

# Lecture12

## The Perron-Frobenius theorem.

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# History.

The theorem we will discuss today (to be stated below) about matrices with non-negative entries, was proved, for matrices with strictly positive entries, by Oskar Perron (1880-1975) in 1907 and extended by Ferdinand Georg Frobenius (1849-1917) to matrices which have non-negative entries and are irreducible (definition below) in 1912.

This theorem has miriads of applications, several of which we will study in this course.

# Non-negative and positive matrices.

We begin with some definitions.

We say that a real matrix  $T$  is **non-negative** (or **positive**) if all the entries of  $T$  are non-negative (or positive). We write  $T \geq 0$  or  $T > 0$ . We will use these definitions primarily for square ( $n \times n$ ) matrices and for column vectors = ( $n \times 1$ ) matrices, although rectangular matrices will come into the picture at one point.

## The positive orthant.

We let

$$Q := \{x \in \mathbb{R}^n : x \geq 0, \quad x \neq 0\}$$

so  $Q$  is the non-negative orthant excluding the origin, which (by abuse of language) we will call the **positive orthant**. Also let

$$C := \{x \geq 0 : \|x\| = 1\}.$$

So  $C$  is the intersection of the positive orthant with the unit sphere.

## Primitive and irreducible non-negative square matrices.

A non-negative matrix square  $T$  is called **primitive** if there is a  $k$  such that all the entries of  $T^k$  are positive. It is called **irreducible** if for any  $i, j$  there is a  $k = k(i, j)$  such that  $(T^k)_{ij} > 0$ .

If  $T$  is irreducible then  $I + T$  is primitive. Indeed, the binomial expansion

$$(I + T)^k = I + kT + \frac{k(k-1)}{2}T^2 + \dots$$

will eventually have positive entries in all positions if  $k$  large enough.

In the statement of the Perron-Frobenius theorem we assume that  $T$  is irreducible. We now state the theorem:

## Theorem

- 1  $T$  has a positive (real) eigenvalue  $\lambda_{\max}$  such that all other eigenvalues of  $T$  satisfy

$$|\lambda| \leq \lambda_{\max}.$$

- 2 Furthermore  $\lambda_{\max}$  has algebraic and geometric multiplicity one, and has an eigenvector  $x$  with  $x > 0$ .
- 3 Any non-negative eigenvector is a multiple of  $x$ .
- 4 More generally, if  $y \geq 0$ ,  $y \neq 0$  is a vector and  $\mu$  is a number such that

$$Ty \leq \mu y$$

then

$$y > 0, \text{ and } \mu \geq \lambda_{\max}$$

with  $\mu = \lambda_{\max}$  if and only if  $y$  is a multiple of  $x$



## Perron-Frobenius theorem, continued.

If  $0 \leq S \leq T$ ,  $S \neq T$  then every eigenvalue  $\sigma$  of  $S$  satisfies

$$|\sigma| < \lambda_{\max}.$$

In particular, all the diagonal minors  $T_{(i)}$  obtained from  $T$  by deleting the  $i$ -th row and column have eigenvalues all of which have absolute value  $< \lambda_{\max}$ .

If  $T$  is primitive, then all other eigenvalues of  $T$  satisfy

$$|\lambda| < \lambda_{\max}.$$

We now embark on the proof of this important theorem.



Let

$$P := (I + T)^k$$

where  $k$  is chosen so large that  $P$  is a positive matrix. Then

$$v \leq w, v \neq w \Rightarrow Pv < Pw.$$

Recall that  $Q$  denotes the positive orthant and that  $C$  denotes the intersection of the unit sphere with the positive orthant. For any  $z \in Q$  let

$$L(z) := \max\{s : sz \leq Tz\} = \min_{1 \leq i \leq n, z_i \neq 0} \frac{(Tz)_i}{z_i}.$$

By definition  $L(rz) = L(z)$  for any  $r > 0$ , so  $L(z)$  depends only on the ray through  $z$ . If  $z \leq y$ ,  $z \neq y$  we have  $Pz < Py$ . Also  $PT = TP$ . So if  $sz \leq Tz$  then

$$sPz \leq PTz = TPz$$

so

$$L(Pz) \geq L(z).$$

$$L(z) := \max\{s : sz \leq Tz\} = \min_{1 \leq i \leq n, z_i \neq 0} \frac{(Tz)_i}{z_i}.$$

$$L(Pz) \geq L(z).$$

Furthermore, if  $L(z)z \neq Tz$  then  $L(z)Pz < TPz$ . So  $L(Pz) > L(z)$  unless  $z$  is an eigenvector of  $T$  with eigenvalue  $L(z)$ .

This suggests that we look for a positive vector which maximizes  $L$ .

## Finding a positive eigenvector.

Consider the image of  $C$  under  $P$ . It is compact (being the image of a compact set under a continuous map) and all of the elements of  $P(C)$  have all their components strictly positive (since  $P$  is positive). Hence the function  $L$  is continuous on  $P(C)$ . Thus  $L$  achieves a maximum value,  $L_{\max}$  on  $P(C)$ . Since  $L(z) \leq L(Pz)$  this is in fact the maximum value of  $L$  on all of  $Q$ , and since  $L(Pz) > L(z)$  unless  $z$  is an eigenvector of  $T$ , we conclude that  $L_{\max}$  **is achieved at an eigenvector, call it**  $x$  of  $T$  and  $x > 0$  with  $L_{\max}$  the eigenvalue. Since  $Tx > 0$  and  $Tx = L_{\max}x$  we have  $L_{\max} > 0$ .

We will now show that this is in fact the maximum eigenvalue in the sense of the theorem. So let  $y$  be any eigenvector with eigenvalue  $\lambda$ , and let  $|y|$  denote the vector whose components are  $|y_j|$ , the absolute values of the components of  $y$ . We have  $|y| \in Q$  and from

$$Ty = \lambda y$$

which says that

$$\lambda y_i = \sum_j T_{ij} y_j$$

and the fact that the  $T_{ij} \geq 0$  we conclude that

$$|\lambda| |y_i| \leq \sum_j T_{ij} |y_j|$$

which we write for short as

$$|\lambda| |y| \leq T |y|.$$

$L_{\max}$  is an eigenvalue of maximum absolute value.

We have shown that

$$|\lambda||y| \leq T|y|.$$

Recalling the definition of  $L$ , this says that  $|\lambda| \leq L(|y|) \leq L_{\max}$ . So we may use the notation

$$\lambda_{\max} := L_{\max}$$

since we have proved that

$$|\lambda| \leq \lambda_{\max}.$$

We have proved item 1 in the theorem.

Notice that we can not have  $\lambda_{\max} = 0$  since then  $T$  would have all eigenvalues zero, and hence be nilpotent, contrary to the assumption that  $T$  is irreducible. So

$$\lambda_{\max} > 0.$$

Suppose that  $0 \leq S \leq T$ . If  $z \in Q$  is a vector such that  $sz \leq Sz$  then since  $Sz \leq Tz$  we get  $sz \leq Tz$  so  $L_S(z) \leq L_T(z)$  for all  $z$  and hence

$$0 \leq S \leq T \Rightarrow L_{\max}(S) \leq L_{\max}(T).$$

We may apply the previous results to  $T^\dagger$ , the transpose of  $T$ , to conclude that it also has a positive maximum eigenvalue. Let us call it  $\eta$ . (We shall soon show that  $\eta = \lambda_{\max}$ .) This means that there is a row vector  $w > 0$  such that

$$w^\dagger T = \eta w^\dagger.$$

Recall that  $x > 0$  denotes the eigenvector with maximum eigenvalue  $\lambda_{\max}$  of  $T$ . We have

$$w^\dagger T x = \eta w^\dagger x = \lambda_{\max} w^\dagger x$$

implying that  $\eta = \lambda_{\max}$  since  $w^\dagger x > 0$ .

Now suppose that  $y \in Q$  and  $Ty \leq \mu y$ . Then

$$\lambda_{\max} w^\dagger y = w^\dagger Ty \leq \mu w^\dagger y$$

implying that  $\lambda_{\max} \leq \mu$ , again using the fact that all the components of  $w$  are positive and some component of  $y$  is positive so  $w^\dagger y > 0$ . In particular, if  $Ty = \mu y$  then  $\mu = \lambda_{\max}$ . Furthermore, if  $y \in Q$  and  $Ty \leq \mu y$  then  $\mu \geq 0$  and

$$0 < Py = (I + T)^{n-1}y \leq (1 + \mu)^{n-1}y$$

so

$$y > 0.$$

This proves the first two assertions in item 4.



If  $\mu = \lambda_{\max}$  then  $w^\dagger(Ty - \lambda_{\max}y) = 0$  but  $Ty - \lambda_{\max}y \leq 0$  and so  $w^\dagger(Ty - \lambda_{\max}y) = 0$  implies that  $Ty = \lambda_{\max}y$ . Then the last assertion of item 4) - that  $y$  is a scalar multiple of  $x$  - will then follow from item 2) - that  $\lambda_{\max}$  has multiplicity one - once we prove item 2), since we have shown that  $y$  must be an eigenvector with eigenvalue  $\lambda_{\max}$ .

Proof that if  $0 \leq S \leq T$ ,  $S \neq T$  then every eigenvalue  $\sigma$  of  $S$  satisfies  $|\sigma| < \lambda_{\max}$ .

Suppose that  $0 \leq S \leq T$  and  $Sz = \sigma z$ ,  $z \neq 0$ . Then

$$T|z| \geq S|z| \geq |\sigma||z|$$

so

$$|\sigma| \leq L_{\max}(T) = \lambda_{\max},$$

as we have already seen. But if  $|\sigma| = \lambda_{\max}$  then  $L(|z|) = L_{\max}(T)$  so  $|z| > 0$  and  $|z|$  is also an eigenvector of  $T$  with the same eigenvalue. But then  $(T - S)|z| = 0$  and this is impossible unless  $S = T$  since  $|z| > 0$ . Replacing the  $i$ -th row and column of  $T$  by zeros give an  $S \geq 0$  with  $S < T$  since the irreducibility of  $T$  precludes all the entries in a row being zero. This proves the assertion that the eigenvalues of  $T_i$  are all less in absolute value than  $\lambda_{\max}$ .

## A lemma in linear algebra.

Let  $T$  be a (square) matrix and let  $\Lambda$  be a diagonal matrix of the same size, with entries  $\lambda_1, \dots, \lambda_n$  along the diagonal. Expanding  $\det(\Lambda - T)$  along the  $i$ -th row shows that

$$\frac{\partial}{\partial \lambda_i} \det(\Lambda - T) = \det(\Lambda_i - T_i)$$

where the subscript  $i$  means the matrix obtained by eliminating the  $i$ -th row and the  $i$ -th column from each matrix.

Setting  $\lambda_i = \lambda$  and applying the chain rule from calculus, we get

$$\frac{d}{d\lambda} \det(\lambda I - T) = \sum_i \det(\lambda I - T_{(i)})$$

So from linear algebra we know that

$$\frac{d}{d\lambda} \det(\lambda I - T) = \sum_i \det(\lambda I - T_{(i)}).$$

Each of the matrices  $\lambda_{\max} I - T_{(i)}$  has strictly positive determinant by what we have just proved. This shows that the derivative of the characteristic polynomial of  $T$  is not zero at  $\lambda_{\max}$ , and therefore the algebraic multiplicity and hence the geometric multiplicity of  $\lambda_{\max}$  is one. This proves 2) and hence all but the last assertion of the theorem, which says that if  $T$  is primitive, then all the other eigenvalues of  $T$  satisfy

$$|\lambda| < \lambda_{\max}.$$

The eigenvalues of  $T^k$  are the  $k$ -th powers of the eigenvalues of  $T$ . So if we want to show that there are no other eigenvalues of a primitive matrix with absolute value equal to  $\lambda_{\max}$ , it is enough to prove this for a positive matrix. Dividing the positive matrix by  $\lambda_{\max}$ , we are reduced to proving the following

### Lemma

*Let  $A > 0$  be a positive matrix with  $\lambda_{\max} = 1$ . Then all other eigenvalues of  $A$  satisfy  $|\lambda| < 1$ .*

# Proof.

Suppose that  $z$  is an eigenvector of  $A$  with eigenvalue  $\lambda$  with  $|\lambda| = 1$ . Then  $|z| = |\lambda z| = |Az| \leq |A||z| = A|z| \Rightarrow |z| \leq A|z|$ . Let  $y := A|z| - |z|$  so  $y \geq 0$ . Suppose (contrary to fact) that  $y \neq 0$ . Then  $Ay > 0$  and  $A|z| > 0$  so there is an  $\epsilon > 0$  so that  $Ay > \epsilon A|z|$  and hence  $A(A|z| - |z|) > \epsilon A|z|$  or

$$B(A|z|) > A|z|, \quad \text{where } B := \frac{1}{1 + \epsilon}A.$$

This implies that  $B^k A|z| > A|z|$  for all  $k$ . But the eigenvalues of  $B$  are all  $< 1$  in absolute value, so  $B^k \rightarrow 0$ . Thus all the entries of  $A|z|$  are  $\leq 0$  contradicting the fact that  $A|z| > 0$ . So  $|z|$  is an eigenvector of  $A$  with eigenvalue 1.

But  $|Az| = |z|$  so  $|Az| = A|z|$  which can only happen if all the entries of  $z$  are of the same sign. So  $z$  must be a multiple of our eigenvector  $x$  since there are no other eigenvectors with all entries of the same sign other than multiples of  $x$ . So  $\lambda = 1$ .  $\square$

## Examples for two by two matrices.

To check whether a matrix with non-negative entries is primitive, or irreducible, or neither, we may replace all of the non-zero entries by ones since this does not affect the classification. The matrix

$$\begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}$$

is (strictly) positive hence primitive. The matrices

$$\begin{pmatrix} 1 & 0 \\ 1 & 1 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix}$$

both have 1 as a double eigenvalue so can not be irreducible.



The matrix  $\begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix}$  satisfies

$$\begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix}^2 = \begin{pmatrix} 2 & 1 \\ 1 & 1 \end{pmatrix}$$

and so is primitive. Similarly for  $\begin{pmatrix} 0 & 1 \\ 1 & 1 \end{pmatrix}$ .

The matrix  $\begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$  is irreducible but not primitive. Its eigenvalues are 1 and  $-1$ .

## Non-negative matrices and directed graphs.

A **directed graph** is a pair consisting of a set  $V$  (called **vertices** or **nodes**) and a subset  $E \subset V \times V$  called (directed) **edges**. The directed edge  $(v_i, v_j)$  “goes from  $v_i$  to  $v_j$ ”. We draw it as an arrow. The **graph associated to the non-negative square matrix**  $M$  of size  $n \times n$  has  $V = \{v_1, \dots, v_n\}$  and the directed edge

$$(v_j, v_i) \in E \iff M_{ij} \neq 0.$$

(Notice the reversal of order in this convention. Sometimes the opposite convention is used.)

The **adjacency matrix**  $A$  of the graph  $(V, E)$  is the  $n \times n$  matrix (where  $n$  is the number of nodes) with  $A_{ij} = 1$  if  $(v_j, v_i) \in E$  and  $= 0$  otherwise.

So if  $(V, E)$  is associated to  $M$  and  $A$  is its adjacency matrix, then  $A$  is obtained from  $M$  by replacing its non-zero entries by ones.

## Paths and powers.

A **path** from a vertex  $v$  to a vertex  $w$  is a finite sequence  $v_0, \dots, v_\ell$  with  $v_0 = v$ ,  $v_\ell = w$  where each  $(v_i, v_{i+1})$  is an edge. The number  $\ell$ , i.e, the number of edges in the path is called the **length** of the path.

If  $A$  is the adjacency matrix of the graph, then  $(A^2)_{ij}$  gives the number of paths of length two joining  $v_j$  to  $v_i$ , and, more generally,  $(A^\ell)_{ij}$  gives the number of paths of length  $\ell$  joining  $v_j$  to  $v_i$ .

So  $M$  is irreducible  $\iff$  its associated graph is **strongly connected** in the sense that for any two vertices  $v_i$  and  $v_j$  there is a path (of some length) joining  $v_i$  to  $v_j$ .

What is a graph theoretical description of primitivity? We discuss this in the next few slides.

## Cycles and primitivity.

A **cycle** is a path starting and ending at the same vertex.

Let  $M$  be primitive with, say  $M^k$  strictly positive. Then the associated graph is strongly connected, indeed every vertex can be joined to every other vertex by a path of length  $k$ . But then every vertex can be joined to itself by a path of length  $k$ , so there are (many) cycles of length  $k$ .

But then  $M^{k+1}$  is also strictly positive and hence there are cycles of length  $k + 1$ . So there are (at least) two cycles whose lengths are relatively prime.

We will now embark on proving the converse:

### Theorem

*If the graph associated to  $M$  is strongly connected and has two cycles of relatively prime lengths, then  $M$  is primitive.*



# Proof.

We will use the following elementary fact from number theory whose proof we will give after using it to prove the theorem:

## Lemma

*Let  $a$  and  $b$  be positive integers with  $\text{g.c.d.}(a, b) = 1$ . Then there is an integer  $B$  such that every integer  $\geq B$  can be written as an integer combination of  $a$  and  $b$  with non-negative coefficients.*

We will prove the theorem from the lemma by showing that for  $k := 3(n - 1) + B$  there is a path of length  $k$  joining any pair of vertices.

## Proof of the theorem from the lemma.

We can construct a path going from  $v$  to  $w$  by going from  $v$  to a point  $x$  on the first cycle, going around this cycle a number of times, then joining  $x$  to a point  $y$  on the second cycle, going around this cycle a number of times, and then going from  $y$  to  $w$ .

The paths from  $v$  to  $x$ , from  $x$  to  $y$ , from  $y$  to  $w$  have total lengths at most  $3(n - 1)$ . But then, by the lemma, we can make up the difference between this total length and  $k$  by going around the cycles an appropriate number of times.  $\square$

## Proof of the lemma.

An integer  $n$  can be written as  $ia + jb$  with  $i$  and  $j$  non-negative integers  $\iff$  it is in one of the following sequences

$$\begin{array}{cccc}
 0, & b, & 2b, & \dots, \\
 a, & b + a, & 2b + a & \dots \\
 \vdots & & & \cdot \\
 (b-1)a, & b + (b-1)a, & 2b + (b-1)a, & \dots
 \end{array}$$

Since  $a$  and  $b$  are relatively prime, the elements of the first column all belong to different conjugacy classes mod  $b$ . So every integer  $n$  can be written as  $n = ra + sb$  where  $0 \leq r < b$ . If  $s < 0$  then  $n < a(b-1)$ .  $\square$

A mild extension of the above argument will show that if there are several (not necessarily two) cycles whose greatest common denominator is one, then  $M$  is primitive.



## Powers of a primitive matrix.

Let  $A$  be a primitive matrix and  $r$  its maximal eigenvalue as given by the Perron-Frobenius theorem. Let  $x > 0$  be a (right-handed) eigenvector of  $A$  with eigenvalue  $r$ , so  $Ax = rx$  and we choose  $x$  so that  $x > 0$ . Let  $y > 0$  be a (row) vector with  $yA = ry$  (also determined up to scalar multiple by a positive number and let us choose  $y$  so that  $y \cdot x = 1$ ).

The rank one matrix  $H := x \otimes y^\dagger$  has image space  $R$ , the one dimensional space spanned by  $x$  and

$$H^2 = H$$

so  $H$  is a projection. The operator  $I - H$  is then also a projection whose image is the null space  $N$  of  $H$ . Also

$AH = Ax \otimes y = rx \otimes y = x \otimes ry = HA$ . So we have the direct sum decomposition of our space as  $R \oplus N$  which is invariant under  $A$ .

We have the direct sum decomposition of our space as  $R \oplus N$  which is invariant under  $A$ .

The restriction of  $A$  to  $N$  has all its eigenvalues strictly less than  $r$  in absolute value, while the restriction of  $A$  to the one dimensional space  $R$  is multiplication by  $r$ . So if we set

$$P := \frac{1}{r}A$$

then the restriction of  $P$  to  $N$  has all its eigenvalues  $< 1$  in absolute value. The above decomposition is invariant under all powers of  $P$  and the restriction of  $P^k$  to  $N$  tends to zero as  $k \rightarrow \infty$ , while the restriction of  $P$  to  $R$  is the identity. So we have proved

$$\lim_{k \rightarrow \infty} \left( \frac{1}{r}A \right)^k = H.$$

## Definition

The **period** of an irreducible non-negative matrix  $A$  is the greatest common divisor of the lengths of the cycles in the associated graph.

Let  $A$  be an irreducible non-negative matrix  $A$  with period  $p > 1$ .  
Let  $v$  be any vertex in the associated graph. For  $0 \leq i < p$  let

$$C_i := \{u \mid \text{there is a path of length } n \text{ from } u \text{ to } v \text{ with } n \equiv i \pmod{p}\}.$$

Since  $A$  is irreducible, every vertex belongs to one of the sets  $C_i$ , and by the definition of  $p$ , it can belong to only one. So the sets  $C_i$  partition the vertex set. Let us relabel the vertices so that the first  $\#(C_0)$  vertices belong to  $C_0$ , the second  $\#(C_1)$  vertices belong to  $C_1$  etc.

This means that we have permutation of the integers  $P$  so that  $PAP^{-1}$  has a block form with rectangular blocks which looks something like a cyclic permutation matrix. For example, for  $p = 4$ , the matrix  $PAP^{-1}$  would look like

$$\begin{pmatrix} 0 & A_1 & 0 & 0 \\ 0 & 0 & A_2 & 0 \\ 0 & 0 & 0 & A_3 \\ A_4 & 0 & 0 & 0 \end{pmatrix}.$$

I want to emphasize that the matrices  $A_i$  are rectangular, not necessarily square.

An example with  $n = 6$  and  $p = 3$  is

$$\begin{pmatrix} 0 & 3 & 7 & 0 & 0 & 0 \\ 0 & 0 & 0 & 2 & 1 & 3 \\ 0 & 0 & 0 & 1 & 0 & 3 \\ 2 & 0 & 0 & 0 & 0 & 0 \\ 3 & 0 & 0 & 0 & 0 & 0 \\ 2 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}.$$

Since the spectral properties of  $PAP^{-1}$  and  $A$  are the same, we will assume from now on that  $A$  is in the block form. To illustrate the next step in Frobenius's analysis, let us go back to the  $p = 4$  example, and raise  $A$  to the fourth power, and obtain a block diagonal matrix:

$$= \begin{pmatrix} \begin{pmatrix} 0 & A_1 & 0 & 0 \\ 0 & 0 & A_2 & 0 \\ 0 & 0 & 0 & A_3 \\ A_4 & 0 & 0 & 0 \end{pmatrix}^4 & & & \\ & \begin{pmatrix} A_1 A_2 A_3 A_4 & 0 & 0 & 0 \\ 0 & A_2 A_3 A_4 A_1 & 0 & 0 \\ 0 & 0 & A_3 A_4 A_1 A_2 & 0 \\ 0 & 0 & 0 & A_4 A_1 A_2 A_3 \end{pmatrix} & & \end{pmatrix}.$$

Each of these diagonal blocks has period one and so is primitive. Also, if  $D(i)$  denotes the  $i$ -th diagonal block, then there are rectangular matrices  $R$  and  $S$  such that

$$D(i) = SR \quad \text{and} \quad D(i+1) = RS.$$

If we take  $i = 2$  in the above example,  $S = A_2$  and  $R = A_3A_4A_1$ .

Therefore, taking their  $k$ -th power, we have

$$D(i)^k = S(RS)^{k-1}R, \quad \text{and} \quad D(i+1)^k = ((RS)^{k-1}R)S.$$

This implies that  $D(i)^k$  and  $D(i+1)^k$  have the same trace. Since the trace of the  $k$ -th power of a matrix is the sum of the  $k$ -th power of its eigenvalues, we conclude that the non-zero eigenvalues of each of the  $D(i)$  are the same.

## Proposition

*Let  $A$  be a non-negative irreducible matrix with period  $p$  and let  $\omega$  be a primitive  $p$ -th root of unity, for example  $\omega = e^{2\pi i/p}$ . Then the matrices  $A$  and  $\omega A$  are conjugate. In particular, if  $c$  is an eigenvalue of  $A$  with multiplicity  $m$  so is  $\omega c$ .*

The following computation for  $p = 3$  explains the general case:



## The non-primitive case.

$$\begin{aligned} & \begin{pmatrix} \omega^{-1}I & 0 & 0 \\ 0 & \omega^{-2}I & 0 \\ 0 & 0 & I \end{pmatrix} \begin{pmatrix} 0 & A_1 & 0 \\ 0 & 0 & A_2 \\ A_3 & 0 & 0 \end{pmatrix} \begin{pmatrix} \omega I & 0 & 0 \\ 0 & \omega^2 I & 0 \\ 0 & 0 & I \end{pmatrix} \\ &= \begin{pmatrix} 0 & \omega A_1 & 0 \\ 0 & 0 & \omega A_2 \\ \omega A_3 & 0 & 0 \end{pmatrix} = \omega \begin{pmatrix} 0 & A_1 & 0 \\ 0 & 0 & A_2 \\ A_3 & 0 & 0 \end{pmatrix}. \quad \square \end{aligned}$$

So we can supplement the Perron-Frobenius theorem in the case that  $A$  is a non-negative irreducible matrix of period  $p$  by

### Theorem

*Let  $A$  be a non-negative irreducible matrix of period  $p$  with maximum real eigenvalue  $\lambda_{\max}$ . The eigenvalues  $\lambda$  of  $A$  with  $|\lambda| = \lambda_{\max}$  are all simple and of the form  $\omega\lambda_{\max}$  as  $\omega$  ranges over the  $p$ -th roots of unity.*

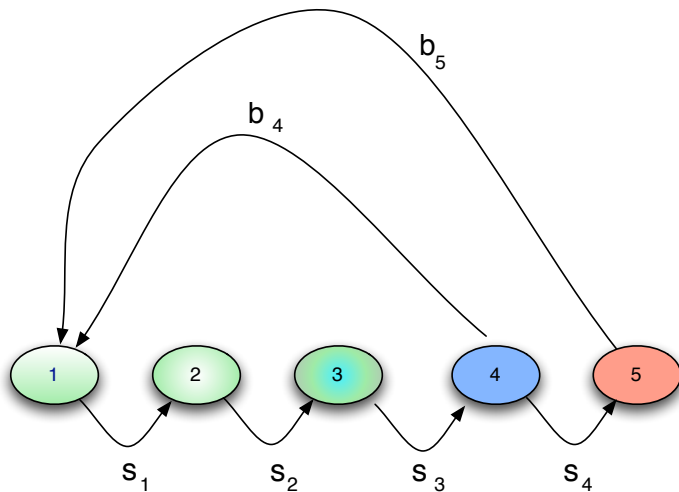
*The spectrum of  $A$  is invariant under multiplication by  $\omega$  where  $\omega$  is a primitive  $p$ -th root of unity.*

## The Leslie model.

In 1945 Leslie introduced a model for the growth of a stratified population: The population to consider consists of the females of a species, and the stratification is by age group. (For example into females under age 5, between 5 and 10, between 10 and 15 etc.) So the population is described by a vector whose size is the number of age groups and whose  $i$ -th component is the number of females in the  $i$ -th age group.

He let  $b_i$  be the expected number of daughters produced by a female in the  $i$ -th age group and  $s_i$  the proportion of females in the  $i$ -th age group who survive (to the next age group) in one time unit.

Example: 5 age groups, the last two child bearing.



# The Leslie matrix.

So the transition after one time unit is given by the **Leslie matrix**

$$L = \begin{pmatrix} b_1 & b_2 & \cdots & b_{n-1} & b_n \\ s_1 & 0 & \cdots & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{pmatrix}.$$

In this matrix we might as well take  $b_n > 0$  as there is no point in taking into consideration those females who are past the age of reproduction as far as the long term behavior of the population is concerned. Also we restrict ourselves to the case where all the  $s_i > 0$  since otherwise the population past age  $i$  will die out.

## The Leslie matrix is irreducible.

$$L = \begin{pmatrix} b_1 & b_2 & \cdots & b_{n-1} & b_n \\ s_1 & 0 & \cdots & \cdots & 0 \\ 0 & s_2 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{pmatrix}, \quad b_n > 0, \quad s_i > 0, \quad i = 1, \dots, n-1.$$

The associated graph then consists of  $n$  vertices with  $v_1 \rightarrow v_2 \rightarrow \cdots \rightarrow v_n$  with  $v_n$  (and possibly others) connected to  $v_1$  and so is strongly connected. So  $L$  is irreducible.

## What is the positive eigenvector?

We might as well take the first component of the positive eigenvector to be 1. The elements in the second to the last positions in  $Lx$  are then determined recursively by

$$x_2 = s_1, \quad x_3 = s_2 x_2, \dots$$

Then the equation  $Lx = rx$  tells us that

$$x_2 = \frac{s_1}{r}, \quad x_3 = \frac{s_1 s_2}{r^2}, \dots$$

and then the first component of  $Lx = rx$  tell us that  $r$  is a solution to the equation

$$p(r) = 1$$

where

$$p(r) = \frac{b_1}{r} + \frac{b_2 s_1}{r^2} + \dots + \frac{b_n s_1 \cdots s_{n-1}}{r^n}.$$

The function

$$p(r) = \frac{b_1}{r} + \frac{b_2 s_1}{r^2} + \cdots + \frac{b_n s_1 \cdots s_{n-1}}{r^n}$$

is defined for  $r > 0$ , is strictly decreasing, tends to  $\infty$  as  $r \rightarrow 0$  and to 0 as  $r \rightarrow \infty$  and so the equation  $p(r) = 1$  has a unique positive root as we expect from the general theory.



## When is the Leslie matrix primitive?

Each  $i$  with  $b_i > 0$  gives rise to a cycle of length  $i$  in the graph. So if there are two  $i$ -s with  $b_i > 0$  which are relatively prime to one another then  $L$  is primitive. (In fact, as mentioned above, an examination of the proof of the corresponding fact in the general Perron-Frobenius theorem shows that it is enough to know that there are  $i$ 's whose greatest common divisor is 1 with  $b_i > 0$ .) In particular, if  $b_i > 0$  and  $b_{i+1} > 0$  for some  $i$  then  $L$  is primitive.

## The limiting behavior when the Leslie matrix is primitive.

If  $L$  is primitive with maximal eigenvalue  $r$  then we know from the general Perron Frobenius theory that the total population grows (or declines) approximate the rate  $r^k$  and that the relative size of the age groups to the general population is proportional to the positive eigenvector (as computed above).

The most famous and (ancient) Leslie matrix is the two by two matrix

$$F = \begin{pmatrix} 1 & 1 \\ 1 & 0 \end{pmatrix}$$

whose powers when applied to  $\begin{pmatrix} 1 \\ 0 \end{pmatrix}$  generate the Fibonacci numbers. The eigenvalues of  $F$  are

$$\frac{1 \pm \sqrt{5}}{2}.$$

## An imprimitive Leslie matrix.

If the females give birth only in the last time period then the Leslie matrix is not primitive. For example, Atlantic salmon die immediately after spawning. Assuming, for example, that there are three age groups, we obtain the Leslie matrix

$$L = \begin{pmatrix} 0 & 0 & b \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{pmatrix}.$$

$$L = \begin{pmatrix} 0 & 0 & b \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{pmatrix}.$$

The characteristic polynomial of this matrix is

$$\lambda^3 - bs_1s_2$$

so if  $F$  is the real root of  $F^3 = bs_1s_2$  the eigenvalues are

$$F, \omega F, \omega^2 F$$

where  $\omega$  is a primitive cube root of unity.

So  $L$  is conjugate to the matrix

$$\begin{pmatrix} 0 & 0 & F \\ F & 0 & 0 \\ 0 & F & 0 \end{pmatrix} = \begin{pmatrix} F & 0 & 0 \\ 0 & F & 0 \\ 0 & 0 & F \end{pmatrix} \begin{pmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}.$$

So

$$\frac{1}{F}L$$

is periodic with period 3.

## Markov chains in a nutshell.

A non-negative matrix  $M$  is a **stochastic** matrix if each of the row sums equal 1. Then the column vector  $\mathbf{1}$  all of whose entries equal 1 is an eigenvector with eigenvalue 1. So if  $M$  is irreducible 1 is the maximal eigenvalue since  $\mathbf{1}$  has all positive entries.

If  $M$  is primitive, then we know from the general theory that

$$M^k \rightarrow \begin{pmatrix} \pi_1 & \pi_2 & \cdots & \pi_n \\ \pi_1 & \pi_2 & \cdots & \pi_n \\ \vdots & \vdots & \vdots & \vdots \\ \pi_1 & \pi_2 & \cdots & \pi_n \end{pmatrix}$$

where  $\mathbf{p} := (\pi_1, \pi_2, \dots, \pi_n)$  is the unique vector whose entries sum to one and satisfies  $\mathbf{p}M = \mathbf{p}$ .

# The Google ranking.

We follow the discussion in Chapters 3 and 4 of *Google's PageRank and Beyond: The Science of Search Engine Rankings* by Amy N. Langville and Carl D. Meyer.

The issue is how to rank the “importance” of URL’s on the web. The idea is to think of a hyperlink from A to B as an endorsement of B. So many inlinks should increase the value of a URL. On the other hand, each inlink should carry a weight. A recommendation should carry more weight if coming from an important source, but less if the source is known to have many outlinks. (If I am known to write many positive letters of recommendation then the value of each decreases, even though I might be an “important” professor.)

## The basic equation.

So we would like the ranking to satisfy an equation like

$$r(P_i) = \sum_{P_j \in B_{P_i}} \frac{r(P_j)}{|P_j|}$$

where  $r(P)$  is the desired ranking,  $B_{P_i}$  is the set of “pages” pointing into  $P_i$ , and  $|P_j|$  is the number of links pointing out of  $P_j$ .



## The matrix $\mathbf{H}$ .

$$r(P_i) = \sum_{P_j \in B_{P_i}} \frac{r(P_j)}{|P_j|}.$$

So if  $\mathbf{r}$  denotes the row vector whose  $i$ -th entry is  $r(P_i)$  and  $\mathbf{H}$  denotes the matrix whose  $ij$  entry is  $1/|P_i|$  if there is a link from  $P_i$  to  $P_j$  then this equation becomes

$$\mathbf{r} = \mathbf{r}\mathbf{H}.$$

The matrix  $\mathbf{H}$  is of size  $n \times n$  where  $n$  is the number of “pages”, roughly 12 billion of so at the current time. We would like to solve the above equation by iteration, as in the case of a Markov chain. Despite the huge size, computing products with  $\mathbf{H}$  is feasible because  $\mathbf{H}$  is sparse, i.e. it consists mostly of zeros.

## Problems with $\mathbf{H}$ , the matrix $\mathbf{S}$ .

The matrix  $\mathbf{H}$  will have some rows consisting entirely of zeros. These correspond to the “dangling nodes”, pages (such as pdf. files etc.) which have no outgoing links. Other than these, the row sums are one.

To fix this problem, Brin and Page, the inventors of Google, replaced the zero rows by rows consisting entirely of  $1/n$  (a very small number). So let  $\mathbf{a}$  denote the column vector whose  $i$ -th entry is 1 if the  $i$ -th row is dangling row, and  $a_i = 0$  otherwise. Let  $\mathbf{e}$  be the row vector consisting entirely of ones. Brin and Page replace  $\mathbf{H}$  by

$$\mathbf{S} := \mathbf{H} + \frac{1}{n} \mathbf{a} \otimes \mathbf{e}.$$

The matrix  $\mathbf{S}$  is now a Markov chain matrix, all rows sum to one.

For example, suppose that node 2 is a dangling mode and that the matrix  $\mathbf{H}$  is

$$\mathbf{H} = \begin{pmatrix} 0 & \frac{1}{2} & \frac{1}{2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{1}{3} & \frac{1}{3} & 0 & 0 & \frac{1}{3} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{2} & \frac{1}{2} \\ 0 & 0 & 0 & 1 & 0 & 0 \end{pmatrix}.$$

Then

$$\mathbf{S} = \begin{pmatrix} 0 & \frac{1}{2} & \frac{1}{2} & 0 & 0 & 0 \\ \frac{1}{6} & \frac{1}{6} & \frac{1}{6} & \frac{1}{6} & \frac{1}{6} & \frac{1}{6} \\ \frac{1}{3} & \frac{1}{3} & 0 & 0 & \frac{1}{3} & 0 \\ 0 & 0 & 0 & 0 & \frac{1}{2} & \frac{1}{2} \\ 0 & 0 & 0 & 1 & 0 & 0 \end{pmatrix}.$$

## Problems with $\mathbf{S}$ , the Google matrix $\mathbf{G}$ .

The rows of  $\mathbf{S}$  sum to one, but we have no reason to believe that  $\mathbf{S}$  is primitive. So Brin and Page replace  $\mathbf{S}$  by

$$\mathbf{G} := \alpha \mathbf{S} + (1 - \alpha) \frac{1}{n} \mathbf{J}$$

where  $\mathbf{J}$  is the matrix all of whose entries are 1, and  $0 < \alpha < 1$  is a real number. (They take  $\alpha = 0.85$ ).

For example, if we start with the  $6 \times 6$  matrix  $\mathbf{H}$  as above, and take  $\alpha = .9$ , the corresponding Google matrix  $\mathbf{G}$  is

$$\begin{pmatrix} 1/60 & 7/15 & 7/15 & 1/60 & 1/60 & 1/60 \\ 1/6 & 1/6 & 1/6 & 1/6 & 1/6 & 1/6 \\ 19/60 & 19/60 & 1/60 & 1/60 & 19/60 & 1/60 \\ 1/60 & 1/60 & 1/60 & 1/60 & 7/15 & 7/15 \\ 1/60 & 1/60 & 1/60 & 7/15 & 1/60 & 7/15 \\ 1/60 & 1/60 & 1/60 & 11/12 & 1/60 & 1/60 \end{pmatrix}.$$

The rows of  $\mathbf{G}$  sum to one, and are all positive. So, in principle,  $\mathbf{G}^k$  converges to a matrix whose rows are all equal to  $\mathbf{s}$  where  $\mathbf{s}$  is a solution to

$$\mathbf{s} = \mathbf{s} \cdot \mathbf{G}.$$

MATLAB gives the eigenvalues of  $G$  as

$$-0.3705, -0.0896, 0.6101, 1.0000, -0.4500, -0.4500.$$

The row vector giving the (left) eigenvector with eigenvalue 1 normalized to have row sum 1 is

$$(0.0372, 0.0540, 0.0415, 0.3751, 0.2060, 0.2862).$$

MATLAB computes  $G^{10}$  as

$$\begin{pmatrix} 0.0394 & 0.0578 & 0.0440 & 0.3714 & 0.2044 & 0.2829 \\ 0.0384 & 0.0560 & 0.0429 & 0.3728 & 0.2053 & 0.2846 \\ 0.0389 & 0.0568 & 0.0435 & 0.3707 & 0.2060 & 0.2841 \\ 0.0370 & 0.0535 & 0.0412 & 0.3769 & 0.2049 & 0.2865 \\ 0.0370 & 0.0535 & 0.0412 & 0.3766 & 0.2052 & 0.2865 \\ 0.0370 & 0.0535 & 0.0412 & 0.3732 & 0.2083 & 0.2868 \end{pmatrix}.$$

This is close to, but not quite the limiting value.

MATLAB computes  $G^{20}$  as

$$\begin{pmatrix} 0.0372 & 0.0540 & 0.0415 & 0.3751 & 0.2060 & 0.2862 \\ 0.0372 & 0.0540 & 0.0415 & 0.3751 & 0.2060 & 0.2862 \\ 0.0372 & 0.0540 & 0.0415 & 0.3751 & 0.2060 & 0.2862 \\ 0.0372 & 0.0540 & 0.0415 & 0.3751 & 0.2060 & 0.2862 \\ 0.0372 & 0.0540 & 0.0415 & 0.3751 & 0.2060 & 0.2862 \\ 0.0372 & 0.0540 & 0.0415 & 0.3751 & 0.2060 & 0.2862 \end{pmatrix},$$

which has the correct limiting value to four decimal places in all positions. This is what we would expect, since if we take the second largest eigenvalue, which is 0.6101, and raise it to the 20th power, we get .000051.. .



In our example, we have seen that the stationary vector with row sum equal to one is

$$\mathbf{s} = (.03721 \quad .05396 \quad .04151 \quad .3751 \quad .206 \quad .2862).$$

The interpretation of the first entry, for example, is that 3.721% of the time, the random surfer visits page 1. The pages of this tiny web are therefore ranked by their importance as (4,6,5,2,3,1). But, in real life, where 6 is replaced by 12 billion, as  $\mathbf{G}$  is not sparse, taking powers of  $\mathbf{G}$  is impossible due to its size.

## Avoiding multiplying by $G$ .

We can avoid multiplying with  $\mathbf{G}$ . Instead, use the iterations scheme

$$\begin{aligned}\mathbf{s}_{k+1} &= \mathbf{s}_k \cdot \mathbf{G} \\ &= \alpha \mathbf{s}_k \cdot \mathbf{S} + \frac{1-\alpha}{n} \mathbf{s}_k \mathbf{J} \\ &= \alpha \mathbf{s}_k \cdot \mathbf{H} + \frac{1}{n} (\alpha \mathbf{s}_k \cdot \mathbf{a} + 1 - \alpha) \mathbf{e}\end{aligned}$$

since  $\mathbf{J} = \mathbf{e}^\dagger \otimes \mathbf{e}$  and  $\mathbf{s}_k \cdot \mathbf{e}^\dagger = 1$ . Now only sparse multiplications are involved.

## Why does this converge and what is the rate of convergence?

Let  $1, \lambda_2, \dots$  be the spectrum of  $\mathbf{S}$  and let  $1, \mu_2, \dots$  be the spectrum of  $\mathbf{G}$  (arranged in decreasing order, so that  $\lambda_2 < 1$  and  $\mu_2 < 1$ ). We will show that

### Theorem

$$\lambda_i = \alpha \mu_i, \quad i = 2, 3, \dots, n.$$

This implies that  $\lambda_2 < \alpha$  since  $\mu_2 < 1$ . Since

$$(0.85)^{50} \doteq 0.000296$$

this shows that at the 50th iteration one can expect 2-3 decimal places of accuracy.

## Proof of the theorem.

Let  $\mathbf{f} := \mathbf{e}^\dagger$  so  $\mathbf{f}$  is the column vector all of whose entries are 1. Since the row sums of  $\mathbf{S}$  equal 1, we have  $\mathbf{S} \cdot \mathbf{f} = \mathbf{f}$ . Let  $\mathbf{Q}$  be an invertible matrix whose first column is  $\mathbf{f}$ , so  $\mathbf{Q} = (\mathbf{f}, \mathbf{X})$  for some matrix  $\mathbf{X}$  with  $n$  rows and  $n - 1$  columns. Write  $\mathbf{Q}^{-1}$  as

$\mathbf{Q}^{-1} = \begin{pmatrix} \mathbf{y} \\ \mathbf{Y} \end{pmatrix}$  where  $\mathbf{y}$  is a row vector with  $n$  entries and  $\mathbf{Y}$  is a matrix with  $n - 1$  rows and  $n$  columns. The fact that  $\mathbf{Q}^{-1}\mathbf{Q} = \mathbf{I}$

implies that

$$\mathbf{y} \cdot \mathbf{f} = 1 \quad \text{and} \quad \mathbf{Y} \cdot \mathbf{f} = \mathbf{0}.$$

We have

$$\mathbf{Q}^{-1}\mathbf{S}\mathbf{Q} = \begin{pmatrix} \mathbf{y} \cdot \mathbf{f} & \mathbf{y}\mathbf{S}\mathbf{X} \\ \mathbf{Y} \cdot \mathbf{f} & \mathbf{Y}\mathbf{S}\mathbf{X} \end{pmatrix} = \begin{pmatrix} 1 & \mathbf{y}\mathbf{S}\mathbf{X} \\ \mathbf{0} & \mathbf{Y}\mathbf{S}\mathbf{X} \end{pmatrix},$$

So the eigenvalues of  $\mathbf{Y}\mathbf{S}\mathbf{X}$  are  $\lambda_2, \lambda_3, \dots$

## Proof of the theorem, concluded.

Now  $\mathbf{J}$  is a matrix all of whose columns equal  $\mathbf{f}$ . So  $\mathbf{Q}^{-1}\mathbf{J}$  has ones in the top row and zeros elsewhere. So

$$\mathbf{Q}^{-1}\mathbf{J}\mathbf{Q} = \begin{pmatrix} 1 & \mathbf{e} \cdot \mathbf{X} \\ 0 & \mathbf{0} \end{pmatrix}$$

Hence

$$\mathbf{Q}^{-1}\mathbf{H}\mathbf{Q} = \mathbf{Q}^{-1}(\alpha\mathbf{S} + (1 - \alpha)\mathbf{J})\mathbf{Q} = \begin{pmatrix} 1 & \alpha\mathbf{y}\mathbf{S}\mathbf{X} + (1 - \alpha)\mathbf{e} \cdot \mathbf{X} \\ 0 & \alpha\mathbf{Y}\mathbf{S}\mathbf{X} \end{pmatrix}.$$

So the eigenvalues of  $\mathbf{G}$  are  $1, \alpha\lambda_2, \alpha\lambda_3 \dots$ .  $\square$

We return to the study of properties of a primitive matrix. (In the biological literature this has the better name: a “power positive matrix”, but we will stick with the mathematics terminology.)

Let  $A$  be a primitive matrix,  $r$  its maximal eigenvalue,  $x$  a right eigenvector with eigenvalue  $r$ ,  $y$  a left eigenvector with eigenvalue  $r$  with  $y \cdot x = 1$  and  $H$  the one dimensional projection operator  $H = x \otimes y$  so

$$H = \lim_{k \rightarrow \infty} \left( \frac{1}{r} A \right)^k.$$

If  $e_j$  is the (column) vector with 1 in the  $j$ -th position and zeros elsewhere, then

$$He_j = y_j x.$$

If  $e_j$  is the (column) vector with 1 in the  $j$ -th position and zeros elsewhere, then

$$He_j = y_j x.$$

This equation has a “biological” interpretation due to R.A.Fisher: If we think of the components of a column vector as referring to stages of development (as, for example, in the Leslie matrix), then the components of  $y$  can be interpreted as giving the relative “reproductive value” of each stage:

Think of different stages as alternate investment opportunities in long-term population growth. If you could put one dollar into any one of these investments (one individual in any of the stages) what is their relative payoff in the long run (the relative size of the resulting population in the distant future)? The above equation shows that it is proportional to  $y_j$ .

# Eigenvalue sensitivity to changes in the matrix elements.

The Perron-Frobenius theorem tells us that if we increase any matrix element in a primitive matrix,  $A$ , then the dominant eigenvalue  $r$  increases. But by how much? To answer this question, consider the equation

$$y \cdot A \cdot x = r \quad y \cdot x = 1.$$

In this equation, think of the entries of  $A$  as  $n^2$  independent variables, and  $x, y, r$  as functions of these variables.



$$y \cdot A \cdot x = r.$$

In this equation, think of the entries of  $A = (a_{ij})$  as  $n^2$  independent variables, and  $x, y, r$  as functions of these variables, and take the partial derivative with respect to the  $ij$ -th entry,  $a_{ij}$ . The left hand side gives

$$\frac{\partial y}{\partial a_{ij}} \cdot A \cdot x + y \cdot \frac{\partial A}{\partial a_{ij}} \cdot x + y \cdot A \cdot \frac{\partial x}{\partial a_{ij}}.$$

But  $\frac{\partial A}{\partial a_{ij}}$  is the matrix with 1 in the  $ij$ -th position and zeros elsewhere, and the sum of the first and third terms above are (since  $Ax = rx$  and  $yA = ry$ )

$$r \left( \frac{\partial y}{\partial a_{ij}} \cdot x + y \cdot \frac{\partial x}{\partial a_{ij}} \right) = r \frac{\partial (y \cdot x)}{\partial a_{ij}} = 0$$

since  $y \cdot x \equiv 1$ .

$$y \cdot A \cdot x = r.$$

In this equation, think of the entries of  $A = (a_{ij})$  as  $n^2$  independent variables, and  $x, y, r$  as functions of these variables, and take the partial derivative with respect to the  $ij$ -th entry,  $a_{ij}$ . The left hand side gives  $y_i x_j$  while the right hand side gives  $\frac{\partial r}{\partial a_{ij}}$ . So we have proved

$$\frac{\partial r}{\partial a_{ij}} = y_i x_j.$$

In the next few slides we will explain how this equation is used to “explain” why there is aging. The ensuing slides are taken verbatim from the book *Dynamical Models in Biology* by Ellner and Guckenheimer, pages 50-51. This explanation is derived by modeling a life cycle in which there is no aging, and then asking whether a little bit of aging would lead to increased Darwinian fitness as measured by  $r$ .

A no aging life cycle - an alternative not seen in nature - means that females start reproducing at some age  $m$  (for maturity), and thereafter have constant fecundity  $f_j = f$  and survival  $p_j = p < 1$  for all ages  $j \geq m$  in the Leslie matrix. We have taken  $p < 1$  to represent an age-independent rate of accidental deaths unrelated to aging. The eigenvalue sensitivity formula

$$\frac{\partial r}{\partial a_{ij}} = y_i x_j$$

lets us compute the relative eigenvalue sensitivities at different ages for this life cycle without any hard calculations, so long as  $r = 1$ . Populations can't grow or decline without limit, so  $r$  must be near 1.

$$\frac{\partial r}{\partial a_{ij}} = y_i x_j.$$

The reproductive value of adults,  $y_i$ ,  $i \geq m$  is independent of age because all adults have exactly the same future prospects and therefore make the same long-term contribution to future generations. On the other hand, the stable age distribution  $x_j$  goes down with age. With  $r = 1$  the number of  $m$  year olds is constant, so we can compute the number of  $m + k$  year olds at time  $t$  to be  $n_{m+k}(t) = n_m(t - k)p^k = n_m(t)p^k$ . That is, in order to be age  $(m + k)$  now, you must have been  $m$  years old  $k$  years ago, and you must have survived for the  $k$  years between then and now. Therefore  $x_j$  is proportional to  $p^{j-m}$  for  $j \geq m$ .

$$\frac{\partial r}{\partial a_{ij}} = y_i x_j.$$

$y_i$ ,  $i \geq m$  is independent of  $i$ .  $x_j$  is proportional to  $\rho^{j-m}$  for  $j \geq m$ .

Consequently, the relative sensitivity of  $r$  to changes in either the fecundity  $a_{1,j}$  or survival  $a_{j+1,j}$  of age- $j$  females, is proportional to  $\rho^{j-m}$ . In both cases, as  $j$  changes the relevant  $x_j$  is proportional to  $\rho^{j-m}$  while the reproductive value  $y_j$  stays the same. This has two consequences:

- 1 The strength of selection against deleterious mutations acting late in life is weaker than selection against deleterious mutations acting early in life.
- 2 Mutations that increase survival or fecundity early in life, at the expense of an equal decrease later in life, will be favored by natural selection.

These are known, respectively, as the *Mutation Accumulation* and *Antagonistic Pleiotropy* theories of aging.