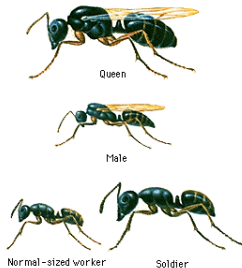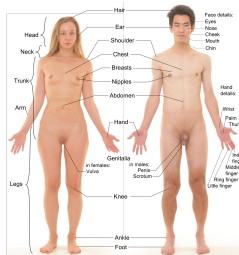Kin selection and
the gene's eye view of evolution
(part 1)

The ultimate reproductive puzzle

- Three type of individuals: males, females, and workers.

- Workers do not reproduce and soldiers self-sacrifice to defend the colony.

- Workers and queens have fundamentally different morphologies and fate.

The ultimate reproductive puzzle

- Somatic cells forming the body of multicellular organisms do not reproduce and work for the good of the germ line.

- Germ line cell giving rise to gametes (ovules and sperm) have fundamentally different fates than somatic cells: immortality for the first death for the latter.

The ultimate reproductive puzzle

The notion of self-sacrifice to help others in human societies has long attracted attention.

- It is extolled by all major religions (e.g., "thou shalt open thine hand wide unto him, and shalt surely lend him sufficient for his need" Deuteronomy 15:8).

- It has been discussed by eminent philosophers and military strategist: "The moral law causes the people to follow their leader regardless of their lives, undismayed by any danger" Sun Tzu

The ultimate reproductive puzzle

- The biomass of social insects is about the same as that of all humans.

- How is it possible that sterility is adaptive at such a massive scale since natural selection favor alleles that increase survival, fecundity, and mating success?

- Why aren't alleles causing self-sacrifice counter-selected?

- Sterile social insects puzzled Darwin and remained a reproductive puzzle for about a century until W. D. Hamilton in 1964 provided a pivotal insight.

The answer to the puzzle

"Despite the principle of the survival of the fittest the ultimate criterion which determines whether a gene will spread is not whether the behavior is to the benefit of the behaver but whether it is to the benefit of the gene"
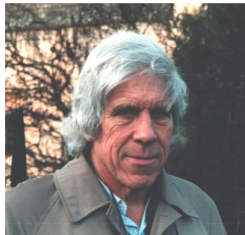
W. D. Hamilton

Hence, to understand the evolution of self-sacrifice we need to focus on fitness benefits to the genes and not on that of individuals.

The answer to the puzzle

- Selection favors alleles that leave on average more replicate copies in the offspring generation, regardless of how it affects particular individuals carrying the allele.

- An allele causing an individual to self sacrifice can be favored by natural selection if the behavior benefit replicate copies of the allele in other individuals; that is, if the recipient of the behavior is related to the actor.

This is the so-called gene eye's view (or gene-centered view) of evolution.

The gene's eye view of evolution

- The gene eye's view of evolution not only explains self-sacrifice but illuminates many other phenotypes or biological phenomena such as cooperation and conflict within the family, the evolution of sex, and maybe even warfare between pre-state societies.

- The gene eye's view of evolution is at the heart of sociobiology and evolutionary psychology.

- This is the attempt to explain (social) behavior in humans and other species within an evolutionary lens.

The gene's eye view of evolution

- We are going to study in more detail the evolution of self-sacrifice, i.e., under what conditions is this possible. This will show that it is useful to delineate between four broad categories of behavior: selfishness, altruism, cooperation, and spite.

- We will study the adaptive dynamics of self-sacrifice and more generally social behavior.

- To that end we need first to understand the concept of relatedness between pairs of individuals.

The relatedness coefficient

- We denote by r the relatedness coefficient between two individuals.

- We define relatedness between two individuals as the probability that a gene (randomly) taken in one individual under scrutiny (called the focal individual or the actor) has an identical-by-descent copy in the second individual (often called the recipient). The two genes will thus be of the same allelic type.

Focal individual   Interaction partner

To be identical-by-descent two genes must descend from the same recent common ancestor (e.g., a parent, a grand-parent).

Relatedness between parent and offspring

We consider the relatedness between parent and offspring from the point of view of an offspring (the focal individual) under random mating.

With probability $1/2$ any gene of an individual is transmitted to its offspring. Or said differently: take a gene in an individual, then with probability $1/2$ it comes from Dad and with probability $1/2$ it comes from Mom.
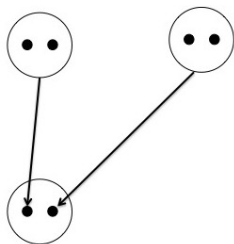
Relatedness between parent and offspring

The probability $r_{o,p}$ that a gene in the offspring has a copy that is identical-by-descent with a gene in the parent under focus (either Mom or Dad) is

$$r_{o,p} = \frac{1}{2}$$
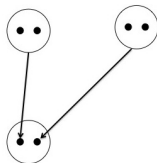
- With probability $1/2$ the gene in the offspring comes from the parent under focus (either Mom or Dad), and is then necessarily identical-by-descent to a gene in the parent.

- With probability $1/2$ the gene sampled in the offspring comes from its other parent. Then, if parents are unrelated (as occur under random mating) there no identity-by-descent relationship between the genes.
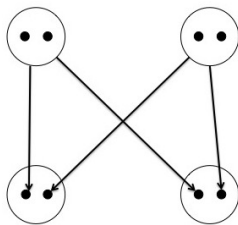
Relatedness between parent and offspring

Under random mating the relatedness between an offspring and any of its parent (Mom or Dad) is

$$r_{\text{o,p}} = \frac{1}{2}$$

Exactly the same expression would be obtained if we were to evaluate the relatedness between between parent and offspring from the point of view of the parent.
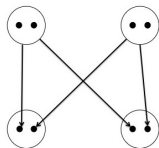
Relatedness between full siblings

We seek the probability r_{sib} that a gene in an offspring under focus has a copy that is identical-by-descent with a gene in its sibling in a random mating population (no inbreeding).

Relatedness between full siblings

Assuming random mating we have

$$r_{\mathrm{sib}} = \frac{1}{2} \times \frac{1}{2} + \frac{1}{2} \times \frac{1}{2} = \frac{1}{2}$$

- With probability $1/2$ the gene in the offspring under focus comes from its father. The paternal gene in the second offspring is identical-by-descent with probability $1/2$.

- With probability $1/2$ the gene in the offspring under focus comes from its mother. The maternal gene in the second offspring is identical-by-descent with probability $1/2$.

- When pairs of genes in offspring do not come from the same parent, they are unrelated under random mating.

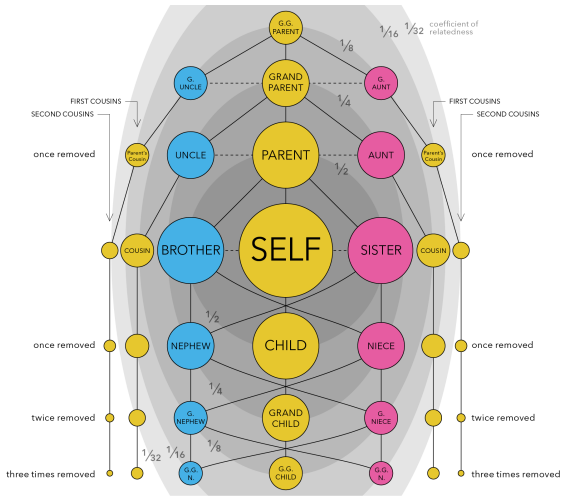# Relatedness between siblings

Hence, under random mating the relatedness between siblings is

$$r_{\mathrm{sib}} = \frac{1}{2}$$

This is the relatedness of an individual to

- Any of its parent (Mom or Dad).

- Any offspring.

- Its full sibling.

Circles of relatives under random mating

The respective circles are for $r = 1/2$, $r = 1/4$, $r = 1/8$, $r = 1/16$, etc...

Interpretation of relatedness

- Relatedness can be interpreted as a discount rate.

- It measures the likelihood that the other individual in a pair transmits to its own offspring a replicate copy of a gene residing in a focal individual, relative to the likelihood that the focal individual transmits that gene to its offspring.
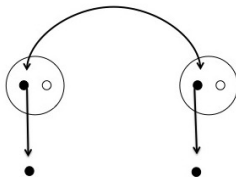
This is very useful to understand the evolution of behavior as it gives the "valuation" of another body relatives to one's own body in terms of allele transmission to the next generation.

Modeling interactions between relatives

- We are now going to build a model for understanding the evolution of a quantitative trait when interactions occur between relatives.

- We will consider a family structured population (interaction between siblings or parent-offspring) and assume additive gene action.

- But the general logic applies to any situation where relatives interact, for instance to group structured populations of small size.

Evolutionary invasion analysis for interactions between relatives

Suppose a mutation A appears in an otherwise monomorphic B diploid population.

Since any mutation arises as a single copy, this means that A necessarily arises in an heterozygote individual with a strategy denoted x.
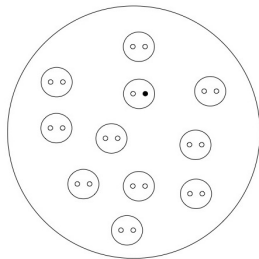

We want to characterize the condition under which A cannot invade a population of homozygotes that express strategy y. To this end, we only need to consider the fitness of an heterozygote AB individual and can neglect homozygotes for BB.

Two type of interactions

Eventhough A is rare, a heterozygote AB may interact with two categories of individuals:

❶ Heterozygotes AB with phenotype x ("mutants").

❷ Homozygotes BB with phenotype y ("residents").
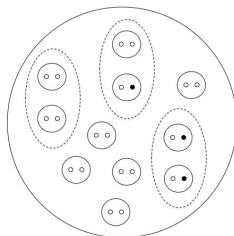
This is so because interactions between family members can occur, for instance two sibling from the same cohort may interact.

Fitness of an individual

We denote by $w(x, x_\mathrm{r})$ the expected fitness (per ploidy) of an individual with phenotype x when interacting with a relative that expresses phenotype x_r (in a population where individuals at large have phenotype y).

The key point now is that the relative may either be heterozygote for A or homozygote (so $x_\mathrm{r} \in \{x, y\}$)
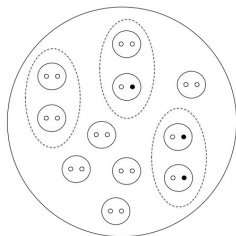
Gene fitness

The average gene fitness of an individual expressing mutant phenotype x in a population where individuals express resident phenotype y is

$$W(x,y) = r \underbrace{w(x,x)}_{x_{\mathrm{r}}=x} + (1-r) \underbrace{w(x,y)}_{x_{\mathrm{r}}=y}$$

- The mutant either interacts with another mutant, probability r, or with a resident, probability $1-r$.

- Fitness $W(x,y)$ the expected number of gene copies produced over one generation by an average A copy and is thus a measure of gene fitness. This will determine whether the mutant allele will spread or not the mutant allele will invade the population.

Uninvadability

We can now characterize the condition under which a phenotype (strategy) is uninvadable by any other strategy.

A resident strategy y is said to be uninvadable if

$$W(x, y) \leq 1 \qquad \forall x \in \mathcal{X}$$

Hence, an uninvadable strategy is resistant to invasion by any mutant phenotype.

The selection gradient

In order to evaluate uninvadable strategies it is useful to define the the selection gradient

$$S(y) = \left. \frac{\partial W(x, y)}{\partial x} \right|_{x=y}$$
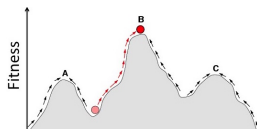
The selection gradient is the marginal change in the fitness of a female when she varies her strategy in a population expressing strategy y. It thus characterizes the direction of selection on the female trait in a population at y.

The selection gradient

The selection gradient is defined from (gene) fitness $W(x, y)$. Hence, the model involves two fitness concepts.

- Gene fitness $W(x, y)$ is the expected number of gene copies produced over one generation by an average mutant copy.

- Individual fitness $w(x, x_{\mathrm{r}})$ is the expected number of offspring produced by a focal individual, and is thus a measure of fitness defined at the individual level.

What are the consequence for the selection gradient?

The selection gradient

The selection gradient for interaction between relatives is given by

$$S(y) = \frac{\partial w(x, x_{\mathrm{r}})}{\partial x} + \frac{\partial w(x, x_{\mathrm{r}})}{\partial x_{\mathrm{r}}} r$$

where all derivatives are evaluated at $x = x_{\mathrm{r}} = y$.[1] The selection gradient consists of two terms:

❶ The change in fitness $\partial w(x, x_{\mathrm{r}})/\partial x$ to the focal individual when it varies its behavior.

❷ The change in fitness $\partial w(x, x_{\mathrm{r}})/\partial x_{\mathrm{r}}$ to the focal individual when its related partner varies its behavior.

---

[1]Hence, formally the equation reads

$$S(y) = \left.\frac{\partial w(x, x_{\mathrm{r}})}{\partial x}\right|_{x=x_{\mathrm{r}}=y} + \left.\frac{\partial w(x, x_{\mathrm{r}})}{\partial x_{\mathrm{r}}}\right|_{x=x_{\mathrm{r}}=y} \times r$$

The selection gradient

The selection gradient is

$$S(y) = \underbrace{\frac{\partial w(x, x_{\mathrm{r}})}{\partial x}}_{\text{direct effect}} + \underbrace{\frac{\partial w(x, x_{\mathrm{r}})}{\partial x_{\mathrm{r}}}}_{\text{indirect effect}} r$$

- Here $\partial w(x, x_{\mathrm{r}})/\partial x$ is the direct effect on fitness.

- Here $\partial w(x, x_{\mathrm{r}})/\partial x_{\mathrm{r}}$ is the indirect effect on fitness.

- The net effect $S(y)$ on gene fitness is also called the inclusive fitness effect.

Hamilton's rule

A mutant introduced into a resident y population spreads if

$$S(y) > 0$$

This can be written as

$$rb - c > 0 \qquad \text{or} \qquad rb > c$$

where

- $c = -\frac{\partial w(x, x_r)}{\partial x}$ is the individual "cost" (or $-c = \frac{\partial w(x, x_r)}{\partial x}$).

- $b = \frac{\partial w(x, x_r)}{\partial x_r}$ is the "benefit" to the individual.

Hamilton's rule

The mutant spreads if

$$rb - c > 0 \qquad \text{or} \qquad rb > c$$

Selection on a mutant allele depends on two measures of value.

❶ Marginal individual fitness cost and benefit, c and b.

❷ Relatedness r between interactants, which can be thought as a discount rate.

Importantly, the cost $-c$ and benefit b can be of the same sign. Nothing forces $-c < 0$ but it is useful to think in terms of cost and benefit.

Inclusive fitness effect

There are two ways to look at fitness effects.

① One can group actions by recipient: $-c$ is the effect on self and b is the effect from others.

② One can group actions by actor ("inclusive fitness" approach): $-c$ is the effect on self and b is the effect on others.

The four fundamental type of social behaviors

❶ **Altruism**. This is defined to occur when $c > 0$ (negative effect on self) and $b > 0$ (positive effect on recipient). Here we have a fitness cost to self and benefit to others.

❷ **Cooperation**. This is defined to occur when $c < 0$ (positive effect on self) and $b > 0$ (positive effect on recipient). Here we have a fitness benefit to self and to others.

❸ **Selfishness**. This is defined to occur when $c < 0$ (positive effect on self) and $b < 0$ (negative effect on recipient). Here we have a fitness benefit to self and a fitness cost to others.

❹ **Spite**. This is defined to occur when $c > 0$ (negative effect on self) and $b < 0$ (negative effect on recipient). Here we have a fitness cost to self and to others.

Marginal substitution rate

At equilibrium, we have $S(y) = 0$, which implies that

$$\frac{c}{b} = r$$

This can be thought of as a marginal substitution rate: this is the number of units of own fitness a focal individual is willing to exchange for one unit of fitness to an individual that is related by r.

If interacted individuals are unrelated, an individual should not behave altruistically towards another.

Example: self-sacrifice

Let us now consider that x is the probability of committing self-sacrifice ($x \in [0, 1]$). The survival of an individual with self-sacrificing probability x when its relative (taken as its sibling) expresses probability x_r of self sacrifice is assumed to be given by

$$s_J(x, x_r) = x \times 0 + (1 - x)\left[(1 - x_r)s_b + x_r(s_b + B)\right]$$

which gives

$$s_J(x, x_r) = (1 - x)(s_b + Bx_r)$$

- s_b is the baseline survival of an individual.

- B is the increase in survival when an individual that has not committed self-sacrifice interacts with a self-sacrificing sibling.

Example: self-sacrifice

The fitness of a focal individual with self-sacrificing probability x when its sibling expresses self-sacrificing probability x_r in a population where the self-sacrificing probability is y is assumed to be given by[2]

$$w(x, x_r) = k \cdot s_J(x, x_r)$$

_____
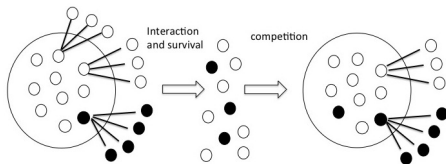
[2]k is a constant of proportionality taking density-dependence into account as well as offspring number production by the focal individual when it has reached adulthood.

Self-sacrifice: direct and indirect effects

Using fitness $w(x, x_\mathrm{r}) = k s_\mathrm{J}(x, x_\mathrm{r})$ and survival
$s_\mathrm{J}(x, x_\mathrm{r}) = (1 - x)(s_\mathrm{b} + B x_\mathrm{r})$ we have that the direct effect on self
is

$$-c = \left. \frac{\partial w(x, x_\mathrm{r})}{\partial x} \right|_{x = x_\mathrm{r} = y} = -k \cdot (s_\mathrm{b} + By)$$
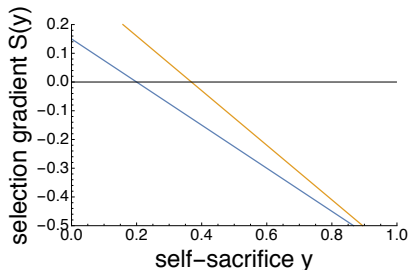
and the indirect effect is

$$b = \left. \frac{\partial w(x, x_\mathrm{r})}{\partial x_\mathrm{r}} \right|_{x = x_\mathrm{r} = y} = k \cdot (1 - y)B$$

Self-sacrifice: selection gradient

The selection gradient on the probability of self-sacrifice is

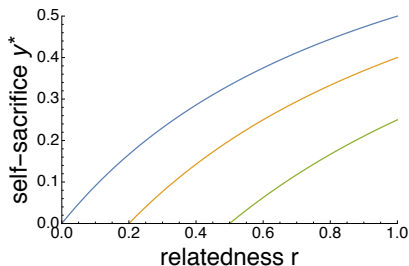$$S(y) = k \cdot [-(s_{\mathrm{b}} + By) + B(1-y)r]$$

Parameters $k = 1$, $s_{\mathrm{b}} = 0.1$, $B = 0.5$ and $r = 0.5$ (blue line) and $r = 0.9$ (yellow line).

Self-sacrifice: the singular point

The unique interior singular strategy y^* satisfying $S(y^*) = 0$ is given by

$$y^* = \frac{rB - s_{\mathrm{b}}}{B(1 + r)}$$

Parameters $B = 0.5$ and $s_{\mathrm{b}} = 0$ (blue),
$s_{\mathrm{b}} = 0.1$ (yellow) and 0.25 (green).

The probability of self-sacrifice goes to zero as relatedness goes to zero.

Take home messages

- The unit of selection is ultimately the gene determining behavior and not the individual expressing behavior.

- Selection acts on replicators and not on reproducers.

- It is evolutionary rational to jump into icy water and risk ones own life to save 2 (full) siblings, 4 nephews, 8 grand-cousins, etc.

- Blood is thicker than water.