# Mathematics Cheat Sheet for Population Biology

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# 1 Introduction

If you fake it long enough, there comes a point where you aren't faking it any more. Here are some tips to help you along the way...

# 2 Calculus

**Derivative** The definition of a derivative is as follows. For some function f(x),

$$f'(x) = \lim_{h \to 0} \frac{f(x+h) - f(x)}{h}.$$

# 2.1 Differentiation Rules

It is useful to remember the following rules for differentiation. Let f(x) and g(x) be two functions

#### 2.1.1 Linearity

$$\frac{d}{dx}\left(af(x) + bg(x)\right) = af'(x) + bg'(x)$$

for constants a and b.

### 2.1.2 Product rule

$$\frac{d}{dx}\left(f(x)g(x)\right) = f'(x)g(x) + f(x)g'(x)$$

2.1.3 Chain rule

$$\frac{d}{dx}g(f(x)) = g'(f(x))f'(x)$$

#### 2.1.4 Quotient Rule

$$\frac{d}{dx}\frac{f(x)}{g(x)} = \frac{f'(x)g(x) - f(x)g'(x)}{g(x)^2}$$

#### 2.1.5 Some Basic Derivatives

$$\frac{d}{dx}x^{a} = ax^{a-1}$$
$$\frac{d}{dx}\frac{1}{x^{a}} = -\frac{a}{x^{a+1}}$$
$$\frac{d}{dx}e^{x} = e^{x}$$
$$\frac{d}{dx}a^{x} = a^{x}\log a$$
$$\frac{d}{dx}\log|x| = \frac{1}{x}$$

#### 2.1.6 Convexity and Concavity

It is very easy to get confused about the convexity and concavity of a function. The technical mathematical definition is actually somewhat at odds with the colloquial usage. Let f(x) be a twice differentiable function in an interval I. Then:

$$f''(x) \ge 0 \implies f(x) \text{ convex}$$
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$$f''(x) \le 0 \implies f(x) \text{ concave}$$

If you think about a profit function as a function of time, a convex function would show increasing marginal returns, while a concave function would show decreasing marginal returns.

This leads into an important theorem (particularly for stochastic demography), known as Jensen's Inequality. For a convex function f(x),

$$\mathbb{E}\left[f(X)\right] \ge f(\mathbb{E}\left[X\right]).$$

## 2.2 Taylor Series

$$T(x) = \sum_{k=0}^{\infty} \frac{f^{(k)}(a)}{k!} (x-a)^k$$

where  $f^{(k)}(a)$  denotes the kth derivative of f evaluated at a, and  $k! = k(k-1)(k-2)\dots(1)$ .

For example, we can approximate  $e^r$  at a = 0:

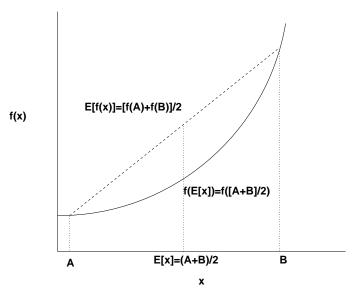


Figure 1: Illustration of Jensen's Inequality.

$$e^r \approx 1 + r + \frac{r^2}{2} + \frac{r^3}{6} \dots$$

Expanding  $\log(1+x)$  around a = 0 yields:

$$\log(1+x) \approx x - \frac{x^2}{2} + \frac{x^3}{3} - \dots$$

# 2.3 Jacobian

For a system of equations, F(x) and  $G(\lambda)$ , the Jacobian matrix is

$$\mathbf{J} = \left(\begin{array}{cc} \partial F/\partial x & \partial F/\partial \lambda \\ \partial G/\partial x & \partial G/\partial \lambda \end{array}\right).$$

This is very important for the analysis of stability of interacting models such as those for epidemics and predator-prey systems. The equilibrium of a system is stable if and only if the real parts of all the eigenvalues of  $\mathbf{J}$  are negative.

#### 2.4 Integration

### Linearity

$$\int \left[af(x) + bg(x)\right] dx = a \int f(x)dx + b \int g(x)dx$$

**Integration by Parts** 

$$\int u \cdot v' \, dx = u \cdot v - \int v \cdot u' \, dx$$

Some Useful Facts About Integrals

$$\int \frac{f'(x)}{f(x)} dx = \log |f(x)|$$
$$\int x^a dx = \frac{x^{a+1}}{a+1}, \quad a \neq -1$$
$$\int e^x dx = e^x$$
$$\int \frac{dx}{x} = \log |x|$$

# 2.5 Definite Integrals

$$\int_{a}^{b} f(x)dx = [F(x)]_{a}^{b} = F(b) - F(a)$$

#### 2.5.1 Expectation

For a continuous random variable X with probability density function f(x), the expected value, or mean, is

$$\mathbb{E}(X) = \int_{\Omega} x f(x) dx$$

where the integral is taken over the set of all possible outcomes  $\Omega$ .

For example, the average age of mothers of newborns in a stable population:

$$A_B = \int_{\alpha}^{\beta} a e^{-ra} l(a) m(a) da$$

Since (from the Euler-Lotka equation) the probability that a mother will be a years old in a stable population is  $f(a) = e^{-ra}l(a)m(a)$ .

#### Some Properties of Expectation

$$\mathbb{E}[aX] = a\mathbb{E}[X]$$

For two discrete random variables, X and Y,

$$\mathbb{E}[X+Y] = \mathbb{E}[X] + \mathbb{E}[Y]$$

# 2.5.2 Variance

For a continuous random variable X with probability density function f(x) and expected value  $\mu$ , the variance is

$$\mathbb{W}(X) = \int_{\Omega} (x - \mu)^2 f(x) dx$$

A useful formula for calculating variances:

$$\mathbb{W}[X] = \mathbb{E}[X^2] - (\mathbb{E}[X])^2$$

### 2.6 Exponents and Logarithms

**Properties of Exponentials** 

$$x^{a}x^{b} = x^{a+b}$$
$$\frac{x^{a}}{x^{b}} = x^{a-b}$$
$$x^{a} = e^{a\log x}$$

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**Complex Case** 

$$e^{z} = e^{a+bi} = e^{a}e^{bi} = e^{a}(\cos b + i\sin b)$$
$$(x^{a})^{b} = x^{ab}$$
$$x^{-a} = \frac{1}{x^{a}}$$

The logarithm to the base e, where e is defined as

$$e = \lim_{n \to \infty} \left( 1 + \frac{1}{n} \right)^n$$

Assume that  $\log \equiv \log_e$ . Logarithms to other bases will be marked as such. For example:  $\log_{10}$ ,  $\log_2$ , etc.

This is an important for demography:

$$\lim_{n \to \infty} \left( 1 + \frac{r}{n} \right)^n = e^r$$

#### **Properties of Logarithms**

$$\log x^a = a \log x$$
$$\log ab = \log a + \log b$$

$$\log \frac{a}{b} = \log a - \log b$$

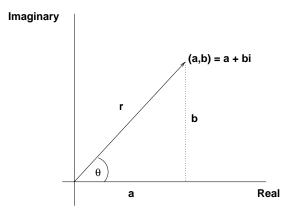


Figure 2: Argand diagram representing a complex number z = a + bi.

**Complex Numbers** We encounter complex numbers frequently when we calculate the eigenvalues of projection matrices, so it is useful to know something about them. Imaginary number:  $i = \sqrt{-1}$ . Complex number: z = a + bi, where a is the real part and b is a coefficient on the imaginary part.

It is useful to represent imaginary numbers in their polar form. Define axes where the abscissa represents the real part of a complex number and the ordinate represents the imaginary part (these axes are known as an *Argand diagram*). This vector, a + bi can be represented by the angle  $\theta$  and the radius of the vector rooted at the origin to point (a, b). Using trigonometric definitions,  $a = r \sin \theta$  and  $b = r \cos \theta$ , we see that

$$z = a + ib = r(\cos\theta + i\sin\theta).$$

Believe it or not, this comes in handy when we interpret the transient dynamics of a population.

Let z be a complex number with real part a and imaginary part b,

$$z = a + bi$$

Then the complex conjugate of z is

$$\bar{z} = a - bi$$

Non-real eigenvalues of demographic projection matrices come in conjugate pairs.

# 3 Linear Algebra

A matrix is a rectangular array of numbers

$$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

A vector is simply a list of numbers

$$\mathbf{n}(t) = \left[ \begin{array}{c} n_1 \\ n_2 \\ n_3 \end{array} \right]$$

A scalar is a single number:  $\lambda=1.05$ 

We refer to individual matrix elements by indexing them by their row and column positions. A matrix is typically named by a capital (bold) letter (e.g., **A**). An element of matrix **A** is given by a lowercase a subscripted with its indices. These indices are subscripted following the the lowercase letter, first by row, then by column. For example,  $a_{21}$  is the element of **A** which is in the second row and first column.

#### Matrix Multiplication

$$\left[\begin{array}{cc}a_{11}&a_{12}\\a_{21}&a_{22}\end{array}\right]\left[\begin{array}{c}n_{1}\\n_{2}\end{array}\right] = \left[\begin{array}{c}a_{11}n_{1}+a_{12}n_{2}\\a_{21}n_{1}+a_{22}n_{2}\end{array}\right]$$

Multiply each row element-wise by the column For Example,

$$\begin{bmatrix} 2 & 3 \\ 4 & 5 \end{bmatrix} \begin{bmatrix} 6 \\ 7 \end{bmatrix} = \begin{bmatrix} (2 \cdot 6) + (3 \cdot 7) \\ (4 \cdot 6) + (5 \cdot 7) \end{bmatrix} = \begin{bmatrix} 33 \\ 59 \end{bmatrix}$$

## Matrix Addition or Subtraction

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} + \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix} = \begin{bmatrix} a_{11} + b_{11} & a_{12} + b_{12} \\ a_{21} + b_{21} & a_{22} + b_{22} \end{bmatrix}$$
$$\begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix} + \begin{bmatrix} 5 & 6 \\ 7 & 8 \end{bmatrix} = \begin{bmatrix} 6 & 8 \\ 10 & 12 \end{bmatrix}$$

Multiplying a Matrix by a Scalar

$$\lambda \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} \lambda a_{11} & \lambda a_{12} \\ \lambda a_{21} & \lambda a_{22} \end{bmatrix}$$
$$4 \begin{bmatrix} 2 & 3 \\ 4 & 5 \end{bmatrix} = \begin{bmatrix} 8 & 12 \\ 16 & 20 \end{bmatrix}$$

**Systems of Equations** Matrix notation was invented to make solving simultaneous equations easier.

$$y_1 = ax_1 + bx_2$$
$$y_2 = cx_1 + dx_2$$

In matrix notation:

$$\left[\begin{array}{c} y_1 \\ y_2 \end{array}\right] = \left[\begin{array}{c} a & b \\ c & d \end{array}\right] \left[\begin{array}{c} x_1 \\ x_2 \end{array}\right]$$

#### 3.1 Eigenvalues and Eigenvectors

A scalar  $\lambda$  is an eigenvalue of a square matrix **A** and  $\mathbf{w} \neq \mathbf{0}$  is its associated eigenvector if

$$\mathbf{A}\mathbf{w} = \lambda \mathbf{w}.$$

Eigenvalues of **A** are calculated as the roots of the characteristic equation,

$$\det(\mathbf{A} - \lambda \mathbf{I}) = 0,$$

where **I** is the identity matrix, a square matrix with ones along the diagonal and zeros elsewhere. For example, we can calculate the eigenvalues for the matrix,

$$\mathbf{A} = \left[ \begin{array}{cc} f_1 & f_2 \\ p_1 & 0 \end{array} \right].$$

Solve the characteristic equation  $det(\mathbf{A} - \lambda \mathbf{I}) = 0$ :

$$(\mathbf{A} - \lambda \mathbf{I}) = \begin{bmatrix} f_1 & f_2 \\ p_1 & 0 \end{bmatrix} - \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix} = \begin{bmatrix} f_1 - \lambda & f_2 \\ p_1 & -\lambda \end{bmatrix}$$
$$\det(\mathbf{A} - \lambda \mathbf{I}) = -(f_1 - \lambda)\lambda - f_2 p_1$$

$$\lambda^2 - f_1\lambda - f_2p_1 = 0$$

Use the quadratic equation to solve for  $\lambda$ :

$$\frac{-f_1 \pm \sqrt{f_1^2 - 4f_2p_1}}{2f_1}$$

Numerical Example Define:

$$\mathbf{A} = \begin{bmatrix} 1.5 & 2\\ 0.5 & 0 \end{bmatrix}$$

$$\det(\mathbf{A} - \lambda \mathbf{I}) = \begin{bmatrix} 1.5 - \lambda & 2\\ 0.5 & -\lambda \end{bmatrix}$$

$$\lambda^2 - 1.5\lambda - 1 = 0$$
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$$(\lambda - 2)(\lambda + 0.5) = 0$$

The roots of this are  $\lambda = 2$  and  $\lambda = -0.5$ . A  $k \times k$  matrix will have k eigenvalues. If a matrix is non-negative, irreducible, and primitive, one of these eigenvalues is guaranteed to be real, positive, and strictly greater than all the others.

Analytic Formula for Eigenvalues: The  $2\times 2$  Case

$$\mathbf{A} = \left[ \begin{array}{cc} a & b \\ c & d \end{array} \right]$$

The eigenvalues are:

$$\lambda_{\pm} = \frac{T}{2} \pm \sqrt{(T/2)^2 - D}$$

where T = a + d is the trace and D = ad - bc is the determinant of matrix **A**.