural selection

Logistic and **exponential** growth models consider every member of the population to **reproduce at the same rate**.

However, in many systems, ***genetic variation*** in characteristics related to **survival** and **reproduction** mean that some members of a population reproduce more effectively than others.

Population genetics models can allow us to track the **frequency** of different **variants** in the population.

Natural selection in action

CDC director warns Covid variants could reverse the recent drop in cases and hospitalizations

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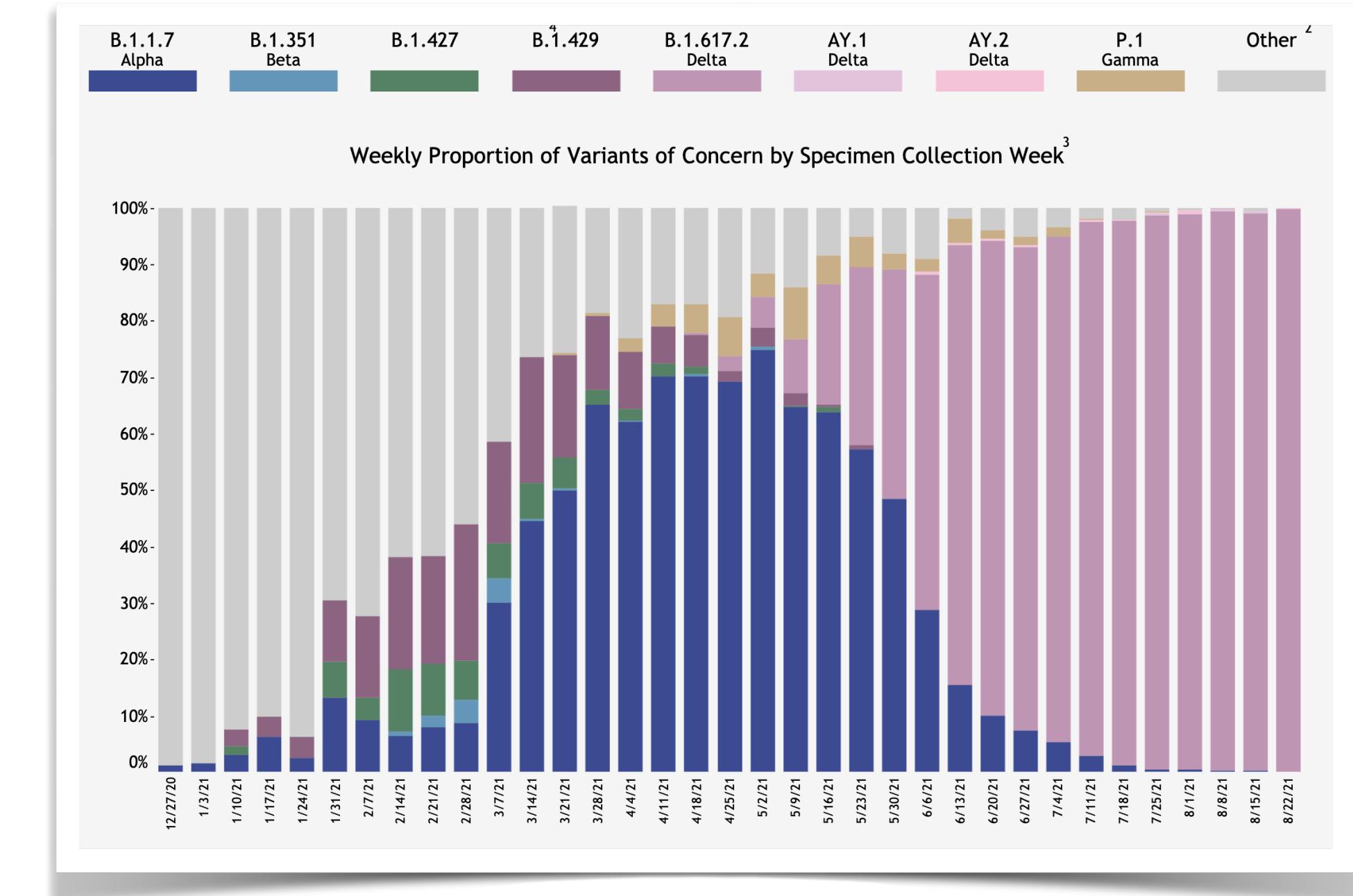
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Feb 2021

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KEY POINTS

- New variants are a “threat” to the U.S. and could reverse the recent declines in Covid-19 cases and hospitalizations, CDC Director Dr. Rochelle Walensky said Monday.
- “Please continue to wear a mask and stay 6 feet apart from people you don’t live with. Avoid travel, crowds and poorly ventilated spaces and get vaccinated when it’s available to you,” she added.



COVID-19 “variants” have emerged and are spreading faster than the wild type virus.
2021: wildtype → alpha → delta → omicron 2022: omicron → BA.4, BA.5 and more

Haploid and Diploid cells

Ploidy: the number of *sets* of chromosomes in a cell (or in the cells of an organism).

Diploid: *two sets.*

- Human somatic cells
- Nearly *all* mammals are diploid (somatic cells)
- Typical reproduction by *meiosis*.
- *P. falciparum*, mosquito life stage (zygote)

Haploid: *one set.* [Note: usage of *haploid* is a little ambiguous, c.f. *monoploid*]

- Human gamete cells
- Typical reproduction by *mitosis*.
- *P. falciparum*, blood stages (sporozoite, trophozoite, gametocyte, etc.)

Haploid models of natural selection

Consider a population of two types of individuals, A and a .

We will assume that both types **breed true**, meaning:

if you're $A \rightarrow$ offspring A

if you're $a \rightarrow$ offspring a

not true for apples

Haploid models of natural selection

Consider a population of two types of individuals, A and a .

We will assume that both types **breed true**, meaning that individuals of type A produce only type A offspring, and individuals of type a produce only type a offspring.

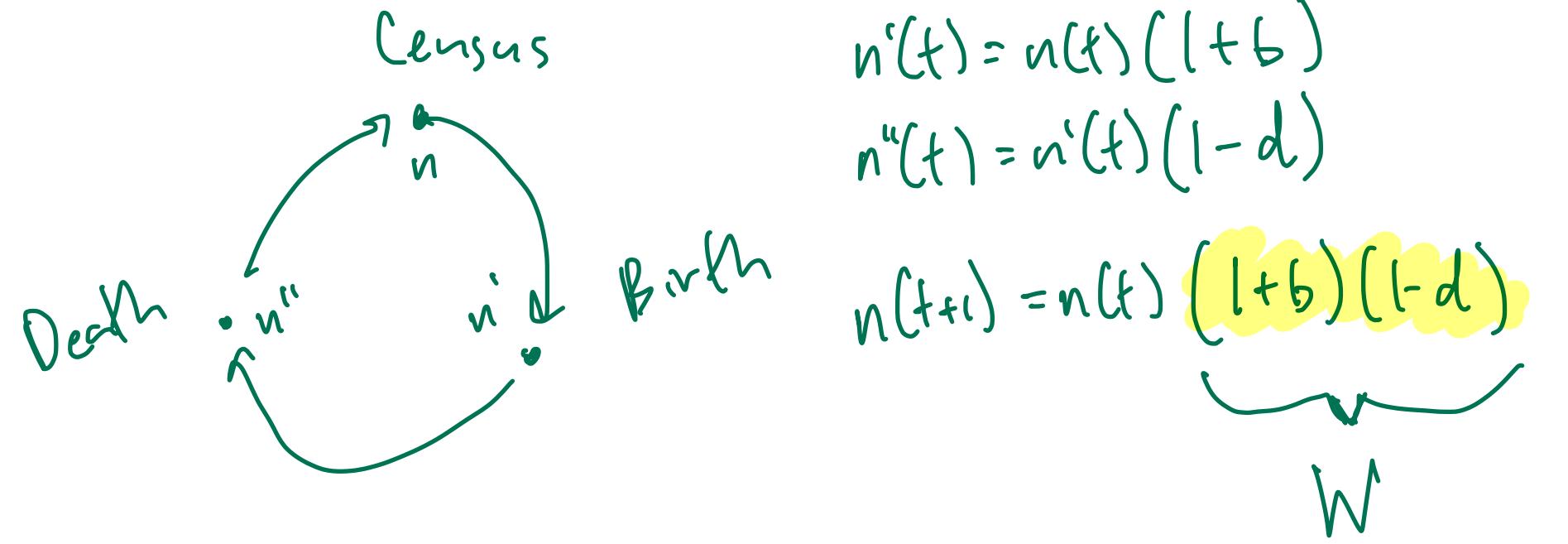
- This simple model describes a **haploid** population with **two alleles**: A and a .
- Alternative interpretation (of the same model): also describes two types of individuals A and a within an asexual population, e.g. two variants.

Haploid models of natural selection

Consider a population of two types of individuals, A and a .

Let the number of each type of individual be given by n_A and n_a .

Consider a typical birth-death process [see previous lectures] and use the traditional letters of evolutionary biology W_A , W_a for the reproductive factors. **Diagram:**



$$n'(t) = n(t)(1+b)$$

$$n''(t) = n'(t)(1-d)$$

$$n(t+1) = n(t) (1+b)(1-d)$$

W

$$n_A(t+1) = n_A(t) W_A$$

$$n_a(t+1) = n_a(t) W_a$$

$$W_A = (1+b_A)(1-d_A)$$

$$W_a = (1+b_a)(1-d_a)$$

Haploid models of natural selection

Consider a population of two types of individuals, A and a .

Let the number of each type of individual be given by n_A and n_a .

We'll consider a typical birth-death process [see previous lectures] and use the traditional letters of evolutionary biology W_A , W_a for the reproductive factors.

Note:

$$W_A = (1 - d_A)(1 + b_A)$$

$$W_a = (1 - d_a)(1 + b_a)$$

Haploid models of natural selection

Consider a population of two types of individuals, A and a .

Let the number of each type of individual be given by n_A and n_a .

$$n_A(t+1) = W_A n_A(t)$$

$$n_a(t+1) = W_a n_a(t)$$

exp. growth

exp. growth

$$W_A = \frac{n_A(t+1)}{n_A(t)}$$

Let p and q be the proportions of type A and type a individuals in the population, respectively. How can we express p and q in terms of our variables?

$$p(t) = \frac{n_A(t)}{n_A(t) + n_a(t)}$$

$$q(t) = \frac{n_a(t)}{n_A(t) + n_a(t)}$$

$$\textcircled{1} \quad n_A(t) + n_a(t) \neq 0$$

$$\textcircled{2} \quad 0 \leq p(t) \leq 1$$

$$0 \leq q(t) \leq 1$$

$$\textcircled{3} \quad p(t) + q(t) = 1$$

\textcircled{4} I only need p or q . They are complementary, i.e., redundant.
→ track p .

What are **three properties** of p and q ?

Haploid models of natural selection

$$P(t) = \frac{n_A(t)}{n_A(t) + n_a(t)}$$

$$q(t) = 1 - P(t)$$

Let's derive an update (or recursion) equation for p , the proportion of indiv's who are A .

$$P(t+1) = \frac{n_A(t+1)}{n_A(t+1) + n_a(t+1)}$$

defn
of P

recursions
for $n_A(t+1)$
 $n_a(t+1)$

$$= \frac{\left[n_A(t) W_A \right]}{\left[n_A(t) W_A + n_a(t) W_a \right]} \cdot \frac{\frac{1}{n_A(t) + n_a(t)}}{\frac{1}{n_A(t) + n_a(t)}}$$

$$= \frac{W_A P(t)}{W_A P(t) + W_a (1 - P(t))}$$

$$\boxed{P(t+1) = \frac{W_A P(t)}{W_A P(t) + W_a (1 - P(t))}}$$

$$= \frac{W_A \frac{n_A(t)}{n_A(t) + n_a(t)}}{W_A \frac{n_A(t)}{n_A(t) + n_a(t)} + W_a \frac{n_a(t)}{n_A(t) + n_a(t)}}$$

Side note:

How would you know to divide the top and bottom by $n_A(t) + n_a(t)$?

This is an insight that comes from lots of practice with these kinds of equations.

“If it works once it’s a trick. If it works twice it’s a method.”

- Paul Martin, Colorado School of Mines

One reason that I'm so excited to teach this class:

I get to teach you all the tricks and all the methods!

Haploid models of natural selection

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An update (or recursion) equation for p with *relative fitness*:

$$p(t+1) = \frac{[w_A p(t)]}{[w_A p(t) + w_a (1-p(t))]} \cdot \frac{\frac{1}{w_a}}{\frac{1}{w_a}} \rightarrow p(t+1) = \frac{\frac{w_A}{w_a} p(t)}{\frac{w_A}{w_a} p(t) + 1 - p(t)}$$

$$V_A \equiv \frac{w_A}{w_a}$$

How can we interpret V_A ?

Relative reproduction rate

→ How many A's do I get per A
relative to a's per a, each Δt

$$p(t+1) = \frac{V_A p(t)}{V_A p(t) + 1 - p(t)}$$

Relative Fitness

Haploid models of natural selection

$$p(t+1) = \frac{V_A p(t)}{V_A p(t) + (1 - p(t))}$$

The dynamics of allele frequency depend *only* on the relative fitnesses of the two alleles. This has some big implications!

1. What if resource availability fluctuates over time, such that the number of offspring per parent becomes $\sin(3\pi t + 2/7)W_A$ and $\sin(3\pi t + 2/7)W_a$?

$$\text{new } V_A = \frac{\sin(3\pi t + 2/7) W_A}{\sin(3\pi t + 2/7) W_a} = \frac{W_A}{W_a} = \text{old } V_A$$

Haploid models of natural selection

$$p(t+1) = \frac{V_A p(t)}{V_A p(t) + (1 - p(t))}$$

The dynamics of allele frequency depend *only on* the relative fitnesses of the two alleles. This has some big implications!

2. What if the number of offspring per parent actually depends on the total population size $n_A + n_a$, in a way that affects W_A and W_a by the same factor?

$$\text{new } V_A = \frac{f(n_A + n_a) W_A}{f(n_A + n_a) W_a} = \text{old } V_A$$

Haploid models of natural selection

$$p(t+1) = \frac{V_A p(t)}{V_A p(t) + (1 - p(t))}$$

The dynamics of allele frequency depend *only on* the relative fitnesses of the two alleles. This has some big implications!

→ Evolutionary change can be studied without reference to the ecological context, provided that the context affects reproduction of both alleles by the same factor.

However, this does not hold if the context differs between the alleles!

Haploid models of natural selection

Let's use $p(t+1) = \frac{W_A p(t)}{W_A p(t) + W_a(1 - p(t))}$ to see how allele frequencies change!

$$\begin{aligned}\Delta p &= p(t+1) - p(t) = \frac{W_A p(t)}{W_A p(t) + W_a(1 - p(t))} - p(t) \frac{W_A p(t) + W_a(1 - p(t))}{W_A p(t) + W_a(1 - p(t))} \\ &= \frac{W_A p(t) - p(t) W_A p(t) - p(t) W_a(1 - p(t))}{W_A p(t) + W_a(1 - p(t))} \\ &= \frac{W_A p(t)(1 - p(t)) - p(t) W_a(1 - p(t))}{W_A p(t) + W_a(1 - p(t))} \\ &= \frac{p(t)(1 - p(t)) [W_A - W_a]}{W_A p(t) + W_a(1 - p(t))} \cdot \frac{\frac{1}{W_a}}{\frac{1}{W_a}}\end{aligned}$$

$$\boxed{\Delta p = \frac{p(t)(1 - p(t)) S_d}{1 + S_d p(t)}}$$

$$S_d \equiv \frac{W_A - W_a}{W_a}$$

$$= V_A - 1$$

proportional diff.
in fitness.

Haploid models of natural selection

Let's use $p(t + 1) = \frac{W_A p(t)}{W_A P(t) + W_a(1 - p(t))}$ to see how allele frequencies change!

$\Delta p = \frac{s_d p(t)(1 - p(t))}{1 + s_d p(t)}$ describes the frequency change in alleles over 1 generation.

But let's see what happens in *continuous time*...

$$\frac{dp}{dt} = \lim_{\Delta t \rightarrow 0} \frac{\Delta p}{\Delta t}$$

Haploid models of natural selection – continuous

We can derive an ODE by assuming that in a little bit of time Δt the number of births is $b\Delta t$ and the number of deaths is $d\Delta t$.

$$W_A(\Delta t) = (1 + b_A \Delta t)(1 - d_A \Delta t) = 1 + (b_A - d_A)\Delta t - b_A d_A (\Delta t)^2$$

$$W_a(\Delta t) = (1 + b_a \Delta t)(1 - d_a \Delta t) = 1 + (b_a - d_a)\Delta t - b_a d_a (\Delta t)^2$$

$$\text{Since } s_d = \frac{W_A - W_a}{W_a}, s_d = \frac{[(b_A - d_A) - (b_a - d_a)]\Delta t - (b_A d_A - b_a d_a)(\Delta t)^2}{1 - (b_a - d_a)\Delta t - b_a d_a (\Delta t)^2}$$

Haploid models of natural selection – continuous

$$s_d(\Delta t) =$$

Haploid models of natural selection – continuous

$$s_d(\Delta t) = \frac{W_A(\Delta t) - W_a(\Delta t)}{W_A(\Delta t)} = \frac{[(b_A - d_A) - (b_a - d_a)]\Delta t - [b_A d_A - b_a d_a]\Delta t^2}{1 + (b_a - d_a)\Delta t - b_a d_a \Delta t^2}$$

$$\frac{dp}{dt} = \lim_{\Delta t \rightarrow 0} \frac{\Delta p}{\Delta t} = \frac{s_d(\Delta t) p(t) (1-p(t))}{\Delta t (1 + s_d(\Delta t) p(t))} = \boxed{\left[(b_A - d_A) - (b_a - d_a) \right] p(t) (1-p(t)) = \frac{dp}{dt}}$$

s_c

$$\lim_{\Delta t \rightarrow 0} \frac{s_d(\Delta t)}{\Delta t} = \frac{\cancel{\left[(b_A - d_A) - (b_a - d_a) \right] \Delta t} - \cancel{\left[b_A d_A - b_a d_a \right] \Delta t^2}}{\cancel{\Delta t} \left[1 + (b_a - d_a) \Delta t - b_a d_a \Delta t^2 \right]}$$

↑ stays ↑ 0 ↑ 0

$$= (b_A - d_A) - (b_a - d_a)$$

$$\lim_{\Delta t \rightarrow 0} s_d(\Delta t) = 0$$

Haploid models of natural selection – continuous

$$\frac{dp}{dt} = s_c p(t)(1 - p(t))$$

where $s_c = (b_A - d_A) - (b_a - d_a)$ is the selection coefficient in continuous time.

TFW u see an old friend



Oh hello old friend!

Where have we seen this equation before?

$$\frac{dp}{dt} = s_c p(t) \left(1 - \frac{p(t)}{1}\right)$$

$$\frac{dn}{dt} = r_c n(t) \left(1 - \frac{n(t)}{K}\right)$$

pop. proportion of variant

logistic growth

Structurally same:

- 1st order
- nonlinear
- separable
- solution.

s_c pos or neg.

$0 \leq p(t) \leq 1$

$r_c \geq 0$

$n(t) \geq 0$