# Brandvain and Coop. Sperm dependent female meiotic drive

### Model 1. Female drive depends on sperm haplotype (single pleitropic locus)

The B allele is transmited with probability, d, in heterozygous females when fertilized by B-bearing sperm.
x represents the deviation from Hardy - Weinberg Equilibrium

# Setup

In[512]:=
```
(*Allele and Genotype frequencies*)
ClearAll["Global`*"]
fA = 1 - fB;
fAA  =  fA^2 + fA fB x;
fAB  =  2 fA fB (1 - x);
fBB =  fB^2 + fA fB x;
```

## Drive

In[338]:=
```
(*Genotype frequencies after drive*)
fAA_Drive = FullSimplify[fA (fAA + fAB / 2)];
fAB_Drive  = FullSimplify[fB (fAA + fAB * (1 - d)) + fA (fAB / 2 + fBB)];
fBB_Drive  = FullSimplify[fB (fAB d + fBB )];
```

## Selection

In[341]:=
```
wAA = 1; wAB = 1 - hs; wBB = 1 - s; (*genotypic fitnesses*)
W̄ = FullSimplify[fAA_Drive wAA + fAB_Drive wAB + fBB_Drive wBB]; (*mean fitness*)
fAA_Sel = FullSimplify[(fAA_Drive * wAA) / W̄];
fAB_Sel = FullSimplify[(fAB_Drive * wAB) / W̄];
fBB_Sel = FullSimplify[(fBB_Drive wBB) / W̄];
fA_Sel = FullSimplify[fAA_Sel + fAB_Sel / 2];
fB_Sel = FullSimplify[fBB_Sel + fAB_Sel / 2];
ΔfA = FullSimplify[fA_Sel - fA];
ΔfB = FullSimplify[fB_Sel - fB];
```

# Analysis

Note, we assume no deviation from Hardy-Weinberg [i.e. x=0] for all analytical results, and therefore these answers are approximations. In the supplamentary material we show thats results of exact recursions are remarkably consistant from these approximate analystical solutions.

# Assuming the cost of drive is fully recessive [i.e. hs is zero]

## Invasion

In[350]:=
```
ΔfBinvade = (FullSimplify[ΔfB /. hs → 0 /. x → 0] / fB^2 /. fB → 0)
```

Out[350]=
$$\frac{1}{2}(-1 + d(2 - 4 s))$$

In[351]:=
```
spermDepReceesiveInvade = Solve[ΔfBinvade == 0, s]
```

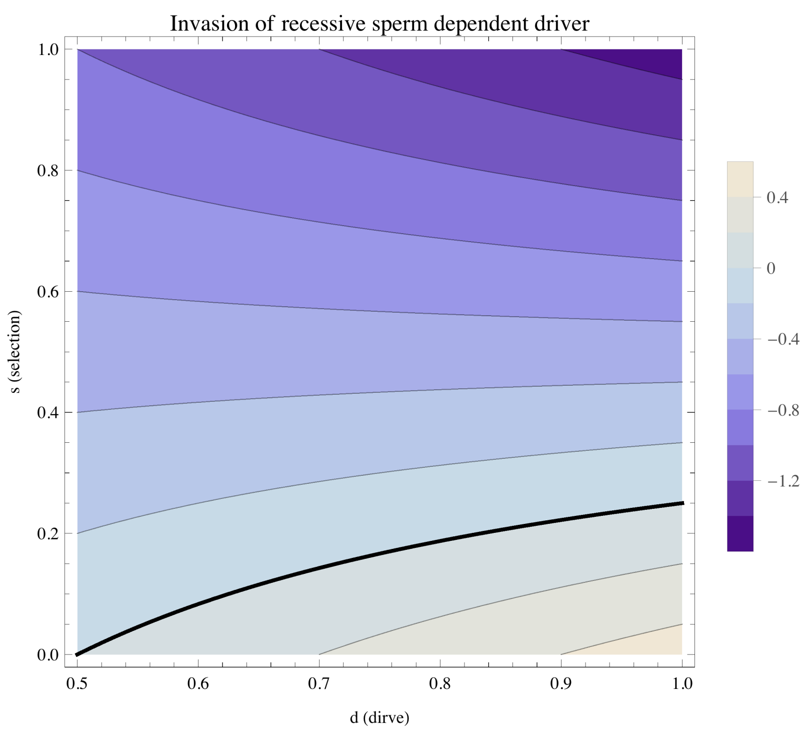
Out[351]=
$$\left\{\left\{s \to \frac{-1 + 2 d}{4 d}\right\}\right\}$$

In[352]:=
```
plotInvasion4spermDepRecessive =
  Plot[s /. spermDepReceesiveInvade [[1]], {d, .5, 1}, PlotStyle → {Black, Thick}];
```

In[353]:=
```
plotRelChange4RarespermDepRecessive = ContourPlot[{ΔfBinvade}, {d, 0.5, 1}, {s, 0, 1},
   PlotLegends → Automatic, FrameLabel → {"d (dirve)", "s (selection)"},
   PlotLabel → "Invasion of recessive sperm dependent driver"];
```

In[354]:=
```
Show[plotRelChange4RarespermDepRecessive, plotInvasion4spermDepRecessive]
```

Out[354]=




## Fixation

In[355]:=
```
ΔfBfix = FullSimplify[FullSimplify[ΔfB /. hs → 0 /. x → 0] / fA] /. fB → 1
```

Out[355]=
$$\frac{-1 + 2 d - 2 s}{2 - 2 s}$$

In[356]:=
```
spermDepReceesiveFix = Solve[ΔfBfix == 0, s]
```

Out[356]= $\left\{\left\{s \to \frac{1}{2}(-1+2\,d)\right\}\right\}$

In[357]:=
```
(s /. spermDepReceesiveFix [[1]])
```

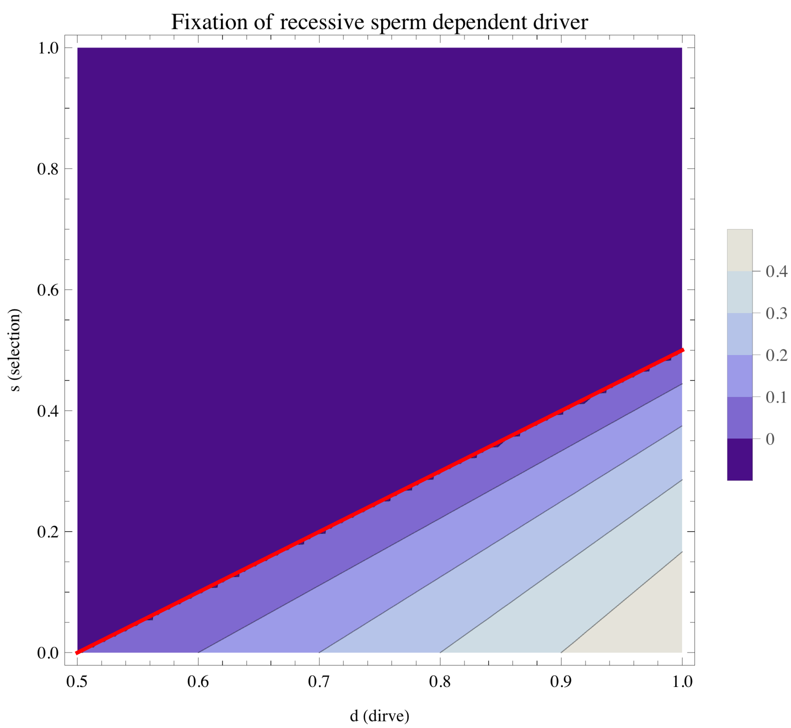
Out[357]= $\frac{1}{2}(-1+2\,d)$

In[358]:=
```
plotFixation4spermDepRecessive =
  Plot[s /. spermDepReceesiveFix [[1]], {d, .5, 1}, PlotStyle → {Red, Thick}];
```

In[359]:=
```
(*Note we artificially rescaled z to be -.1 for all negative values*)
plotRelChange4CommonSpermDepRecessive =
  ContourPlot[If[s > (s /. spermDepReceesiveFix [[1]]), -.1, ΔfBfix], {d, 0.5, 1},
   {s, 0, 1}, PlotLegends → Automatic, FrameLabel → {"d (dirve)", "s (selection)"},
   PlotLabel → "Fixation of recessive sperm dependent driver"];
```

In[360]:=
```
Show[plotRelChange4CommonSpermDepRecessive, plotFixation4spermDepRecessive]
```

Out[360]=




## Bistability Point

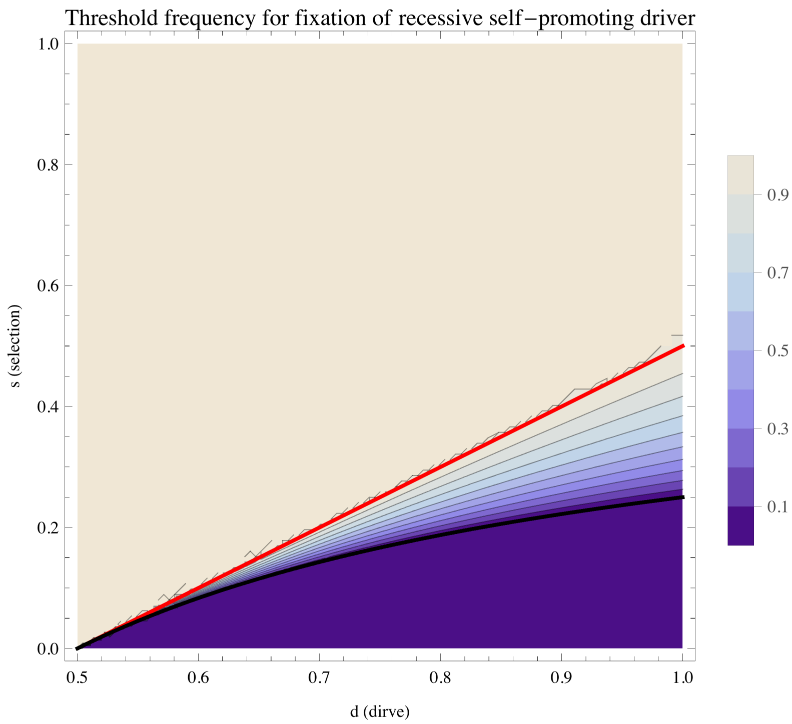
In[361]:=
```
FBbistabSpermDepReceesive = Solve[FullSimplify[ΔfB /. hs → 0 /. x → 0] == 0, fB][[4]]
```

Out[361]= $\left\{fB \to \frac{1-2\,d+4\,d\,s}{-2\,s+4\,d\,s}\right\}$

In[367]:=
```
bistab = ContourPlot[(If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabSpermDepReceesive,
    {d, .5, 1}, {s, 0, 1}, PlotLegends → Automatic,
    FrameLabel → {"d (dirve)", "s (selection)"}, PlotLabel →
     "Threshold frequency for fixation of recessive self-promoting driver"];
```

In[368]:=
```
Show[bistab, plotFixation4spermDepRecessive, plotInvasion4spermDepRecessive]
```

Out[368]=




# Assuming the cost of drive is not fully recessive [i.e. hs is nonzero]

## Invasion

Note with any heterozgous cost (i.e. hs > 0) a self - promoting driver cannot invade

In[369]:=
```
FullSimplify[FullSimplify[ΔfB /. x → 0] / fB] /. fB → 0
```

Out[369]= $-hs$

## Fixation

In[370]:=
```
ΔfBfix = FullSimplify[FullSimplify[FullSimplify[ΔfB /. x → 0] / fA] /. fB → 1]
```

Out[370]= $$\frac{1 + 2\,d\,(-1 + hs) - 3\,hs + 2\,s}{2\,(-1 + s)}$$

In[371]:=
```
spermDepNotReceesiveFix = Solve[ΔfBfix == 0, s]
```

Out[371]= $$\left\{\left\{s \to \frac{1}{2}\,(-1 + 2\,d + 3\,hs - 2\,d\,hs)\right\}\right\}$$

In[372]:=
```
spermDepAddFix = Solve[ΔfBfix == 0 /. hs → s / 2, s]
```

Out[372]= $$\left\{\left\{s \to \frac{2\,(-1 + 2\,d)}{1 + 2\,d}\right\}\right\}$$

```
In[373]:= plotspermDepAddFix =
  Plot[s /. spermDepAddReceesiveFix , {d, .5, 1}, PlotStyle → {Red, Thick}];
```

## Bistability Point

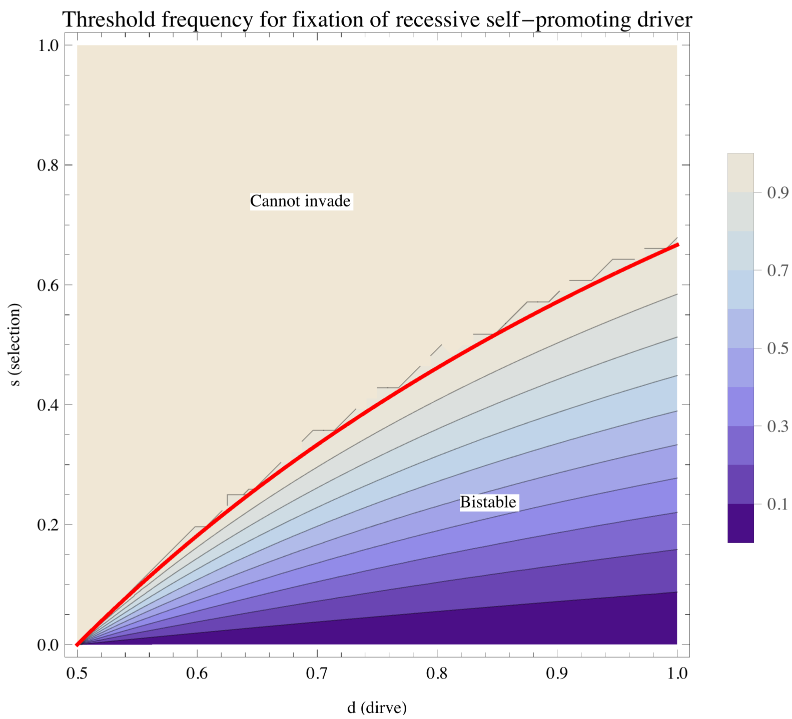
```
In[374]:= FBbistabSpermDepNotReceesive = Solve[FullSimplify[ΔfB /. x → 0] == 0, fB][[3]]
```

Out[374]=
$$\left\{fB \to \left(-1 + 2\,d + 3\,hs + 2\,d\,hs - 4\,d\,s - \sqrt{-8\,hs\,(-2\,hs + 4\,d\,hs + 2\,s - 4\,d\,s) + (1 - 2\,d - 3\,hs - 2\,d\,hs + 4\,d\,s)^2}\right) \Big/ (2\,(-2\,hs + 4\,d\,hs + 2\,s - 4\,d\,s))\right\}$$

An Example of a non - recessive driver [Assuming additivity]

```
In[375]:= bistab = ContourPlot[
   (If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabSpermDepNotReceesive /. hs → (s / 2),
   {d, .5, 1}, {s, 0, 1}, PlotLegends → Automatic,
   FrameLabel → {"d (dirve)", "s (selection)"}, PlotLabel →
    "Threshold frequency for fixation of recessive self-promoting driver"];

In[376]:= Show[bistab, plotspermDepAddFix]
```



### Model 2. Female drive depends on male genotype (single pleitropic locus)

The B allele is transmited with probability, d and dh, in heterozygous females when fertilized BB and AB males, respectively.
x represents the deviation from Hardy - Weinberg Equilibrium

# Setup

In[517]:=
```
(*Allele and Genotype frequencies*)
ClearAll["Global`*"]
fA = 1 - fB;
fAA = fA^2 + fA fB x;
fAB = 2 fA fB (1 - x);
fBB = fB^2 + fA fB x;
```

## Drive

In[377]:=
```
(*Genotype frequencies after drive*)
fAA_Drive = FullSimplify[fAA (fAA + fAB / 2) + fAB (fAA / 2 + fAB (1 - dh) / 2)];
fAB_Drive = FullSimplify[
   fAA (fAB / 2 + fBB) + fAB (fAA / 2 + fAB / 2 + fBB (1 - d)) + fBB (fAA + fAB / 2)];
fBB_Drive = FullSimplify[fAB (fAB dh / 2 + fBB d) + fBB (fAB / 2 + fBB)];
```

## Selection

In[380]:=
```
wAA = 1; wAB = 1 - hs; wBB = 1 - s; (*genotypic fitnesses*)
W̄ = FullSimplify[fAA_Drive wAA + fAB_Drive wAB + fBB_Drive wBB]; (*mean fitness*)
fAA_Sel = FullSimplify[(fAA_Drive * wAA) / W̄];
fAB_Sel = FullSimplify[(fAB_Drive * wAB) / W̄];
fBB_Sel = FullSimplify[(fBB_Drive wBB) / W̄];
fA_Sel = FullSimplify[fAA_Sel + fAB_Sel / 2];
fB_Sel = FullSimplify[fBB_Sel + fAB_Sel / 2];
ΔfA = FullSimplify[fA_Sel - fA];
ΔfB = FullSimplify[fB_Sel - fB];
```

# Analysis

## Analytical example - recessive fitness cost

### Invasion

In[450]:=
```
invasion4maleDepRecessive =
 Solve[((FullSimplify[(ΔfB /. x → 0 /. hs → 0)] / fB^2) /. fB → 0) == 0, s]
```

Out[450]= $\left\{\left\{s \to \frac{-1+2\,dh}{2\,dh}\right\}\right\}$

In[500]:=
```
plotiInvasion4maleDepRecessive = Plot[s /. invasion4maleDepRecessive /. dh -> d,
   {d, .5, 1}, PlotStyle -> {Black, Thick}];
```

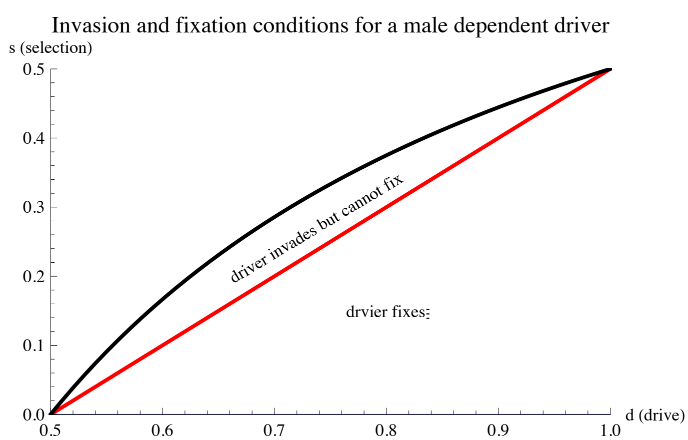
### Fixation

In[451]:=
```
fixation4maleDepRecessive =
 Solve[(FullSimplify[(FullSimplify[(ΔfB /. x → 0 /. hs → 0) / fA] /. fB → 1)]) == 0, s]
```

Out[451]= $\left\{\left\{s \to \frac{1}{2}\,(-1+2\,d)\right\}\right\}$

In[502]:=
```
plotFixation4maleDepRecessive = Plot[s /. fixation4maleDepRecessive /. dh -> d,
   {d, .5, 1}, PlotStyle -> {Red, Thick}];
```

In[511]:=
```
Show[Plot[0, {d, 0.5, 1},
  AxesLabel → {"d (drive)", "s (selection)"}, PlotRange → {{.5, 1}, {0, .5}},
  PlotLabel → "Invasion and fixation conditions for a male dependent driver"],
 plotFixation4maleDepRecessive, plotiInvasion4maleDepRecessive]
```



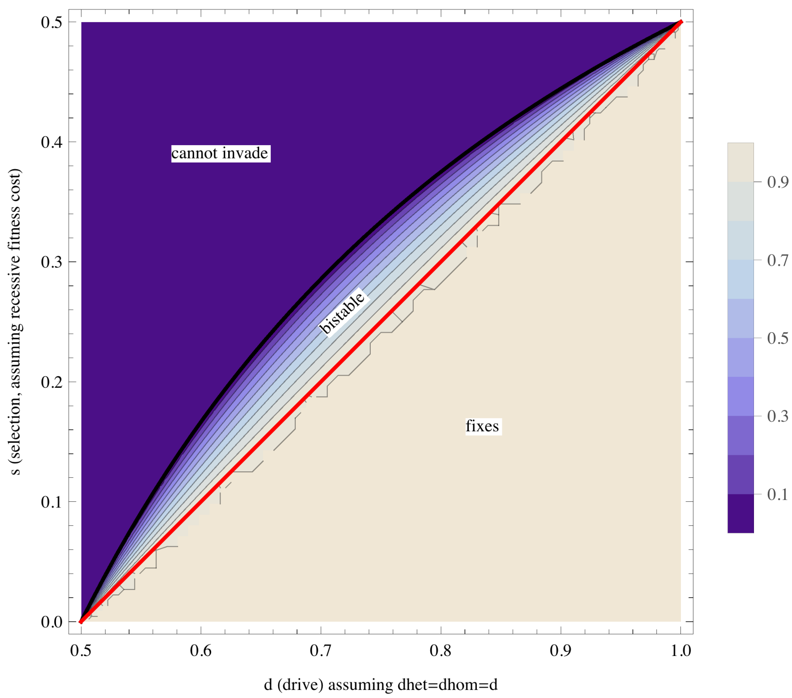

### Bistability

In[463]:=
```
FBbistabMaleepReceesive =
 Solve[FullSimplify[ΔfB /. x → 0 /. hs → 0 /. dh → d] == 0, fB][[4]]
```

Out[463]= $\left\{fB \to \frac{2\,(1-2\,d+2\,d\,s)}{(-1+2\,d)\,(-1+2\,s)}\right\}$

```
In[506]:= bistab = ContourPlot[ (If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabMaleepReceesive,
    {d, 0.5, 1}, {s, 0, .5}, PlotLegends → Automatic,
    FrameLabel → {"d (drive) assuming dhet=dhom=d",
      "s (selection, assuming recessive fitness cost)"}];

In[507]:= Show[bistab, plotiInvasion4maleDepRecessive, plotFixation4maleDepRecessive]
```




## Model 3. Female drive depends on sperm haplotype (two tightly linked loci)

We have one locus with two alleles, A (non-driving) and B (traditional driver), as well as a tightly linked locus where one allele  modifies drive. Assuming no recombination this functions as a third allele, C. We assume that

# Setup

In[1503]:=
```
ClearAll["Global`*"]
fA =.
fAA =.
fAB =.
fAC =.
fBB =.
fBC =.
fCC =.
minormod = {d1 → d0 + ϵ};
SUMTOONE = { fA -> 1 - (fB + fC) };
HWE =
  {fAA -> fA^2, fAB → 2 fA fB, fAC → 2 fA fC, fBB → fB^2, fBC → 2 fB fC, fCC → fC^2};
GENOFREQS = {fA → fAA + fAB / 2 + fAC / 2,
   fB → fBB + fAB / 2 + fBC / 2, fC → fCC + fBC / 2 + fBC / 2};
```

## Drive

```
(*Here we caculate all genotypes after drive. For book-
 keeping purposes we distinguish between reciprocal homozygotes,
but remove this distinction belowsum them below*)
```

In[1515]:=
```
AAn =
  FullSimplify[fAA * fAA * 1 + fAA * fAB * 1 / 2 + fAA * fAC * 1 / 2 + fAA * fBB * 0 + fAA * fBC * 0 +
    fAA * fCC * 0 + fAB * fAA * (1 - d0) + fAB * fAB * (1 - d0) / 2 + fAB * fAC * (1 - d0) / 2 +
    fAB * fBB * 0 + fAB * fBC * 0 + fAB * fCC * 0 + fAC * fAA * (1 - d0) + fAC * fAB * (1 - d0) / 2 +
    fAC * fAC * (1 - d0) / 2 + fAC * fBB * 0 + fAC * fBC * 0 + fAC * fCC * 0 + fBB * fAA * 0 +
    fBB * fAB * 0 + fBB * fAC * 0 + fBB * fBB * 0 + fBB * fBC * 0 + fBB * fCC * 0 + fBC * fAA * 0 +
    fBC * fAB * 0 + fBC * fAC * 0 + fBC * fBB * 0 + fBC * fBC * 0 + fBC * fCC * 0 + fCC * fAA * 0 +
    fCC * fAB * 0 + fCC * fAC * 0 + fCC * fBB * 0 + fCC * fBC * 0 + fCC * fCC * 0 + 0];
ABn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 1 / 2 + fAA * fAC * 0 + fAA * fBB * 1 +
    fAA * fBC * 1 / 2 + fAA * fCC * 0 + fAB * fAA * 0 + fAB * fAB * (1 - d0) / 2 +
    fAB * fAC * 0 + fAB * fBB * (1 - d0) + fAB * fBC * (1 - d0) / 2 + fAB * fCC * 0 +
    fAC * fAA * 0 + fAC * fAB * (1 - d0) / 2 + fAC * fAC * 0 + fAC * fBB * (1 - d0) +
    fAC * fBC * (1 - d0) / 2 + fAC * fCC * 0 + fBB * fAA * 0 + fBB * fAB * 0 + fBB * fAC * 0 +
    fBB * fBB * 0 + fBB * fBC * 0 + fBB * fCC * 0 + fBC * fAA * 0 + fBC * fAB * 0 +
    fBC * fAC * 0 + fBC * fBB * 0 + fBC * fBC * 0 + fBC * fCC * 0 + fCC * fAA * 0 +
    fCC * fAB * 0 + fCC * fAC * 0 + fCC * fBB * 0 + fCC * fBC * 0 + fCC * fCC * 0 + 0];
ACn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * fAC * 1 / 2 + fAA * fBB * 0 +
    fAA * fBC * 1 / 2 + fAA * fCC * 1 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * fAC * (1 - d1) / 2 +
    fAB * fBB * 0 + fAB * fBC * (1 - d1) / 2 + fAB * fCC * (1 - d1) + fAC * fAA * 0 + fAC * fAB * 0 +
    fAC * fAC * (1 - d1) / 2 + fAC * fBB * 0 + fAC * fBC * (1 - d1) / 2 + fAC * fCC * (1 - d1) +
    fBB * fAA * 0 + fBB * fAB * 0 + fBB * fAC * 0 + fBB * fBB * 0 + fBB * fBC * 0 + fBB * fCC * 0 +
    fBC * fAA * 0 + fBC * fAB * 0 + fBC * fAC * 0 + fBC * fBB * 0 + fBC * fBC * 0 + fBC * fCC * 0 +
    fCC * fAA * 0 + fCC * fAB * 0 + fCC * fAC * 0 + fCC * fBB * 0 + fCC * fBC * 0 + fCC * fCC * 0 + 0];
BAn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * fAC * 0 + fAA * fBB * 0 + fAA * fBC * 0 +
    fAA * fCC * 0 + fAB * fAA * d0 + fAB * fAB * d0 / 2 + fAB * fAC * d0 / 2 + fAB * fBB * 0 +
    fAB * fBC * 0 + fAB * fCC * 0 + fAC * fAA * 0 + fAC * fAB * 0 + fAC * fAC * 0 + fAC * fBB * 0 +
    fAC * fBC * 0 + fAC * fCC * 0 + fBB * fAA * 1 + fBB * fAB * 1 / 2 + fBB * fAC * 1 / 2 +
    fBB * fBB * 0 + fBB * fBC * 0 + fBB * fCC * 0 + fBC * fAA * 1 / 2 + fBC * fAB * 1 / 4 +
    fBC * fAC * 1 / 4 + fBC * fBB * 0 + fBC * fBC * 0 + fBC * fCC * 0 + fCC * fAA * 0 +
```

```
    fCC * fAB * 0 + fCC * fAC * 0 + fCC * fBB * 0 + fCC * fBC * 0 + fCC * fCC * 0 + 0];
BBn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * fAC * 0 + fAA * fBB * 0 + fAA * fBC * 0 +
    fAA * fCC * 0 + fAB * fAA * 0 + fAB * fAB * d0 / 2 + fAB * fAC * 0 + fAB * fBB * d0 +
    fAB * fBC * d0 / 2 + fAB * fCC * 0 + fAC * fAA * 0 + fAC * fAB * 0 + fAC * fAC * 0 +
    fAC * fBB * 0 + fAC * fBC * 0 + fAC * fCC * 0 + fBB * fAA * 0 + fBB * fAB * 1 / 2 + fBB * fAC * 0 +
    fBB * fBB * 1 + fBB * fBC * 1 / 2 + fBB * fCC * 0 + fBC * fAA * 0 + fBC * fAB * 1 / 4 +
    fBC * fAC * 0 + fBC * fBB * 1 / 2 + fBC * fBC * 1 / 4 + fBC * fCC * 0 + fCC * fAA * 0 +
    fCC * fAB * 0 + fCC * fAC * 0 + fCC * fBB * 0 + fCC * fBC * 0 + fCC * fCC * 0 + 0];
BCn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * fAC * 0 + fAA * fBB * 0 +
    fAA * fBC * 0 + fAA * fCC * 0 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * fAC * (d1) / 2 +
    fAB * fBB * 0 + fAB * fBC * (d1) / 2 + fAB * fCC * d1 + fAC * fAA * 0 + fAC * fAB * 0 +
    fAC * fAC * 0 + fAC * fBB * 0 + fAC * fBC * 0 + fAC * fCC * 0 + fBB * fAA * 0 + fBB * fAB * 0 +
    fBB * fAC * 1 / 2 + fBB * fBB * 0 + fBB * fBC * 1 / 2 + fBB * fCC * 1 + fBC * fAA * 0 +
    fBC * fAB * 0 + fBC * fAC * 1 / 4 + fBC * fBB * 0 + fBC * fBC * 1 / 4 + fBC * fCC * 1 / 2 +
    fCC * fAA * 0 + fCC * fAB * 0 + fCC * fAC * 0 + fCC * fBB * 0 + fCC * fBC * 0 + fCC * fCC * 0 + 0];
CAn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * fAC * 0 + fAA * fBB * 0 +
    fAA * fBC * 0 + fAA * fCC * 0 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * fAC * 0 + fAB * fBB * 0 +
    fAB * fBC * 0 + fAB * fCC * 0 + fAC * fAA * d0 + fAC * fAB * d0 / 2 + fAC * fAC * d0 / 2 +
    fAC * fBB * 0 + fAC * fBC * 0 + fAC * fCC * 0 + fBB * fAA * 0 + fBB * fAB * 0 + fBB * fAC * 0 +
    fBB * fBB * 0 + fBB * fBC * 0 + fBB * fCC * 0 + fBC * fAA * 1 / 2 + fBC * fAB * 1 / 4 +
    fBC * fAC * 1 / 4 + fBC * fBB * 0 + fBC * fBC * 0 + fBC * fCC * 0 + fCC * fAA * 1 +
    fCC * fAB * 1 / 2 + fCC * fAC * 1 / 2 + fCC * fBB * 0 + fCC * fBC * 0 + fCC * fCC * 0 + 0];
CBn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * fAC * 0 + fAA * fBB * 0 + fAA * fBC * 0 +
    fAA * fCC * 0 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * fAC * 0 + fAB * fBB * 0 + fAB * fBC * 0 +
    fAB * fCC * 0 + fAC * fAA * 0 + fAC * fAB * d0 / 2 + fAC * fAC * 0 + fAC * fBB * d0 +
    fAC * fBC * d0 / 2 + fAC * fCC * 0 + fBB * fAA * 0 + fBB * fAB * 0 + fBB * fAC * 0 +
    fBB * fBB * 0 + fBB * fBC * 0 + fBB * fCC * 0 + fBC * fAA * 0 + fBC * fAB * 1 / 4 +
    fBC * fAC * 0 + fBC * fBB * 1 / 2 + fBC * fBC * 1 / 4 + fBC * fCC * 0 + fCC * fAA * 0 +
    fCC * fAB * 1 / 2 + fCC * fAC * 0 + fCC * fBB * 1 + fCC * fBC * 1 / 2 + fCC * fCC * 0 + 0];
CCn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * fAC * 0 + fAA * fBB * 0 +
    fAA * fBC * 0 + fAA * fCC * 0 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * fAC * 0 + fAB * fBB * 0 +
    fAB * fBC * 0 + fAB * fCC * 0 + fAC * fAA * 0 + fAC * fAB * 0 + fAC * fAC * d1 / 2 +
    fAC * fBB * 0 + fAC * fBC * d1 / 2 + fAC * fCC * d1 + fBB * fAA * 0 + fBB * fAB * 0 +
    fBB * fAC * 0 + fBB * fBB * 0 + fBB * fBC * 0 + fBB * fCC * 0 + fBC * fAA * 0 + fBC * fAB * 0 +
    fBC * fAC * 1 / 4 + fBC * fBB * 0 + fBC * fBC * 1 / 4 + fBC * fCC * 1 / 2 + fCC * fAA * 0 +
    fCC * fAB * 0 + fCC * fAC * 1 / 2 + fCC * fBB * 0 + fCC * fBC * 1 / 2 + fCC * fCC * 1 + 0];
```

In[1524]:=
```
(*Genotype frequencies after drive*)
fAA_Drive = FullSimplify[AAn];
fAB_Drive = FullSimplify[ABn + BAn];
fAC_Drive = FullSimplify[ACn + CAn];
fBB_Drive = FullSimplify[BBn];
fBC_Drive = FullSimplify[BCn + CBn];
fCC_Drive = FullSimplify[CCn];
(*check, do allele freqs sum to one?*)
FullSimplify[
 FullSimplify[fAA_Drive + fAB_Drive + fAC_Drive + fBB_Drive + fBC_Drive + fCC_Drive] /. HWE /. SUMTOONE]
```

Out[1530]= 1

# Selection

In[1531]:=
```
wAA = 1; wAC = wAB = 1 - hs; wBB = wBC = wCC = 1 - s;
W̄ = FullSimplify[
    (wAA fAA_Drive + wAB fAB_Drive + wAC fAC_Drive + wBB fBB_Drive + wBC fBC_Drive + wCC fCC_Drive)];
FullSimplify[W̄ /. HWE /. SUMTOONE /. hs → 0]
```

Out[1533]= $1 + (fB + fC)\ (-2\ d1\ fC + 2\ d0\ fB\ (-1 + fB + fC) - (fB + fC)\ (fB + fC - 2\ d1\ fC))\ s$

In[1534]:=
```
fAA_Sel = fAA_Drive wAA / W̄;
fAB_Sel = fAB_Drive wAB / W̄;
fAC_Sel = fAC_Drive wAC / W̄;
fBB_Sel = fBB_Drive wBB / W̄;
fBC_Sel = fBC_Drive wBC / W̄;
fCC_Sel = fCC_Drive wCC / W̄;
fA_Sel = FullSimplify[fAA_Sel + (fAB_Sel + fAC_Sel) / 2];
fB_Sel = FullSimplify[fBB_Sel + (fAB_Sel + fBC_Sel) / 2];
fC_Sel = FullSimplify[fCC_Sel + (fAC_Sel + fBC_Sel) / 2];
ΔfA = FullSimplify[fA_Sel - fA];
ΔfB = FullSimplify[fB_Sel - fB];
ΔfC = FullSimplify[fC_Sel - fC];

(*Check: do genotype freqs after selection sum to one?*)
FullSimplify[fA_Sel + fB_Sel + fC_Sel]
```

Out[1546]= 1

## Analysis - a standard driver [i.e. C is absent]

Note, we assume no deviation from Hardy - Weinberg for all analytical results, and therefore these answers are approximations. In the supplamentary material we show thats results of exact recursions are remarkably consistant from these approximate analystical solutions.

**Invasion of standard driver** [note the driver always invades when it has a recessive fitness cost]

In[1592]:=
```
invasionStandardDriver = Solve[
  (FullSimplify[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) / fB] /. fB → 0) == 0, hs]
```

Out[1592]= $\left\{\left\{hs \to \frac{-1 + 2\ d0}{1 + 2\ d0}\right\}\right\}$

**Fixation of standard driver**

In[1593]:=
```
fixationStandardDriver = Solve[
  (FullSimplify[(ΔfB / fA /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0)] /. fB → 1) == 0, s]
```

Out[1593]= $\left\{\left\{s \to \frac{1}{2}\ (-1 + 2\ d0 + 3\ hs - 2\ d0\ hs)\right\}\right\}$

```
(*fixation of a standard recessive driver*)
fixationStandardDriver /. hs → 0
```

Out[1594]= $\left\{\left\{s \to \frac{1}{2}\ (-1 + 2\ d0)\right\}\right\}$

## Equilibrium

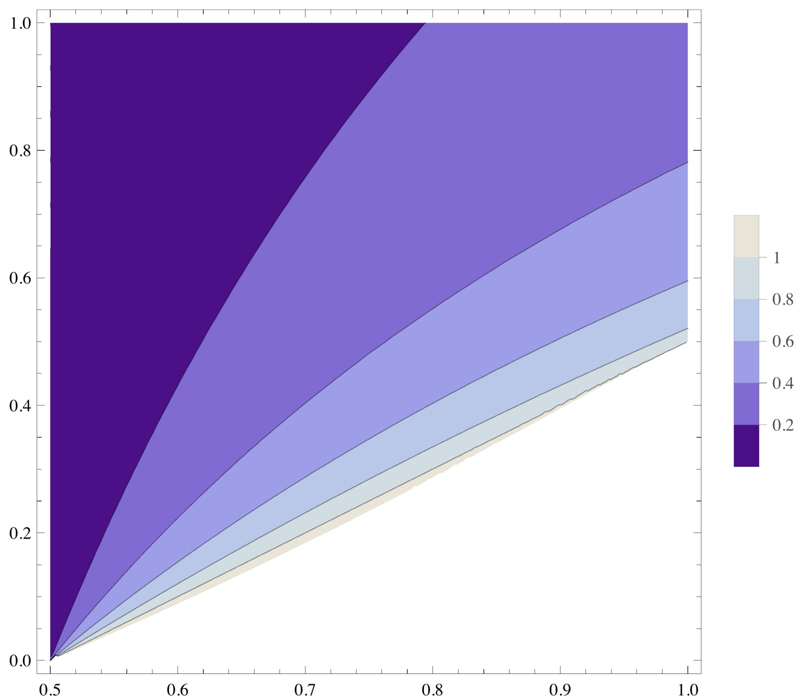
In[1562]:=
```
eqfB = Solve[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) == 0, fB][[4]]
```

Out[1562]=
$$\left\{fB \to \left(8\, d0\, hs - 4\, d0\, s + \sqrt{-4\,(1 - 2\, d0 + hs + 2\, d0\, hs)\,(-4\, hs + 8\, d0\, hs + 2\, s - 4\, d0\, s) + (-8\, d0\, hs + 4\, d0\, s)^2}\right) \Big/ \left(2\,(-4\, hs + 8\, d0\, hs + 2\, s - 4\, d0\, s)\right)\right\}$$

```
(*Plot of equilibrium frequency of standard driver assuming full recessivity*)
```

In[1564]:=
```
ContourPlot[fB /. eqfB /. hs → 0, {d0, .5, 1}, {s, 0, 1}, PlotLegends → Automatic]
```

Out[1564]=



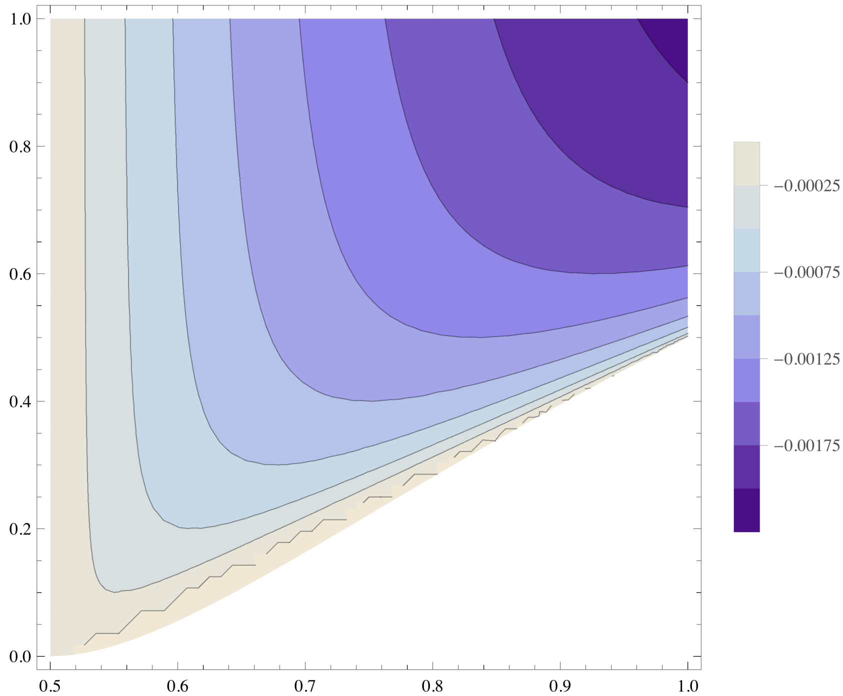

**Invasion of sperm dept drive**

In[1565]:=
```
wbarDeltaSpermDrive = FullSimplify[
  FullSimplify[W̄ ΔfC / (fC) /. HWE /. SUMTOONE] /. fC → 0 /. eqfB /. minormod]
```

Out[1565]=
$$\frac{1}{2\,(1 - 2\, d0)^2\,(2\, hs - s)}\,(hs - s)\left(-1 - hs - \sqrt{2}\,\sqrt{(1 + hs - 2\, d0\,(2 + d0\,(-2 + s)))\,(2\, hs - s)} + 2\, d0\,(2\,(-1 + d0)\,(-1 + hs) + s)\right)\epsilon$$

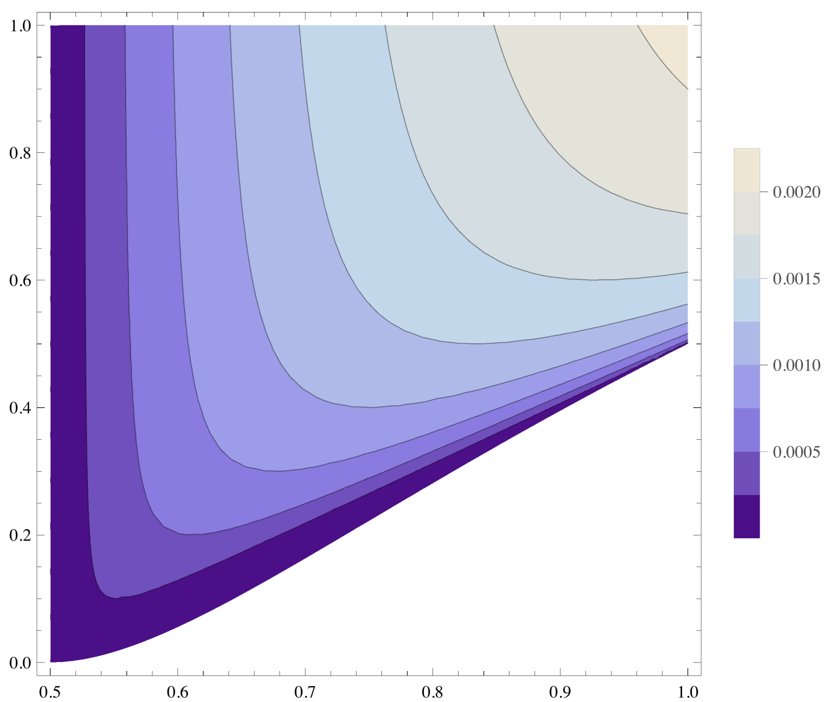
In[1581]:=
```
ContourPlot[
  (If[fB > .999, 0, If[fB < 0.0000001, 0, wbarDeltaSpermDrive]]) /. eqfB /. ϵ → 0.01 /.
   hs → 0, {d0, 0.5, 1}, {s, 0, 1}, PlotLegends → Automatic]
```

Out[1581]=



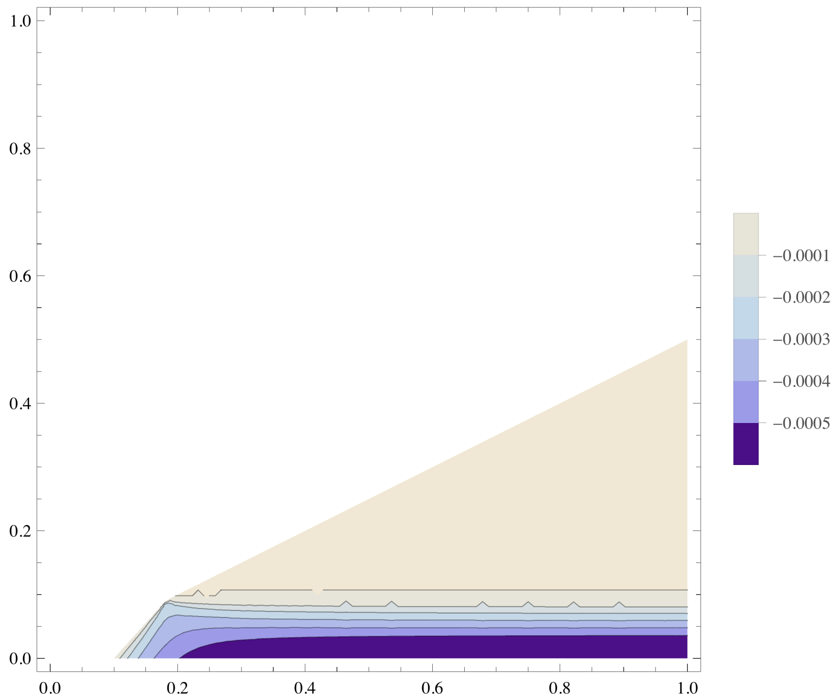

In[1580]:=
```
ContourPlot[
  (If[fB > .999, 0, If[fB < 0.0000001, 0, wbarDeltaSpermDrive]]) /. eqfB /. ϵ → -0.01 /.
   hs → 0, {d0, 0.5, 1}, {s, 0, 1}, PlotLegends → Automatic]
```

Out[1580]=



In[1582]:=
```
ContourPlot[
 (If[fB > 1, 1 / 0, If[fB < 0.0000001, 0, wbarDeltaSpermDrive]] /. eqfB /. ϵ → 0.01 /.
   d0 → .6), {s, 0, 1}, {hs, 0, 1}, PlotLegends → Automatic]
```

Out[1582]=




In[1583]:=
```
ContourPlot[
 (If[fB > 1, 1 / 0, If[fB <= 0.00000000000001, 0, wbarDeltaSpermDrive]] /. eqfB /.
    ϵ → 0.01 /. d0 → .98), {s, 0, 1}, {hs, 0, 1}, PlotLegends → Automatic]
```

Out[1583]=