ESM S1: Parent-offspring conflict

We were all young once -- an intragenomic perspective an parent-offspring conflict

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Resource function

The **resources** that a mother possesses are limited by ***R*** (represented by *res* in the *Mathematica* code below) and can be invested by the mother in increasing either the **survival probability of the offspring, *s*** or the **survival probability of the mother, *q***. If the mother survives, she produces an additional offspring.

The mother can increase *s* at the expense of *q* or vice versa, but neither of these probabilities can ever exceed 1. After one period, which consists of producing and caring for an offspring as well as survival of the mother, the mother is in the same position as before and has the same amount of resources to spend in the next period.

Since *s* and *q* are interdependent, it is sufficient to consider one of these variables as dependent for the analysis. We choose *s*, which lets us write *q* as a function of *R* and *s*:

$q = 1 - \frac{1}{R(1-s)}$

In order to see how this is derived, we first define the total resources as a function of *s* and *q*:

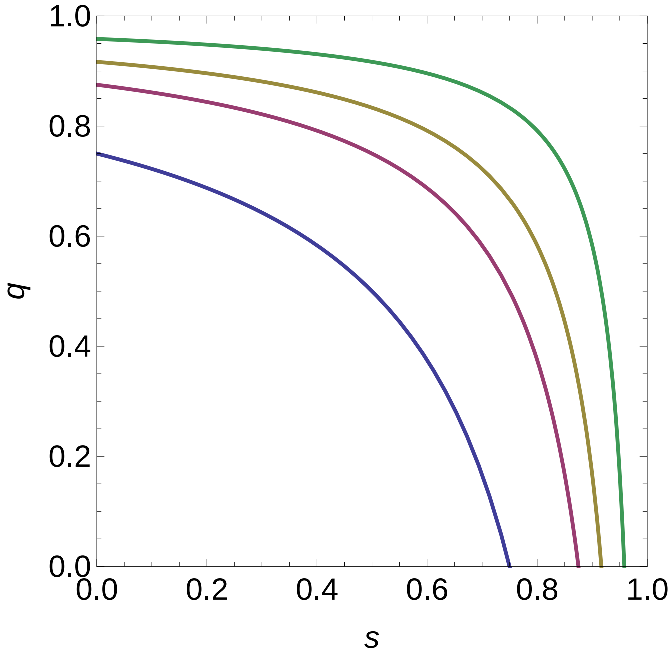
$$R = \frac{1}{(q-1)\,(s-1)}$$

We chose this function for the resource limitation because of several advantages. First, the marginal returns in investing in *s* or *q* are decreasing, which should be expected. Second, *s* and *q* can never exceed 1, which should be expected for probabilities. And third, this function will allow us later to derive analytical results. Other functions that share these properties should lead to similar results.

Next, we solve this function for *q*, defining *q* as a function of *s* and *R*

$$q = \frac{1}{R\,(s-1)} + 1$$

Now, we can plot *q* as a function of *s* for different total resource levels *R* with *R*=4 (blue), *R*=8 (purple), *R*=12 (yellow), and *R*=24 (green). Increasing *R* shifts the resulting response curves to the upper right. That means, the more resources are available, the higher *s* and *q* can be at the same time. The effect of varying *R* can be studied more closely in Interactive Figure S1.

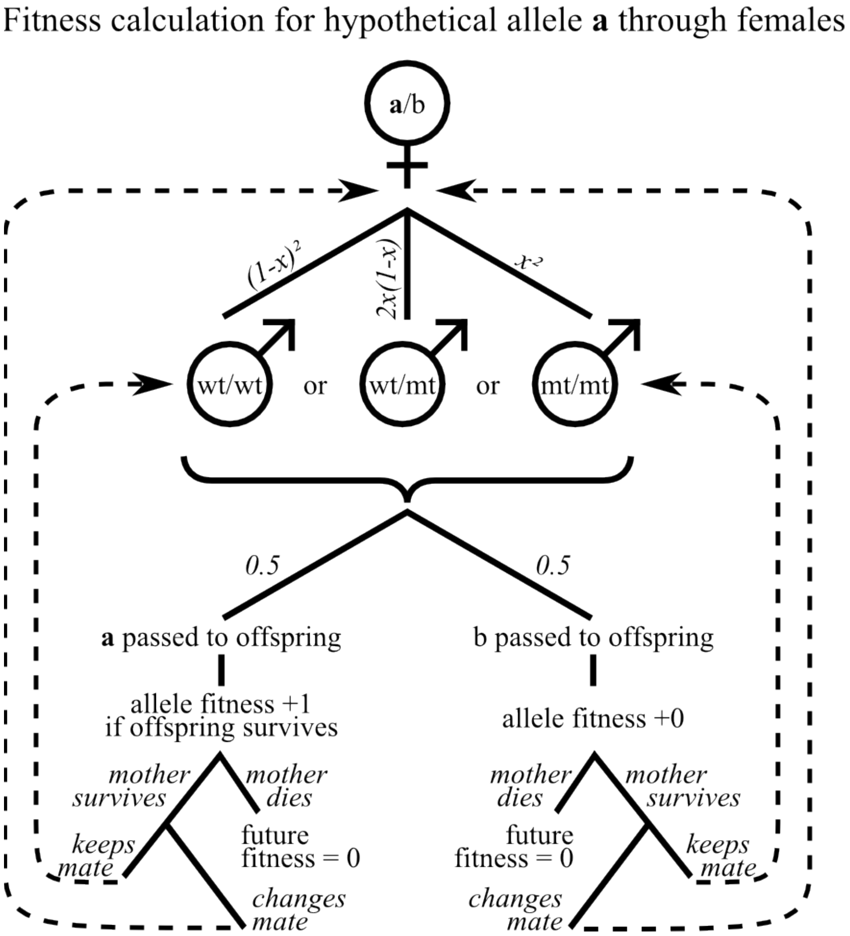


Deriving fitness functions from the game tree – demand function genes

Two groups of genes exist in the context of our model: genes that affect how much an offspring demands, and genes that affect how much a mother supplies. The net supply received by a given offspring from a given mother is a function of both groups of genes, and this net supply will affect the fitness functions of the respective alleles.

We assume that demand is affected by some trait, e.g. the begging intensity, whereas supply is affected by the reaction to this trait, for example the parental attention to begging. It has to be assumed that the net supply is elastic with regard to begging and attention (or whatever trait is considered); else, there would not be any evolution in this trait. To the eyes of evolution, what matters is the net effect on parental care produced by a mutation in the considered traits, and we therefore characterise alleles simply by this net effect. Thereby, we do not need to address questions regarding the exact mechanistic realization of begging and of providing parental care.

Having said that, we focus our attention solely on the s values that wildtypes and mutants produce, s_{wt} and s_{mt}, respectively. The corresponding values of q are q_{wt} and q_{mt}. To derive fitness functions, it is best to consider a game tree that incorporates all possible outcomes.



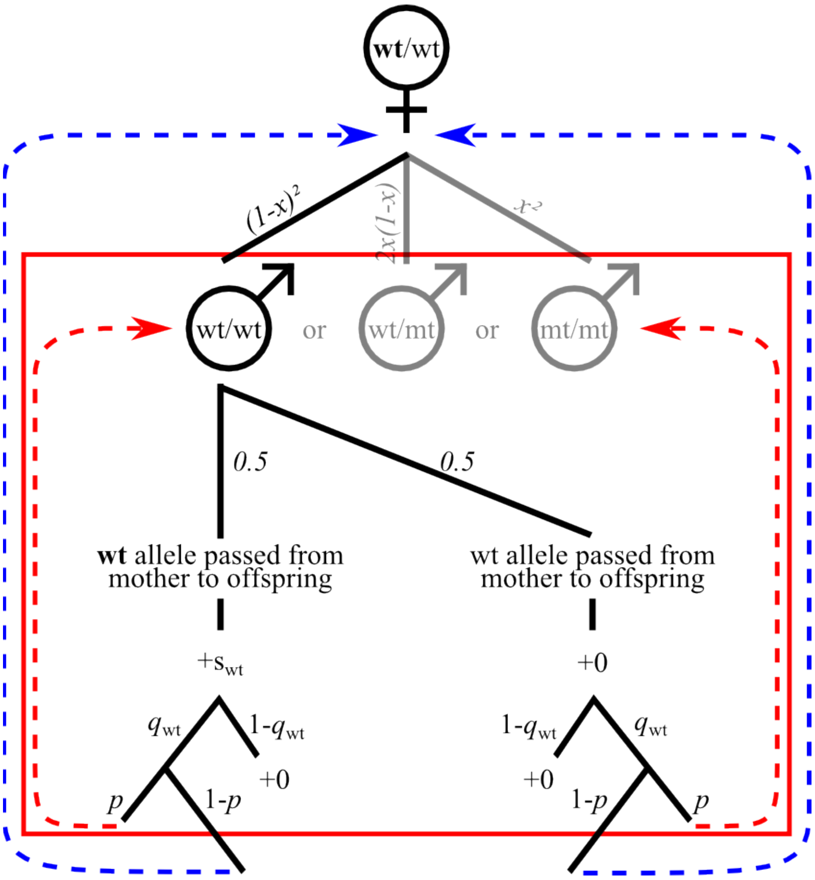
Above: Game tree of female life cycle, allowing to determine the fitness of wildtype and mutant alleles accumulated through females. Probabilities are shown in italics, x is the **frequency of the mutant allele in the population**. The mother carries two alleles, which are neutrally called **a** and b and have to be replaced by the mutant or wildtype allele when actually making the calculations. At the beginning of the life cycle, a female encounters a mate. This male can either be a homozygous wildtype, a homozygous mutant, or heterozygous, with probability $(1\text{-}x)^2$, x^2, and $2x(1\text{-}x)$, respectively. The **a** allele is in focus here, and its fitness only increases when this allele **a** is passed down to the offspring by the mother and when this **a**-bearing offspring then survives. Offspring survival probability depends on the genetic setup of the offspring; if it carries a dominant mutant that increases demand, the offspring has a higher survival probability. This comes at a cost, though, as the higher exhaustion of the mother will decrease her survival probability and hence the potential number of future siblings of this offspring.

After producing an offspring, the mother may or may not survive and she may or may not change her mate. If she survives and keeps her mate, she is in the same spot as after having encountered her mate the first time, as we assume that there are no aging effects. This property will simplify fitness calcuations, as will be seen below. If the female survives and changes mates, she will be in the same spot as before she encountered her previous mate. This property will also be used to simplify the fitness calculation.

Depending on the genetic setup of the parents and the laws of inheritance, an offspring expresses either the wildtype feature (*wt*) or the mutant feature (*mt*). If the offspring expresses the wildtype phenotype, it will curb the demand in a way that 1) it will receive a survival probability of s_{wt} and that 2) leaves the mother with sufficient resources to have a survival probability of q_{wt}. If the offspring has the mutant phenotype, it receives s_{mt} and the mother is left with q_{mt} instead.

Allele fitness derived from females

We begin our analysis by assuming that the female has already found a mate, which has one of the three possible genetic setups. Furthermore, we begin by first only considering the fitness accumulated through one male. This is shown as the “small loop” framed by the red square in the figure below.



First, we consider the case that the female and the male are homozygous wildtypes (see figure above). Proceeding step by step, we first note that our focus wildtype allele is passed down with probability 0.5 (even though the other allele is identical, we only concentrate on the focal allele). Given the parental genetic setup, the offspring will also be a homozygous wildtype, so its survival probability is s_{wt} , which is added to the focal allele's fitness. Consequently, the mother's survival probability is q_{wt}, and if she survives, she will keep her mate with probability p (which is unaffected by the genetic background). So, in case the mother survives and keeps her mate, we are back where we started. Similarly, with probability 0.5, the non-focal allele is passed down. In that case, nothing is added to the focal allele's fitness. Still, it is possible that the mother survives (with probability q_{wt}, as this offspring will also be a homozygous wildtype) and keeps her mate, at which point we are also back to where we started.

When denoting **allele fitness *w*** as $w_{f,A/b}(c/d)$, where *f* indicates that we are dealing with fitness through females, *A/b* is the mother's genetic background, where the capital letter indicates the focal allele, and *c/d* is the father's genetic background, we may start by writing down:

$$w_{f,\text{WT/wt}}(\text{wt}/\text{wt}) = 0.5\left(s_{\text{wt}} + q_{\text{wt}} \times p \times w_{f,\text{WT/wt}}(\text{wt}/\text{wt})\right) + 0.5\left(0 + q_{\text{wt}} \times p \times w_{f,\text{WT/wt}}(\text{wt}/\text{wt})\right) + \ldots$$

Moreover, we have to consider the possibility that the mother survives but does not keep her mate, which happens with probability $q_{\text{wt}}(1-p)$. Then she will return to the "big loop" (blue arrows). This completes the equation to:

$$w_{f,\text{WT/wt}}(\text{wt}/\text{wt}) = 0.5\left(s_{\text{wt}} + q_{\text{wt}} \times p \times w_{f,\text{WT/wt}}(\text{wt}/\text{wt})\right) + \\ 0.5\left(0 + q_{\text{wt}} \times p \times w_{f,\text{WT/wt}}(\text{wt}/\text{wt})\right) + 0.5\, q_{\text{wt}}(1-p)\, w_{f,\text{WT,wt}} + 0.5\, q_{\text{wt}}(1-p)\, w_{f,\text{WT/wt}}$$

where $w_{f,\text{WT/wt}}$ is the total allele fitness of a wildtype allele through female homozygous wildtypes, regardless of the genetic background of the male partner. This equation being recursive $\left(w_{f,\text{WT/wt}}(\text{wt}/\text{wt})\right.$ appears on both sides of the equation), it has to be solved for $w_{f,\text{WT/wt}}(\text{wt}/\text{wt})$, which gives:

$$w_{f,\text{WT/wt}}(\text{wt}/\text{wt}) = \frac{s_{\text{wt}} - 2\,(p-1)\,q_{\text{wt}}\,w_{f,\text{WT/wt}}}{2 - 2\,p\,q_{\text{wt}}}$$

We will progress analogously to calculate the partial allele fitnesses in case the female is mated to a heterozygous male or to a homozygous mutant, keeping in mind that if the offspring inherits a mutant allele, its survival probability will be changed to s_{mt} and the mother’s survival probability to q_{mt}.

With a wt/mt male:

$$w_{\mathrm{f,WT/wt}}(\mathrm{wt/mt}) =$$

$$-\frac{-2\,(p-1)\,w_{f,\mathrm{WT/wt}}\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})+s_{\mathrm{mt}}+s_{\mathrm{wt}}}{2\,(p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2)}$$

With a mt/mt male:

$$w_{\mathrm{f,WT/wt}}(\mathrm{mt/mt}) =$$

$$\frac{s_{\mathrm{mt}}-2\,(p-1)\,q_{\mathrm{mt}}\,w_{f,\mathrm{WT/wt}}}{2-2\,p\,q_{\mathrm{mt}}}$$

In the next step, we return to the big loop (blue arrows in figure above). A female encounters a wt/wt male with probability $(1\text{-}x)^2$, a wt/mt male with probability $2x(1\text{-}x)$, and a mt/mt male with probability x^2. So the total fitness a wildtype allele derives from females is:

$w_{f,\mathrm{WT/wt}} = (1-x)^2\,w_{f,\mathrm{WT/wt}}(\mathrm{wt/wt}) + 2\,x(1-x)\,w_{f,\mathrm{WT/wt}}(\mathrm{wt/mt}) + x^2\,w_{f,\mathrm{WT/wt}}(\mathrm{mt/mt})$

As this equation is again recursive, we solve it for $w_{f,\mathrm{WT/wt}}$:

$$w_{\mathrm{f,WT/wt}} =$$

$$\left(s_{\mathrm{mt}}\,x\,(p\,q_{\mathrm{wt}}-1)\,(p\,(q_{\mathrm{mt}}\,(x-2)-q_{\mathrm{wt}}\,x)+2)-s_{\mathrm{wt}}\,(x-1)\,(p\,q_{\mathrm{mt}}-1)\,(p\,x\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})-p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})+2)\right)\Big/\left(-2\,(p-1)\,p\,x^2\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})^2+4\,(p-1)\,x\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})+2\,(q_{\mathrm{wt}}-1)\,(p\,q_{\mathrm{mt}}-1)\,(p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2)\right)$$

Using the same method as described above, we may also calculate the allele fitness of wildtype alleles derived from heterozygous females, as well as the allele fitness of mutant alleles derived from heterozygous females and from homozygous females.

Wildtype allele from heterozygous females:

$$w_{\mathrm{f,WT/mt}} =$$

$$\left(s_{\mathrm{mt}}\,x\,(p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2)\,(p\,(q_{\mathrm{mt}}\,(x-4)-q_{\mathrm{wt}}\,x)+4)-2\,s_{\mathrm{wt}}\,(x-1)\,(p\,q_{\mathrm{mt}}-1)\,(p\,(q_{\mathrm{mt}}\,(x-3)-q_{\mathrm{wt}}\,(x+1))+4)\right)\Big/\left(-2\,(p-1)\,p\,x^2\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})^2+8\,(p-1)\,x\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})+2\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}+q_{\mathrm{wt}}-2)\,(p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4)\right)$$

Mutant allele from heterozygous females:

$$w_{\mathrm{f,MT/wt}} =$$

$$\left(s_{\mathrm{mt}}\left(-p^2\,x^2\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})^2+4\,p\,x\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})-2\,(p\,q_{\mathrm{mt}}-1)\,(p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4)\right)\right)\Big/\left(-2\,(p-1)\,p\,x^2\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})^2+8\,(p-1)\,x\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})+2\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}+q_{\mathrm{wt}}-2)\,(p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4)\right)$$

Mutant allele from homozygous mutant females:

$$w_{\mathrm{f,MT/mt}} =$$

$$\frac{s_{\mathrm{mt}}}{2-2\,q_{\mathrm{mt}}}$$

In summary, we have:

1) wildtype allele from homozygous female wildtype

$w_{f,\mathrm{WT/wt}} =$

$$(s_{\mathrm{mt}}\, x\, (p\, q_{\mathrm{wt}} - 1)\, (p\, (q_{\mathrm{mt}}\, (x - 2) - q_{\mathrm{wt}}\, x) + 2) - s_{\mathrm{wt}}\, (x - 1)\, (p\, q_{\mathrm{mt}} - 1)\, (p\, x\, (q_{\mathrm{mt}} - q_{\mathrm{wt}}) - p\, (q_{\mathrm{mt}} + q_{\mathrm{wt}}) + 2)) \Big/ \left(-2\, (p - 1)\, p\, x^2\, (q_{\mathrm{mt}} - q_{\mathrm{wt}})^2 + 4\, (p - 1)\, x\, (p\, q_{\mathrm{mt}} - 1)\, (q_{\mathrm{mt}} - q_{\mathrm{wt}}) + 2\, (q_{\mathrm{wt}} - 1)\, (p\, q_{\mathrm{mt}} - 1)\, (p\, (q_{\mathrm{mt}} + q_{\mathrm{wt}}) - 2)\right)$$

2) wildtype allele from heterozygous female

$w_{f,\mathrm{WT/mt}} =$

$$(s_{\mathrm{mt}}\, x\, (p\, (q_{\mathrm{mt}} + q_{\mathrm{wt}}) - 2)\, (p\, (q_{\mathrm{mt}}\, (x - 4) - q_{\mathrm{wt}}\, x) + 4) - 2\, s_{\mathrm{wt}}\, (x - 1)\, (p\, q_{\mathrm{mt}} - 1)\, (p\, (q_{\mathrm{mt}}\, (x - 3) - q_{\mathrm{wt}}\, (x + 1)) + 4)) \Big/ \left(-2\, (p - 1)\, p\, x^2\, (q_{\mathrm{mt}} - q_{\mathrm{wt}})^2 + 8\, (p - 1)\, x\, (p\, q_{\mathrm{mt}} - 1)\, (q_{\mathrm{mt}} - q_{\mathrm{wt}}) + 2\, (p\, q_{\mathrm{mt}} - 1)\, (q_{\mathrm{mt}} + q_{\mathrm{wt}} - 2)\, (p\, (3\, q_{\mathrm{mt}} + q_{\mathrm{wt}}) - 4)\right)$$

3) mutant allele from heterozygous female

$w_{f,\mathrm{MT/wt}} =$

$$\left(s_{\mathrm{mt}}\, \left(-p^2\, x^2\, (q_{\mathrm{mt}} - q_{\mathrm{wt}})^2 + 4\, p\, x\, (p\, q_{\mathrm{mt}} - 1)\, (q_{\mathrm{mt}} - q_{\mathrm{wt}}) - 2\, (p\, q_{\mathrm{mt}} - 1)\, (p\, (3\, q_{\mathrm{mt}} + q_{\mathrm{wt}}) - 4)\right)\right) \Big/ \left(-2\, (p - 1)\, p\, x^2\, (q_{\mathrm{mt}} - q_{\mathrm{wt}})^2 + 8\, (p - 1)\, x\, (p\, q_{\mathrm{mt}} - 1)\, (q_{\mathrm{mt}} - q_{\mathrm{wt}}) + 2\, (p\, q_{\mathrm{mt}} - 1)\, (q_{\mathrm{mt}} + q_{\mathrm{wt}} - 2)\, (p\, (3\, q_{\mathrm{mt}} + q_{\mathrm{wt}}) - 4)\right)$$

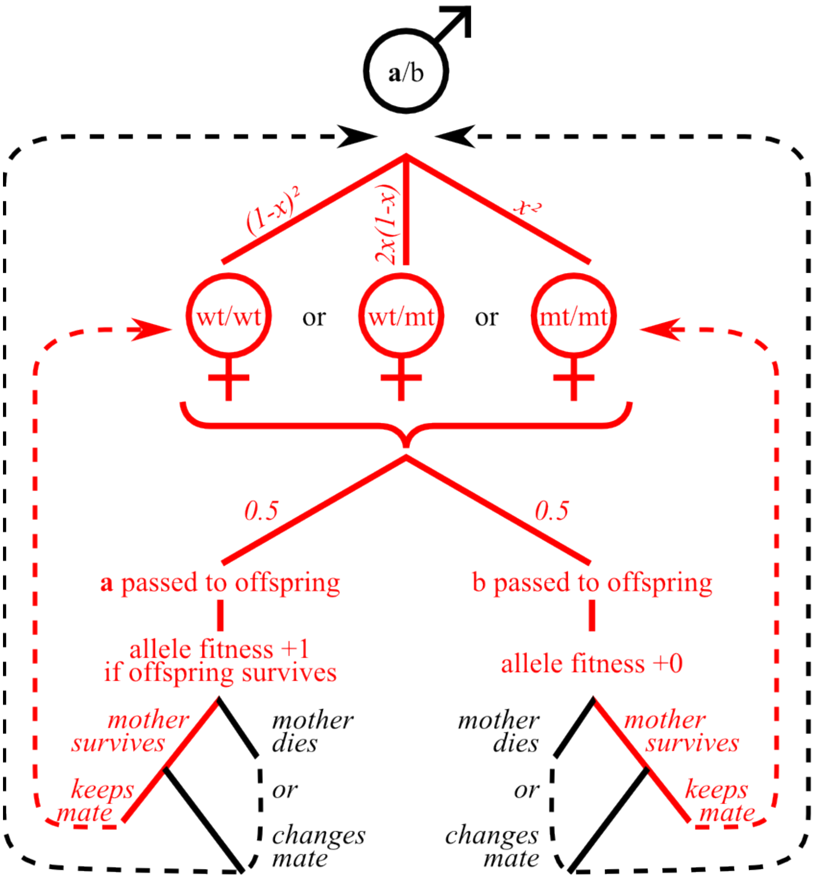
4) mutant allele from homozygous female mutant

$w_{f,\mathrm{MT/mt}} = \frac{s_{\mathrm{mt}}}{2-2\, q_{\mathrm{mt}}}$

Male fitness functions

First, we calculate the fitness that a male derives from one particular female (red paths in the game tree shown below). The probability that a male stays with a female for one additional breeding season corresponds to the **monogamy rate *p***. Therefore, the partial allele fitness functions for males are exactly the same as those for females, except that the future fitness derived from a specific female is 0 not only when this female dies (with probability 1-*q*) but also when the male changes to another female (with probability 1-*p*).

Fitness calculation for hypothetical allele **a** through males



Proceeding analogously as for females, we may now derive the wildtype allele fitness from homozygous males:

$$W_{m,WT/wt} =$$

$$\frac{x\,(x-1)\,(s_{mt}+s_{wt})}{p\,(q_{mt}+q_{wt})-2} + \frac{s_{mt}\,x^2}{2-2\,p\,q_{mt}} - \frac{s_{wt}\,(x-1)^2}{2\,p\,q_{wt}-2}$$

Wildtype allele fitness from homozygous males:

$$W_{m,WT/mt} =$$

$$\frac{2\,x\,(x-1)\,(s_{mt}+s_{wt})}{p\,(3\,q_{mt}+q_{wt})-4} - \frac{s_{wt}\,(x-1)^2}{p\,(q_{mt}+q_{wt})-2} + \frac{s_{mt}\,x^2}{2-2\,p\,q_{mt}}$$

Mutant allele fitness from heterozygous males:

$$W_{m,MT/wt} =$$

$$s_{mt}\left(-\frac{(x-1)^2}{p\,(q_{mt}+q_{wt})-2} + \frac{4\,x\,(x-1)}{p\,(3\,q_{mt}+q_{wt})-4} + \frac{x^2}{2-2\,p\,q_{mt}}\right)$$

Mutant allele fitness from homozygous males:

$$W_{m,MT/mt} =$$

$$\frac{s_{\mathrm{mt}}}{2-2\,p\,q_{\mathrm{mt}}}$$

In summary, the allele fitness functions derived from males are:

1) wildtype allele from homozygous wildtype male:

$$w_{m,\mathrm{WT/wt}}=\frac{x\,(x-1)\,(s_{\mathrm{mt}}+s_{\mathrm{wt}})}{p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2}+\frac{s_{\mathrm{mt}}\,x^2}{2-2\,p\,q_{\mathrm{mt}}}-\frac{s_{\mathrm{wt}}\,(x-1)^2}{2\,p\,q_{\mathrm{wt}}-2}$$

2) wildtype allele from heterozygous male:

$$w_{m,\mathrm{WT/mt}}=\frac{2\,x\,(x-1)\,(s_{\mathrm{mt}}+s_{\mathrm{wt}})}{p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4}-\frac{s_{\mathrm{wt}}\,(x-1)^2}{p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2}+\frac{s_{\mathrm{mt}}\,x^2}{2-2\,p\,q_{\mathrm{mt}}}$$

3) mutant allele from heterozygous male:

$$w_{m,\mathrm{MT/wt}}=s_{\mathrm{mt}}\left(-\frac{(x-1)^2}{p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2}+\frac{4\,x\,(x-1)}{p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4}+\frac{x^2}{2-2\,p\,q_{\mathrm{mt}}}\right)$$

4) mutant allele from homozygous mutant male:

$$w_{m,\mathrm{MT/mt}}=\frac{s_{\mathrm{mt}}}{2-2\,p\,q_{\mathrm{mt}}}$$

Number of mates

Since the fitness functions for males derived so far only take into account the fitness a male derives from one female, the total average number of mates per male has to be considered as well in order to complete the fitness functions. This quantity can be calculated quite easily. Knowing that the total fitness of males equals the total fitness of females because each offspring has exactly one father and one mother and assuming the usual sex ratio of 50:50, we can calculate the **number of mates per male, *m***, as the ratio between average female and average male fitness.

$$w_f=m\cdot w_m$$

$$m=w_f\,/\,w_m$$

$$m=\frac{(1-x)^2\,w_{f,\mathrm{WT/wt}}+x(1-x)\,w_{f,\mathrm{WT/mt}}+x(1-x)\,w_{m,\mathrm{MT/wt}}+x^2\,w_{f,\mathrm{MT/mt}}}{(1-x)^2\,w_{m,\mathrm{WT/wt}}+x(1-x)\,w_{m,\mathrm{WT/mt}}+x(1-x)\,w_{m,\mathrm{MT/wt}}+x^2\,w_{m,\mathrm{MT/mt}}}$$

$$
\begin{aligned}
m = {}& \\
&\Bigg(\Big(s_{\mathrm{mt}}\,(1-x)\,x\,\Big(-p^2\,x^2\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})^2+4\,p\,x\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})-2\,(p\,q_{\mathrm{mt}}-1)\,(p\,(3\\
&\quad q_{\mathrm{mt}}+q_{\mathrm{wt}})-4)\Big)\Big)\Big/\Big(-2\,(p-1)\,p\,x^2\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})^2+8\,(p-1)\,x\,(\\
&\quad p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})+2\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}+q_{\mathrm{wt}}-2)\,(p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4)\Big)\\
&\quad+\Big((x-1)^2\,(s_{\mathrm{mt}}\,x\,(p\,q_{\mathrm{wt}}-1)\,(p\,(q_{\mathrm{mt}}\,(x-2)-q_{\mathrm{wt}}\,x)+2)-s_{\mathrm{wt}}\,(x-1)\,(p\\
&\quad q_{\mathrm{mt}}-1)\,(p\,(q_{\mathrm{mt}}\,(x-1)-q_{\mathrm{wt}}\,(x+1))+2))\Big)\Big/\Big(-2\,(p-1)\,p\,x^2\,(\\
&\quad q_{\mathrm{mt}}-q_{\mathrm{wt}})^2+4\,(p-1)\,x\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})+2\,(q_{\mathrm{wt}}-1)\,(p\,q_{\mathrm{mt}}-\\
&\quad 1)\,(p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2)\Big)+((1-x)\,x\,(s_{\mathrm{mt}}\,x\,(p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2)\,(p\,(q_{\mathrm{mt}}\,(\\
&\quad x-4)-q_{\mathrm{wt}}\,x)+4)-2\,s_{\mathrm{wt}}\,(x-1)\,(p\,q_{\mathrm{mt}}-1)\,(p\,(q_{\mathrm{mt}}\,(x-3)-\\
&\quad q_{\mathrm{wt}}\,(x+1))+4)))\Big/\Big(-2\,(p-1)\,p\,x^2\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})^2+8\,(p-1)\,x\,(\\
&\quad p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}-q_{\mathrm{wt}})+2\,(p\,q_{\mathrm{mt}}-1)\,(q_{\mathrm{mt}}+q_{\mathrm{wt}}-2)\,(p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4)\Big)\\
&\quad+\frac{s_{\mathrm{mt}}\,x^2}{2-2\,q_{\mathrm{mt}}}\Bigg)\Bigg/\Bigg((x-1)^2\left(\frac{x\,(x-1)\,(s_{\mathrm{mt}}+s_{\mathrm{wt}})}{p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2}+\frac{s_{\mathrm{mt}}\,x^2}{2-2\,p\,q_{\mathrm{mt}}}-\frac{s_{\mathrm{wt}}\,(x-1)^2}{2\,p\,q_{\mathrm{wt}}-2}\right)\\
&\quad+(1-x)\,x\left(\frac{2\,x\,(x-1)\,(s_{\mathrm{mt}}+s_{\mathrm{wt}})}{p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4}-\frac{s_{\mathrm{wt}}\,(x-1)^2}{p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2}+\frac{s_{\mathrm{mt}}\,x^2}{2-2\,p\,q_{\mathrm{mt}}}\right)+s_{\mathrm{mt}}\,(1\\
&\quad-x)\,x\left(-\frac{(x-1)^2}{p\,(q_{\mathrm{mt}}+q_{\mathrm{wt}})-2}+\frac{4\,x\,(x-1)}{p\,(3\,q_{\mathrm{mt}}+q_{\mathrm{wt}})-4}+\frac{x^2}{2-2\,p\,q_{\mathrm{mt}}}\right)+\frac{s_{\mathrm{mt}}\,x^2}{2-2\,p\,q_{\mathrm{mt}}}\Bigg)
\end{aligned}
$$

Fitness of wildtype and mutant alleles through both sexes

We now have the ingredients to calculate the fitness of wildtype and mutant alleles of demand function genes. These are simply the corresponding allele fitnesses, weighted by the contribution by females and by males toward that fitness:

1) fitness of the wildtype allele:

$$w_{\mathrm{WT}} = \frac{1}{2}\left((1-x)\, w_{f,\mathrm{WT/wt}} + x \cdot w_{f,\mathrm{WT/mt}}\right) + \frac{1}{2}\, m\left((1-x)\, w_{m,\mathrm{WT/wt}} + x \cdot w_{m,\mathrm{WT/mt}}\right)$$

(Note that we now replace s_{mt} with $s+\Delta s$ and q_{wt} and q_{mt} by the corresponding functions as derived from the resource constraint.)

$$\mathrm{w}_{\mathrm{WT}} \;=$$

$$\frac{1}{2} R \Bigg(((1-x)((s-1) s (p (R (\triangle s+s-1)+1)-R (\triangle s+s-1)) (x-1) (p (2 (R (s-$$

$$1)+1) (s-1)+\triangle s (2 R (s-1)+x+1))-2 R (s-1) ($$

$$\triangle s+s-1))-(\triangle s+s-1) (\triangle s+s) (-s R+R+p (R (s-1)+1)) x$$

$$(p (2 s+2 R (s-1) (\triangle s+s-1)+\triangle s x-2)-2 R (s-1) (\triangle s+s-1)))$$

$$) \big/ \big(-\triangle s^2 (p-1) p R x^2-2 \triangle s (p-1) R (s-1) (p (R (\triangle s+s-1)+1)-R$$

$$(\triangle s+s-1)) x+(p (\triangle s (2 R (s-1)+1)+2 (R (s-1)+1) (s-1))-$$

$$2 R (s-1) (\triangle s+s-1)) (p (R (\triangle s+s-1)+1)-R (\triangle s+s-1))\big)+(($$

$$\triangle s+s-1) x (2 (s-1) s (p (R (\triangle s+s-1)+1)-R (\triangle s+s-1)) (x-1) ($$

$$p (4 (R (s-1)+1) (s-1)+\triangle s (4 R (s-1)+x+1))-4 R (s-1) ($$

$$\triangle s+s-1))-(\triangle s+s) (p (\triangle s (2 R (s-1)+1)+2 (R (s-1)+1)$$

$$(s-1))-2 R (s-1) (\triangle s+s-1)) x (p (4 s+4 R (s-1) (\triangle s+$$

$$s-1)+\triangle s x-4)-4 R (s-1) (\triangle s+s-1)))) \big/ \big(-\triangle s^2 (p-1$$

$$) p R (\triangle s+s-1) x^2-4 \triangle s (p-1) R (s-1) (\triangle s+s-1) (p (R (\triangle s+s-$$

$$1)+1)-R (\triangle s+s-1)) x+(\triangle s+2 s-2) (p (\triangle s (4 R (s-1)+$$

$$1)+4 (R (s-1)+1) (s-1))-4 R (s-1) (\triangle s+s-1)) (p (R$$

$$(\triangle s+s-1)+1)-R (\triangle s+s-1))\big)+\Bigg(\Bigg((1-x) \Bigg(-$$

$$\frac{R (s-1) s (x-1)^2}{2 (-s R+R+p (R (s-1)+1))}+$$

$$\frac{(\triangle s+2 s) x (x-1)}{\frac{p (\triangle s (2 R (s-1)+1)+2 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)}-2}+\frac{(\triangle s+s) x^2}{2-\frac{2 p (R (\triangle s+s-1)+1)}{R (\triangle s+s-1)}}\Bigg)+x \Bigg(-$$

$$\frac{s (x-1)^2}{\frac{p (\triangle s (2 R (s-1)+1)+2 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)}-2}+$$

$$\frac{2 (\triangle s+2 s) x (x-1)}{\frac{p (\triangle s (4 R (s-1)+1)+4 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)}-4}+\frac{(\triangle s+s) x^2}{2-\frac{2 p (R (\triangle s+s-1)+1)}{R (\triangle s+s-1)}}\Bigg)\Bigg) \Bigg(\Bigg(R^2 ($$

$$s-1)^2 (\triangle s+s) (1-x) x \Bigg(-\frac{\triangle s^2 p^2 x^2}{R^2 (s-1)^2 (\triangle s+s-1)^2}-(4 \triangle s p ($$

$$p (R (\triangle s+s-1)+1)-R (\triangle s+s-1)) x) \big/ \big(R^2 (s-1) (\triangle s+$$

$$s-1)^2\big)-2 ((p (\triangle s (4 R (s-1)+1)+4 (R (s-1)+1)$$

$$(s-1)))/(R(s-1)(\Delta s+s-1))-4)\Big($$

$$\frac{p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}-1\Big)\Big)(\Delta s+s-1)^3\Big)\Big/\Big(-\Delta s^2(p-1)pR$$

$$(\Delta s+s-1)x^2-4\Delta s(p-1)R(s-1)(\Delta s+s-1)(p(R(\Delta s+s-1$$

$$)+1)-R(\Delta s+s-1))x+(\Delta s+2s-2)(p(\Delta s(4R(s$$

$$-1)+1)+4(R(s-1)+1)(s-1))-4R(s-1)($$

$$\Delta s+s-1))(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))\Big)-(\Delta s+s$$

$$)x^2(\Delta s+s-1)+((1-x)x(2(s-1)s(p(R(\Delta s+s-1)+1)-R($$

$$\Delta s+s-1))(x-1)(p(4(R(s-1)+1)(s-1)+\Delta s(4R($$

$$s-1)+x+1))-4R(s-1)(\Delta s+s-1))-(\Delta s+s$$

$$)(p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))-2R(s$$

$$-1)(\Delta s+s-1))x(p(4s+4R(s-1)(\Delta s+s-1)+\Delta s$$

$$x-4)-4R(s-1)(\Delta s+s-1)))(\Delta s+s-1))\Big/\Big(-\Delta s^2($$

$$p-1)pR(\Delta s+s-1)x^2-4\Delta s(p-1)R(s-1)(\Delta s+s-1)(p($$

$$R(\Delta s+s-1)+1)-R(\Delta s+s-1))x+(\Delta s+2s-2)(p(\Delta s($$

$$4R(s-1)+1)+4(R(s-1)+1)(s-1))-4R(s-1)($$

$$\Delta s+s-1))(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))\Big)+\Big((x-1)$$

$$(2(R(s-1)+1)(s-1)+\Delta s(2R(s-1)+x+1))-2R(s$$

$$-1)(\Delta s+s-1))-(\Delta s+s-1)(\Delta s+s)(-sR+R+p(R($$

$$s-1)+1))x(p(2s+2R(s-1)(\Delta s+s-1)+\Delta s\,x-$$

$$2)-2R(s-1)(\Delta s+s-1))))\Big)\Big/\Big(-\Delta s^2(p-1)pRx^2-2$$

$$\Delta s(p-1)R(s-1)(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))x+(p($$

$$\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))-2R(s-1)($$

$$\Delta s+s-1))(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))\Big)\Bigg)\Bigg/\Bigg(\Bigg(-$$

$$\frac{R(s-1)s(x-1)^2}{2(-sR+R+p(R(s-1)+1))}+$$

$$\frac{(\Delta s+2s)x(x-1)}{\frac{p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-2}+\frac{(\Delta s+s)x^2}{2-\frac{2p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}}\Bigg)(x-1)^2+$$

$$\frac{(\Delta s+s)x^2}{2-\frac{2p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}}+(\Delta s+s)(1-x)x\Bigg(-$$

$$\frac{(x-1)^2}{\frac{p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-2}+$$

$$\frac{4x(x-1)}{\frac{p(\Delta s(4R(s-1)+1)+4(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-4}+\frac{x^2}{2-\frac{2p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}}\Bigg)+(1-x)x$$

$$\Bigg(-\frac{s(x-1)^2}{\frac{p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-2}+$$

$$\frac{2\,(\triangle s+2\,s)\,x\,(x-1)}{\frac{p\,(\triangle s\,(4\,R\,(s-1)+1)+4\,(R\,(s-1)+1)\,(s-1))}{R\,(s-1)\,(\triangle s+s-1)}-4}+\frac{(\triangle s+s)\,x^2}{2-\frac{2\,p\,(R\,(\triangle s+s-1)+1)}{R\,(\triangle s+s-1)}}\Bigg)\Bigg)\Bigg)$$

Here, w_{WT} is the total allele fitness of the wildtype allele.

2) fitness of the mutant allele:

$$w_{\mathrm{MT}}=\frac{1}{2}\left((1-x)\,w_{f,\mathrm{MT/wt}}+x\cdot w_{f,\mathrm{MT/mt}}\right)+\frac{1}{2}\,m\left((1-x)\,w_{m,\mathrm{MT/wt}}+x\cdot w_{m,\mathrm{MT/mt}}\right)$$

$$\mathrm{w_{MT}}\;=$$

$$\frac{1}{2}\,R\,(\triangle s+s)\,\Bigg(\Bigg(R^2\,(s-1)^2\,(1-x)\,\Bigg(-\frac{\triangle s^2\,p^2\,x^2}{R^2\,(s-1)^2\,(\triangle s+s-1)^2}-(4\,\triangle s\,p\,(p\,(R\,(\triangle s+s$$

$$-1)+1)-R\,(\triangle s+s-1))\,x)\Big/\left(R^2\,(s-1)\,(\triangle s+s-1)^2\right)-$$

$$2\,((p\,(\triangle s\,(4\,R\,(s-1)+1)+4\,(R\,(s-1)+1)\,(s-1)))\,/\,(R\,(s-1)\,(\triangle s$$

$$+s-1))-4)\,\left(\frac{p\,(R\,(\triangle s+s-1)+1)}{R\,(\triangle s+s-1)}-1\right)\Bigg)\,(\triangle s+s-1)^3\Bigg)\Big/\,($$

$$-\triangle s^2\,(p-1)\,p\,R\,(\triangle s+s-1)\,x^2-4\,\triangle s\,(p-1)\,R\,(s-1)\,(\triangle s+s-1)\,(p\,(R\,($$

$$\triangle s+s-1)+1)-R\,(\triangle s+s-1))\,x+(\triangle s+2\,s-2)\,(p\,(\triangle s\,(4\,R\,(s$$

$$-1)+1)+4\,(R\,(s-1)+1)\,(s-1))-4\,R\,(s-1)\,(\triangle s+s-$$

$$1))\,(p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\Big)-x\,(\triangle s+s-1)+\Bigg(\Bigg($$

$$\frac{x}{2-\frac{2\,p\,(R\,(\triangle s+s-1)+1)}{R\,(\triangle s+s-1)}}+(1-x)\,\Bigg(-\frac{(x-1)^2}{\frac{p\,(\triangle s\,(2\,R\,(s-1)+1)+2\,(R\,(s-1)+1)\,(s-1))}{R\,(s-1)\,(\triangle s+s-1)}-2}+$$

$$\frac{4\,x\,(x-1)}{\frac{p\,(\triangle s\,(4\,R\,(s-1)+1)+4\,(R\,(s-1)+1)\,(s-1))}{R\,(s-1)\,(\triangle s+s-1)}-4}+\frac{x^2}{2-\frac{2\,p\,(R\,(\triangle s+s-1)+1)}{R\,(\triangle s+s-1)}}\Bigg)\Bigg)\,\Bigg(\Bigg(R^2\,($$

$$s-1)^2\,(\triangle s+s)\,(1-x)\,x\,\Bigg(-\frac{\triangle s^2\,p^2\,x^2}{R^2\,(s-1)^2\,(\triangle s+s-1)^2}-(4\,\triangle s\,p\,($$

$$p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\,x)\Big/\left(R^2\,(s-1)\,(\triangle s+\right.$$

$$\left.s-1)^2\right)-2\,((p\,(\triangle s\,(4\,R\,(s-1)+1)+4\,(R\,(s-1)+1)$$

$$(s-1)))\,/\,(R\,(s-1)\,(\triangle s+s-1))-4)\,\Bigg($$

$$\frac{p\,(R\,(\triangle s+s-1)+1)}{R\,(\triangle s+s-1)}-1\Bigg)\Bigg)\,(\triangle s+s-1)^3\Bigg)\Big/\,\left(-\triangle s^2\,(p-1)\,p\,R\right.$$

$$(\triangle s+s-1)\,x^2-4\,\triangle s\,(p-1)\,R\,(s-1)\,(\triangle s+s-1)\,(p\,(R\,(\triangle s+s-1$$

$$)+1)-R\,(\triangle s+s-1))\,x+(\triangle s+2\,s-2)\,(p\,(\triangle s\,(4\,R\,(s$$

$$-1)+1)+4\,(R\,(s-1)+1)\,(s-1))-4\,R\,(s-1)\,($$

$$\left.\triangle s+s-1))\,(p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\right)-(\triangle s+s$$

$$)\,x^2\,(\triangle s+s-1)+((1-x)\,x\,(2\,(s-1)\,s\,(p\,(R\,(\triangle s+s-1)+1)-R\,($$

$$\triangle s+s-1))\,(x-1)\,(p\,(4\,(R\,(s-1)+1)\,(s-1)+\triangle s\,(4\,R\,($$

$$s-1)+x+1))-4\,R\,(s-1)\,(\triangle s+s-1))-(\triangle s+s$$

$$)\,(p\,(\triangle s\,(2\,R\,(s-1)+1)+2\,(R\,(s-1)+1)\,(s-1))-2\,R\,(s$$

$$-1) (\triangle s + s - 1)) x (p (4 s + 4 R (s - 1) (\triangle s + s - 1) + \triangle s$$
$$x - 4) - 4 R (s - 1) (\triangle s + s - 1))) (\triangle s + s - 1)) \Big/ \Big(-\triangle s^2 ($$
$$p - 1) p R (\triangle s + s - 1) x^2 - 4 \triangle s (p - 1) R (s - 1) (\triangle s + s - 1) (p ($$
$$R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)) x + (\triangle s + 2 s - 2) (p (\triangle s ($$
$$4 R (s - 1) + 1) + 4 (R (s - 1) + 1) (s - 1)) - 4 R (s - 1) ($$
$$\triangle s + s - 1)) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)))\Big) + \Big((x - 1)$$
$$(2 (R (s - 1) + 1) (s - 1) + \triangle s (2 R (s - 1) + x + 1)) - 2 R (s$$
$$- 1) (\triangle s + s - 1)) - (\triangle s + s - 1) (\triangle s + s) (-s R + R + p (R ($$
$$s - 1) + 1)) x (p (2 s + 2 R (s - 1) (\triangle s + s - 1) + \triangle s x -$$
$$2) - 2 R (s - 1) (\triangle s + s - 1))))\Big) \Big/ \Big(-\triangle s^2 (p - 1) p R x^2 - 2$$
$$\triangle s (p - 1) R (s - 1) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)) x + (p ($$
$$\triangle s (2 R (s - 1) + 1) + 2 (R (s - 1) + 1) (s - 1)) - 2 R (s - 1) ($$
$$\triangle s + s - 1)) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1))\Big)\Bigg)\Bigg) \Bigg/ \Bigg(\Bigg(\Bigg(-$$

$$\frac{R (s - 1) s (x - 1)^2}{2 (-s R + R + p (R (s - 1) + 1))} +$$

$$\frac{(\triangle s + 2 s) x (x - 1)}{\frac{p (\triangle s (2 R (s-1)+1)+2 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)} - 2} + \frac{(\triangle s + s) x^2}{2 - \frac{2 p (R (\triangle s+s-1)+1)}{R (\triangle s+s-1)}}\Bigg) (x - 1)^2 +$$

$$\frac{(\triangle s + s) x^2}{2 - \frac{2 p (R (\triangle s+s-1)+1)}{R (\triangle s+s-1)}} + (\triangle s + s) (1 - x) x \Bigg(-$$

$$\frac{(x - 1)^2}{\frac{p (\triangle s (2 R (s-1)+1)+2 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)} - 2} +$$

$$\frac{4 x (x - 1)}{\frac{p (\triangle s (4 R (s-1)+1)+4 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)} - 4} + \frac{x^2}{2 - \frac{2 p (R (\triangle s+s-1)+1)}{R (\triangle s+s-1)}}\Bigg) + (1 - x) x$$

$$\Bigg(- \frac{s (x - 1)^2}{\frac{p (\triangle s (2 R (s-1)+1)+2 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)} - 2} +$$

$$\frac{2 (\triangle s + 2 s) x (x - 1)}{\frac{p (\triangle s (4 R (s-1)+1)+4 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)} - 4} + \frac{(\triangle s + s) x^2}{2 - \frac{2 p (R (\triangle s+s-1)+1)}{R (\triangle s+s-1)}}\Bigg)\Bigg)\Bigg)\Bigg)$$

The fitness difference Δ*w* is then:

$$\triangle w =$$

$$\frac{1}{2} R (\triangle s + s) \Bigg(\Bigg(R^2 (s - 1)^2 (1 - x) \Bigg(- \frac{\triangle s^2 p^2 x^2}{R^2 (s - 1)^2 (\triangle s + s - 1)^2} - (4 \triangle s p (p (R (\triangle s + s$$
$$- 1) + 1) - R (\triangle s + s - 1)) x) \Big/ \Big(R^2 (s - 1) (\triangle s + s - 1)^2\Big)$$
$$- 2 ((p (\triangle s (4 R (s - 1) + 1) + 4 (R (s - 1) + 1) (s - 1))) / (R (s - 1$$

$$) (\triangle s + s - 1)) - 4) \left(\frac{p (R (\triangle s + s - 1) + 1)}{R (\triangle s + s - 1)} - 1\right)) (\triangle s + s - 1)^3)$$

$$s - 1) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)) x + (\triangle s + 2 s - 2) (p (\triangle s$$

$$(4 R (s - 1) + 1) + 4 (R (s - 1) + 1) (s - 1)) - 4 R (s - 1) (\triangle s + s$$

$$- 1)) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1))) - x (\triangle s + s - 1) + ($$

$$\left(\frac{x}{2 - \frac{2 p (R (\triangle s+s-1)+1)}{R (\triangle s+s-1)}} + (1 - x) \left(-\frac{(x - 1)^2}{\frac{p (\triangle s (2 R (s-1)+1)+2 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)} - 2} +\right.\right.$$

$$\left.\left.\frac{4 x (x - 1)}{\frac{p (\triangle s (4 R (s-1)+1)+4 (R (s-1)+1) (s-1))}{R (s-1) (\triangle s+s-1)} - 4} + \frac{x^2}{2 - \frac{2 p (R (\triangle s+s-1)+1)}{R (\triangle s+s-1)}}\right)\right) ((R^2$$

$$(s - 1)^2 (\triangle s + s) (1 - x) x \left(-\frac{\triangle s^2 p^2 x^2}{R^2 (s - 1)^2 (\triangle s + s - 1)^2} - (4 \triangle s p (p\right.$$

$$(R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)) x) / (R^2 (s - 1) (\triangle s$$

$$+ s - 1)^2) - 2 ((p (\triangle s (4 R (s - 1) + 1) + 4 (R (s - 1) +$$

$$1) (s - 1))) / (R (s - 1) (\triangle s + s - 1)) - 4) ($$

$$\left.\frac{p (R (\triangle s + s - 1) + 1)}{R (\triangle s + s - 1)} - 1)\right) (\triangle s + s - 1)^3) / (-\triangle s^2 (p - 1) p$$

$$R (\triangle s + s - 1) x^2 - 4 \triangle s (p - 1) R (s - 1) (\triangle s + s - 1) (p (R (\triangle s + s$$

$$- 1) + 1) - R (\triangle s + s - 1)) x + (\triangle s + 2 s - 2) (p (\triangle s (4 R$$

$$(s - 1) + 1) + 4 (R (s - 1) + 1) (s - 1)) - 4 R (s - 1)$$

$$(\triangle s + s - 1)) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1))) - (\triangle s +$$

$$s) x^2 (\triangle s + s - 1) + ((1 - x) x (2 (s - 1) s (p (R (\triangle s + s - 1) + 1) -$$

$$R (\triangle s + s - 1)) (x - 1) (p (4 (R (s - 1) + 1) (s - 1) + \triangle s (4 R$$

$$(s - 1) + x + 1)) - 4 R (s - 1) (\triangle s + s - 1)) - (\triangle s +$$

$$s) (p (\triangle s (2 R (s - 1) + 1) + 2 (R (s - 1) + 1) (s - 1)) - 2 R$$

$$(s - 1) (\triangle s + s - 1)) x (p (4 s + 4 R (s - 1) (\triangle s + s - 1) +$$

$$\triangle s x - 4) - 4 R (s - 1) (\triangle s + s - 1))) (\triangle s + s - 1)) / (-$$

$$\triangle s^2 (p - 1) p R (\triangle s + s - 1) x^2 - 4 \triangle s (p - 1) R (s - 1) (\triangle s + s - 1$$

$$) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)) x + (\triangle s + 2 s - 2) (p ($$

$$\triangle s (4 R (s - 1) + 1) + 4 (R (s - 1) + 1) (s - 1)) - 4 R (s - 1)$$

$$(\triangle s + s - 1)) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1))) + ((x -$$

$$1)^2 ((s - 1) s (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)) (x - 1)$$

$$(p (2 (R (s - 1) + 1) (s - 1) + \triangle s (2 R (s - 1) + x + 1)) - 2 R (s$$

$$- 1) (\triangle s + s - 1)) - (\triangle s + s - 1) (\triangle s + s) (-s R + R + p (R$$

$$(s - 1) + 1)) x (p (2 s + 2 R (s - 1) (\triangle s + s - 1) + \triangle s x$$

$$- 2) - 2 R (s - 1) (\triangle s + s - 1)))) / (-\triangle s^2 (p - 1) p R x^2$$

$$- 2 \triangle s (p - 1) R (s - 1) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)) x +$$

$$(p (\triangle s (2 R (s - 1) + 1) + 2 (R (s - 1) + 1) (s - 1)) - 2 R (s - 1) ($$

$$\triangle s + s - 1)) (p (R (\triangle s + s - 1) + 1) - R (\triangle s + s - 1)))) / ((($$

$$-\frac{R(s-1)s(x-1)^2}{2(-sR+R+p(R(s-1)+1))}+$$

$$\frac{(\Delta s+2s)x(x-1)}{\frac{p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-2}+\frac{(\Delta s+s)x^2}{2-\frac{2p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}}\Bigg)(x-1)^2$$

$$+\frac{(\Delta s+s)x^2}{2-\frac{2p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}}+(\Delta s+s)(1-x)x\Bigg(-$$

$$\frac{(x-1)^2}{\frac{p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-2}+$$

$$\frac{4x(x-1)}{\frac{p(\Delta s(4R(s-1)+1)+4(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-4}+\frac{x^2}{2-\frac{2p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}}\Bigg)+(1-x)$$

$$x\Bigg(-\frac{s(x-1)^2}{\frac{p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-2}+$$

$$\frac{2(\Delta s+2s)x(x-1)}{\frac{p(\Delta s(4R(s-1)+1)+4(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-4}+\frac{(\Delta s+s)x^2}{2-\frac{2p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}}\Bigg)\Bigg)\Bigg)\Bigg)-\frac{1}{2}R\Bigg($$

$$((1-x)((s-1)s(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))(x-1)(p(2(R(s-1)+1)(s-1)+\Delta s(2R(s-1)+x+1))-2R(s-1)(\Delta s+s-1))-(\Delta s+s-1)(\Delta s+s)(-sR+R+p(R(s-1)+1))x(p(2s+2R(s-1)(\Delta s+s-1)+\Delta s x-2)-2R(s-1)(\Delta s+s-1))))\Big/\Big(-\Delta s^2(p-1)pRx^2-2\Delta s(p-1)R(s-1)(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))x+(p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))-2R(s-1)(\Delta s+s-1))(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))\Big)+((\Delta s+s-1)x(2(s-1)s(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))(x-1)(p(4(R(s-1)+1)(s-1)+\Delta s(4R(s-1)+x+1))-4R(s-1)(\Delta s+s-1))-(\Delta s+s)(p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))-2R(s-1)(\Delta s+s-1))x(p(4s+4R(s-1)(\Delta s+s-1)+\Delta s x-4)-4R(s-1)(\Delta s+s-1))))\Big/\Big(-\Delta s^2(p-1)pR(\Delta s+s-1)x^2-4\Delta s(p-1)R(s-1)(\Delta s+s-1)(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))x+(\Delta s+2s-2)(p(\Delta s(4R(s-1)+1)+4(R(s-1)+1)(s-1))-4R(s-1)(\Delta s+s-1))(p(R(\Delta s+s-1)+1)-R(\Delta s+s-1))\Big)+\Bigg(\Bigg((1-x)\Bigg(-$$

$$\frac{R(s-1)s(x-1)^2}{2(-sR+R+p(R(s-1)+1))}+$$

$$\frac{(\Delta s+2s)x(x-1)}{\frac{p(\Delta s(2R(s-1)+1)+2(R(s-1)+1)(s-1))}{R(s-1)(\Delta s+s-1)}-2}+\frac{(\Delta s+s)x^2}{2-\frac{2p(R(\Delta s+s-1)+1)}{R(\Delta s+s-1)}}\Bigg)+x\Bigg(-$$

$$\frac{s\,(x-1)^2}{\frac{p\,(\triangle s\,(2\,R\,(s-1)+1)+2\,(R\,(s-1)+1)\,(s-1))}{R\,(s-1)\,(\triangle s+s-1)}-2}+$$

$$\frac{2\,(\triangle s+2\,s)\,x\,(x-1)}{\frac{p\,(\triangle s\,(4\,R\,(s-1)+1)+4\,(R\,(s-1)+1)\,(s-1))}{R\,(s-1)\,(\triangle s+s-1)}-4}+\frac{(\triangle s+s)\,x^2}{2-\frac{2\,p\,(R\,(\triangle s+s-1)+1)}{R\,(\triangle s+s-1)}}\Bigg)\Bigg)\;\Bigg(\Bigg(\Bigg(R^2$$

$$(s-1)^2\,(\triangle s+s)\,(1-x)\,x\,\Bigg(-\frac{\triangle s^2\,p^2\,x^2}{R^2\,(s-1)^2\,(\triangle s+s-1)^2}-(4\,\triangle s\,p\,(p$$

$$(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\,x)\Big/\Big(R^2\,(s-1)\,(\triangle s$$

$$+s-1)^2\Big)-2\,((p\,(\triangle s\,(4\,R\,(s-1)+1)+4\,(R\,(s-1)+$$

$$1)\,(s-1)))\,/\,(R\,(s-1)\,(\triangle s+s-1))-4)\,\Bigg($$

$$\frac{p\,(R\,(\triangle s+s-1)+1)}{R\,(\triangle s+s-1)}-1\Bigg)\Bigg)\,(\triangle s+s-1)^3\Bigg)\Bigg/\Big(-\triangle s^2\,(p-1)\,p$$

$$R\,(\triangle s+s-1)\,x^2-4\,\triangle s\,(p-1)\,R\,(s-1)\,(\triangle s+s-1)\,(p\,(R\,(\triangle s+s$$

$$-1)+1)-R\,(\triangle s+s-1))\,x+(\triangle s+2\,s-2)\,(p\,(\triangle s\,(4\,R$$

$$(s-1)+1)+4\,(R\,(s-1)+1)\,(s-1))-4\,R\,(s-1)$$

$$(\triangle s+s-1))\,(p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\Big)-(\triangle s+$$

$$s)\,x^2\,(\triangle s+s-1)+((1-x)\,x\,(2\,(s-1)\,s\,(p\,(R\,(\triangle s+s-1)+1)-$$

$$R\,(\triangle s+s-1))\,(x-1)\,(p\,(4\,(R\,(s-1)+1)\,(s-1)+\triangle s\,(4\,R$$

$$(s-1)+x+1))-4\,R\,(s-1)\,(\triangle s+s-1))-(\triangle s+$$

$$s)\,(p\,(\triangle s\,(2\,R\,(s-1)+1)+2\,(R\,(s-1)+1)\,(s-1))-2\,R$$

$$(s-1)\,(\triangle s+s-1))\,x\,(p\,(4\,s+4\,R\,(s-1)\,(\triangle s+s-1)+$$

$$\triangle s\,x-4)-4\,R\,(s-1)\,(\triangle s+s-1)))\,(\triangle s+s-1))\Big/\Big(-$$

$$\triangle s^2\,(p-1)\,p\,R\,(\triangle s+s-1)\,x^2-4\,\triangle s\,(p-1)\,R\,(s-1)\,(\triangle s+s-1$$

$$)\,(p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\,x+(\triangle s+2\,s-2)\,(p\,($$

$$\triangle s\,(4\,R\,(s-1)+1)+4\,(R\,(s-1)+1)\,(s-1))-4\,R\,(s-1)$$

$$(\triangle s+s-1))\,(p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\Big)+\Big((x-$$

$$1)^2\,((s-1)\,s\,(p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\,(x-1)$$

$$(p\,(2\,(R\,(s-1)+1)\,(s-1)+\triangle s\,(2\,R\,(s-1)+x+1))-2\,R\,(s$$

$$-1)\,(\triangle s+s-1))-(\triangle s+s-1)\,(\triangle s+s)\,(-s\,R+R+p\,(R$$

$$(s-1)+1))\,x\,(p\,(2\,s+2\,R\,(s-1)\,(\triangle s+s-1)+\triangle s\,x$$

$$-2)-2\,R\,(s-1)\,(\triangle s+s-1))))\Big)\Big/\Big(-\triangle s^2\,(p-1)\,p\,R\,x^2$$

$$-2\,\triangle s\,(p-1)\,R\,(s-1)\,(p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\,x+$$

$$(p\,(\triangle s\,(2\,R\,(s-1)+1)+2\,(R\,(s-1)+1)\,(s-1))-2\,R\,(s-1)\,($$

$$\triangle s+s-1))\,(p\,(R\,(\triangle s+s-1)+1)-R\,(\triangle s+s-1))\Big)\Bigg)\Bigg)\Bigg/\Bigg(\Bigg(\Bigg($$

$$-\frac{R\,(s-1)\,s\,(x-1)^2}{2\,(-s\,R+R+p\,(R\,(s-1)+1))}+$$

$$\frac{(\triangle s+2\,s)\,x\,(x-1)}{\frac{p\,(\triangle s\,(2\,R\,(s-1)+1)+2\,(R\,(s-1)+1)\,(s-1))}{R\,(s-1)\,(\triangle s+s-1)}-2}+\frac{(\triangle s+s)\,x^2}{2-\frac{2\,p\,(R\,(\triangle s+s-1)+1)}{R\,(\triangle s+s-1)}}\Bigg)\,(x-1)^2$$

$$+\frac{(\triangle s + s)\ x^2}{2 - \frac{2\,p\ (R\ (\triangle s+s-1)+1)}{R\ (\triangle s+s-1)}} + (\triangle s + s)\ (1 - x)\ x \left(- \right.$$

$$\frac{(x - 1)^2}{\frac{p\ (\triangle s\ (2\,R\ (s-1)+1)+2\ (R\ (s-1)+1)\ (s-1))}{R\ (s-1)\ (\triangle s+s-1)} - 2} +$$

$$\left. \frac{4\,x\ (x - 1)}{\frac{p\ (\triangle s\ (4\,R\ (s-1)+1)+4\ (R\ (s-1)+1)\ (s-1))}{R\ (s-1)\ (\triangle s+s-1)} - 4} + \frac{x^2}{2 - \frac{2\,p\ (R\ (\triangle s+s-1)+1)}{R\ (\triangle s+s-1)}} \right) + (1 - x)$$

$$x \left(- \frac{s\ (x - 1)^2}{\frac{p\ (\triangle s\ (2\,R\ (s-1)+1)+2\ (R\ (s-1)+1)\ (s-1))}{R\ (s-1)\ (\triangle s+s-1)} - 2} + \right.$$

$$\left.\left.\left. \frac{2\ (\triangle s + 2\,s)\ x\ (x - 1)}{\frac{p\ (\triangle s\ (4\,R\ (s-1)+1)+4\ (R\ (s-1)+1)\ (s-1))}{R\ (s-1)\ (\triangle s+s-1)} - 4} + \frac{(\triangle s + s)\ x^2}{2 - \frac{2\,p\ (R\ (\triangle s+s-1)+1)}{R\ (\triangle s+s-1)}} \right)\right)\right)$$

Supply function genes

We have now determined the allele fitness functions for genes affecting demand. Additionally, we have to calculate the allele fitness function for genes affecting supply. In contrast to demand function genes, supply function genes act only in mothers. This makes this part easier for two reasons:

1) Mutations in supply function genes (which are assumed to be dominant) are active regardless of which allele was inherited by the offspring.
2) Supply function genes are not expressed by males, and we can thus leave males out of the equation.

As a result, whether a mutation in a supply function gene is rare or common does not affect its fitness. Given a certain genetic background of the mother, the father may carry any alleles he likes, it will not affect the outcome for mother or offspring (which was not the case for demand function genes). There is thus no frequency-dependence of supply function genes.

With these simplifications in mind, we may use the same methods as previously to calculate the corresponding fitness functions. In the following, the **fitness functions of supply function genes** are denoted as ***v***, with subscripts as before**.**

Fitness of wildtype and mutant alleles

Wildtype alleles derived from homozygous wildtype females receive the wildtype level of supply. Wildtype and mutant alleles derived from heterozygous females, as well as mutant alleles derived from mutant homozygous females, receive the mutant level of supply.

Allele fitness of the wildtype allele derived from a homozygous wildtype female:

$$v_{f,\mathrm{WT}} = \tfrac{1}{2}\,R(1 - s)\,s$$

$$\mathrm{v}_{\mathrm{f,WT}} =$$

$$\frac{s_{\mathrm{wt}}}{2 - 2\,q_{\mathrm{wt}}}$$

$$=$$

$$-\frac{1}{2}\,R\ (s - 1)\ s$$

Allele fitness of the wildtype and mutant allele derived from a heterozygous female, and from the mutant allele derived from homozygous mutant females:

$$v_{f,\mathrm{WT/mt}} = v_{f,\mathrm{wt/MT}} = v_{f,\mathrm{MT}} = \tfrac{1}{2}\,R(1 - s - \Delta\mathrm{s})\,(s + \Delta\mathrm{s})$$

$$\mathrm{v}_{\mathrm{f,WT/mt}} = \mathrm{v}_{\mathrm{f,MT/wt}} = \mathrm{v}_{\mathrm{f,MT/MT}} =$$

$$\frac{s_{\mathrm{mt}}}{2 - 2\, q_{\mathrm{mt}}}$$

$$=$$

$$-\frac{1}{2} R\, (\triangle\mathrm{s} + s - 1)\, (\triangle\mathrm{s} + s)$$

Supply function genes neither are expressed in males (males do not provide parental care in this model), nor do they affect maternal care differently for different offspring genotypes. Evolution of supply function genes is therefore not influenced by males, allowing us to ignore them when calculating stable levels attained by supply function genes.

Overall, to calculate the average fitness of supply function alleles, we have to weigh the different fitness functions by the frequency of the mutant allele:

$$v_{\mathrm{WT}} = (1 - x)\, v_{f,\mathrm{WT/wt}} + x \cdot v_{f,\mathrm{WT/mt}} =$$

$$-\frac{1}{2} R\, \left(s\, (2\, \triangle\mathrm{s}\, x - 1) + (\triangle\mathrm{s} - 1)\, \triangle\mathrm{s}\, x + s^2\right)$$

$$v_{\mathrm{MT}} = (1 - x)\, v_{f,\mathrm{MT/wt}} + x \cdot v_{f,\mathrm{MT/mt}} =$$

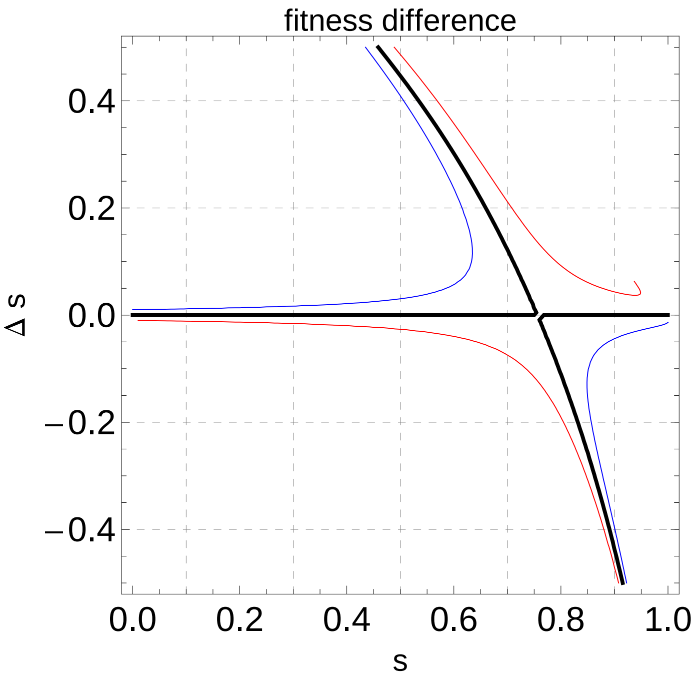
$$-\frac{1}{2} R\, \left(\triangle\mathrm{s}^2 + \triangle\mathrm{s}\, (2\, s - 1) + (s - 1)\, s\right)$$

Frequency – dependence

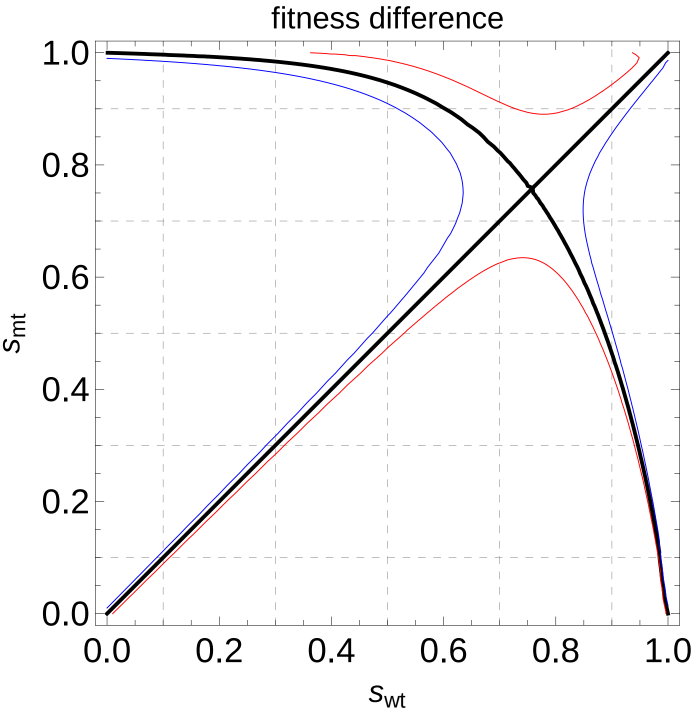
Demand function genes

As argued above, the effect of mutations in supply function genes is not frequency-dependent, whereas the effect of demand function genes is. We now analyze this latter frequency-dependence in more detail.

To this end, we create **fitness difference isoclines** (presented as functions of s and Δs) and **pairwise invasibility plots** (same content, but presented as functions of s_{wt} and s_{mt}), always with blue denoting isoclines with mutant alleles having higher fitness than wildtype alleles and red isoclines with wildtype alleles having higher fitness than mutant alleles. Black lines indicate the zero fitness difference isoclines. As a result, mutants can invade in areas with positive fitness differences (i.e. containing blue lines) and wildtypes prevails in areas with negative fitness differences (i.e. containing red lines).



Pairwise invasibility plot:



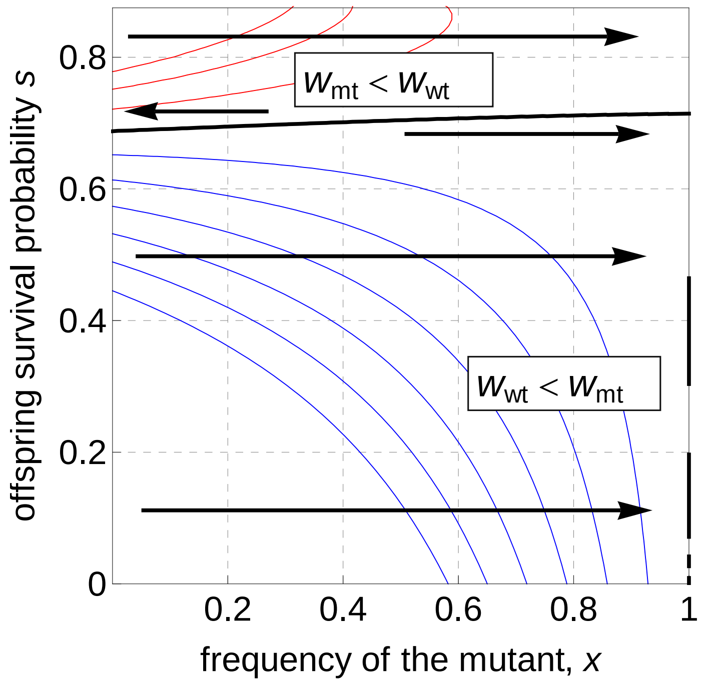
The parameter values for the two figures above are R=10, p=0.5, and x=0.5.

In equilibrium, every mutation with Δ*s* unequal 0 causes a net fitness loss (evolutionary stability). Vertical shifts from the equilibrium thus lead to areas where the fitness difference between mutant and wildtype alleles is negative. Furthermore, (horizontal) shifts of monomorphic populations should lead to a fitness loss (convergence stability). Therefore, the equilibrium value of *s* can be found at the intersection of the zero fitness isoclines, where horizontal shifts are positive and vertical shifts are negative.

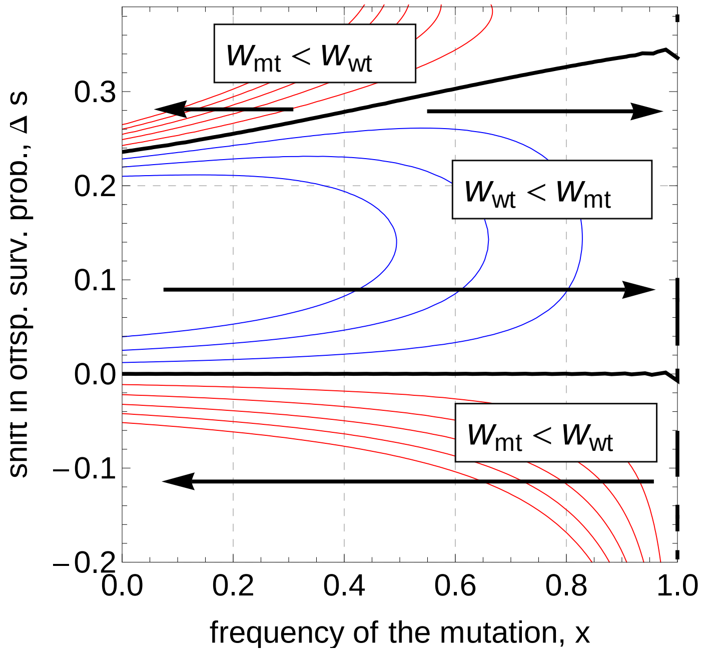
Unfortunately, it is impossible to solve for this equilibrium analytically. (Solving dwall==0 for Δs fails to deliver a result.)

One assumption that would simplify the matter is that mutant alleles, given that they have a higher fitness than wildtypes alleles when rare, will always replace the wildtype allele. This assumption is often made, and although we cannot prove it for our case, we can at least illustrate that the selection gradient increases the more frequent the mutant becomes. To this end, we show fitness isoclines as a function of one of the parameters or variables and as a function of the mutant frequency *x*. If the mutant can always invade when initially at an advantage, we should expect that the area of positive fitness for mutants never shrinks when x increases. Below are shown some examples with the fitness difference expressed, in turn, as a function of our parameters s, Δs, R, and p.

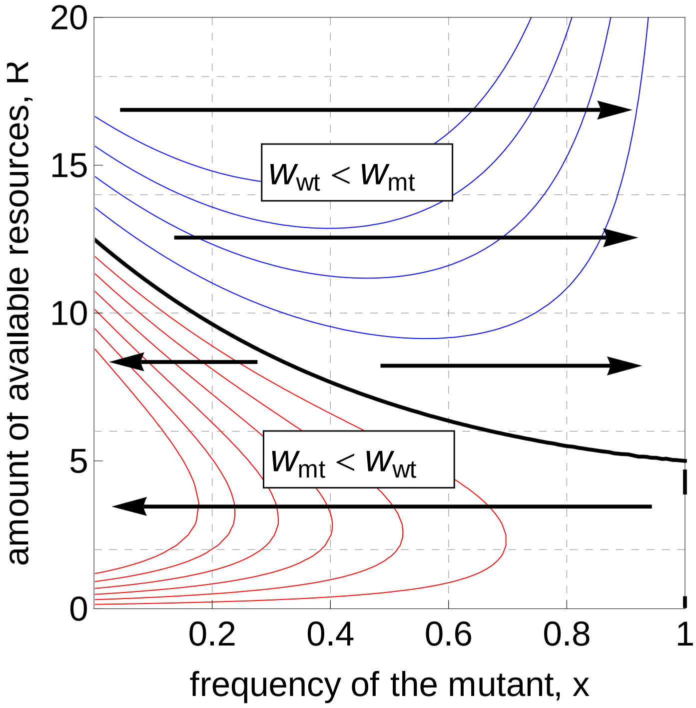
Fitness difference as a function of s



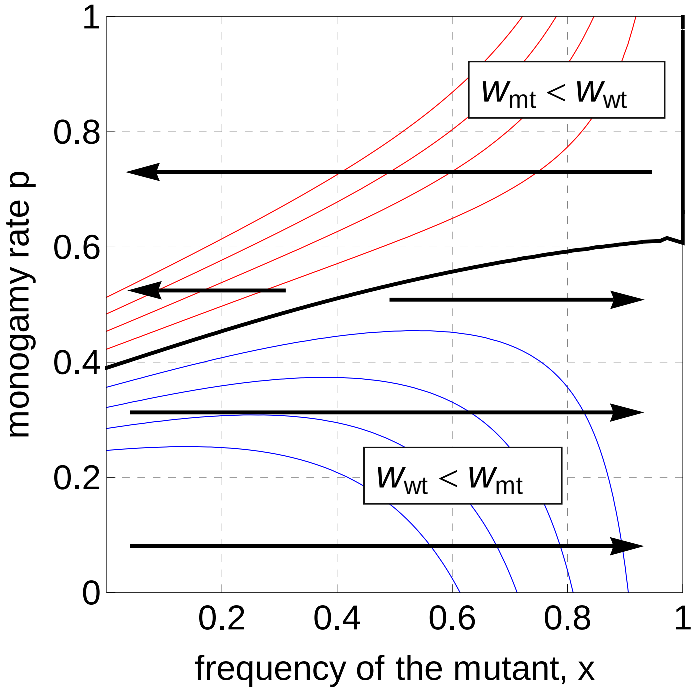
Fitness difference as a function of Δs



Fitness difference as a function of R



Fitness difference as a function of *p*



As these examples illustrate, if the mutant can invade, it will always be fixed in the population. This finding can be illustrated by exploring Interactive Figure S2: First adjust the parameters in such a way that the mutant has a fitness advantage over the wildtype when rare (i.e. for low *x*). Then increase the frequency of the mutant by shifting the slider for *x* towards higher values. As you will see, the fitness advantage for the mutant never vanishes (i.e. the mutant fitness function remains above the wildtype fitness function), meaning that it will be positively selected for until it is fixed in the population.

Evolutionary stability

Evolutionary stability for demand function genes

Although we find that for some parameter regions, there is an invasion barrier for the mutant allele (i.e. the mutant allele has to cross a certain frequency in the population before being able to invade), the mutant allele will always replace the wildtype if the mutant allele has higher initial fitness. We can therefore narrow down our analysis on whether a mutant allele can invade if initially rare.

To find the evolutionarily stable state, we use the following reasoning. For every wildtype offspring survival probability s, there is a mutation with an effect Δs that would have exactly the same fitness as the wildtype, i.e. $w_{\mathrm{wt}} = w_{\mathrm{mt}}$. For instance, if R=8, p=1, and s=0.5, then a mutant with an effect of Δs=0.25, i.e. a mutant that greatly increases the provided resources through higher demand, would have the same fitness as the wildtype. However, for all parameter values, there is one value of s and one value only for which this Δs equals 0. This must be an equilibrium value of s. Since mutants that cause deviations from that s have lower fitness, that s is evolutionarily stable; since monomorphic populations in the neighborhood are prone to invasion, it is convergence stable.

Using the logic that there is only one value of s for which the deviation Δs that leads to the same fitness is Δs=0, we can solve for that value of s. We want to find values of Δs that equalise the fitness of wildtype and mutant. (There are three solutions. The first, Δs is trivial and can be discarded. The other two, when solved for s, give the same results, so one can be ignored.)

$$0$$

$$\left(8\,p\,R\,s^2-\sqrt{\left(\left(-8\,p\,R\,s^2+15\,p\,R\,s-7\,p\,R-7\,p\,s+6\,p+8\,R\,s^2-15\,R\,s+7\,R\right)^2-4\,(-3\,p\,R\,s+3\,p\,R-2\,p+3\,R\,s-3\,R)\left(-5\,p\,R\,s^3+14\,p\,R\,s^2-13\,p\,R\,s+4\,p\,R-6\,p\,s^2+10\,p\,s-4\,p+5\,R\,s^3-14\,R\,s^2+13\,R\,s-4\,R\right)\right)}-15\,p\,R\,s+7\,p\,R+7\,p\,s-6\,p-8\,R\,s^2+15\,R\,s-7\,R\right)\Big/\left(2\,(-3\,p\,R\,s+3\,p\,R-2\,p+3\,R\,s-3\,R)\right)$$

$$\left(8\,p\,R\,s^2+\sqrt{\left(\left(-8\,p\,R\,s^2+15\,p\,R\,s-7\,p\,R-7\,p\,s+6\,p+8\,R\,s^2-15\,R\,s+7\,R\right)^2-4\,(-3\,p\,R\,s+3\,p\,R-2\,p+3\,R\,s-3\,R)\left(-5\,p\,R\,s^3+14\,p\,R\,s^2-13\,p\,R\,s+4\,p\,R-6\,p\,s^2+10\,p\,s-4\,p+5\,R\,s^3-14\,R\,s^2+13\,R\,s-4\,R\right)\right)}-15\,p\,R\,s+7\,p\,R+7\,p\,s-6\,p-8\,R\,s^2+15\,R\,s-7\,R\right)\Big/\left(2\,(-3\,p\,R\,s+3\,p\,R-2\,p+3\,R\,s-3\,R)\right)$$

Next we want to find values of s for which the equalizing Δs is equal to 0. To this end, we first solve the fitness difference for Δs, then set the resulting Δs equal to zero and solve for s. Finally, we explore the solutions graphically in a 3D-plot.

$$s_{\mathrm{ESS}}^{\mathrm{dem}} =$$

$$1$$

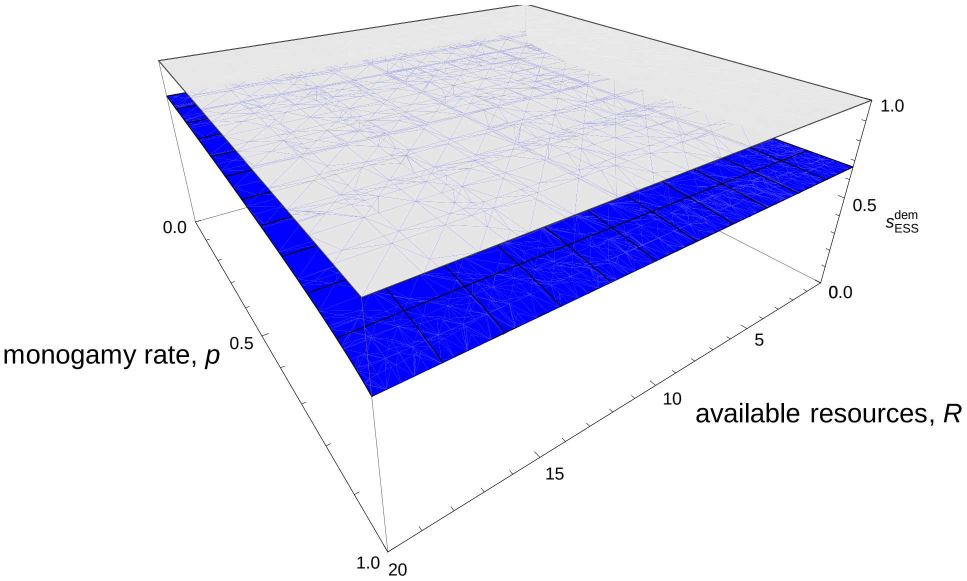
or

$$\frac{1}{10\,(p\,R-R)}\left(-\sqrt{p^2\,R^2-28\,p^2\,R+36\,p^2-2\,p\,R^2+28\,p\,R+R^2}+9\,p\,R-6\,p-9\,R\right)$$

or

$$\frac{1}{10\,(p\,R-R)}\left(\sqrt{p^2\,R^2-28\,p^2\,R+36\,p^2-2\,p\,R^2+28\,p\,R+R^2}+9\,p\,R-6\,p-9\,R\right)$$

The first solution is trivial and can be discarded. We next plot the second and third solution to test whether they are inside the analyzed domain.



As the plot shows, the third of the three offered solutions is correct, whereas second is outside the boundaries (or a red plane would have been visible),. We can thus determine the ESS-value of *s* as

$s_{\mathrm{ESS}}^{\mathrm{dem}}$ =

$$\frac{\sqrt{36\,p^2+(p-1)^2\,R^2-28\,(p-1)\,p\,R}+9\,(p-1)\,R-6\,p}{10\,(p-1)\,R}$$

As a particular result, in the limit of *p* equal to 1 (strict monogamy, which reduces parent-offspring conflict to a minimum), the ESS value of *s* becomes 2/3, regardless of *R*; in the limit of *p* equal to 0 (strict polygamy, which creates the most parent-offspring conflict), the ESS value of *s* becomes 4/5.

For the limit of p → 1, $s_{\mathrm{ESS}}^{\mathrm{dem}}$ =

$$\frac{2}{3}$$

For $p = 0$, $s_{\mathrm{ESS}}^{\mathrm{dem}}$ =

$$\frac{4}{5}$$

Evolutionary stability for supply function genes

The same logic as for demand function genes can be applied to supply function genes. However, we can save ourselves the trouble of the assumption that the mutation is rare because no frequency-dependence exists anyway.

$$0$$

$$1-2\,s$$

The first solution is trivial: When the mutation has no effect, mutants alleles will have the same fitness as wildtype alleles. This result can be discarded, and we continue by setting the second solution to zero and solving for the evolutionarily stable value of *s*.

$s_{\mathrm{ESS}}^{\mathrm{sup}}$ =

$$\frac{1}{2}$$

The result for supply function genes is much simpler than for demand function genes: Supply function genes should always aim at providing resources until the survival probability rate of the offspring is 50%. The remainder of the resources is used to increase the survival probability rate *q* of the mother.

Unsurprisingly, this ESS value of *s* for supply function genes is also the value that maximises the expected number of offspring produced by a female. The reason is that when supply function genes mutate, all offspring are affected in the same degree. This contrasts with mutations in demand function genes, which only affect those offspring that inherit it. Because of the indiscriminate nature of supply function genes, they maximise their fitness when they maximise the total number of offspring.

Comparison of supply and demand function genes

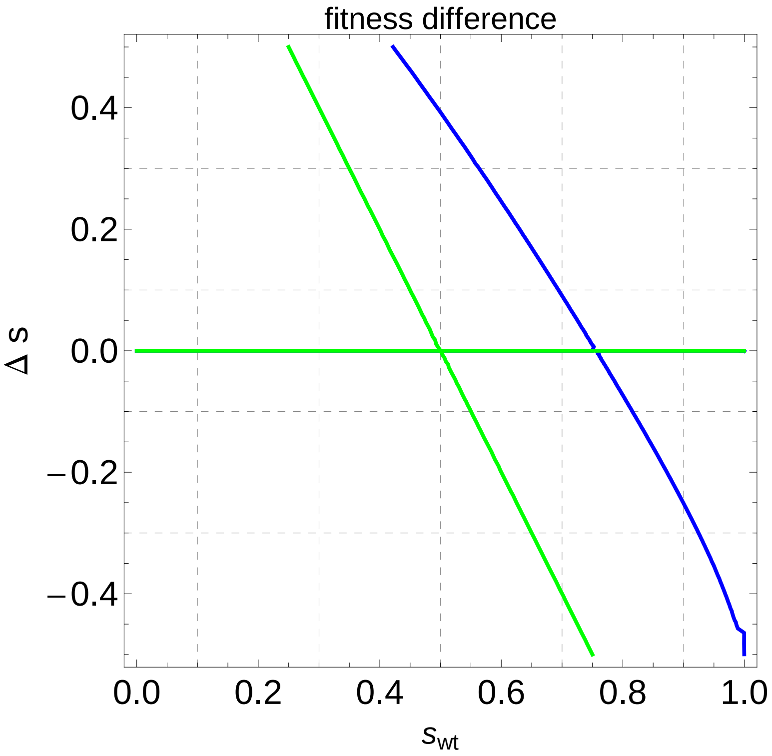
Within the constraints, the evolutionarily stable value for demand function genes is never less than 2/3, which is strictly greater than the evolutionarily stable value for supply function genes. There is thus always conflict between supply and demand function genes. These two distinct stable values determine the 'battleground' of parent-offspring conflict.

This battleground can be explored in more detail in Interactive Figure S3. This figure allows to adjust resource level *R* and monogamy rate *p* and to compare the resulting ESS-values for demand and supply.

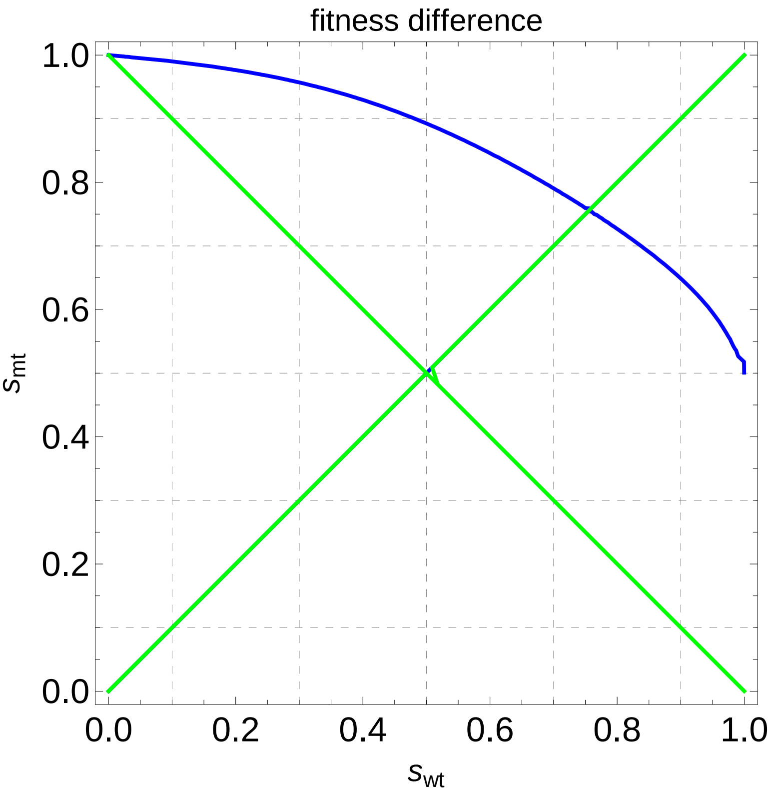
There is also an upper limit for demand function genes; it is 4/5 and is reached for *p*=0, regardless of the value of *R*. We should thus expect that under all circumstances, demand function genes should aim at increasing supply so as to reach an offspring survival probability of at least 2/3 but no more than 4/5.

Pairwise invasibility plots for both demand (blue lines) and supply functions (green lines) are shown below, the first with s_{wt} and Δ*s* as variables, the second with s_{wt} and s_{mt} as variables. In each diagram, ESS values are to be found at the intersections of the lines. Between the two intersections lies the 'battleground'. When the wildtype level of *s* is within this battleground, genes affecting demand will tend to increase parental investment, whereas genes affecting supply will tend to decrease parental investment. This resembles the classic conflict between offspring and parents, since the former group of genes is expressed in an individual while it is offspring, whereas the latter is expressed in an individual while it is parent. In reality, an individual carries both types of genes, though, so the conflict actually is intragenomic in nature.

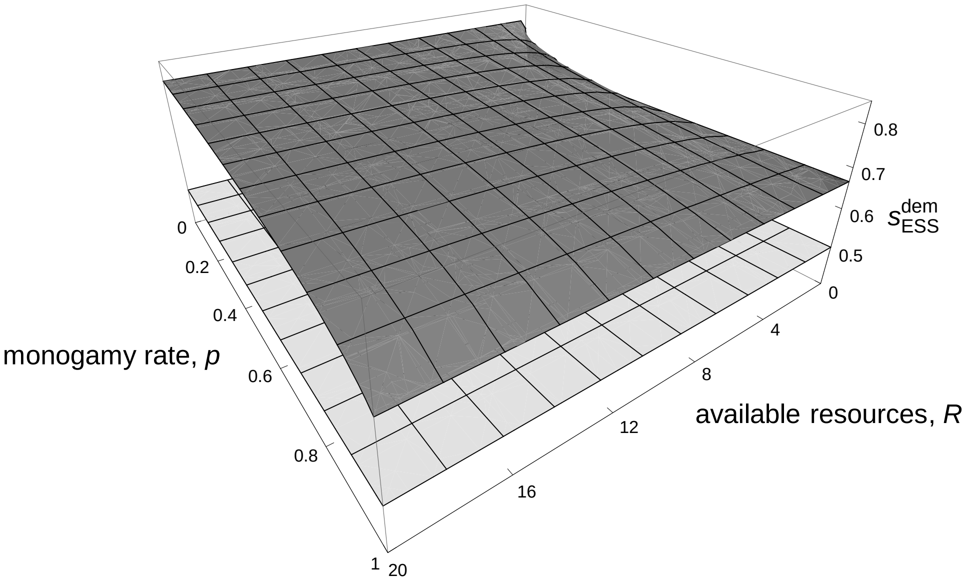
Without further resolution models, the evolutionary endpoint of the battle between demand and supply function genes cannot be determined.



Above: Fitness isoclines for supply (green lines) and for demand function genes (blue lines). Equilibrium values are at the intersections of the isoclines. Between the two equilibria lies the 'battleground of parent-offspring conflict'. (Note, however, that temporarily overshooting beyond the demand function optimum is possible.)



Above: Pairwise invasibility plot for supply (green dashed lines) and for demand function genes (blue solid lines). Equilibrium values are at the intersections of the isoclines. Between the two equilibria lies the 'battleground of parent-offspring conflict'.



Above: A comparison of the evolutionarily stable value of *s* as a function of *R* and *p*. Demand function genes: dark gray; supply function genes: light gray. Regardless of parameter values, optima for demand and supply function genes never overlap, meaning that there is always potential for conflict.

Results of previous studies

The most read book that treats parent-offspring conflict from a theoretical viewpoint is by Mock and Parker (The Evolution of Sibling Rivalry, 1997). On p. 144, the authors derive the equation for the evolution of interbrood parent-offspring conflict. Specifically, for them, a mutant that extracts more resources from the parents has a fitness advantage as long as:

$$f(m_w + \Delta) - f(m_w) > r \cdot \pi \cdot f(m_w + \Delta)$$

Here, f is the fitness of the offspring, m_w is the wildtype amount of resources taken by an offspring, Δ is the shift in taken resources caused by the mutation, r is the coefficient of relatedness, and π is the reduction in the probability to have a subsequent sibling in the future. Translated in the terms we use for our model, this equation changes into:

$$s_{\mathrm{mt}} - s_{\mathrm{wt}} > r \cdot (q_{\mathrm{wt}} - q_{\mathrm{mt}}) \cdot s_{\mathrm{mt}}$$

To see this, keep in mind that parental investment in our model affects offspring fitness only with regard to the survival probability, but this simplification should not alter the conclusions.

Having the conditions for the spread of the mutation, we know that in equilibrium, the inequation above has to become an equality :

$$s_{\mathrm{mt}} - s_{\mathrm{wt}} = r \cdot (q_{\mathrm{wt}} - q_{\mathrm{mt}}) \cdot s_{\mathrm{mt}}$$

Entering our variables, we arrive at:

$$\triangle s =$$

$$\frac{\triangle s\,(p+1)\,(\triangle s + s)}{4\,R\,(s-1)\,(\triangle s + s - 1)}$$

The coefficient of relatedness r is taken as 1/4 (the probability that the specific allele is also inherited by the subsequent sibling through the mother) plus p/4 (the probability that the specific allele is also inherited by the subsequent sibling through the father).

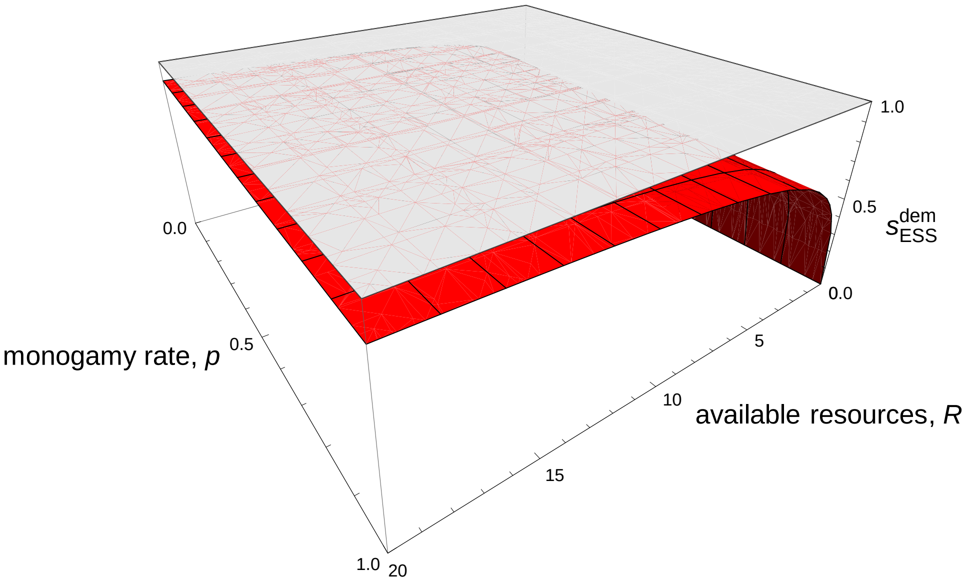
With the same logic as above, we can derive the evolutionarily stable value of s as a function of R and p:

$$s_{\mathrm{ESS}}^{\mathrm{M\&P}}\ (\text{evolutionarily stable value of } s \text{ for demand functions according to Mock\&Parker's calculation}) =$$

$$\frac{-\sqrt{p+1}\,\sqrt{p+16\,R+1}+p+8\,R+1}{8\,R}$$

or

$$\frac{\sqrt{p+1}\,\sqrt{p+16\,R+1}+p+8\,R+1}{8\,R}$$



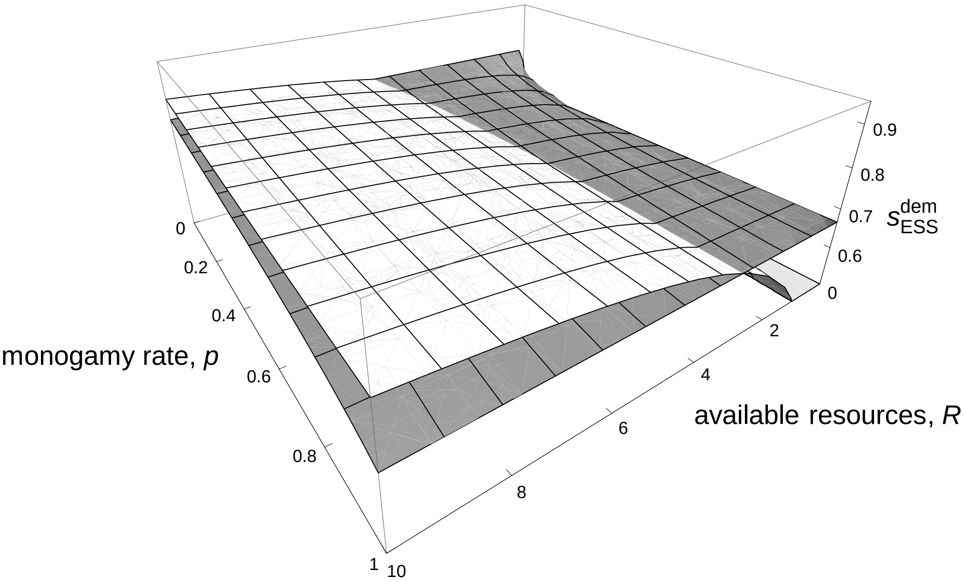
As the plot shows, the second of the offered solutions is out of boundaries (or a blue plane would have been visible), so the first solution is the correct one.

The evolutionarily stable value for demand function genes according to Mock and Parker's model is thus:

$$s_{\mathrm{ESS}}^{\mathrm{M\&P}} =$$

$$\frac{-\sqrt{p+1}\,\sqrt{p+16R+1}+p+8R+1}{8R}$$

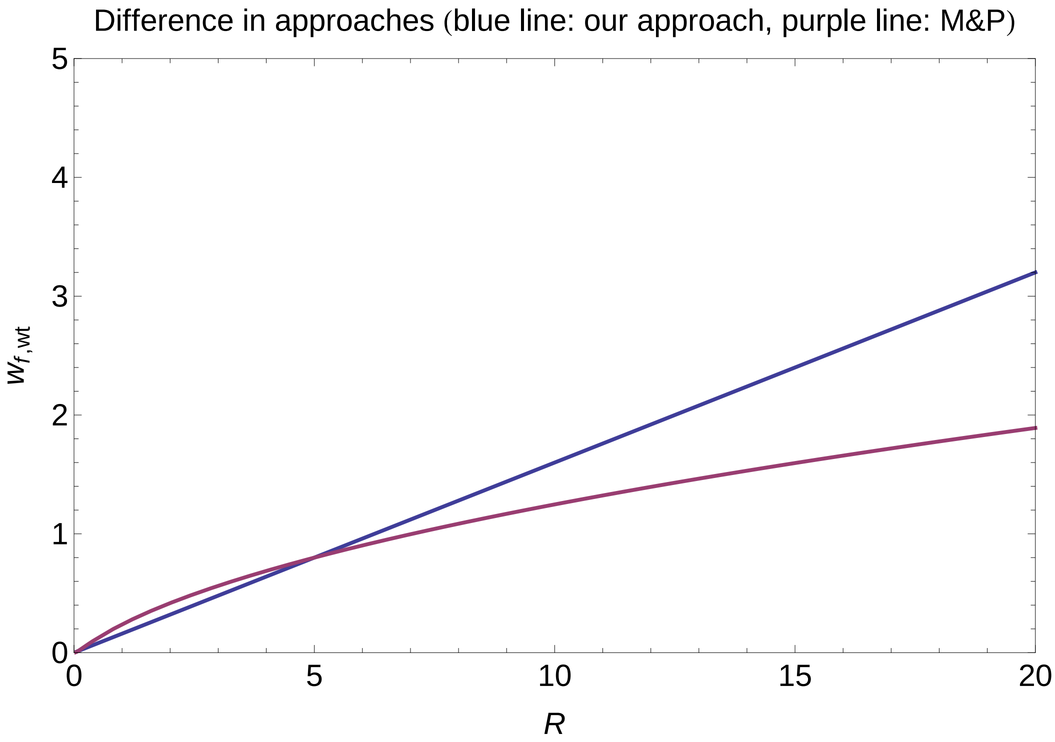
We can now plot the different predictions for the stable ESS offspring demand of our model and Mock and Parker’s model as a function of the monogamy rate *p* and the available resources *R*.



The gray surface displays our results, the white surface those derived from Mock and Parker (M&P). M&P’s model generally overestimates the equilibrium level of *s*, except for low *R*.This is because M&P’s model implicitly assume that only one future sibling is to be expected. When more future siblings are to be expected, the damage by selfishly demanding more resources is greater. Therefore, M&P’s mutants are "too greedy", demanding too much. When less future siblings are expected, the reverse is true. The number of expected future siblings depends on *R*, which reflects the results seen above.

Quantitative differences in the approaches

We found that our approach yielded a minimum for the evolutionarily stable value of offspring demand of 2/3; the maximum was at 4/5. In contrast, M&P’s model leads to a minimum of 0 (reached for *R*=0) and a maximum of 1 (reached for *p*=0). These results are less sensible than our results.



Above: Our model and M&P's model generate quantitatively different predictions.This is reflected for instance in the total fitness which our model (blue line) predicts to be higher than M&P's model (purple line) does. This difference is especially pronounced for high resource levels. The trend is only reversed for very low resource levels. Assumptions in this figure: The equilibrium in favour of demand function genes is reached, p=0.

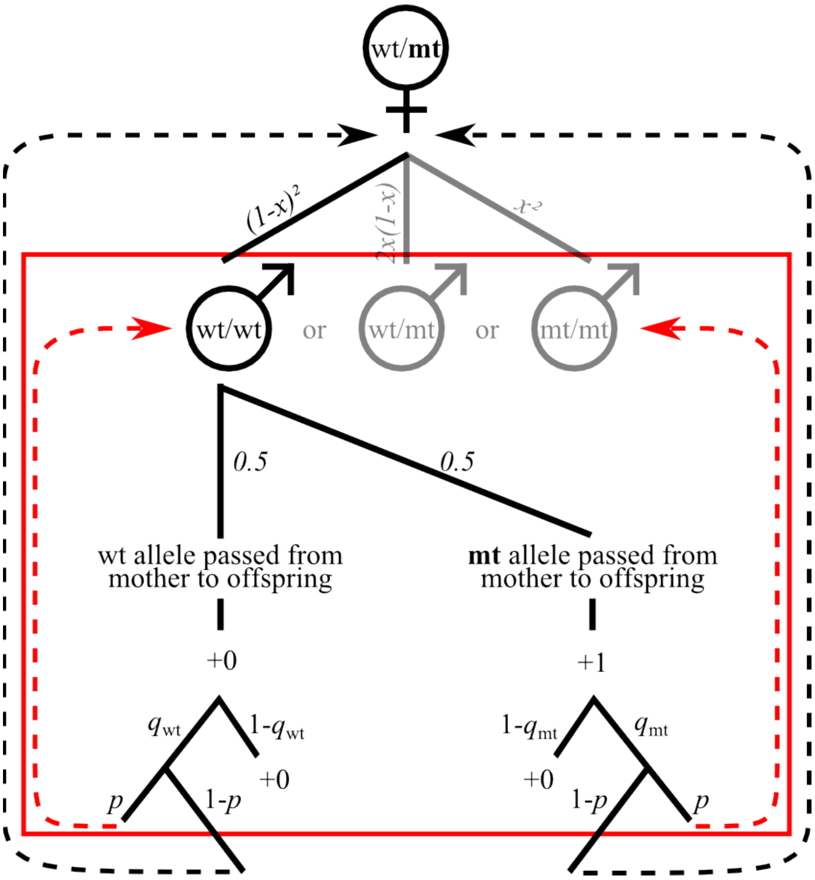
An important measure of the intensity of parent-offspring conflict is its potential impact on total fitness. The difference in the approaches can be substantial. For example, assume that POC is resolved completely in favor of demand function genes. Then, for R=8 and p=*0.5*, there is a difference in total fitness of ≈0.25 offspring, a 16.5% difference. For the more extreme case of R=16 and p=1, the difference grows to ≈1.39 offspring, a difference of 39.0%. To explore the quantitative differences between the approaches in more detail, have a look at Interactive Figure S4.

Accounting for more offspring

As we argue in the main text, the trouble with previous approaches to interbrood POC is that they implicitly assumed exactly one subsequent offspring to be produced. In this section, we show that if all potential future offspring are taken into account, an approach based on kin selection can actually yield the correct results.

Calculating the probability of a heterozygous female or male to produce exactly *n* mutant offspring

Let $P_f(\boldsymbol{n})$ be the **probability that a female produces exactly *n* mutant offspring**. The probability that an offspring inherits the wildtype allele from the mother is 0.5, as is the probability that it inherits the mutant allele.



$$P_f[0] =$$

$$\frac{q_{wt}-1}{q_{wt}-2}$$

$$P_f[1] =$$

$$-\frac{q_{mt}+q_{wt}-2}{(q_{wt}-2)^2}$$

$$P_f[n, n>1] =$$

$$-\frac{P_f[n-1]\, q_{mt}}{q_{wt}-2}$$

$$=$$

$$-\frac{(q_{mt}+q_{wt}-2)\left(\frac{q_{mt}}{2-q_{wt}}\right)^n}{(q_{wt}-2)^2}$$

With *o* being the number of future offspring that are taken into account in the equation, we have:

```
⌗ of mutant offsp., probability
```

$$\begin{pmatrix} 0 & \frac{q_{\text{wt}}-1}{q_{\text{wt}}-2} \\ 1 & \frac{-q_{\text{mt}}-q_{\text{wt}}+2}{(q_{\text{wt}}-2)^2} \\ 2 & -\frac{q_{\text{mt}}\,(-q_{\text{mt}}-q_{\text{wt}}+2)}{(q_{\text{wt}}-2)^3} \\ 3 & \frac{q_{\text{mt}}^2\,(-q_{\text{mt}}-q_{\text{wt}}+2)}{(q_{\text{wt}}-2)^4} \\ 4 & -\frac{q_{\text{mt}}^3\,(-q_{\text{mt}}-q_{\text{wt}}+2)}{(q_{\text{wt}}-2)^5} \\ 5 & \frac{q_{\text{mt}}^4\,(-q_{\text{mt}}-q_{\text{wt}}+2)}{(q_{\text{wt}}-2)^6} \end{pmatrix}$$

Here is a numerical example with six future offspring taken into account at most, including a test whether all probabilities add up to one, which they do.

```
Probabilities for 0 to 6 mutant offspring:
```

$$\left\{\frac{1}{3}, \frac{1}{3}, \frac{1}{6}, \frac{1}{12}, \frac{1}{24}, \frac{1}{48}, \frac{1}{96}\right\}$$

```
Sum of the probabilities for a high number of mutant offspring:

1.
```

Let P_m **(*n*)** be the **probability that a male produces exactly *n* mutant offspring with a specific female**. Then, the same reasoning is true as for females, except that one has to consider the additional possibility that a male changes mates from one period to the other, 1-*p*.

$\text{P}_{\text{m}}[0]$ =

$$\frac{p\, q_{\text{wt}} - 1}{p\, q_{\text{wt}} - 2}$$

$\text{P}_{\text{m}}[1]$ =

$$\frac{2 - p\,(q_{\text{mt}} + q_{\text{wt}})}{(p\, q_{\text{wt}} - 2)^2}$$

$\text{P}_{\text{m}}[n, n>1]$ =

$$\frac{p\, P_m[n-1]\, q_{\text{mt}}}{2 - p\, q_{\text{wt}}}$$

=

$$\frac{(2 - p\,(q_{\text{mt}} + q_{\text{wt}}))\left(\frac{p\, q_{\text{mt}}}{2 - p\, q_{\text{wt}}}\right)^n}{(p\, q_{\text{wt}} - 2)^2}$$

```
# of mutant offsp., probability
```

$$\left(\begin{array}{cc}
0 & \frac{p\,q_{\text{wt}}-1}{p\,q_{\text{wt}}-2} \\
1 & \frac{-p\,q_{\text{mt}}-p\,q_{\text{wt}}+2}{(p\,q_{\text{wt}}-2)^2} \\
2 & -\frac{p\,q_{\text{mt}}\,(-p\,q_{\text{mt}}-p\,q_{\text{wt}}+2)}{(p\,q_{\text{wt}}-2)^3} \\
3 & \frac{p^2\,q_{\text{mt}}^2\,(-p\,q_{\text{mt}}-p\,q_{\text{wt}}+2)}{(p\,q_{\text{wt}}-2)^4} \\
4 & -\frac{p^3\,q_{\text{mt}}^3\,(-p\,q_{\text{mt}}-p\,q_{\text{wt}}+2)}{(p\,q_{\text{wt}}-2)^5} \\
5 & \frac{p^4\,q_{\text{mt}}^4\,(-p\,q_{\text{mt}}-p\,q_{\text{wt}}+2)}{(p\,q_{\text{wt}}-2)^6}
\end{array}\right)$$

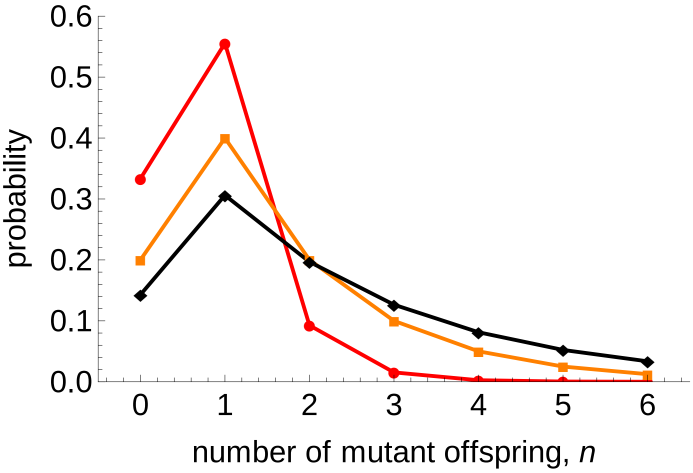
Numerical example with same parameters as in the one for females shown above and with the same test for consistency.

```
Probabilities for 0 to 6 mutant offspring:
```

$$\left\{\frac{3}{7}, \frac{22}{49}, \frac{33}{343}, \frac{99}{4802}, \frac{297}{67\,228}, \frac{891}{941\,192}, \frac{2673}{13\,176\,688}\right\}$$

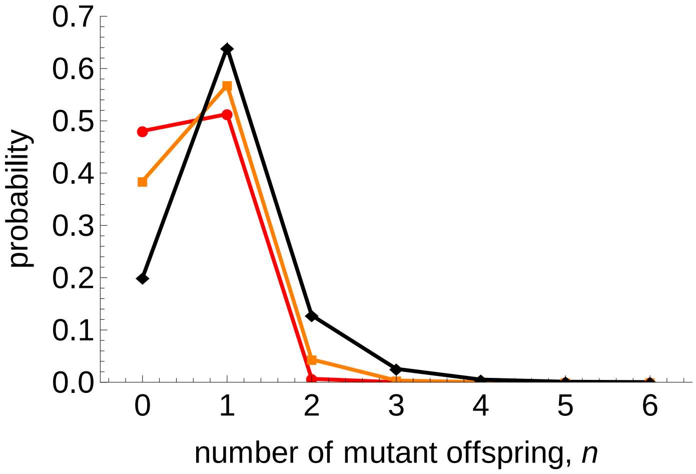
```
Sum of the probabilities for a high number of mutant offspring:

1.
```

We can plot the probabilities of a female to produce exactly *n* mutant offspring as a function of *n*, assuming the mutant to be rare:



Above: Plot of the probability of a female to produce exactly *n* mutant offspring as a function of *n* assuming the mutant to be rare, $s_{\text{wt}} = 1/2$, $s_{\text{mt}} = 2/3$, and for *R*=4 (red), *R*=8 (orange), and *R*=12 (black).

We can do produce a similar plot for the probability of a male to produce exactly *n* mutant offspring:



Above: Plot of the probability of a male to produce exactly *n* mutant offspring with a specific female as a function of *n* assuming the mutant to be rare, $s_{wt} = 1/2$, $s_{mt} = 2/3$, $R=8$, and for $p=1/10$ (red), $p=1/2$ (orange), and $p=1$ (black).

Knowing the probabilities of certain events to take place, we can calculate the approximated fitness function of wildtype alleles as a function the number of offspring taken into account.

`Approximated fitness for 3 considered mutant offspring:`

$$\left(R\,(s-1)\,(\Delta s+s)\left(-\left((p\,(R\,(s-1)+1)+R\,(-s)+R)\,(p\,(\Delta s\,(2\,R\,(s-1)+1)+2\,(s-1)\,(R\,(s-1)+1))-2\,R\,(s-1)\,(\Delta s+s-1))\left(p^2\left(\Delta s^2\left(2\,R^2\,(s-1)^2+1\right)+4\,\Delta s\,R\,(s-1)^2\,(R\,(s-1)+1)+2\,(s-1)^2\,(R\,(s-1)+1)^2\right)-4\,\Delta s\,p\,R\,(s-1)\,(\Delta s+s-1)+4\,R^2\,(s-1)^2\,(\right.\right.\right.$$
$$\left.\left.\left. 2\,s-2)\left(\Delta s^2\left(6\,R^2\,(s-1)^2-4\,R\,(s-1)+1\right)+12\,\Delta s\,R^2\,(s-1)^3+2\,(s-1)^2\left(3\,R^2\,(s-1)^2+2\,R\,(s-1)+1\right)\right)\right)\Big/(R\,(-s)+R+1)^4\right)\right)\Big/\left(2\,(\Delta s+s-1)^3\right)$$

Hamilton's rule simply states *r*·*b*>*c*. Crucially, in this formula, the **coefficient of relatedness *r*** only appears as a linear term. Using the approximation above, we can show that when more future siblings are taken into account, *r* enters the equation in a non-linear fashion (note that we substituted 4*r*-1 as an approximation for the monogamy rate *p*). The specific results depend on how many offspring are taken into account, in this case first one, then two, and finally three:

`1 offspring:`

$$w_{mt} =$$

$$\frac{3\left(5357-17\,488\,r+14\,448\,r^2\right)}{125\,(11-12\,r)^2}$$

`2 offspring:`

$$w_{mt} =$$

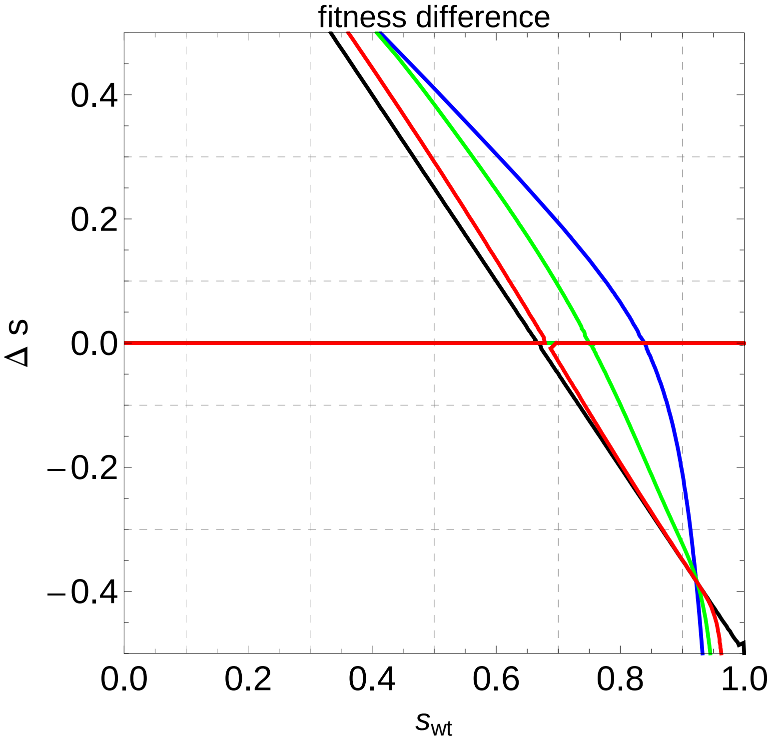
$$-\frac{3\left(390\,467-826\,892\,r-421\,936\,r^2+1\,216\,704\,r^3\right)}{1250\,(-11+12\,r)^3}$$

`3 offspring:`

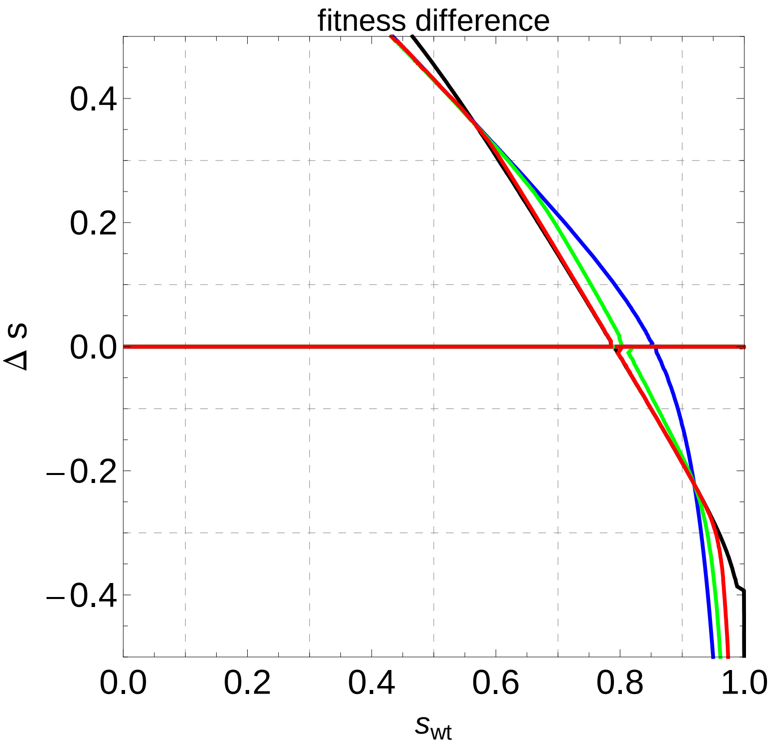
$$w_{mt} =$$

$$\left(3\left(239\,394\,991-1\,152\,927\,688\,r+2\,389\,418\,944\,r^2-2\,754\,959\,232\,r^3+1\,453\,614\,336\,r^4\right)\right)\Big/\left(50\,000\,(11-12\,r)^4\right)$$

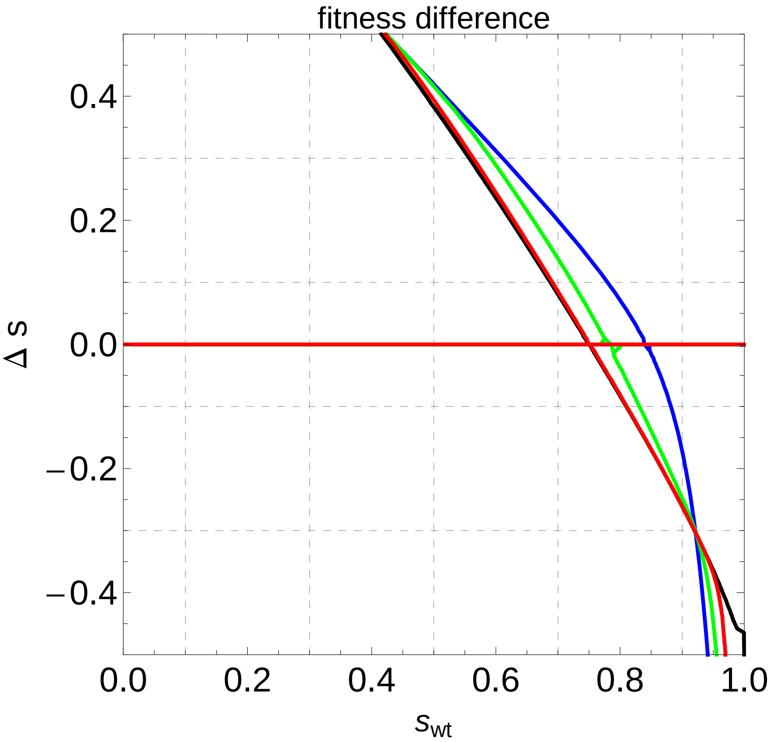
Now, we can plot the difference in the evolutionarily stable value of *s* as a function of the number of potential future offspring taken into account. As these plots show, the more offspring are taken into account, the closer the approximation is to the correct value. These differences depend on the value of the monogamy rate *p* and the amount of resource *R*. We plot them first for high, low, and intermediate monogamy as well as for different resource levels at intermediate monogamy.



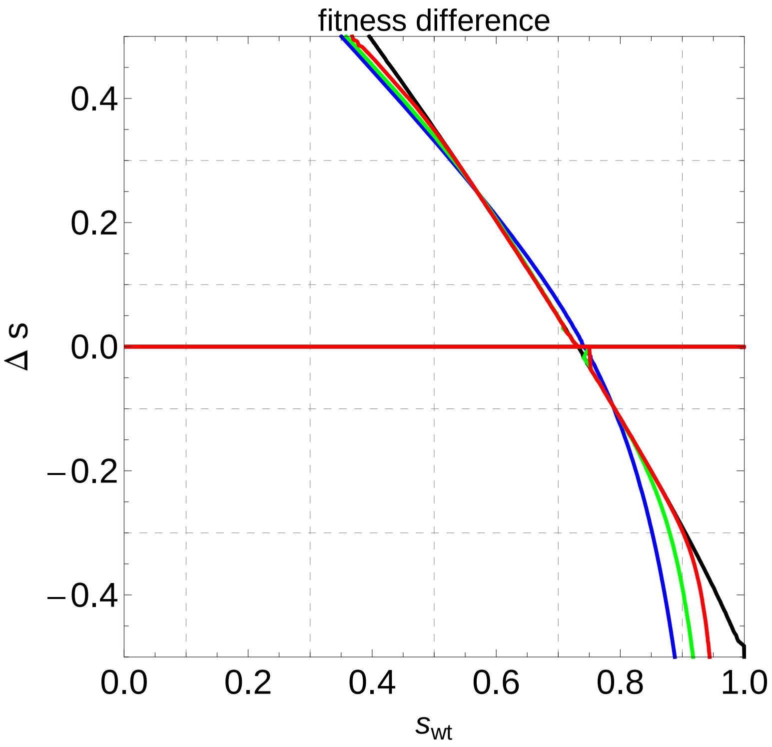
Above: Fitness isoclines for our calculated *s* (black line) and the approximations, with the blue line approximating for 2 future siblings, green for 4 future siblings, and red for 8 future siblings. Other parameters are *R*=8, *p*=1, and the mutation is assumed to be rare.



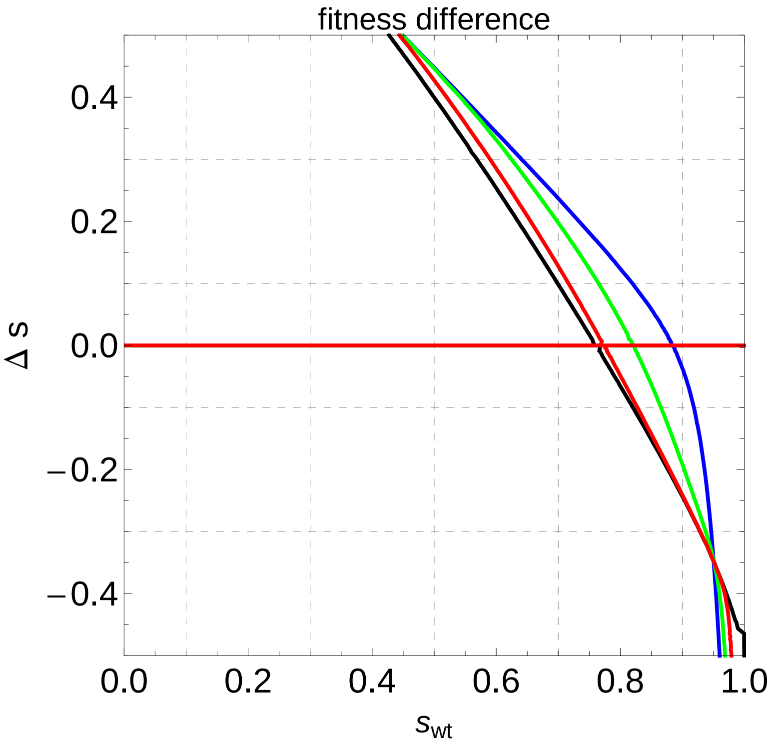
Above: Fitness isoclines for our calculated *s* (black line) and the approximations, with the blue line approximating for 2 future siblings, green for 4 future siblings, and red for 8 future siblings. Other parameters are *R*=8, *p*=0.1, the mutation is assumed to be rare.



Above: Fitness isoclines for our calculated *s* (black line) and the approximations, with the blue line approximating for 2 future siblings, green for 4 future siblings, and red for 8 future siblings. Other parameters are *R*=8, *p*=0.5, the mutation is assumed to be rare.



Above: Fitness isoclines for our calculated *s* (black line) and the approximations, with the blue line approximating for 2 future siblings, green for 4 future siblings, and red for 8 future siblings. Other parameters are *R*=4, *p*=0.5, the mutation is assumed to be rare.



Above: Fitness isoclines for our calculated *s* (black line) and the approximations, with the blue line approximating for 2 future siblings, green for 4 future siblings, and red for 8 future siblings. Other parameters are *R*=12, *p*=0.5, the mutation is assumed to be rare.

Proof that in the limit of considering infinitely many future offspring the approximation converges to the correct result

If we allow for a potentially infinite number of future offspring to be taken into account, the approximation should converge towards the correct result. To prove this, we have to reformulate the fitness equation to:

$$w_{\text{mt}} = 0.5\,(s + \Delta s)\,c_1 \sum_{i=1}^{\infty} \left(i \cdot c_2^{\,i-1}\right) + 0.5\,m(s + \Delta s)\,c_3 \sum_{i=1}^{\infty} \left(i \cdot c_4^{\,i-1}\right)$$

The fitness approximated for an infinite number of offspring is:

$$\frac{1}{2}\,(\triangle s + s)\left(\frac{c_1}{(c_2 - 1)^2} + \frac{c_3\, m}{(c_4 - 1)^2}\right)$$

with:

$$c_1 = -\frac{q_{\text{mt}} + q_{\text{wt}} - 2}{(q_{\text{wt}} - 2)^2}$$
$$c_2 = \frac{q_{\text{mt}}}{2 - q_{\text{wt}}}$$
$$c_3 = \frac{2 - p\,(q_{\text{mt}} + q_{\text{wt}})}{(p\,q_{\text{wt}} - 2)^2}$$
$$c_4 = \frac{p\,q_{\text{mt}}}{2 - p\,q_{\text{wt}}}$$

(remember that *m* is the number of expected mates per male and *p* is the monogamy rate).

Entering c_1, c_2, c_3, and c_4 into the fitness equation, we arrive at:

$w_{\text{mt,approx}} =$

$$-(R\,(s-1)\,(\triangle s + s - 1)\,(\triangle s + s)\,(p\,(\triangle s\,(3\,R\,(s-1)+2) + 4\,(s-1)\,(R\,(s-1)+1)) - R\,(s-1)\,(3\,\triangle s + 4\,s - 4)))\,/\,(2\,(\triangle s + 2\,s - 2)\,(p\,(\triangle s\,(2\,R\,(s-1)+1) + 2\,(s-1)\,(R\,(s-1)+1)) - 2\,R\,(s-1)\,(\triangle s + s - 1)))$$

Again, we assumed the mutant to be rare.

The fitness difference between a mutant and a wildtype allele is then:

$\triangle w_{\text{approx}} =$

$$-\left(\triangle s\,R\,(s-1)\,\left(p\,\left(\triangle s^2\,(3\,R\,(s-1)+2) + \triangle s\,\left(R\,\left(8\,s^2 - 15\,s + 7\right) + 7\,s - 6\right) + (s-1)\,\left(R\,\left(5\,s^2 - 9\,s + 4\right) + 6\,s - 4\right)\right) - R\,(s-1)\,\left(3\,\triangle s^2 + \triangle s\,(8\,s - 7) + 5\,s^2 - 9\,s + 4\right)\right)\right) \Big/ (2\,(\triangle s + 2\,s - 2)\,(p\,(\triangle s\,(2\,R\,(s-1)+1) + 2\,(s-1)\,(R\,(s-1)+1)) - 2\,R\,(s-1)\,(\triangle s + s - 1)))$$

If the approximation is equal to the real results, the difference should be zero, which it indeed is, as can be shown both analytically and graphically.

This function is not identical to the difference in fitness as calculated in our direct fitness approach, as it was derived under different assumptions (we assumed from the beginning on that the mutant is rare). However, when solving our initial function, we used the same assumptions; therefore, the solutions should still be the same. Indeed, when we solve the two fitness difference functions for the equilibrium, using the mentioned assumption, the results are exactly equal. This shows that at the end of the day, our second, indirect approach is capable of providing identical results.

Difference in the three solutions between the direct and indirect fitness approach, using the same assumptions;

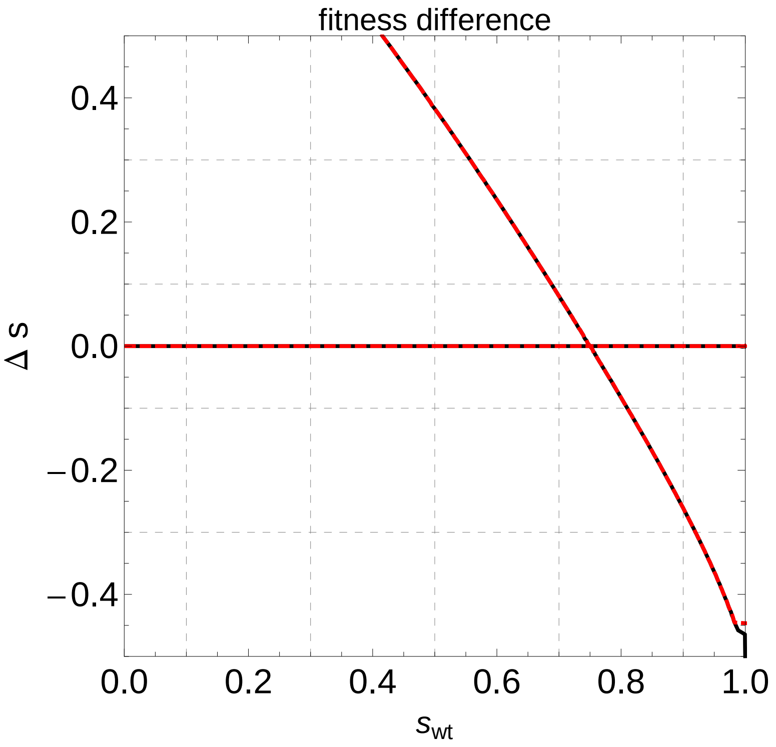
first solution:

```
0
```

second solution:

```
0

third solution:

0
```

This result can also be shown graphically:



Above: The results from our calculation (solid black lines) and the results from the approximation if infinitely many future offspring are considered (red dashed lines) completely overlap. In this example, *R*=8 and *p*=0.5.