

Brandvain and Coop. Sperm dependent female meiotic drive

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

The B allele is transmitted with probability, d, in heterozygous females when fertilized by B-bearing sperm.

x represents the deviation from Hardy - Weinberg Equilibrium

Setup

```
In[1914]:= (*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[1919]:= (*Genotype frequencies after drive*)
fAADrive = FullSimplify[fA (fAA + fAB / 2)];
fABDrive = FullSimplify[fB (fAA + fAB * (1 - d)) + fA (fAB / 2 + fBB)];
fBBDrive = FullSimplify[fB (fAB d + fBB)];
```

Selection

```
In[1922]:= wAA = 1; wAB = 1 - hs; wBB = 1 - s; (*genotypic fitnesses*)
W = FullSimplify[fAADrive wAA + fABDrive wAB + fBBDrive wBB]; (*mean fitness*)
fAASel = FullSimplify[(fAADrive * wAA) / W];
fABSel = FullSimplify[(fABDrive * wAB) / W];
fBBSel = FullSimplify[(fBBDrive wBB) / W];
fASel = FullSimplify[fAASel + fABSel / 2];
fBSel = FullSimplify[fBBSel + fABSel / 2];
ΔfA = FullSimplify[fASel - fA];
ΔfB = FullSimplify[fBSel - 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 supplementary 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[1931]:= ΔfBinvade = (FullSimplify[ΔfB /. hs → 0 /. x → 0] / fB^2 /. fB → 0)

Out[1931]=  $\frac{1}{2} (-1 + d (2 - 4 s))$ 

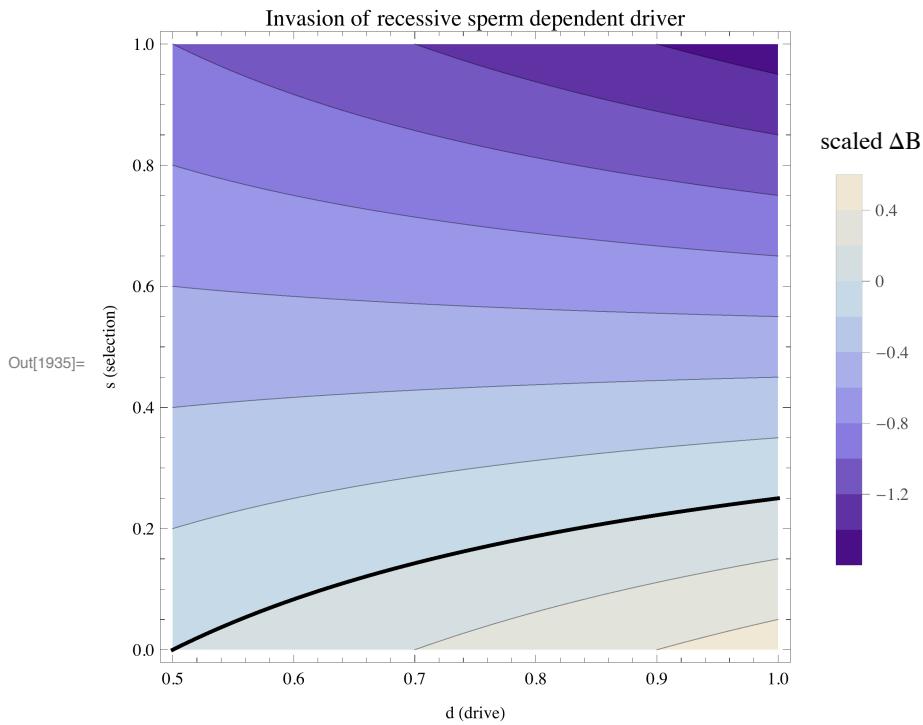
In[1932]:= spermDepRecessiveInvade = Solve[ΔfBinvade == 0, s]

Out[1932]=  $\left\{ \left\{ s \rightarrow \frac{-1 + 2 d}{4 d} \right\} \right\}$ 

In[1933]:= plotInvasion4spermDepRecessive =
  Plot[s /. spermDepRecessiveInvade [[1]], {d, .5, 1}, PlotStyle → {Black, Thick}];

In[1934]:= 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[1935]:= Show[plotRelChange4RarespermDepRecessive, plotInvasion4spermDepRecessive]
```



Fixation

```
In[1936]:= ΔfBfix = FullSimplify[FullSimplify[ΔfB /. hs → 0 /. x → 0] / fA] /. fB → 1

Out[1936]=  $\frac{-1 + 2 d - 2 s}{2 - 2 s}$ 
```

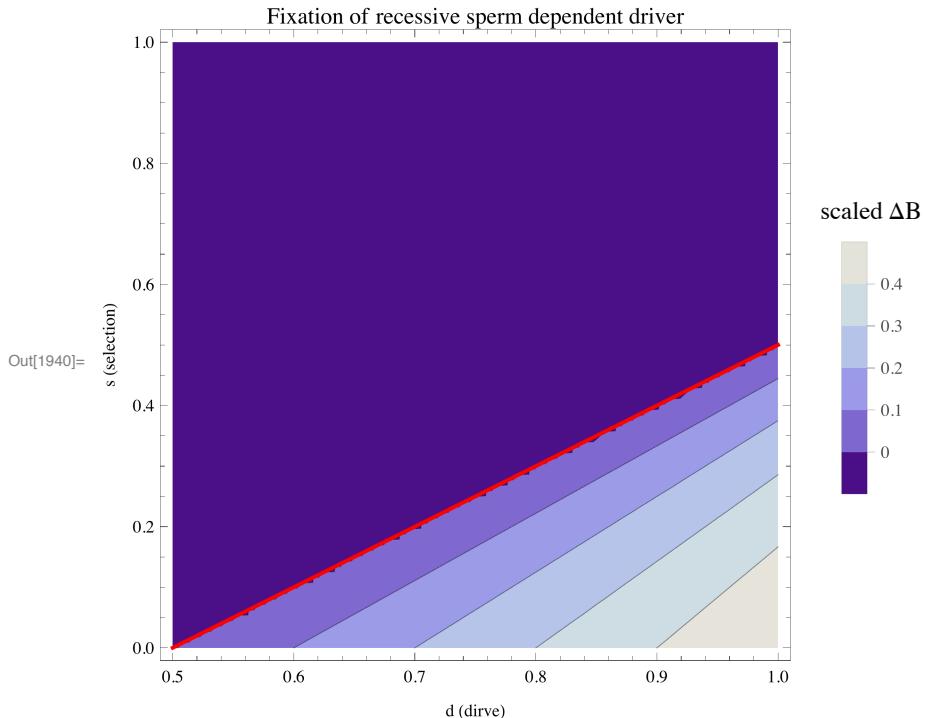
```
In[1937]:= spermDepRecessiveFix = Solve[ $\Delta f_B$ fix == 0, s]
Out[1937]=  $\left\{ \left\{ s \rightarrow \frac{1}{2} (-1 + 2 d) \right\} \right\}$ 

In[357]:= (s /. spermDepRecessiveFix [[1]])
Out[357]=  $\frac{1}{2} (-1 + 2 d)$ 

In[1938]:= plotFixation4spermDepRecessive =
  Plot[s /. spermDepRecessiveFix [[1]], {d, .5, 1}, PlotStyle -> {Red, Thick}];

In[1939]:= (*Note we artificially rescaled z to be -.1 for all negative values*)
plotRelChange4CommonSpermDepRecessive =
  ContourPlot[If[s > (s /. spermDepRecessiveFix [[1]]), -.1,  $\Delta f_B$ fix], {d, 0.5, 1},
  {s, 0, 1}, PlotLegends -> BarLegend[Automatic, LegendLabel -> "scaled  $\Delta B$ ", FrameLabel -> {"d (dirve)", "s (selection)"}, PlotLabel -> "Fixation of recessive sperm dependent driver"];

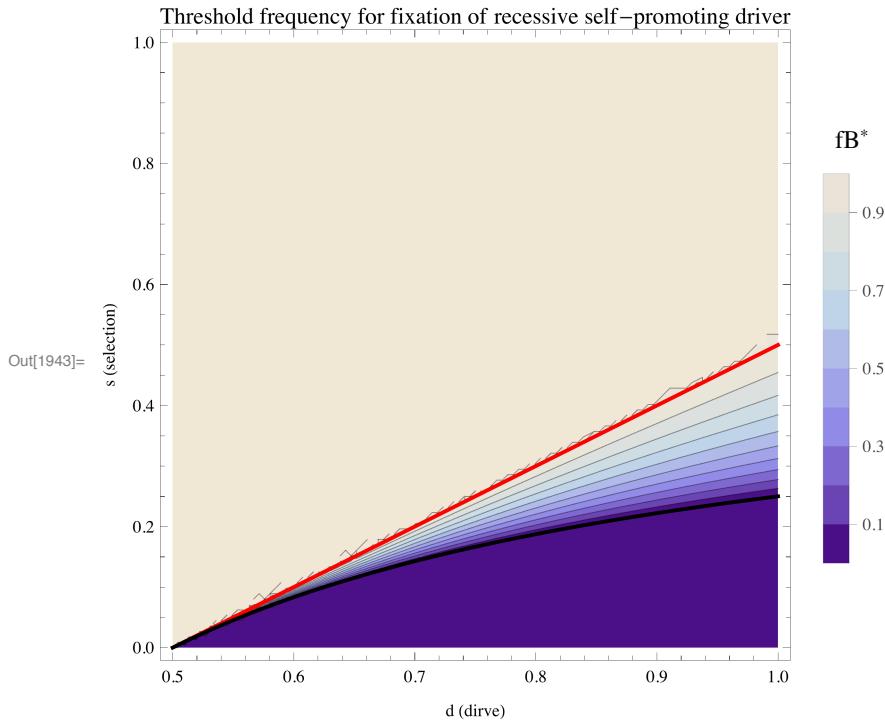
In[1940]:= Show[plotRelChange4CommonSpermDepRecessive, plotFixation4spermDepRecessive]
```



Bistability Point

```
In[1941]:= FBbistabSpermDepRecessive = Solve[FullSimplify[ $\Delta f_B$  /. hs -> 0 /. x -> 0] == 0, fB] [[4]]
Out[1941]=  $\left\{ f_B \rightarrow \frac{1 - 2 d + 4 d s}{-2 s + 4 d s} \right\}$ 
```

```
In[1942]:= bistab = ContourPlot[(If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabSpermDepRecessive,
  {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[1943]:= Show[bistab, plotFixation4spermDepRecessive, plotInvasion4spermDepRecessive]
```



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

Invasion

Note with any heterozygous 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]:= spermDepNotRecessiveFix = Solve[ΔfBfix == 0, s]
Out[371]= 
$$\left\{ \left\{ s \rightarrow \frac{1}{2} (-1 + 2 d) \right\} \right\}$$

```

```
In[1948]:= spermDepAddFix = Solve[ΔfBfix == 0 /. hs → s / 2, s]
Out[1948]= {s → 1/2 (-1 + 2 d)}
```

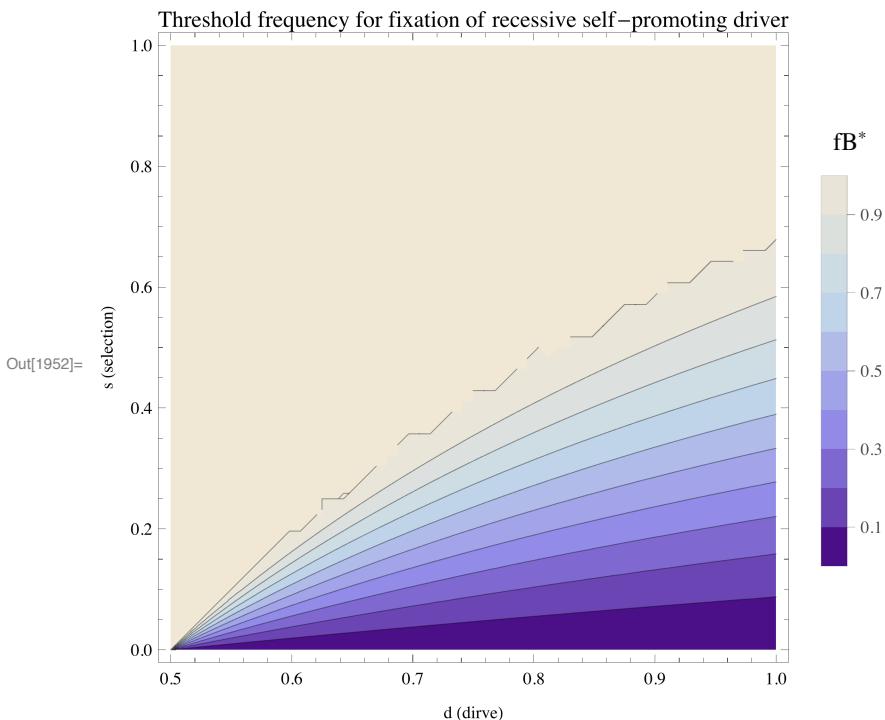
```
In[1949]:= plotspermDepAddFix =
  Plot[s /. spermDepAddReceesiveFix, {d, .5, 1}, PlotStyle → {Red, Thick}];
```

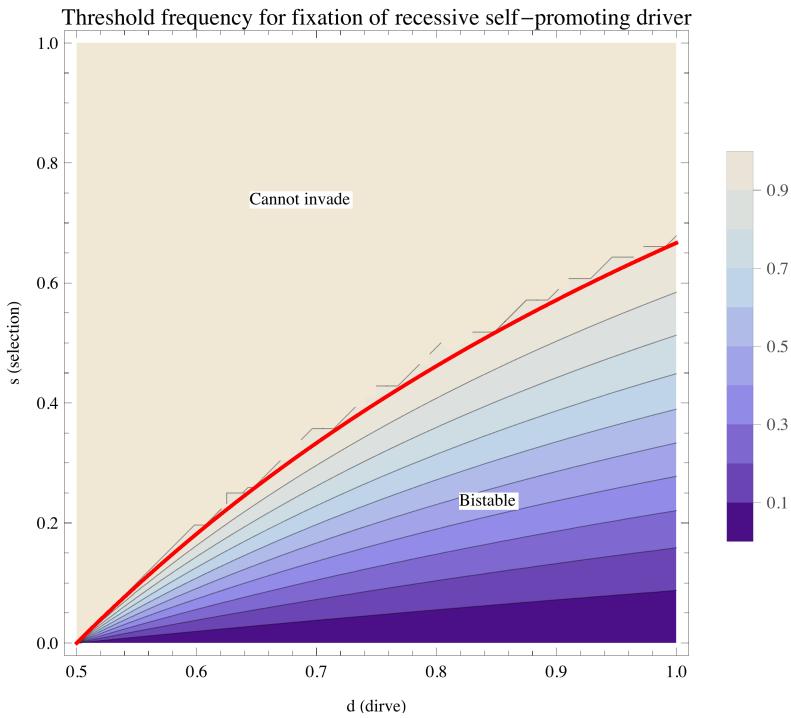
Bistability Point

```
In[1950]:= FBbistabSpermDepNotReceesive = Solve[FullSimplify[ΔfB /. x → 0] == 0, fB][[3]]
Out[1950]= {fB → ((-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])/(2 (-2 hs + 4 d hs + 2 s - 4 d s))}
```

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

```
In[1951]:= 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[1952]:= Show[bistab, plotspermDepAddFix]
```





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

The B allele is transmitted 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[1953]:= (*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[1958]:= (*Genotype frequencies after drive*)
fAADrive = FullSimplify[fAA (fAA + fAB / 2) + fAB (fAA / 2 + fAB (1 - dh) / 2)];
fABDrive = FullSimplify[
  fAA (fAB / 2 + fBB) + fAB (fAA / 2 + fAB / 2 + fBB (1 - d)) + fBB (fAA + fAB / 2)];
fBBDrive = FullSimplify[fAB (fAB dh / 2 + fBB d) + fBB (fAB / 2 + fBB)];
```

Selection

```
In[1961]:= wAA = 1; wAB = 1 - hs; wBB = 1 - s; (*genotypic fitnesses*)
W = FullSimplify[fAADrive wAA + fABDrive wAB + fBBDrive wBB]; (*mean fitness*)
fAASel = FullSimplify[(fAADrive * wAA) / W];
fABSel = FullSimplify[(fABDrive * wAB) / W];
fBBSel = FullSimplify[(fBBDrive wBB) / W];
fASel = FullSimplify[fAASel + fABSel / 2];
fBSel = FullSimplify[fBBSel + fABSel / 2];
ΔfA = FullSimplify[fASel - fA];
ΔfB = FullSimplify[fBSel - fB];
```

Analysis

Analytical example - recessive fitness cost

Invasion

```
In[1970]:= invasion4maleDepRecessive =
  Solve[((FullSimplify[(ΔfB /. x → 0 /. hs → 0)] / fB^2) /. fB → 0) == 0, s]
Out[1970]= {s → -1 + 2 dh / (2 dh)}
```

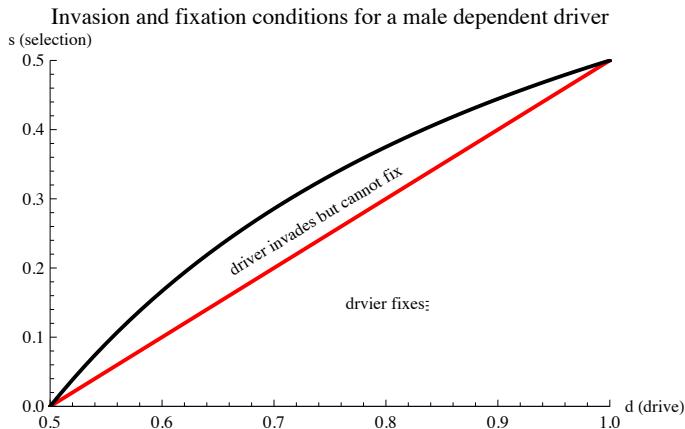
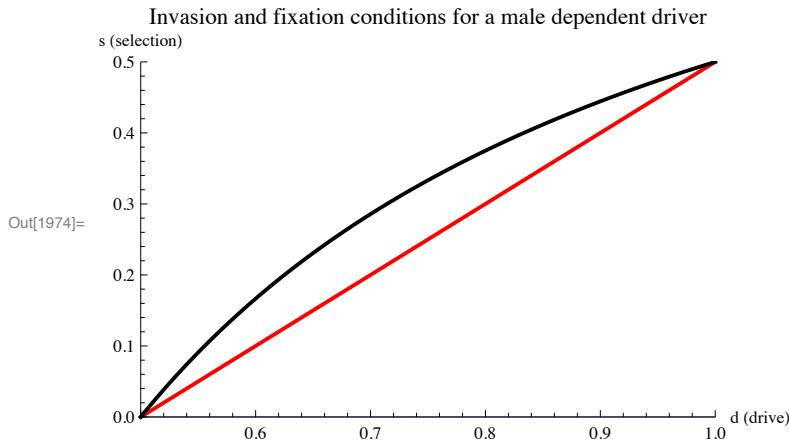
```
In[1971]:= plotInvasion4maleDepRecessive = Plot[s /. invasion4maleDepRecessive /. dh → d,
  {d, .5, 1}, PlotStyle -> {Black, Thick}];
```

Fixation

```
In[1972]:= fixation4maleDepRecessive =
  Solve[(FullSimplify[(FullSimplify[(ΔfB /. x → 0 /. hs → 0) / fA] /. fB → 1)]) == 0, s]
Out[1972]= {s → 1 / (2 (-1 + 2 d))}
```

```
In[1973]:= plotFixation4maleDepRecessive = Plot[s /. fixation4maleDepRecessive /. dh → d,
  {d, .5, 1}, PlotStyle -> {Red, Thick}];
```

```
In[1974]:= 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]
```

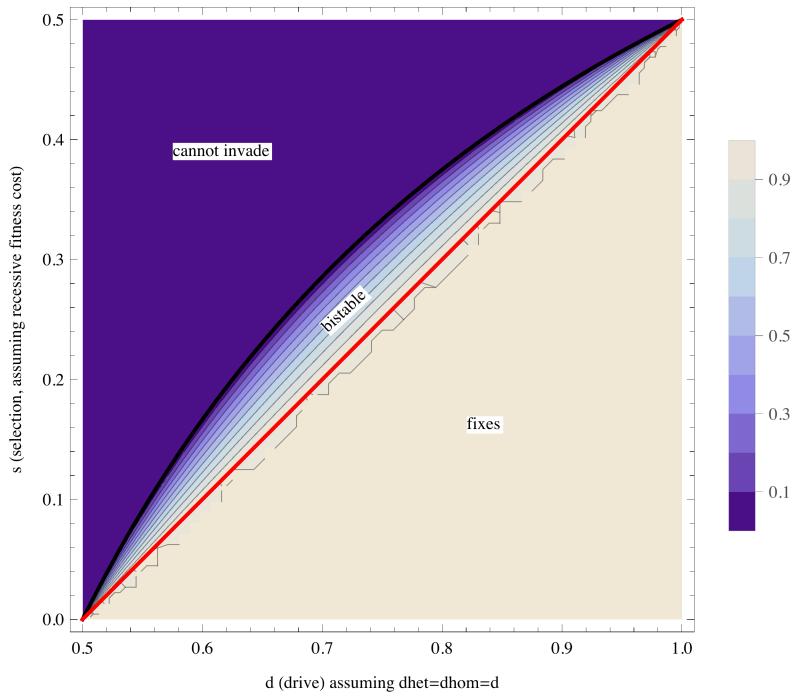
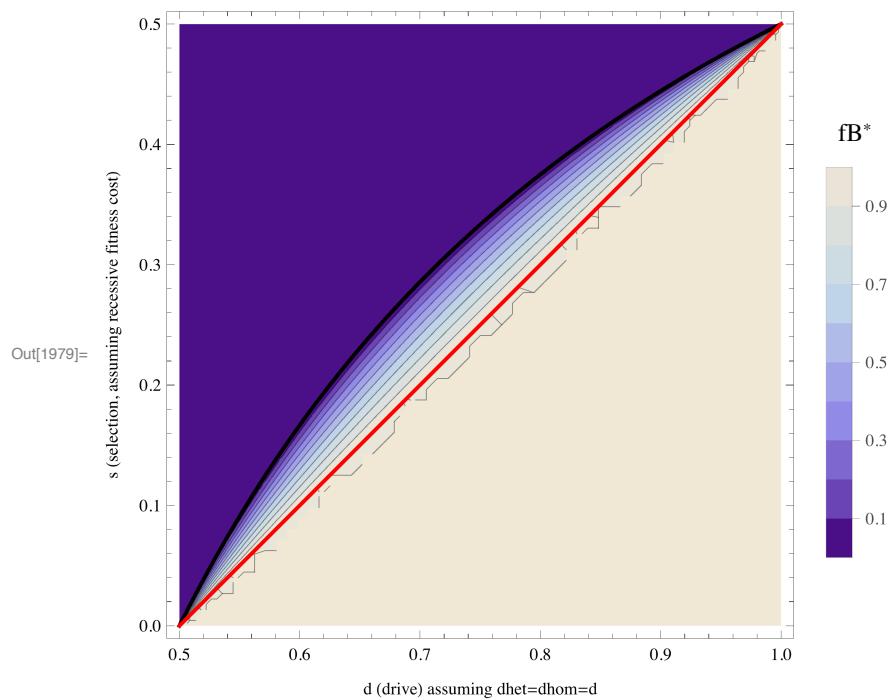


Bistability

```
In[1975]:= FBbistabMaleepRecessive =
Solve[FullSimplify[\Delta fB /. x -> 0 /. hs -> 0 /. dh -> d == 0, fB][[4]]]
Out[1975]= {fB ->  $\frac{2(1 - 2d + 2ds)}{(-1 + 2d)(-1 + 2s)}$ }
```

```
In[1978]:= bistab = ContourPlot[(If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabMaleepRecessive,
{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[1979]:= `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. When C increases drive in heterozygous females it fertilizes, it is a drive enhancer (the B+ allele in our ms).

When C decreases drive in heterozygous females it fertilizes, it is a drive suppressor (the B- allele in our ms).

Setup

```
In[1980]:= 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 + fAC / 2};
```

Drive

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

```
In[1992]:= AAAn =
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 +
```



```

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[2001]:= (*Genotype frequencies after drive*)
fAADrive = FullSimplify[AAn];
fABDrive = FullSimplify[ABn + BAn];
fACDrive = FullSimplify[ACn + CAn];
fBBDrive = FullSimplify[BBn];
fBCDrive = FullSimplify[BCn + CBn];
fCCDrive = FullSimplify[CCn];
(*check, do allele freqs sum to one?*)
FullSimplify[
FullSimplify[fAADrive + fABDrive + fACDrive + fBBDrive + fBCDrive + fCCDrive] /. HWE /. SUMTOONE]

Out[2007]= 1

```

Selection

```

In[2008]:= wAA = 1; wAC = wAB = 1 - hs; wBB = wBC = wCC = 1 - s;
W = FullSimplify[
(wAA fAADrive + wAB fABDrive + wAC fACDrive + wBB fBBDrive + wBC fBCDrive + wCC fCCDrive)];
FullSimplify[W /. HWE /. SUMTOONE /. hs → 0]

Out[2010]= 1 + (fB + fC) (-2 d1 fC + 2 d0 fB (-1 + fB + fC) - (fB + fC) (fB + fC - 2 d1 fC)) s

```

```

In[2011]:= fAASel = fAADrive wAA / W;
fABSel = fABDrive wAB / W;
fACSel = fACDrive wAC / W;
fBBSel = fBBDrive wBB / W;
fBCSel = fBCDrive wBC / W;
fCCSel = fCCDrive wCC / W;
fASel = FullSimplify[fAASel + (fABSel + fACSel) / 2];
fBSel = FullSimplify[fBBSel + (fABSel + fBCSel) / 2];
fCSel = FullSimplify[fCCSel + (fACSel + fBCSel) / 2];
ΔfA = FullSimplify[fASel - fA];
ΔfB = FullSimplify[fBSel - fB];
ΔfC = FullSimplify[fCSel - fC];

(*Check: do genotype freqs after selection sum to one?*)
FullSimplify[fASel + fBSel + fCSel]

Out[2023]= 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 supplementary material we show thats results of exact recursions are remarkably consistant from these approximate analistical solutions.

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

```
In[2024]:= invasionStandardDriver = Solve[
  FullSimplify[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) / . fB] /. fB → 0, hs]
Out[2024]= {hs → -1 + 2 d0 / 1 + 2 d0}
```

Fixation of standard driver

```
In[2025]:= fixationStandardDriver = Solve[
  FullSimplify[(ΔfB / fA /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) ] /. fB → 1) == 0, s]
Out[2025]= {s → 1 / 2 (-1 + 2 d0 + 3 hs - 2 d0 hs)}
```

```
In[2026]:= (*fixation of a standard recessive driver*)
fixationStandardDriver /. hs → 0
```

```
Out[2026]= {s → 1 / 2 (-1 + 2 d0)}
```

Equilibrium

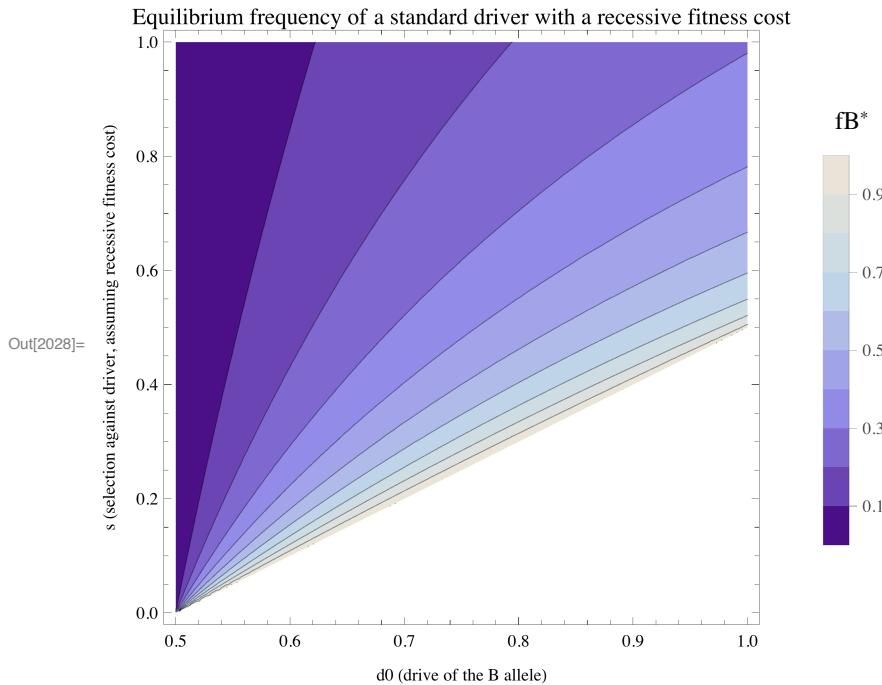
(*Equilibrium frequency of a standard driver*)

```
In[2027]:= eqfB = Solve[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) == 0, fB][[4]]
```

```
Out[2027]= {fB → (8 d0 hs - 4 d0 s +
  √(-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)) /
  (2 (-4 hs + 8 d0 hs + 2 s - 4 d0 s))}
```

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

```
In[2028]:= 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)"}]
```



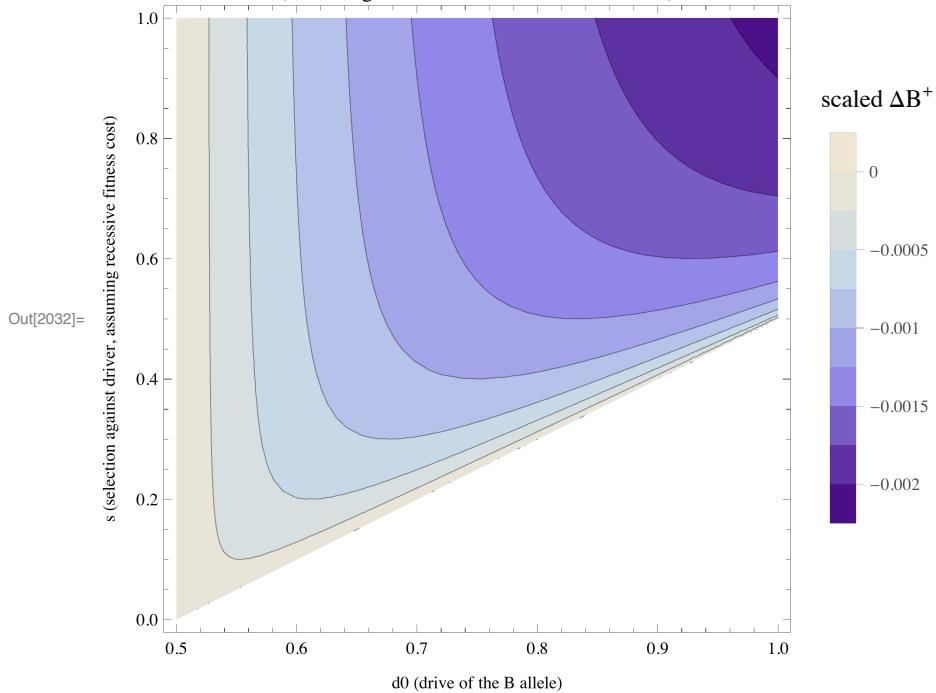
Invasion of sperm acting drive modifier tightly linked with the driver, and on the driving background

```
In[2029]:= (*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[ $\bar{W} \Delta fC / (fC) /. HWE /. SUMTOONE$ ] /. fC → 0 /. eqfB /. minormod]  
  
Out[2029]= 
$$\frac{1}{2 (1 - 2 d0)^2 (2 hs - s)} (hs - s)$$
  

$$\left( -1 - hs - \sqrt{2} \sqrt{(1 + hs - 2 d0 (2 + d0 (-2 + s))) (2 hs - s)} + 2 d0 (2 (-1 + d0) (-1 + hs) + s) \right) \in$$
  
  
In[2030]:= (*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[2032]:= 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)"}]
```

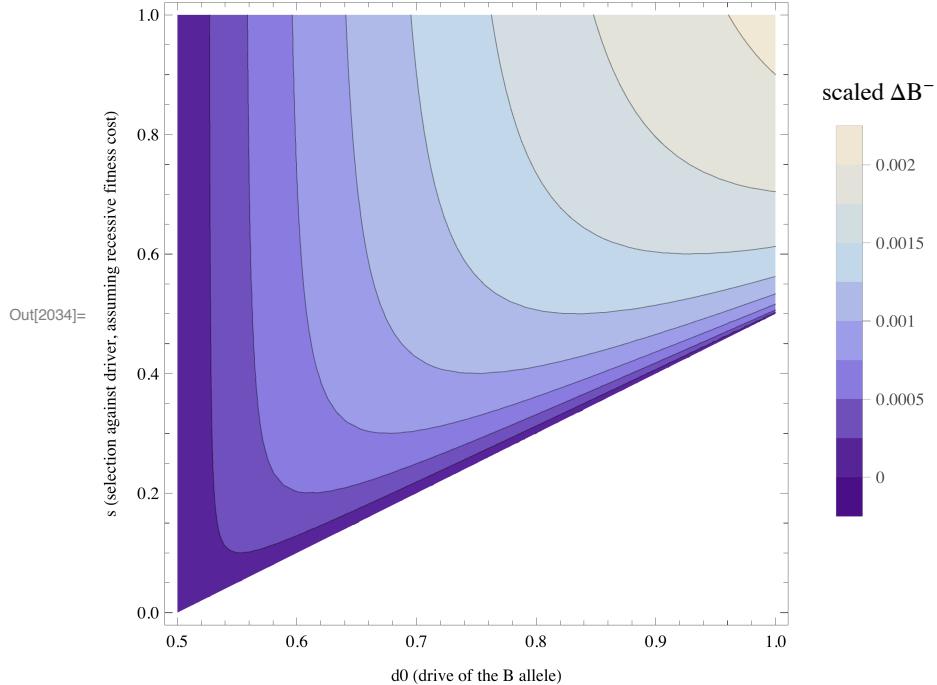
A sperm-acting drive enhancer (the B^+ haplotype) cannot invade
(assuming a recessive fitness cost of drive)



(*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 suppressor always invades*)

```
In[2034]:= 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)"}]
```

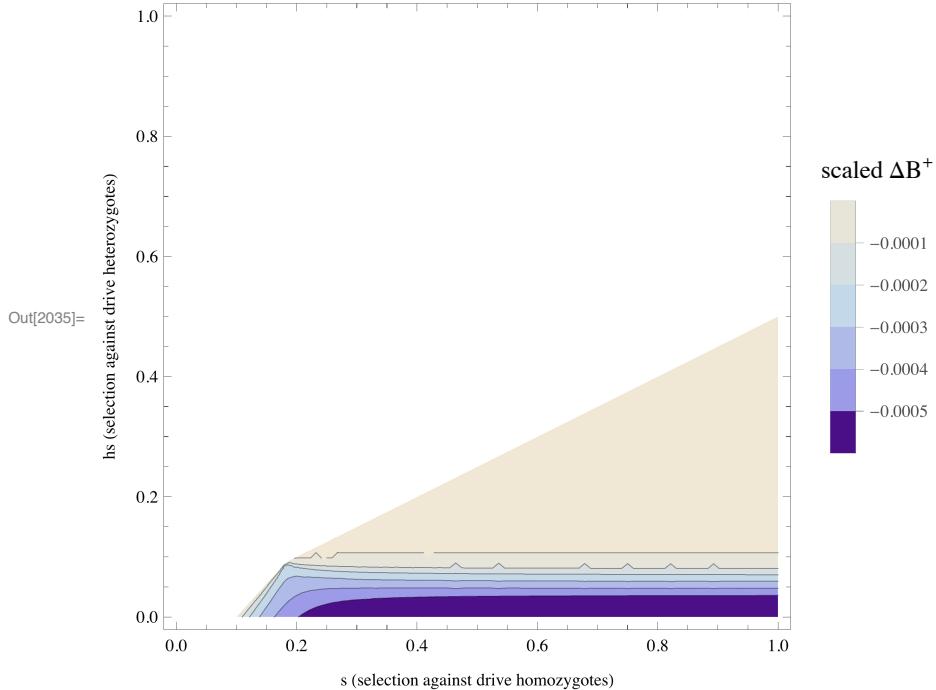
A sperm-acting drive suppressor (the B^- haplotype) always invades
(assuming a recessive fitness cost of drive)



Out[2034]=

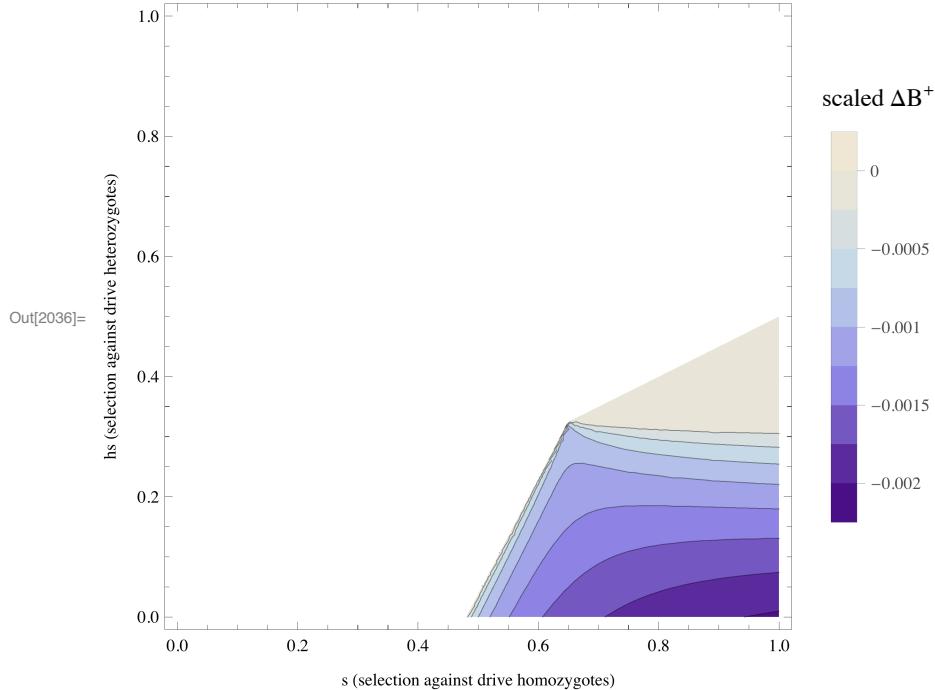
```
In[2035]:= (*Plotting change this change in frequency when hte extent
of drive is mild [d0 = .6] and the sperm acting locus is rare
and increase drive. NOTE: This sperm enhancer never invades*)
ContourPlot[(If[fB > 1, 1/0, If[fB < 0.0000001, 0, wbarDeltaSpermDrive]] /. eqfB /.
 $\epsilon \rightarrow 0.01 /.$  d0  $\rightarrow .6)$ , {s, 0, 1}, {hs, 0, 1},
PlotLegends  $\rightarrow$  BarLegend[Automatic, LegendLabel  $\rightarrow$  "scaled  $\Delta B^+$ "], PlotLabel  $\rightarrow$ 
"A sperm-acting drive enhancer (the  $B^+$  haplotype) cannot invade\n(assuming
drive-selection equilibrium of a modest driver, d0 = .6)",
FrameLabel  $\rightarrow$  {"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 modest driver, $d0 = .6$)



```
In[2036]:= (*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 /.
 $\epsilon \rightarrow 0.01 /.$  d0  $\rightarrow .98$ ), {s, 0, 1}, {hs, 0, 1},
PlotLegends  $\rightarrow$  BarLegend[Automatic, LegendLabel  $\rightarrow$  "scaled  $\Delta B^+$ "], PlotLabel  $\rightarrow$ 
"A sperm-acting drive enhancer (the  $B^+$  haplotype) cannot invade\n(assuming
drive-selection equilibrium of a strong driver, d0 = .98)",
FrameLabel  $\rightarrow$  {"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, $d0 = .98$)



Out[2036]=

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

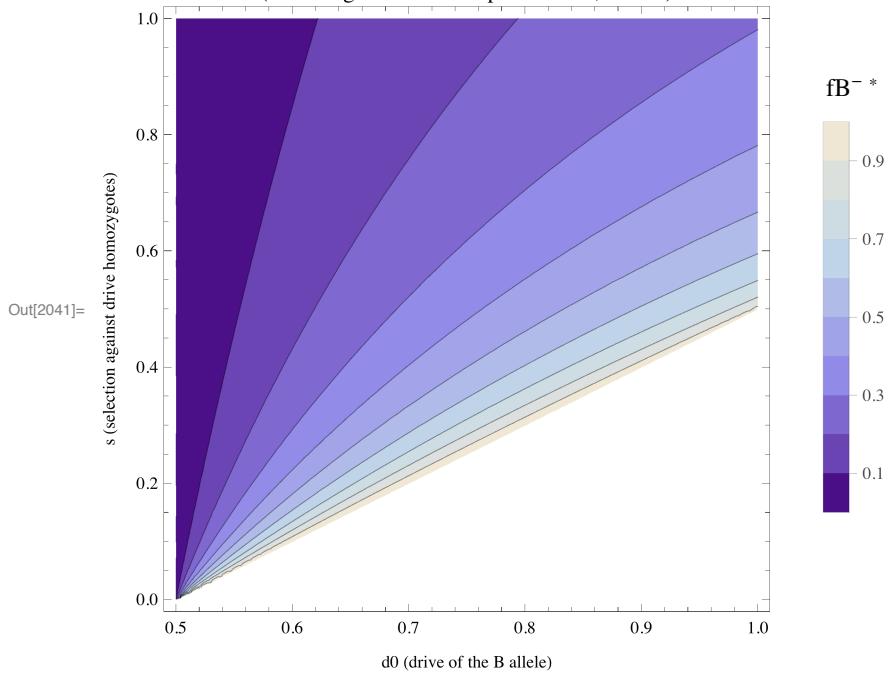
Equilibrium frequency of drive suppressor

```
In[2038]:= eqfC = Solve[(FullSimplify[ΔfC /. HWE /. SUMTOONE /. minormod /. fB  $\rightarrow$  0] == 0, fc][[4]];
(*Equilibrium frequency of a linked, coupled,
drive suppressor when the fitness costs of drive are recessive*)
```

```
In[2041]:= 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 → "Equilibrium 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)"}]
```

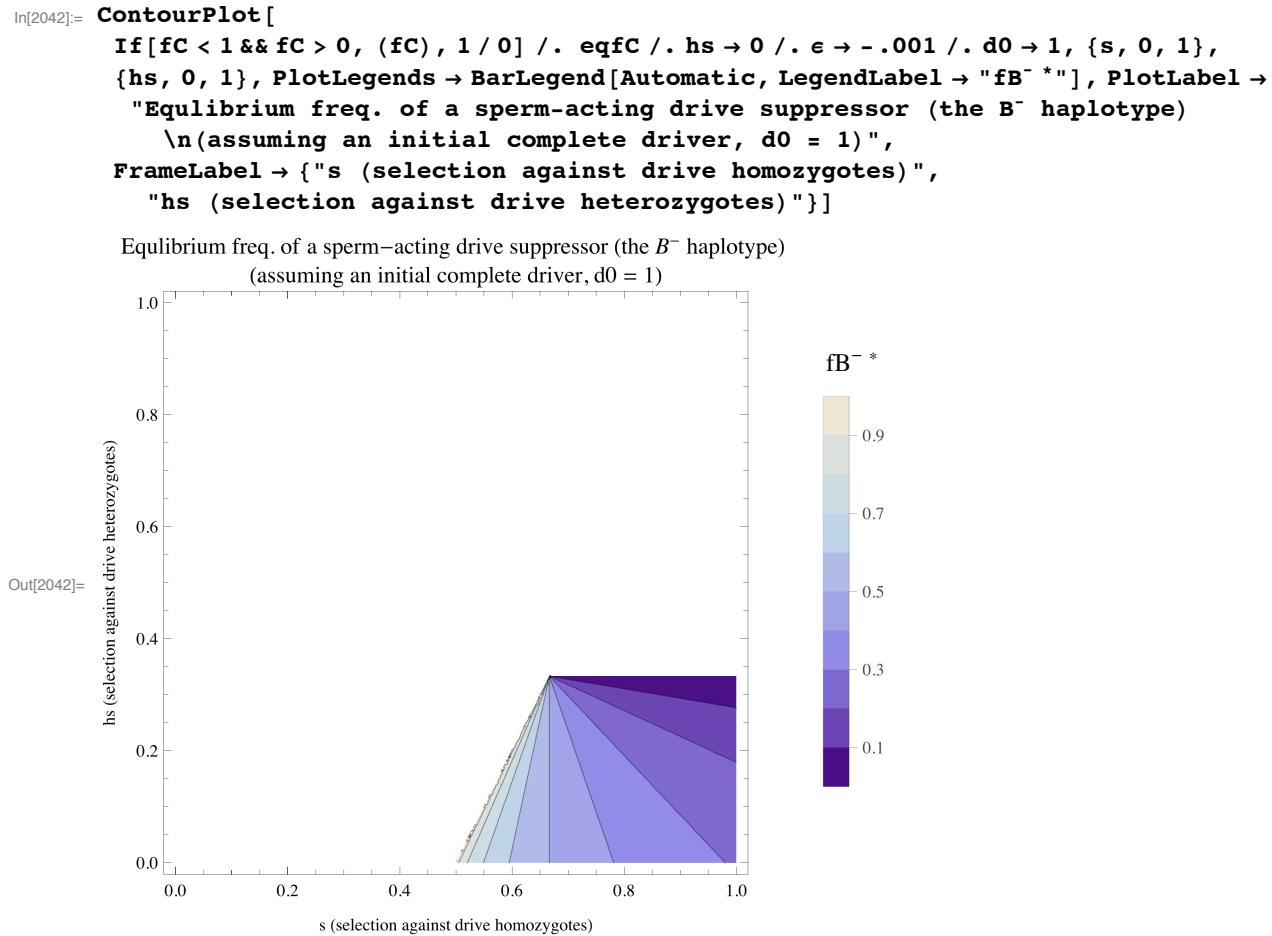
Equilibrium freq. of sperm-acting drive suppressor (the B^- haplotype)

(assuming an initial complete driver, $d_0 = 1$)



```
Out[2041]=
```

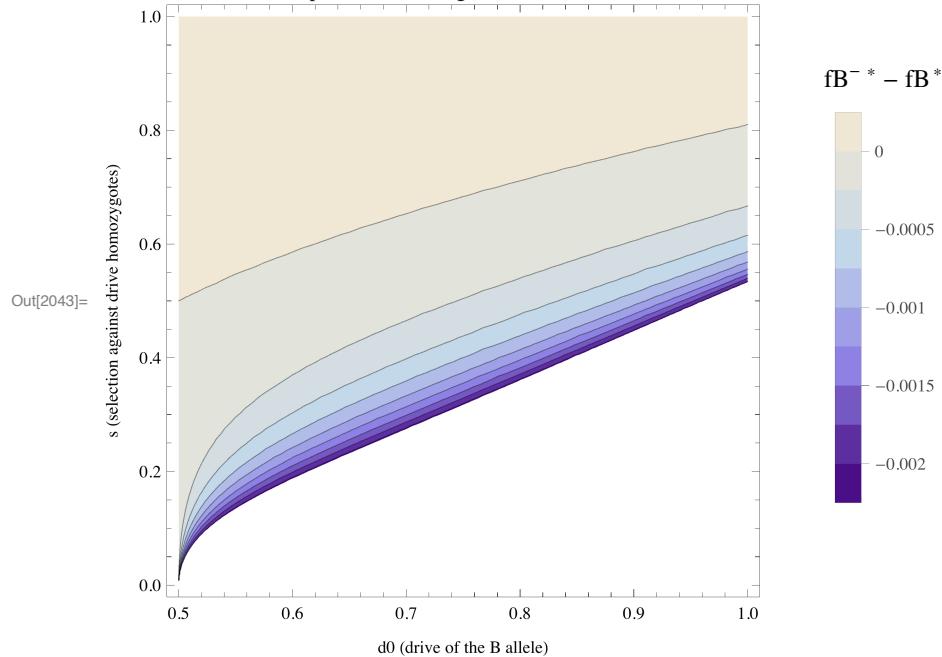
(*Equilibrium frequency of a linked, coupled,
drive suppressor when drive is complete*)

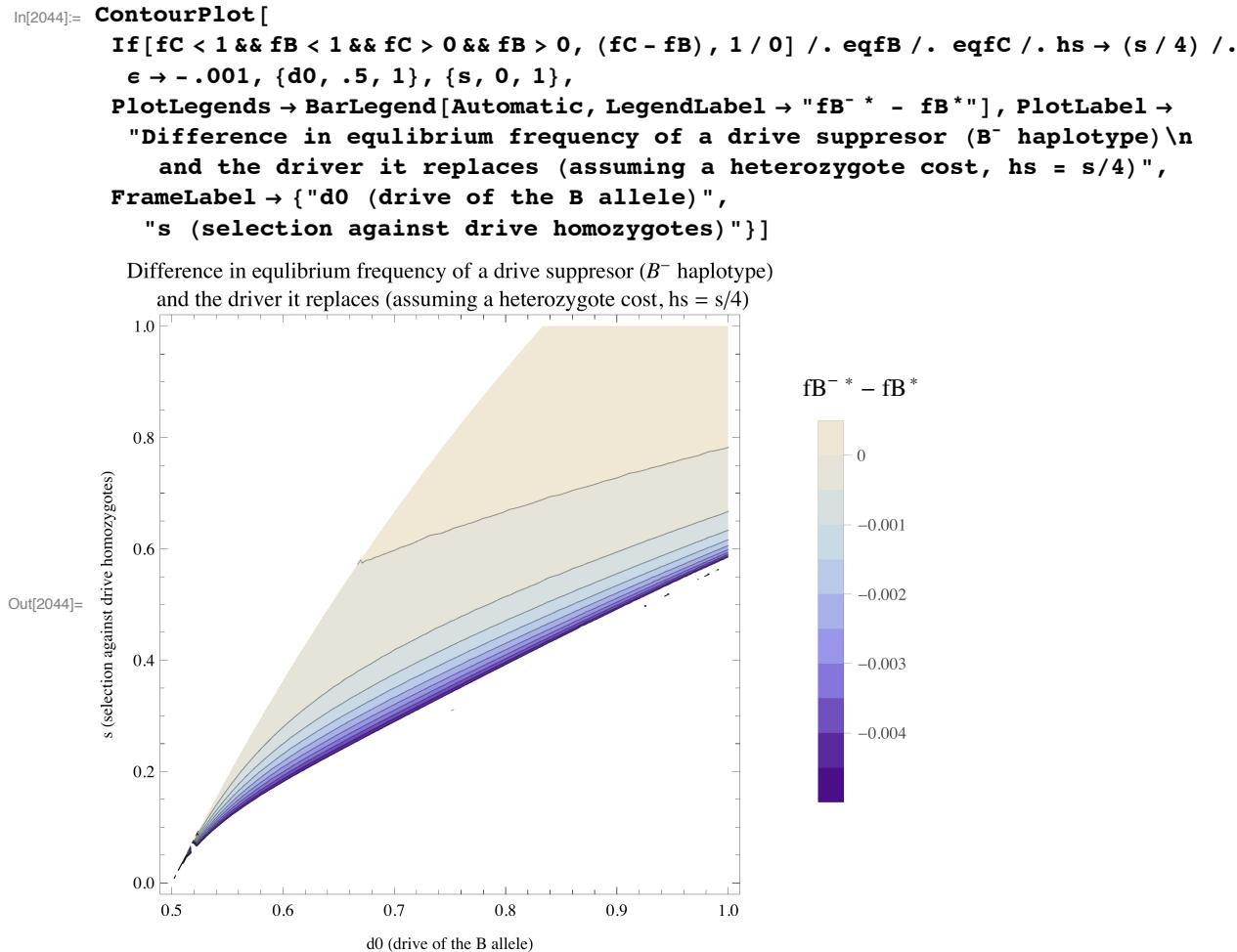


Equilibrium frequency of drive/sperm acting suppressor haplotype is often less than that of the standard driver it replaces.

```
In[2043]:= (*Difference 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 equilibrium frequency of a drive suppressor (B^- haplotype)\nand
    the driver it replaces (assuming a recessive cost of the drive allele)",
  FrameLabel → {"d0 (drive of the B allele)", "s (selection against drive homozygotes)"}]
```

Difference in equilibrium frequency of a drive suppressor (B^- haplotype)
and the driver it replaces (assuming a recessive cost of the drive allele)

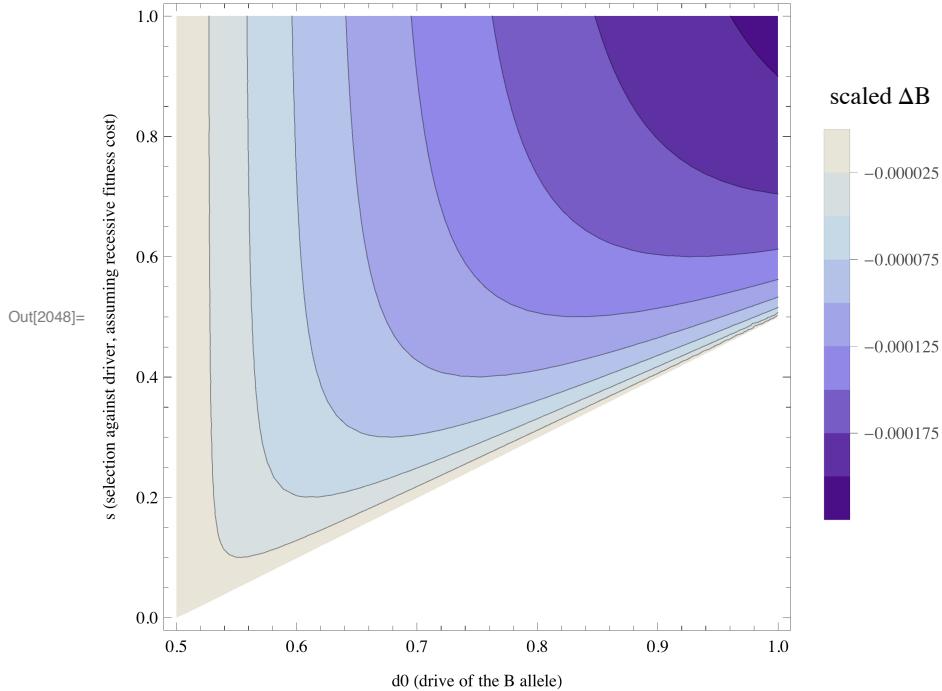




In[2047]:= (*change in frequency of a rare traditional driver when the drive-sperm suppressor haplotype and the ondriving hplotype
 are at drive selection equilibrium, mutliplied by
 Wbar/fC [this value is always positive and will not influence the sign]*)
 wbarDeltaTradDrive = FullSimplify[
 FullSimplify[$\bar{W} \Delta fB / (fB) /. HWE /. SUMTOONE$] /. fB → 0 /. eqfC /. minormod];
 (*Plotting the change in frequency of a rare traditional driving haplotype when the sperm drive suppressor is at drive selection balance. ASSUMING the fitness cost of drive is fully recessive. NOTE: This sperm enhancer of drive cannot invade*)

```
In[2048]:= 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 suppressor ( $B^-$  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)"}]
```

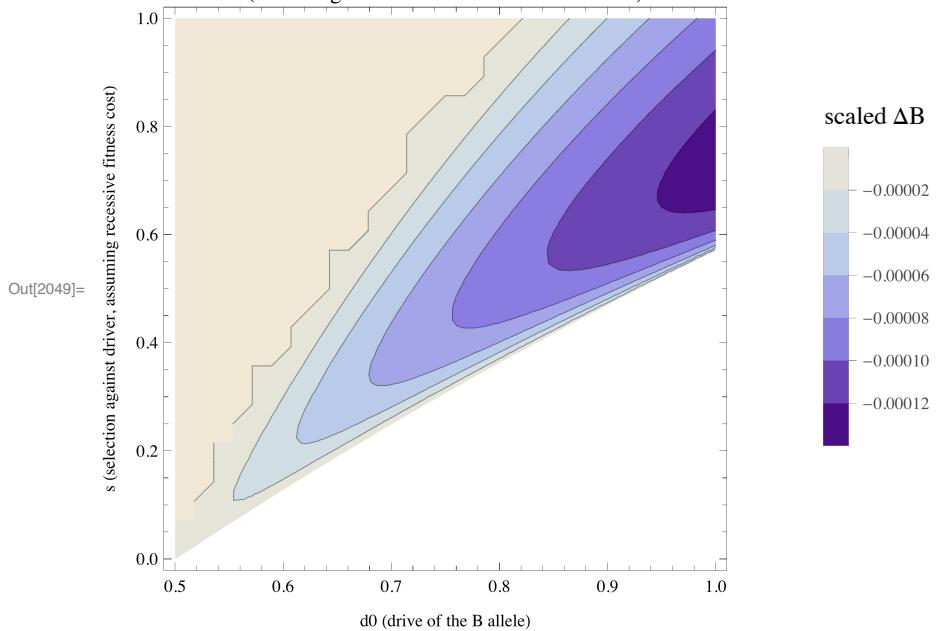
A fixed drive suppressor (B^- haplotype) cannot be displaced by
a traditional driver (assuming a recessive fitness cost of drive)



(*Plotting the change in frequency of a rare traditional
driving haplotype when the sperm drive suppressor 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[2049]:= 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 suppressor 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)"}]
```

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



```
In[2052]:= 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 suppressor cannot
  be displaced by a traditional \n(assuming perfect drive)",
  FrameLabel → {"s (selection against drive homozygotes)",
  "hs (selection against drive heterozygotes)"}]
```

A fixed sperm-acting drive suppressor cannot be displaced by a traditional
(assuming perfect drive)

