# Brandvain and Coop. Sperm dependent female meiotic drive

In[2053]:=

### 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[2054]:=
```
(*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[2059]:=
```
(*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[2062]:=
```
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[2071]:=
```
ΔfBinvade = (FullSimplify[ΔfB /. hs → 0 /. x → 0] / fB^2 /. fB → 0)
```

Out[2071]=
$$\frac{1}{2}\left(-1+d\,(2-4\,s)\right)$$

In[2072]:=
```
spermDepReceesiveInvade = Solve[ΔfBinvade == 0, s]
```

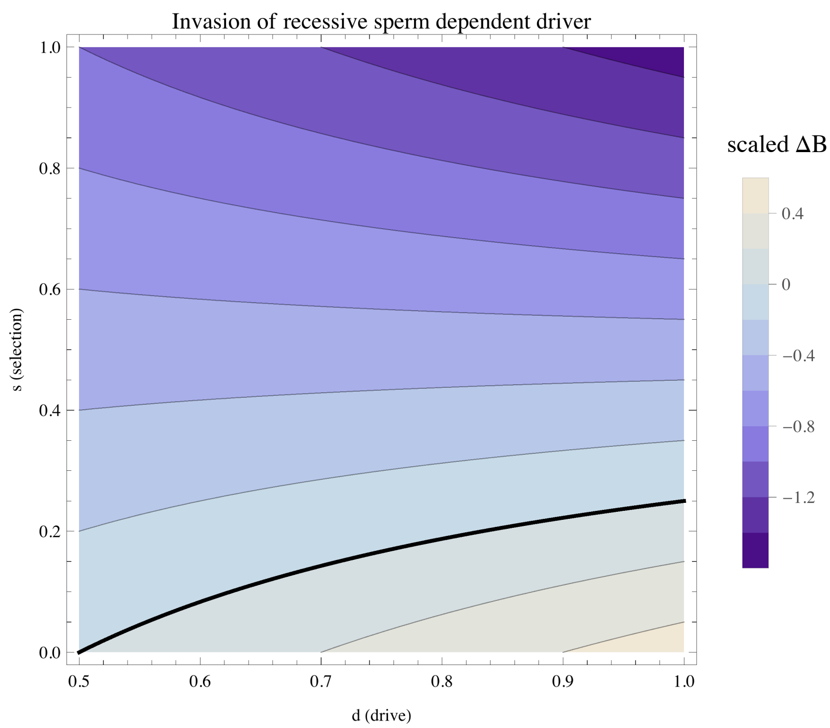
Out[2072]=
$$\left\{\left\{s\to\frac{-1+2\,d}{4\,d}\right\}\right\}$$

In[2073]:=
```
plotInvasion4spermDepRecessive =
  Plot[s /. spermDepReceesiveInvade [[1]], {d, .5, 1}, PlotStyle → {Black, Thick}];
```

In[2074]:=
```
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"];
```

In[2075]:=
```
Show[plotRelChange4RarespermDepRecessive, plotInvasion4spermDepRecessive]
```

Out[2075]=




## Fixation

In[2076]:=
```
ΔfBfix = FullSimplify[FullSimplify[ΔfB /. hs → 0 /. x → 0] / fA] /. fB → 1
```

Out[2076]=
$$\frac{-1+2\,d-2\,s}{2-2\,s}$$

In[2077]:= 
```
spermDepReceesiveFix = Solve[ΔfBfix == 0, s]
```

Out[2077]= $\left\{\left\{s \to \frac{1}{2}(-1+2d)\right\}\right\}$

In[2078]:= 
```
(s /. spermDepReceesiveFix [[1]])
```

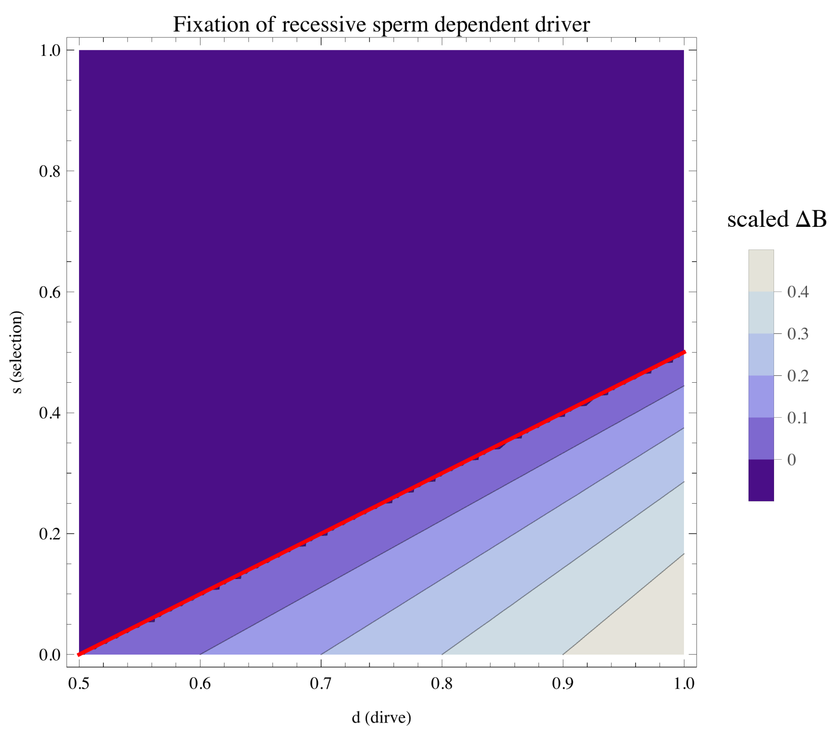
Out[2078]= $\frac{1}{2}(-1+2d)$

In[2079]:= 
```
plotFixation4spermDepRecessive =
  Plot[s /. spermDepReceesiveFix [[1]], {d, .5, 1}, PlotStyle → {Red, Thick}];
```

In[2080]:= 
```
(*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"];
```

In[2081]:= 
```
Show[plotRelChange4CommonSpermDepRecessive, plotFixation4spermDepRecessive]
```

Out[2081]=




## Bistability Point

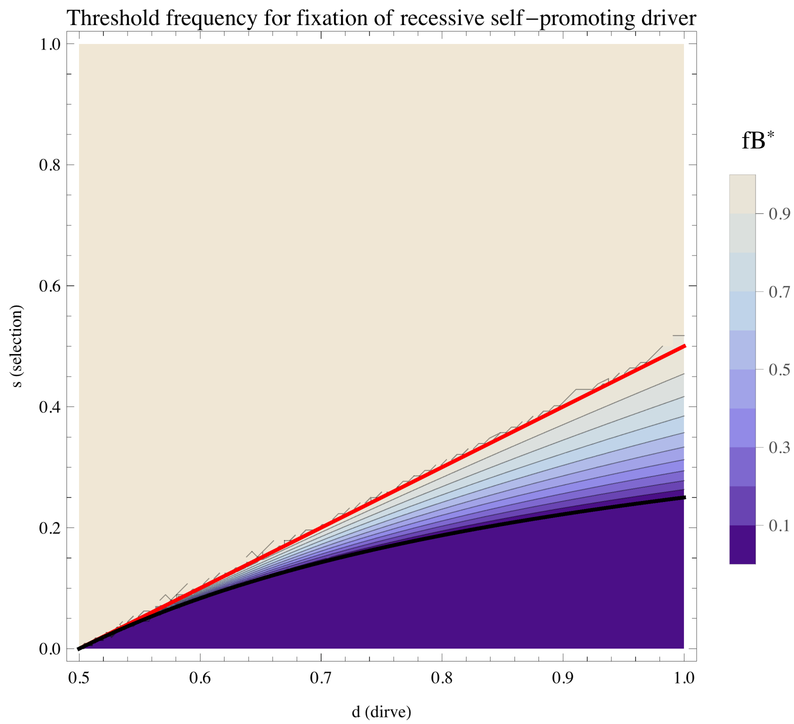
In[2082]:= 
```
FBbistabSpermDepReceesive = Solve[FullSimplify[ΔfB /. hs → 0 /. x → 0] == 0, fB][[4]]
```

Out[2082]= $\left\{fB \to \frac{1-2d+4ds}{-2s+4ds}\right\}$

In[2083]:=
```
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"];
```

In[2084]:=
```
Show[bistab, plotFixation4spermDepRecessive, plotInvasion4spermDepRecessive]
```

Out[2084]=




# 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[2085]:=
```
FullSimplify[FullSimplify[ΔfB /. x → 0] / fB] /. fB → 0
```

Out[2085]= $-hs$

## Fixation

In[2086]:=
```
ΔfBfix = FullSimplify[FullSimplify[FullSimplify[ΔfB /. x → 0] / fA] /. fB → 1]
```

Out[2086]= $$\frac{1 + 2\, d\, (-1 + hs) - 3\, hs + 2\, s}{2\, (-1 + s)}$$

In[2087]:=
```
spermDepNotReceesiveFix = Solve[ΔfBfix == 0, s]
```

Out[2087]= $$\left\{\left\{s \to \frac{1}{2}\, (-1 + 2\, d + 3\, hs - 2\, d\, hs)\right\}\right\}$$

In[2088]:=
```
spermDepAddFix = Solve[ΔfBfix == 0 /. hs → s / 2, s]
```

Out[2088]=
$$\left\{\left\{s \to \frac{2\,(-1+2\,d)}{1+2\,d}\right\}\right\}$$

In[2089]:=
```
plotspermDepAddFix =
  Plot[s /. spermDepAddReceesiveFix , {d, .5, 1}, PlotStyle → {Red, Thick}];
```

## Bistability Point

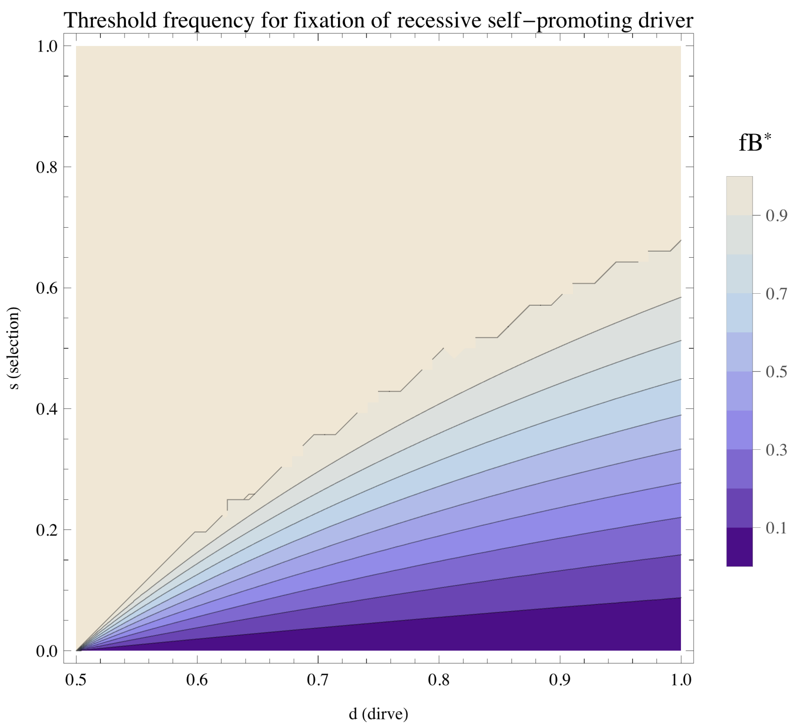
In[2090]:=
```
FBbistabSpermDepNotReceesive = Solve[FullSimplify[ΔfB /. x → 0] == 0, fB][[3]]
```

Out[2090]=
$$\left\{fB \to \left(-1+2\,d+3\,hs+2\,d\,hs-4\,d\,s-\sqrt{-8\,hs\,(-2\,hs+4\,d\,hs+2\,s-4\,d\,s)+(1-2\,d-3\,hs-2\,d\,hs+4\,d\,s)^2}\right)\Big/\left(2\,(-2\,hs+4\,d\,hs+2\,s-4\,d\,s)\right)\right\}$$

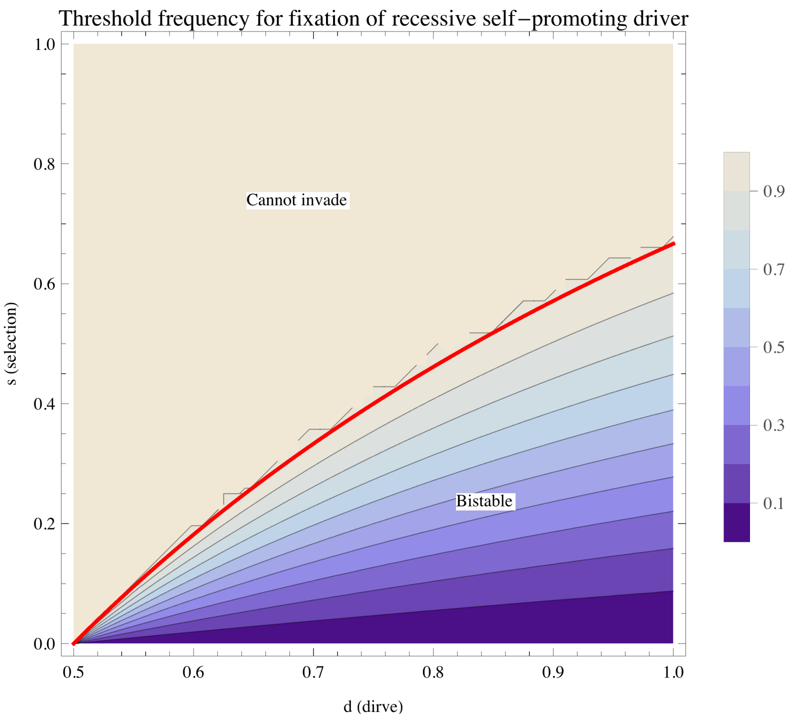
An Example of a non - recessive driver [Assuming additivity]

In[2091]:=
```
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"];
```

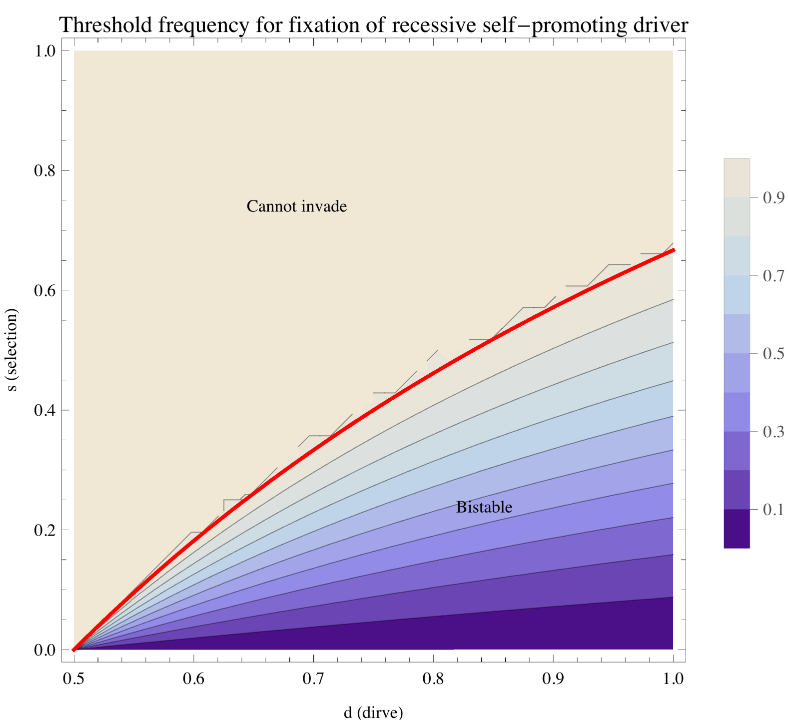
In[2092]:=
```
Show[bistab, plotspermDepAddFix]
```

Out[2092]=


In[2093]:=




Out[2093]=



In[2094]:=

### 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[2095]:=
```
(*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[2100]:=
```
(*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[2103]:=
```
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[2112]:=
```
invasion4maleDepRecessive =
 Solve[((FullSimplify[(ΔfB /. x → 0 /. hs → 0)] / fB^2) /. fB → 0) == 0, s]
```

Out[2112]= $\left\{\left\{s \to \frac{-1 + 2\,dh}{2\,dh}\right\}\right\}$

In[2113]:=
```
plotiInvasion4maleDepRecessive = Plot[s /. invasion4maleDepRecessive /. dh -> d,
   {d, .5, 1}, PlotStyle -> {Black, Thick}];
```

### Fixation

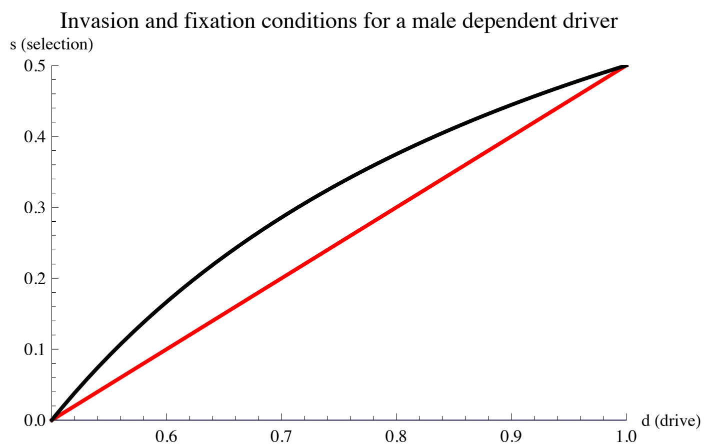
In[2114]:=
```
fixation4maleDepRecessive =
 Solve[(FullSimplify[(FullSimplify[(ΔfB /. x → 0 /. hs → 0) / fA] /. fB → 1)]) == 0, s]
```

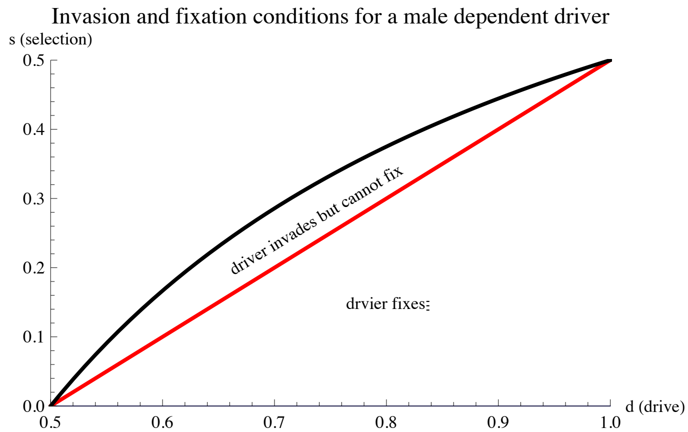
Out[2114]= $\left\{\left\{s \to \frac{1}{2}\,(-1 + 2\,d)\right\}\right\}$

In[2115]:=
```
plotFixation4maleDepRecessive = Plot[s /. fixation4maleDepRecessive /. dh -> d,
   {d, .5, 1}, PlotStyle -> {Red, Thick}];
```

In[2116]:=
```
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]
```

Out[2116]=






## Bistability

In[2117]:=
```
FBbistabMaleepReceesive =
 Solve[FullSimplify[ΔfB /. x → 0 /. hs → 0 /. dh → d] == 0, fB][[4]]
```

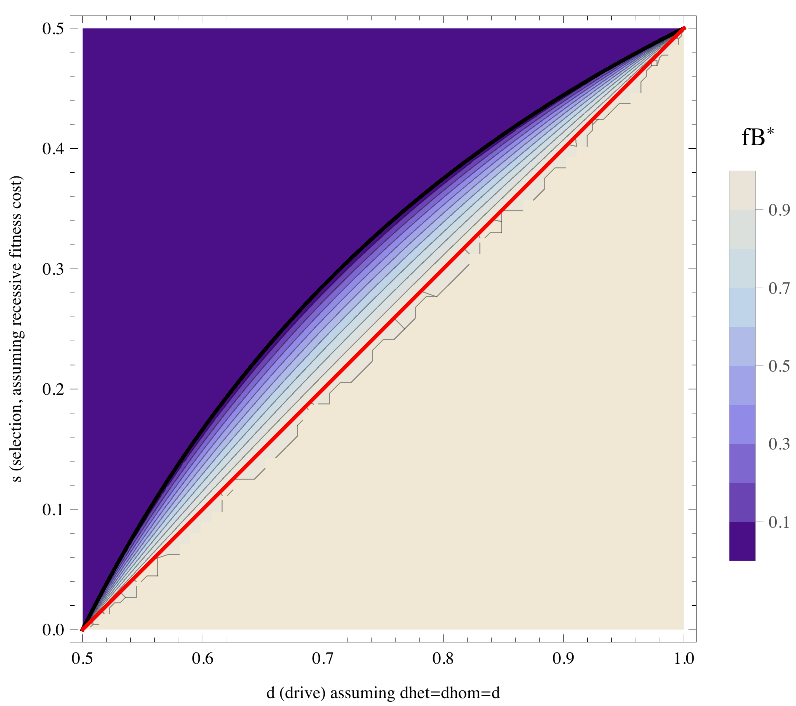
Out[2117]=
$$\left\{fB \to \frac{2\ (1 - 2\,d + 2\,d\,s)}{(-1 + 2\,d)\ (-1 + 2\,s)}\right\}$$

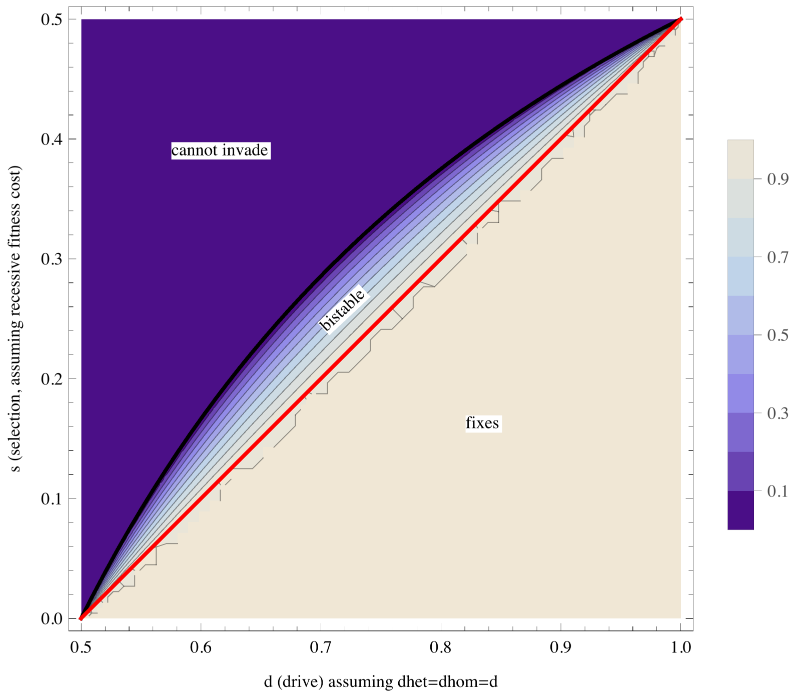
In[2118]:=

In[2119]:=
```
bistab = ContourPlot[ (If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabMaleepReceesive,
   {d, 0.5, 1}, {s, 0, .5}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB*"],
   FrameLabel → {"d (drive) assuming dhet=dhom=d",
     "s (selection, assuming recessive fitness cost)"}];
```

In[2120]:=
```
Show[bistab, plotiInvasion4maleDepRecessive, plotFixation4maleDepRecessive]
```

Out[2120]=






In[2121]:=

## 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.
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

In[2122]:=
```
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};
```

In[2134]:=

## Drive

In[2135]:=
```
(*Here we caculate all genotypes after drive. For book-
 keeping purposes we distinguish between reciprocal homozygotes,
but remove this distinction belowsum them below*)
```

In[2136]:=
```
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[2145]:=
```
(*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[2151]= 1

# Selection

In[2152]:=
```
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[2154]= $1 + (fB + fC)\ (-2\ d1\ fC + 2\ d0\ fB\ (-1 + fB + fC) - (fB + fC)\ (fB + fC - 2\ d1\ fC))\ s$

In[2155]:=
```
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[2167]= 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[2168]:=
```
invasionStandardDriver = Solve[
  (FullSimplify[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) / fB] /. fB → 0) == 0, hs]
```

Out[2168]= $\left\{\left\{hs \to \frac{-1 + 2\ d0}{1 + 2\ d0}\right\}\right\}$

**Fixation of standard driver**

In[2169]:=
```
fixationStandardDriver = Solve[
  (FullSimplify[(ΔfB / fA /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0)] /. fB → 1) == 0, s]
```

Out[2169]= $\left\{\left\{s \to \frac{1}{2}\ (-1 + 2\ d0 + 3\ hs - 2\ d0\ hs)\right\}\right\}$

In[2170]:=
```
(*fixation of a standard recessive driver*)
fixationStandardDriver /. hs → 0
```

Out[2170]= $\left\{\left\{s \to \frac{1}{2}\ (-1 + 2\ d0)\right\}\right\}$

## Equilibrium

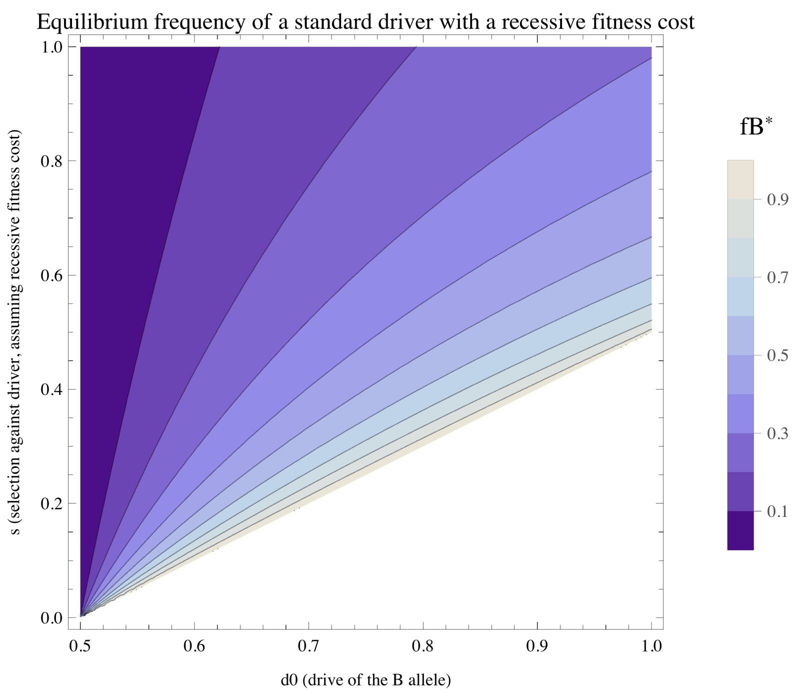
In[2171]:=
```
(*Equilibrium frequency of a standard driver]*)
```

In[2172]:=
```
eqfB = Solve[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) == 0, fB][[4]]
```

Out[2172]=
$$\left\{fB \to \left(8\ d0\ hs - 4\ d0\ s + \sqrt{-4\ (1 - 2\ d0 + hs + 2\ d0\ hs)\ (-4\ hs + 8\ d0\ hs + 2\ s - 4\ d0\ s) + (-8\ d0\ hs + 4\ d0\ s)^2}\right) \Big/ (2\ (-4\ hs + 8\ d0\ hs + 2\ s - 4\ d0\ s))\right\}$$

In[2173]:=
```
(*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

In[2174]:=
```
(*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]
```

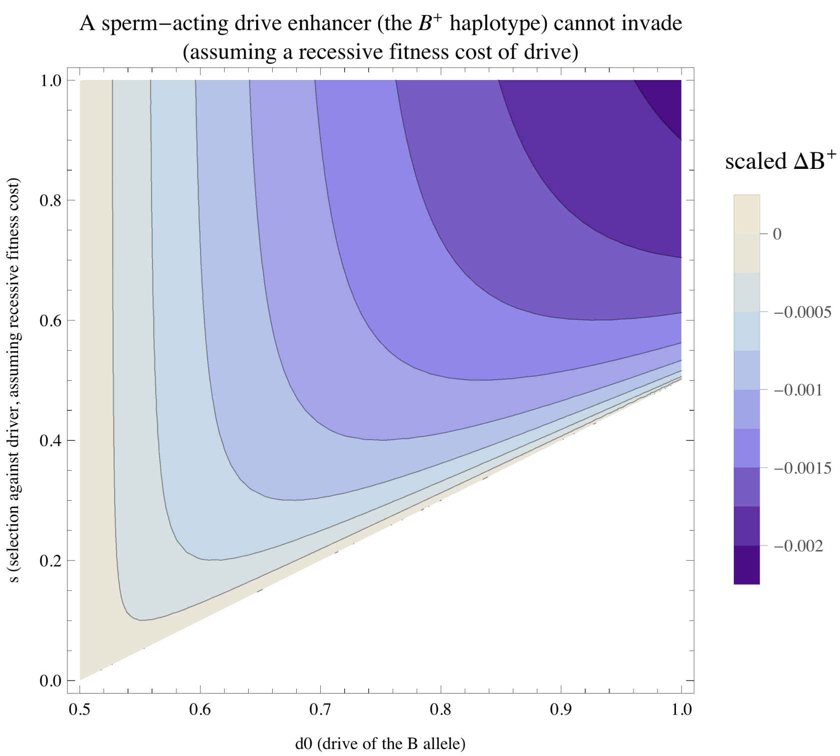
Out[2174]=

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

In[2175]:=
```
(*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*)
```

In[2176]:=
```
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)"}]
```

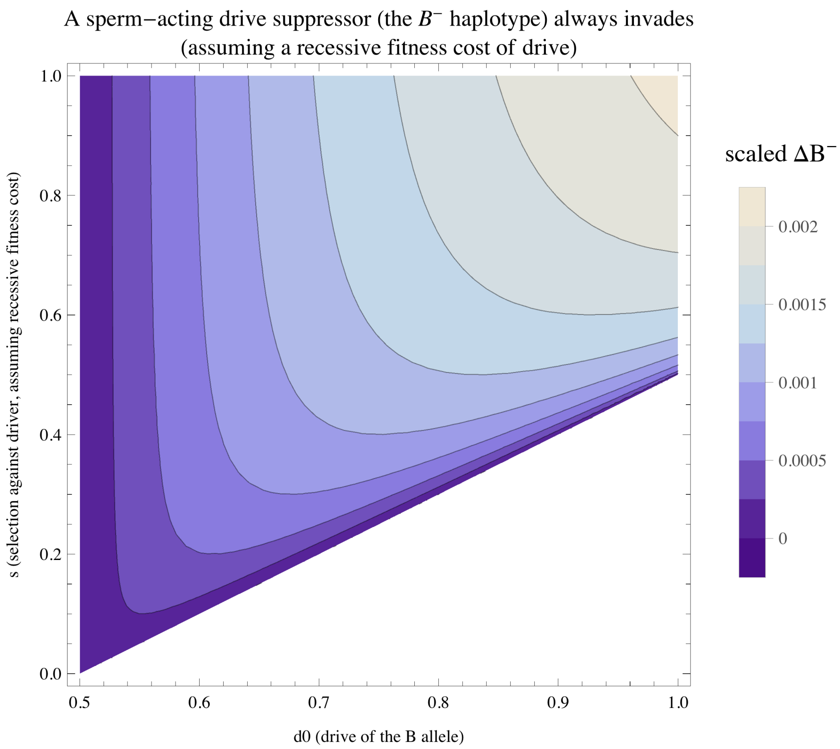
Out[2176]=



In[2177]:=
```
(*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*)
```

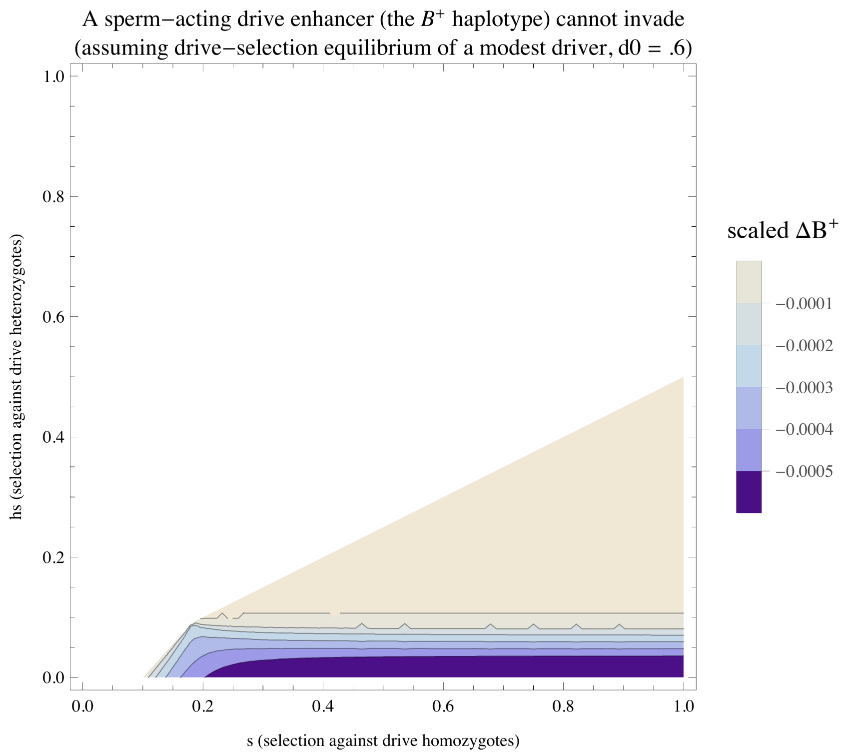
In[2178]:=
```
ContourPlot[
 If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDrive]] /. eqfB /. ϵ → -0.01 /. hs → 0,
 {d0, 0.5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB⁻"],
 PlotLabel → "A sperm-acting drive suppressor (the B⁻ haplotype)
    always invades\n(assuming a recessive fitness cost of drive)",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```

Out[2178]=



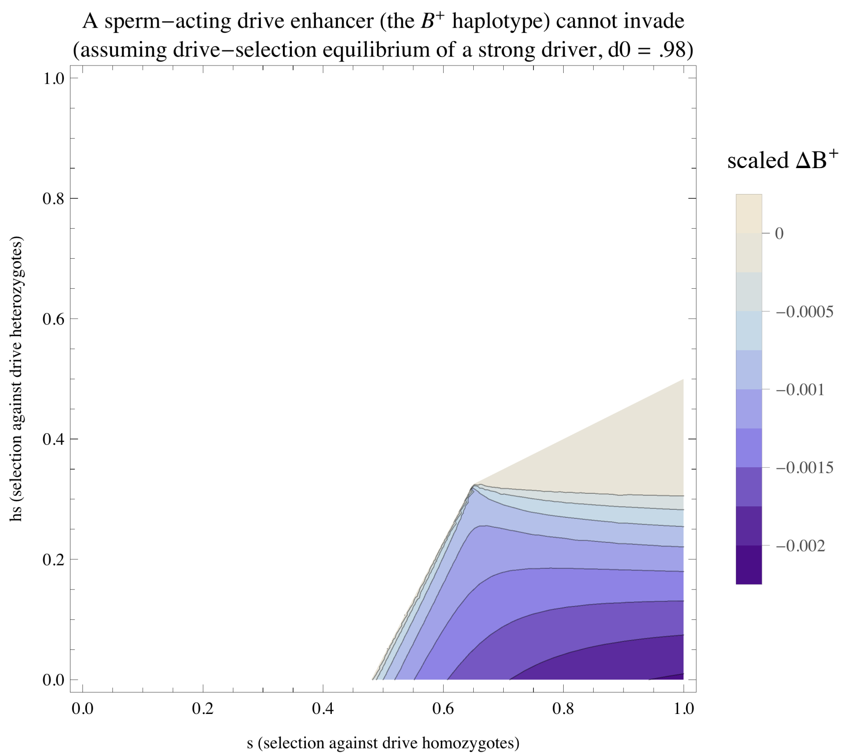
In[2179]:=
```
(*Plotting change this change in frequency when hte extent
 of drive is mild [d0 = .6] and the sperm acting locus is rare
 and increase drive. NOTE: This sperm enhancer never invades*)
ContourPlot[(If[fB > 1, 1 / 0, If[fB < 0.0000001, 0, wbarDeltaSpermDrive]] /. eqfB /.
    ϵ → 0.01 /. 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)"}]
```

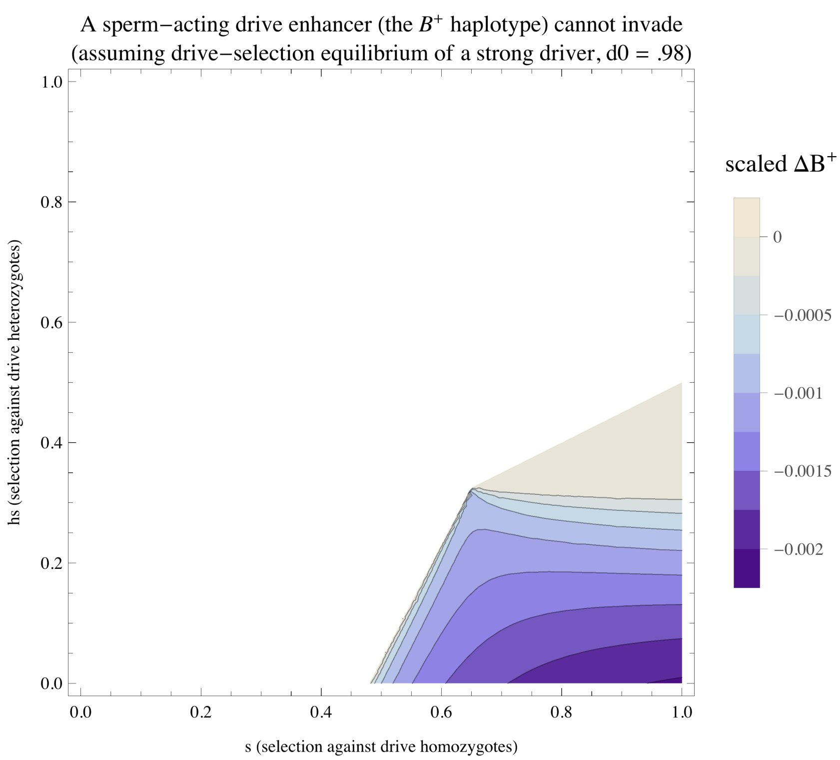
Out[2179]=




In[2180]:=
```
(*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)"}]
```

Out[2180]=


A sperm−acting drive enhancer (the $B^{+}$ haplotype) cannot invade
(assuming drive−selection equilibrium of a strong driver, d0 = .98)
hs (selection against drive heterozygotes)
s (selection against drive homozygotes)
scaled $\Delta B^{+}$
0
−0.0005
−0.001
−0.0015
−0.002
0.0
0.2
0.4
0.6
0.8
1.0


A sperm−acting drive enhancer (the $B^{+}$ haplotype) cannot invade
(assuming drive−selection equilibrium of a strong driver, d0 = .98)
hs (selection against drive heterozygotes)
s (selection against drive homozygotes)
scaled $\Delta B^{+}$
0
−0.0005
−0.001
−0.0015
−0.002
0.0
0.2
0.4
0.6
0.8
1.0

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

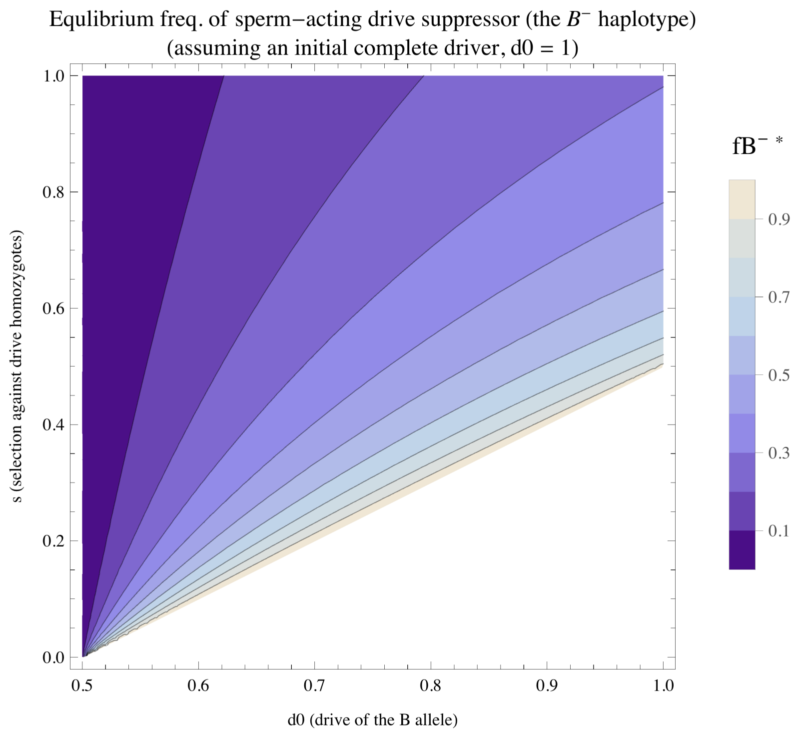
## Equilibrium frequency of drive suppresor

In[2181]:=
```
eqfC = Solve[(FullSimplify[ΔfC /. HWE /. SUMTOONE /. minormod /. fB → 0]) == 0, fC][[4]];
```

In[2182]:=
```
(*Equilibrium frequency of a linked, coupled,
drive suppressor when the fitness costs of drive are recessive*)
```

In[2183]:=
```
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)"}]
```

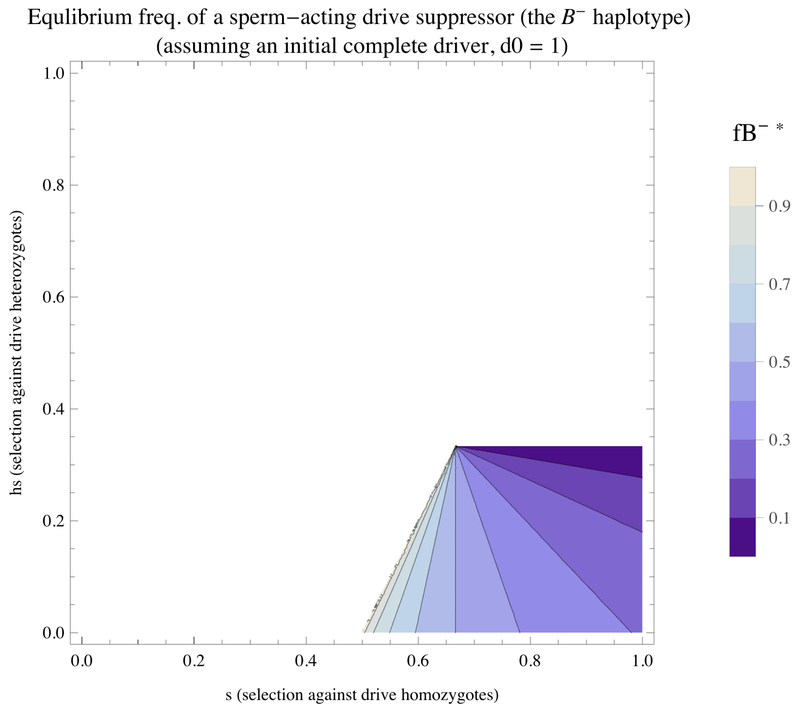
Out[2183]=




In[2184]:=
```
(*Equilibrium frequency of a linked, coupled,
drive suppressor when drive is complete*)
```

In[2185]:=
```
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)"}]
```

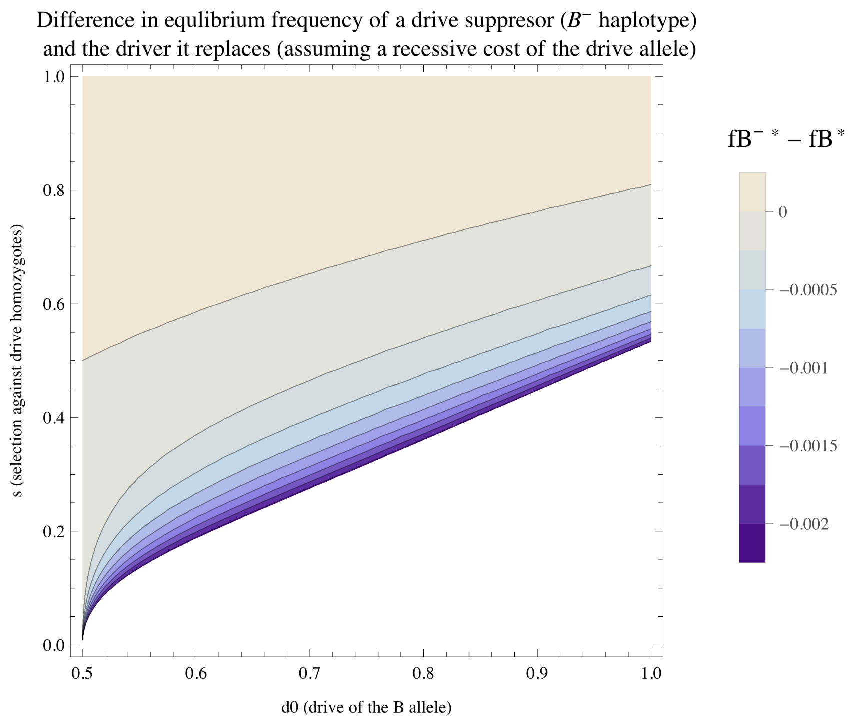
Out[2185]=




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

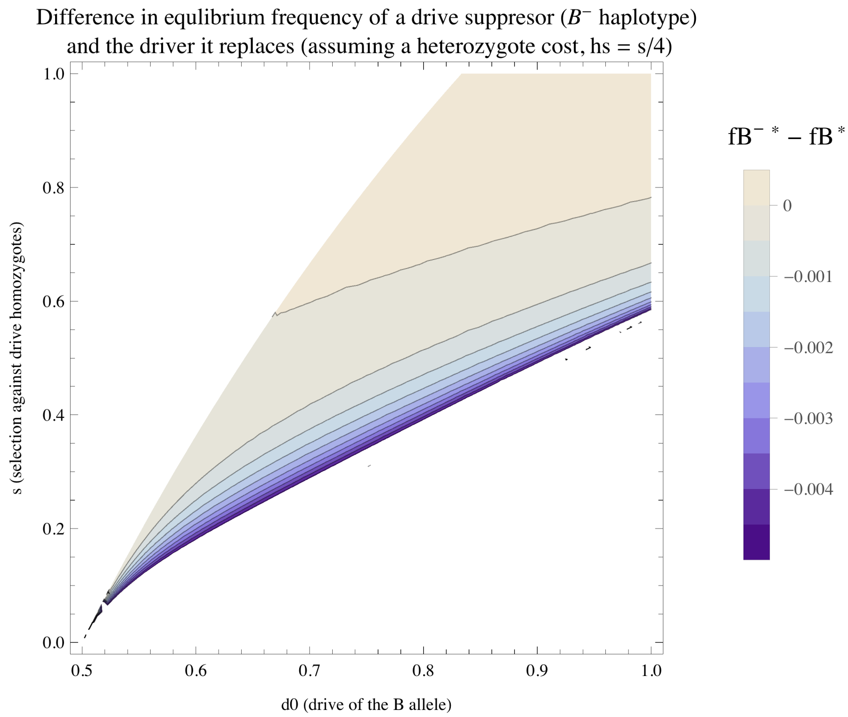
In[2186]:=
```
(*Differecce in equilibrium frequency of the B- and B haplotypes*)
ContourPlot[
 If[fC < 1 && fB < 1 && fC > 0 && fB > 0, (fC - fB), 1 / 0] /. eqfB /. eqfC /. hs → 0 /.
   ϵ → - .001, {d0, .5, 1}, {s, 0, 1},
 PlotLegends → BarLegend[Automatic, LegendLabel → "fB⁻ * - fB*"], PlotLabel →
  "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)"}]
```

Out[2186]=



In[2187]:=
```
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)"}]
```

Out[2187]=

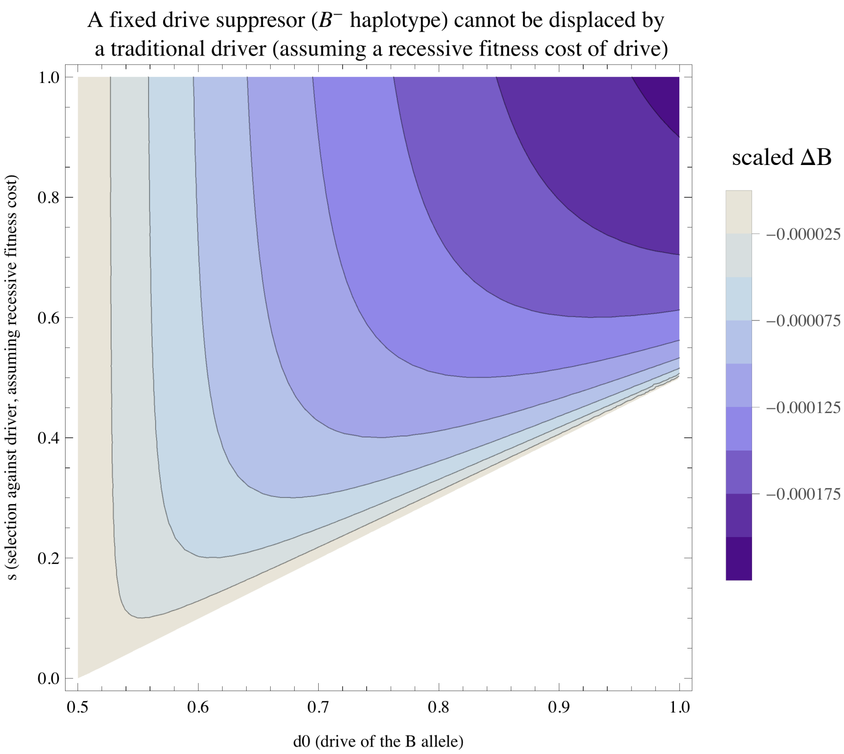



In[2188]:=
```
(*change in frequency of a rare traditional driver when the drive-
 sperm suppressor haplotype and the ondriving hplotype
  are at drive selection equilibrium, mutliplied by
 Wbar/fC [this value is always positive and will not influence the sign]*)
wbarDeltaTradDrive = FullSimplify[
   FullSimplify[W̄ ΔfB / (fB) /. HWE /. SUMTOONE] /. fB → 0 /. eqfC /. minormod];
```

In[2189]:=
```
(*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*)
```

In[2190]:=
```
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)"}]
```

Out[2190]=

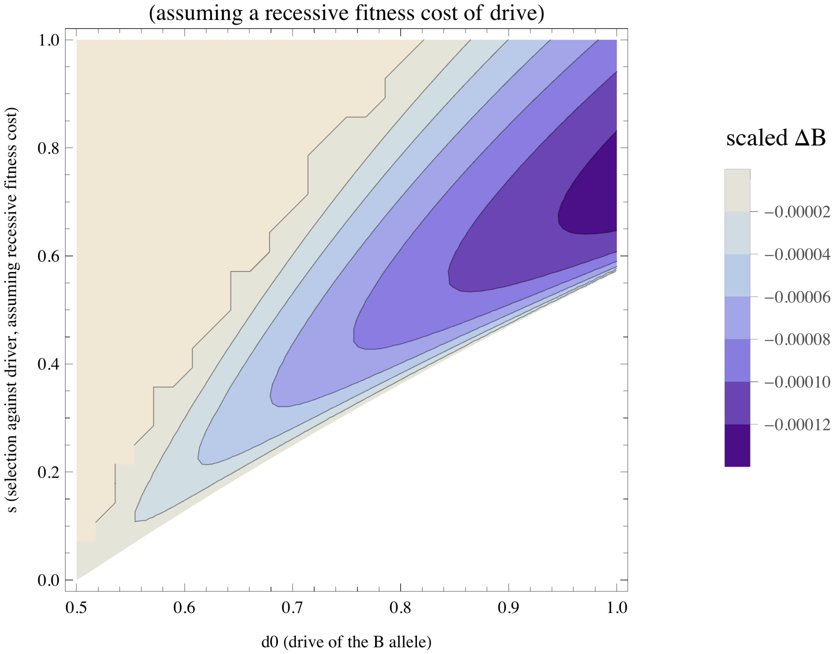



In[2191]:=
```
(*Plotting the change in frequency of a rare traditional
 driving haplotype when the sperm drive suppresor is at drive
 selection balance. ASSUMING a fitness cost of drive in homozygotes
 (hs→s/4). NOTE: This sperm enhancer of drive cannot invade*)
```

In[2192]:=
```
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)"}]
```

Out[2192]=

A fixed sperm−acting drive suppresor cannot be displaced by a traditional
(assuming a recessive fitness cost of drive)



In[2193]:=
```
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)"}]
```

Out[2193]=