

Brandvain and Coop.

Sperm dependent female meiotic drive.

In[1]=

Model I. Tadtional female drive

Set up

```
In[2]= (*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[7]= fAAdrive = FullSimplify[fA (fAA + fAB (1 - d))];
fABdrive = FullSimplify[fA (fBB + fAB d) + fB (fAA + fAB (1 - d))];
fBBdrive = FullSimplify[fB (fAB d + fBB)];
```

Selection

```
In[10]= wAA = 1; wAB = 1 - hs; wBB = 1 - s; (*genotypic fitnesses*)
W̄ = FullSimplify[fAAdrive wAA + fABdrive wAB + fBBdrive wBB]; (*mean fitness*)
fAAsel = FullSimplify[(fAAdrive * wAA) / W̄];
fABsel = FullSimplify[(fABdrive * wAB) / W̄];
fBBsel = FullSimplify[(fBBdrive wBB) / W̄];
fAsel = FullSimplify[fAAsel + fABsel / 2];
fBsel = FullSimplify[fBBsel + fABsel / 2];
ΔfA = FullSimplify[fAsel - fA];
ΔfB = FullSimplify[fBsel - fB];
```

Analysis

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

Invasion

In[19]:= **scaledDeltaDriveWhenRare** = (FullSimplify[$\Delta f_B / (f_B * (1 - f_B)) / . x \rightarrow 0$] /. **fB** $\rightarrow 0$)

Out[19]=
$$\frac{1}{2} (-1 - 2 d (-1 + h s) - h s)$$

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.

In[20]:= **invasionCrit** = Solve[scaledDeltaDriveWhenRare == 0, **hs**]

Out[20]=
$$\left\{ \left\{ h s \rightarrow \frac{-1 + 2 d}{1 + 2 d} \right\} \right\}$$

Fixation

In[21]:= **scaledDeltaDriveWhenCommon** = (FullSimplify[$\Delta f_B / (f_B * (1 - f_B)) / . x \rightarrow 0$] /. **fB** $\rightarrow 1$)

Out[21]=
$$\frac{1 + h s + 2 (d (-1 + h s) - 2 h s + s)}{2 (-1 + s)}$$

We solve for fixation conditions when recessive or not.

In[22]:= **fixationCritRecessive** = Solve[scaledDeltaDriveWhenCommon == 0, **s**] /. **hs** $\rightarrow 0$
fixationCritNotRecessive = Solve[scaledDeltaDriveWhenCommon == 0, **s**]

Out[22]=
$$\left\{ \left\{ s \rightarrow \frac{1}{2} (-1 + 2 d) \right\} \right\}$$

Out[23]=
$$\left\{ \left\{ s \rightarrow \frac{1}{2} (-1 + 2 d + 3 h s - 2 d h s) \right\} \right\}$$

Equilibrium

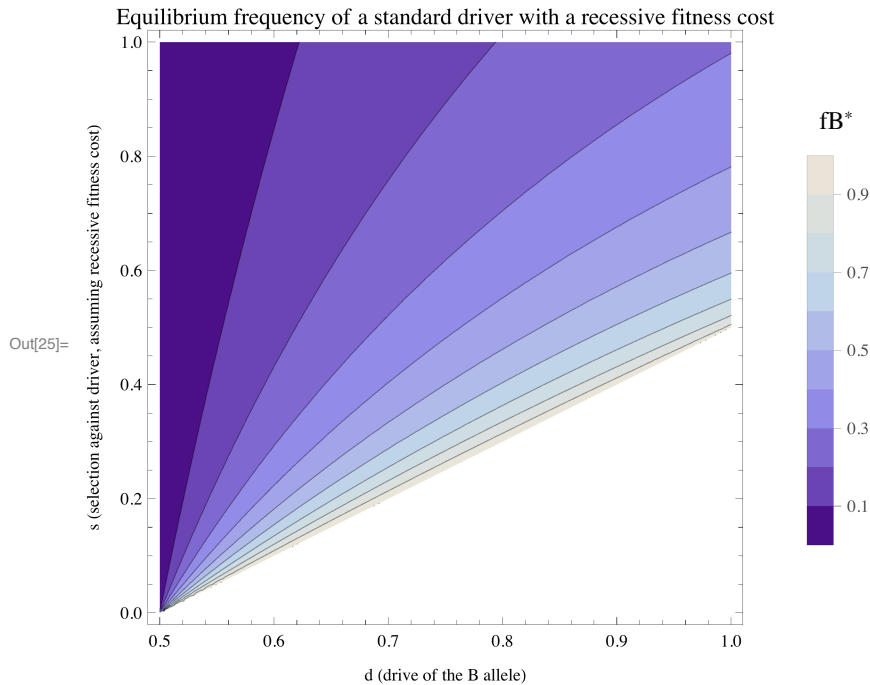
We identify the equilibrium frequency of the standard driver

In[24]:= **eqfB** = Solve[(FullSimplify[$\Delta f_B / . x \rightarrow 0$]) == 0, **fB**][[4]]

Out[24]=
$$\left\{ f_B \rightarrow \frac{\left(8 d h s - 4 d s + \sqrt{(-4 (1 - 2 d + h s + 2 d h s) (-4 h s + 8 d h s + 2 s - 4 d s) + (-8 d h s + 4 d s)^2)} \right)}{2 (-4 h s + 8 d h s + 2 s - 4 d s)} \right\}$$

We plot this equilibrium frequency assuming a recessive fitness cost.

```
In[25]:= 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)"}]
```



```
In[26]:= FullSimplify[fAADrive + fABDrive + fBBDrive]
```

Out[26]= 1

Model 2. Female drive depends on sperm haplotype (single pleiotropic 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[27]:= (*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[32]:= (*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[35]:= wAA = 1; wAB = 1 - hs; wBB = 1 - s; (*genotypic fitnesses*)
W̄ = FullSimplify[fAADrive wAA + fABDrive wAB + fBBDrive wBB]; (*mean fitness*)
fAAsel = FullSimplify[(fAADrive * wAA) / W̄];
fABsel = FullSimplify[(fABDrive * wAB) / W̄];
fBBsel = FullSimplify[(fBBDrive wBB) / W̄];
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 that results of exact recursions are remarkably consistent from these approximate analytical solutions.

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

Invasion

```
In[44]:= ΔfBinvasive = (FullSimplify[ΔfB /. hs → 0 /. x → 0] / fB^2 /. fB → 0)
```

```
Out[44]=  $\frac{1}{2} (-1 + d (2 - 4 s))$ 
```

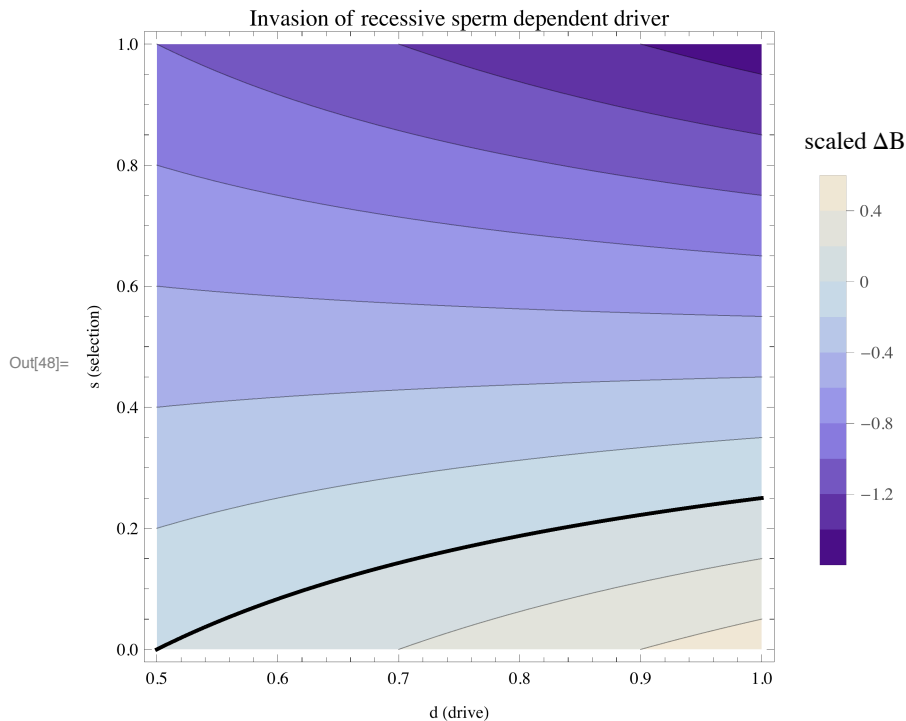
```
In[45]:= spermDepRecessiveInvasive = Solve[ΔfBinvasive == 0, s]
```

```
Out[45]=  $\left\{ \left\{ s \rightarrow \frac{-1 + 2 d}{4 d} \right\} \right\}$ 
```

```
In[46]:= plotInvasion4spermDepRecessive =
  Plot[s /. spermDepRecessiveInvasive [[1]], {d, .5, 1}, PlotStyle → {Black, Thick}];
```

```
In[47]:= plotRelChange4RarespermDepRecessive = ContourPlot[{ΔfBinvasive}, {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[48]:= Show[plotRelChange4RarespermDepRecessive, plotInvasion4spermDepRecessive]
```



Fixation

```
In[49]:= ΔfBfix = FullSimplify[FullSimplify[ΔfB /. hs → 0 /. x → 0] / fA] /. fB → 1
```

$$\text{Out[49]= } \frac{-1 + 2d - 2s}{2 - 2s}$$

```
In[50]:= spermDepRecessiveFix = Solve[ΔfBfix == 0, s]
```

$$\text{Out[50]= } \left\{ \left\{ s \rightarrow \frac{1}{2} (-1 + 2d) \right\} \right\}$$

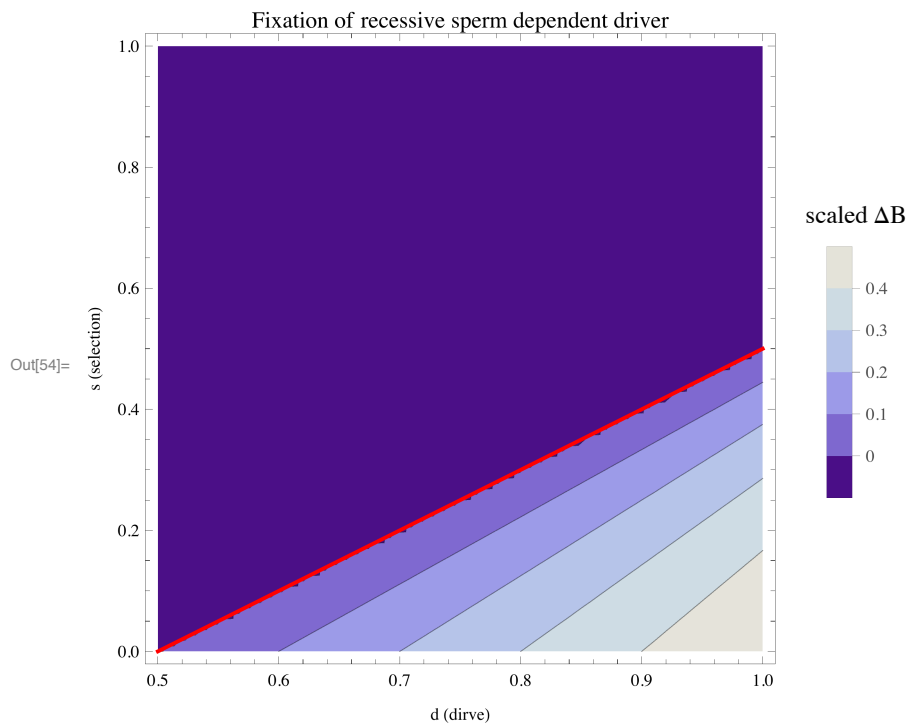
```
In[51]:= (s /. spermDepRecessiveFix [[1]])
```

$$\text{Out[51]= } \frac{1}{2} (-1 + 2d)$$

```
In[52]:= plotFixation4spermDepRecessive =  
Plot[s /. spermDepRecessiveFix [[1]], {d, .5, 1}, PlotStyle → {Red, Thick}];
```

```
In[53]:= (*Note we artificially rescaled z to be -.1 for all negative values*)  
plotRelChange4CommonSpermDepRecessive =  
ContourPlot[If[s > (s /. spermDepRecessiveFix [[1])], -.1, ΔfBfix], {d, 0.5, 1},  
{s, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB"],  
FrameLabel → {"d (drive)", "s (selection)"},  
PlotLabel → "Fixation of recessive sperm dependent driver"];
```

```
In[54]:= Show[plotRelChange4CommonSpermDepRecessive, plotFixation4spermDepRecessive]
```



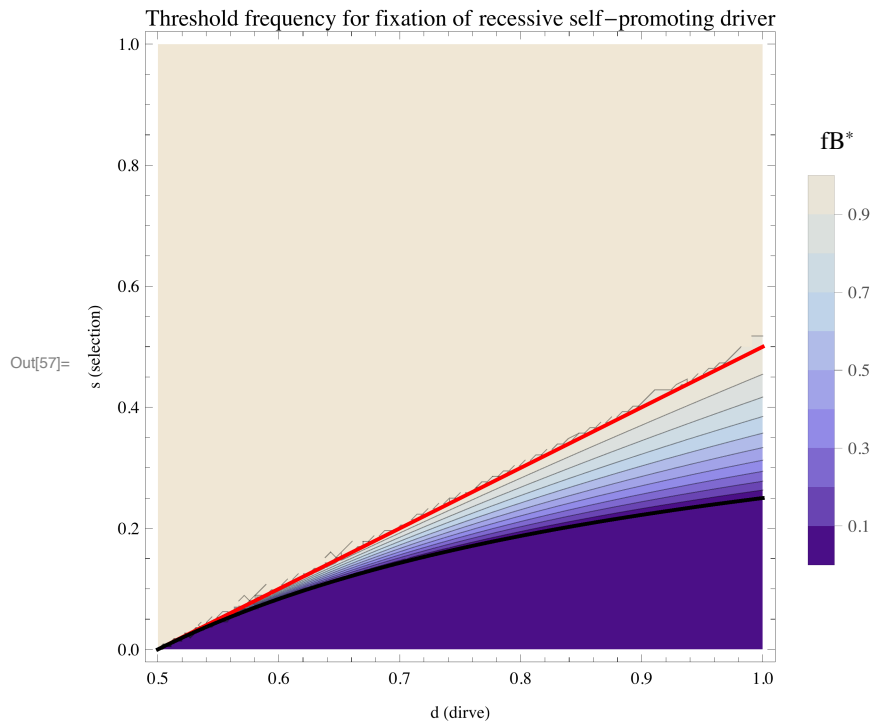
Bistability Point

```
In[55]:= FBbistabSpermDepRecessive = Solve[FullSimplify[ΔfB /. hs → 0 /. x → 0] == 0, fB][[4]]
```

Out[55]= $\left\{ fB \rightarrow \frac{1 - 2d + 4ds}{-2s + 4ds} \right\}$

```
In[56]:= 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[57]:= **Show[bistab, plotFixation4spermDepRecessive, plotInvasion4spermDepRecessive]**



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

Invasion

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

In[58]:= **FullSimplify[FullSimplify[$\Delta f_B /. x \rightarrow 0$] / f_B] /. $f_B \rightarrow 0$**

Out[58]= $-h_s$

Fixation

In[59]:= **$\Delta f_{Bfix} = \text{FullSimplify}[\text{FullSimplify}[\text{FullSimplify}[\Delta f_B /. x \rightarrow 0] / f_A] /. f_B \rightarrow 1]$**

Out[59]=
$$\frac{1 + 2 d (-1 + h_s) - 3 h_s + 2 s}{2 (-1 + s)}$$

In[60]:= **spermDepNotRecessiveFix = Solve[$\Delta f_{Bfix} == 0, s$]**

Out[60]=
$$\left\{ \left\{ s \rightarrow \frac{1}{2} (-1 + 2 d + 3 h_s - 2 d h_s) \right\} \right\}$$

In[61]:= **spermDepAddFix = Solve[$\Delta f_{Bfix} == 0 /. h_s \rightarrow s / 2, s$]**

Out[61]=
$$\left\{ \left\{ s \rightarrow \frac{2 (-1 + 2 d)}{1 + 2 d} \right\} \right\}$$

```
In[62]:= plotspermDepAddFix =
Plot[s /. spermDepAddRecessiveFix , {d, .5, 1}, PlotStyle -> {Red, Thick}];
ReplaceAll::reps : {spermDepAddRecessiveFix} is neither a list of
replacement rules nor a valid dispatch table, and so cannot be used for replacing. >>
```

Bistability Point

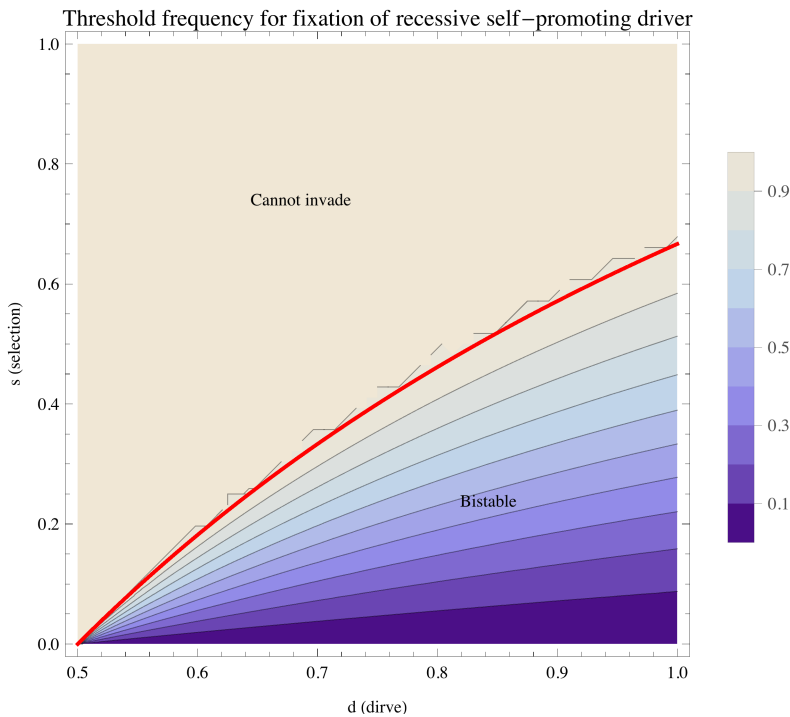
```
In[63]:= FBbistabSpermDepNotRecessive = Solve[FullSimplify[ΔfB /. x -> 0] == 0, fB][[3]]
```

$$\text{Out[63]= } \left\{ fB \rightarrow \left(-1 + 2 d + 3 h s + 2 d h s - 4 d s - \sqrt{(-8 h s (-2 h s + 4 d h s + 2 s - 4 d s) + (1 - 2 d - 3 h s - 2 d h s + 4 d s)^2)} \right) / (2 (-2 h s + 4 d h s + 2 s - 4 d s)) \right\}$$

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

```
In[64]:= bistab = ContourPlot[
(If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabSpermDepNotRecessive /. 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[65]:= Show[bistab, plotspermDepAddFix]
```



In[67]:=

Model 3. Female drive depends on male genotype (single pleiotropic locus)

The B allele is transmitted with probability, d and d_h , in heterozygous females when fertilized BB and AB males, respectively.

x represents the deviation from Hardy - Weinberg Equilibrium

Setup

```
In[68]:= (*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[73]:= (*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

```
In[76]:= wAA = 1; wAB = 1 - hs; wBB = 1 - s; (*genotypic fitnesses*)
W_bar = FullSimplify[fAA_drive wAA + fAB_drive wAB + fBB_drive wBB]; (*mean fitness*)
fAA_sel = FullSimplify[(fAA_drive * wAA) / W_bar];
fAB_sel = FullSimplify[(fAB_drive * wAB) / W_bar];
fBB_sel = FullSimplify[(fBB_drive wBB) / W_bar];
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];
```

```
In[85]:= FullSimplify[fAADrive + fABDrive + fBBDrive]
```

```
Out[85]= 1
```

Analysis

Analytical example - recessive fitness cost

Invasion

```
In[86]:= invasion4maleDepRecessive =  
Solve[ ((FullSimplify[(ΔfB /. x → 0 /. hs → 0)] / fB^2) /. fB → 0) == 0, s]
```

```
Out[86]= {{s →  $\frac{-1 + 2 d_{het}}{2 d_{het}}$ }}
```

```
In[87]:= plotInvasion4maleDepRecessive =  
Plot[s /. invasion4maleDepRecessive /. dhet -> dhom,  
{dhom, .5, 1}, PlotStyle -> {Black, Thick}];
```

Fixation

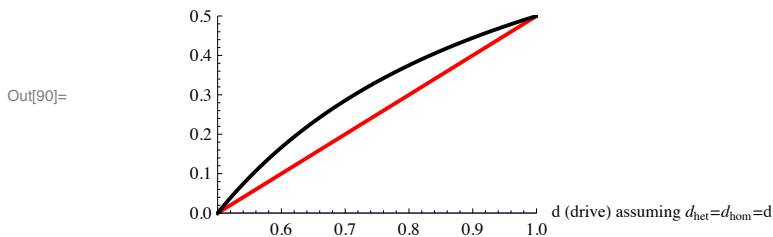
```
In[88]:= fixation4maleDepRecessive =  
Solve[(FullSimplify[(FullSimplify[(ΔfB /. x → 0 /. hs → 0) / fA] /. fB → 1])] == 0, s]
```

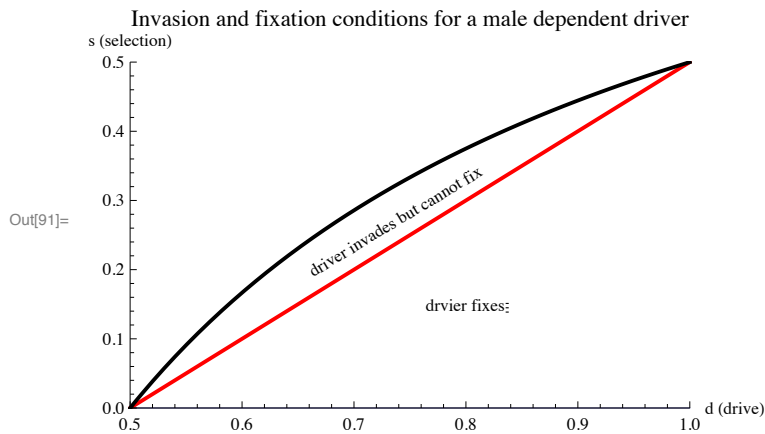
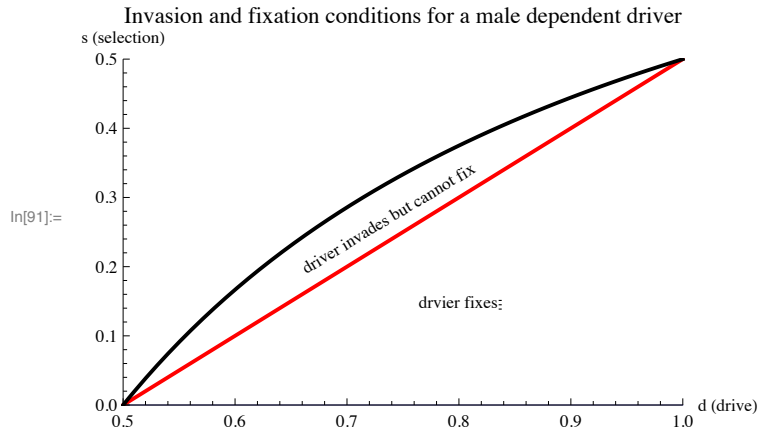
```
Out[88]= {{s →  $\frac{1}{2} (-1 + 2 d_{hom})$ }}
```

```
In[89]:= plotFixation4maleDepRecessive = Plot[s /. fixation4maleDepRecessive /. dhet -> dhom,  
{dhom, .5, 1}, PlotStyle -> {Red, Thick}];
```

```
In[90]:= Show[Plot[0, {dhom, 0.5, 1}, AxesLabel -> {"d (drive) assuming dhet=dhom=d",  
"s (selection against drive homozygotes)"}, PlotRange -> {{.5, 1}, {0, .5}},  
PlotLabel -> "Invasion and fixation conditions for a male dependent driver"],  
plotFixation4maleDepRecessive, plotInvasion4maleDepRecessive]
```

Invasion and fixation conditions for a male dependent driver
s (selection against drive homozygotes)





Equilibrium

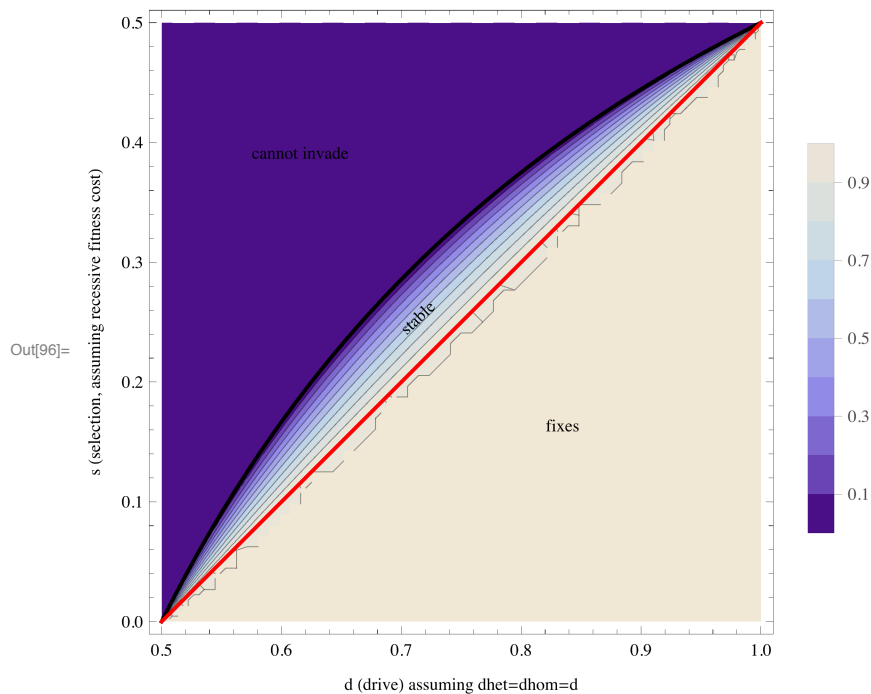
In[92]= **FBeqMaleepRecessive =**
Solve[FullSimplify[$\Delta fB /. x \rightarrow 0 /. hs \rightarrow 0 /. d_{het} \rightarrow d_{hom}] == 0, fB][[4]]$

Out[92]= $\left\{ fB \rightarrow \frac{2 (1 - 2 d_{hom} + 2 s d_{hom})}{(-1 + 2 s) (-1 + 2 d_{hom})} \right\}$

In[93]=

In[94]= **eqfig = ContourPlot[(If[fB < 0, 0, If[fB > 1, 1, fB]) /. FBeqMaleepRecessive,**
{d_{hom}, 0.5, 1}, {s, 0, .5}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB*"],
FrameLabel → {"d (drive) assuming d_{het}=d_{hom}=d",
"s (selection, assuming recessive fitness cost)"}];

```
In[95]:= Show[eqfig, plotInvasion4maleDepRecessive, plotFixation4maleDepRecessive]
```



```
In[97]:=
```

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 tightly-linked locus is on the B background.

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[98]:= 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 + fFC / 2};
```

```
In[110]:=
```

Drive

```
In[111]:= (*Here we caculate all genotypes after drive. For book-
keeping purposes we distinguish between reciprocal homozygotes,
but remove this distinction belowsun them below*)
```

```
In[112]:= 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];
BAAn = 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 * 0 + 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[121]:= (*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[127]= 1
```

Selection

```
In[128]:= wAA = 1; wAC = wAB = 1 - hs; wBB = wBC = wCC = 1 - s;
W̄ = FullSimplify[
  (wAA fAADrive + wAB fABDrive + wAC fACDrive + wBB fBBDrive + wBC fBCDrive + wCC fCCDrive);
  (*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]
Out[130]= 1 + (fB + fC) (-2 d1 fC + 2 d0 fB (-1 + fB + fC) - (fB + fC) (fB + fC - 2 d1 fC)) s
```

```
In[131]:= fAAsel = fAADrive wAA / W̄;
fABsel = fABDrive wAB / W̄;
fACsel = fACDrive wAC / W̄;
fBBsel = fBBDrive wBB / W̄;
fBCsel = fBCDrive wBC / W̄;
fCCsel = fCCDrive wCC / W̄;
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[143]= 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 supplementary material we show that results of exact recursions are remarkably consistent from these approximate analytical solutions.

Invasion of standard driver - note the driver always invades when it has a recessive fitness cost. Reassuringly, this reproduces model 1.

```
In[144]:= invasionStandardDriver = Solve[
  (FullSimplify[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) / fB] /. fB → 0) == 0, hs]
```

```
Out[144]= {{hs →  $\frac{-1 + 2 d0}{1 + 2 d0}$ }}
```

Fixation of standard driver

```
In[145]:= fixationStandardDriver = Solve[
  (FullSimplify[(ΔfB / fA /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0]) /. fB → 1) == 0, s]
```

```
Out[145]:= {{s →  $\frac{1}{2} (-1 + 2 d0 + 3 hs - 2 d0 hs)$ }}
```

```
In[146]:= (*fixation of a standard recessive driver*)
fixationStandardDriver /. hs → 0
```

```
Out[146]:= {{s →  $\frac{1}{2} (-1 + 2 d0)$ }}
```

Equilibrium

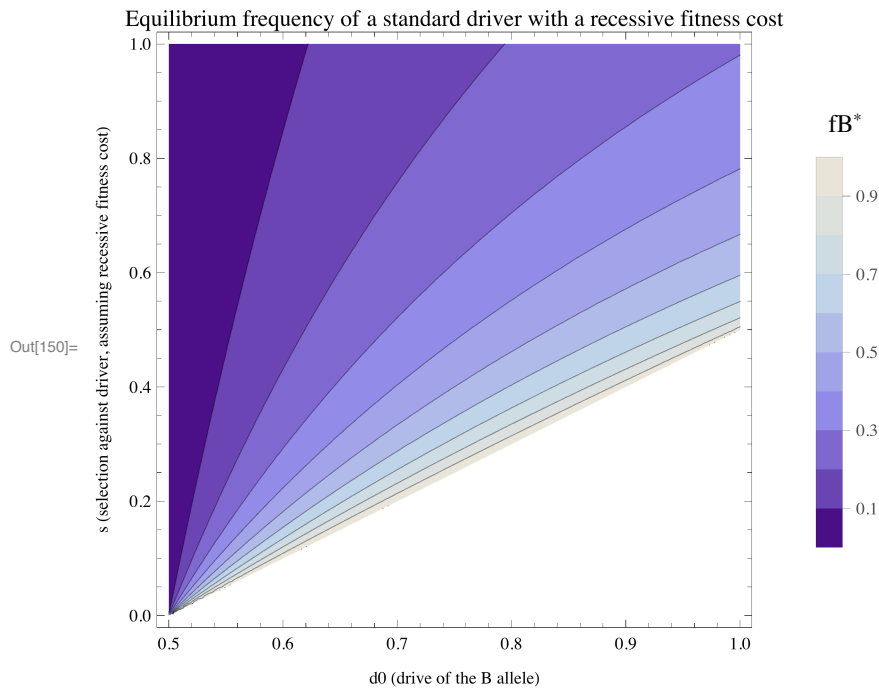
```
In[147]:= (*Equilibrium frequency of a standard driver*)
```

```
In[148]:= eqfB = Solve[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) == 0, fB][[4]]
```

```
Out[148]:= {fB →  $\left( 8 d0 hs - 4 d0 s + \sqrt{-4 (1 - 2 d0 + hs + 2 d0 hs) (-4 hs + 8 d0 hs + 2 s - 4 d0 s) + (-8 d0 hs + 4 d0 s)^2} \right) / (2 (-4 hs + 8 d0 hs + 2 s - 4 d0 s))$ }
```

```
In[149]:= (*Plot of equilibrium frequency of standard driver assuming full recessivity*)
```

```
In[150]:= 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[151]:= (*change in frequency of the drive modifier when rare and when alleles
at the drive locus are in drive-viability equilibrium, multiplied by
Wbar/fC [this value is always positive and will not influence the sign]*)
wbarDeltaSpermDrive = FullSimplify[
  FullSimplify[ $\bar{W} \Delta f_C / (f_C)$  /. HWE /. SUMTOONE] /. fC  $\rightarrow$  0 /. eqfB /. minormod]
```

```
Out[151]= 
$$\frac{1}{2 (1 - 2 d_0)^2 (2 h s - s)} (h s - s)$$


$$\left( -1 - h s - \sqrt{2} \sqrt{(1 + h s - 2 d_0 (2 + d_0 (-2 + s)))} (2 h s - s) + 2 d_0 (2 (-1 + d_0) (-1 + h s) + s) \right) \epsilon$$

```

```
In[152]:= (*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[153]:= ContourPlot[
  If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDrive]] /. eqfB /. e -> 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)"}]
```

Greater::nord : Invalid comparison with 7.49301 - 83.3298 *i* attempted. >>

Greater::nord : Invalid comparison with 7.49301 - 83.3298 *i* attempted. >>

Power::infty : Infinite expression $\frac{1}{0}$ encountered. >>

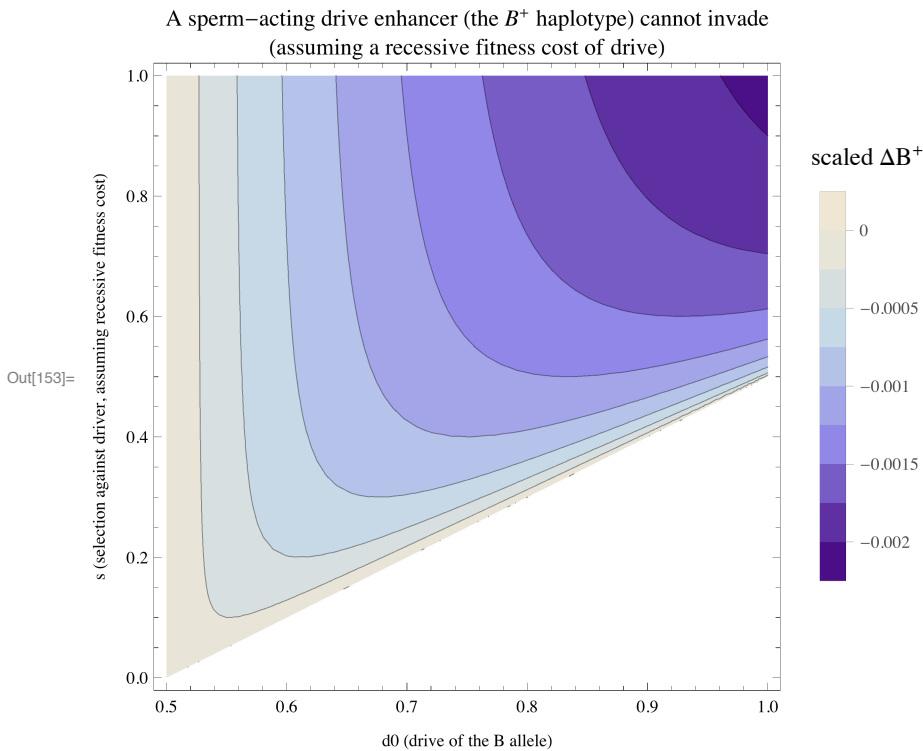
Power::infty : Infinite expression $\frac{1}{0.1}$ encountered. >>

Greater::nord : Invalid comparison with 3.99825 - 83.5704 *i* attempted. >>

General::stop : Further output of Greater::nord will be suppressed during this calculation. >>

Power::infty : Infinite expression $\frac{1}{0}$ encountered. >>

General::stop : Further output of Power::infty will be suppressed during this calculation. >>



```
In[154]:= (*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[155]:= ContourPlot[
  If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDrive]] /. eqfB /. e -> -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)"}]
```

Greater::nord : Invalid comparison with 7.49301 - 83.3298 i attempted. >>

Greater::nord : Invalid comparison with 7.49301 - 83.3298 i attempted. >>

Power::infty : Infinite expression $\frac{1}{0}$ encountered. >>

Power::infty : Infinite expression $\frac{1}{0.1}$ encountered. >>

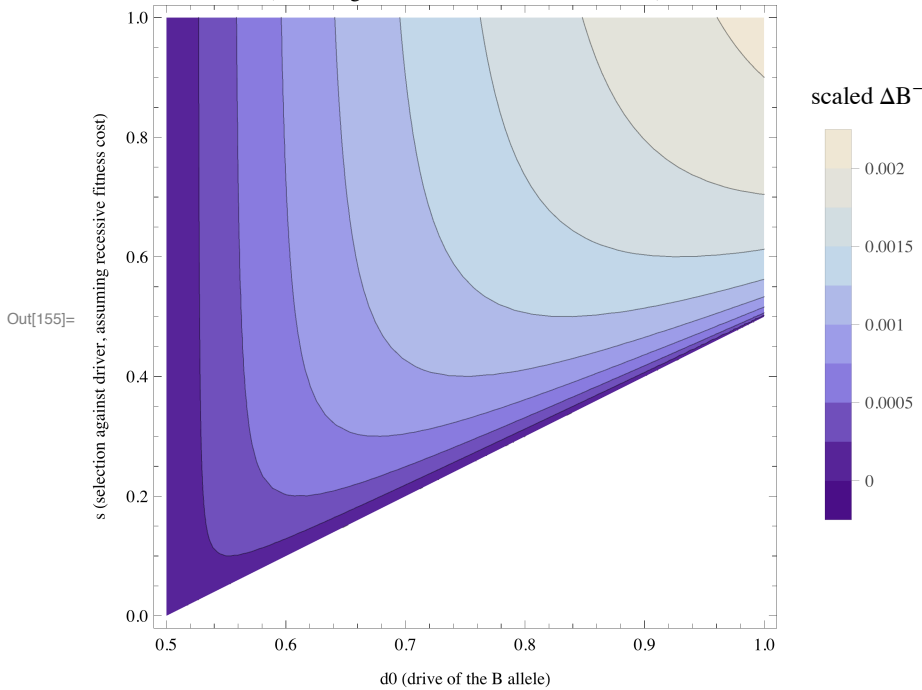
Greater::nord : Invalid comparison with 3.99825 - 83.5704 i attempted. >>

General::stop : Further output of Greater::nord will be suppressed during this calculation. >>

Power::infty : Infinite expression $\frac{1}{0}$ encountered. >>

General::stop : Further output of Power::infty will be suppressed during this calculation. >>

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



```
In[156]:= (*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 < 0.000001, 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)"}]
```

Power::infy : Infinite expression $\frac{1}{0}$ encountered. >>

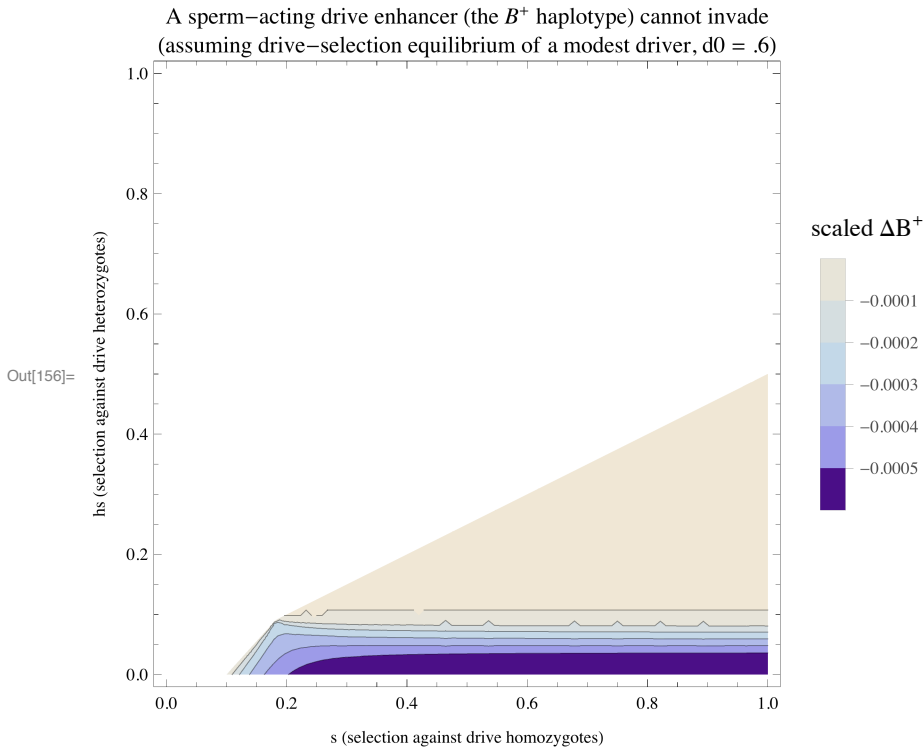
Power::infy : Infinite expression $\frac{1}{0}$ encountered. >>

Power::infy : Infinite expression $\frac{1}{0}$ encountered. >>

General::stop : Further output of Power::infy will be suppressed during this calculation. >>

Greater::nord : Invalid comparison with 3. + 63.2179 i attempted. >>

Greater::nord : Invalid comparison with 3. + 63.2179 i attempted. >>



```
In[157]:= (*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)"}]
```

Power::infty : Infinite expression $\frac{1}{0}$ encountered. >>

Greater::nord : Invalid comparison with 1.02083 - 2.442 i attempted. >>

Greater::nord : Invalid comparison with 1.02083 - 2.442 i attempted. >>

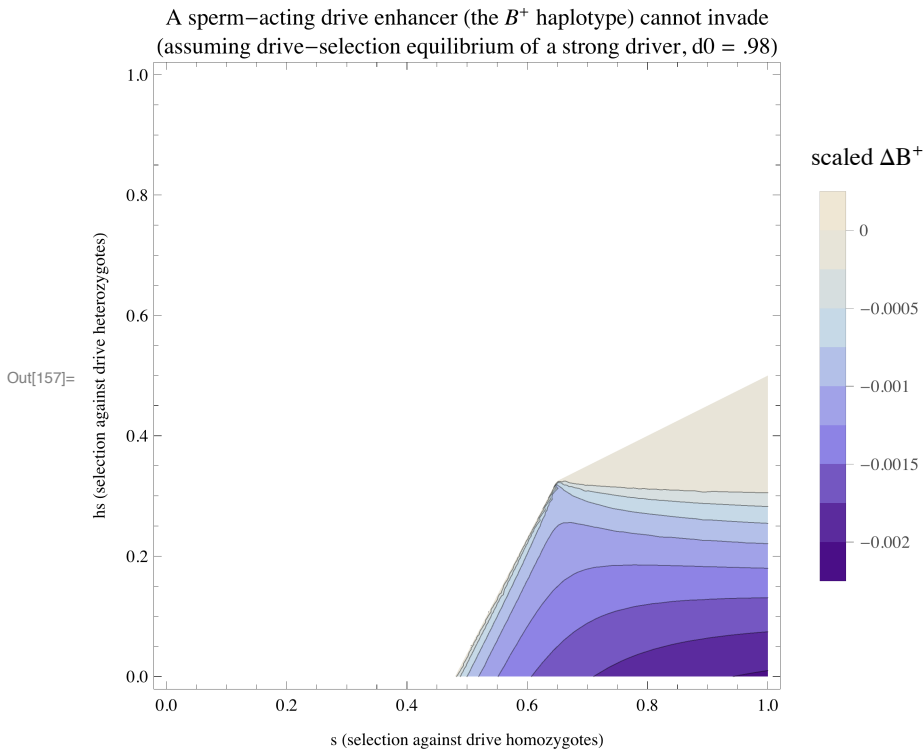
Power::infty : Infinite expression $\frac{1}{0}$ encountered. >>

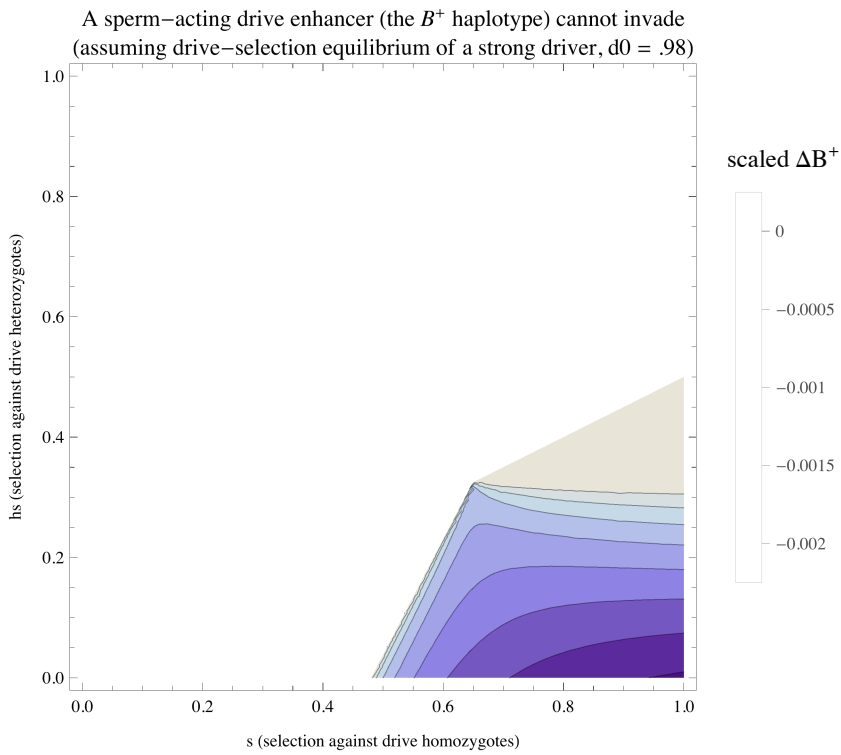
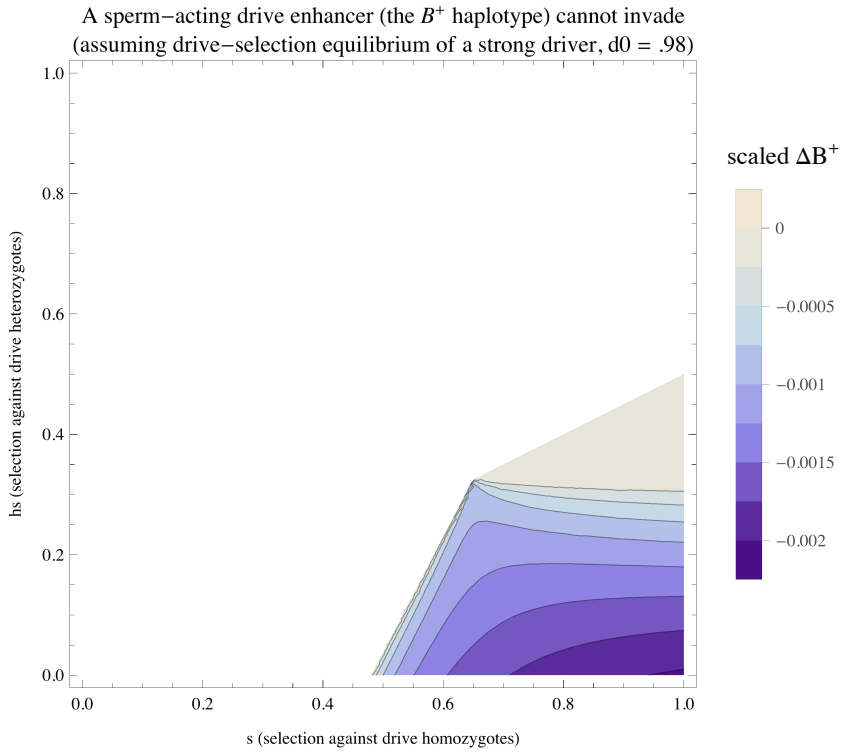
Power::infty : Infinite expression $\frac{1}{0.1}$ encountered. >>

General::stop : Further output of Power::infty will be suppressed during this calculation. >>

Greater::nord : Invalid comparison with 1.02083 - 1.56808 i attempted. >>

General::stop : Further output of Greater::nord will be suppressed during this calculation. >>





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

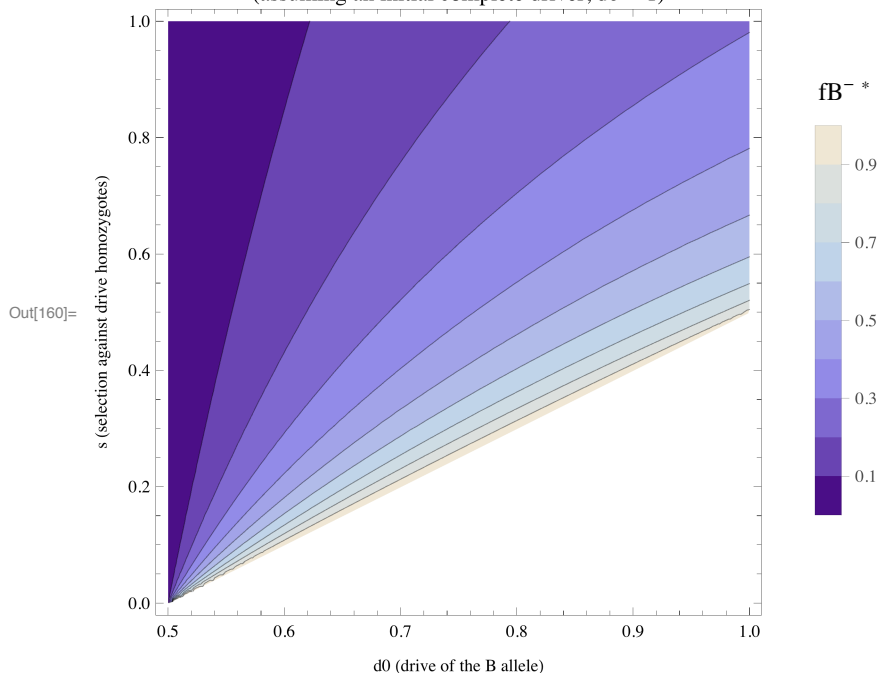
Equilibrium frequency of drive suppressor

```
In[158]:= eqfC = Solve[(FullSimplify[ΔfC /. HWE /. SUMTOONE /. minormod /. fB → 0]) == 0, fC][[4]];
```

```
In[159]:= (*Equilibrium frequency of a linked, coupled,
drive suppressor when the fitness costs of drive are recessive*)
```

```
In[160]:= 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, d0 = 1)



```
In[161]:= (*Equilibrium frequency of a linked, coupled,
drive suppressor when drive is complete*)
```

```
In[162]:= 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 -> "Equilibrium 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)"}]
```

Power::infy : Infinite expression $\frac{1}{0}$ encountered. >>

Less::nord : Invalid comparison with $1.00802 - 2.45019 i$ attempted. >>

Greater::nord : Invalid comparison with $1.00802 - 2.45019 i$ attempted. >>

Less::nord : Invalid comparison with $1.00802 - 2.45019 i$ attempted. >>

Greater::nord : Invalid comparison with $1.00802 - 2.45019 i$ attempted. >>

Power::infy : Infinite expression $\frac{1}{0}$ encountered. >>

Power::infy : Infinite expression $\frac{1}{0.1}$ encountered. >>

General::stop : Further output of Power::infy will be suppressed during this calculation. >>

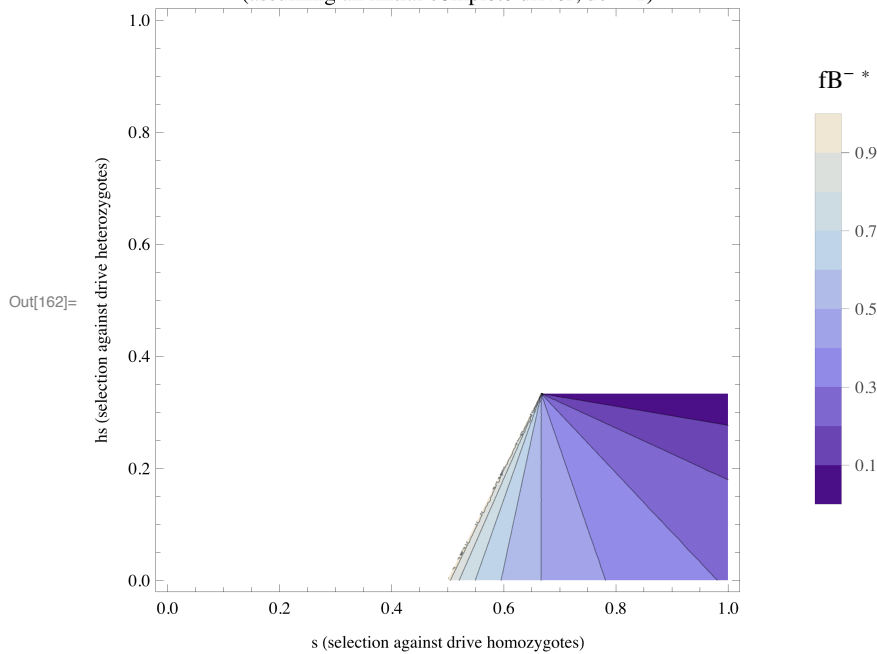
Less::nord : Invalid comparison with $1.00451 - 1.58082 i$ attempted. >>

General::stop : Further output of Less::nord will be suppressed during this calculation. >>

Greater::nord : Invalid comparison with $1.00451 - 1.58082 i$ attempted. >>

General::stop : Further output of Greater::nord will be suppressed during this calculation. >>

Equilibrium freq. of a sperm-acting drive suppressor (the B⁻ haplotype)
(assuming an initial complete driver, d0 = 1)



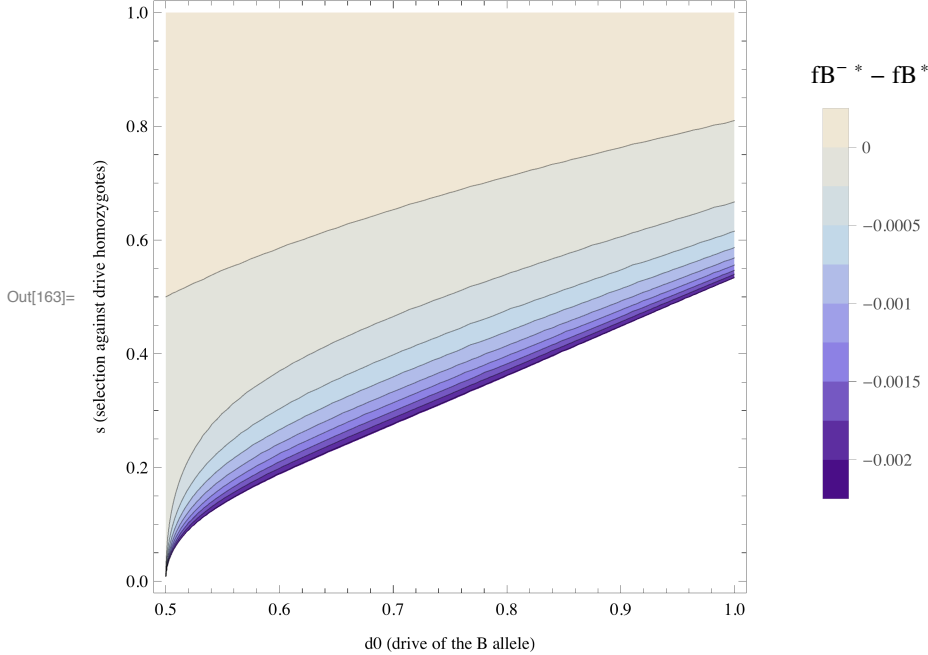
Equilibrium frequency of drive/sperm acting suppressor haplotype is often less than that of the standard driver it replaces.


```

In[163]:= (*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)\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)"}]

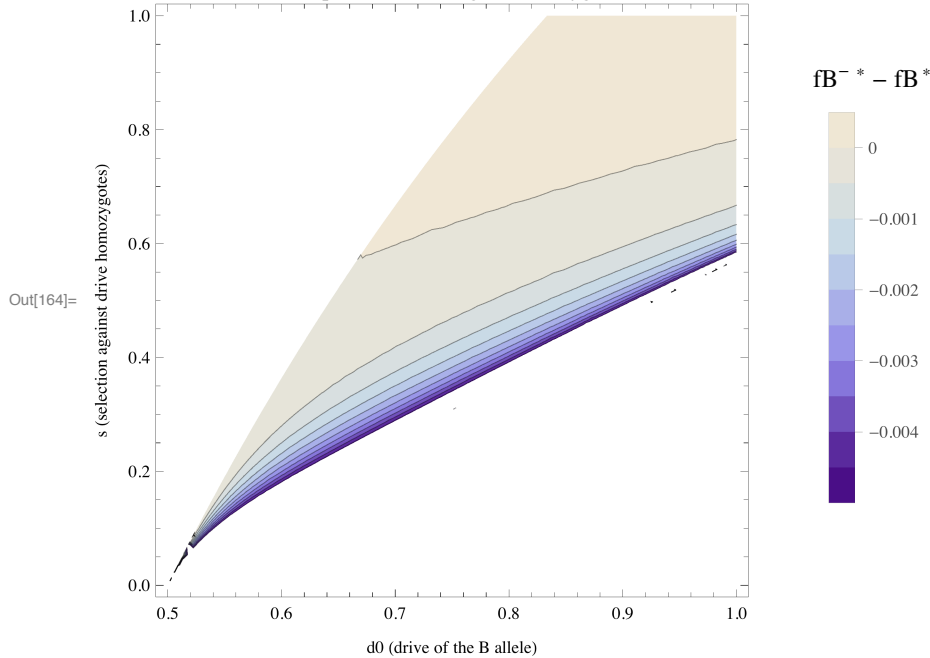
```

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



```
In[164]:= 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 equilibrium frequency of a drive suppressor (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)"}]
```

Difference in equilibrium frequency of a drive suppressor (B⁻ haplotype)
and the driver it replaces (assuming a heterozygote cost, hs = s/4)



```
In[165]:= (*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[ $\bar{w} \Delta f_B / (f_B)$  /. HWE /. SUMTOONE] /. fB → 0 /. eqfC /. minormod];
```

```
In[166]:= (*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[167]:= 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)"}]
```

Power::infty : Infinite expression $\frac{1}{0}$ encountered. >>

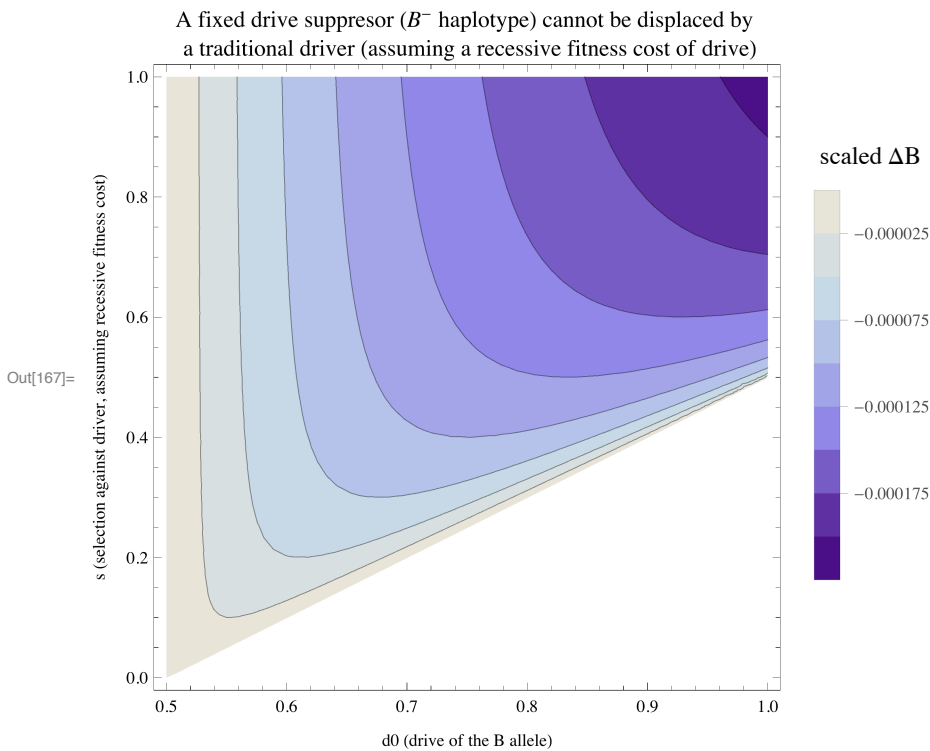
Greater::nord : Invalid comparison with 53.7184 - 64.9128 i attempted. >>

Greater::nord : Invalid comparison with 53.7184 - 64.9128 i attempted. >>

Power::infty : Infinite expression $\frac{1}{0}$ encountered. >>

Power::infty : Infinite expression $\frac{1}{0.1}$ encountered. >>

General::stop : Further output of Power::infty will be suppressed during this calculation. >>



```
In[168]:= (*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[169]:= 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)"}]
```

Power::infy : Infinite expression $\frac{1}{0}$ encountered. >>

Greater::nord : Invalid comparison with 104.123 - 58.7778 i attempted. >>

Greater::nord : Invalid comparison with 104.123 - 58.7778 i attempted. >>

Power::infy : Infinite expression $\frac{1}{0}$ encountered. >>

Power::infy : Infinite expression $\frac{1}{0.1}$ encountered. >>

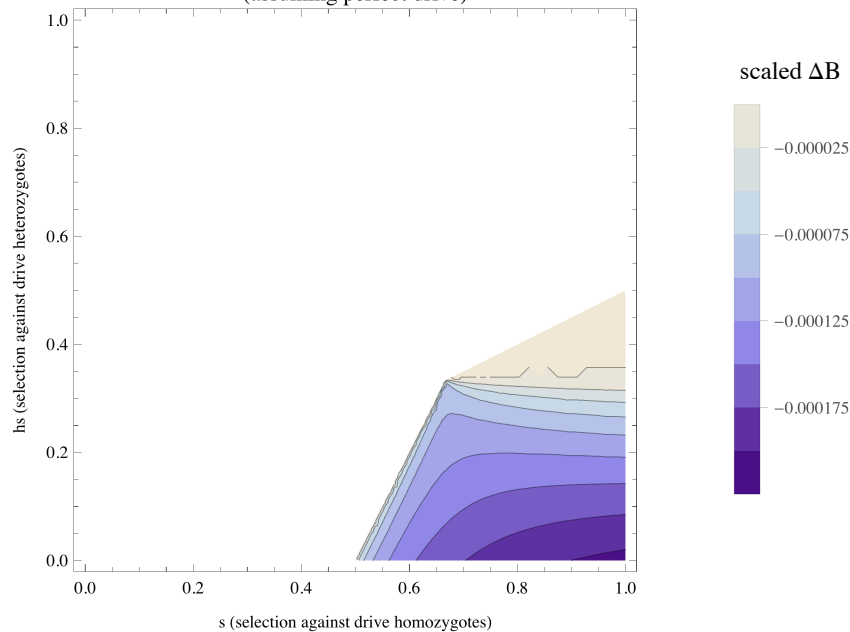
General::stop : Further output of Power::infy will be suppressed during this calculation. >>

Greater::nord : Invalid comparison with 69.1031 - 97.0611 i attempted. >>

General::stop : Further output of Greater::nord will be suppressed during this calculation. >>

```
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)



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 tightly-linked locus is on the A background. 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 A+ allele [not discussed in our ms]).

When C decreases drive in heterozygous 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 calculate 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 +
```



```

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[AA_n];
fAB_Drive = FullSimplify[AB_n + BA_n];
fAC_Drive = FullSimplify[AC_n + CA_n];
fBB_Drive = FullSimplify[BB_n];
fBC_Drive = FullSimplify[BC_n + CB_n];
fCC_Drive = FullSimplify[CC_n];
(*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;
W_bar = 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[W_bar /. HWE /. SUMTOONE /. hs -> 0]
1 + (2 d0 (-1 + fB) - fB) fB^2 s

fAA_Sel = fAA_Drive wAA / W_bar;
fAB_Sel = fAB_Drive wAB / W_bar;
fAC_Sel = fAC_Drive wAC / W_bar;
fBB_Sel = fBB_Drive wBB / W_bar;
fBC_Sel = fBC_Drive wBC / W_bar;
fCC_Sel = fCC_Drive wCC / W_bar;
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[W_bar 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 REENTER 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]];
```

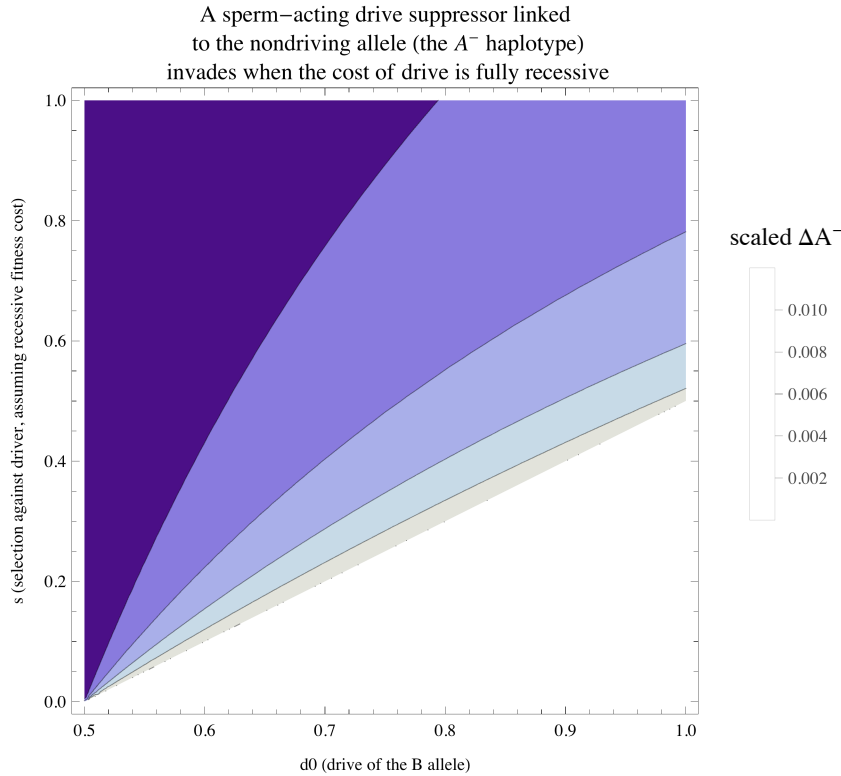
Invasion of sperm acting drive modifier tightly linked with the driver, on the non-driving background

(*change in frequency of the drive modifier when rare and when alleles at the drive locus are in drive-viability equilibrium, multiplied by \bar{w}_B/f_C^2 [this value is always positive and will not influence the sign]*)

```
wbarDeltaSpermDriveRecessive = FullSimplify[
  (FullSimplify[ $\bar{w} \Delta f_C / (f_C^2)$  /. HWE /. SUMTOONE /. eqfB /. hs → 0]) /. minormod]
  (
$$\frac{-2 d_0 s + \sqrt{2} \sqrt{(-1 + 2 d_0 (2 + d_0 (-2 + s))) s}}{2 (-1 + 2 d_0) s} \in$$
)
```



```
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, multiplied by \bar{w}/f_C [this value is always positive and will not influence the sign]*)

```
wbarDeltaSpermDrive = FullSimplify[
  FullSimplify[ $\bar{w} \Delta f_C / (f_C) /. HWE /. SUMTOONE$ ] /. fC → 0 /. eqfB /. minormod]
-  $\frac{1}{2 (1 - 2 d_0)^2 (2 h s - s)} h s (-1 - h s - \sqrt{2} \sqrt{(1 + h s - 2 d_0 (2 + d_0 (-2 + s))) (2 h s - s) + 2 d_0 (2 (-1 + d_0) (-1 + h s) + s)}) \epsilon$ 
```

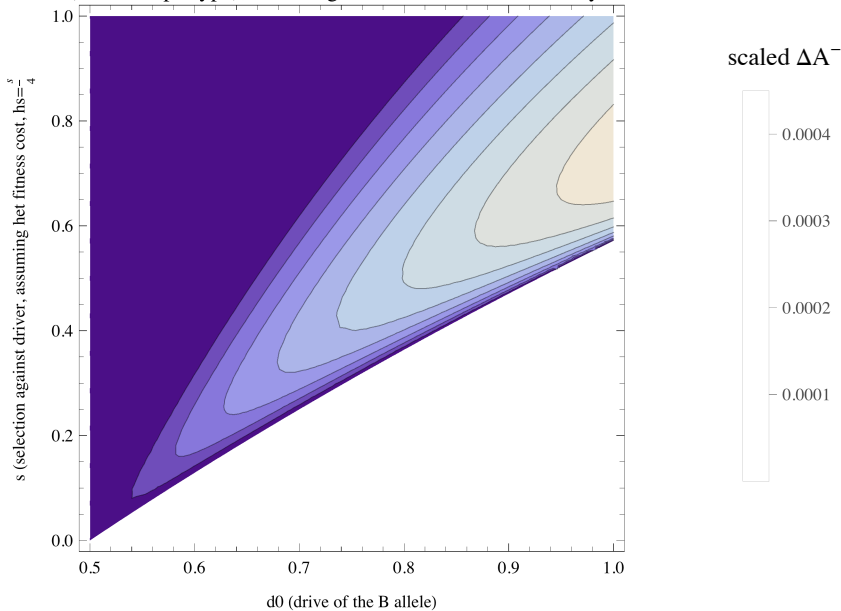
(*Plotting change this change in frequency when the sperm acting locus is rare, increases drive, and when the fitness cost of drive is fully recessive. NOTE: This sperm enhancer of drive cannot invade*)

```

ContourPlot[
  If[fB > 1, 1 / 0, If[fB < 0.0001, 0, wbarDeltaSpermDrive]] /. eqfB /. e -> -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,  $hs = \frac{s}{4}$ )"}]

```

Invasion of a sperm-acting drive suppressor linked to the nondriving allele (the A⁻ haplotype), assuming the cost of drive is not fully recessive.



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

In addition to 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 d_0 , but changes to d_1 when fertilized by an 'F' bearing sperm

Setup

```

ClearAll["Global`*"]

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*)
{fA → 1 - fB, fE → 1 - fF}

```

Drive

```

fAAEEdrive = 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]
fABEEdrive = 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]
fBBEEDrive = 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]
fAAEFDrive = 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]
fAAFF_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 * 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]
fABFF_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 * 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]
fBBFF_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 * 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]

```

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

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

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

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

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

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

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

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

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

Selection

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

$\bar{W} = \text{FullSimplify}[(\text{fAAEE}_{\text{Drive}} \text{wAAEE} + \text{fAAEF}_{\text{Drive}} \text{wAAEF} + \text{fAAFF}_{\text{Drive}} \text{wAAFF}$
 $+ \text{fABEE}_{\text{Drive}} \text{wABEE} + \text{fABEF}_{\text{Drive}} \text{wABEF} + \text{fABFF}_{\text{Drive}} \text{wABFF}$
 $+ \text{fBBEE}_{\text{Drive}} \text{wBBEE} + \text{fBBEF}_{\text{Drive}} \text{wBBEF} + \text{fBBFF}_{\text{Drive}} \text{wBBFF}$
 $)];$

```

fAAEE_Sel = FullSimplify[fAAEE_Drive wAAEE / W];
fABEE_Sel = FullSimplify[fABEE_Drive wABEE / W];
fBBEE_Sel = FullSimplify[fBBEE_Drive wBBEE / W];
fAAEF_Sel = FullSimplify[fAAEF_Drive wAAEF / W];
fABEF_Sel = FullSimplify[fABEF_Drive wABEF / W];
fBBEF_Sel = FullSimplify[fBBEF_Drive wBBEF / W];
fAAFF_Sel = FullSimplify[fAAFF_Drive wAAFF / W];
fABFF_Sel = FullSimplify[fABFF_Drive wABFF / W];
fBBFF_Sel = FullSimplify[fBBFF_Drive wBBFF / W];
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[W 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 rearrangement,
  invasionOfUnlinkedModeifier = -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

```
fixationOfUnlinkedModifier = FullSimplify[
  FullSimplify[ $\bar{W} \Delta fF / (1 - fF) /. \text{randomHaps} /. D \rightarrow 0 /. \text{sum2one} /. \text{minormod} ] /. fF \rightarrow 1 ]
  (*this assumes no LD and random mating*)
  (-1 + fB) fB (hs - 2 fB hs + fB s) \epsilon
  (*Thus the invasion and fixation conditions are equivalent*)$ 
```

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

In addition to 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 d_0 , but changes to d_1 when fertilized by an 'F' bearing sperm

Setup

```
ClearAll["Global`*"]

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

Drive

```
fAAEEdrive = 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 - dh) / 2)) + (fABEF * fABEE * ((1 - dh) / 4)) + (fABEF * fBBEE * 0) +
(fABEF * fAAEF * ((1 - dh) / 4)) + (fABEF * fABEF * ((1 - dh) / 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]
fBBEEDrive = 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 * (dh / 2)) + (fABEF * fABEE * (1 / 4)) +
(fABEF * fBBEE * ((1 - dh) / 2)) + (fABEF * fAAEF * (dh / 4)) + (fABEF * fABEF * (1 / 8)) +
(fABEF * fBBEF * ((1 - dh) / 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]
fBBEEDrive = 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 * (dh / 4)) +
(fABEF * fBBEE * (dh / 2)) + (fABEF * fAAEF * 0) + (fABEF * fABEF * (dh / 8)) +
(fABEF * fBBEF * (dh / 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) +

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(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 - d0) / 2)) + (fABEE * fABEF * ((1 - d0) / 4)) +
(fABEE * fBBEF * 0) + (fABEE * fAAFF * (1 - d0)) + (fABEE * fABFF * ((1 - d0) / 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 - dh) / 2)) + (fABEF * fABEE * ((1 - dh) / 4)) +
(fABEF * fBBEE * 0) + (fABEF * fAAEF * ((1 - dh) / 2)) + (fABEF * fABEF * ((1 - dh) / 4)) +
(fABEF * fBBEF * 0) + (fABEF * fAAFF * ((1 - dh) / 2)) + (fABEF * fABFF * ((1 - dh) / 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 * (1 - d1)) + (fABFF * fABEE * ((1 - d1) / 2)) + (fABFF * fBBEE * 0) +
(fABFF * fAAEF * ((1 - d1) / 2)) + (fABFF * fABEF * ((1 - d1) / 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 * (d0 / 2)) + (fABEE * fABEF * (1 / 4)) +
(fABEE * fBBEF * ((1 - d0) / 2)) + (fABEE * fAAFF * (d0)) + (fABEE * fABFF * (1 / 2)) +
(fABEE * fBBFF * (1 - d0)) + (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 * (dh / 2)) + (fABEF * fABEE * (1 / 4)) +
(fABEF * fBBEE * ((1 - dh) / 2)) + (fABEF * fAAEF * (dh / 2)) + (fABEF * fABEF * (1 / 4)) +
(fABEF * fBBEF * ((1 - dh) / 2)) + (fABEF * fAAFF * (dh / 2)) + (fABEF * fABFF * (1 / 4)) +
(fABEF * fBBFF * ((1 - dh) / 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 * (d1)) +
(fABFF * fABEE * (1 / 2)) + (fABFF * fBBEE * (1 - d1)) + (fABFF * fAAEF * (d1 / 2)) +
(fABFF * fABEF * (1 / 4)) + (fABFF * fBBEF * ((1 - d1) / 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 * (d0 / 4)) +
(fABEE * fBBEF * (d0 / 2)) + (fABEE * fAAFF * 0) + (fABEE * fABFF * (d0 / 2)) +

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(fABEE * fBBFF * d0) + (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 * (dh / 4)) + (fABEF * fBBEE * (dh / 2)) + (fABEF * fAAEF * 0) +
(fABEF * fABEF * (dh / 4)) + (fABEF * fBBEF * (dh / 2)) + (fABEF * fAAFF * 0) +
(fABEF * fABFF * (dh / 4)) + (fABEF * fBBFF * (dh / 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 * (d1 / 2)) + (fABFF * fBBEE * (d1)) +
(fABFF * fAAEF * 0) + (fABFF * fABEF * (d1 / 4)) + (fABFF * fBBEF * (d1 / 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]
fAAFF_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 * 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 - dh) / 4)) + (fABEF * fABEF * ((1 - dh) / 8)) +
(fABEF * fBBEF * 0) + (fABEF * fAAFF * ((1 - dh) / 2)) + (fABEF * fABFF * ((1 - dh) / 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]
fABFF_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 * 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 * (dh / 4)) + (fABEF * fABEF * (1 / 8)) +
(fABEF * fBBEF * ((1 - dh) / 4)) + (fABEF * fAAFF * (dh / 2)) + (fABEF * fABFF * (1 / 4)) +
(fABEF * fBBFF * ((1 - dh) / 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) +

```

$$\begin{aligned}
& (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] \\
fBBFF_{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 * 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 * (dh / 8)) + (fABEF * fBBEF * (dh / 4)) + \\
& (fABEF * fAAFF * 0) + (fABEF * fABFF * (dh / 4)) + (fABEF * fBBFF * (dh / 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 fAAEE + 2 (fAAEF + fABEE) + fABEF) \\
& (2 fAAEE + fAAEF + 2 fABEE - 2 d0 fABEE + fABEF - dh fABEF) \\
\frac{1}{8} & (4 fABEE^2 + 4 fABEE fABEF + fABEF^2 + 12 fABEE fBBEE - 8 d0 fABEE fBBEE + \\
& 6 fABEF fBBEE - 4 dh fABEF fBBEE + 6 fABEE fBBEF - 4 d0 fABEE fBBEF + 3 fABEF fBBEF - \\
& 2 dh fABEF fBBEF + fAAEF (2 fABEE + 4 d0 fABEE + fABEF + 2 dh fABEF + 8 fBBEE + 4 fBBEF) + \\
& 2 fAAEE ((2 + 4 d0) fABEE + fABEF + 2 dh fABEF + 8 fBBEE + 4 fBBEF)) \\
\frac{1}{8} & (2 d0 fABEE + dh fABEF + 2 fBBEE + fBBEF) (2 fABEE + fABEF + 4 fBBEE + 2 fBBEF) \\
\frac{1}{4} & (2 fAAEF^2 + 6 fAAFF fABEE - 4 d0 fAAFF fABEE + 3 fAAFF fABEF - \\
& 2 dh fAAFF fABEF + 2 fABEE fABEF - d0 fABEE fABEF - dh fABEE fABEF + \\
& fABEF^2 - dh fABEF^2 - (2 (-2 + d0 + d1) fABEE + (-2 + d1 + dh) fABEF) fABFF + \\
& fAAEE (4 fAAEF + 8 fAAFF + 3 fABEF - 2 dh fABEF + 6 fABFF - 4 d1 fABFF) + \\
& fAAEF (4 fAAFF + 3 fABEE - 2 d0 fABEE + 3 fABEF - 2 dh fABEF + 3 fABFF - 2 d1 fABFF))
\end{aligned}$$

$$\frac{1}{4} \left(2 \text{fABEE} \text{fABEF} + \text{fABEF}^2 + 4 \text{fABEE} \text{fABFF} + 2 \text{fABEF} \text{fABFF} + 3 \text{fABEF} \text{fBBEE} - \right.$$

$$2 \text{dh} \text{fABEF} \text{fBBEE} + 6 \text{fABFF} \text{fBBEE} - 4 \text{d1} \text{fABFF} \text{fBBEE} + 3 \text{fABEE} \text{fBBEF} -$$

$$2 \text{d0} \text{fABEE} \text{fBBEF} + 3 \text{fABEF} \text{fBBEF} - 2 \text{dh} \text{fABEF} \text{fBBEF} + 3 \text{fABFF} \text{fBBEF} -$$

$$2 \text{d1} \text{fABFF} \text{fBBEF} + \text{fAAFF} \left((2 + 4 \text{d0}) \text{fABEE} + \text{fABEF} + 2 \text{dh} \text{fABEF} + 8 \text{fBBEE} + 4 \text{fBBEF} \right) +$$

$$6 \text{fABEE} \text{fBBFF} - 4 \text{d0} \text{fABEE} \text{fBBFF} + 3 \text{fABEF} \text{fBBFF} - 2 \text{dh} \text{fABEF} \text{fBBFF} +$$

$$\text{fAAEF} \left(\text{fABEF} + 2 \text{dh} \text{fABEF} + 2 \text{fABFF} + 4 \text{d1} \text{fABFF} + 4 \text{fBBEF} + 8 \text{fBBFF} \right) + \text{fAAEF}$$

$$\left(\text{fABEE} + 2 \text{d0} \text{fABEE} + \text{fABEF} + 2 \text{dh} \text{fABEF} + \text{fABFF} + 2 \text{d1} \text{fABFF} + 4 \left(\text{fBBEE} + \text{fBBEF} + \text{fBBFF} \right) \right)$$

$$\frac{1}{4} \left(2 \text{d1} \text{fABEE} \text{fABFF} + \text{d1} \text{fABEF} \text{fABFF} + \text{fABEF} \text{fBBEE} + 2 \text{fABFF} \text{fBBEE} + \right.$$

$$4 \text{d1} \text{fABFF} \text{fBBEE} + \text{fABEE} \text{fBBEF} + \text{fABEF} \text{fBBEF} + \text{fABFF} \text{fBBEF} + 2 \text{d1} \text{fABFF} \text{fBBEF} +$$

$$4 \text{fBBEE} \text{fBBEF} + 2 \text{fBBEF}^2 + (2 \text{fABEE} + \text{fABEF} + 8 \text{fBBEE} + 4 \text{fBBEF}) \text{fBBFF} +$$

$$\text{dh} \text{fABEF} \left(\text{fABEE} + \text{fABEF} + \text{fABFF} + 2 \left(\text{fBBEE} + \text{fBBEF} + \text{fBBFF} \right) \right) +$$

$$\text{d0} \text{fABEE} \left(\text{fABEF} + 2 \left(\text{fABFF} + \text{fBBEF} + 2 \text{fBBFF} \right) \right)$$

$$\frac{1}{8} \left(2 \text{fAAEF} + 4 \text{fAAFF} + \text{fABEF} + 2 \text{fABFF} \right)$$

$$\left(\text{fAAEF} + 2 \text{fAAFF} + \text{fABEF} - \text{dh} \text{fABEF} + 2 \text{fABFF} - 2 \text{d1} \text{fABFF} \right)$$

$$\frac{1}{8} \left(\text{fABEF}^2 + 4 \text{fABEF} \text{fABFF} + 4 \text{fABFF}^2 + 3 \text{fABEF} \text{fBBEF} - 2 \text{dh} \text{fABEF} \text{fBBEF} + 6 \text{fABFF} \text{fBBEF} - \right.$$

$$4 \text{d1} \text{fABFF} \text{fBBEF} + 6 \text{fABEF} \text{fBBFF} - 4 \text{dh} \text{fABEF} \text{fBBFF} + 12 \text{fABFF} \text{fBBFF} -$$

$$8 \text{d1} \text{fABFF} \text{fBBFF} + \text{fAAEF} \left(\text{fABEF} + 2 \text{dh} \text{fABEF} + 2 \text{fABFF} + 4 \text{d1} \text{fABFF} + 4 \text{fBBEF} + 8 \text{fBBFF} \right) +$$

$$2 \text{fAAFF} \left(\text{fABEF} + 2 \text{dh} \text{fABEF} + 2 \text{fABFF} + 4 \text{d1} \text{fABFF} + 4 \text{fBBEF} + 8 \text{fBBFF} \right)$$

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

Selection

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

$\bar{W} = \text{FullSimplify} [(\text{fAAEE}_{\text{Drive}} \text{wAAEE} + \text{fAAEF}_{\text{Drive}} \text{wAAEF} + \text{fAAFF}_{\text{Drive}} \text{wAAFF}$
 $+ \text{fABEE}_{\text{Drive}} \text{wABEE} + \text{fABEF}_{\text{Drive}} \text{wABEF} + \text{fABFF}_{\text{Drive}} \text{wABFF}$
 $+ \text{fBBEE}_{\text{Drive}} \text{wBBEE} + \text{fBBEF}_{\text{Drive}} \text{wBBEF} + \text{fBBFF}_{\text{Drive}} \text{wBBFF}$
 $)];$

```

fAAEE_Sel = FullSimplify[fAAEE_Drive wAAEE / W];
fABEE_Sel = FullSimplify[fABEE_Drive wABEE / W];
fBBEE_Sel = FullSimplify[fBBEE_Drive wBBEE / W];
fAAEF_Sel = FullSimplify[fAAEF_Drive wAAEF / W];
fABEF_Sel = FullSimplify[fABEF_Drive wABEF / W];
fBBEF_Sel = FullSimplify[fBBEF_Drive wBBEF / W];
fAAFF_Sel = FullSimplify[fAAFF_Drive wAAFF / W];
fABFF_Sel = FullSimplify[fABFF_Drive wABFF / W];
fBBFF_Sel = FullSimplify[fBBFF_Drive wBBFF / W];
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 egg-acting drive modifier unlinked to the driver

```

invasionOfUnlinkedModifier =
  FullSimplify[W ΔfF / fF /. randomHaps /. D → 0 /. dh → d1 /. sum2one /. minormod] /.
  fF → 0 (*this assumes no LD and random mating*)
- (-1 + fB) fB ((-1 + 2 fB) hs - fB s) ε

(*With some rearrangement,
  invasionOfUnlinkedModeifier= -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 eggs-acting drive modifier unlinked to the driver

```

fixationOfUnlinkedModifier = FullSimplify[FullSimplify[
   $\bar{W} \Delta fF / (1 - fF)^2 /. \text{randomHaps} /. D \rightarrow 0 /. dh \rightarrow d1 /. \text{sum2one} /. \text{minormod} /.$ 
   $hs \rightarrow 0]] /. fF \rightarrow 1 (*\text{this assumes no LD and random mating}*)
(-1 + fB) fB^2 s \in
(*Thus the invasion and fixation conditions are equivalent*)$ 
```