Brandvain and Coop.
Sperm dependent female meiotic drive.

Model 1. Taditional female drive

Set up

```
(*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

```
fAA_Drive = FullSimplify[fA (fAA + fAB (1 - d))];
fAB_Drive  = FullSimplify[fA (fBB + fAB d) + fB (fAA + fAB (1 - d))];
fBB_Drive  = FullSimplify[fB (fAB d + fBB )];
```

Selection

```
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

For all analyses we assume HWE (i.e. x = 0), we relax this assumption in numerical iterations

Invasion

```
scaledDeltaDriveWhenRare = (FullSimplify[ΔfB / (fB * (1 - fB)) /. x → 0] /. fB → 0)
```

$$\frac{1}{2}(-1-2\,d\,(-1+hs)-hs)$$

Noting that the change in frequency of a standard driver is independent of s when rare, we solve for the value of hs required for invasion.

```
invasionCrit = Solve[scaledDeltaDriveWhenRare == 0, hs]
```

$$\left\{\left\{hs \to \frac{-1+2\,d}{1+2\,d}\right\}\right\}$$

Fixation

```
scaledDeltaDriveWhenCommon = (FullSimplify[ΔfB / (fB * (1 - fB)) /. x → 0] /. fB → 1)
```

$$\frac{1+hs+2\,(d\,(-1+hs)-2\,hs+s)}{2\,(-1+s)}$$

We solve for fixation conditions when recessive or not.

```
fixationCritRecessive = Solve[scaledDeltaDriveWhenCommon == 0, s] /. hs → 0
fixationCritNotRecessive = Solve[scaledDeltaDriveWhenCommon == 0, s]
```

$$\left\{\left\{s \to \frac{1}{2}(-1+2\,d)\right\}\right\}$$

$$\left\{\left\{s \to \frac{1}{2}(-1+2\,d+3\,hs-2\,d\,hs)\right\}\right\}$$

Equilibrium

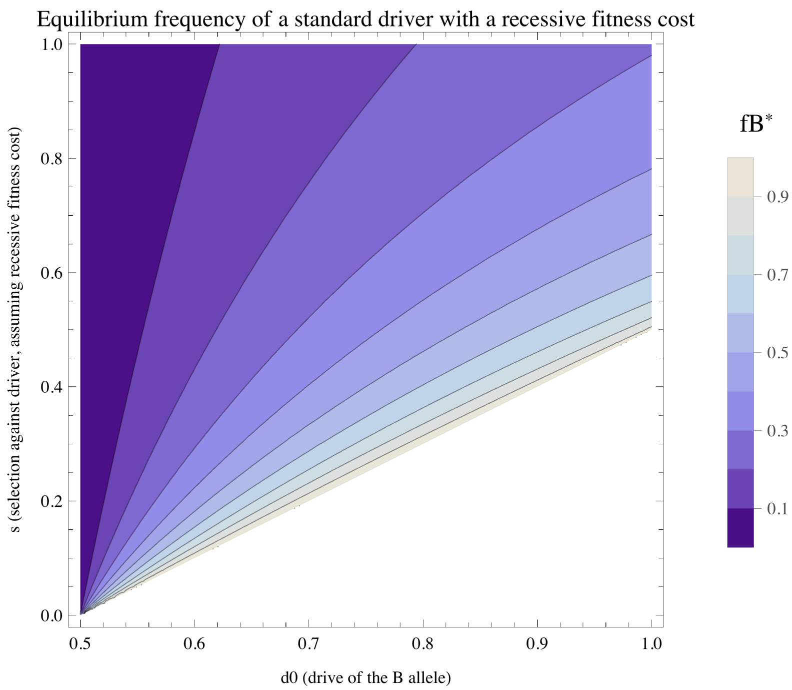
We identify the equilibrium frequency of the standard driver

```
eqfB = Solve[(FullSimplify[(ΔfB /. x → 0)]) == 0, fB][[4]]
```

$$\left\{fB \to \frac{8\,d\,hs-4\,d\,s+\sqrt{-4\,(1-2\,d+hs+2\,d\,hs)\,(-4\,hs+8\,d\,hs+2\,s-4\,d\,s)+(-8\,d\,hs+4\,d\,s)^2}}{2\,(-4\,hs+8\,d\,hs+2\,s-4\,d\,s)}\right\}$$

We plot this equilibrium frequency assuming a recessive fitness cost.

```
ContourPlot[If[fB > 1, 1 / 0, If[fB < 0, 1 / 0, fB]] /. eqfB /. hs → 0, {d, .5, 1},
 {s, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB*"], PlotLabel →
  "Equilibrium frequency of a standard driver with a recessive fitness cost",
 FrameLabel → {"d (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```




```
FullSimplify[fAA_Drive + fAB_Drive + fBB_Drive]
```

1

Model 2. 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

```
(*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

```
(*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

```
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

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

$$\frac{1}{2}(-1+d(2-4s))$$

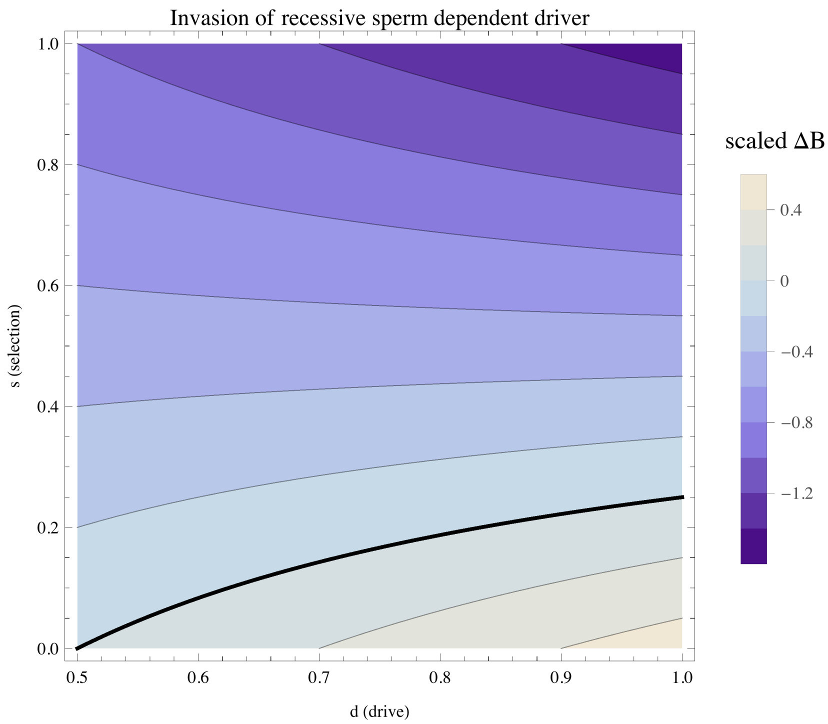
```
spermDepReceesiveInvade = Solve[ΔfBinvade == 0, s]
```

$$\left\{\left\{s\to\frac{-1+2d}{4d}\right\}\right\}$$

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

plotRelChange4RarespermDepRecessive = ContourPlot[{ΔfBinvade}, {d, 0.5, 1},
   {s, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB"],
   FrameLabel → {"d (drive)", "s (selection)"},
   PlotLabel → "Invasion of recessive sperm dependent driver"];
```

```
Show[plotRelChange4RarespermDepRecessive, plotInvasion4spermDepRecessive]
```



Fixation

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

$$\frac{-1 + 2\,d - 2\,s}{2 - 2\,s}$$

```
spermDepReceesiveFix  = Solve[ΔfBfix == 0, s]
```

$$\left\{\left\{s \to \frac{1}{2}\,(-1 + 2\,d)\right\}\right\}$$

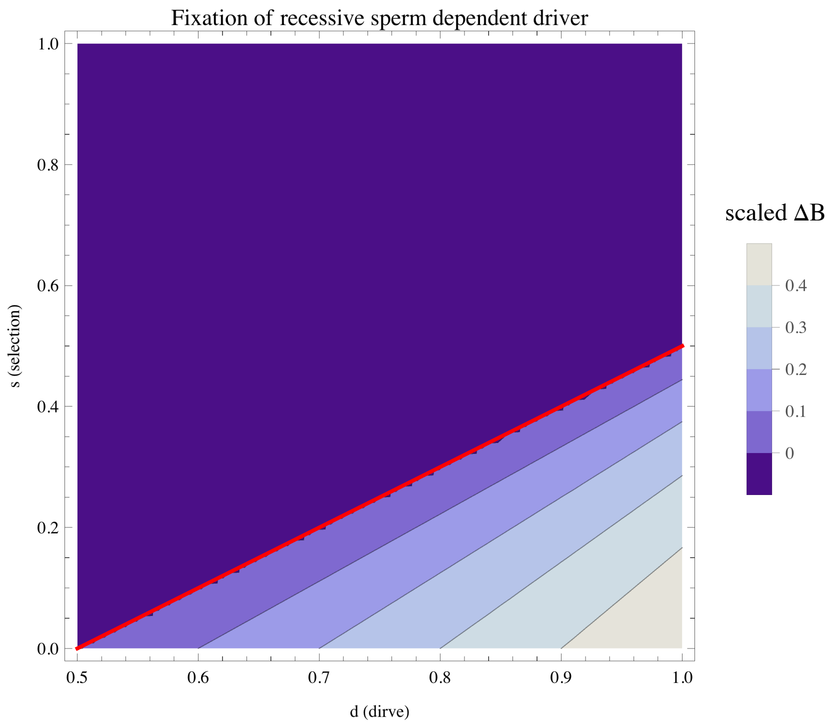
```
(s /. spermDepReceesiveFix [[1]])
```

$$\frac{1}{2}\,(-1 + 2\,d)$$

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

```
(*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 → BarLegend[Automatic, LegendLabel → "scaled ΔB"],
   FrameLabel → {"d (dirve)", "s (selection)"},
   PlotLabel → "Fixation of recessive sperm dependent driver"];
```

```
Show[plotRelChange4CommonSpermDepRecessive, plotFixation4spermDepRecessive]
```



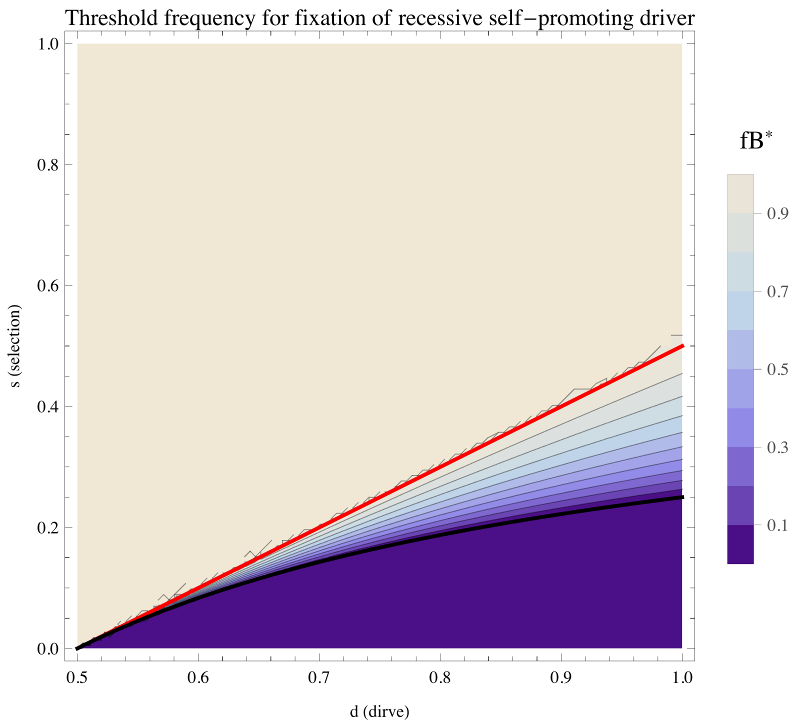
Bistability Point

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

$$\left\{fB \to \frac{1 - 2 d + 4 d s}{-2 s + 4 d s}\right\}$$

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

```
Show[bistab, plotFixation4spermDepRecessive, plotInvasion4spermDepRecessive]
```



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

```
FullSimplify[FullSimplify[ΔfB /. x → 0] / fB] /. fB → 0
```

$-\text{hs}$

Fixation

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

$$\frac{1 + 2\,d\,(-1 + \text{hs}) - 3\,\text{hs} + 2\,s}{2\,(-1 + s)}$$

```
spermDepNotReceesiveFix = Solve[ΔfBfix == 0, s]
```

$$\left\{\left\{s \to \frac{1}{2}\,(-1 + 2\,d + 3\,\text{hs} - 2\,d\,\text{hs})\right\}\right\}$$

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

$$\left\{\left\{s \to \frac{2\,(-1 + 2\,d)}{1 + 2\,d}\right\}\right\}$$

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

Bistability Point

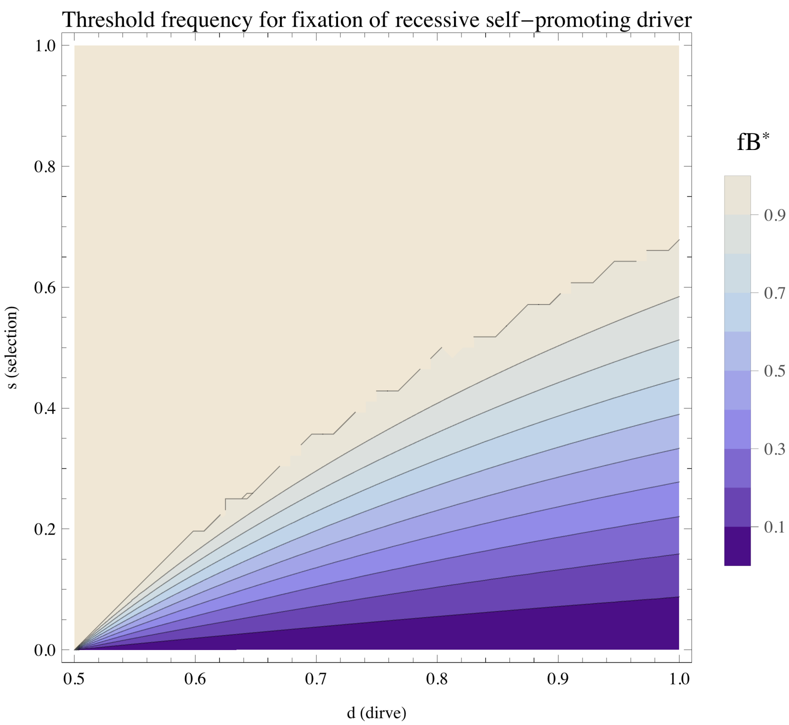
```
FBbistabSpermDepNotReceesive = Solve[FullSimplify[ΔfB /. x → 0] == 0, fB][[3]]
```

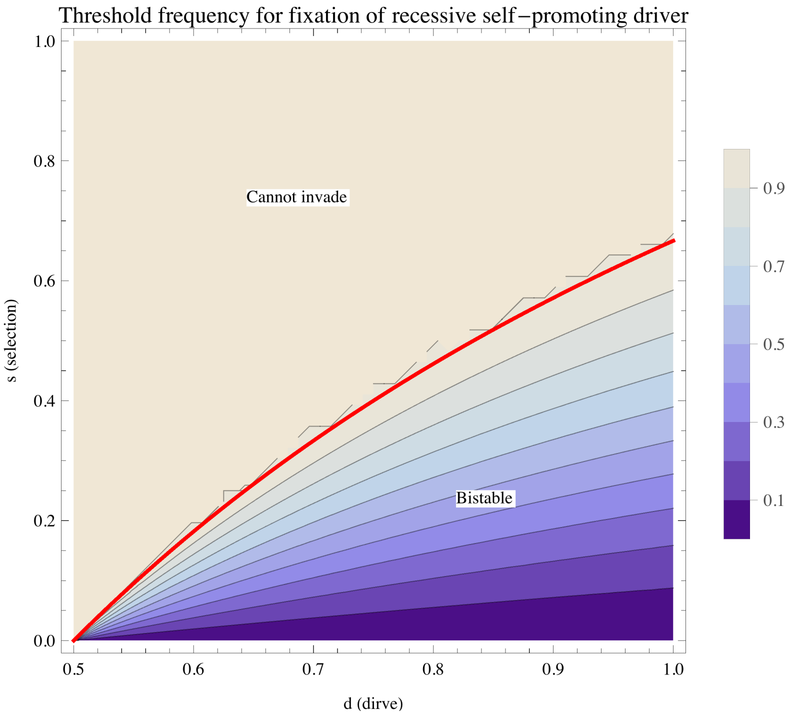
$$\left\{fB \to \left(-1 + 2\,d + 3\,hs + 2\,d\,hs - 4\,d\,s - \sqrt{-8\,hs\,(-2\,hs + 4\,d\,hs + 2\,s - 4\,d\,s) + (1 - 2\,d - 3\,hs - 2\,d\,hs + 4\,d\,s)^2}\right) \Big/ (2\,(-2\,hs + 4\,d\,hs + 2\,s - 4\,d\,s))\right\}$$

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

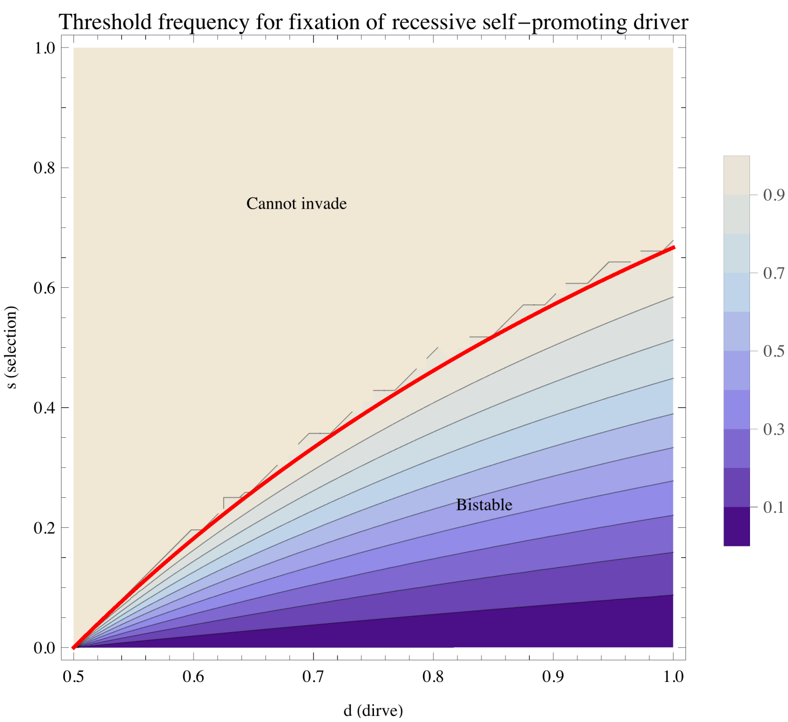
```
bistab = ContourPlot[
   (If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabSpermDepNotReceesive /. hs → (s / 2),
   {d, .5, 1}, {s, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB*"],
   FrameLabel → {"d (dirve)", "s (selection)"}, PlotLabel →
    "Threshold frequency for fixation of recessive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

```
Show[bistab, plotspermDepAddFix]
```





Threshold frequency for fixation of recessive self−promoting driver
Cannot invade
Bistable
s (selection)
d (dirve)
1.0
0.8
0.6
0.4
0.2
0.0
0.5
0.6
0.7
0.8
0.9
1.0
0.9
0.7
0.5
0.3
0.1



Threshold frequency for fixation of recessive self−promoting driver
Cannot invade
Bistable
s (selection)
d (dirve)
1.0
0.8
0.6
0.4
0.2
0.0
0.5
0.6
0.7
0.8
0.9
1.0
0.9
0.7
0.5
0.3
0.1

Model 3. 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

```
(*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

```
(*Genotype frequencies after drive*)
fAA_Drive = FullSimplify[fAA (fAA + fAB / 2) + fAB (fAA / 2 + fAB (1 - d_het) / 2)];
fAB_Drive  = FullSimplify[
   fAA (fAB / 2 + fBB) + fAB (fAA / 2 + fAB / 2 + fBB (1 - d_hom)) + fBB (fAA + fAB / 2)];
fBB_Drive  = FullSimplify[fAB (fAB d_het / 2 + fBB d_hom) + fBB (fAB / 2 + fBB)];
```

Selection

```
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];
```

```
FullSimplify[fAA_Drive + fAB_Drive + fBB_Drive]
```

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Analysis

Analytical example - recessive fitness cost

Invasion

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

$$\left\{\left\{s \to \frac{-1 + 2\, d_{het}}{2\, d_{het}}\right\}\right\}$$

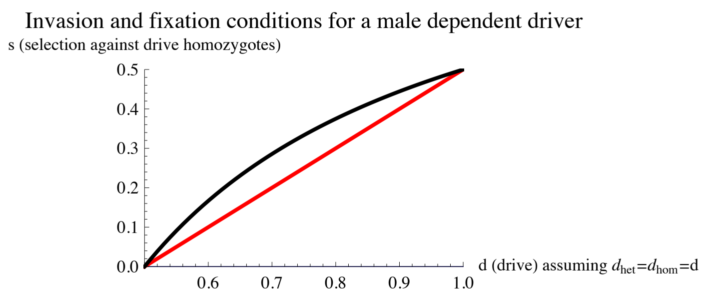
```
plotiInvasion4maleDepRecessive =
  Plot[s /. invasion4maleDepRecessive /. d_het -> d_hom,
   {d_hom, .5, 1}, PlotStyle -> {Black, Thick}];
```

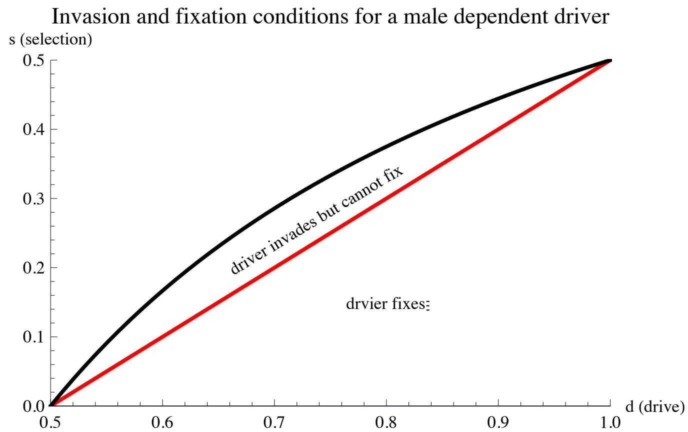
Fixation

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

$$\left\{\left\{s \to \frac{1}{2}\,(-1 + 2\, d_{hom})\right\}\right\}$$

```
plotFixation4maleDepRecessive = Plot[s /. fixation4maleDepRecessive /. d_het -> d_hom,
   {d_hom, .5, 1}, PlotStyle -> {Red, Thick}];

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





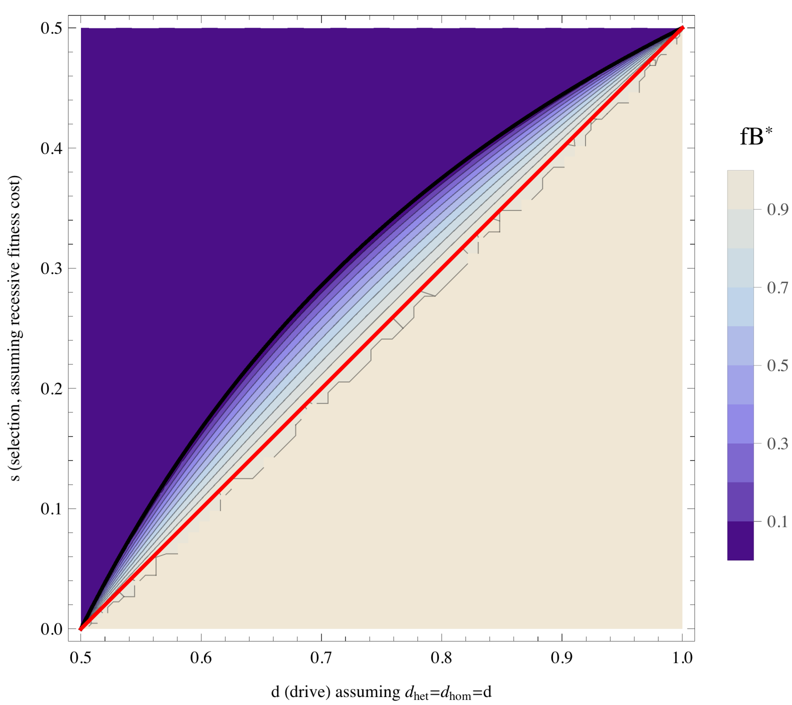
Equlibrium

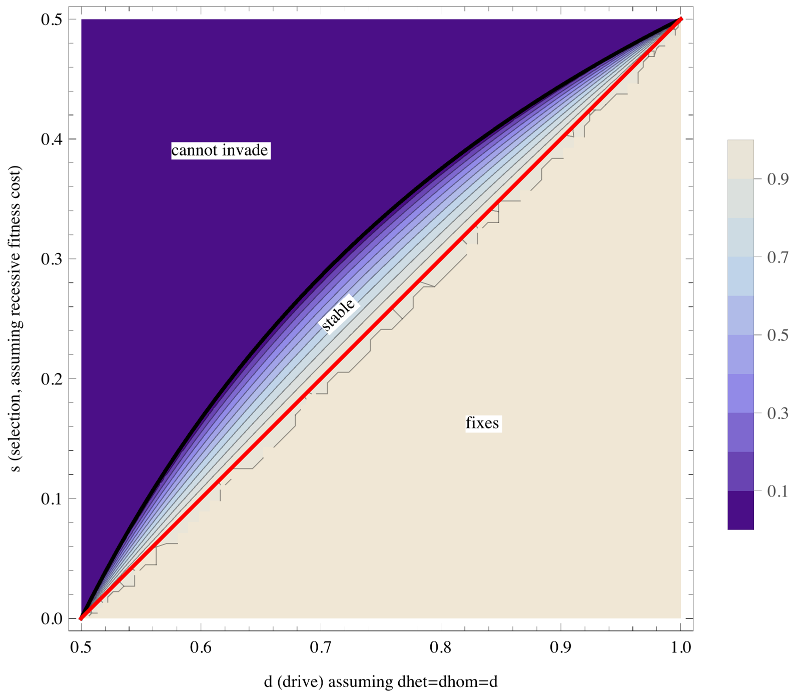
```
FBeqMaleepReceesive =
 Solve[FullSimplify[ΔfB /. x → 0 /. hs → 0 /. dhet → dhom] == 0, fB][[4]]
```

$$\left\{fB \to \frac{2\,(1 - 2\,d_{hom} + 2\,s\,d_{hom})}{(-1 + 2\,s)\,(-1 + 2\,d_{hom})}\right\}$$

```
eqfig = ContourPlot[ (If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBeqMaleepReceesive,
   {dhom, 0.5, 1}, {s, 0, .5}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB*"],
   FrameLabel → {"d (drive) assuming dhet=dhom=d",
     "s (selection, assuming recessive fitness cost)"}];
```

```
Show[eqfig, plotiInvasion4maleDepRecessive, plotFixation4maleDepRecessive]
```





Model 4. Female drive depends on sperm haplotype (two tightly linked, loci in coupling phase)

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. This tighly-linked locus is on the B background.
When C increases drive in heterozgous females it fertilizes, it is a drive enhancer (the B+ allele in our ms).
When C decreases drive in heterozgous females it fertilizes, it is a drive suppressor (the B- allele in our ms).

Setup

```
ClearAll["Global`*"]
fA =.
fAA =.
fAB =.
fAC =.
fBB =.
fBC =.
fCC =.
minormod = {d1 → d0 + ϵ}
 (*assuming the sperm acting modifier additively increases drive by epsilon*);
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*)

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];

(*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]
1
```

Selection

```
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)];
(*Because the C allele arises on the B background we assume
 it has the same impact on individual fitness*)
FullSimplify[W̄ /. HWE /. SUMTOONE /. hs → 0]
```

$1 + (fB + fC) (-2\,d1\,fC + 2\,d0\,fB (-1 + fB + fC) - (fB + fC) (fB + fC - 2\,d1\,fC))\,s$

```
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]
```

1

Analysis

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. Reassuringly, this reproduces model 1.

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

$\left\{\left\{hs \to \frac{-1 + 2\,d0}{1 + 2\,d0}\right\}\right\}$

Fixation of standard driver

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

$$\left\{\left\{s \to \frac{1}{2}\,(-1 + 2\,d0 + 3\,hs - 2\,d0\,hs)\right\}\right\}$$

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

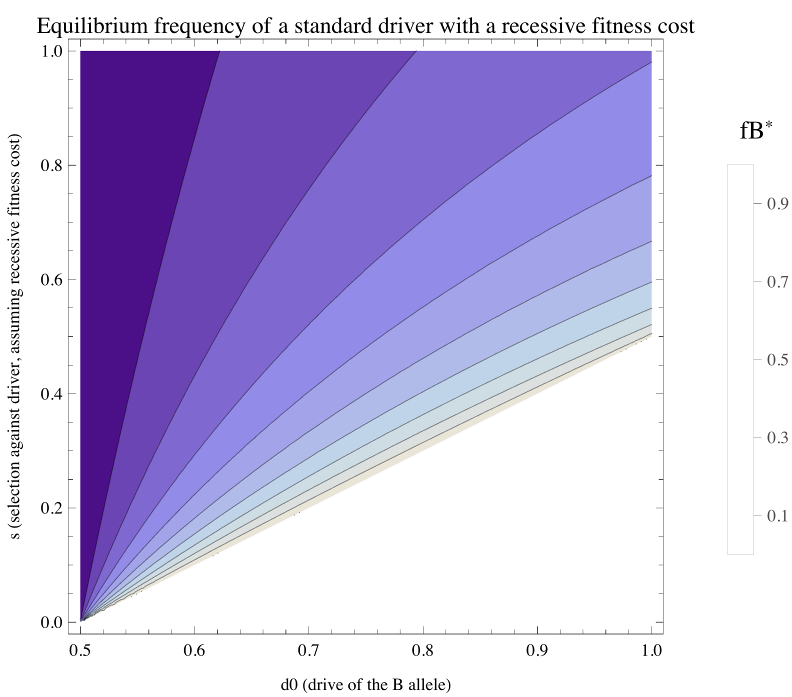
$$\left\{\left\{s \to \frac{1}{2}\,(-1 + 2\,d0)\right\}\right\}$$

Equilibrium

```
(*Equilibrium frequency of a standard driver]*)

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

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

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

ContourPlot[If[fB > 1, 1 / 0, If[fB < 0, 1 / 0, fB]] /. eqfB /. hs → 0, {d0, .5, 1},
 {s, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB*"], PlotLabel →
  "Equilibrium frequency of a standard driver with a recessive fitness cost",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```



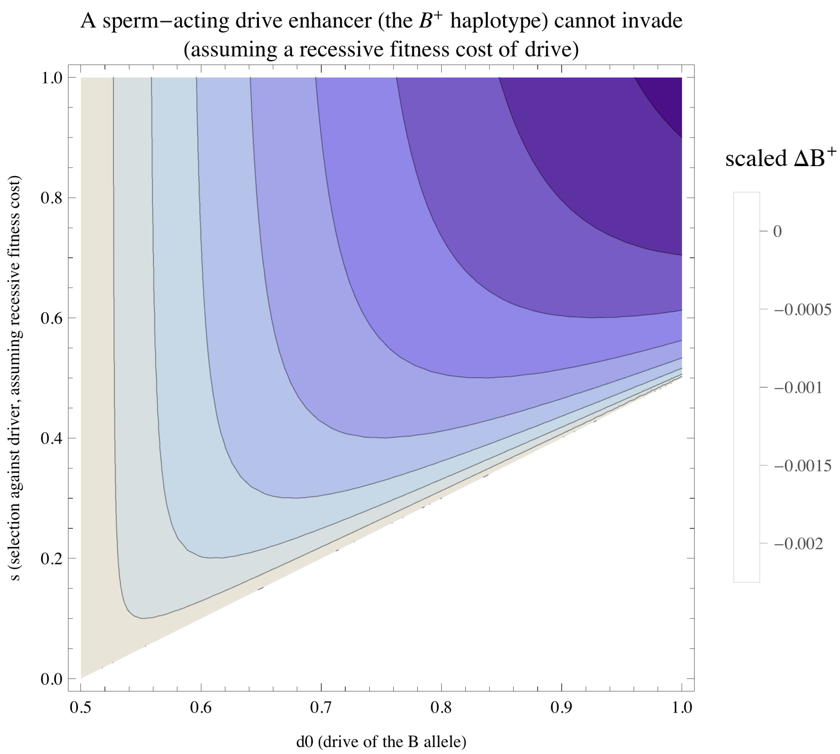
Invasion of sperm acting drive modifier tighly linked with the

driver, and on the driving background

```
(*change in frequency of the drive modifier when rare and when alleles
  at the drive locus are in drive-viability equilibrium, mutliplied by
 Wbar/fC [this value is always positive and will not influence the sign]*)
wbarDeltaSpermDrive = FullSimplify[
  FullSimplify[W̄ ΔfC / (fC) /. HWE /. SUMTOONE] /. fC → 0 /. eqfB /. minormod]
```

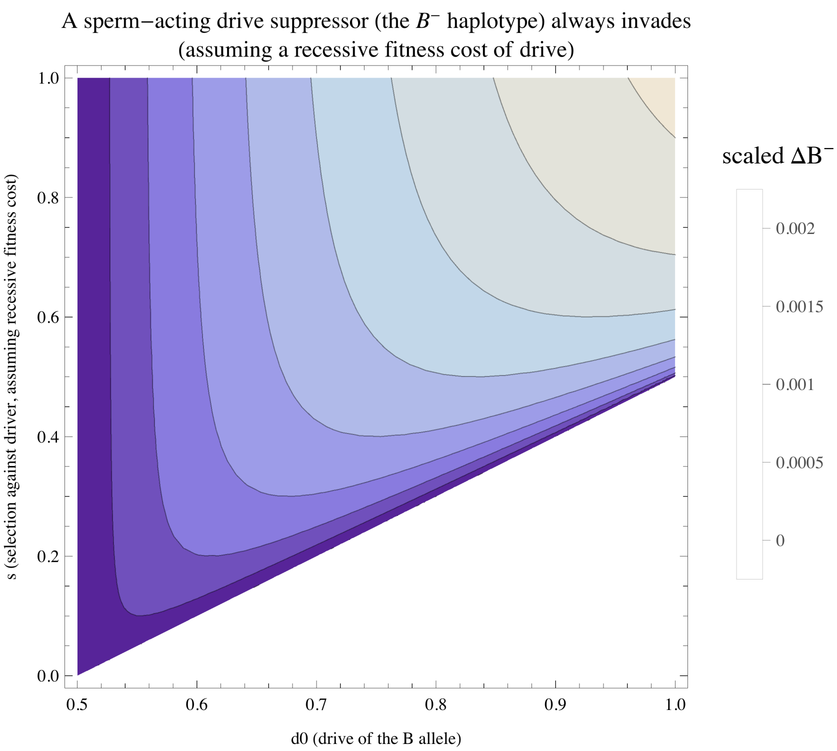
$$\frac{1}{2\,(1-2\,d0)^2\,(2\,hs-s)}(hs-s)\left(-1-hs-\sqrt{2}\,\sqrt{(1+hs-2\,d0\,(2+d0\,(-2+s)))\,(2\,hs-s)}+2\,d0\,(2\,(-1+d0)\,(-1+hs)+s)\right)\epsilon$$

```
(*Plotting change this change in frequency when the sperm acting locus is rare,
increases drive, and when the fitness cost of drive is fully
 recessive. NOTE: This sperm enhancer of drive cannot invade*)

ContourPlot[
 If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDrive]] /. eqfB /. ϵ → 0.01 /. hs → 0,
 {d0, 0.5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB⁺"],
 PlotLabel → "A sperm-acting drive enhancer (the B⁺ haplotype)
    cannot invade\n(assuming a recessive fitness cost of drive)",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```

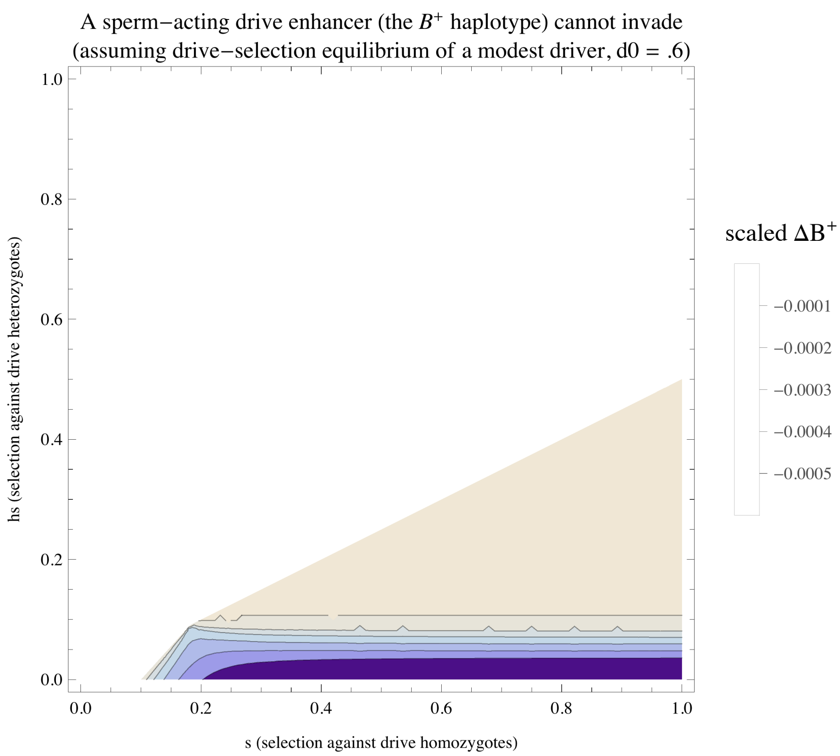



```
(*Plotting change this change in frequency when the sperm acting
 locus is rare and decreases drive, and when the fitness cost of
 drive is fully recessive. NOTE: This sperm suppresor always invades*)
```

```
ContourPlot[
 If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDrive]] /. eqfB /. ϵ → -0.01 /. hs → 0,
 {d0, 0.5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB⁻"],
 PlotLabel → "A sperm-acting drive suppressor (the B⁻ haplotype)
    always invades\n(assuming a recessive fitness cost of drive)",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```

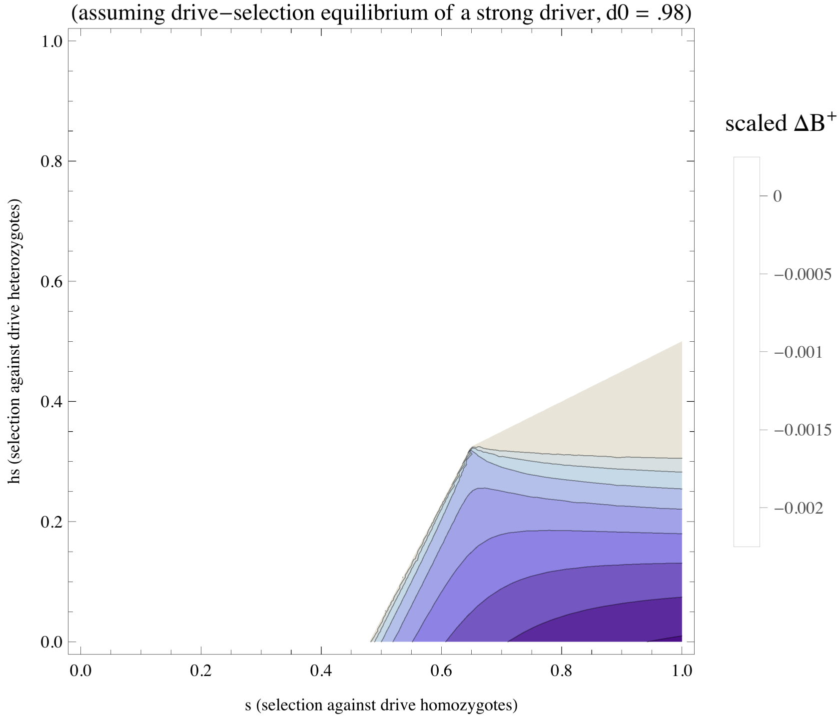


```
(*Plotting change this change in frequency when hte extent
 of drive is mild [d0 = .6] and the sperm acting locus is rare
 and increase drive. NOTE: This sperm enhancer never invades*)
ContourPlot[(If[fB > 1, 1 / 0, If[fB < 0.0000001, 0, wbarDeltaSpermDrive]] /. eqfB /.
    ϵ → 0.01 /. d0 → .6), {s, 0, 1}, {hs, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB⁺"], PlotLabel →
  "A sperm-acting drive enhancer (the B⁺ haplotype) cannot invade\n(assuming
    drive-selection equilibrium of a modest driver, d0 = .6)",
 FrameLabel → {"s (selection against drive homozygotes)",
   "hs (selection against drive heterozygotes)"}]
```

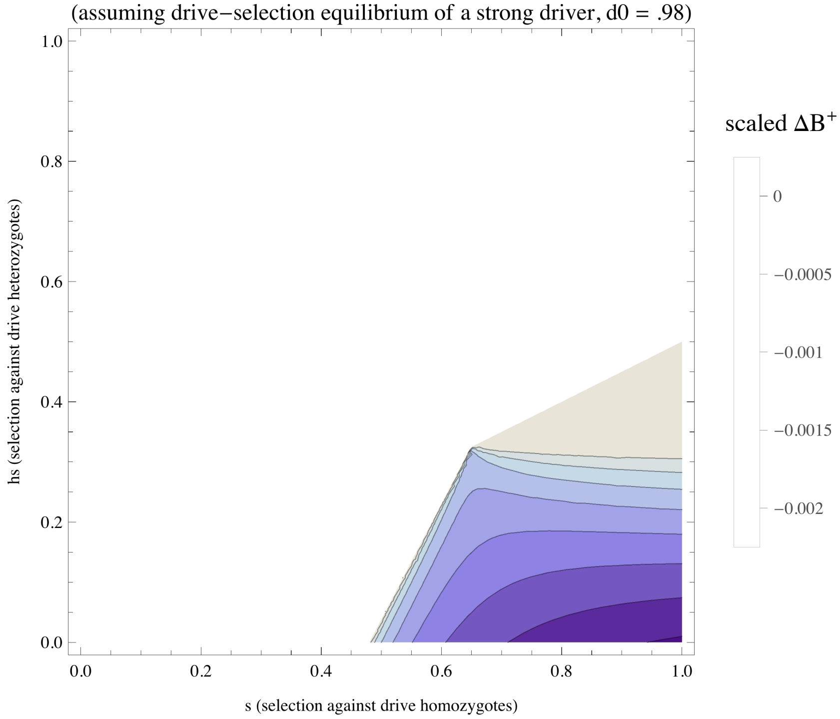



```
(*Plotting change this change in frequency when hte extent of
 drive is mild [d0 = .98] and the sperm acting locus is rare and
 increase drive. NOTE: This sperm enhancer never invades*)ContourPlot[
 (If[fB > 1, 1 / 0, If[fB <= 0.001, -0.000000001, wbarDeltaSpermDrive]] /. eqfB /.
    ϵ → 0.01 /. d0 → .98), {s, 0, 1}, {hs, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB⁺"], PlotLabel →
  "A sperm-acting drive enhancer (the B⁺ haplotype) cannot invade\n(assuming
    drive-selection equilibrium of a strong driver, d0 = .98)",
 FrameLabel → {"s (selection against drive homozygotes)",
   "hs (selection against drive heterozygotes)"}]
```

A sperm−acting drive enhancer (the B^+ haplotype) cannot invade
(assuming drive−selection equilibrium of a strong driver, d0 = .98)



A sperm−acting drive enhancer (the B^+ haplotype) cannot invade
(assuming drive−selection equilibrium of a strong driver, d0 = .98)



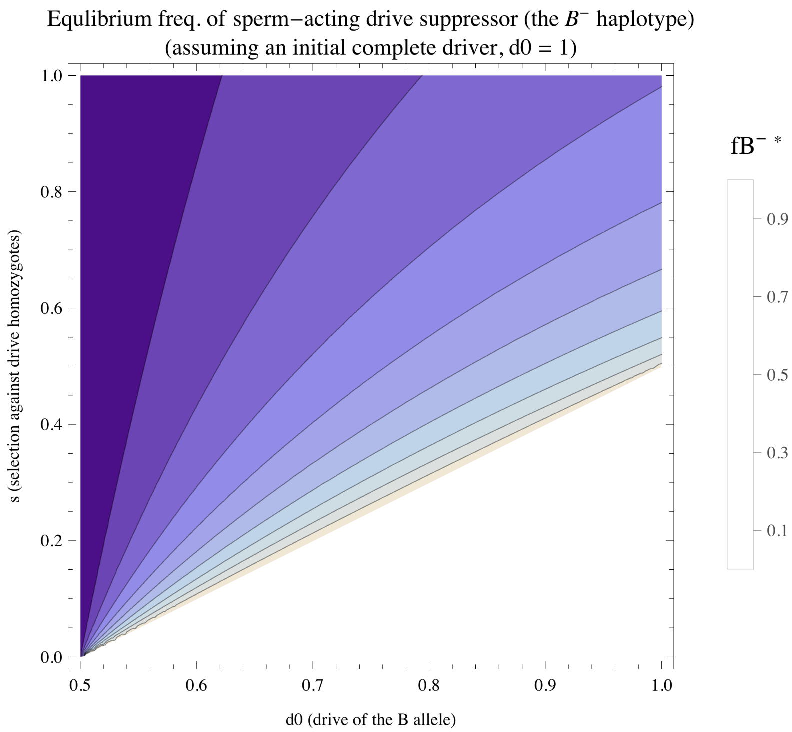
Replacement of traditional driver by sperm acting drive suppressor tighly linked with the driver, and on the driving background

Equilibrium frequency of drive suppresor

```
eqfC = Solve[(FullSimplify[ΔfC /. HWE /. SUMTOONE /. minormod /. fB → 0]) == 0, fC][[4]];
```

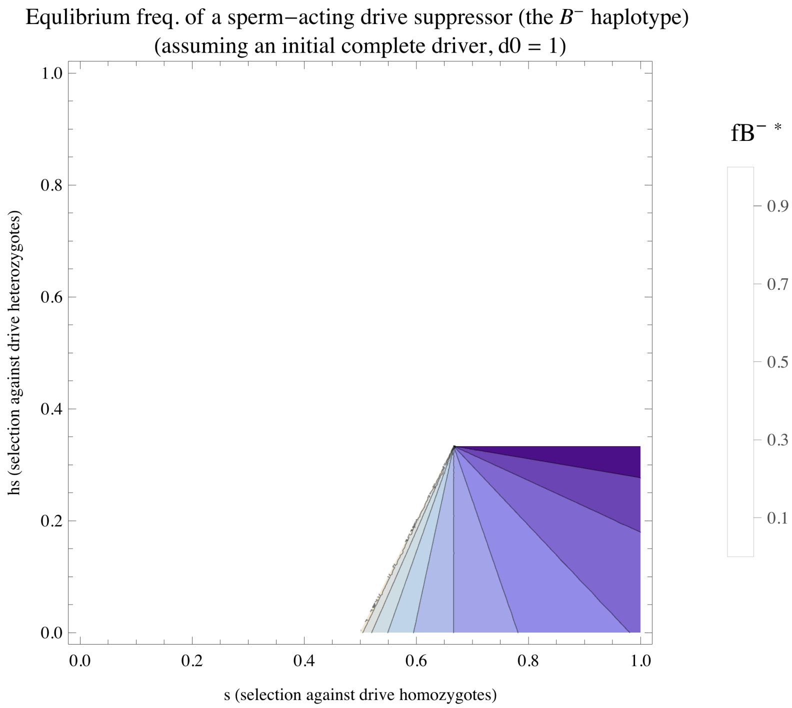
```
(*Equilibrium frequency of a linked, coupled,
drive suppressor when the fitness costs of drive are recessive*)
```

```
ContourPlot[If[fC < 1 && fC > 0, (fC), 1 / 0] /. eqfC /. hs → 0 /. ϵ → -.001,
 {d0, .5, 1}, {s, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB⁻ *"],
 PlotLabel → "Equlibrium freq. of sperm-acting drive suppressor (the B⁻
    haplotype)\n(assuming an initial complete driver, d0 = 1)", FrameLabel →
  {"d0 (drive of the B allele)", "s (selection against drive homozygotes)"}]
```



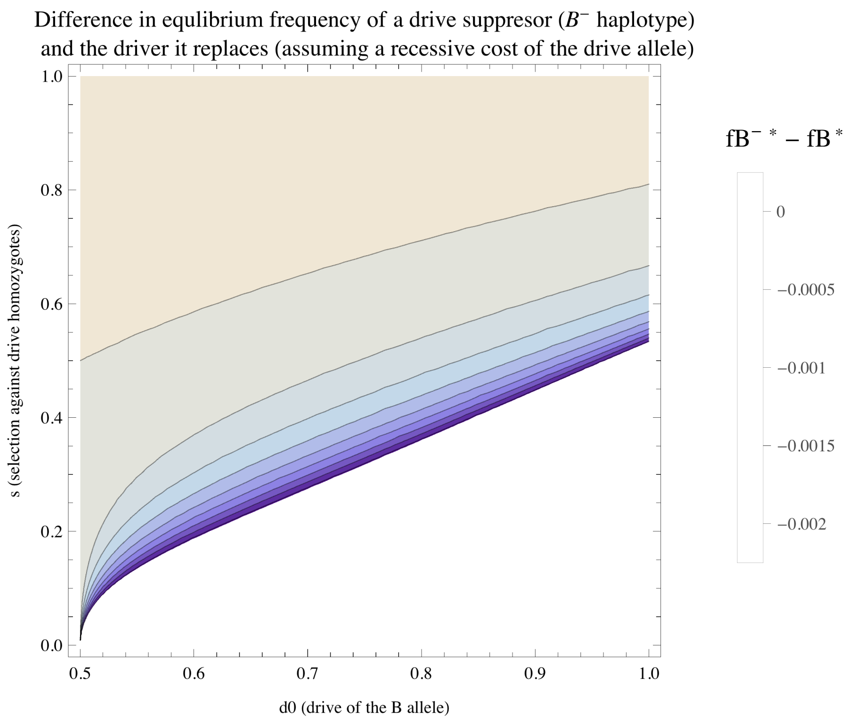

```
(*Equilibrium frequency of a linked, coupled,
drive suppressor when drive is complete*)
```

```
ContourPlot[If[fC < 1 && fC > 0, (fC), 1 / 0] /. eqfC /. hs → 0 /. ϵ → -.001 /. d0 → 1,
 {s, 0, 1}, {hs, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB⁻ *"],
 PlotLabel → "Equlibrium freq. of a sperm-acting drive suppressor (the
    B⁻ haplotype) \n(assuming an initial complete driver, d0 = 1)",
 FrameLabel → {"s (selection against drive homozygotes)",
   "hs (selection against drive heterozygotes)"}]
```

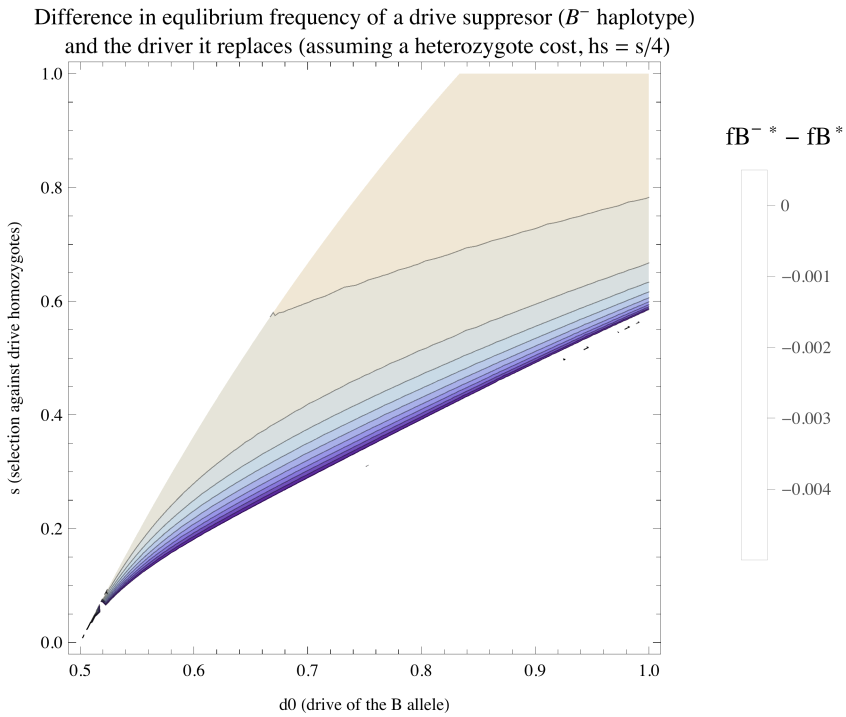


Equilibrium frequency of drive/sperm acting suppresor haplotype is often less than that of the standard driver it replaces.

```
(*Differecce in equilibrium frequency of the B- and B haplotypes*)
ContourPlot[
 If[fC < 1 && fB < 1 && fC > 0 && fB > 0, (fC - fB), 1 / 0] /. eqfB /. eqfC /. hs → 0 /.
  ϵ → - .001, {d0, .5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "fB⁻ * - fB*"], PlotLabel →
  "Difference in equlibrium frequency of a drive suppresor (B⁻ haplotype)\n and
    the driver it replaces (assuming a recessive cost of the drive allele)",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against drive homozygotes)"}]
```

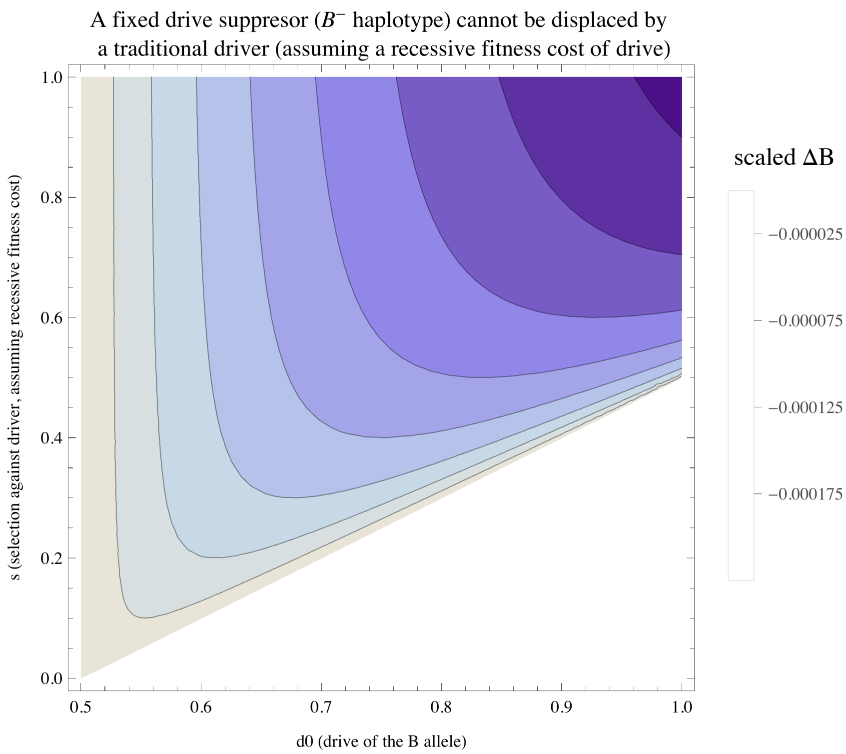


```
ContourPlot[
 If[fC < 1 && fB < 1 && fC > 0 && fB > 0, (fC - fB), 1 / 0] /. eqfB /. eqfC /. hs → (s / 4) /.
  ϵ → - .001, {d0, .5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "fB⁻ * - fB*"], PlotLabel →
  "Difference in equlibrium frequency of a drive suppresor (B⁻ haplotype)\n
    and the driver it replaces (assuming a heterozygote cost, hs = s/4)",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against drive homozygotes)"}]
```



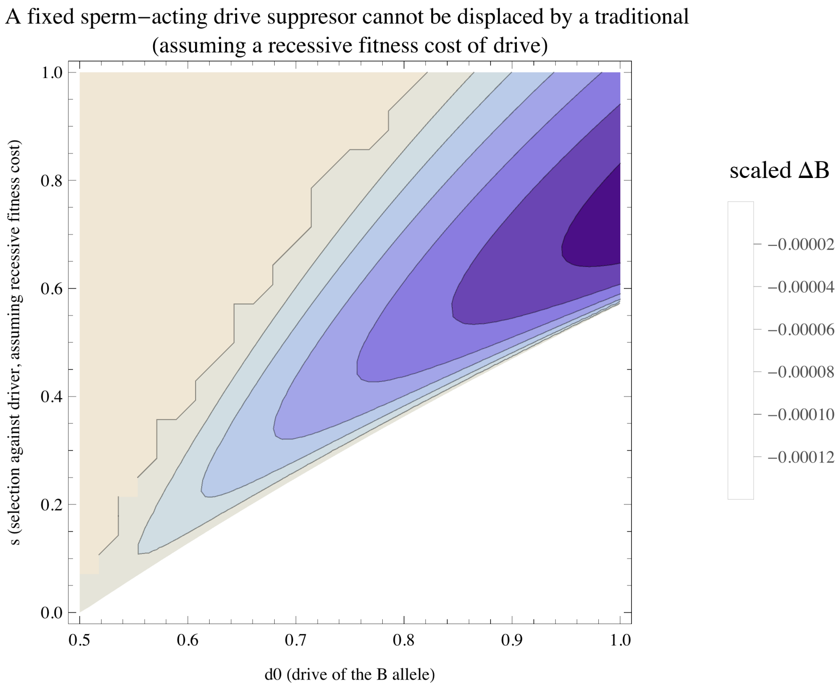

```
(*change in frequency of a rare traditional driver when the drive-
 sperm suppressor haplotype and the ondriving hplotype
  are at drive selection equilibrium, mutliplied by
 Wbar/fC [this value is always positive and will not influence the sign]*)
wbarDeltaTradDrive = FullSimplify[
   FullSimplify[W̄ ΔfB / (fB) /. HWE /. SUMTOONE] /. fB → 0 /. eqfC /. minormod];

(*Plotting the change in frequency of a rare traditional
 driving haplotype when the sperm drive suppresor is at drive
 selection balance. ASSUMING the fitness cost of drive is fully
 recessive. NOTE: This sperm enhancer of drive cannot invade*)
```

```
ContourPlot[
 If[fC > 1, 1 / 0, If[fC < 0.0001, 0, wbarDeltaTradDrive]] /. eqfC /. ϵ → -0.001 /. hs → 0,
 {d0, 0.5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB"],
 PlotLabel → "A fixed drive suppresor (B⁻ haplotype) cannot be displaced by \n a
    traditional driver (assuming a recessive fitness cost of drive)",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```

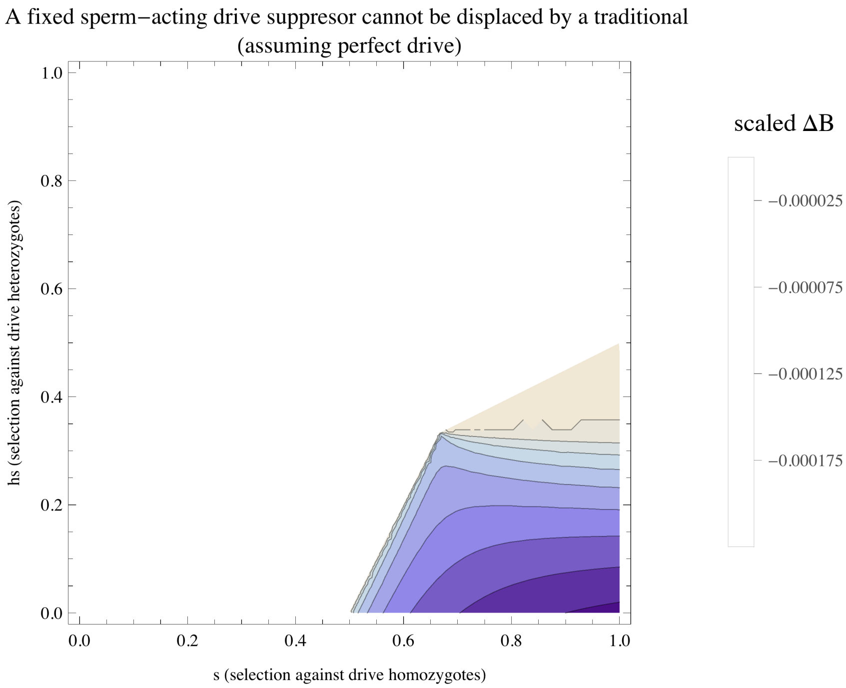



```
(*Plotting the change in frequency of a rare traditional
 driving haplotype when the sperm drive suppresor is at drive
 selection balance. ASSUMING a fitness cost of drive in homozygotes
 (hs→s/4). NOTE: This sperm enhancer of drive cannot invade*)
```

```
ContourPlot[
 If[fC > 1, 1 / 0, If[fC < 0.0001, 0, wbarDeltaTradDrive]] /. eqfC /. ϵ → -0.001 /.
  hs → s / 4, {d0, 0.5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB"],
 PlotLabel → "A fixed sperm-acting drive suppresor cannot be displaced
    by a traditional \n(assuming a recessive fitness cost of drive)",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```



```
ContourPlot[
 If[fC > 1, 1 / 0, If[fC < 0.0001, 0, wbarDeltaTradDrive]] /. eqfC /. ϵ → -0.001 /. d0 → 1,
 {s, 0, 1}, {hs, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB"],
 PlotLabel → "A fixed sperm-acting drive suppresor cannot
    be displaced by a traditional \n(assuming perfect drive)",
 FrameLabel → {"s (selection against drive homozygotes)",
   "hs (selection against drive heterozygotes)"}]
```



Model 5. Female drive depends on sperm haplotype (two tightly linked, loci in repulsion phase)

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. This tighly-linked locus is on the A background. Assuming no recombination this functions as a third allele, C.
When C increases drive in heterozgous females it fertilizes, it is a drive enhancer (the A+ allele [not discussed in our ms]).
When C decreases drive in heterozgous females it fertilizes, it is a drive suppressor (the A- allele in our ms).

Setup

```
ClearAll["Global`*"]
fA =.
fAA =.
fAB =.
fAC =.
fBB =.
fBC =.
fCC =.
minormod = {d1 → d0 + ϵ}
 (*assuming the sperm acting modifier additively increases drive by epsilon*);
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*)

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 / 2 + fAC * fAB * 1 / 4 +
     fAC * fAC * 1 / 4 + 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 / 4 +
     fAC * fAC * 0 + fAC * fBB * 1 / 2 + fAC * fBC * 1 / 4 + 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 / 4 + fAC * fBB * 0 + fAC * fBC * 1 / 4 + fAC * fCC * 1 / 2 + 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 * d0 + fBC * fAB * d0 / 2 +
    fBC * fAC * (d0) / 2 + 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 * d0 / 2 +
    fBC * fAC * 0 + fBC * fBB * d0 + fBC * fBC * (d0) / 2 + 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 * (d1) / 2 + fBC * fBB * 0 + fBC * fBC * (d1) / 2 + fBC * fCC * d1 +
    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 * 1 / 2 + fAC * fAB * 1 / 4 + fAC * fAC * 1 / 4 +
    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 - d0) + fBC * fAB * (1 - d0) / 2 +
    fBC * fAC * (1 - d0) / 2 + 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 * 1 / 4 + fAC * fAC * 0 + fAC * fBB * 1 / 2 +
    fAC * fBC * 1 / 4 + 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 - d0) / 2 +
    fBC * fAC * 0 + fBC * fBB * (1 - d0) + fBC * fBC * (1 - d0) / 2 + 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 * 1 / 4 + fAC * fBB * 0 + fAC * fBC * 1 / 4 +
    fAC * fCC * 1 / 2 + 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 - d1) / 2 +
    fBC * fBB * 0 + fBC * fBC * (1 - d1) / 2 + fBC * fCC * (1 - d1) + fCC * fAA * 0 +
    fCC * fAB * 0 + fCC * fAC * 1 / 2 + fCC * fBB * 0 + fCC * fBC * 1 / 2 + fCC * fCC * 1 + 0];

(*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]

1
```

Selection

```
wAA = wAC = wCC = 1; wAB = wBC = 1 - hs; wBB = 1 - s;
W̄ = FullSimplify[
   (wAA fAA_Drive + wAB fAB_Drive + wAC fAC_Drive + wBB fBB_Drive + wBC fBC_Drive + wCC fCC_Drive)];
(*Because the C allele arises on the B background we assume
 it has the same impact on individual fitness*)
FullSimplify[W̄ /. HWE /. SUMTOONE /. hs → 0]
```

$1 + (2\,d0\,(-1 + fB) - fB)\,fB^2\,s$

```
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]
```

1

```
FullSimplify[W̄ fAC_Sel /. HWE /. SUMTOONE]
```

$2\,(-1 + (-1 + d0 + d1)\,fB)\,fC\,(-1 + fB + fC)$

Analysis

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

THIS IS THE SAME AS ABOVE, AND WE RENETER IT SIMPLY TO LOAD RESULTS INTO MEMORY. PLOTS ARE NOT RECREATED

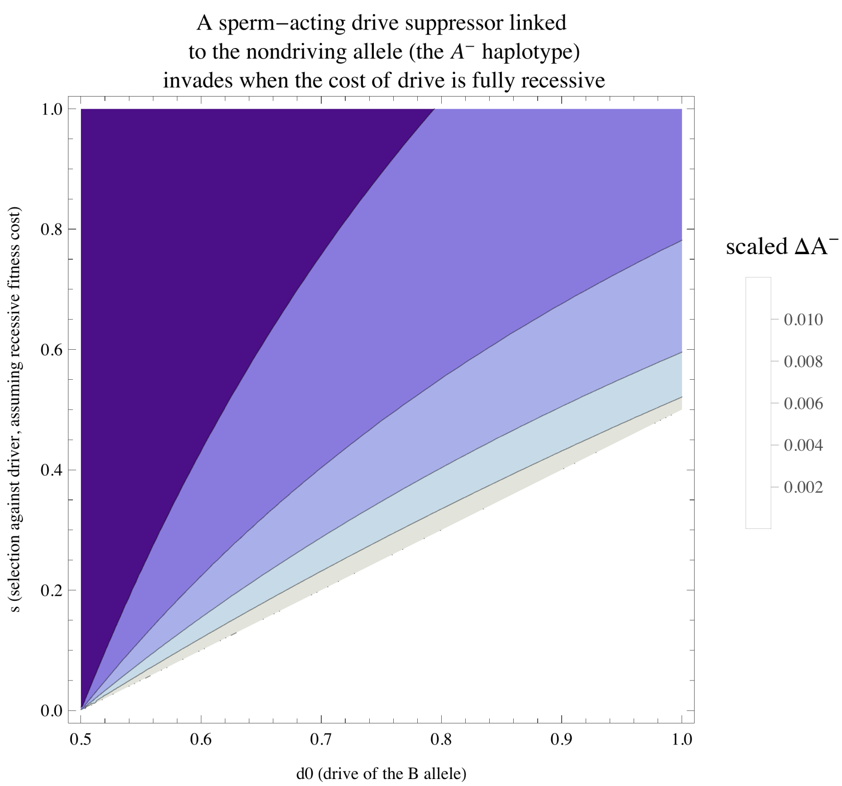
```
invasionStandardDriver = Solve[
   (FullSimplify[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) / fB] /. fB → 0) == 0,
   hs];
fixationStandardDriver = Solve[
   (FullSimplify[(ΔfB / fA /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0)] /. fB → 1) == 0,
   s];
eqfB = Solve[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) == 0, fB][[4]];
```

Invasion of sperm acting drive modifier tighly linked with the driver, on the non-driving background

```
(*change in frequency of the drive modifier when rare and when alleles
  at the drive locus are in drive-viability equilibrium, mutliplied by
 Wbar/fC^2 [this value is always positive and will not influence the sign]*)
wbarDeltaSpermDriveRecessive = FullSimplify[
  (FullSimplify[W̄ ΔfC / (fC^2) /. HWE /. SUMTOONE /. eqfB /. hs → 0]) /. minormod]
```

$$\frac{\left(-2\,d0\,s+\sqrt{2}\,\sqrt{(-1+2\,d0\,(2+d0\,(-2+s)))\,s}\right)\,\epsilon}{2\,(-1+2\,d0)\,s}$$

```
ContourPlot[
 If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDriveRecessive]] /. eqfB /.
   ϵ → -0.01 /. hs → 0, {d0, 0.5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔA⁻"],
 PlotLabel → "A sperm-acting drive suppressor linked\n to the nondriving allele
    (the A⁻ haplotype)\n invades when the cost of drive is fully recessive",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```

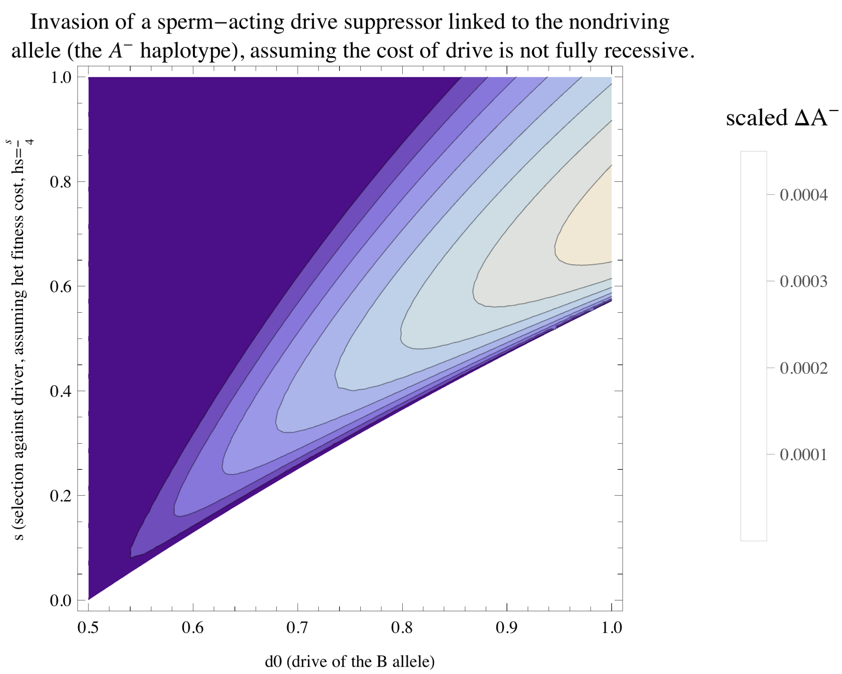



```
(*change in frequency of the drive modifier when rare and when alleles
  at the drive locus are in drive-viability equilibrium, mutliplied by
 Wbar/fC [this value is always positive and will not influence the sign]*)
```

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

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

```
(*Plotting change this change in frequency when the sperm acting locus is rare,
increases drive, and when the fitness cost of drive is fully
 recessive. NOTE: This sperm enhancer of drive cannot invade*)

ContourPlot[
 If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDrive]] /. eqfB /. ϵ → -0.01 /.
  hs → s / 4, {d0, 0.5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔA⁻"], PlotLabel →
  "Invasion of a sperm-acting drive suppressor linked to the nondriving\n allele
    (the A⁻ haplotype), assuming the cost of drive is not fully recessive.",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming het fitness cost, hs=s/4"}]
```



Model 6. Female drive depends on sperm genotype at an unlinked locus

In addition two our one locus with two alleles, A (non-driving) and B (traditional driver), we have a second locus with loci, E and F. We are concerned with the invasion and fixation of the F allele, which acts to modify drive when it fertilizes a heterozygote. Drive of the B allele is d0, but changes to d1 when fertilized by an ‘F’ bearing sperm

Setup

In[196]:=
```
fA =.; fB =.; fE =.; fF =.;
fAE = fA fE + D;
fAF = fA fF - D;
fBE = fB fE - D;
fBF = fB fF + D;
randomHaps = {fAAEE → FullSimplify[fAE fAE],
   fABEE → FullSimplify[2 fAE fBE], fBBEE → FullSimplify[fBE fBE],
   fAAEF → FullSimplify[2 fAE fAF], fABEF → FullSimplify[2 (fAE fBF + fAF fBE)],
   fBBEF → FullSimplify[2 fBE fBF], fAAFF → FullSimplify[fAF fAF],
   fABFF → FullSimplify[2 fAF fBF], fBBFF → FullSimplify[fBF fBF]};
sum2one = {fA → 1 - fB, fE → 1 - fF}
minormod = {d1 → d0 + ϵ}
  (*assuming the sperm acting modifier additively increases drive by epsilon*);
```

Out[202]=
```
{fA → 1 - fB, fE → 1 - fF}
```

Drive

```
fAAEE_Drive = FullSimplify[
  fAAEE * fAAEE * 1 + fAAEE * fABEE * 1 / 2 + fAAEE * fBBEE * 0 + fAAEE * fAAEF * 1 / 2 +
   fAAEE * fABEF * 1 / 4 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 0 + fAAEE * fABFF * 0 +
   fAAEE * fBBFF * 0 + fABEE * fAAEE * (1 - d0) + fABEE * fABEE * (1 - d0) / 2 + fABEE * fBBEE * 0 +
   fABEE * fAAEF * (1 - d0) / 2 + fABEE * fABEF * (1 - d0) / 4 + fABEE * fBBEF * 0 +
   fABEE * fAAFF * 0 + fABEE * fABFF * 0 + fABEE * fBBFF * 0 + fBBEE * fAAEE * 0 +
   fBBEE * fABEE * 0 + fBBEE * fBBEE * 0 + fBBEE * fAAEF * 0 + fBBEE * fABEF * 0 +
   fBBEE * fBBEF * 0 + fBBEE * fAAFF * 0 + fBBEE * fABFF * 0 + fBBEE * fBBFF * 0 +
   fAAEF * fAAEE * 1 / 2 + fAAEF * fABEE * 1 / 4 + fAAEF * fBBEE * 0 + fAAEF * fAAEF * 1 / 4 +
   fAAEF * fABEF * 1 / 8 + fAAEF * fBBEF * 0 + fAAEF * fAAFF * 0 + fAAEF * fABFF * 0 +
   fAAEF * fBBFF * 0 + fABEF * fAAEE * (1 - d0) / 2 + fABEF * fABEE * (1 - d0) / 4 +
```

```
    fABEF * fBBEE * 0 + fABEF * fAAEF * (1 - d0) / 4 + fABEF * fABEF * (1 - d0) / 8 +
    fABEF * fBBEF * 0 + fABEF * fAAFF * 0 + fABEF * fABFF * 0 + fABEF * fBBFF * 0 +
    fBBEF * fAAEE * 0 + fBBEF * fABEE * 0 + fBBEF * fBBEE * 0 + fBBEF * fAAEF * 0 +
    fBBEF * fABEF * 0 + fBBEF * fBBEF * 0 + fBBEF * fAAFF * 0 + fBBEF * fABFF * 0 +
    fBBEF * fBBFF * 0 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 + fAAFF * fBBEE * 0 +
    fAAFF * fAAEF * 0 + fAAFF * fABEF * 0 + fAAFF * fBBEF * 0 + fAAFF * fAAFF * 0 +
    fAAFF * fABFF * 0 + fAAFF * fBBFF * 0 + fABFF * fAAEE * 0 + fABFF * fABEE * 0 +
    fABFF * fBBEE * 0 + fABFF * fAAEF * 0 + fABFF * fABEF * 0 + fABFF * fBBEF * 0 +
    fABFF * fAAFF * 0 + fABFF * fABFF * 0 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 0 +
    fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 0 +
    fBBFF * fBBEF * 0 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]
fABEE_Drive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 1 / 2 + fAAEE * fBBEE * 1 +
    fAAEE * fAAEF * 0 + fAAEE * fABEF * 1 / 4 + fAAEE * fBBEF * 1 / 2 + fAAEE * fAAFF * 0 +
    fAAEE * fABFF * 0 + fAAEE * fBBFF * 0 + fABEE * fAAEE * d0 + fABEE * fABEE * 1 / 2 +
    fABEE * fBBEE * (1 - d0) + fABEE * fAAEF * d0 / 2 + fABEE * fABEF * 1 / 4 +
    fABEE * fBBEF * (1 - d0) / 2 + fABEE * fAAFF * 0 + fABEE * fABFF * 0 + fABEE * fBBFF * 0 +
    fBBEE * fAAEE * 1 + fBBEE * fABEE * 1 / 2 + fBBEE * fBBEE * 0 + fBBEE * fAAEF * 1 / 2 +
    fBBEE * fABEF * 1 / 4 + fBBEE * fBBEF * 0 + fBBEE * fAAFF * 0 + fBBEE * fABFF * 0 +
    fBBEE * fBBFF * 0 + fAAEF * fAAEE * 0 + fAAEF * fABEE * 1 / 4 + fAAEF * fBBEE * 1 / 2 +
    fAAEF * fAAEF * 0 + fAAEF * fABEF * 1 / 8 + fAAEF * fBBEF * 1 / 4 + fAAEF * fAAFF * 0 +
    fAAEF * fABFF * 0 + fAAEF * fBBFF * 0 + fABEF * fAAEE * d0 / 2 + fABEF * fABEE * 1 / 4 +
    fABEF * fBBEE * (1 - d0) / 2 + fABEF * fAAEF * d0 / 4 + fABEF * fABEF * 1 / 8 +
    fABEF * fBBEF * (1 - d0) / 4 + fABEF * fAAFF * 0 + fABEF * fABFF * 0 + fABEF * fBBFF * 0 +
    fBBEF * fAAEE * 1 / 2 + fBBEF * fABEE * 1 / 4 + fBBEF * fBBEE * 0 + fBBEF * fAAEF * 1 / 4 +
    fBBEF * fABEF * 1 / 8 + fBBEF * fBBEF * 0 + fBBEF * fAAFF * 0 + fBBEF * fABFF * 0 +
    fBBEF * fBBFF * 0 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 + fAAFF * fBBEE * 0 +
    fAAFF * fAAEF * 0 + fAAFF * fABEF * 0 + fAAFF * fBBEF * 0 + fAAFF * fAAFF * 0 +
    fAAFF * fABFF * 0 + fAAFF * fBBFF * 0 + fABFF * fAAEE * 0 + fABFF * fABEE * 0 +
    fABFF * fBBEE * 0 + fABFF * fAAEF * 0 + fABFF * fABEF * 0 + fABFF * fBBEF * 0 +
    fABFF * fAAFF * 0 + fABFF * fABFF * 0 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 0 +
    fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 0 +
    fBBFF * fBBEF * 0 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]
fBBEE_Drive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 0 + fAAEE * fBBEE * 0 +
    fAAEE * fAAEF * 0 + fAAEE * fABEF * 0 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 0 +
    fAAEE * fABFF * 0 + fAAEE * fBBFF * 0 + fABEE * fAAEE * 0 + fABEE * fABEE * d0 / 2 +
    fABEE * fBBEE * d0 + fABEE * fAAEF * 0 + fABEE * fABEF * (d0 / 4) +
    fABEE * fBBEF * d0 / 2 + fABEE * fAAFF * 0 + fABEE * fABFF * 0 + fABEE * fBBFF * 0 +
    fBBEE * fAAEE * 0 + fBBEE * fABEE * 1 / 2 + fBBEE * fBBEE * 1 + fBBEE * fAAEF * 0 +
    fBBEE * fABEF * 1 / 4 + fBBEE * fBBEF * 1 / 2 + fBBEE * fAAFF * 0 + fBBEE * fABFF * 0 +
    fBBEE * fBBFF * 0 + fAAEF * fAAEE * 0 + fAAEF * fABEE * 0 + fAAEF * fBBEE * 0 +
    fAAEF * fAAEF * 0 + fAAEF * fABEF * 0 + fAAEF * fBBEF * 0 + fAAEF * fAAFF * 0 +
    fAAEF * fABFF * 0 + fAAEF * fBBFF * 0 + fABEF * fAAEE * 0 + fABEF * fABEE * (d0 / 4) +
    fABEF * fBBEE * d0 / 2 + fABEF * fAAEF * 0 + fABEF * fABEF * (d0 / 8) +
    fABEF * fBBEF * d0 / 4 + fABEF * fAAFF * 0 + fABEF * fABFF * 0 + fABEF * fBBFF * 0 +
    fBBEF * fAAEE * 0 + fBBEF * fABEE * 1 / 4 + fBBEF * fBBEE * 1 / 2 + fBBEF * fAAEF * 0 +
    fBBEF * fABEF * 1 / 8 + fBBEF * fBBEF * 1 / 4 + fBBEF * fAAFF * 0 + fBBEF * fABFF * 0 +
    fBBEF * fBBFF * 0 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 + fAAFF * fBBEE * 0 +
    fAAFF * fAAEF * 0 + fAAFF * fABEF * 0 + fAAFF * fBBEF * 0 + fAAFF * fAAFF * 0 +
    fAAFF * fABFF * 0 + fAAFF * fBBFF * 0 + fABFF * fAAEE * 0 + fABFF * fABEE * 0 +
    fABFF * fBBEE * 0 + fABFF * fAAEF * 0 + fABFF * fABEF * 0 + fABFF * fBBEF * 0 +
    fABFF * fAAFF * 0 + fABFF * fABFF * 0 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 0 +
    fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 0 +
    fBBFF * fBBEF * 0 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]
fAAEF_Drive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 0 + fAAEE * fBBEE * 0 +
    fAAEE * fAAEF * 1 / 2 + fAAEE * fABEF * 1 / 4 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 1 +
```

```
    fAAEE * fABFF * 1 / 2 + fAAEE * fBBFF * 0 + fABEE * fAAEE * 0 + fABEE * fABEE * 0 +
    fABEE * fBBEE * 0 + fABEE * fAAEF * (1 - d1) / 2 + fABEE * fABEF * (1 - d1) / 4 +
    fABEE * fBBEF * 0 + fABEE * fAAFF * (1 - d1) + fABEE * fABFF * (1 - d1) / 2 +
    fABEE * fBBFF * 0 + fBBEE * fAAEE * 0 + fBBEE * fABEE * 0 + fBBEE * fBBEE * 0 +
    fBBEE * fAAEF * 0 + fBBEE * fABEF * 0 + fBBEE * fBBEF * 0 + fBBEE * fAAFF * 0 +
    fBBEE * fABFF * 0 + fBBEE * fBBFF * 0 + fAAEF * fAAEE * 1 / 2 + fAAEF * fABEE * 1 / 4 +
    fAAEF * fBBEE * 0 + fAAEF * fAAEF * 1 / 2 + fAAEF * fABEF * 1 / 4 + fAAEF * fBBEF * 0 +
    fAAEF * fAAFF * 1 / 2 + fAAEF * fABFF * 1 / 4 + fAAEF * fBBFF * 0 + fABEF * fAAEE * (1 - d0) / 2 +
    fABEF * fABEE * (1 - d0) / 4 + fABEF * fBBEE * 0 + fABEF * fAAEF * ((1 - d0) / 4 + (1 - d1) / 4) +
    fABEF * fABEF * ((1 - d0) / 8 + (1 - d1) / 8) + fABEF * fBBEF * 0 + fABEF * fAAFF * (1 - d1) / 2 +
    fABEF * fABFF * (1 - d1) / 4 + fABEF * fBBFF * 0 + fBBEF * fAAEE * 0 + fBBEF * fABEE * 0 +
    fBBEF * fBBEE * 0 + fBBEF * fAAEF * 0 + fBBEF * fABEF * 0 + fBBEF * fBBEF * 0 +
    fBBEF * fAAFF * 0 + fBBEF * fABFF * 0 + fBBEF * fBBFF * 0 + fAAFF * fAAEE * 1 +
    fAAFF * fABEE * 1 / 2 + fAAFF * fBBEE * 0 + fAAFF * fAAEF * 1 / 2 + fAAFF * fABEF * 1 / 4 +
    fAAFF * fBBEF * 0 + fAAFF * fAAFF * 0 + fAAFF * fABFF * 0 + fAAFF * fBBFF * 0 +
    fABFF * fAAEE * d0 + fABFF * fABEE * (1 - d0) / 2 + fABFF * fBBEE * 0 +
    fABFF * fAAEF * (1 - d0) / 2 + fABFF * fABEF * (1 - d0) / 4 + fABFF * fBBEF * 0 +
    fABFF * fAAFF * 0 + fABFF * fABFF * 0 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 0 +
    fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 0 +
    fBBFF * fBBEF * 0 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]
fABEF_Drive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 0 + fAAEE * fBBEE * 0 +
    fAAEE * fAAEF * 0 + fAAEE * fABEF * 1 / 4 + fAAEE * fBBEF * 1 / 2 + fAAEE * fAAFF * 0 +
    fAAEE * fABFF * 1 / 2 + fAAEE * fBBFF * 1 + fABEE * fAAEE * 0 + fABEE * fABEE * 0 +
    fABEE * fBBEE * 0 + fABEE * fAAEF * d1 / 2 + fABEE * fABEF * 1 / 4 +
    fABEE * fBBEF * (1 - d1) / 2 + fABEE * fAAFF * d1 + fABEE * fABFF * 1 / 2 +
    fABEE * fBBFF * (1 - d1) + fBBEE * fAAEE * 0 + fBBEE * fABEE * 0 + fBBEE * fBBEE * 0 +
    fBBEE * fAAEF * 1 / 2 + fBBEE * fABEF * 1 / 4 + fBBEE * fBBEF * 0 + fBBEE * fAAFF * 1 +
    fBBEE * fABFF * 1 / 2 + fBBEE * fBBFF * 0 + fAAEF * fAAEE * 0 + fAAEF * fABEE * 1 / 4 +
    fAAEF * fBBEE * 1 / 2 + fAAEF * fAAEF * 0 + fAAEF * fABEF * 1 / 4 + fAAEF * fBBEF * 1 / 2 +
    fAAEF * fAAFF * 0 + fAAEF * fABFF * 1 / 4 + fAAEF * fBBFF * 1 / 2 + fABEF * fAAEE * d0 / 2 +
    fABEF * fABEE * 1 / 4 + fABEF * fBBEE * (1 - d0) / 2 + fABEF * fAAEF * (d0 / 4 + d1 / 4) +
    fABEF * fABEF * 1 / 4 + fABEF * fBBEF * ((1 - d0) / 4 + (1 - d1) / 4) + fABEF * fAAFF * d1 / 2 +
    fABEF * fABFF * 1 / 4 + fABEF * fBBFF * (1 - d1) / 2 + fBBEF * fAAEE * 1 / 2 +
    fBBEF * fABEE * 1 / 4 + fBBEF * fBBEE * 0 + fBBEF * fAAEF * 1 / 2 + fBBEF * fABEF * 1 / 4 +
    fBBEF * fBBEF * 0 + fBBEF * fAAFF * 1 / 2 + fBBEF * fABFF * 1 / 4 + fBBEF * fBBFF * 0 +
    fAAFF * fAAEE * 0 + fAAFF * fABEE * 1 / 2 + fAAFF * fBBEE * 1 + fAAFF * fAAEF * 0 +
    fAAFF * fABEF * 1 / 4 + fAAFF * fBBEF * 1 / 2 + fAAFF * fAAFF * 0 + fAAFF * fABFF * 0 +
    fAAFF * fBBFF * 0 + fABFF * fAAEE * (1 - d0) + fABFF * fABEE * 1 / 2 + fABFF * fBBEE * d0 +
    fABFF * fAAEF * d0 / 2 + fABFF * fABEF * 1 / 4 + fABFF * fBBEF * (1 - d0) / 2 +
    fABFF * fAAFF * 0 + fABFF * fABFF * 0 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 1 +
    fBBFF * fABEE * 1 / 2 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 1 / 2 + fBBFF * fABEF * 1 / 4 +
    fBBFF * fBBEF * 0 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]
fBBEF_Drive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 0 + fAAEE * fBBEE * 0 +
    fAAEE * fAAEF * 0 + fAAEE * fABEF * 0 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 0 +
    fAAEE * fABFF * 0 + fAAEE * fBBFF * 0 + fABEE * fAAEE * 0 + fABEE * fABEE * 0 +
    fABEE * fBBEE * 0 + fABEE * fAAEF * 0 + fABEE * fABEF * d1 / 4 + fABEE * fBBEF * d1 / 2 +
    fABEE * fAAFF * 0 + fABEE * fABFF * d1 / 2 + fABEE * fBBFF * d1 + fBBEE * fAAEE * 0 +
    fBBEE * fABEE * 0 + fBBEE * fBBEE * 0 + fBBEE * fAAEF * 0 + fBBEE * fABEF * 1 / 4 +
    fBBEE * fBBEF * 1 / 2 + fBBEE * fAAFF * 0 + fBBEE * fABFF * 1 / 2 + fBBEE * fBBFF * 1 +
    fAAEF * fAAEE * 0 + fAAEF * fABEE * 0 + fAAEF * fBBEE * 0 + fAAEF * fAAEF * 0 +
    fAAEF * fABEF * 0 + fAAEF * fBBEF * 0 + fAAEF * fAAFF * 0 + fAAEF * fABFF * 0 +
    fAAEF * fBBFF * 0 + fABEF * fAAEE * 0 + fABEF * fABEE * (d0 / 4) + fABEF * fBBEE * (d0 / 2) +
    fABEF * fAAEF * 0 + fABEF * fABEF * (d0 / 8 + d1 / 8) + fABEF * fBBEF * (d0 / 4 + d1 / 4) +
    fABEF * fAAFF * 0 + fABEF * fABFF * d1 / 4 + fABEF * fBBFF * (d1 / 2) +
    fBBEF * fAAEE * 0 + fBBEF * fABEE * 1 / 4 + fBBEF * fBBEE * 1 / 2 + fBBEF * fAAEF * 0 +
```

```
    fBBEF * fABEF * 1 / 4 + fBBEF * fBBEF * 1 / 2 + fBBEF * fAAFF * 0 + fBBEF * fABFF * 1 / 4 +
    fBBEF * fBBFF * 1 / 2 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 + fAAFF * fBBEE * 0 +
    fAAFF * fAAEF * 0 + fAAFF * fABEF * 0 + fAAFF * fBBEF * 0 + fAAFF * fAAFF * 0 +
    fAAFF * fABFF * 0 + fAAFF * fBBFF * 0 + fABFF * fAAEE * 0 + fABFF * fABEE * d0 / 2 +
    fABFF * fBBEE * (1 - d0) + fABFF * fAAEF * 0 + fABFF * fABEF * d0 / 4 + fABFF * fBBEF * d0 / 2 +
    fABFF * fAAFF * 0 + fABFF * fABFF * 0 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 0 +
    fBBFF * fABEE * 1 / 2 + fBBFF * fBBEE * 1 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 1 / 4 +
    fBBFF * fBBEF * 1 / 2 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]
fAAFFDrive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 0 + fAAEE * fBBEE * 0 +
    fAAEE * fAAEF * 0 + fAAEE * fABEF * 0 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 0 +
    fAAEE * fABFF * 0 + fAAEE * fBBFF * 0 + fABEE * fAAEE * 0 + fABEE * fABEE * 0 +
    fABEE * fBBEE * 0 + fABEE * fAAEF * 0 + fABEE * fABEF * 0 + fABEE * fBBEF * 0 +
    fABEE * fAAFF * 0 + fABEE * fABFF * 0 + fABEE * fBBFF * 0 + fBBEE * fAAEE * 0 +
    fBBEE * fABEE * 0 + fBBEE * fBBEE * 0 + fBBEE * fAAEF * 0 + fBBEE * fABEF * 0 +
    fBBEE * fBBEF * 0 + fBBEE * fAAFF * 0 + fBBEE * fABFF * 0 + fBBEE * fBBFF * 0 +
    fAAEF * fAAEE * 0 + fAAEF * fABEE * 0 + fAAEF * fBBEE * 0 + fAAEF * fAAEF * 1 / 4 +
    fAAEF * fABEF * 1 / 8 + fAAEF * fBBEF * 0 + fAAEF * fAAFF * 1 / 2 +
    fAAEF * fABFF * 1 / 4 + fAAEF * fBBFF * 0 + fABEF * fAAEE * 0 + fABEF * fABEE * 0 +
    fABEF * fBBEE * 0 + fABEF * fAAEF * (1 - d1) / 4 + fABEF * fABEF * (1 - d1) / 8 +
    fABEF * fBBEF * 0 + fABEF * fAAFF * (1 - d1) / 2 + fABEF * fABFF * (1 - d1) / 4 +
    fABEF * fBBFF * 0 + fBBEF * fAAEE * 0 + fBBEF * fABEE * 0 + fBBEF * fBBEE * 0 +
    fBBEF * fAAEF * 0 + fBBEF * fABEF * 0 + fBBEF * fBBEF * 0 + fBBEF * fAAFF * 0 +
    fBBEF * fABFF * 0 + fBBEF * fBBFF * 0 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 +
    fAAFF * fBBEE * 0 + fAAFF * fAAEF * 1 / 2 + fAAFF * fABEF * 1 / 4 + fAAFF * fBBEF * 0 +
    fAAFF * fAAFF * 1 + fAAFF * fABFF * 1 / 2 + fAAFF * fBBFF * 0 + fABFF * fAAEE * 0 +
    fABFF * fABEE * 0 + fABFF * fBBEE * 0 + fABFF * fAAEF * (1 - d1) / 2 +
    fABFF * fABEF * (1 - d1) / 4 + fABFF * fBBEF * 0 + fABFF * fAAFF * (1 - d1) +
    fABFF * fABFF * (1 - d1) / 2 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 0 +
    fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 0 +
    fBBFF * fBBEF * 0 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]
fABFFDrive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 0 + fAAEE * fBBEE * 0 +
    fAAEE * fAAEF * 0 + fAAEE * fABEF * 0 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 0 +
    fAAEE * fABFF * 0 + fAAEE * fBBFF * 0 + fABEE * fAAEE * 0 + fABEE * fABEE * 0 +
    fABEE * fBBEE * 0 + fABEE * fAAEF * 0 + fABEE * fABEF * 0 + fABEE * fBBEF * 0 +
    fABEE * fAAFF * 0 + fABEE * fABFF * 0 + fABEE * fBBFF * 0 + fBBEE * fAAEE * 0 +
    fBBEE * fABEE * 0 + fBBEE * fBBEE * 0 + fBBEE * fAAEF * 0 + fBBEE * fABEF * 0 +
    fBBEE * fBBEF * 0 + fBBEE * fAAFF * 0 + fBBEE * fABFF * 0 + fBBEE * fBBFF * 0 +
    fAAEF * fAAEE * 0 + fAAEF * fABEE * 0 + fAAEF * fBBEE * 0 + fAAEF * fAAEF * 0 +
    fAAEF * fABEF * 1 / 8 + fAAEF * fBBEF * 1 / 4 + fAAEF * fAAFF * 0 + fAAEF * fABFF * 1 / 4 +
    fAAEF * fBBFF * 1 / 2 + fABEF * fAAEE * 0 + fABEF * fABEE * 0 + fABEF * fBBEE * 0 +
    fABEF * fAAEF * d1 / 4 + fABEF * fABEF * 1 / 8 + fABEF * fBBEF * (1 - d1) / 4 +
    fABEF * fAAFF * d1 / 2 + fABEF * fABFF * 1 / 4 + fABEF * fBBFF * (1 - d1) / 2 +
    fBBEF * fAAEE * 0 + fBBEF * fABEE * 0 + fBBEF * fBBEE * 0 + fBBEF * fAAEF * 1 / 4 +
    fBBEF * fABEF * 1 / 8 + fBBEF * fBBEF * 0 + fBBEF * fAAFF * 1 / 2 + fBBEF * fABFF * 1 / 4 +
    fBBEF * fBBFF * 0 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 + fAAFF * fBBEE * 0 +
    fAAFF * fAAEF * 0 + fAAFF * fABEF * 1 / 4 + fAAFF * fBBEF * 1 / 2 + fAAFF * fAAFF * 0 +
    fAAFF * fABFF * 1 / 2 + fAAFF * fBBFF * 1 + fABFF * fAAEE * 0 + fABFF * fABEE * 0 +
    fABFF * fBBEE * 0 + fABFF * fAAEF * d1 / 2 + fABFF * fABEF * 1 / 4 + fABFF * fBBEF * (1 - d1) / 2 +
    fABFF * fAAFF * d1 + fABFF * fABFF * 1 / 2 + fABFF * fBBFF * (1 - d1) + fBBFF * fAAEE * 0 +
    fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 1 / 2 + fBBFF * fABEF * 1 / 4 +
    fBBFF * fBBEF * 0 + fBBFF * fAAFF * 1 + fBBFF * fABFF * 1 / 2 + fBBFF * fBBFF * 0 + 0]
fBBFFDrive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 0 + fAAEE * fBBEE * 0 +
    fAAEE * fAAEF * 0 + fAAEE * fABEF * 0 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 0 +
    fAAEE * fABFF * 0 + fAAEE * fBBFF * 0 + fABEE * fAAEE * 0 + fABEE * fABEE * 0 +
    fABEE * fBBEE * 0 + fABEE * fAAEF * 0 + fABEE * fABEF * 0 + fABEE * fBBEF * 0 +
```

```
fABEE * fAAFF * 0 + fABEE * fABFF * 0 + fABEE * fBBFF * 0 + fBBEE * fAAEE * 0 +
fBBEE * fABEE * 0 + fBBEE * fBBEE * 0 + fBBEE * fAAEF * 0 + fBBEE * fABEF * 0 +
fBBEE * fBBEF * 0 + fBBEE * fAAFF * 0 + fBBEE * fABFF * 0 + fBBEE * fBBFF * 0 +
fAAEF * fAAEE * 0 + fAAEF * fABEE * 0 + fAAEF * fBBEE * 0 + fAAEF * fAAEF * 0 +
fAAEF * fABEF * 0 + fAAEF * fBBEF * 0 + fAAEF * fAAFF * 0 + fAAEF * fABFF * 0 +
fAAEF * fBBFF * 0 + fABEF * fAAEE * 0 + fABEF * fABEE * 0 + fABEF * fBBEE * 0 +
fABEF * fAAEF * 0 + fABEF * fABEF * d1 / 8 + fABEF * fBBEF * d1 / 4 +
fABEF * fAAFF * 0 + fABEF * fABFF * d1 / 4 + fABEF * fBBFF * d1 / 2 +
fBBEF * fAAEE * 0 + fBBEF * fABEE * 0 + fBBEF * fBBEE * 0 + fBBEF * fAAEF * 0 +
fBBEF * fABEF * 1 / 8 + fBBEF * fBBEF * 1 / 4 + fBBEF * fAAFF * 0 + fBBEF * fABFF * 1 / 4 +
fBBEF * fBBFF * 1 / 2 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 + fAAFF * fBBEE * 0 +
fAAFF * fAAEF * 0 + fAAFF * fABEF * 0 + fAAFF * fBBEF * 0 + fAAFF * fAAFF * 0 +
fAAFF * fABFF * 0 + fAAFF * fBBFF * 0 + fABFF * fAAEE * 0 + fABFF * fABEE * 0 +
fABFF * fBBEE * 0 + fABFF * fAAEF * 0 + fABFF * fABEF * d1 / 4 + fABFF * fBBEF * d1 / 2 +
fABFF * fAAFF * 0 + fABFF * fABFF * d1 / 2 + fABFF * fBBFF * (d1) + fBBFF * fAAEE * 0 +
fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 1 / 4 +
fBBFF * fBBEF * 1 / 2 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 1 / 2 + fBBFF * fBBFF * 1 + 0]
```

$$\frac{1}{8}\,(4\,\mathrm{fAAEE}+2\,(\mathrm{fAAEF}+\mathrm{fABEE})+\mathrm{fABEF})\,(2\,\mathrm{fAAEE}+\mathrm{fAAEF}-(-1+\mathrm{d0})\,(2\,\mathrm{fABEE}+\mathrm{fABEF}))$$

$$\frac{1}{8}\,(\mathrm{fAAEF}\,(2\,\mathrm{fABEE}+4\,\mathrm{d0}\,\mathrm{fABEE}+\mathrm{fABEF}+2\,\mathrm{d0}\,\mathrm{fABEF}+8\,\mathrm{fBBEE}+4\,\mathrm{fBBEF})+ 2\,\mathrm{fAAEE}\,((2+4\,\mathrm{d0})\,\mathrm{fABEE}+\mathrm{fABEF}+2\,\mathrm{d0}\,\mathrm{fABEF}+8\,\mathrm{fBBEE}+4\,\mathrm{fBBEF})+ (2\,\mathrm{fABEE}+\mathrm{fABEF})\,(2\,\mathrm{fABEE}+\mathrm{fABEF}-(-3+2\,\mathrm{d0})\,(2\,\mathrm{fBBEE}+\mathrm{fBBEF})))$$

$$\frac{1}{8}\,(\mathrm{d0}\,(2\,\mathrm{fABEE}+\mathrm{fABEF})+2\,\mathrm{fBBEE}+\mathrm{fBBEF})\,(2\,\mathrm{fABEE}+\mathrm{fABEF}+4\,\mathrm{fBBEE}+2\,\mathrm{fBBEF})$$

$$\frac{1}{8}\left(4\,\mathrm{fAAEF}^2+2\,\mathrm{fAAEE}\,(4\,\mathrm{fAAEF}+8\,\mathrm{fAAFF}+3\,\mathrm{fABEF}-2\,\mathrm{d0}\,\mathrm{fABEF}+2\,\mathrm{fABFF}+4\,\mathrm{d0}\,\mathrm{fABFF})- (2\,\mathrm{fABEE}+\mathrm{fABEF})\,((-6+4\,\mathrm{d1})\,\mathrm{fAAFF}+(-2+\mathrm{d0}+\mathrm{d1})\,(\mathrm{fABEF}+2\,\mathrm{fABFF}))+ \mathrm{fAAEF}\,(8\,\mathrm{fAAFF}-2\,((-3+2\,\mathrm{d1})\,\mathrm{fABEE}+(-3+\mathrm{d0}+\mathrm{d1})\,\mathrm{fABEF}+(-3+2\,\mathrm{d0})\,\mathrm{fABFF}))\right)$$

$$\frac{1}{4}\left(2\,\mathrm{fABEE}\,\mathrm{fABEF}+\mathrm{fABEF}^2+4\,\mathrm{fABEE}\,\mathrm{fABFF}+2\,\mathrm{fABEF}\,\mathrm{fABFF}+3\,\mathrm{fABEF}\,\mathrm{fBBEE}- 2\,\mathrm{d0}\,\mathrm{fABEF}\,\mathrm{fBBEE}+2\,\mathrm{fABFF}\,\mathrm{fBBEE}+4\,\mathrm{d0}\,\mathrm{fABFF}\,\mathrm{fBBEE}+3\,\mathrm{fABEE}\,\mathrm{fBBEF}- 2\,\mathrm{d1}\,\mathrm{fABEE}\,\mathrm{fBBEF}+3\,\mathrm{fABEF}\,\mathrm{fBBEF}-\mathrm{d0}\,\mathrm{fABEF}\,\mathrm{fBBEF}-\mathrm{d1}\,\mathrm{fABEF}\,\mathrm{fBBEF}+3\,\mathrm{fABFF}\,\mathrm{fBBEF}- 2\,\mathrm{d0}\,\mathrm{fABFF}\,\mathrm{fBBEF}+\mathrm{fAAFF}\,((2+4\,\mathrm{d1})\,\mathrm{fABEE}+\mathrm{fABEF}+2\,\mathrm{d1}\,\mathrm{fABEF}+8\,\mathrm{fBBEE}+4\,\mathrm{fBBEF})- (-3+2\,\mathrm{d1})\,(2\,\mathrm{fABEE}+\mathrm{fABEF})\,\mathrm{fBBFF}+ \mathrm{fAAEE}\,(\mathrm{fABEF}+2\,\mathrm{d0}\,\mathrm{fABEF}+6\,\mathrm{fABFF}-4\,\mathrm{d0}\,\mathrm{fABFF}+4\,\mathrm{fBBEF}+8\,\mathrm{fBBFF})+\mathrm{fAAEF}\, (\mathrm{fABEE}+2\,\mathrm{d1}\,\mathrm{fABEE}+(1+\mathrm{d0}+\mathrm{d1})\,\mathrm{fABEF}+\mathrm{fABFF}+2\,\mathrm{d0}\,\mathrm{fABFF}+4\,(\mathrm{fBBEE}+\mathrm{fBBEF}+\mathrm{fBBFF}))\right)$$

$$\frac{1}{8}\left(\mathrm{d0}\,\left(\mathrm{fABEF}^2+2\,\mathrm{fABEE}\,(\mathrm{fABEF}+2\,\mathrm{fABFF})+ 4\,\mathrm{fABFF}\,(-2\,\mathrm{fBBEE}+\mathrm{fBBEF})+2\,\mathrm{fABEF}\,(\mathrm{fABFF}+2\,\mathrm{fBBEE}+\mathrm{fBBEF})\right)+ 2\,(\mathrm{fABFF}\,(6\,\mathrm{fBBEE}+\mathrm{fBBEF})+\mathrm{fABEF}\,(\mathrm{fBBEE}+\mathrm{fBBEF}+\mathrm{fBBFF})+ (\mathrm{fABEE}+4\,\mathrm{fBBEE}+2\,\mathrm{fBBEF})\,(\mathrm{fBBEF}+2\,\mathrm{fBBFF}))+ \mathrm{d1}\,(2\,\mathrm{fABEE}+\mathrm{fABEF})\,(\mathrm{fABEF}+2\,(\mathrm{fABFF}+\mathrm{fBBEF}+2\,\mathrm{fBBFF}))\right)$$

$$\frac{1}{8}\,(2\,\mathrm{fAAEF}+4\,\mathrm{fAAFF}+\mathrm{fABEF}+2\,\mathrm{fABFF})\,(\mathrm{fAAEF}+2\,\mathrm{fAAFF}-(-1+\mathrm{d1})\,(\mathrm{fABEF}+2\,\mathrm{fABFF}))$$

$$\frac{1}{8}\left(\text{fAAEF}\left(\text{fABEF}+2\,\text{d1 fABEF}+2\,\text{fABFF}+4\,\text{d1 fABFF}+4\,\text{fBBEF}+8\,\text{fBBFF}\right)+2\,\text{fAAFF}\left(\text{fABEF}+2\,\text{d1 fABEF}+2\,\text{fABFF}+4\,\text{d1 fABFF}+4\,\text{fBBEF}+8\,\text{fBBFF}\right)+\left(\text{fABEF}+2\,\text{fABFF}\right)\left(\text{fABEF}+2\,\text{fABFF}-(-3+2\,\text{d1})\left(\text{fBBEF}+2\,\text{fBBFF}\right)\right)\right)$$

$$\frac{1}{8}\left(\text{d1}\left(\text{fABEF}+2\,\text{fABFF}\right)+\text{fBBEF}+2\,\text{fBBFF}\right)\left(\text{fABEF}+2\left(\text{fABFF}+\text{fBBEF}+2\,\text{fBBFF}\right)\right)$$

Selection

```
wAAEE = wAAEF = wAAFF = 1;
wABEE = wABEF = wABFF = 1 - hs;
wBBEE = wBBEF = wBBFF = 1 - s;

W̄ = FullSimplify[(fAAEE_Drive wAAEE + fAAEF_Drive wAAEF + fAAFF_Drive wAAFF
      + fABEE_Drive wABEE + fABEF_Drive wABEF + fABFF_Drive wABFF
      + fBBEE_Drive wBBEE + fBBEF_Drive wBBEF + fBBFF_Drive wBBFF
   )];

fAAEE_Sel = FullSimplify[fAAEE_Drive wAAEE / W̄];
fABEE_Sel = FullSimplify[fABEE_Drive wABEE / W̄];
fBBEE_Sel = FullSimplify[fBBEE_Drive wBBEE / W̄];
fAAEF_Sel = FullSimplify[fAAEF_Drive wAAEF / W̄];
fABEF_Sel = FullSimplify[fABEF_Drive wABEF / W̄];
fBBEF_Sel = FullSimplify[fBBEF_Drive wBBEF / W̄];
fAAFF_Sel = FullSimplify[fAAFF_Drive wAAFF / W̄];
fABFF_Sel = FullSimplify[fABFF_Drive wABFF / W̄];
fBBFF_Sel = FullSimplify[fBBFF_Drive wBBFF / W̄];
fA_Sel = FullSimplify[fAAEE_Sel + fAAEF_Sel + fAAFF_Sel + (fABEE_Sel + fABEF_Sel + fABFF_Sel) / 2];
fB_Sel = FullSimplify[fBBEE_Sel + fBBEF_Sel + fBBFF_Sel + (fABEE_Sel + fABEF_Sel + fABFF_Sel) / 2];
fE_Sel = FullSimplify[fAAEE_Sel + fABEE_Sel + fBBEE_Sel + (fAAEF_Sel + fABEF_Sel + fBBEF_Sel) / 2];
fF_Sel = FullSimplify[fAAFF_Sel + fABFF_Sel + fBBFF_Sel + (fAAEF_Sel + fABEF_Sel + fBBEF_Sel) / 2];
ΔfA = FullSimplify[fA_Sel - fA];
ΔfB = FullSimplify[fB_Sel - fB];
ΔfE = FullSimplify[fE_Sel - fE];
ΔfF = FullSimplify[fF_Sel - fF];

(*ΔfC=FullSimplify[fC_Sel-fC];*)

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

1

1

Analysis

Invasion of sperm-acting drive modifier unlinked to the driver

```
invasionOfUnlinkedModeifier =
 FullSimplify[W̄ ΔfF / fF /. randomHaps /. D → 0 /. sum2one /. minormod] /.
  fF → 0(*this assumes no LD and random mating*)
```

```
-(-1 + fB) fB ((-1 + 2 fB) hs - fB s) ϵ
```

```
(*With some rearangement,
   invasionOfUnlikedModeifier= -ϵ fA fB(fB s+(fA-fB) hs))
  So long as sh⩽s, [
 i.e. the driver does not have an underdominant effect on fitness]  this is
 guaranteed to be positive when ϵ is negative [i.e. the modifier dampens drive]*)
```

Fixation of sperm-acting drive modifier unlinked to the driver

```
fixationOfUnlinkedModeifier = FullSimplify[
  FullSimplify[W̄ ΔfF / (1 - fF) /. randomHaps /. D → 0 /. sum2one /. minormod] /. fF → 1]
  (*this assumes no LD and random mating*)
```

```
(-1 + fB) fB (hs - 2 fB hs + fB s) ϵ
```

```
(*Thus the invasion and fixation conditions are equivalent*)
```