Brandvain and Coop. Sperm dependent female meiotic drive

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

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

Setup

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

Drive

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

Selection

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

Analysis

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

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

Invasion

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

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

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

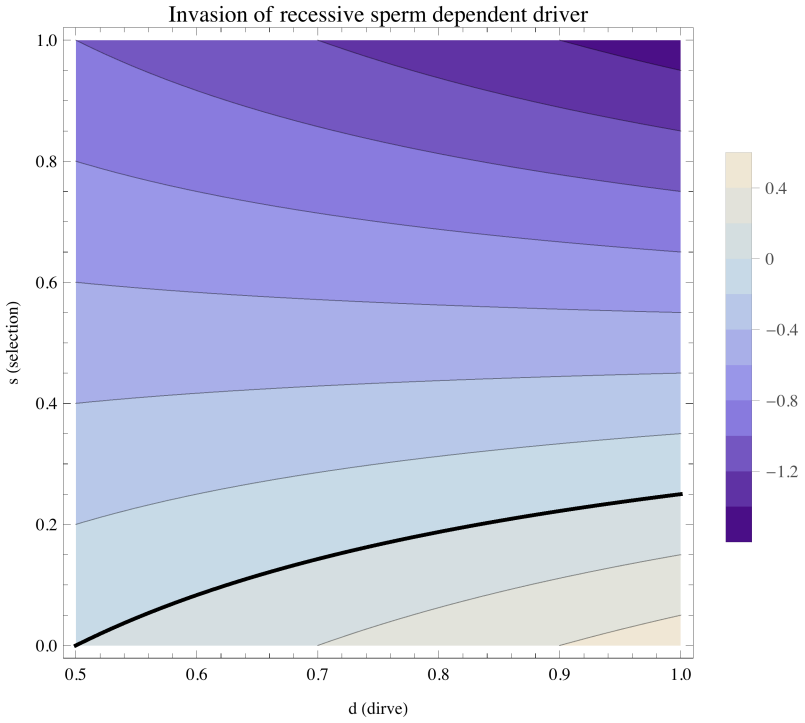
Out[351]=
$$\left\{\left\{s \to \frac{-1+2\,d}{4\,d}\right\}\right\}$$

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

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

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

Out[354]=



Fixation

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

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

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

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

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

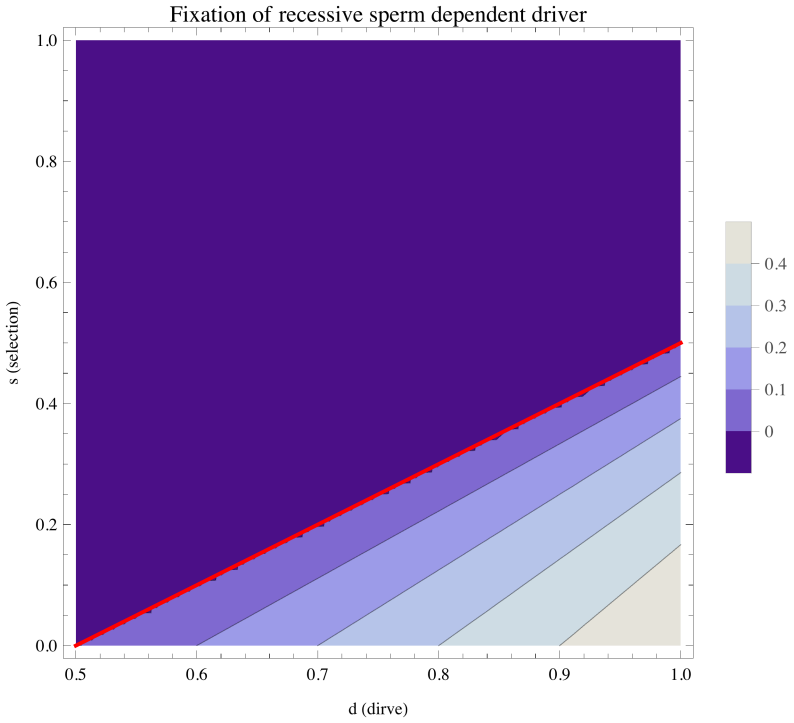
Out[357]=
$$\frac{1}{2}\ (-1+2\,d)$$

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

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

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

Out[360]=



Bistability Point

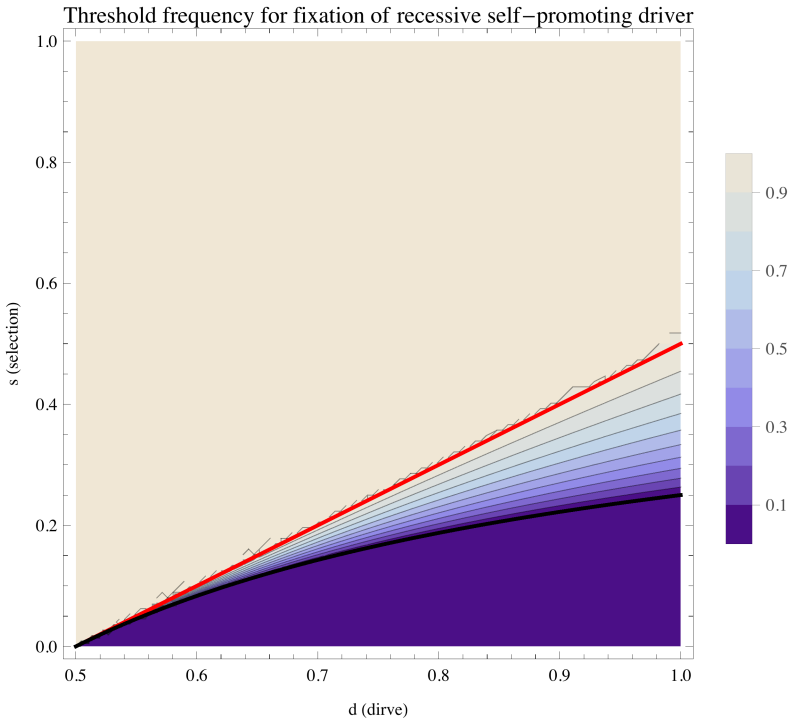
In[361]:=
```
FBbistabSpermDepReceesive = Solve[FullSimplify[ΔfB /. hs → 0 /. x → 0] == 0, fB][[4]]
```

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

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

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

Out[368]=



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

Invasion

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

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

Out[369]=
```
-hs
```

Fixation

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

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

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

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

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

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

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

Bistability Point

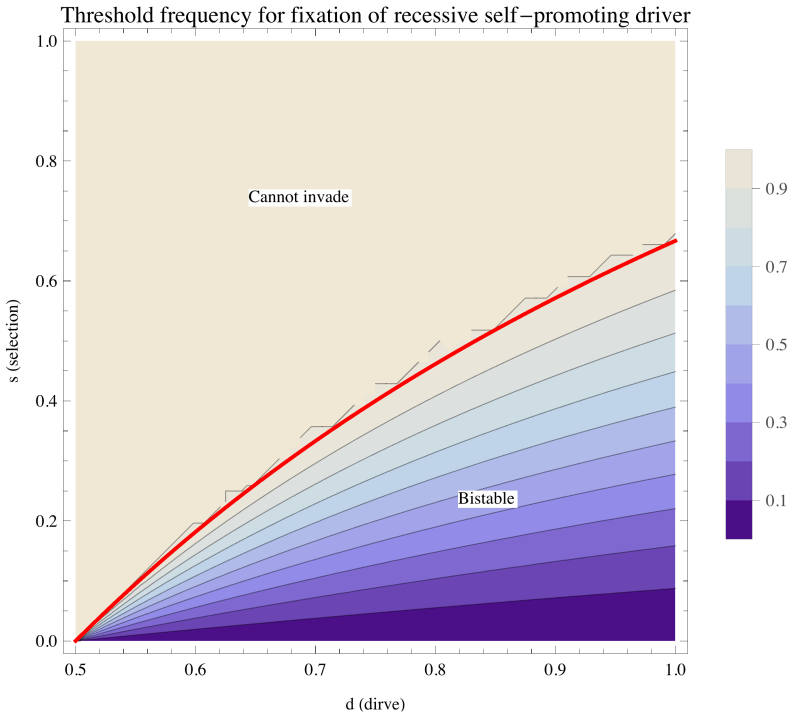
In[374]:=
```
FBbistabSpermDepNotReceesive = Solve[FullSimplify[ΔfB /. x → 0] == 0, fB][[3]]
```

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

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

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

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



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

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

Setup

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

Drive

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

Selection

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

Analysis

Analytical example - recessive fitness cost

Invasion

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

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

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

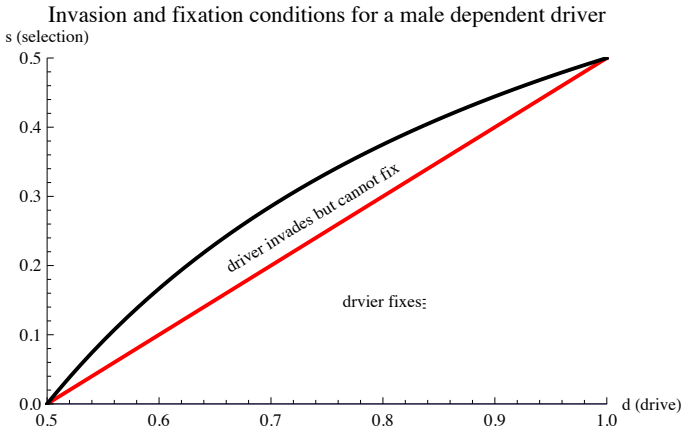
Fixation

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

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

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

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



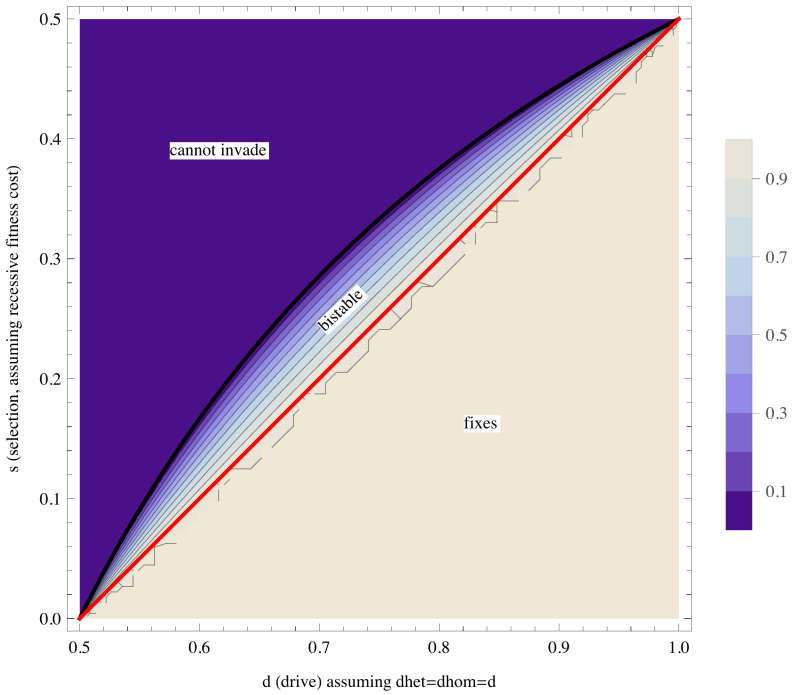
Bistability

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

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

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

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



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

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

Setup

```
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*)
```

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

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

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

Out[1530]= 1

Selection

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

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

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

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

Out[1546]= 1

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

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

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

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

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

Fixation of standard driver

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

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

In[1594]:=
```
(*fixation of a standard recessive driver*)
fixationStandardDriver /. hs → 0
```

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

Equilibrium

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

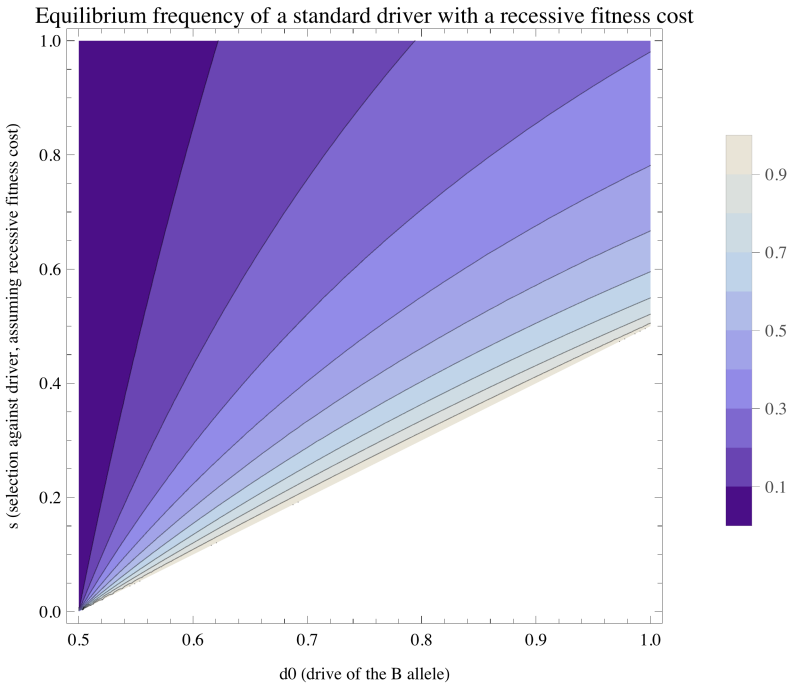
In[1562]:=
```
eqfB = Solve[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) == 0, fB][[4]]
```

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

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

In[1624]:=
```
ContourPlot[If[fB > 1, 1 / 0, If[fB < 0, 1 / 0, fB]] /. eqfB /. hs → 0,
 {d0, .5, 1}, {s, 0, 1}, PlotLegends → Automatic, 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)"}]
```

Out[1624]=



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

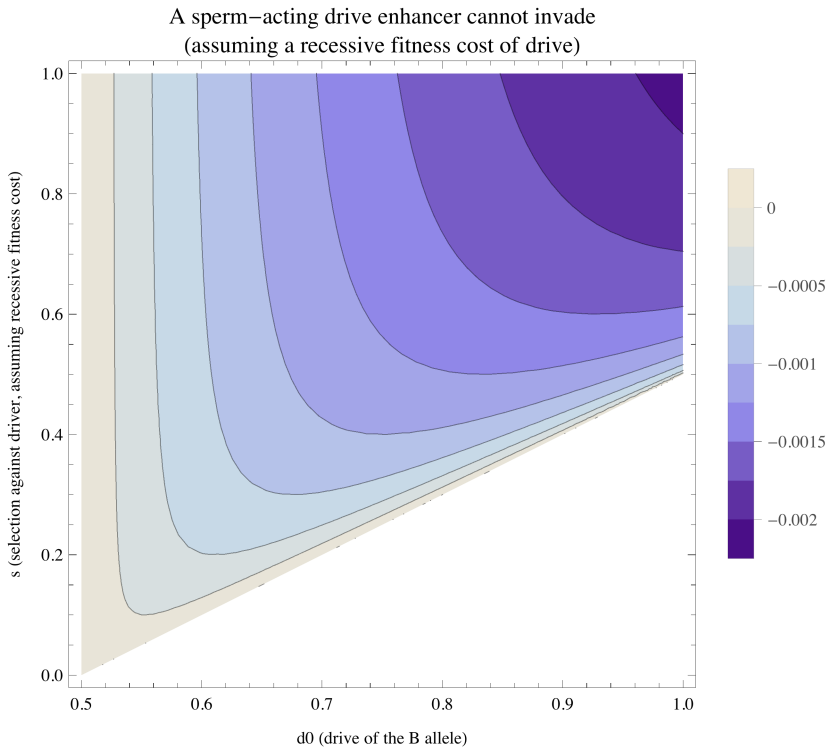
```
(*change in frequency of the drive modifier when rare and when alleles
  at the drive locus are in drive-viability equilibrium, mutliplied by
 Wbar/fC [this value is always positive and will not influence the sign]*)
wbarDeltaSpermDrive = FullSimplify[
  FullSimplify[\[Overline]W ΔfC / (fC) /. HWE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

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

```
(*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[1633]:=
```
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 → Automatic,
 PlotLabel → "A sperm-acting drive enhancer 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)"}]
```

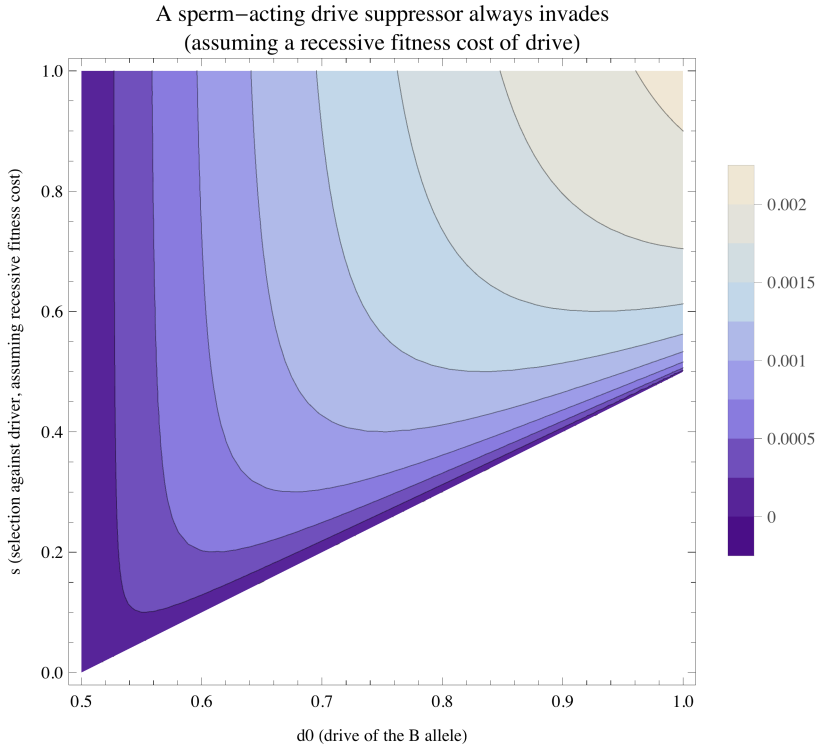
Out[1633]=




```
(*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*)
```

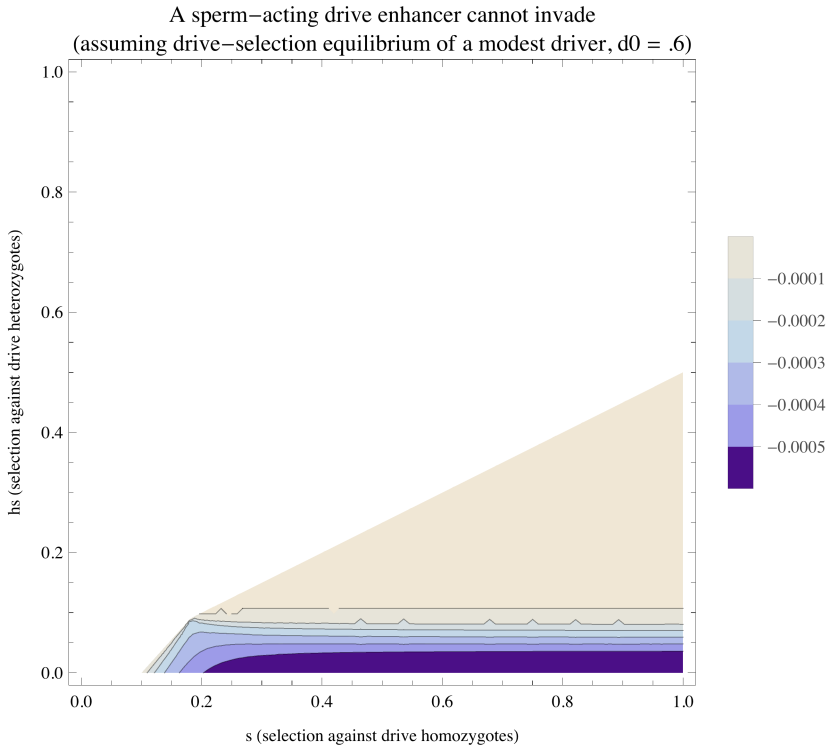
In[1634]:=
```
ContourPlot[
 If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDrive]] /. eqfB /. ϵ → -0.01 /. hs → 0,
 {d0, 0.5, 1}, {s, 0, 1}, PlotLegends → Automatic, PlotLegends → Automatic,
 PlotLabel → "A sperm-acting drive suppressor always
    invades\n(assuming a recessive fitness cost of drive)",
 FrameLabel → {"d0 (drive of the B allele)",
   "s (selection against driver, assuming recessive fitness cost)"}]
```

Out[1634]=



```
(*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 → Automatic,
 PlotLabel → "A sperm-acting drive enhancer 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[1642]=



```
(*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, wbarDeltaSpermDrive]] /. eqfB /. ϵ → 0.01 /.
   d0 → .98), {s, 0, 1}, {hs, 0, 1}, PlotLegends → Automatic,
 PlotLabel → "A sperm-acting drive enhancer 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[1645]=