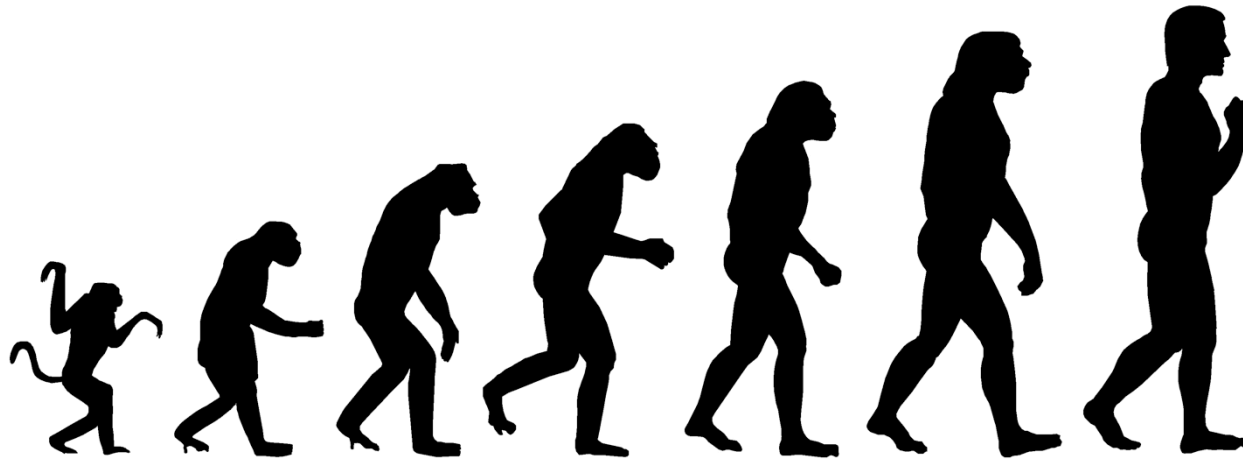


# Evolution

Matt Keeling



MA 999: Topics in Mathematical Modelling

Tuesday 11-12

Thursday 2-4

# Evolution

Lecture 1 Tuesday 6<sup>th</sup> 11-12

**Introduction.** Evidence for evolution. Fitness. Competition.

Lecture 2 Thursday 8<sup>th</sup> 2-3

**Games & Genes.**

Lecture 3 Thursday 8<sup>th</sup> 3-4

**Computer-based practicals** – example programs and questions.

Lecture 4 Tuesday 13<sup>th</sup> 11-12

**Sex and Speciation.** Sexual selection. Males as parasites. Why sexual reproduction? How do new species arise.

Lecture 5 Thursday 15<sup>th</sup> 2-3

**Disease evolution.** Why aren't we all wiped out by killer infections?

Lecture 6 Thursday 15<sup>th</sup> 3-4

**Computer-based practicals** – example programs and questions.

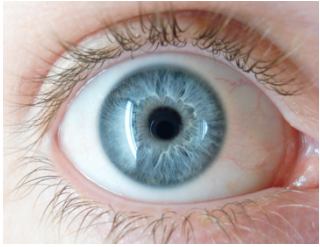
# Games and Genes

## **Genes.**

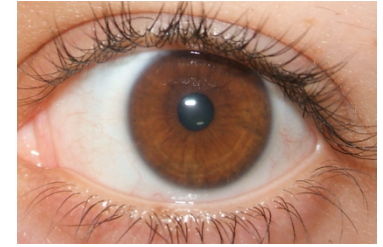
Obvious, we all know now that our behaviour/fitness is largely governed by our genes. Here we'll consider traits which are governed by two alleles at a single locus.

## **Games.**

Two-player games provide a robust and easy mathematical framework to deal with the interaction (and competition) between individuals 'playing' different strategies. We'll consider the mathematics and some classic examples.

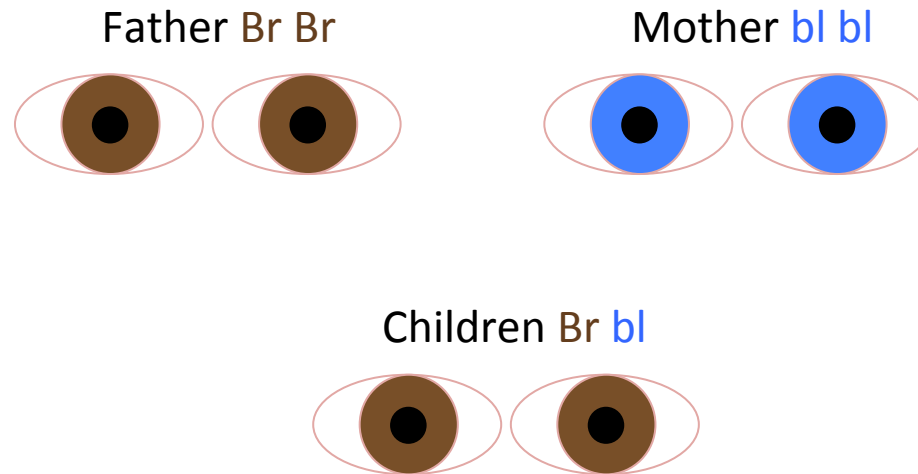


# Genes



The classic example is eye colour. Blue and Brown eyes are (mostly) governed by a single locus. The colour of someone's eyes is determined by the 2 genes they inherit from their parents.

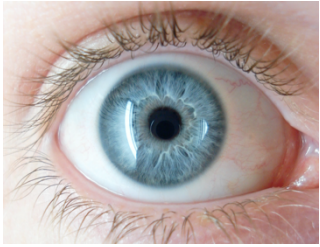
In this example the Brown allele(**Br**) is dominant, and the Blue allele(**bl**) is recessive.



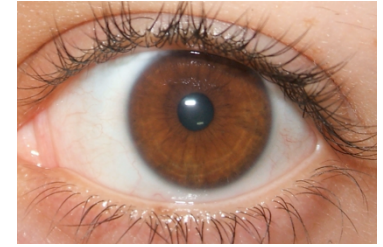
This example is easy – all children are **Br bl** and have brown eyes.

This shows the difference between **genotype** and **phenotype**.

(Please don't ask about green eyes !! )

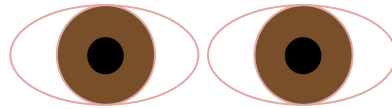


# Genes

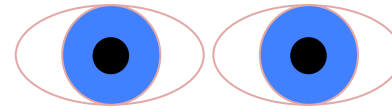


Other combinations.

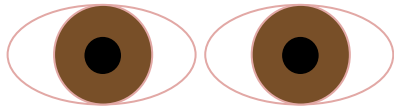
Father Br bl



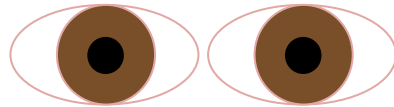
Mother bl bl



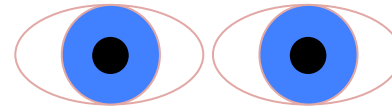
Children Br bl



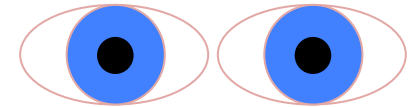
Children Br bl



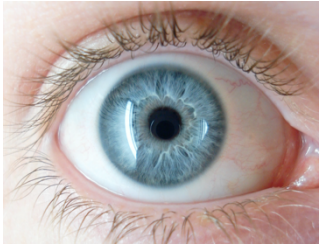
Children bl bl



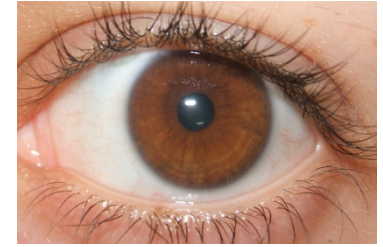
Children bl bl



In this combination of Brown-eyed Father and Blue-eyed Mother there is a 50:50 ratio in the children.

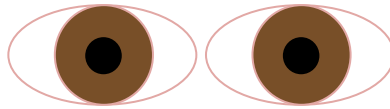


# Genes

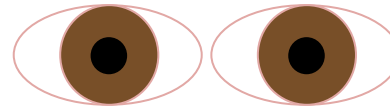


Other combinations.

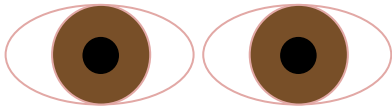
Father Br Br



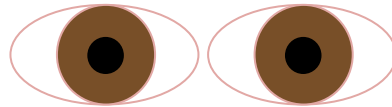
Mother Br bl



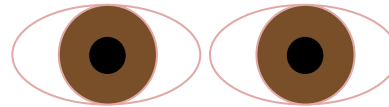
Children Br Br



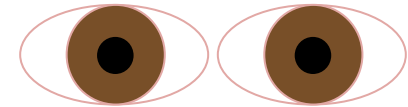
Children Br Br



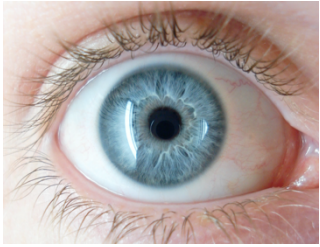
Children Br bl



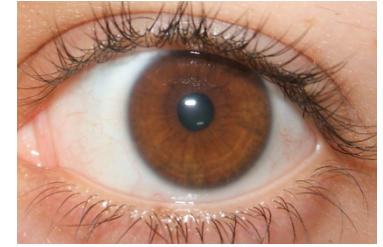
Children Br bl



This clearly illustrates the dominance of the Brown eye allele.

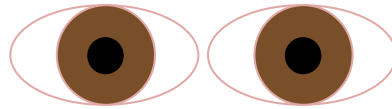


# Genes

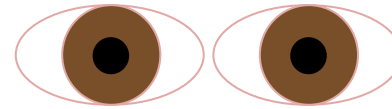


Finally the slightly odd one:

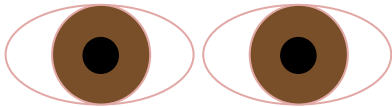
Father Br bl



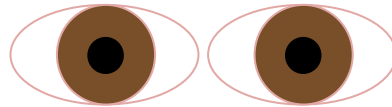
Mother Br bl



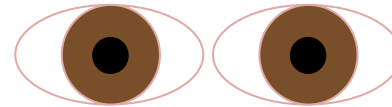
Children Br Br



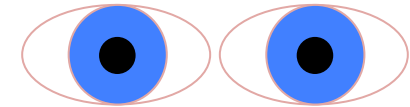
Children Br bl



Children Br bl

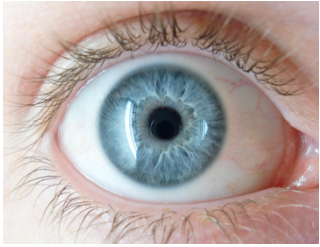


Children bl bl

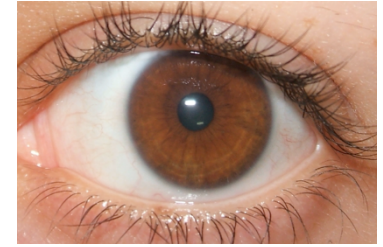


So due to the fact that a Brown-eyed parent can be “hiding” a blue gene, it is possible for two Brown-eyed parents to have a Blue-eyed child.

Notice that there are always **four** ways of putting together the parents’ genes – even if often these lead to the same combination.



# Genes



In general, we can use these caricatures to define population-level distributions.

If we assume that mating is **random**...

– that is blue-eyed individuals don't preferentially partner other blue-eyed people

...then the **Hardy-Weinberg Ratio** says that

If  $X_i$  is the proportion of allele  $A_i$  in the population then the proportion of the population who are type  $A_i A_j$  is simply  $X_i X_j$ .

So if the proportion of blue-eye alleles in the population is  $b$  (and say  $b=0.2$ ) then:

$$\text{Br Br} = (1-b)^2 = 0.64 \quad \text{Br bl} = \text{bl Br} = b(1-b) = 0.16 \quad \text{bl bl} = b^2 = 0.04$$

So only 4% of the population would have blue eyes.



# Genes

Usually we don't think of eye-colour as giving a substantial evolutionary advantage (although clearly there is some dependence on latitude). Let's consider three different examples and their mathematical models:

**Haemophilia.** Recessive genetic disorder – individuals of type hh have problems producing blood clotting agents. (Note this gene is on the X chromosome, so affects males differently to females – but we'll ignore this complication).

**Fatal Mutation.** What if there was a mutation that was dominant and gave a lower fitness?

**Sickle-cell disease.** Again this is recessive; type aa suffer from extreme anaemia, type Aa and AA do not – but type Aa has some level of protection against malaria.

# Genes

Consider alleles of type A and a. The dynamics are described by:

$$\begin{aligned}\frac{da}{dt} &= [\text{Fitness of a-type offspring}] - a \times [\text{Fitness of average offspring}] \\ &= \left[ W_{aa} a^2 + \frac{1}{2} W_{aA} a(1-a) + \frac{1}{2} W_{Aa} (1-a)a \right] - a \times \left[ W_{aa} a^2 + 2W_{aA} a(1-a) + W_{AA} (1-a)^2 \right] \\ &= W_{aa} a^2 (1-a) + W_{aA} a(1-a)(1-2a) - W_{AA} a(1-a)^2 \\ &= a(1-a) \left[ W_{aa} a + W_{aA} (1-2a) - W_{AA} (1-a) \right]\end{aligned}$$

Where the  $W$  terms are the reproductive fitnesses of each allele combination.

This allows us to experiment with different real-world examples.

# Two-Player Games

A two-player game can be defined by a pay-off matrix; this gives the payoff an individual playing strategy  $s$  gains when playing against strategy  $s'$ .

		$s_1$	$s_2$
<b>Pay-off to strategy</b>	$s_1$	A	B
	$s_2$	C	D

We then want to suppose that each strategy reproduces based on its pay-off matrix:

$$\frac{ds_1}{dt} = s_1 s_1 A + s_1 s_2 B$$

$$\frac{ds_2}{dt} = s_2 s_1 C + s_2 s_2 D$$

$$\frac{ds}{dt} = \frac{d}{dt} \left( \frac{s_1}{s_1 + s_2} \right) = s(1-s) [sA + (1-s)B - sC - (1-s)D]$$

# Two-Player Games

More generally, we would like to set  $P_i$  as the proportion of individuals playing strategy  $i$ , and set  $\mathbf{W}$  to be the pay-off matrix.

In this case, the generalised model is:

$$\frac{dP_i}{dt} = [\mathbf{W}P]_i P_i - [P^T \mathbf{W}P] P_i$$

If we then define the average fitness (per individual) within this populations to be:

$$\bar{\omega} = P^T \mathbf{W}P$$

then we find that if  $\mathbf{W}$  is symmetric, then fitness always increases over time.

# Two-Player Games: mixed strategies

Suppose now instead of playing pure strategies  $s_1$  and  $s_2$ , the two players decide to randomly play a mixed strategy (ie playing  $s_1$  a proportion  $p$  of the time). Setting  $P=(p \ 1-p)^T$  and  $Q=(q \ 1-q)^T$ , we have:

		$p$	$q$
<b>Pay-off to strategy</b>	$p$	$P^T W P$	$P^T W Q$
	$q$	$Q^T W P$	$P^T W Q$

The most famous example of this type of 2-player game is the hawk-dove model:

$$W = \begin{pmatrix} D & H \\ 1 & 0 \\ A (> 1) & -B (< 0) \end{pmatrix} \begin{matrix} D \\ H \end{matrix}$$

Where doves are peaceful and share a resource, whereas hawks are competitive and fight for a resource.

# Two-Player Games: ESS

An Evolutionary Stable Strategy (or ESS) is a strategy (pure or mixed) that cannot be invaded. Mathematically this means that  $P$  is an ESS if:

$$Q^T \mathbf{W} P \leq P^T \mathbf{W} P \quad \forall Q$$

That is, there is no other strategy ( $Q$ ) that can invade a population of  $P$ 's.

Note:

- 1) An ESS does **not** optimise fitness, it is simply more fit than others in its own environment.
- 2) Multiple ESS can easily exist.
- 3) Often we can consider a *local* ESS, which is sufficient if mutation is short-range.

An ESS is **strongly** or **continuously** stable if it is also an evolutionary attractor:

$$P^T \mathbf{W} Q \geq Q^T \mathbf{W} Q \quad \forall Q$$

That is, it can out-compete all other strategies.

# Two-Player Games: Bishop-Canning theorem

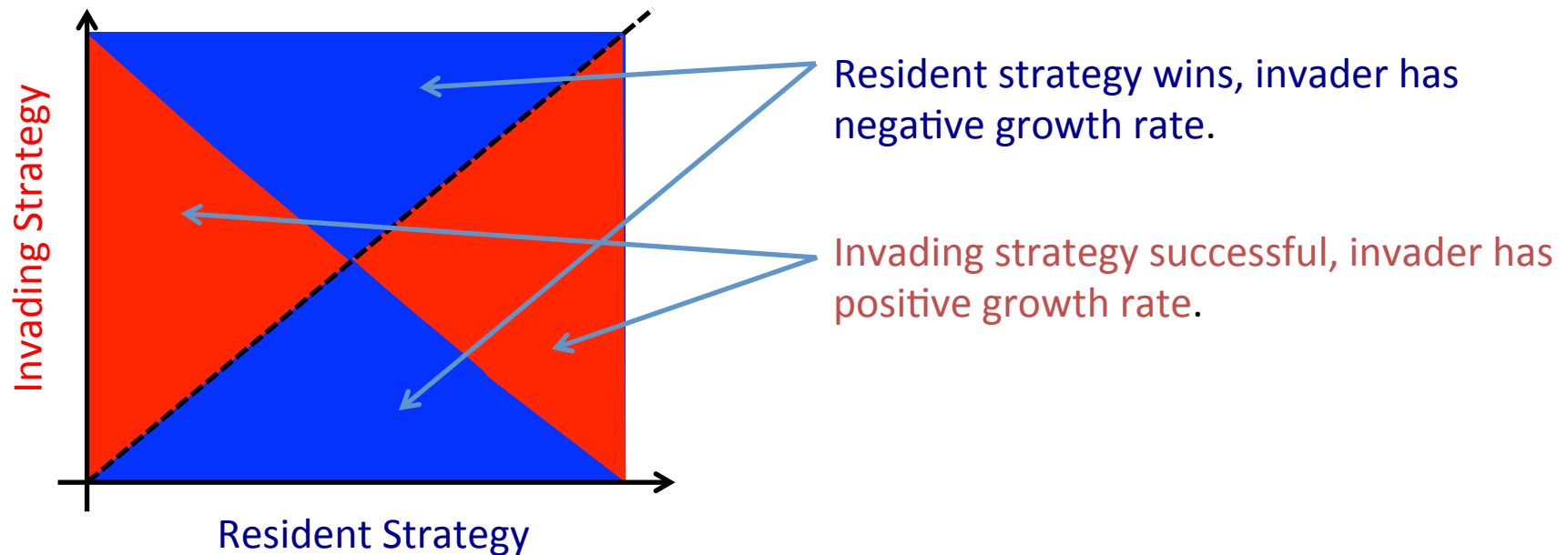
If  $P$  is an ESS composed of pure strategies  $s_1, s_2, \dots, s_n$ ; then in an environment of all  $P$  the payoff to all pure strategies is equal to that of the ESS.

$$s_i^T \mathbf{W}P = P^T \mathbf{W}P \quad \forall i$$

The proof of this comes from realising that  $P$  is a linear combination of the pure strategies; so if the equality does not hold, then some strategy will perform better than  $P$ , so it cannot be an ESS.

# Invasion Plots

These provide an ideal means of rapidly visualising the evolutionary behaviour.



This form of invasion plot (or Pairwise invasibility plot) is associated with a **strongly stable ESS**. At the cross-over point, nothing else can invade (so its an ESS); also the strategy is able to invade any other strategy.