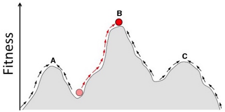
Kin selection and
the gene's eye view of evolution
(part 2)

The selfish, cooperative, altruistic, or spiteful individual

The selection gradient on a phenotype affecting social behavior is[1]

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



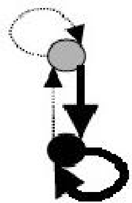
with derivatives evaluated at $x = x_{\mathrm{r}} = y$. The four fundamental type of social behaviors are

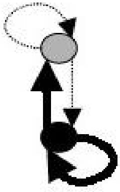
1. **Altruism**: $c > 0$ and $b > 0$.
2. **Cooperation**: $c < 0$ and $b > 0$.
3. **Selfishness**: $c < 0$ and $b < 0$.
4. **Spite**: $c > 0$ and $b < 0$.

[1] Recall that $w(x, x_{\mathrm{r}})$ is the fitness (per ploidy) to an individual with phenotype x when interacting with a relative with phenotype x_{r} in a population where individuals at large have phenotype y.

Inclusive fitness effect

There are two ways to look at the $-c$ and b 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 selfish, cooperative, altruistic, or spiteful individual

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

- If $r = 0$ selection favors what is best to the individual (like "*Homo economicus*").
- If $r = 1$ selection favors what is best to the group (group fitness is maximized). There are no conflicts of interests.

Relatedness thus tends to align the interest of individuals within groups and reduce conflict. Relatedness between somatic and germ line cells is one, this explains the apparent "harmony" within the individual.

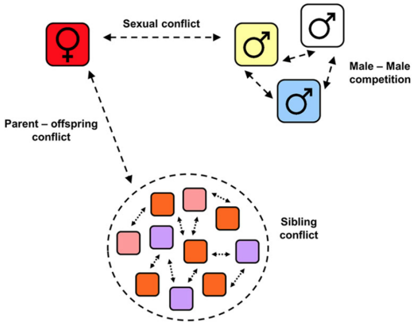
Family life permeates the animal kingdom

- Interactions among family members such as between parent and offspring or between siblings permeate throughout the animal kingdom.
- Many animals care for their young. This is called parental care.

How should parents allocate their resources to their offspring? How should the maternal (or paternal) pie be divided?

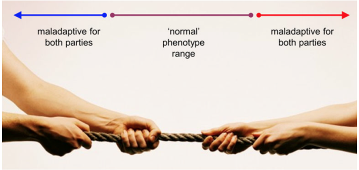
The web of family interactions and potential conflicts

Answering the question of how parents should allocate resources to offspring is complicated as many actors are involved and conflict occurs at different levels around reproduction.



Parent-offspring conflict over maternal care

- There is certainly some degree of coordination between maternal supply and offspring demand.
- But since mother and offspring are related only by one half, we expect a differential expression of genes in mothers and their offspring concerning the supply and demand for resources.



Tug of war over resource allocation!

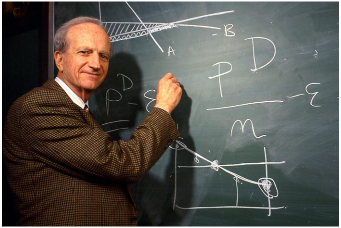
Three type of conflicts over maternal care

1. Conflict between mother and offspring.
2. Conflict between siblings.
3. Conflict between the paternally inherited gene (patrigene) and the maternally inherited gene (matrigene) within an offspring (intragenomic conflict).

We will start by considering a model of resource allocation within the family from economics and then turn towards evolutionary biology.

The rotten kid theorem

The rotten kid theorem says that offspring, even if they are greedy, will act to help one another because Mom has dictatorial powers and thus the power to align interests as she ultimately decides on resource allocation.



Garry Becker, who addressed from the perspective of (micro)-economics topics that traditionally belonged to sociology, like racial discrimination, crime, family organization, and drug addiction.

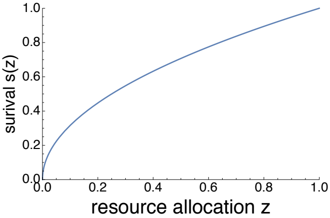
The rotten kid theorem

- But can the incentives of offspring really be fullly aligned?
- Why should Mom have full power? Offspring may have psychological tactics to deceive their mother (and father), like tantrums or other manipulations.
- Let us look at resource allocation to offspring using an evolutionary perspective.

We look at evolution of resource allocation when mother is in control and then when offspring are in control of the allocation, and each case try to determine the convergence stable level of resource allocation.

Allocation of resources to offspring

Suppose a mother allocates resources to offspring and an offspring receiving amount of resources z has survival $s(z)$, which is assumed monotonically increasing and having diminishing returns.



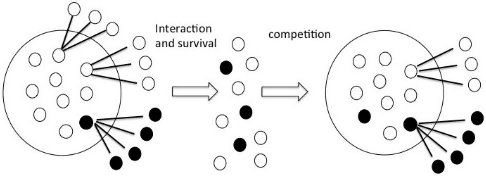
Graph with survival function $s(z) = z^{1/2}$ (concave function).

Allocation controlled by parents

Suppose a (dictatorial) mother has one unit of resource and allocates amount $x \in [0,1]$ of resources to her first offspring and amount $1-x$ to her second offspring. Her fitness is taken to be the sum of the survival of her two offspring:[2]

$$w(x,y) = k\left[\underbrace{s(x)}_{\substack{\text{offspring}\\ \text{one}}} + \underbrace{s(1-x)}_{\substack{\text{offspring}\\ \text{two}}}\right]$$

for some constant k taking density-dependence into account.

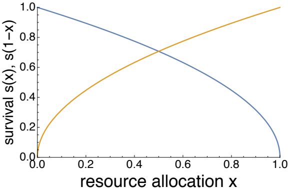


[2] k is a constant of proportionality taking density-dependence into account.

Allocation controlled by parents

With the (concave) survival function $s(x) = x^{1/2}$, the fitness is

$$w(x, y) = k\,[s(x) + s(1-x)] = k\left[x^{1/2} + (1-x)^{1/2}\right]$$



$s(x) = x^{1/2}$ (yellow) and $s(1-x) = (1-x)^{1/2}$ (blue).

This displays the trade-off between allocating resources to the first and to the second offspring.

Selection gradient on resource allocation

The selection gradient on resource allocation is

$$S(y) = \left. \frac{\partial w(x,y)}{\partial x} \right|_{x=y}$$

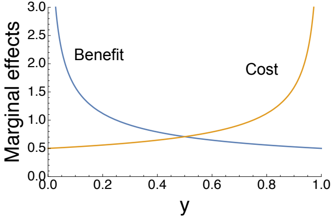
whereby

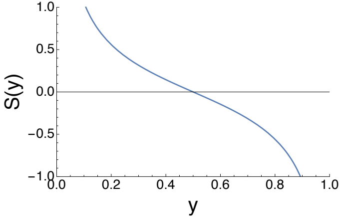
$$S(y) = k \left[\underbrace{\frac{y^{-1/2}}{2}}_{\text{marginal benefit}} - \underbrace{\frac{(1-y)^{-1/2}}{2}}_{\text{marginal cost}} \right]$$

The trade-off thus results in a marginal cost and benefit to the mother, which must equalize at equilibrium.

Selection gradient on resource allocation

The trade-off implies that there should be an interior solution.





The singular strategy balances marginal cost and benefit and is found by solving $S(y^*) = 0$, which gives

$$y^{*(-1/2)} = (1 - y^*)^{-1/2}$$

From this graph we see that the singular strategy is $y^* = 1/2$.

Equal allocation is uninvadable and convergence stable

Equal allocation of resources, $y^* = 1/2$, is favored by evolution and regardless of the shape of the survival function as long as it is increasing with diminishing returns.

- Equal allocation, $y^* = 1/2$, of resources to offspring is convergence stable and can also be shown to be uninvadable.
- Hence mother's should tend to treat their offspring equally.

But what about offspring control of resource allocation?

Allocation controlled by offspring

Let us now denote by x the level of allocation when an offspring is in control of the trait.

- Since there are two offspring it is unlikely that one is in control all of the time.
- We assume that the two offspring are of equal strength.
- We let each offspring to be in control of the allocation half of the time.

These assumptions will allow us to determine what is evolutionary optimal from the point of view of the genes in the offspring.

Allocation controlled by offspring

The expected survival of a focal offspring with level of allocation x when its sibling has level x_r is

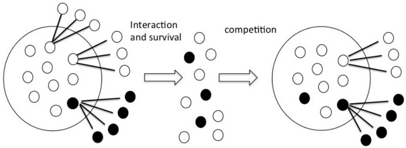
$$s_\mathrm{J}(x, x_\mathrm{r}) = \frac{1}{2}s(x) + \frac{1}{2}s(1 - x_\mathrm{r})$$

- With probability $1/2$ the focal offspring is in control of the allocation and has survival $s(x)$ (it gets amount of resources x).
- With probability $1/2$ its sibling is in control of allocation in which case the focal has survival $s(1 - x_\mathrm{r})$ (it gets amount of resources $1 - x_\mathrm{r}$).

Allocation controlled by offspring

The fitness to a focal individual with allocation level x when its sibling expresses allocation level x_r in a population where individuals at large express allocation level y is assumed to be proportional to survival[3]

$$w(x, x_\mathrm{r}) = ks_\mathrm{J}(x, x_\mathrm{r})$$



[3] k is a constant of proportionality taking density-dependence into account as will as offspring production by the focal when it has reached adulthood.

Selection gradient on resource allocation

We need to compute the selection gradient

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

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

- The change in the fitness of an individual when it varies its behavior.
- The change in the fitness of an individual when its sibing varies its behavior.

Selection gradient on resource allocation

With the survival function $s(x) = x^{1/2}$, the direct fitness effect is

$$\left.\frac{\partial w(x, x_\mathrm{r})}{\partial x}\right|_{x=x_\mathrm{r}=y} = \frac{k}{2} \left.\frac{\partial s(x)}{\partial x}\right|_{x=x_\mathrm{r}=y} = \frac{k}{2} \times \frac{y^{-1/2}}{2}$$

which is a benefit. The indirect fitness effect is

$$\left.\frac{\partial w(x, x_\mathrm{r})}{\partial x_\mathrm{r}}\right|_{x=x_\mathrm{r}=y} = \frac{k}{2} \left.\frac{\partial s(1 - x_\mathrm{r})}{\partial x_\mathrm{r}}\right|_{x=x_\mathrm{r}=y} = -\frac{k}{2} \times \frac{(1-y)^{-1/2}}{2}$$

which is a cost.

Hence, the behavior classifies as "selfishness".

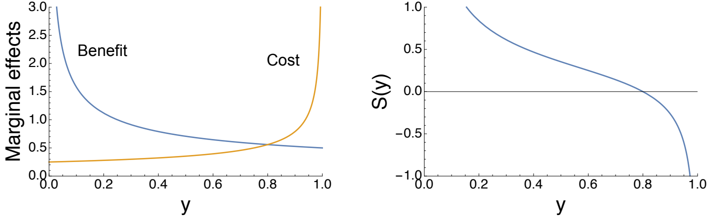
Selection gradient on resource allocation

The selection gradient is

$$S(y) = \frac{k}{2}\left[\underbrace{\frac{y^{-1/2}}{2}}_{\text{marginal benefit}} - \underbrace{\frac{(1-y)^{-1/2}}{2}}_{\text{marginal cost}} r\right]$$

- The marginal cost is discounted by r.
- The net marginal cost is lower than under mother control of the trait.

Selection gradient on resource allocation



Graph with survival function $s(y) = y^{1/2}$ and $r = 0.5$

The singular strategy balances marginal cost and benefit and is found by solving $S(y^*) = 0$, which gives

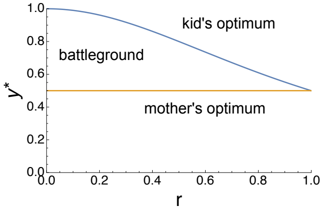
$$y^{*(-1/2)} = (1 - y^*)^{-1/2} \times r$$

so an offspring should claim more than $1/2$ of the resource.

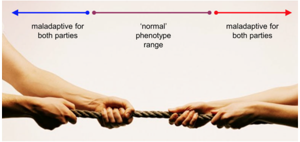
The battleground

The convergence stable (and uninvadable) amount of resources claimed by the offspring is

$$y^* = \frac{1}{1 + r^2}$$



The model predicts a battle-ground over resource allocation: offspring are selected to take more than Mom is selected to give.



Conflict between siblings over maternal care

- It follows from the model that there will be sibling conflict over parental resource allocation (sibling rivalry).
- The underlying logic is similar to parent-offspring conflict as sibling are related by half.
- The conflict is increasing with multiple paternity as r decreases. The conflict should be lowest among monozygotic twins ($r = 1$). Hence, among half-sibs you have stronger conflict.

Documented examples of parent-offspring conflict

- **Birds**: siblicide is often observed in nestling birds, the strongest or dominant individual tends to kill the other.

- **Social insects**: conflict over production of males (haploid) and females (diploid). Female workers are more related to their sisters than to their brothers to try to obtain a sex ratio of 3:1 (females to males) in the colony. However, queens are equally related to both sons and daughters, so they prefer a sex ratio of 1:1.

Outcome of parental-offspring conflict

There are two broad categories of outcomes of the conflict.

- Only the parent can influence the outcome. Its allocation can always be imposed by *force majeure* (like in the rotten kid theorem). For instance by provisioning resources to egg before fertilization like in turtles.
- But it is more likely that both parent and offspring influence the outcome. One expects that offspring will evolve psychological and physiological solicitation mechanisms to favor resource allocation to them (tantrums may be an example of that). Mother's (and father's) will evolve mechanisms for not being too much manipulated by the offspring.

A surprising example of parent-offspring conflict

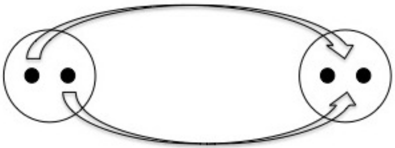
Humans (and mice): mother-offspring conflict during pregnancy

- There is strong evidence that genes expressed in the foetus are selected to take more resources than is optimal to Mom to give.
- Placenta secretes hormones decreasing Mom's sensitivity to insulin[4] so that she delivers more sugar into the blood that benefits the offspring.
- What is most remarkable about this is that it involves the expression of patrigenes and the silencing of matrigenes thus leading to intragenomic conflict within an individual.

[4] Insulin is an hormone secreted by the pancreas and favoring the absorption of sugar that is transported by blood. The embryo expresses insulin-like growth factor 2 (IGF 2), which down regulates the expression of Mom's insulin and promotes embryonic growth.

Parent of origin specific relatedness

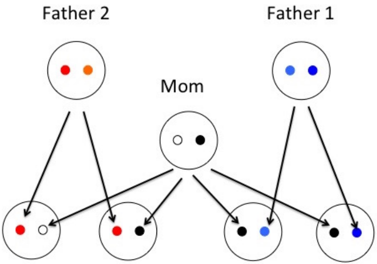
- $r^{♀}$ relatedness between a matrigene and a gene in a receptor: probability that the matrigene in one individual has a copy that is identical-by-descent with a gene in the other individual.
- $r^{♂}$ relatedness between a patrigene and a gene in a receptor: probability that the patrigene in one individual has a copy that is identical-by-descent with a gene in the other individual.[5]



[5] Standard relatedness is the average over patrigene and matrigene relatedness $r = (1/2)r^{♀} + (1/2)r^{♂}$.

Parent of origin specific relatedness

Under multiple paternity an individual is more related to its siblings through its mother than through its father.



The relatedness $r^{\male}$ between siblings from the perspective of a patrigene can be different from the relatedness $r^{\female}$ from the perspective of a matrigene. Under multiple paternity: $r^{\female} > r^{\male}$.

Parent of origin specific expression of phenotypic effects

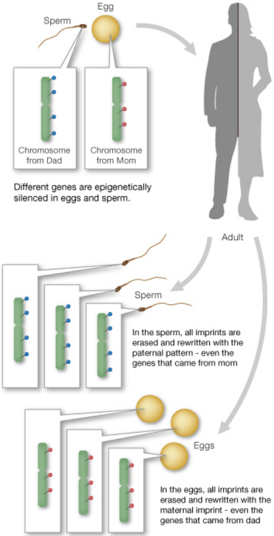
- Under multiple paternity $r^{♀} > r^{♂}$. The patrigene in an offspring should "claim" more resources than the matrigene.
- Asymmetry in relatedness predicts that the matrigene has a different optimum for resource allocation than the patrigene.
- This should result in a parent of origin specific phenotypic expression. The phenotype of an individual can be decomposed into two contributions:

$$y = \underbrace{y^{♀}}_{\substack{\text{maternal} \\ \text{gene}}} + \underbrace{y^{♂}}_{\substack{\text{paternal} \\ \text{gene}}}$$

Is this possible?

Genomic imprinting

Genomic imprints on DNA (some molecule marking DNA) are erased and reset in each generation. Imprinted genes subtend parent of origin specific gene expression.



Selective inactivation of the matrigene if $r^{♀} > r^{♂}$

- There is a selection gradient, say $S^{♂}(y^{♂})$, on patrigene trait expression and a selection gradient, say $S^{♀}(y^{♀})$, on matrigene trait expression. Hence, we can conceive of a paternal uninvadable trait $(y^{♂^*})$ an a maternal uninvadable trait $(y^{♀^*})$.

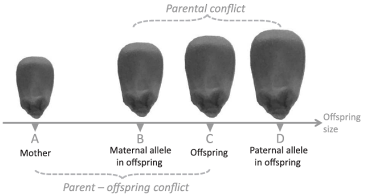
- When $r^{♀} > r^{♂}$ the maternal inherited gene gets silenced: $y^{♀^*} = 0$.

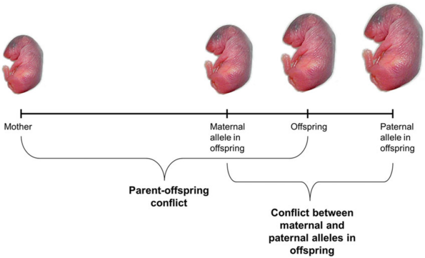
- This is so because when $y = y^{♂} + y^{♀}$ is below the paternal optimum $(y^{♂^*})$, alleles increasing paternal expression will be favored by selection (increasing $y^{♂}$ is favored) and alleles reducing maternal expression will be favored (decreasing $y^{♀}$ is favored).

The "loudest voice" wins the conflict and there is paternal expression of the phenotype ($y^* = y^{♂^*}$ so $y^{♀^*} = 0$) is convergence stable.

Summary: conflict with the family

Evolutionary prediction: different allocation optima from the perspective of different "actors": gene(s) in mother, average gene(s) in offspring, patrigene(s), and matrigene(s).





In maize, this conflict has been shown to occur in seed size.
Evolutionary prediction: Psychological and mental attitudes related to parental supply (and demand from offspring) may thus be adaptations.

Summary: conflict within the family

- No conflict if $r = 1$. This is the case for most bodily function and so there can be full harmony within individuals or interacting units.

- Conflict if $r = 0$. Then different parties have different interests and we are back into classical "game theory".

- But in general $1 > r > 0$. A gene-centered perspective predicts the occurrence of diverse conflicts within the family and they have all been documented (no alternative parsimonious theory in the social sciences to explain these).

Summary on the gene's eye view of evolution

Adaptations are not good to the individual ("the reproducer") but good to the gene ("the replicator"). In other words, the unit of selection is the gene, not the individual nor the group.

"*I am pretending to a unity that, deep inside myself, I now know does not exist. I am fundamentally mixed, male with female, parent and offspring, warring segments of chromosomes that interlocked in strife millions of years before the River Severn ever saw the Celts and Saxons of Housman's poem–before Europe as a whole existed or saw any of the human violence that became later, for sure, embedded in my ancestry.*"

(Hamilton 1996, Narrow Roads of Gene Land, volume 1)

Exam date

The exam is on January 30 and January 31