

# Brandvain and Coop. Sperm dependent female meiotic drive.

In[1]:=

## Model I. Traditional female drive

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### 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*)
W = FullSimplify[fAADrive wAA + fABDrive wAB + fBBDrive wBB]; (*mean fitness*)
fAASel = FullSimplify[(fAADrive * wAA) / W];
fABSel = FullSimplify[(fABDrive * wAB) / W];
fBBSel = FullSimplify[(fBBDrive wBB) / W];
fASel = FullSimplify[fAASel + fABSel / 2];
fBSel = FullSimplify[fBBSel + fABSel / 2];
ΔfA = FullSimplify[fASel - fA];
ΔfB = FullSimplify[fBSel - fB];
```

---

### Analysis

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

## Invasion

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

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

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

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

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

## Fixation

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

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

We solve for fixation conditions when recessive or not.

```
In[22]:= fixationCritRecessive = Solve[scaledDeltaDriveWhenCommon == 0, s] /. hs → 0  
fixationCritNotRecessive = Solve[scaledDeltaDriveWhenCommon == 0, s]
```

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

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

## Equilibrium

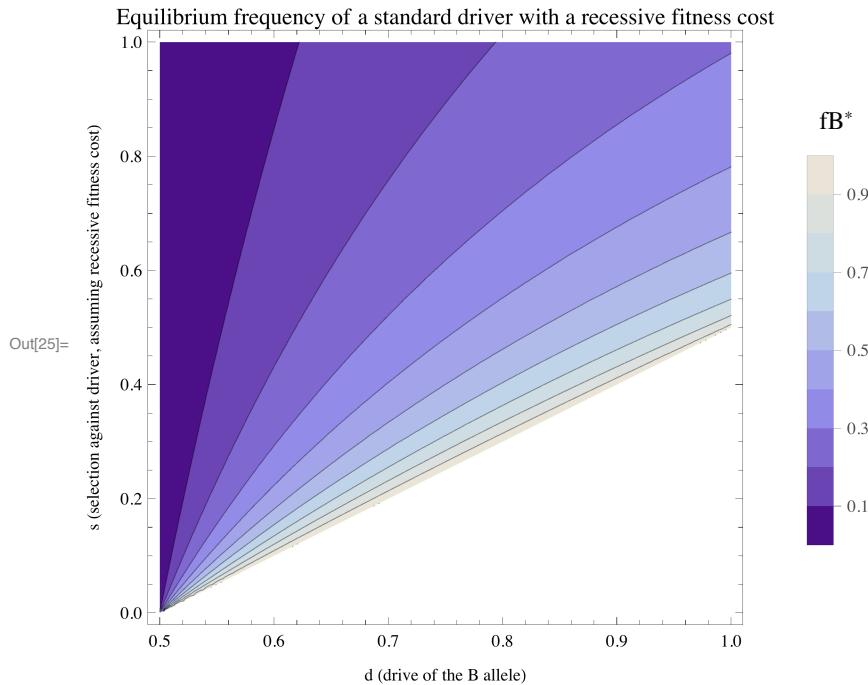
We identify the equilibrium frequency of the standard driver

```
In[24]:= eqfB = Solve[(FullSimplify[(\Delta fB /. x → 0)]) == 0, fB][[4]]
```

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

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[fAA Drive + fAB Drive + fBB Drive]
```

```
Out[26]= 1
```

## Model 2. Female drive depends on sperm haplotype (single pleitropic locus)

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

x represents the deviation from Hardy - Weinberg Equilibrium

## Setup

```
In[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*)
W = FullSimplify[fAAdrive wAA + fABdrive wAB + fBBdrive wBB]; (*mean fitness*)
fAAsel = FullSimplify[(fAAdrive * wAA) / W];
fABsel = FullSimplify[(fABdrive * wAB) / W];
fBBsel = FullSimplify[(fBBdrive wBB) / W];
fAsel = FullSimplify[fAAsel + fABsel / 2];
fBsel = FullSimplify[fBBsel + fABsel / 2];
ΔfA = FullSimplify[fAsel - fA];
ΔfB = FullSimplify[fBsel - fB];
```

## Analysis

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

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

## Invasion

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

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

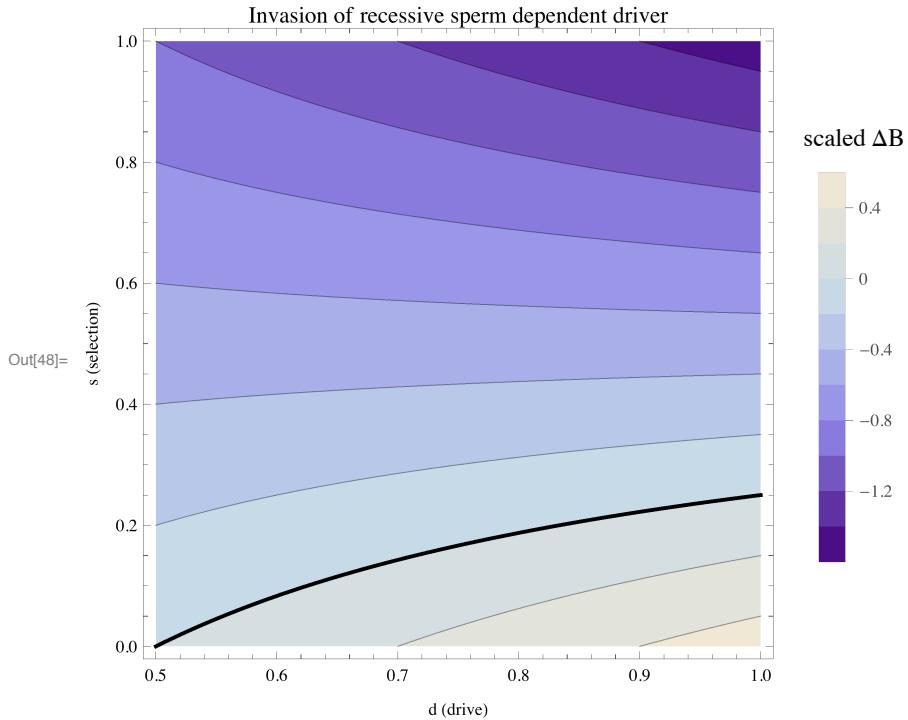
In[45]:= spermDepRecessiveInvade = Solve[ΔfBinvade == 0, s]

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

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

In[47]:= plotRelChange4RarespermDepRecessive = ContourPlot[{ΔfBinvade}, {d, 0.5, 1},
{s, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "scaled ΔB"],
FrameLabel → {"d (drive)", "s (selection)"}, PlotLabel → "Invasion of recessive sperm dependent driver"];
```

```
In[48]:= Show[plotRelChange4RarespermDepRecessive, plotInvasion4spermDepRecessive]
```



## Fixation

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

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

Out[49]=

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

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

Out[50]=

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

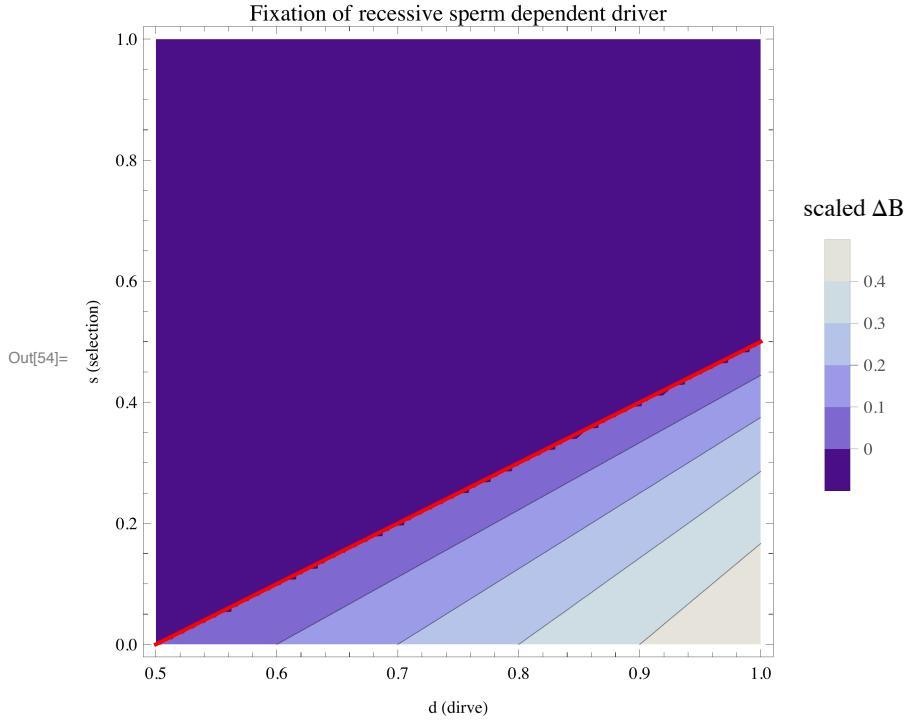
$$\frac{1}{2} (-1 + 2 d)$$

Out[51]=

```
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]
```



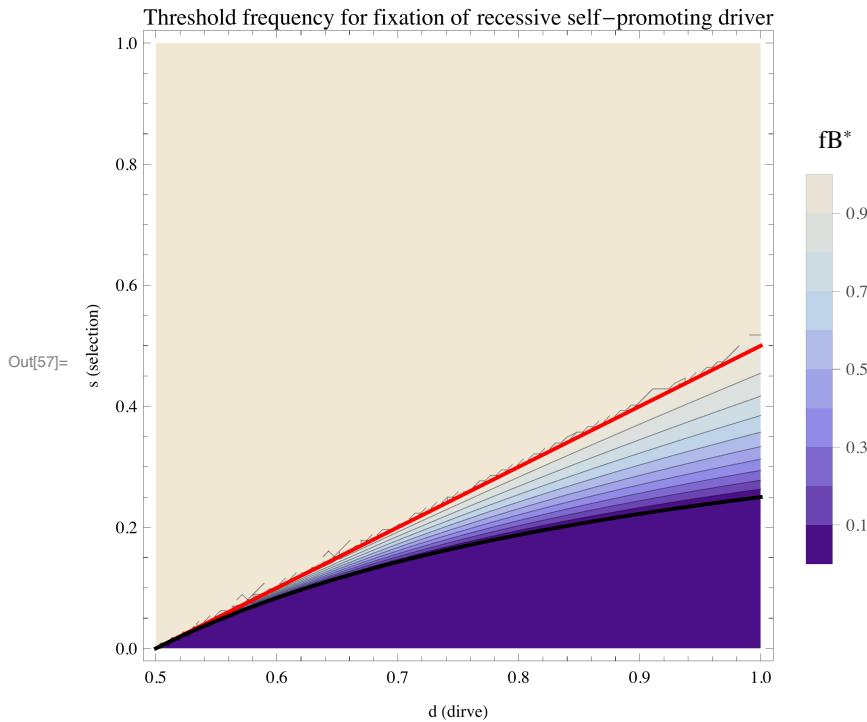
## Bistability Point

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

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

```
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. hs is nonzero]**

## Invasion

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

```
In[58]:= FullSimplify[FullSimplify[ΔfB /. x → 0] / fB] /. fB → 0
```

```
Out[58]= -hs
```

## Fixation

```
In[59]:= ΔfBfix = FullSimplify[FullSimplify[FullSimplify[ΔfB /. x → 0] / fA] /. fB → 1]
```

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

```

```
In[60]:= spermDepNotRecessiveFix = Solve[ΔfBfix == 0, s]
```

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

```

```
In[61]:= spermDepAddFix = Solve[ΔfBfix == 0 /. hs → s / 2, s]
```

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

```

```
In[62]:= plotspermDepAddFix =
  Plot[s /. spermDepAddReceesiveFix, {d, .5, 1}, PlotStyle -> {Red, Thick}];

ReplaceAll::reps : {spermDepAddReceesiveFix} is neither a list of
replacement rules nor a valid dispatch table, and so cannot be used for replacing. >>
```

## Bistability Point

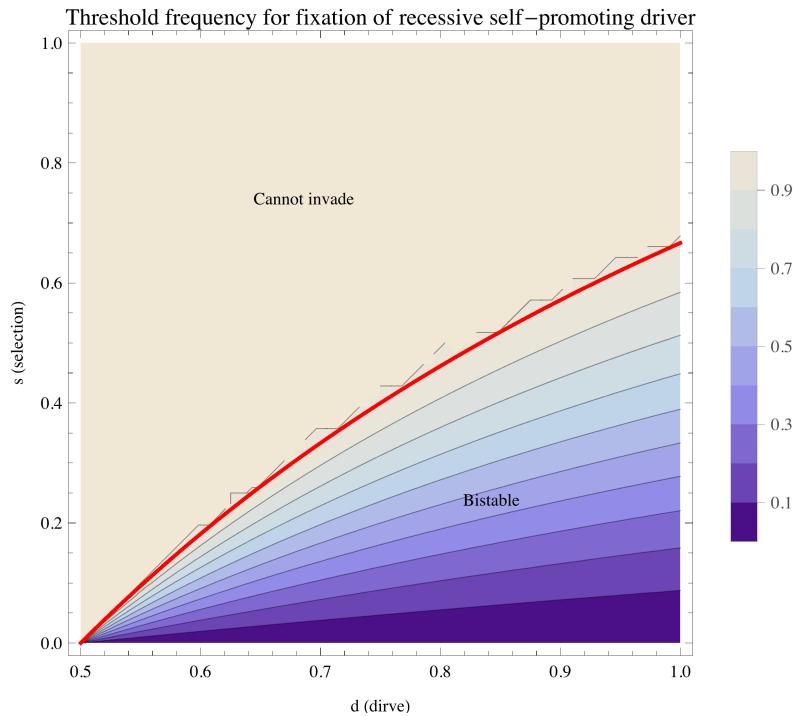
```
In[63]:= FBbistabSpermDepNotReceesive = Solve[FullSimplify[\Delta fB /. x -> 0] == 0, fB][[3]]

Out[63]= {fB -> (-1 + 2 d + 3 hs + 2 d hs - 4 d s -
  Sqrt[(-8 hs (-2 hs + 4 d hs + 2 s - 4 d s) + (1 - 2 d - 3 hs - 2 d hs + 4 d s)^2)])/
  (2 (-2 hs + 4 d hs + 2 s - 4 d s))}
```

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

```
In[64]:= bistab = ContourPlot[
  (If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBbistabSpermDepNotReceesive /. hs -> (s/2),
  {d, .5, 1}, {s, 0, 1}, PlotLegends -> BarLegend[Automatic, LegendLabel -> "fB*"],
  FrameLabel -> {"d (dirve)", "s (selection)"}, PlotLabel ->
  "Threshold frequency for fixation of recessive self-promoting driver"];

In[65]:= Show[bistab, plotspermDepAddFix]
```



```
In[67]:=
```

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

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

x represents the deviation from Hardy - Weinberg Equilibrium

## Setup

```
In[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*)
fAADrive = FullSimplify[fAA (fAA + fAB / 2) + fAB (fAA / 2 + fAB (1 - dhet) / 2)];
fABDrive = FullSimplify[
  fAA (fAB / 2 + fBB) + fAB (fAA / 2 + fAB / 2 + fBB (1 - dhom)) + fBB (fAA + fAB / 2)];
fBBDrive = FullSimplify[fAB (fAB dhet / 2 + fBB dhom) + fBB (fAB / 2 + fBB)];
```

## Selection

```
In[76]:= wAA = 1; wAB = 1 - hs; wBB = 1 - s; (*genotypic fitnesses*)
W = FullSimplify[fAADrive wAA + fABDrive wAB + fBBDrive wBB]; (*mean fitness*)
fAASel = FullSimplify[(fAADrive * wAA) / W];
fABSel = FullSimplify[(fABDrive * wAB) / W];
fBBSel = FullSimplify[(fBBDrive wBB) / W];
fASel = FullSimplify[fAASel + fABSel / 2];
fBSel = FullSimplify[fBBSel + fABSel / 2];
ΔfA = FullSimplify[fASel - fA];
ΔfB = FullSimplify[fBSel - fB];
```

```
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 → (-1 + 2 dhet) / (2 dhet)}
```

```
In[87]:= plotiInvasion4maleDepRecessive =
  Plot[s /. invasion4maleDepRecessive /. dhet → dhom,
  {dhom, .5, 1}, PlotStyle -> {Black, Thick}];
```

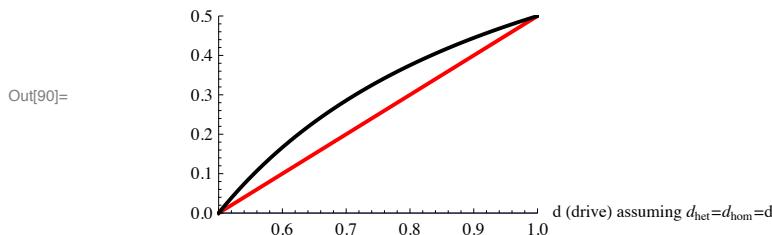
#### Fixation

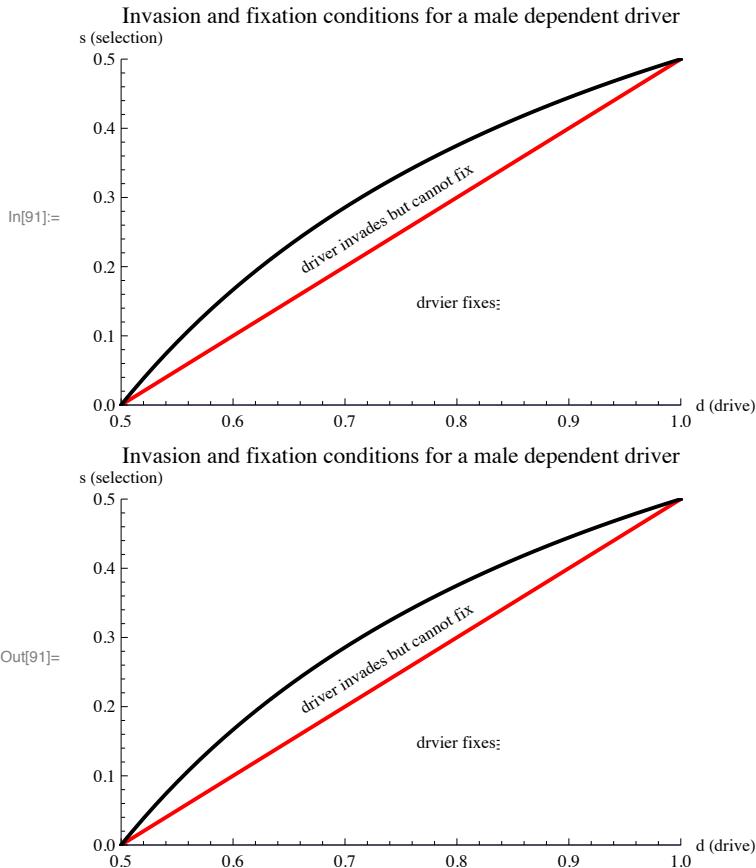
```
In[88]:= fixation4maleDepRecessive =
  Solve[(FullSimplify[(FullSimplify[(ΔfB /. x → 0 /. hs → 0) / fA] /. fB → 1)]) == 0, s]
Out[88]= {s → 1/2 (-1 + 2 dhom)}

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, plotiInvasion4maleDepRecessive]
```

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



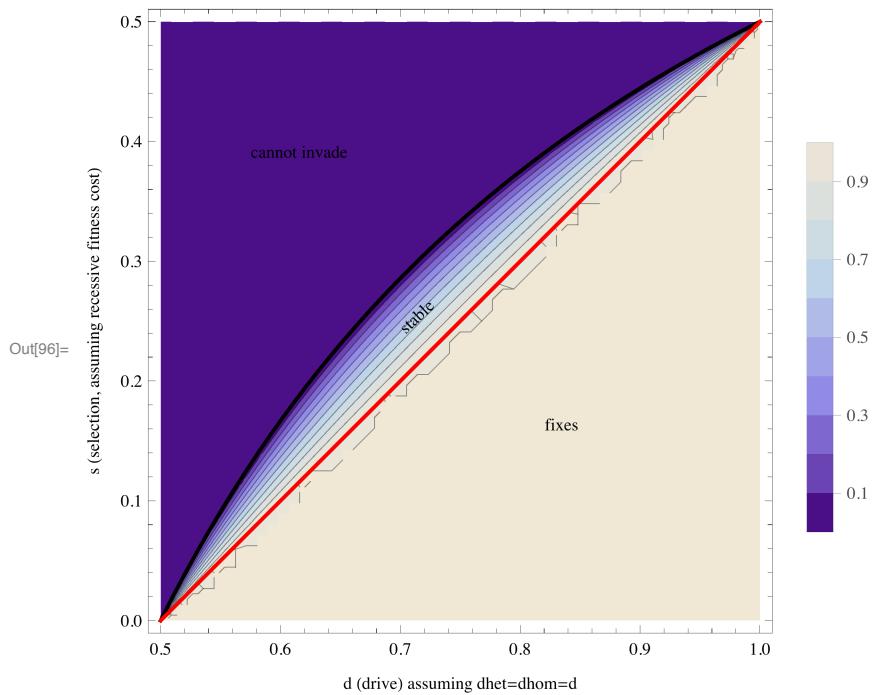


## Equilibrium

```
In[92]:= FBeqMaleepRecessive =
  Solve[FullSimplify[\Delta fB /. x → 0 /. hs → 0 /. dhet → dhom] == 0, fB][[4]]
Out[92]= {fB → 2 (1 - 2 dhom + 2 s dhom) / (-1 + 2 s) (-1 + 2 dhom)}

In[93]:= eqfig = ContourPlot[(If[fB < 0, 0, If[fB > 1, 1, fB]]) /. FBeqMaleepRecessive,
  {dhom, 0.5, 1}, {s, 0, .5}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB*"],
  FrameLabel → {"d (drive) assuming dhet=dhom=d",
  "s (selection, assuming recessive fitness cost)"}];
```

```
In[95]:= Show[eqfig, plotiInvasion4maleDepRecessive, 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 + fAC / 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 belowsum 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];
BAn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * fAC * 0 + fAA * fBB * 0 + fAA * fBC * 0 +
fAA * fCC * 0 + fAB * fAA * d0 + fAB * fAB * d0 / 2 + fAB * fAC * d0 / 2 + fAB * fBB * 0 +
fAB * fBC * 0 + fAB * fCC * 0 + fAC * fAA * 0 + fAC * fAB * 0 + fAC * fAC * 0 + fAC * fBB * 0 +
fAC * fBC * 0 + fAC * fCC * 0 + fBB * fAA * 1 + fBB * fAB * 1 / 2 + fBB * fAC * 1 / 2 +
fBB * fBB * 0 + fBB * fBC * 0 + fBB * fCC * 0 + fBC * fAA * 1 / 2 + fBC * fAB * 1 / 4 +
```

```

fBC * FAC * 1 / 4 + fBC * fBB * 0 + fBC * fBC * 0 + fBC * FCC * 0 + FCC * FAA * 0 +
FCC * fAB * 0 + FCC * FAC * 0 + FCC * fBB * 0 + FCC * fBC * 0 + FCC * FCC * 0 + 0];
BBn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * FAC * 0 + fAA * fBB * 0 + fAA * fBC * 0 +
fAA * FCC * 0 + fAB * fAA * 0 + fAB * fAB * d0 / 2 + fAB * FAC * 0 + fAB * fBB * d0 +
fAB * fBC * d0 / 2 + fAB * FCC * 0 + FAC * fAA * 0 + FAC * fAB * 0 + FAC * FAC * 0 +
FAC * fBB * 0 + FAC * fBC * 0 + FAC * FCC * 0 + fBB * fAA * 0 + fBB * fAB * 1 / 2 + fBB * FAC * 0 +
fBB * fBB * 1 + fBB * fBC * 1 / 2 + fBB * FCC * 0 + fBC * fAA * 0 + fBC * fAB * 1 / 4 +
fBC * FAC * 0 + fBC * fBB * 1 / 2 + fBC * fBC * 1 / 4 + fBC * FCC * 0 + FCC * fAA * 0 +
FCC * fAB * 0 + FCC * FAC * 0 + FCC * fBB * 0 + FCC * fBC * 0 + FCC * FCC * 0 + 0];
BCn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * FAC * 0 + fAA * fBB * 0 +
fAA * fBC * 0 + fAA * FCC * 0 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * FAC * (d1) / 2 +
fAB * fBB * 0 + fAB * fBC * (d1) / 2 + fAB * FCC * d1 + FAC * fAA * 0 + FAC * fAB * 0 +
FAC * FAC * 0 + FAC * fBB * 0 + FAC * fBC * 0 + FAC * FCC * 0 + fBB * fAA * 0 + fBB * fAB * 0 +
fBB * FAC * 1 / 2 + fBB * fBB * 0 + fBB * fBC * 1 / 2 + fBB * FCC * 1 + fBC * fAA * 0 +
fBC * fAB * 0 + fBC * FAC * 1 / 4 + fBC * fBB * 0 + fBC * fBC * 1 / 4 + fBC * FCC * 1 / 2 +
FCC * fAA * 0 + FCC * fAB * 0 + FCC * FAC * 0 + FCC * fBB * 0 + FCC * fBC * 0 + FCC * FCC * 0 + 0];
CAn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * FAC * 0 + fAA * fBB * 0 +
fAA * fBC * 0 + fAA * FCC * 0 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * FAC * 0 + fAB * fBB * 0 +
fAB * fBC * 0 + fAB * FCC * 0 + FAC * fAA * d0 + FAC * fAB * d0 / 2 + FAC * FAC * d0 / 2 +
FAC * fBB * 0 + FAC * fBC * 0 + FAC * FCC * 0 + fBB * fAA * 0 + fBB * fAB * 0 + fBB * fAC * 0 +
fBB * fBB * 0 + fBB * fBC * 0 + fBB * FCC * 0 + fBC * fAA * 1 / 2 + fBC * fAB * 1 / 4 +
fBC * FAC * 1 / 4 + fBC * fBB * 0 + fBC * fBC * 0 + fBC * FCC * 0 + FCC * fAA * 1 +
FCC * fAB * 1 / 2 + FCC * FAC * 1 / 2 + FCC * fBB * 0 + FCC * fBC * 0 + FCC * FCC * 0 + 0];
CBn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * FAC * 0 + fAA * fBB * 0 + fAA * fBC * 0 +
fAA * FCC * 0 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * FAC * 0 + fAB * fBB * 0 + fAB * fBC * 0 +
fAB * fCC * 0 + FAC * fAA * 0 + FAC * fAB * d0 / 2 + FAC * FAC * 0 + FAC * fBB * d0 +
FAC * fBC * d0 / 2 + FAC * FCC * 0 + fBB * fAA * 0 + fBB * fAB * 0 + fBB * fAC * 0 +
fBB * fBB * 0 + fBB * fBC * 0 + fBB * FCC * 0 + fBC * fAA * 0 + fBC * fAB * 1 / 4 +
fBC * FAC * 0 + fBC * fBB * 1 / 2 + fBC * fBC * 1 / 4 + fBC * FCC * 0 + FCC * fAA * 0 +
FCC * fAB * 1 / 2 + FCC * FAC * 0 + FCC * fBB * 1 + FCC * fBC * 1 / 2 + FCC * FCC * 0 + 0];
CCn = FullSimplify[fAA * fAA * 0 + fAA * fAB * 0 + fAA * FAC * 0 + fAA * fBB * 0 +
fAA * fBC * 0 + fAA * FCC * 0 + fAB * fAA * 0 + fAB * fAB * 0 + fAB * FAC * 0 + fAB * fBB * 0 +
fAB * fBC * 0 + fAB * FCC * 0 + FAC * fAA * 0 + FAC * fAB * 0 + FAC * FAC * d1 / 2 +
FAC * fBB * 0 + FAC * fBC * d1 / 2 + FAC * FCC * d1 + fBB * fAA * 0 + fBB * fAB * 0 +
fBB * FAC * 0 + fBB * fBB * 0 + fBB * fBC * 0 + fBB * FCC * 0 + fBC * fAA * 0 + fBC * fAB * 0 +
fBC * FAC * 1 / 4 + fBC * fBB * 0 + fBC * fBC * 1 / 4 + fBC * FCC * 1 / 2 + FCC * fAA * 0 +
FCC * fAB * 0 + FCC * FAC * 1 / 2 + FCC * fBB * 0 + FCC * fBC * 1 / 2 + FCC * FCC * 1 + 0];
In[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] /. HWE /. SUMTOONE]
Out[127]= 1

```

## Selection

```
In[128]:= wAA = 1; wAC = wAB = 1 - hs; wBB = wBC = wCC = 1 - s;
W = FullSimplify[
  (wAA fAADrive + wAB fABDrive + wAC fACDrive + wBB fBBDrive + wBC fBCDrive + wCC fCCDrive)];
(*Because the C allele arises on the B background we assume
it has the same impact on individual fitness*)
FullSimplify[W /. 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 / W;
fABSel = fABDrive wAB / W;
fACSel = fACDrive wAC / W;
fBBSel = fBBDrive wBB / W;
fBCSel = fBCDrive wBC / W;
fCCSel = fCCDrive wCC / W;
fASel = FullSimplify[fAASel + (fABSel + fACSel) / 2];
fBSel = FullSimplify[fBBSel + (fABSel + fBCSel) / 2];
fCSel = FullSimplify[fCCSel + (fACSel + fBCSel) / 2];
ΔfA = FullSimplify[fASel - fA];
ΔfB = FullSimplify[fBSel - fB];
ΔfC = FullSimplify[fCSel - fC];

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

Out[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 thats results of exact recursions are remarkably consistant from these approximate analytical solutions.

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

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

Out[144]= {hs → -1 + 2 d0 / (1 + 2 d0)}
```

### Fixation of standard driver

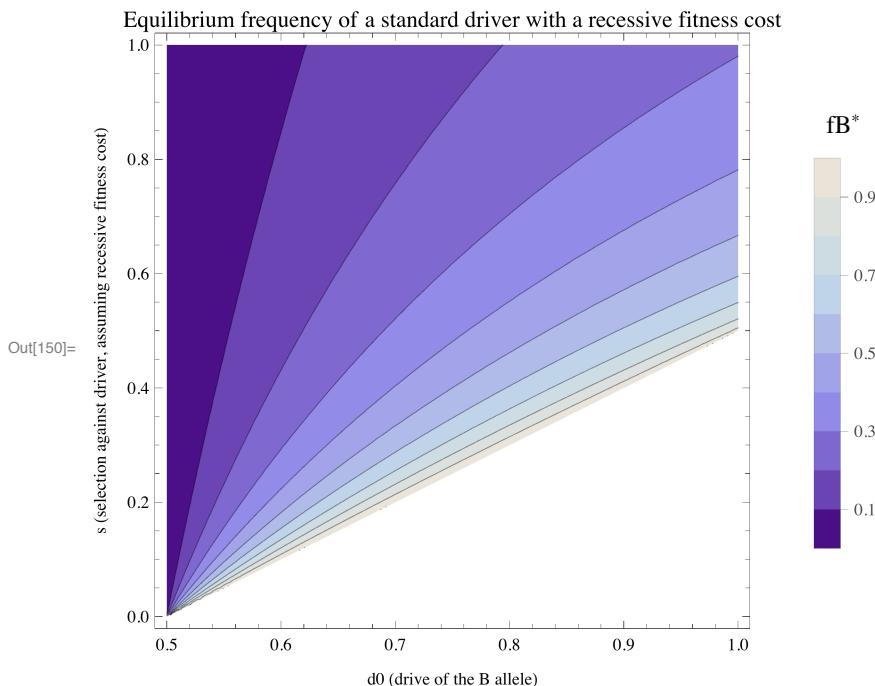
```
In[145]:= fixationStandardDriver = Solve[
  FullSimplify[(ΔfB / fA /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) /. fB → 1] == 0, s]
Out[145]= {s → 1/2 (-1 + 2 d0 + 3 hs - 2 d0 hs)}
```

```
In[146]:= (*fixation of a standard recessive driver*)
fixationStandardDriver /. hs → 0
Out[146]= {s → 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 → (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])/
  (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, mutliplied by
Wbar/fC [this value is always positive and will not influence the sign]*)
wbarDeltaSpermDrive = FullSimplify[
  FullSimplify[\bar{W} \Delta fC / (fC) /. HWE /. SUMTOONE] /. fC \[Rule] 0 /. eqfB /. minormod]
Out[151]= 
$$\frac{1}{2 (1 - 2 d0)^2 (2 hs - s)} (hs - s)$$


$$\left( -1 - hs - \sqrt{2} \sqrt{(1 + hs - 2 d0 (2 + d0 (-2 + s))) (2 hs - s)} + 2 d0 (2 (-1 + d0) (-1 + hs) + s) \right) \in$$


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

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

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

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

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

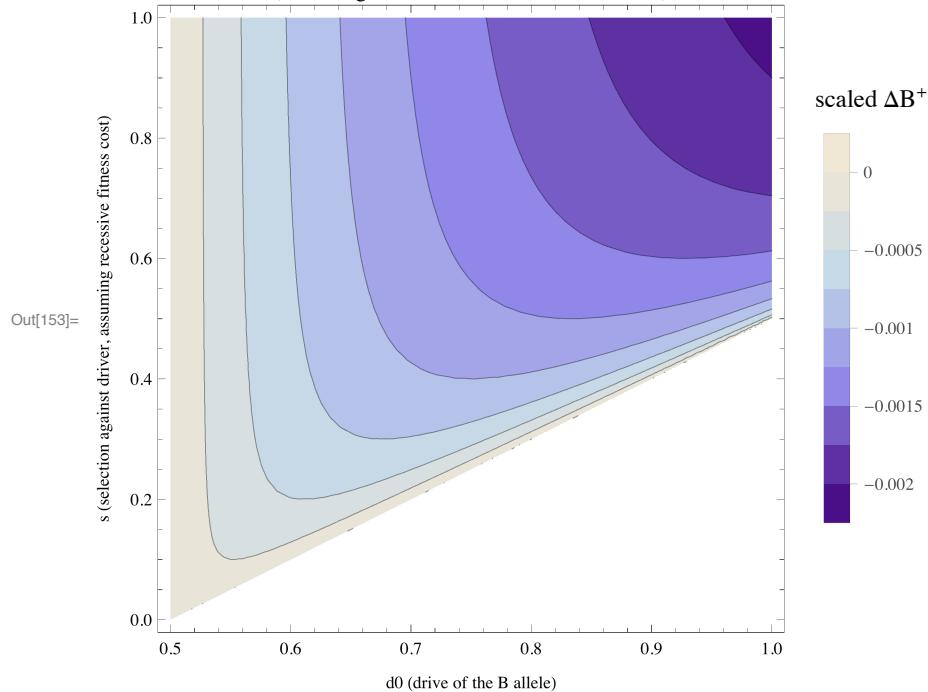
Greater::nord : Invalid comparison with  $3.99825 - 83.5704i$  attempted. >>

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

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

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

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



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

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

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

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

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

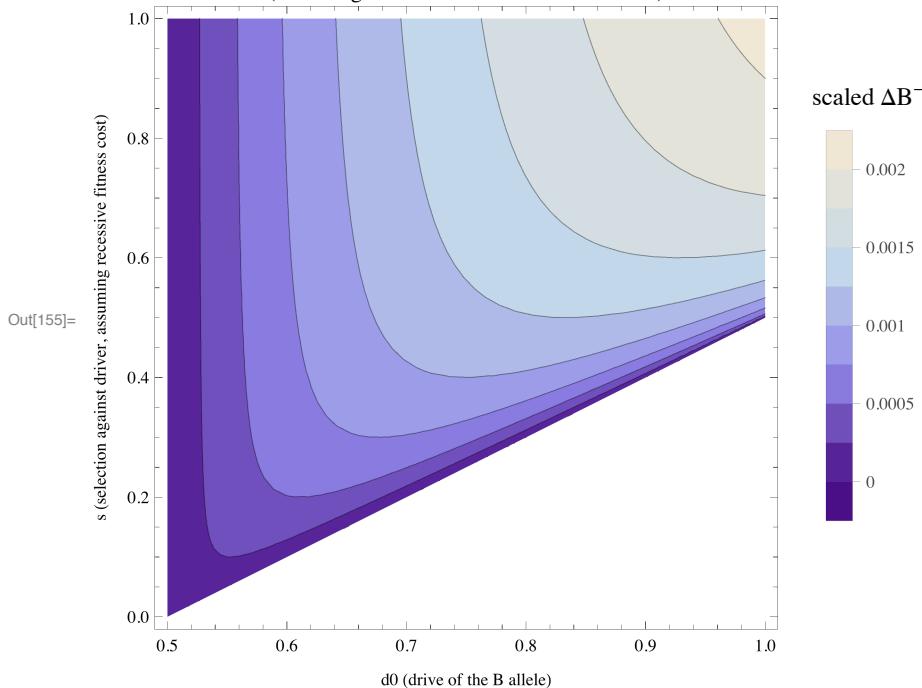
Greater::nord : Invalid comparison with  $3.99825 - 83.5704 i$  attempted. >>

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

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

General::stop : Further output of Power::infy 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 < 0.0000001, 0, wbarDeltaSpermDrive]]) /. eqfB /.
 $\epsilon \rightarrow 0.01 / . d0 \rightarrow .6$ , {s, 0, 1}, {hs, 0, 1},
PlotLegends -> BarLegend[Automatic, LegendLabel -> "scaled  $\Delta B^+$ "], 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. >>

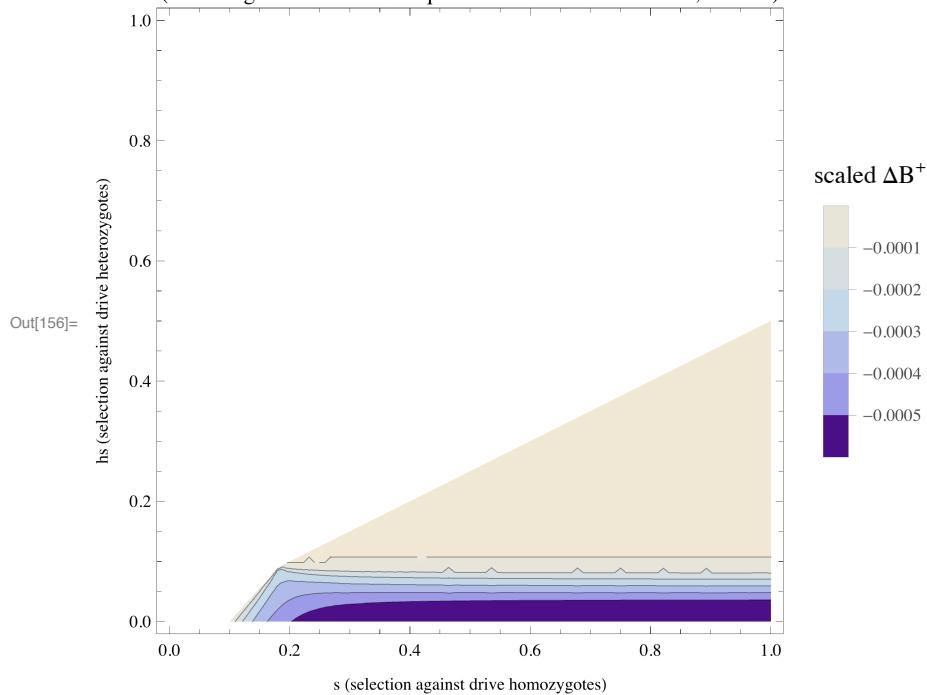
Power::infy : Infinite expression  $\frac{1}{0}$  encountered. >>

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. >>

A sperm-acting drive enhancer (the  $B^+$  haplotype) cannot invade  
(assuming drive-selection equilibrium of a modest driver,  $d0 = .6$ )



```
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 /.
 $\epsilon \rightarrow 0.01 / . d0 \rightarrow .98$ ), {s, 0, 1}, {hs, 0, 1},
PlotLegends -> BarLegend[Automatic, LegendLabel -> "scaled  $\Delta B^+$ "], 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::infy : 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::infy : Infinite expression  $\frac{1}{0.}$  encountered. >>

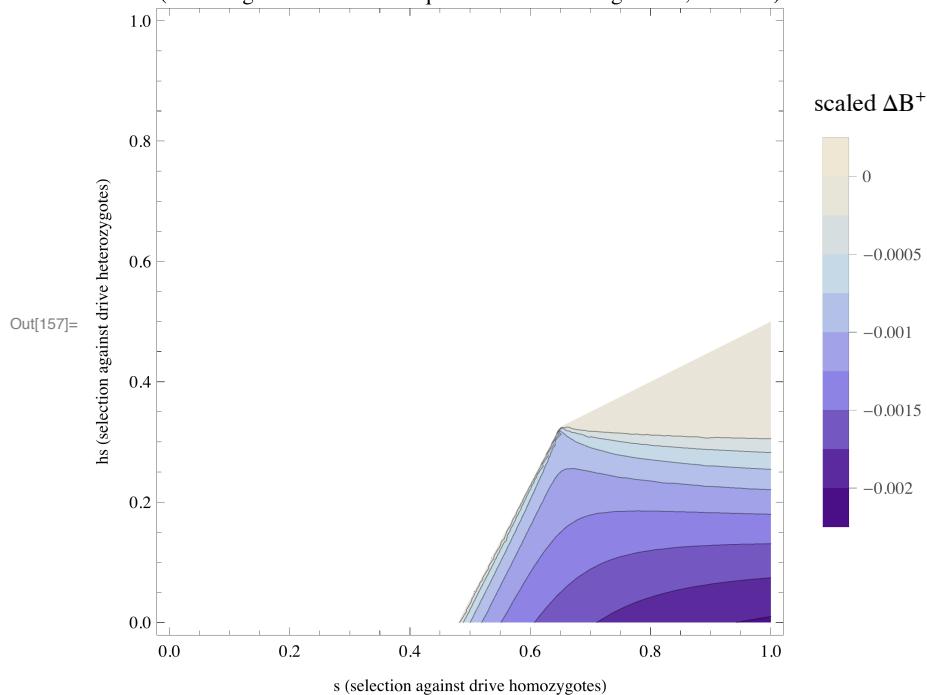
Power::infy : Infinite expression  $\frac{1}{0.^1.}$  encountered. >>

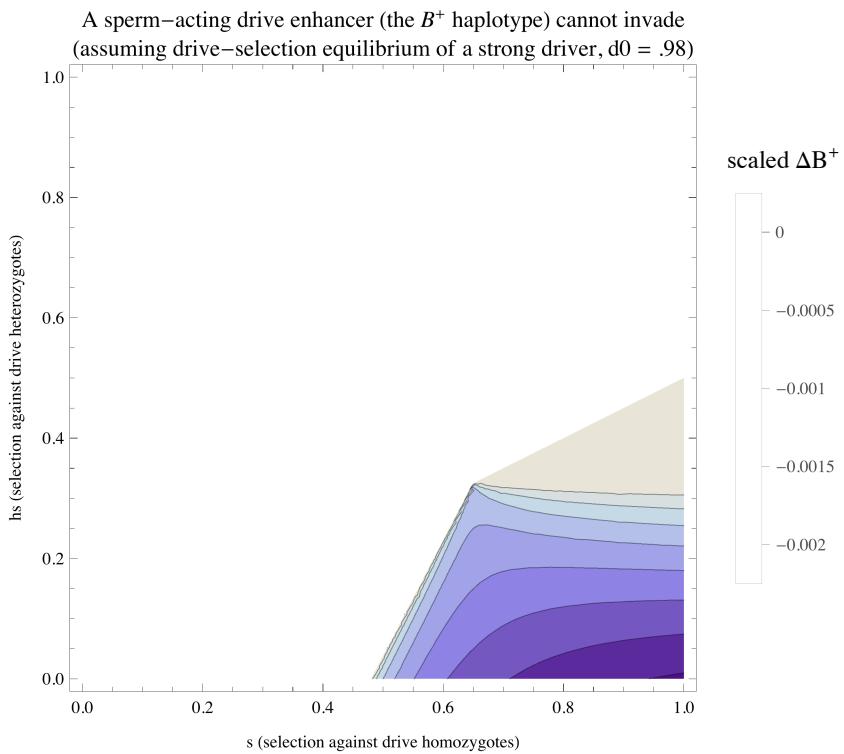
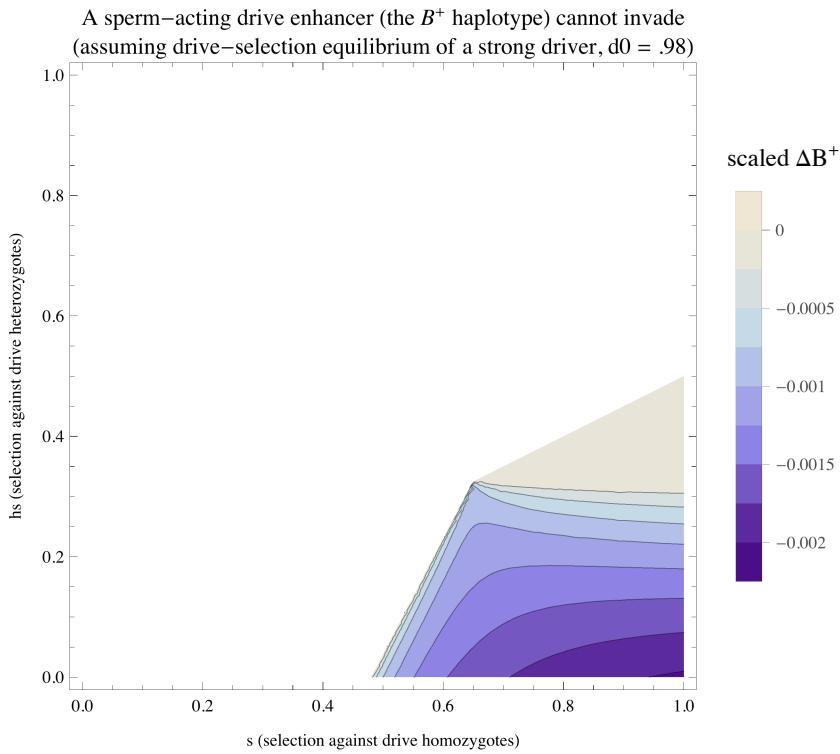
General::stop : Further output of Power::infy will be suppressed during this calculation. >>

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

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

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





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

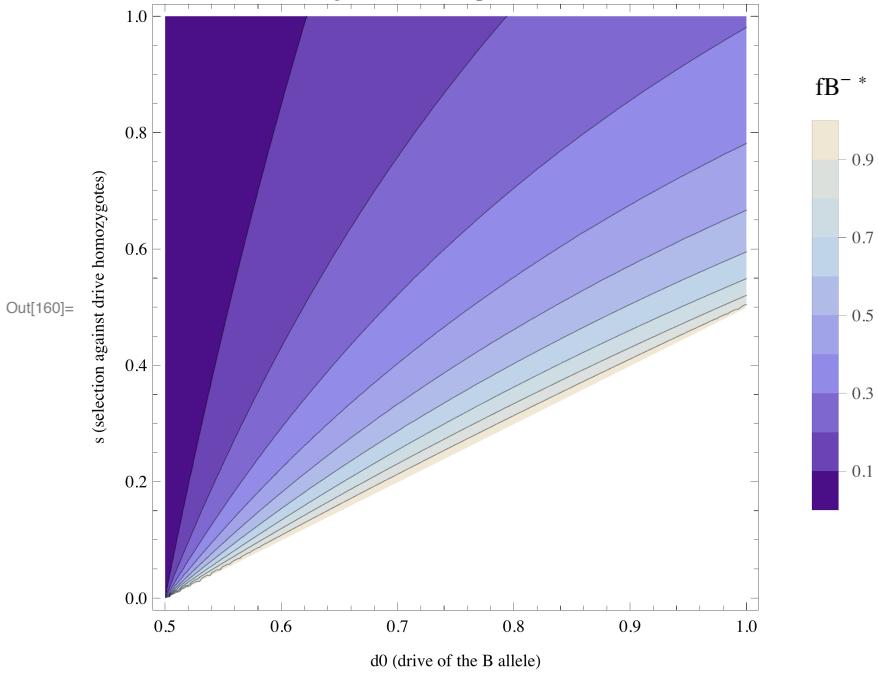
### Equilibrium frequency of drive suppressor

```
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. >>

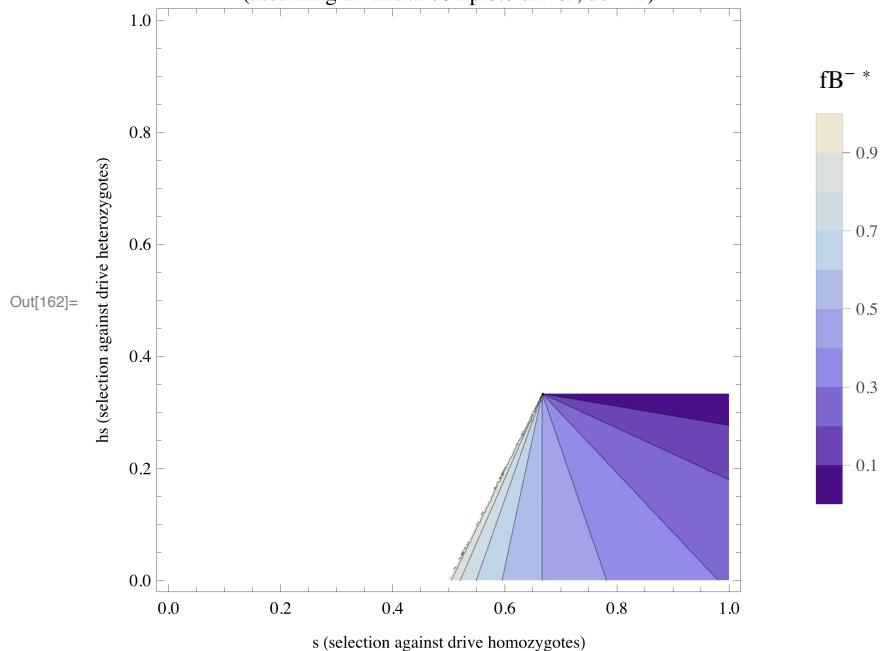
Less::nord : Invalid comparison with  $1.00451 - 1.58082 i$  attempted. >>

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. >>

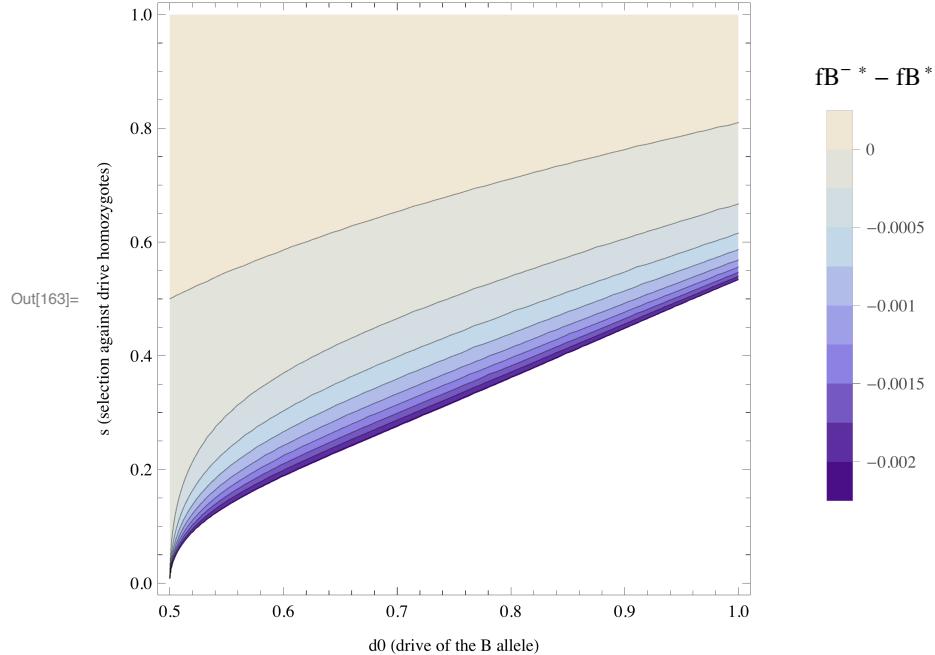
Equilibrium freq. of a sperm-acting drive suppressor (the  $B^-$  haplotype)  
(assuming an initial complete driver,  $d0 = 1$ )

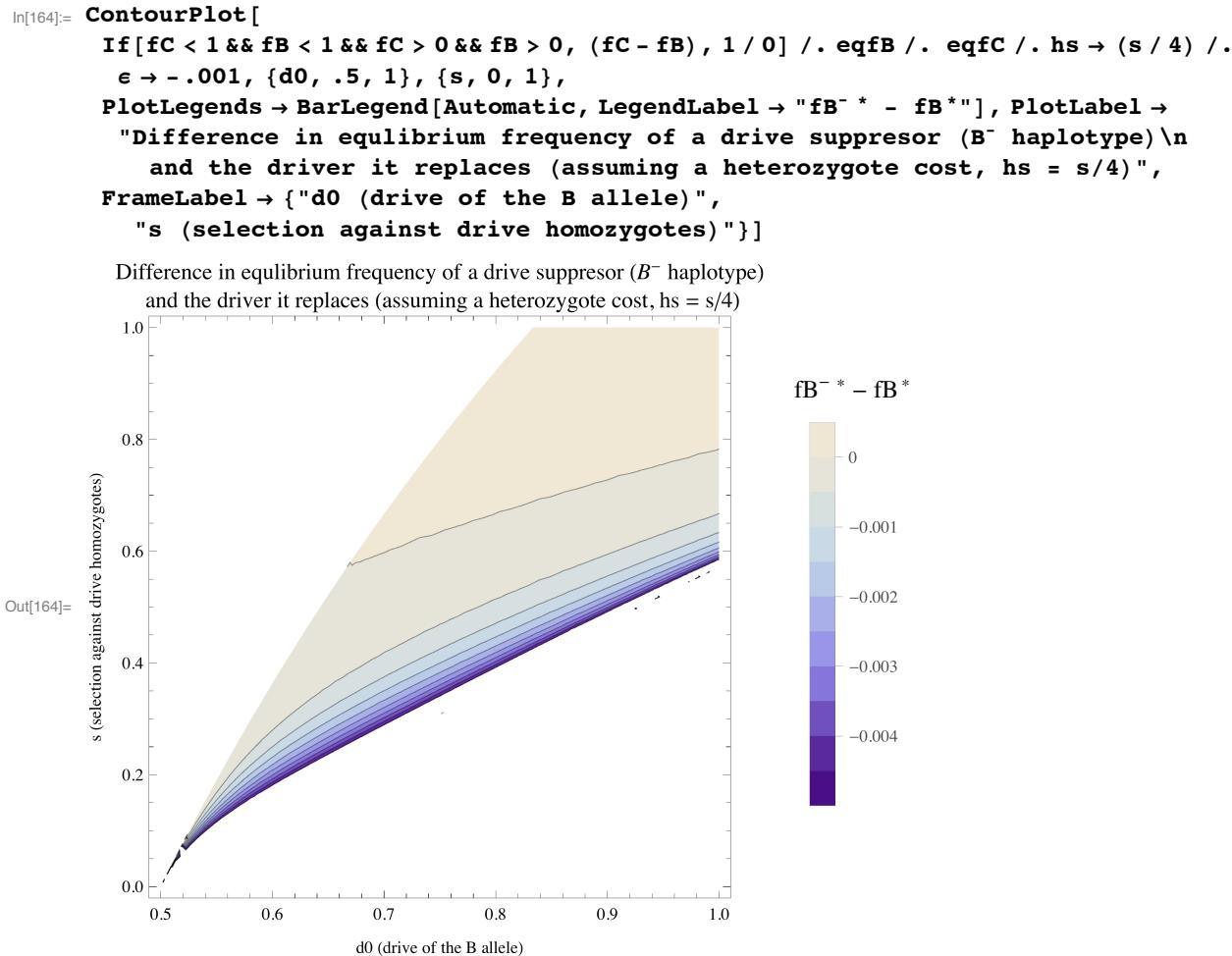


**Equilibrium frequency of drive/sperm acting suppressor haplotype is often less than that of the standard driver it replaces.**

```
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)\nand
    the driver it replaces (assuming a recessive cost of the drive allele)",
  FrameLabel → {"d0 (drive of the B allele)", "s (selection against drive homozygotes)"}]
```

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





In[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[ $\bar{W} \Delta fB / (fB) /. HWE /. SUMTOONE$ ] /. 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::infy : Infinite expression  $\frac{1}{0}$  encountered. >>

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

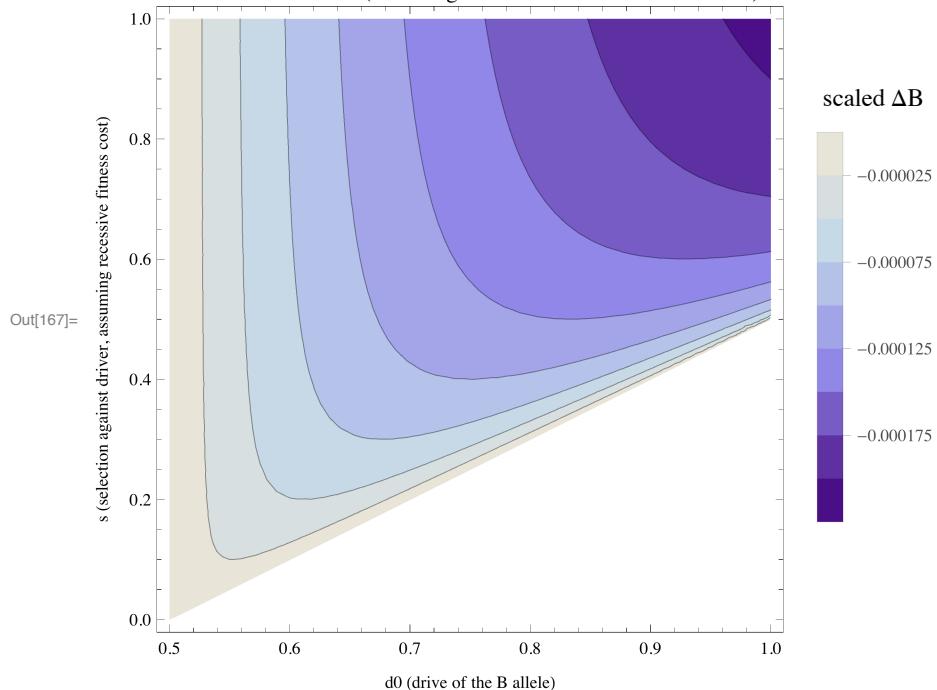
Greater::nord : Invalid comparison with  $53.7184 - 64.9128 i$  attempted. >>

Power::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. >>

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



```
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. >>

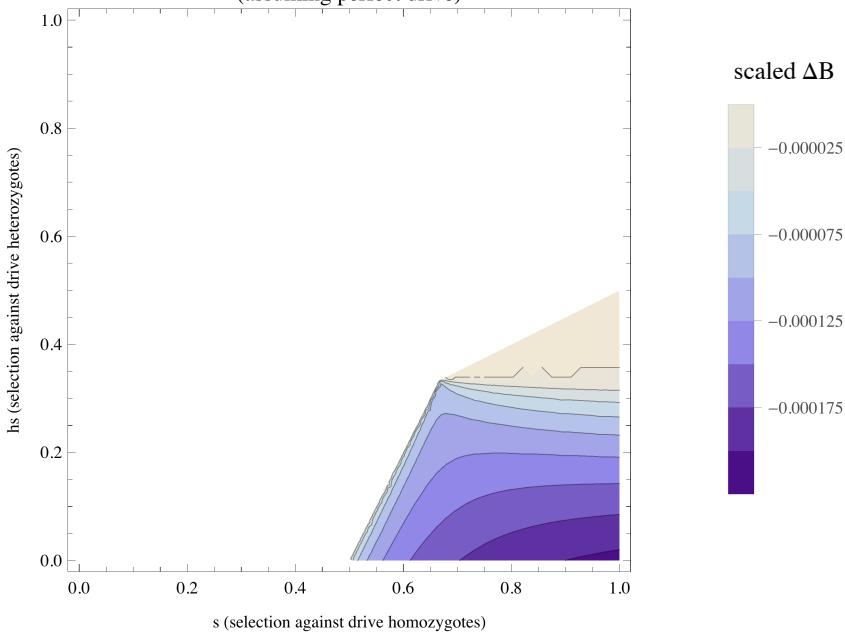
General::stop : Further output of Power::infy will be suppressed during this calculation. >>

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 + fAC / 2};
```

## Drive

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

```
AA_n =
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*)
fAADrive = FullSimplify[AAn];
fABDrive = FullSimplify[ABn + BN];
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]
1

```

## Selection

```

wAA = wAC = wCC = 1; wAB = wBC = 1 - hs; wBB = 1 - s;
W = 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[W /. HWE /. SUMTOONE /. hs → 0]

1 + (2 d0 (-1 + fB) - fB) fB2 s

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

(*Check: do genotype freqs after selection sum to one?*)
FullSimplify[fASel + fBSel + fCSel]
1

FullSimplify[W fACSel /. HWE /. SUMTOONE]
2 (-1 + (-1 + d0 + d1) fB) fC (-1 + fB + fC)

```

# Analysis

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

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

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

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

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

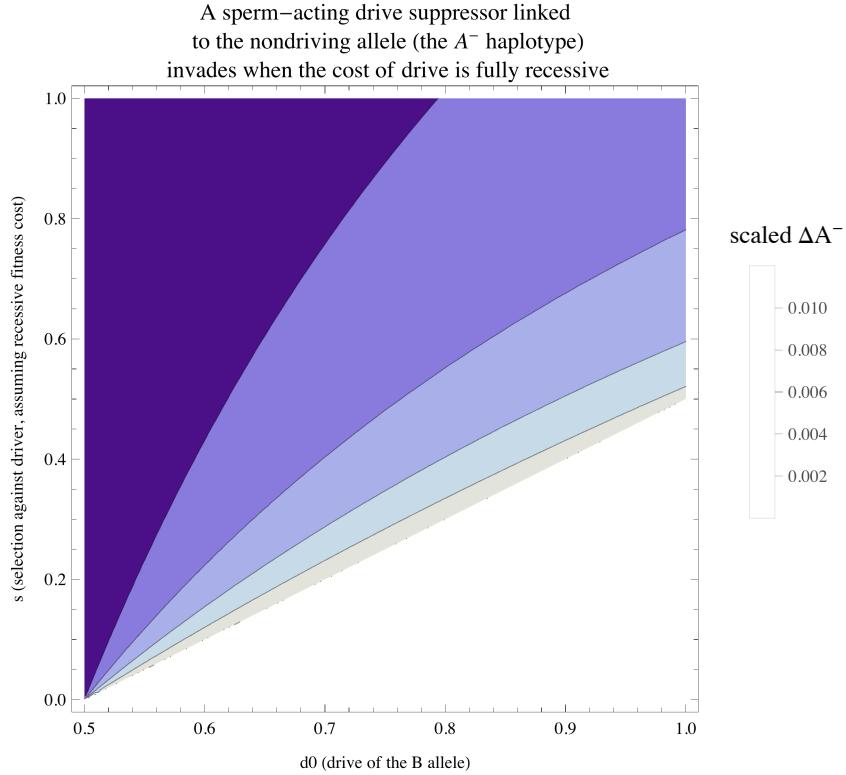
$$\frac{(-2 d0 s + \sqrt{2} \sqrt{(-1 + 2 d0 (2 + d0 (-2 + s))) s})}{2 (-1 + 2 d0) s}$$

```

```

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

```



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

$$\begin{aligned}
 \text{wbarDeltaSpermDrive} = & \text{FullSimplify}[ \\
 & \text{FullSimplify}[\bar{W} \Delta fC / (fC) /. \text{HWE} /. \text{SUMTOONE}] /. fC \rightarrow 0 /. \text{eqfB} /. \text{minormod}] \\
 & - \frac{1}{2 (1 - 2 d0)^2 (2 hs - s)} hs (-1 - hs - \\
 & \sqrt{2} \sqrt{(1 + hs - 2 d0 (2 + d0 (-2 + s))) (2 hs - s)} + 2 d0 (2 (-1 + d0) (-1 + hs) + s)) \in
 \end{aligned}$$

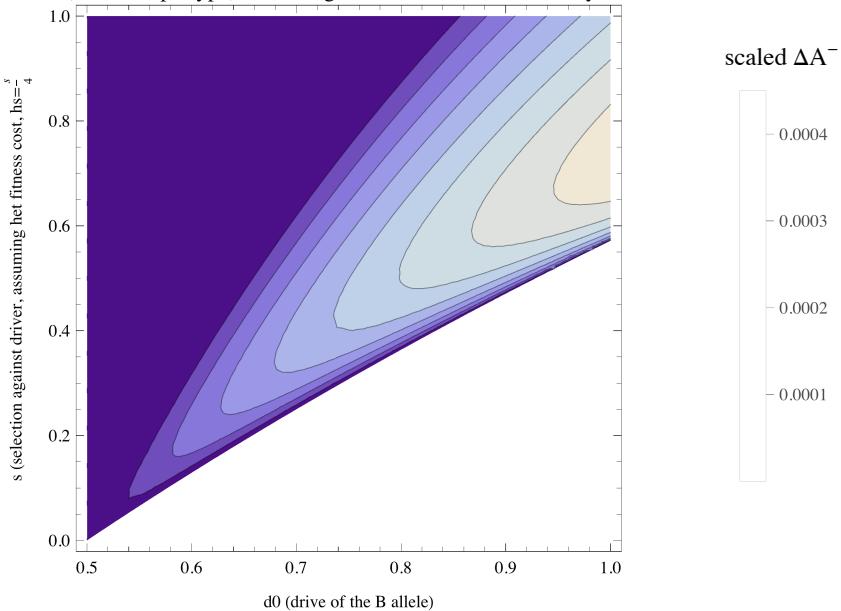
(\*Plotting change this change in frequency when the sperm acting locus is rare,  
increases drive, and when the fitness cost of drive is fully  
recessive. NOTE: This sperm enhancer of drive cannot invade\*)

```

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

```

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

```

fAAEEEDrive = FullSimplify[

fAAEEE * fAAEEE * 1 + fAAEEE * fABEE * 1 / 2 + fAAEEE * fBBEE * 0 + fAAEEE * fAAEF * 1 / 2 +
fAAEEE * fABEF * 1 / 4 + fAAEEE * fBBEF * 0 + fAAEEE * fAAFF * 0 + fAAEEE * fABFF * 0 +
fAAEEE * fBBFF * 0 + fABEE * fAAEEE * (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 * fAAEEE * 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 * fAAEEE * 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 * fAAEEE * (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 * fAAEEE * 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 * fAAEEE * 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 * fAAEEE * 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 * fAAEEE * 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[fAAEEE * fAAEEE * 0 + fAAEEE * fABEE * 1 / 2 + fAAEEE * fBBEE * 1 +
fAAEEE * fAAEF * 0 + fAAEEE * fABEF * 1 / 4 + fAAEEE * fBBEF * 1 / 2 + fAAEEE * fAAFF * 0 +
fAAEEE * fABFF * 0 + fAAEEE * fBBFF * 0 + fABEE * fAAEEE * 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 * fAAEEE * 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 * fAAEEE * 0 + fAAEF * fABEE * 1 / 4 + fAAEF * fBBEE * 1 / 2 +

```

```

fAAAEF * fAAAEF * 0 + fAAAEF * fABEF * 1 / 8 + fAAAEF * fBBEF * 1 / 4 + fAAAEF * fAAFF * 0 +
fAAAEF * fABBF * 0 + fAAAEF * 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]

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

```

```

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

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

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

```

$$\begin{aligned}
& \frac{1}{8} (4 f_{AAEE} + 2 (f_{AAEF} + f_{ABEE}) + f_{ABEF}) (2 f_{AAEE} + f_{AAEF} - (-1 + d_0) (2 f_{ABEE} + f_{ABEF})) \\
& - \frac{1}{8} (f_{AAEF} (2 f_{ABEE} + 4 d_0 f_{ABEE} + f_{ABEF} + 2 d_0 f_{ABEF} + 8 f_{BBEE} + 4 f_{BBEF}) + \\
& 2 f_{AAEE} ((2 + 4 d_0) f_{ABEE} + f_{ABEF} + 2 d_0 f_{ABEF} + 8 f_{BBEE} + 4 f_{BBEF}) + \\
& (2 f_{ABEE} + f_{ABEF}) (2 f_{ABEE} + f_{ABEF} - (-3 + 2 d_0) (2 f_{BBEE} + f_{BBEF}))) \\
& \frac{1}{8} (d_0 (2 f_{ABEE} + f_{ABEF}) + 2 f_{BBEE} + f_{BBEF}) (2 f_{ABEE} + f_{ABEF} + 4 f_{BBEE} + 2 f_{BBEF}) \\
& \frac{1}{8} (4 f_{AAEF}^2 + 2 f_{AAEE} (4 f_{AAEF} + 8 f_{AAFF} + 3 f_{ABEF} - 2 d_0 f_{ABEF} + 2 f_{ABFF} + 4 d_0 f_{ABFF}) - \\
& (2 f_{ABEE} + f_{ABEF}) ((-6 + 4 d_1) f_{AAFF} + (-2 + d_0 + d_1) (f_{ABEF} + 2 f_{ABFF})) + \\
& f_{AAEF} (8 f_{AAFF} - 2 ((-3 + 2 d_1) f_{ABEE} + (-3 + d_0 + d_1) f_{ABEF} + (-3 + 2 d_0) f_{ABFF}))) \\
& \frac{1}{4} (2 f_{ABEE} f_{ABEF} + f_{ABEF}^2 + 4 f_{ABEE} f_{ABFF} + 2 f_{ABEF} f_{ABFF} + 3 f_{ABEF} f_{BBEE} - \\
& 2 d_0 f_{ABEF} f_{BBEE} + 2 f_{ABFF} f_{BBEE} + 4 d_0 f_{ABFF} f_{BBEE} + 3 f_{ABEE} f_{BBEF} - \\
& 2 d_1 f_{ABEE} f_{BBEF} + 3 f_{ABEF} f_{BBEF} - d_0 f_{ABEF} f_{BBEF} - d_1 f_{ABEF} f_{BBEF} + 3 f_{ABFF} f_{BBEF} - \\
& 2 d_0 f_{ABFF} f_{BBEF} + f_{AAFF} ((2 + 4 d_1) f_{ABEE} + f_{ABEF} + 2 d_1 f_{ABEF} + 8 f_{BBEE} + 4 f_{BBEF}) - \\
& (-3 + 2 d_1) (2 f_{ABEE} + f_{ABEF}) f_{BBFF} + \\
& f_{AAEE} (f_{ABEF} + 2 d_0 f_{ABEF} + 6 f_{ABFF} - 4 d_0 f_{ABFF} + 4 f_{BBEF} + 8 f_{BBFF}) + f_{AAEF} \\
& (f_{ABEE} + 2 d_1 f_{ABEE} + (1 + d_0 + d_1) f_{ABEF} + f_{ABFF} + 2 d_0 f_{ABFF} + 4 (f_{BBEE} + f_{BBEF} + f_{BBFF}))) \\
& \frac{1}{8} (d_0 (f_{ABEF}^2 + 2 f_{ABEE} (f_{ABEF} + 2 f_{ABFF}) + \\
& 4 f_{ABFF} (-2 f_{BBEE} + f_{BBEF}) + 2 f_{ABEF} (f_{ABFF} + 2 f_{BBEE} + f_{BBEF})) + \\
& 2 (f_{ABFF} (6 f_{BBEE} + f_{BBEF}) + f_{ABEF} (f_{BBEE} + f_{BBEF} + f_{BBFF}) + \\
& (f_{ABEE} + 4 f_{BBEE} + 2 f_{BBEF}) (f_{BBEF} + 2 f_{BBFF})) + \\
& d_1 (2 f_{ABEE} + f_{ABEF}) (f_{ABEF} + 2 (f_{ABFF} + f_{BBEF} + 2 f_{BBFF}))) \\
& \frac{1}{8} (2 f_{AAEF} + 4 f_{AAFF} + f_{ABEF} + 2 f_{ABFF}) (f_{AAEF} + 2 f_{AAFF} - (-1 + d_1) (f_{ABEF} + 2 f_{ABFF})) \\
& \frac{1}{8} (f_{AAEF} (f_{ABEF} + 2 d_1 f_{ABEF} + 2 f_{ABFF} + 4 d_1 f_{ABFF} + 4 f_{BBEF} + 8 f_{BBFF}) + \\
& 2 f_{AAFF} (f_{ABEF} + 2 d_1 f_{ABEF} + 2 f_{ABFF} + 4 d_1 f_{ABFF} + 4 f_{BBEF} + 8 f_{BBFF}) + \\
& (f_{ABEF} + 2 f_{ABFF}) (f_{ABEF} + 2 f_{ABFF} - (-3 + 2 d_1) (f_{BBEF} + 2 f_{BBFF}))) \\
& \frac{1}{8} (d_1 (f_{ABEF} + 2 f_{ABFF}) + f_{BBEF} + 2 f_{BBFF}) (f_{ABEF} + 2 (f_{ABFF} + f_{BBEF} + 2 f_{BBFF}))
\end{aligned}$$

## Selection

```

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

\bar{W} = FullSimplify[ (fAAEEDrive wAAEE + fAAEFDrive wAAEF + fAAFFDrive wAAFF
+ fABEEDrive wABEE + fABEFDrive wABEF + fABFFDrive wABFF
+ fBBEEDrive wBBEE + fBBEFDrive wBBEF + fBBFFDrive wBBFF
)];

```

```

fAAEEsel = FullSimplify[fAAEEDrive wAAEE /  $\bar{W}$ ] ;
fABEEsel = FullSimplify[fABEEDrive wABEE /  $\bar{W}$ ] ;
fBBEEsel = FullSimplify[fBBEEDrive wBBEE /  $\bar{W}$ ] ;
fAAEFsel = FullSimplify[fAAEFDrive wAAEF /  $\bar{W}$ ] ;
fABEFsel = FullSimplify[fABEFDrive wABEF /  $\bar{W}$ ] ;
fBBEFsel = FullSimplify[fBBEFDrive wBBEF /  $\bar{W}$ ] ;
fAAFFsel = FullSimplify[fAAFFDrive wAAFF /  $\bar{W}$ ] ;
fABFFsel = FullSimplify[fABFFDrive wABFF /  $\bar{W}$ ] ;
fBBFFsel = FullSimplify[fBBFFDrive wBBFF /  $\bar{W}$ ] ;
fAsel = FullSimplify[fAAEEsel + fAAEFsel + fAAFFsel + (fABEEsel + fABEFsel + fABFFsel) / 2] ;
fBsel = FullSimplify[fBBEEsel + fBBEFsel + fBBFFsel + (fABEEsel + fABEFsel + fABFFsel) / 2] ;
fEsel = FullSimplify[fAAEEsel + fABEEsel + fBBEEsel + (fAAEFsel + fABEFsel + fBBEFsel) / 2] ;
fFsel = FullSimplify[fAAFFsel + fABFFsel + fBBFFsel + (fAAEFsel + fABEFsel + fBBEFsel) / 2] ;
ΔfA = FullSimplify[fAsel - fA] ;
ΔfB = FullSimplify[fBsel - fB] ;
ΔfE = FullSimplify[fEsel - fE] ;
ΔfF = FullSimplify[fFsel - fF] ;

(*ΔfC=FullSimplify[fCsel-fC];*)

(*Check: do genotype freqs after selection sum to one?*)
FullSimplify[fAsel + fBsel]
FullSimplify[fEsel + fFsel]
1
1

```

## Analysis

### Invasion of sperm-acting drive modifier unlinked to the driver

```

invasionOfUnlinkedModeifier =
  FullSimplify[ $\bar{W}$  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) ∈

(*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

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

## 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 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 * fBBFF * 0) +
(fABFF * fAAFF * 0) + (fABFF * fABFF * 0) + (fABFF * fBBFF * 0) + 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]
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 - 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 * fBBFF * 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) + (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]
fABEFDrive = 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 * 0) + (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 * 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]
fBBEFDrive = 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]

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

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

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$$\begin{aligned}
& (\text{fAAFF} * \text{FABEE} * 0) + (\text{fAAFF} * \text{FBBEE} * 0) + (\text{fAAFF} * \text{FAAEF} * 0) + (\text{fAAFF} * \text{FABEF} * 1 / 4) + \\
& (\text{fAAFF} * \text{FBBEF} * 1 / 2) + (\text{fAAFF} * \text{FAAFF} * 0) + (\text{fAAFF} * \text{FABFF} * 1 / 2) + (\text{fAAFF} * \text{FBBF} * 1) + \\
& (\text{FABFF} * \text{FAAEE} * 0) + (\text{FABFF} * \text{FABEE} * 0) + (\text{FABFF} * \text{FBBEE} * 0) + (\text{FABFF} * \text{FAAEF} * (\text{d1} / 2)) + \\
& (\text{FABFF} * \text{FABEF} * (1 / 4)) + (\text{FABFF} * \text{FBBEF} * ((1 - \text{d1}) / 2)) + (\text{FABFF} * \text{FAAFF} * (\text{d1})) + \\
& (\text{FABFF} * \text{FABFF} * (1 / 2)) + (\text{FABFF} * \text{FBBF} * (1 - \text{d1})) + (\text{FBBF} * \text{FAAEE} * 0) + \\
& (\text{FBBF} * \text{FABEE} * 0) + (\text{FBBF} * \text{FBBEE} * 0) + (\text{FBBF} * \text{FAAEF} * 1 / 2) + (\text{FBBF} * \text{FABEF} * 1 / 4) + \\
& (\text{FBBF} * \text{FBBEF} * 0) + (\text{FBBF} * \text{FAAFF} * 1) + (\text{FBBF} * \text{FABFF} * 1 / 2) + (\text{FBBF} * \text{FBBF} * 0) + 0] \\
\text{FBBF}_{\text{Drive}} = \text{FullSimplify} [ & (\text{FAAEE} * \text{FAAEE} * 0) + (\text{FAAEE} * \text{FABEE} * 0) + (\text{FAAEE} * \text{FBBEE} * 0) + \\
& (\text{FAAEE} * \text{FAAEF} * 0) + (\text{FAAEE} * \text{FABEF} * 0) + (\text{FAAEE} * \text{FBBF} * 0) + (\text{FAAEE} * \text{FAAFF} * 0) + \\
& (\text{FAAEE} * \text{FABFF} * 0) + (\text{FAAEE} * \text{FBBF} * 0) + (\text{FABEE} * \text{FAAEE} * 0) + (\text{FABEE} * \text{FABEE} * 0) + \\
& (\text{FABEE} * \text{FBBEE} * 0) + (\text{FABEE} * \text{FAAEF} * 0) + (\text{FABEE} * \text{FABEF} * 0) + (\text{FABEE} * \text{FBBF} * 0) + \\
& (\text{FABEE} * \text{FAAFF} * 0) + (\text{FABEE} * \text{FABFF} * 0) + (\text{FABEE} * \text{FBBF} * 0) + (\text{FBBEE} * \text{FAAEE} * 0) + \\
& (\text{FBBEE} * \text{FABEE} * 0) + (\text{FBBEE} * \text{FBBEE} * 0) + (\text{FBBEE} * \text{FAAEF} * 0) + (\text{FBBEE} * \text{FABEF} * 0) + \\
& (\text{FBBEE} * \text{FBBEF} * 0) + (\text{FBBEE} * \text{FAAFF} * 0) + (\text{FBBEE} * \text{FABFF} * 0) + (\text{FBBEE} * \text{FBBF} * 0) + \\
& (\text{FAAEF} * \text{FAAEE} * 0) + (\text{FAAEF} * \text{FABEE} * 0) + (\text{FAAEF} * \text{FBBEE} * 0) + (\text{FAAEF} * \text{FAAEF} * 0) + \\
& (\text{FAAEF} * \text{FABEF} * 0) + (\text{FAAEF} * \text{FBBF} * 0) + (\text{FAAEF} * \text{FAAFF} * 0) + (\text{FAAEF} * \text{FABFF} * 0) + \\
& (\text{FAAEF} * \text{FBBF} * 0) + (\text{FABEF} * \text{FAAEE} * 0) + (\text{FABEF} * \text{FABEE} * 0) + (\text{FABEF} * \text{FBBEE} * 0) + \\
& (\text{FABEF} * \text{FAAEF} * 0) + (\text{FABEF} * \text{FABEF} * (\text{dh} / 8)) + (\text{FABEF} * \text{FBBF} * (\text{dh} / 4)) + \\
& (\text{FABEF} * \text{FAAFF} * 0) + (\text{FABEF} * \text{FABFF} * (\text{dh} / 4)) + (\text{FABEF} * \text{FBBF} * (\text{dh} / 2)) + \\
& (\text{FBBF} * \text{FAAEE} * 0) + (\text{FBBF} * \text{FABEE} * 0) + (\text{FBBF} * \text{FBBEE} * 0) + (\text{FBBF} * \text{FAAEF} * 0) + \\
& (\text{FBBF} * \text{FABEF} * 1 / 8) + (\text{FBBF} * \text{FBBF} * 1 / 4) + (\text{FBBF} * \text{FAAFF} * 0) + \\
& (\text{FBBF} * \text{FABFF} * 1 / 4) + (\text{FBBF} * \text{FBBF} * 1 / 2) + (\text{FAAFF} * \text{FAAEE} * 0) + (\text{FAAFF} * \text{FABEE} * 0) + \\
& (\text{FAAFF} * \text{FBBEE} * 0) + (\text{FAAFF} * \text{FAAEF} * 0) + (\text{FAAFF} * \text{FABEF} * 0) + (\text{FAAFF} * \text{FBBF} * 0) + \\
& (\text{FAAFF} * \text{FAAFF} * 0) + (\text{FAAFF} * \text{FABFF} * 0) + (\text{FAAFF} * \text{FBBF} * 0) + (\text{FABFF} * \text{FAAEE} * 0) + \\
& (\text{FABFF} * \text{FABEE} * 0) + (\text{FABFF} * \text{FBBEE} * 0) + (\text{FABFF} * \text{FAAEF} * 0) + (\text{FABFF} * \text{FABEF} * (\text{d1} / 4)) + \\
& (\text{FABFF} * \text{FBBF} * (\text{d1} / 2)) + (\text{FABFF} * \text{FAAFF} * 0) + (\text{FABFF} * \text{FABFF} * (\text{d1} / 2)) + \\
& (\text{FABFF} * \text{FBBF} * \text{d1}) + (\text{FBBF} * \text{FAAEE} * 0) + (\text{FBBF} * \text{FABEE} * 0) + (\text{FBBF} * \text{FBBEE} * 0) + \\
& (\text{FBBF} * \text{FAAEF} * 0) + (\text{FBBF} * \text{FABEF} * 1 / 4) + (\text{FBBF} * \text{FBBF} * 1 / 2) + \\
& (\text{FBBF} * \text{FAAFF} * 0) + (\text{FBBF} * \text{FABFF} * 1 / 2) + (\text{FBBF} * \text{FBBF} * 1) + 0] \\
\frac{1}{8} & (4 \text{FAAEE} + 2 (\text{FAAEF} + \text{FABEE}) + \text{FABEF}) \\
& (2 \text{FAAEE} + \text{FAAEF} + 2 \text{FABEE} - 2 \text{d0 FABEE} + \text{FABEF} - \text{dh FABEF}) \\
\frac{1}{8} & (4 \text{FABEE}^2 + 4 \text{FABEE FABEF} + \text{FABEF}^2 + 12 \text{FABEE FBEE} - 8 \text{d0 FABEE FBEE} + \\
& 6 \text{FABEF FBEE} - 4 \text{dh FABEF FBEE} + 6 \text{FABEE FBBF} - 4 \text{d0 FABEE FBBF} + 3 \text{FABEF FBBF} - \\
& 2 \text{dh FABEF FBBF} + \text{FAAEF} (2 \text{FABEE} + 4 \text{d0 FABEE} + \text{FABEF} + 2 \text{dh FABEF} + 8 \text{FBEE} + 4 \text{FBBF}) + \\
& 2 \text{FAAEE} ((2 + 4 \text{d0}) \text{FABEE} + \text{FABEF} + 2 \text{dh FABEF} + 8 \text{FBEE} + 4 \text{FBBF})) \\
\frac{1}{8} & (2 \text{d0 FABEE} + \text{dh FABEF} + 2 \text{FBEE} + \text{FBBF}) (2 \text{FABEE} + \text{FABEF} + 4 \text{FBEE} + 2 \text{FBBF}) \\
\frac{1}{4} & (2 \text{FAAEF}^2 + 6 \text{FAAFF FABEE} - 4 \text{d0 FAAFF FABEE} + 3 \text{FAAFF FABEF} - \\
& 2 \text{dh FAAFF FABEF} + 2 \text{FABEE FABEF} - \text{d0 FABEE FABEF} - \text{dh FABEE FABEF} + \\
& \text{FABEF}^2 - \text{dh FABEF}^2 - (2 (-2 + \text{d0} + \text{d1}) \text{FABEE} + (-2 + \text{d1} + \text{dh}) \text{FABEF}) \text{FABFF} + \\
& \text{FAAEF} (4 \text{FAAEF} + 8 \text{FAAFF} + 3 \text{FABEF} - 2 \text{dh FABEF} + 6 \text{FABFF} - 4 \text{d1 FABFF}) + \\
& \text{FAAEF} (4 \text{FAAFF} + 3 \text{FABEE} - 2 \text{d0 FABEE} + 3 \text{FABEF} - 2 \text{dh FABEF} + 3 \text{FABFF} - 2 \text{d1 FABFF})) \\
\end{aligned}$$

$$\begin{aligned}
& \frac{1}{4} \left( 2 f_{ABEE} f_{ABEF} + f_{ABEF}^2 + 4 f_{ABEE} f_{ABFF} + 2 f_{ABEF} f_{ABFF} + 3 f_{ABEF} f_{BBEE} - \right. \\
& \quad 2 dh f_{ABEF} f_{BBEE} + 6 f_{ABFF} f_{BBEE} - 4 d1 f_{ABFF} f_{BBEE} + 3 f_{ABEE} f_{BBEF} - \\
& \quad 2 d0 f_{ABEE} f_{BBEF} + 3 f_{ABEF} f_{BBEF} - 2 dh f_{ABEF} f_{BBEF} + 3 f_{ABFF} f_{BBEF} - \\
& \quad 2 d1 f_{ABFF} f_{BBEF} + f_{AAFF} ((2 + 4 d0) f_{ABEE} + f_{ABEF} + 2 dh f_{ABEF} + 8 f_{BBEE} + 4 f_{BBEF}) + \\
& \quad 6 f_{ABEE} f_{BBFF} - 4 d0 f_{ABEE} f_{BBFF} + 3 f_{ABEF} f_{BBFF} - 2 dh f_{ABEF} f_{BBFF} + \\
& \quad f_{AAEE} (f_{ABEF} + 2 dh f_{ABEF} + 2 f_{ABFF} + 4 d1 f_{ABFF} + 4 f_{BBEF} + 8 f_{BBFF}) + f_{AAEF} \\
& \quad \left. (f_{ABEE} + 2 d0 f_{ABEE} + f_{ABEF} + 2 dh f_{ABEF} + f_{ABFF} + 2 d1 f_{ABFF} + 4 (f_{BBEE} + f_{BBEF} + f_{BBFF})) \right) \\
& \frac{1}{4} \left( 2 d1 f_{ABEE} f_{ABFF} + d1 f_{ABEF} f_{ABFF} + f_{ABEF} f_{BBEE} + 2 f_{ABFF} f_{BBEE} + \right. \\
& \quad 4 d1 f_{ABFF} f_{BBEE} + f_{ABEE} f_{BBEF} + f_{ABEF} f_{BBEF} + f_{ABFF} f_{BBEF} + 2 d1 f_{ABFF} f_{BBEF} + \\
& \quad 4 f_{BBEE} f_{BBEF} + 2 f_{BBEF}^2 + (2 f_{ABEE} + f_{ABEF} + 8 f_{BBEE} + 4 f_{BBEF}) f_{BBFF} + \\
& \quad dh f_{ABEF} (f_{ABEE} + f_{ABEF} + f_{ABFF} + 2 (f_{BBEE} + f_{BBEF} + f_{BBFF})) + \\
& \quad d0 f_{ABEE} (f_{ABEF} + 2 (f_{ABFF} + f_{BBEF} + 2 f_{BBFF})) \left. \right) \\
& \frac{1}{8} (2 f_{AAEF} + 4 f_{AAFF} + f_{ABEF} + 2 f_{ABFF}) \\
& (f_{AAEF} + 2 f_{AAFF} + f_{ABEF} - dh f_{ABEF} + 2 f_{ABFF} - 2 d1 f_{ABFF}) \\
& \frac{1}{8} (f_{ABEF}^2 + 4 f_{ABEF} f_{ABFF} + 4 f_{ABFF}^2 + 3 f_{ABEF} f_{BBEF} - 2 dh f_{ABEF} f_{BBEF} + 6 f_{ABFF} f_{BBEF} - \\
& \quad 4 d1 f_{ABFF} f_{BBEF} + 6 f_{ABEF} f_{BBFF} - 4 dh f_{ABEF} f_{BBFF} + 12 f_{ABFF} f_{BBFF} - \\
& \quad 8 d1 f_{ABFF} f_{BBFF} + f_{AAEF} (f_{ABEF} + 2 dh f_{ABEF} + 2 f_{ABFF} + 4 d1 f_{ABFF} + 4 f_{BBEF} + 8 f_{BBFF}) + \\
& \quad 2 f_{AAFF} (f_{ABEF} + 2 dh f_{ABEF} + 2 f_{ABFF} + 4 d1 f_{ABFF} + 4 f_{BBEF} + 8 f_{BBFF})) \\
& \frac{1}{8} (dh f_{ABEF} + 2 d1 f_{ABFF} + f_{BBEF} + 2 f_{BBFF}) (f_{ABEF} + 2 (f_{ABFF} + f_{BBEF} + 2 f_{BBFF}))
\end{aligned}$$

## Selection

```

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

\bar{W} = FullSimplify[ (fAAEEDrive wAAEE + fAAEFDrive wAAEF + fAAFFDrive wAAFF
+ fABEEDrive wABEE + fABEFDrive wABEF + fABFFDrive wABFF
+ fBBEEDrive wBSEE + fBBEFDrive wBBEF + fBBFFDrive wBBFF
)];

```

```

fAAEESel = FullSimplify[fAAEEDrive wAAEE /  $\bar{W}$ ] ;
fABEESel = FullSimplify[fABEEDrive wABEE /  $\bar{W}$ ] ;
fBBEESel = FullSimplify[fBBEEDrive wBBEE /  $\bar{W}$ ] ;
fAAEFSel = FullSimplify[fAAEFDrive wAAEF /  $\bar{W}$ ] ;
fABEFSel = FullSimplify[fABEFDrive wABEF /  $\bar{W}$ ] ;
fBBEFSel = FullSimplify[fBBEFDrive wBBEF /  $\bar{W}$ ] ;
fAAFFSel = FullSimplify[fAAFFDrive wAAFF /  $\bar{W}$ ] ;
fABFFSel = FullSimplify[fABFFDrive wABFF /  $\bar{W}$ ] ;
fBBFFSel = FullSimplify[fBBFFDrive wBBFF /  $\bar{W}$ ] ;
fASel = FullSimplify[fAAEESel + fAAEFSel + fAAFFSel + (fABEESel + fABEFSel + fABFFSel) / 2] ;
fBSel = FullSimplify[fBBEESel + fBBEFSel + fBBFFSel + (fABEESel + fABEFSel + fABFFSel) / 2] ;
fESel = FullSimplify[fAAEESel + fABEESel + fBBEESel + (fAAEFSel + fABEFSel + fBBEFSel) / 2] ;
fFSel = FullSimplify[fAAFFSel + fABFFSel + fBBFFSel + (fAAEFSel + fABEFSel + fBBEFSel) / 2] ;
ΔfA = FullSimplify[fASel - fA] ;
ΔfB = FullSimplify[fBSel - fB] ;
ΔfE = FullSimplify[fESel - fE] ;
ΔfF = FullSimplify[fFSel - fF] ;

(*ΔfC=FullSimplify[fCSel-fC];*)

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

1
1

```

## Analysis

### Invasion of egg-acting drive modifier unlinked to the driver

```

invasionOfUnlinkedModifier =
  FullSimplify[ $\bar{W}$  ΔfF / fF /. randomHaps /. D → 0 /. dh → d1 /. sumZone /. minormod] /.
    fF → 0 (*this assumes no LD and random mating*)
  - (-1 + fB) fB ((-1 + 2 fB) hs - fB s) ∈

(*With some rearrangement,
  invasionOfUnlinkedModifier= -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[
  W ΔfF / (1 - fF)^2 /. randomHaps /. D → 0 /. dh → d1 /. sum2one /. minormod /.
  hs → 0] /. fF → 1(*this assumes no LD and random mating*)
(- 1 + fB) fB^2 s ∈
(*Thus the invasion and fixation conditions are equivalent*)
```