

# Brandvain and Coop. Sperm dependent female meiotic drive

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

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

x represents the deviation from Hardy - Weinberg Equilibrium

---

## Setup

```
(*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

```
(*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

```
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];
```

---

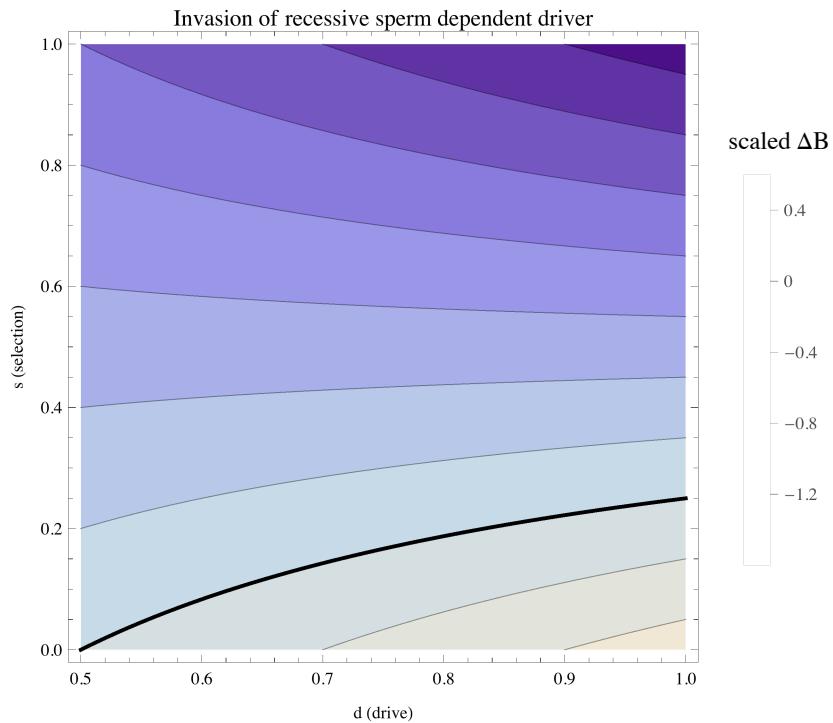
## Analysis

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

```
 $\Delta f_B \text{invade} = (\text{FullSimplify}[\Delta f_B /. hs \rightarrow 0 /. x \rightarrow 0] / f_B^2 /. f_B \rightarrow 0)$ 
 $\frac{1}{2} (-1 + d (2 - 4 s))$ 
 $spermDepRecessiveInvade = \text{Solve}[\Delta f_B \text{invade} == 0, s]$ 
 $\left\{ \left\{ s \rightarrow \frac{-1 + 2 d}{4 d} \right\} \right\}$ 
 $\text{plotInvasion4spermDepRecessive} =$ 
 $\text{Plot}[s /. spermDepRecessiveInvade [[1]], \{d, .5, 1\}, \text{PlotStyle} \rightarrow \{\text{Black}, \text{Thick}\}]$ ;
 $\text{plotRelChange4RarespermDepRecessive} = \text{ContourPlot}[\{\Delta f_B \text{invade}\}, \{d, 0.5, 1\},$ 
 $\{s, 0, 1\}, \text{PlotLegends} \rightarrow \text{BarLegend}[\text{Automatic}, \text{LegendLabel} \rightarrow \text{"scaled } \Delta B"],$ 
 $\text{FrameLabel} \rightarrow \{ "d \text{ (drive)} ", "s \text{ (selection)} " \},$ 
 $\text{PlotLabel} \rightarrow \text{"Invasion of recessive sperm dependent driver"}];$ 
 $\text{Show}[\text{plotRelChange4RarespermDepRecessive}, \text{plotInvasion4spermDepRecessive}]$ 
```



### Fixation

```
 $\Delta f_B \text{fix} = \text{FullSimplify}[\text{FullSimplify}[\Delta f_B /. hs \rightarrow 0 /. x \rightarrow 0] / f_A] /. f_B \rightarrow 1$ 
 $\frac{-1 + 2 d - 2 s}{2 - 2 s}$ 
```

```

spermDepRecessiveFix = Solve[ΔfBfix == 0, s]

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

(s /. spermDepRecessiveFix [[1]])

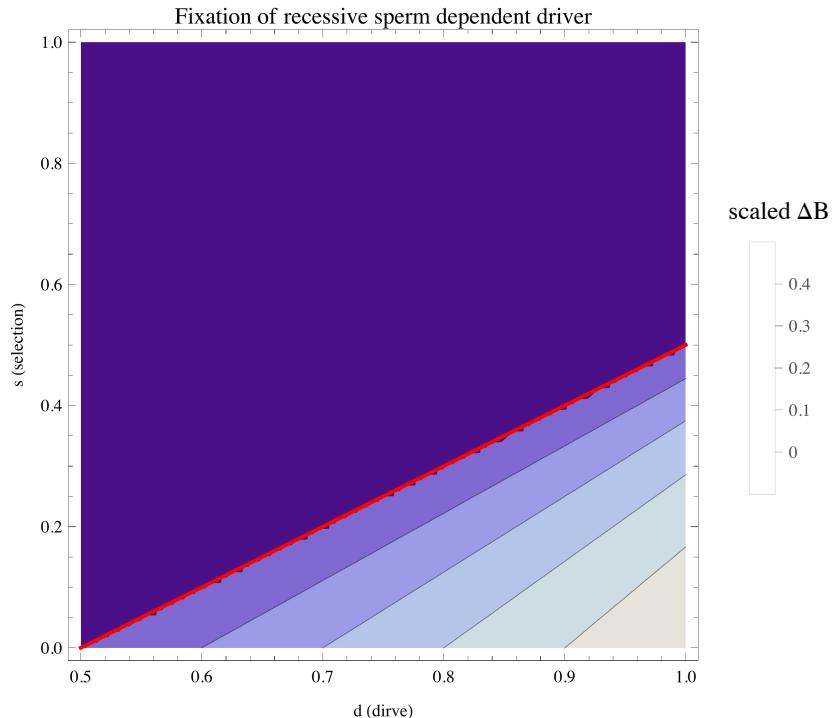
$$\frac{1}{2} (-1 + 2 d)$$


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

(*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 (dirve)", "s (selection)" },
PlotLabel -> "Fixation of recessive sperm dependent driver"];

Show[plotRelChange4CommonSpermDepRecessive, plotFixation4spermDepRecessive]

```



## Bistability Point

```

FBbistabSpermDepRecessive = Solve[FullSimplify[ΔfB /. hs -> 0 /. x -> 0] == 0, fB][[4]]

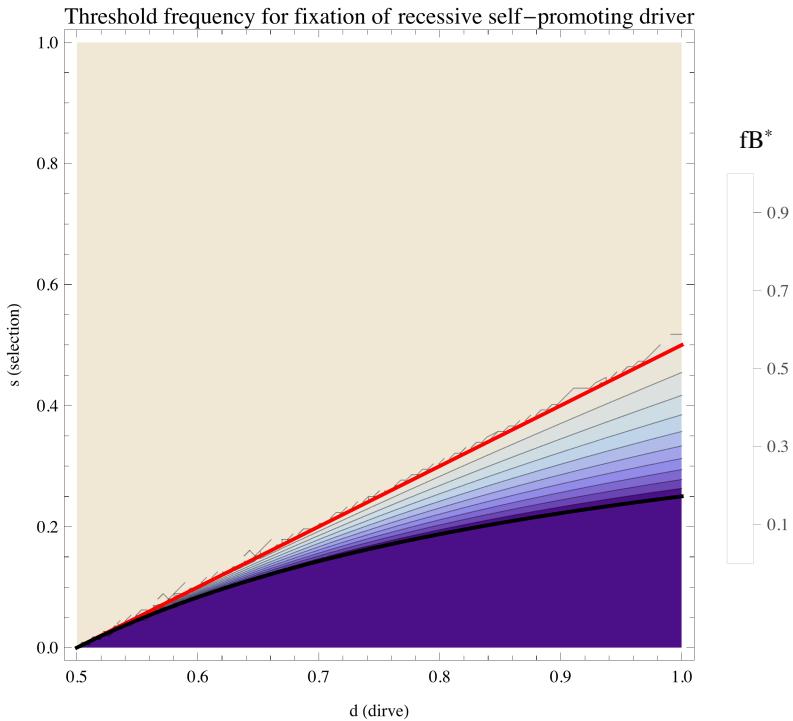
$$\left\{ f_B \rightarrow \frac{1 - 2 d + 4 d s}{-2 s + 4 d s} \right\}$$


```

```

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"];
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

```

FullSimplify[FullSimplify[ΔfB /. x → 0] / fB] /. fB → 0
-hs

```

## Fixation

```

ΔfBfix = FullSimplify[FullSimplify[FullSimplify[ΔfB /. x → 0] / fA] /. fB → 1]

$$\frac{1 + 2 d (-1 + hs) - 3 hs + 2 s}{2 (-1 + s)}$$

spermDepNotRecessiveFix = Solve[ΔfBfix == 0, s]

$$\left\{ \left\{ s \rightarrow \frac{1}{2} (-1 + 2 d + 3 hs - 2 d hs) \right\} \right\}$$


```

```

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

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

```

## Bistability Point

```

FBbistabSpermDepNotReceesive = Solve[FullSimplify[ΔfB /. x → 0] == 0, fB][[3]]
{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)) }

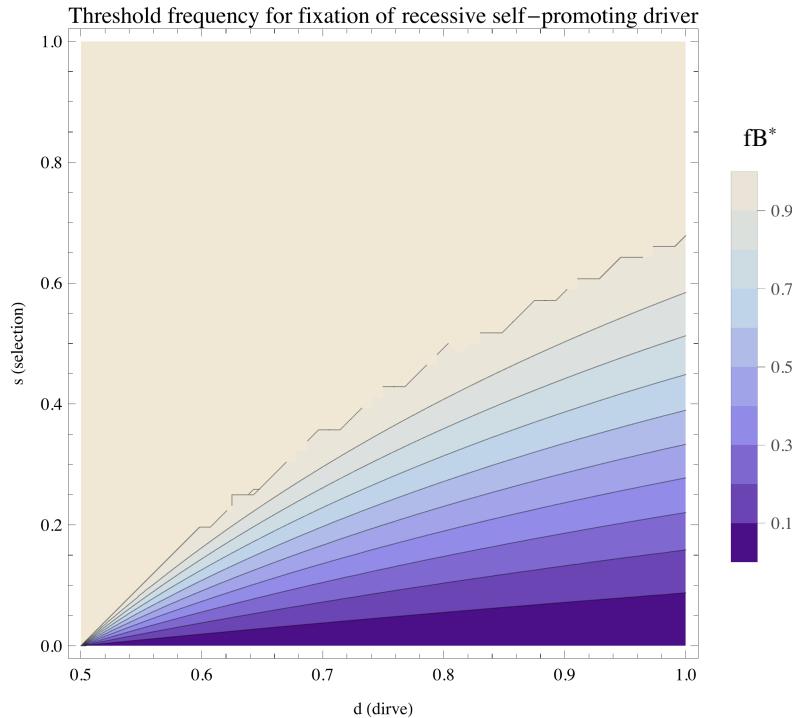
```

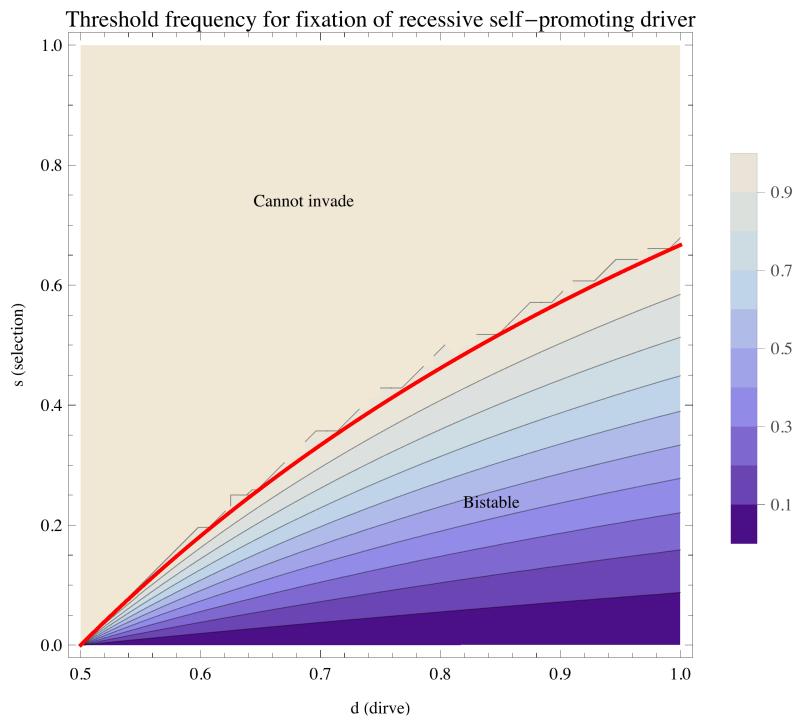
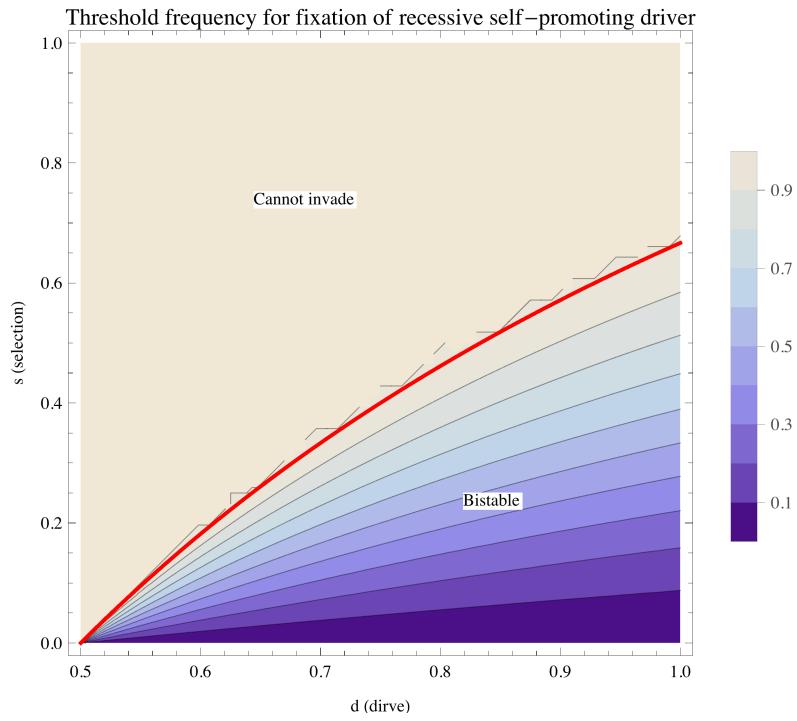
An Example of a non - recessive driver [Assuming additivity]

```

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"];
Show[bistab, plotspermDepAddFix]

```





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

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

x represents the deviation from Hardy - Weinberg Equilibrium

## Setup

```
(*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

```
(*Genotype frequencies after drive*)
fAADrive = FullSimplify[fAA (fAA + fAB / 2) + fAB (fAA / 2 + fAB (1 - dh) / 2)];
fABDrive = FullSimplify[
  fAA (fAB / 2 + fBB) + fAB (fAA / 2 + fAB / 2 + fBB (1 - d)) + fBB (fAA + fAB / 2)];
fBBDrive = FullSimplify[fAB (fAB dh / 2 + fBB d) + fBB (fAB / 2 + fBB)];
```

## Selection

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

## Analysis

### Analytical example - recessive fitness cost

#### Invasion

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

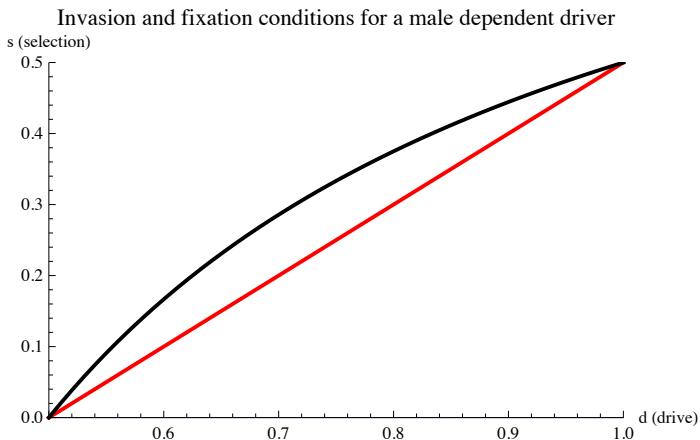
`plotiInvasion4maleDepRecessive = Plot[s /. invasion4maleDepRecessive /. dh → d,
{d, .5, 1}, PlotStyle -> {Black, Thick}];`

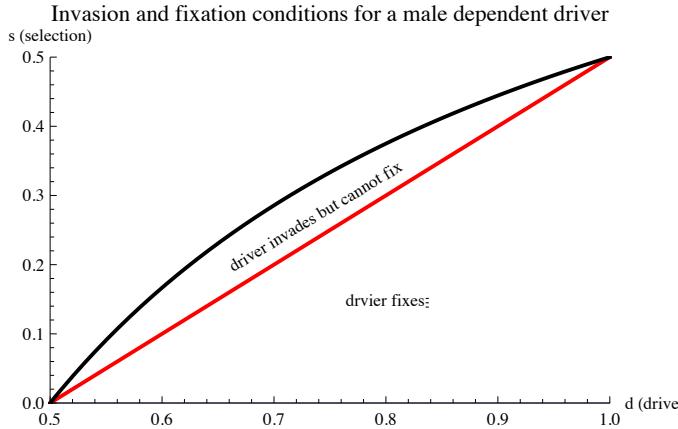
#### Fixation

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

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

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





## Bistability

```

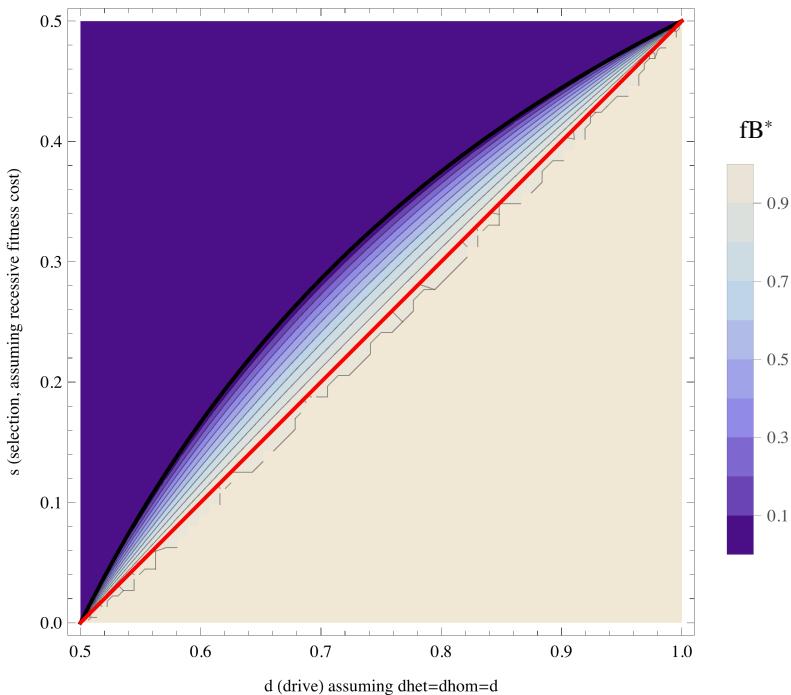
FBbistabMaleepRecessive =
Solve[FullSimplify[ $\Delta f_B$  /. x → 0 /. hs → 0 /. dh → d] == 0, fB][[4]]

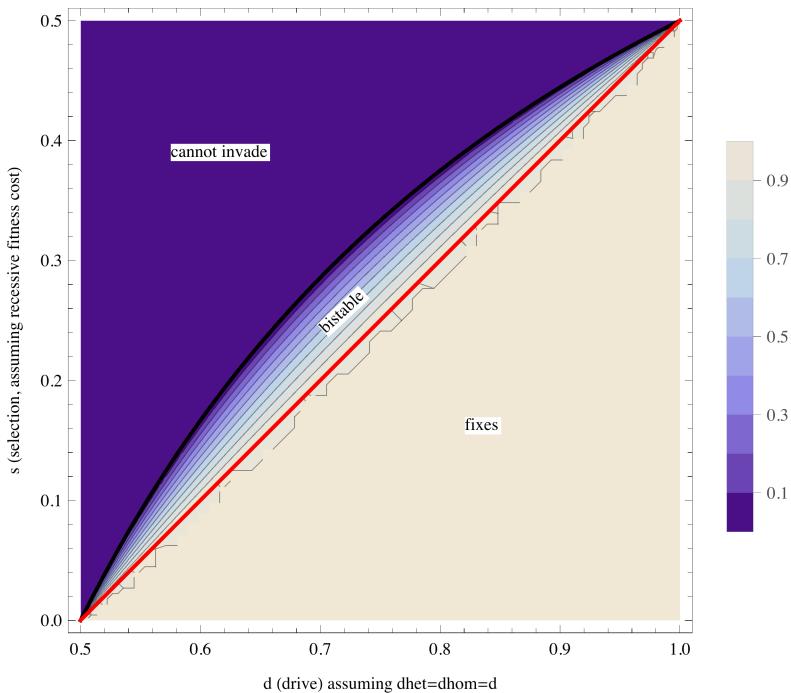
 $\left\{ f_B \rightarrow \frac{2(1 - 2d + 2ds)}{(-1 + 2d)(-1 + 2s)} \right\}$ 

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

Show[bistab, plotiInvasion4maleDepRecessive, plotFixation4maleDepRecessive]

```





### Model 3. 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

## Selection

```
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]

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]
```

## 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]

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

**Fixation of standard driver**

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

```
(*fixation of a standard recessive driver*)
fixationStandardDriver /. hs → 0
```

$$\left\{ \left\{ s \rightarrow \frac{1}{2} (-1 + 2 d_0) \right\} \right\}$$

### Equilibrium

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

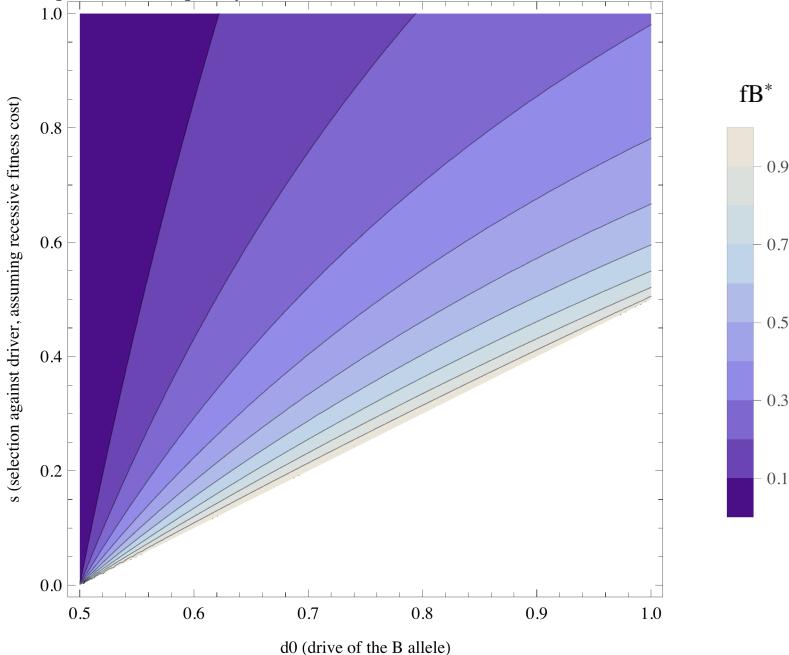
```
eqfB = Solve[(ΔfB /. GENOFREQS /. HWE /. SUMTOONE /. fC → 0) == 0, fB][[4]]
```

$$\left\{ f_B \rightarrow \left( \frac{8 d_0 h_s - 4 d_0 s + \sqrt{-4 (1 - 2 d_0 + h_s + 2 d_0 h_s) (-4 h_s + 8 d_0 h_s + 2 s - 4 d_0 s) + (-8 d_0 h_s + 4 d_0 s)^2}}{2 (-4 h_s + 8 d_0 h_s + 2 s - 4 d_0 s)} \right) \right\}$$

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

```
ContourPlot[If[fB > 1, 1/0, If[fB < 0, 1/0, fB]] /. eqfB /. hs → 0, {d0, .5, 1}, {s, 0, 1}, PlotLegends → BarLegend[Automatic, LegendLabel → "fB*"], PlotLabel → "Equilibrium frequency of a standard driver with a recessive fitness cost", FrameLabel → {"d0 (drive of the B allele)", "s (selection against driver, assuming recessive fitness cost)"}]
```

Equilibrium frequency of a standard driver with a recessive fitness cost



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

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

## background

### Equilibrium frequency of drive suppressor

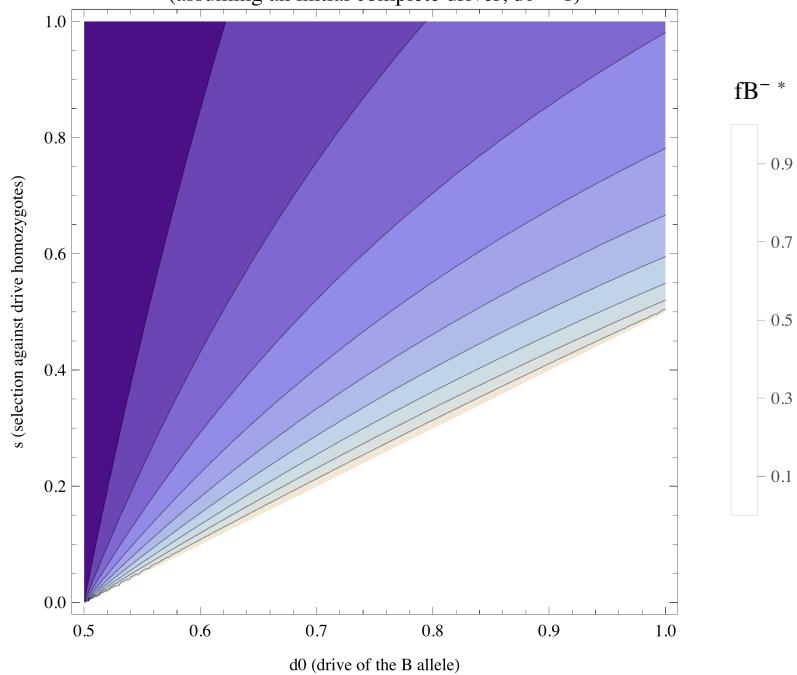
```
eqfC = Solve[(FullSimplify[ΔfC /. HWE /. SUMTOONE /. minormod /. fB → 0]) == 0, fC][[4]];

(*Equilibrium frequency of a linked, coupled,
drive suppressor when the fitness costs of drive are recessive*)

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)"}]
```

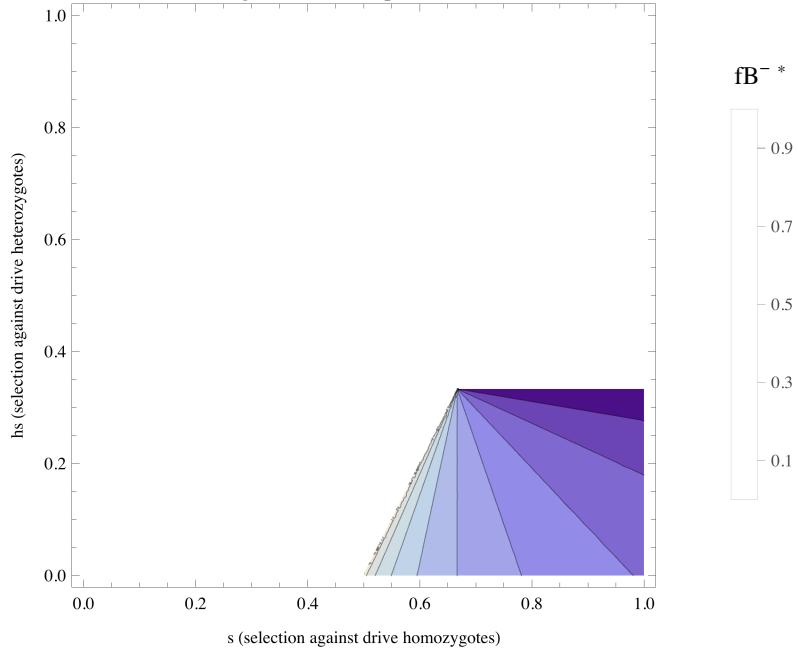
Equilibrium freq. of sperm-acting drive suppressor (the  $B^-$  haplotype)  
(assuming an initial complete driver,  $d0 = 1$ )



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

```
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)"}]
```

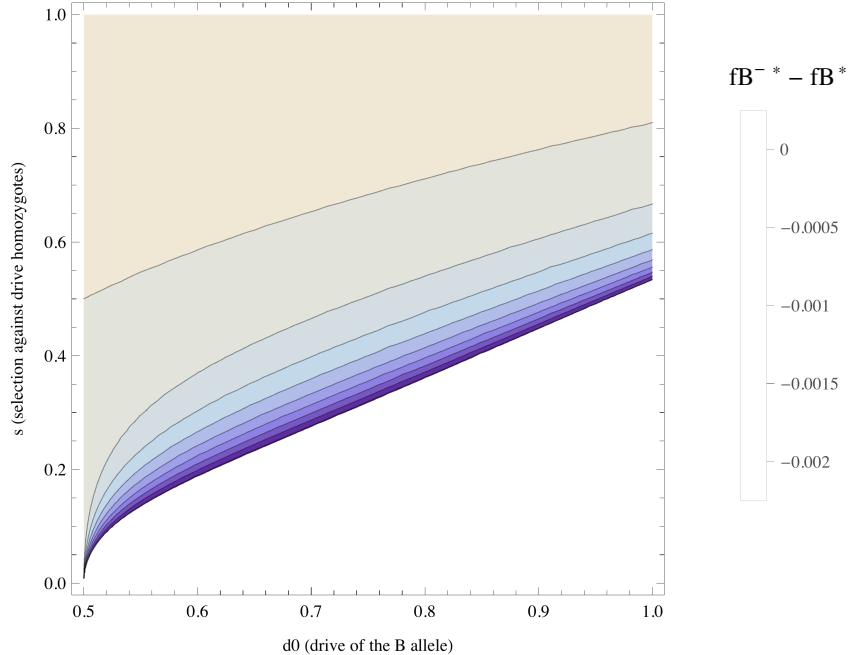
Equilibrium freq. of a sperm-acting drive suppressor (the  $B^-$  haplotype)  
(assuming an initial complete driver,  $d0 = 1$ )



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

```
(*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)

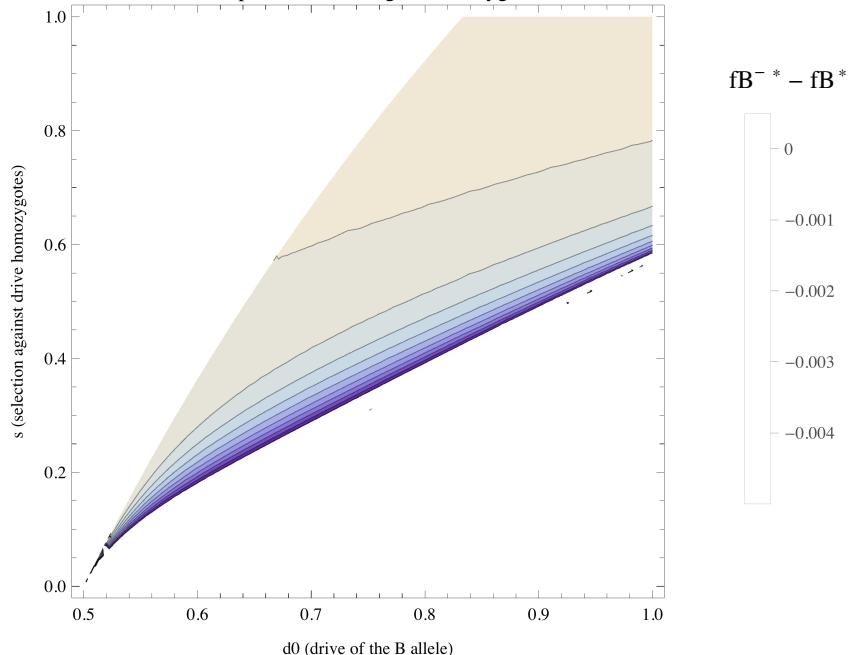


```

ContourPlot[
If[fC < 1 && fB < 1 && fC > 0 && fB > 0, (fC - fB), 1/0] /. eqfB /. eqfC /. hs → (s / 4) /.
ε → -.001, {d0, .5, 1}, {s, 0, 1},
PlotLegends → BarLegend[Automatic, LegendLabel → "fB⁻ * - fB⁹"], PlotLabel →
"Difference in equilibrium frequency of a drive suppressor (B⁻ haplotype)\nand the driver it replaces (assuming a heterozygote cost, hs = s/4)",
FrameLabel → {"d0 (drive of the B allele)", "s (selection against drive homozygotes)"}]

```

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



```

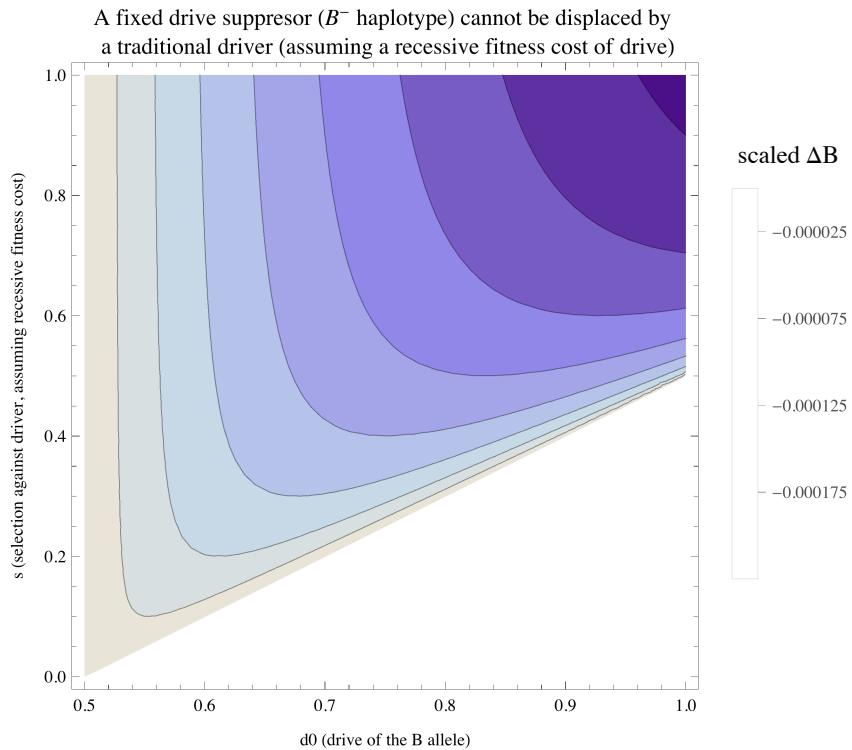
(*change in frequency of a rare traditional driver when the drive-
sperm suppressor haplotype and the ondriving hplotype
are at drive selection equilibrium, mutliplied by
Wbar/fC [this value is always positive and will not influence the sign]*)
wbarDeltaTradDrive = FullSimplify[
FullSimplify[WΔfB / (fB)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

```

```

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)"}]

```



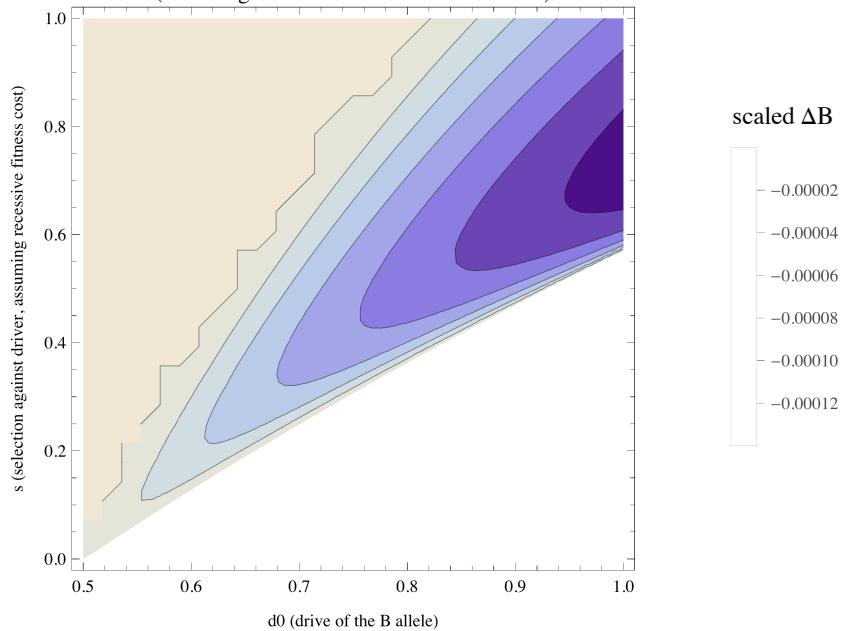
(\*Plotting the change in frequency of a rare traditional driving haplotype when the sperm drive suppressor is at drive selection balance. ASSUMING a fitness cost of drive in homozygotes (hs→s/4). NOTE: This sperm enhancer of drive cannot invade\*)

```

ContourPlot[
 If[fC > 1, 1 / 0, If[fC < 0.0001, 0, wbarDeltaTradDrive]] /. eqfC /. \[Epsilon] \[Rule] -0.001 /.
 hs \[Rule] s / 4, {d0, 0.5, 1}, {s, 0, 1},
 PlotLegends \[Rule] BarLegend[Automatic, LegendLabel \[Rule] "scaled \[Delta]B"],
 PlotLabel \[Rule] "A fixed sperm-acting drive suppressor cannot be displaced
 by a traditional \n(assuming a recessive fitness cost of drive)",
 FrameLabel \[Rule] {"d0 (drive of the B allele)",
 "s (selection against driver, assuming recessive fitness cost)"}]

```

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

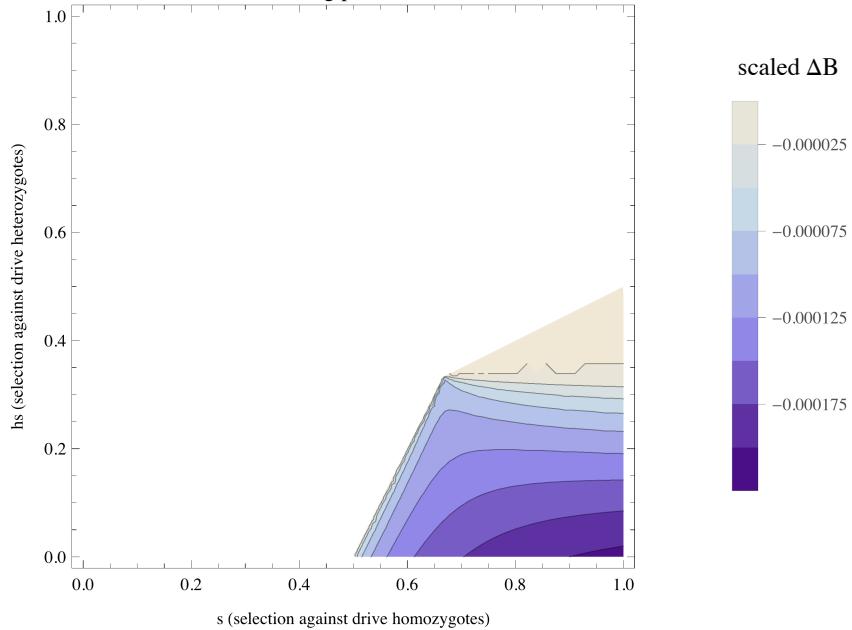


```

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 4. 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 = 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 +
fAC * fAC * 1 / 4 + 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 / 4 +
fAC * fAC * 0 + fAC * fBB * 1 / 2 + fAC * fBC * 1 / 4 + 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 / 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 * 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 * d0 + fBC * fAB * d0 / 2 +
fBC * fAC * (d0) / 2 + 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 / 2 + fBB * fCC * 0 + fBC * fAA * 0 + fBC * fAB * d0 / 2 +
fBC * fAC * 0 + fBC * fBB * d0 + fBC * fBC * (d0) / 2 + 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 * (d1) / 2 + fBC * fBB * 0 + fBC * fBC * (d1) / 2 + fBC * fCC * d1 +
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 * 1 / 2 + fAC * fAB * 1 / 4 + fAC * fAC * 1 / 4 +
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 - d0) + fBC * fAB * (1 - d0) / 2 +
fBC * fAC * (1 - d0) / 2 + 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 * 1 / 4 + fAC * fAC * 0 + fAC * fBB * 1 / 2 +
fAC * fBC * 1 / 4 + 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 - d0) / 2 +
fBC * fAC * 0 + fBC * fBB * (1 - d0) + fBC * fBC * (1 - d0) / 2 + 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 * 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 + Ban];
fACDrive = FullSimplify[ACn + CAN];
fBBDrive = FullSimplify[BBn];
fBCDrive = FullSimplify[BCn + CBn];
fCCDrive = FullSimplify[CCn];
(*check, do allele freqs sum to one?*)
FullSimplify[
FullSimplify[fAADrive + fABDrive + fACDrive + fBBDrive + fBCDrive + fCCDrive] /. HWE /. SUMTOONE]
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[ $\bar{W} \Delta f_C / (f_C^2) /. HWE /. SUMTOONE /. eqfB /. hs \rightarrow 0$ ] /. minormod]

$$\frac{(-2 d_0 s + \sqrt{2} \sqrt{(-1 + 2 d_0 (2 + d_0 (-2 + s))) s})}{2 (-1 + 2 d_0) s}$$

```

**ContourPlot[**

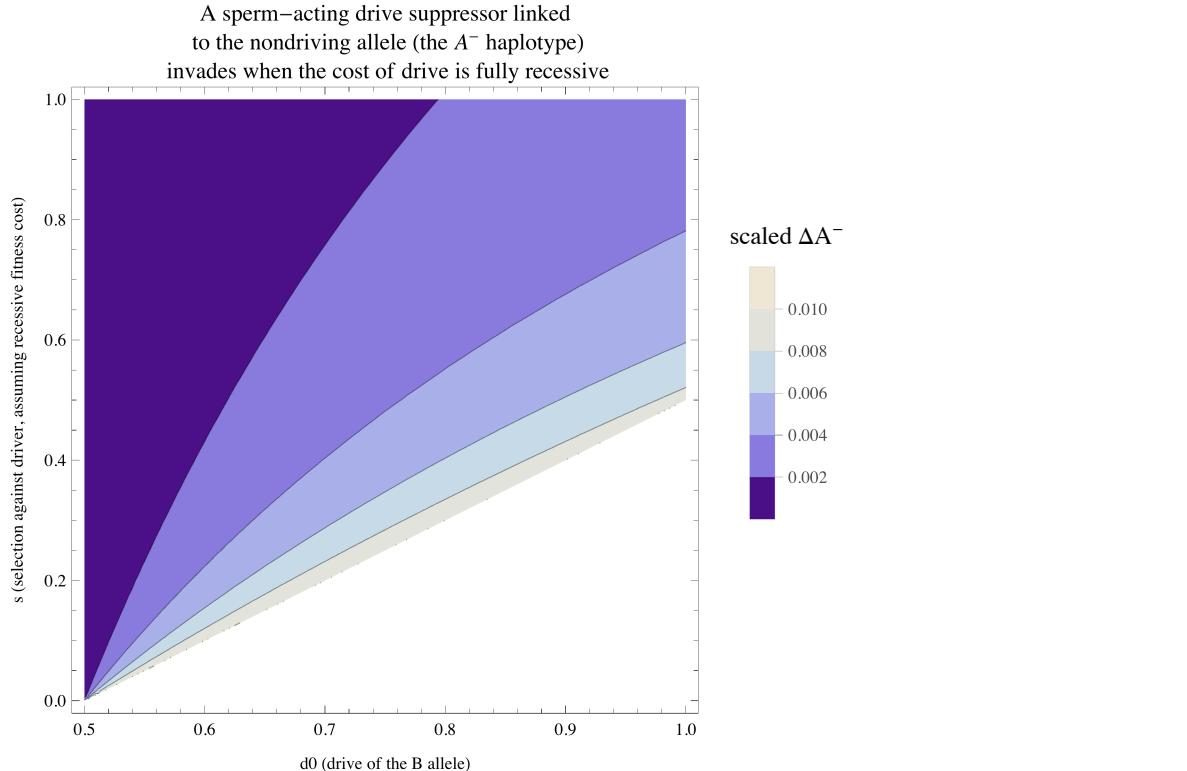
If[fB > 1, 1/0, If[fB < 0.0001, 0, wbarDeltaSpermDriveRecessive]] /. eqfB /.

$\epsilon \rightarrow -0.01 / . hs \rightarrow 0, \{d_0, 0.5, 1\}, \{s, 0, 1\},$

PlotLegends  $\rightarrow$  BarLegend[Automatic, LegendLabel  $\rightarrow$  "scaled  $\Delta A^-$ "],

PlotLabel  $\rightarrow$  "A sperm-acting drive suppressor linked\n to the nondriving allele  
(the  $A^-$  haplotype)\n invades when the cost of drive is fully recessive",

FrameLabel  $\rightarrow$  {" $d_0$  (drive of the B allele)",  
"s (selection against driver, assuming recessive fitness cost)"}]



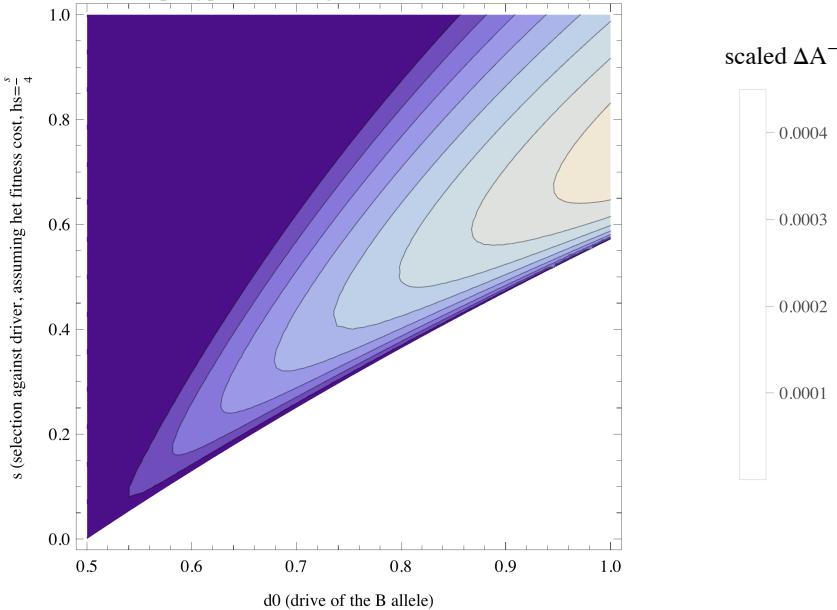
```
(*change in frequency of the drive modifier when rare and when alleles
at the drive locus are in drive-viability equilibrium, mutliplied by
Wbar/fC [this value is always positive and will not influence the sign]*)
```

```
wbarDeltaSpermDrive = FullSimplify[
  FullSimplify[ $\bar{W} \Delta f_C / (f_C) /. HWE /. SUMTOONE] /. f_C \rightarrow 0 /. eqfB /. minormod]
-  $\frac{1}{2 (1 - 2 d_0)^2 (2 h_s - s)} h_s (-1 - h_s -$ 
 $\sqrt{2} \sqrt{(1 + h_s - 2 d_0 (2 + d_0 (-2 + s))) (2 h_s - s)} + 2 d_0 (2 (-1 + d_0) (-1 + h_s) + s)) \in$ 

(*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 /.
 h_s → 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, h_s =  $\frac{s}{4}$ )"}]
```

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 5. 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

```
In[1]:= 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*);
Out[7]= {fA → 1 - fB, fE → 1 - fF}
```

## Drive

```
In[84]:= fAAEEDrive = FullSimplify[
  fAAEE * fAAEE * 1 + fAAEE * fABEE * 1 / 2 + fAAEE * fBBEE * 0 + fAAEE * fAAEF * 1 / 2 +
  fAAEE * fABEF * 1 / 4 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 0 + fAAEE * fABFF * 0 +
  fAAEE * fBBFF * 0 + fABEE * fAAEE * (1 - d0) + fABEE * fABEE * (1 - d0) / 2 + fABEE * fBBEE * 0 +
  fABEE * fAAEF * (1 - d0) / 2 + fABEE * fABEF * (1 - d0) / 4 + fABEE * fBBEF * 0 +
  fABEE * fAAFF * 0 + fABEE * fABFF * 0 + fABEE * fBBFF * 0 + fBBEE * fAAEE * 0 +
  fBBEE * fABEE * 0 + fBBEE * fBBEE * 0 + fBBEE * fAAEF * 0 + fBBEE * fABEF * 0 +
  fBBEE * fBBEF * 0 + fBBEE * fAAFF * 0 + fBBEE * fABFF * 0 + fBBEE * fBBFF * 0 +
  fAAEF * fAAEE * 1 / 2 + fAAEF * fABEE * 1 / 4 + fAAEF * fBBEE * 0 + fAAEF * fAAEF * 1 / 4 +
  fAAEF * fABEF * 1 / 8 + fAAEF * fBBEF * 0 + fAAEF * fAAFF * 0 + fAAEF * fABFF * 0 +
  fAAEF * fBBFF * 0 + fABEF * fAAEE * (1 - d0) / 2 + fABEF * fABEE * (1 - d0) / 4 +
  fABEF * fBBEE * 0 + fABEF * fAAEF * (1 - d0) / 4 + fABEF * fABEF * (1 - d0) / 8 +
```

```

fABEF * fBBEF * 0 + fABEF * fAAFF * 0 + fABEF * fABFF * 0 + fABEF * fBBFF * 0 +
fBBEF * fAAEE * 0 + fBBEF * fABEE * 0 + fBBEF * fBSEE * 0 + fBBEF * fAAEF * 0 +
fBBEF * fABEF * 0 + fBBEF * fBBEF * 0 + fBBEF * fAAFF * 0 + fBBEF * fABFF * 0 +
fBBEF * fBBFF * 0 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 + fAAFF * fBBEE * 0 +
fAAFF * fAAEF * 0 + fAAFF * fABEF * 0 + fAAFF * fBBEF * 0 + fAAFF * fAAFF * 0 +
fAAFF * fABFF * 0 + fAAFF * fBBFF * 0 + fABFF * fAAEE * 0 + fABFF * fABEE * 0 +
fABFF * fBBEE * 0 + fABFF * fAAEF * 0 + fABFF * fABEF * 0 + fABFF * fBBEF * 0 +
fABFF * fAAFF * 0 + fABFF * fABFF * 0 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 0 +
fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 0 +
fBBFF * fBBEF * 0 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]

fABEEDrive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 1 / 2 + fAAEE * fBBEE * 1 +
fAAEE * fAAEF * 0 + fAAEE * fABEF * 1 / 4 + fAAEE * fBBEF * 1 / 2 + fAAEE * fAAFF * 0 +
fAAEE * fABFF * 0 + fAAEE * fBBFF * 0 + fABEE * fAAEE * d0 + fABEE * fABEE * 1 / 2 +
fABEE * fBBEE * (1 - d0) + fABEE * fAAEF * d0 / 2 + fABEE * fABEF * 1 / 4 +
fABEE * fBBEF * (1 - d0) / 2 + fABEE * fAAFF * 0 + fABEE * fABFF * 0 + fABEE * fBBFF * 0 +
fBBEE * fAAEE * 1 + fBSEE * fABEE * 1 / 2 + fBSEE * fBBEE * 0 + fBSEE * fAAEF * 1 / 2 +
fBSEE * fABEF * 1 / 4 + fBSEE * fBBEF * 0 + fBSEE * fAAFF * 0 + fBSEE * fABFF * 0 +
fBSEE * fBBFF * 0 + fAAEF * fAAEE * 0 + fAAEF * fABEE * 1 / 4 + fAAEF * fBBEE * 1 / 2 +
fAAEF * fAAEF * 0 + fAAEF * fABEF * 1 / 8 + fAAEF * fBBEF * 1 / 4 + fAAEF * fAAFF * 0 +
fAAEF * fABFF * 0 + fAAEF * fBBFF * 0 + fABEF * fAAEE * d0 / 2 + fABEF * fABEE * 1 / 4 +
fABEF * fBBEE * (1 - d0) / 2 + fABEF * fAAEF * d0 / 4 + fABEF * fABEF * 1 / 8 +
fABEF * fBBEF * (1 - d0) / 4 + fABEF * fAAFF * 0 + fABEF * fABFF * 0 + fABEF * fBBFF * 0 +
fBBEF * fAAEE * 1 / 2 + fBBEF * fABEE * 1 / 4 + fBBEF * fBBEE * 0 + fBBEF * fAAEF * 1 / 4 +
fBBEF * fABEF * 1 / 8 + fBBEF * fBBEF * 0 + fBBEF * fAAFF * 0 + fBBEF * fABFF * 0 +
fBBEF * fBBFF * 0 + fAAFF * 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 + fBSEE * fABEE * 1 / 2 + fBSEE * fBBEE * 1 + fBSEE * fAAEF * 0 +
fBSEE * fABEF * 1 / 4 + fBSEE * fBBEF * 1 / 2 + fBSEE * fAAFF * 0 + fBSEE * fABFF * 0 +
fBSEE * fBBFF * 0 + fAAEF * fAAEE * 0 + fAAEF * fABEE * 0 + fAAEF * fBBEE * 0 +
fAAEF * fAAEF * 0 + fAAEF * fABEF * 0 + fAAEF * fBBEF * 0 + fAAEF * fAAFF * 0 +
fAAEF * fABFF * 0 + fAAEF * fBBFF * 0 + fABEF * fAAEE * 0 + fABEF * fABEE * (d0 / 4) +
fABEF * fBBEE * d0 / 2 + fABEF * fAAEF * 0 + fABEF * fABEF * (d0 / 8) +
fABEF * fBBEF * d0 / 4 + fABEF * fAAFF * 0 + fABEF * fABFF * 0 + fABEF * fBBFF * 0 +
fBBEF * fAAEE * 0 + fBBEF * fABEE * 1 / 4 + fBBEF * fBBEE * 1 / 2 + fBBEF * fAAEF * 0 +
fBBEF * fABEF * 1 / 8 + fBBEF * fBBEF * 1 / 4 + fBBEF * fAAFF * 0 + fBBEF * fABFF * 0 +
fBBEF * fBBFF * 0 + fAAFF * fAAEE * 0 + fAAFF * fABEE * 0 + fAAFF * fBBEE * 0 +
fAAFF * fAAEF * 0 + fAAFF * fABEF * 0 + fAAFF * fBBEF * 0 + fAAFF * fAAFF * 0 +
fAAFF * fABFF * 0 + fAAFF * fBBFF * 0 + fABFF * fAAEE * 0 + fABFF * fABEE * 0 +
fABFF * fBBEE * 0 + fABFF * fAAEF * 0 + fABFF * fABEF * 0 + fABFF * fBBEF * 0 +
fABFF * fAAFF * 0 + fABFF * fABFF * 0 + fABFF * fBBFF * 0 + fBBFF * fAAEE * 0 +
fBBFF * fABEE * 0 + fBBFF * fBBEE * 0 + fBBFF * fAAEF * 0 + fBBFF * fABEF * 0 +
fBBFF * fBBEF * 0 + fBBFF * fAAFF * 0 + fBBFF * fABFF * 0 + fBBFF * fBBFF * 0 + 0]

fAAEFDrive = FullSimplify[fAAEE * fAAEE * 0 + fAAEE * fABEE * 0 + fAAEE * fBBEE * 0 +
fAAEE * fAAEF * 1 / 2 + fAAEE * fABEF * 1 / 4 + fAAEE * fBBEF * 0 + fAAEE * fAAFF * 1 +
fAAEE * fABFF * 1 / 2 + fAAEE * fBBFF * 0 + fABEE * fAAEE * 0 + fABEE * fABEE * 0 +

```

```

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

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 * 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 * 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

```

$$\begin{aligned}
& f_{BBEE} * f_{ABEE} * 0 + f_{BBEE} * f_{BBEE} * 0 + f_{BBEE} * f_{AAEF} * 0 + f_{BBEE} * f_{ABEF} * 0 + \\
& f_{BBEE} * f_{BBEF} * 0 + f_{BBEE} * f_{AAFF} * 0 + f_{BBEE} * f_{ABFF} * 0 + f_{BBEE} * f_{BBFF} * 0 + \\
& f_{AAEF} * f_{AAEE} * 0 + f_{AAEF} * f_{ABEE} * 0 + f_{AAEF} * f_{BBEE} * 0 + f_{AAEF} * f_{AAEF} * 0 + \\
& f_{AAEF} * f_{ABEF} * 0 + f_{AAEF} * f_{BBEF} * 0 + f_{AAEF} * f_{AAFF} * 0 + f_{AAEF} * f_{ABFF} * 0 + \\
& f_{AAEF} * f_{BBFF} * 0 + f_{ABEF} * f_{AAEE} * 0 + f_{ABEF} * f_{ABEE} * 0 + f_{ABEF} * f_{BBEE} * 0 + \\
& f_{ABEF} * f_{AAEF} * 0 + f_{ABEF} * f_{ABEF} * d1 / 8 + f_{ABEF} * f_{BBEF} * d1 / 4 + \\
& f_{ABEF} * f_{AAFF} * 0 + f_{ABEF} * f_{ABFF} * d1 / 4 + f_{ABEF} * f_{BBFF} * d1 / 2 + \\
& f_{BBEF} * f_{AAEE} * 0 + f_{BBEF} * f_{ABEE} * 0 + f_{BBEF} * f_{BBEE} * 0 + f_{BBEF} * f_{AAEF} * 0 + \\
& f_{BBEF} * f_{ABEF} * 1 / 8 + f_{BBEF} * f_{BBEF} * 1 / 4 + f_{BBEF} * f_{AAFF} * 0 + f_{BBEF} * f_{ABFF} * 1 / 4 + \\
& f_{BBEF} * f_{BBFF} * 1 / 2 + f_{AAFF} * f_{AAEE} * 0 + f_{AAFF} * f_{ABEE} * 0 + f_{AAFF} * f_{BBEE} * 0 + \\
& f_{AAFF} * f_{AAEF} * 0 + f_{AAFF} * f_{ABEF} * 0 + f_{AAFF} * f_{BBEF} * 0 + f_{AAFF} * f_{AAFF} * 0 + \\
& f_{AAFF} * f_{ABFF} * 0 + f_{AAFF} * f_{BBFF} * 0 + f_{ABFF} * f_{AAEE} * 0 + f_{ABFF} * f_{ABEE} * 0 + \\
& f_{ABFF} * f_{BBEE} * 0 + f_{ABFF} * f_{AAEF} * 0 + f_{ABFF} * f_{ABEF} * d1 / 4 + f_{ABFF} * f_{BBEF} * d1 / 2 + \\
& f_{ABFF} * f_{AAFF} * 0 + f_{ABFF} * f_{ABFF} * d1 / 2 + f_{ABFF} * f_{BBFF} * (d1) + f_{BBFF} * f_{AAEE} * 0 + \\
& f_{BBFF} * f_{ABEE} * 0 + f_{BBFF} * f_{BBEE} * 0 + f_{BBFF} * f_{AAEF} * 0 + f_{BBFF} * f_{ABEF} * 1 / 4 + \\
& f_{BBFF} * f_{BBEF} * 1 / 2 + f_{BBFF} * f_{AAFF} * 0 + f_{BBFF} * f_{ABFF} * 1 / 2 + f_{BBFF} * f_{BBFF} * 1 + 0] \\
\text{Out}[84]= & \frac{1}{8} (4 f_{AAEE} + 2 (f_{AAEF} + f_{ABEE}) + f_{ABEF}) (2 f_{AAEE} + f_{AAEF} - (-1 + d0) (2 f_{ABEE} + f_{ABEF})) \\
\text{Out}[85]= & \frac{1}{8} (f_{AAEF} (2 f_{ABEE} + 4 d0 f_{ABEE} + f_{ABEF} + 2 d0 f_{ABEF} + 8 f_{BBEE} + 4 f_{BBEF}) + \\
& 2 f_{AAEE} ((2 + 4 d0) f_{ABEE} + f_{ABEF} + 2 d0 f_{ABEF} + 8 f_{BBEE} + 4 f_{BBEF}) + \\
& (2 f_{ABEE} + f_{ABEF}) (2 f_{ABEE} + f_{ABEF} - (-3 + 2 d0) (2 f_{BBEE} + f_{BBEF}))) \\
\text{Out}[86]= & \frac{1}{8} (d0 (2 f_{ABEE} + f_{ABEF}) + 2 f_{BBEE} + f_{BBEF}) (2 f_{ABEE} + f_{ABEF} + 4 f_{BBEE} + 2 f_{BBEF}) \\
\text{Out}[87]= & \frac{1}{8} (4 f_{AAEF}^2 + 2 f_{AAEE} (4 f_{AAEF} + 8 f_{AAFF} + 3 f_{ABEF} - 2 d0 f_{ABEF} + 2 f_{ABFF} + 4 d0 f_{ABFF}) - \\
& (2 f_{ABEE} + f_{ABEF}) ((-6 + 4 d1) f_{AAFF} + (-2 + d0 + d1) (f_{ABEF} + 2 f_{ABFF})) + \\
& f_{AAEF} (8 f_{AAFF} - 2 ((-3 + 2 d1) f_{ABEE} + (-3 + d0 + d1) f_{ABEF} + (-3 + 2 d0) f_{ABFF}))) \\
\text{Out}[88]= & \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 d0 f_{ABEF} f_{BBEE} + 2 f_{ABFF} f_{BBEE} + 4 d0 f_{ABFF} f_{BBEE} + 3 f_{ABEE} f_{BBEF} - \\
& 2 d1 f_{ABEE} f_{BBEF} + 3 f_{ABEF} f_{BBEF} - d0 f_{ABEF} f_{BBEF} - d1 f_{ABEF} f_{BBEF} + 3 f_{ABFF} f_{BBEF} - \\
& 2 d0 f_{ABFF} f_{BBEF} + f_{AAFF} ((2 + 4 d1) f_{ABEE} + f_{ABEF} + 2 d1 f_{ABEF} + 8 f_{BBEE} + 4 f_{BBEF}) - \\
& (-3 + 2 d1) (2 f_{ABEE} + f_{ABEF}) f_{BBFF} + \\
& f_{AAEE} (f_{ABEF} + 2 d0 f_{ABEF} + 6 f_{ABFF} - 4 d0 f_{ABFF} + 4 f_{BBEF} + 8 f_{BBFF}) + f_{AAEF} \\
& (f_{ABEE} + 2 d1 f_{ABEE} + (1 + d0 + d1) f_{ABEF} + f_{ABFF} + 2 d0 f_{ABFF} + 4 (f_{BBEE} + f_{BBEF} + f_{BBFF}))) \\
\text{Out}[89]= & \frac{1}{8} (d0 (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})) + \\
& d1 (2 f_{ABEE} + f_{ABEF}) (f_{ABEF} + 2 (f_{ABFF} + f_{BBEF} + 2 f_{BBFF}))) \\
\text{Out}[90]= & \frac{1}{8} (2 f_{AAEF} + 4 f_{AAFF} + f_{ABEF} + 2 f_{ABFF}) (f_{AAEF} + 2 f_{AAFF} - (-1 + d1) (f_{ABEF} + 2 f_{ABFF}))
\end{aligned}$$

```

Out[91]= 
$$\frac{1}{8} \left( fAAEF (fABEF + 2 d1 fABEF + 2 fABFF + 4 d1 fABFF + 4 fBBEF + 8 fBBFF) + 2 fAAFF (fABEF + 2 d1 fABEF + 2 fABFF + 4 d1 fABFF + 4 fBBEF + 8 fBBFF) + (fABEF + 2 fABFF) (fABEF + 2 fABFF - (-3 + 2 d1) (fBBEF + 2 fBBFF)) \right)$$


Out[92]= 
$$\frac{1}{8} (d1 (fABEF + 2 fABFF) + fBBEF + 2 fBBFF) (fABEF + 2 (fABFF + fBBEF + 2 fBBFF))$$


```

## Selection

```

In[93]:= wAAEE = wAAEF = wAFF = 1;
wABEE = wABEF = wABFF = 1 - hs;
wBEE = wBEF = wBFF = 1 - s;

In[96]:=  $\bar{W} = \text{FullSimplify}[(fAAE_{\text{Drive}} wAAE + fAAE_{\text{Drive}} wAAE + fAAFF_{\text{Drive}} wAFF + fABE_{\text{Drive}} wABE + fABE_{\text{Drive}} wABE + fABFF_{\text{Drive}} wABFF + fBBE_{\text{Drive}} wBEE + fBBE_{\text{Drive}} wBEE + fBBFF_{\text{Drive}} wBFF)]$ 

In[97]:= fAAE_{\text{Sel}} = FullSimplify[fAAE_{\text{Drive}} wAAE / \bar{W}];
fABE_{\text{Sel}} = FullSimplify[fABE_{\text{Drive}} wABE / \bar{W}];
fBBE_{\text{Sel}} = FullSimplify[fBBE_{\text{Drive}} wBEE / \bar{W}];
fAAE_{\text{Sel}} = FullSimplify[fAAE_{\text{Drive}} wAAE / \bar{W}];
fABE_{\text{Sel}} = FullSimplify[fABE_{\text{Drive}} wABE / \bar{W}];
fBBE_{\text{Sel}} = FullSimplify[fBBE_{\text{Drive}} wBEE / \bar{W}];
fAFF_{\text{Sel}} = FullSimplify[fAFF_{\text{Drive}} wAFF / \bar{W}];
fABFF_{\text{Sel}} = FullSimplify[fABFF_{\text{Drive}} wABFF / \bar{W}];
fBBFF_{\text{Sel}} = FullSimplify[fBBFF_{\text{Drive}} wBFF / \bar{W}];

fA_{\text{Sel}} = FullSimplify[fAAE_{\text{Sel}} + fAAE_{\text{Sel}} + fAAFF_{\text{Sel}} + (fABE_{\text{Sel}} + fABE_{\text{Sel}} + fABFF_{\text{Sel}}) / 2];
fB_{\text{Sel}} = FullSimplify[fBBE_{\text{Sel}} + fBBE_{\text{Sel}} + fBBFF_{\text{Sel}} + (fABE_{\text{Sel}} + fABE_{\text{Sel}} + fABFF_{\text{Sel}}) / 2];
fE_{\text{Sel}} = FullSimplify[fAAE_{\text{Sel}} + fABE_{\text{Sel}} + fBBE_{\text{Sel}} + (fAAE_{\text{Sel}} + fABE_{\text{Sel}} + fBBE_{\text{Sel}}) / 2];
fF_{\text{Sel}} = FullSimplify[fAFF_{\text{Sel}} + fABFF_{\text{Sel}} + fBBFF_{\text{Sel}} + (fAAE_{\text{Sel}} + fABE_{\text{Sel}} + fBBE_{\text{Sel}}) / 2];
\Delta fA = FullSimplify[fA_{\text{Sel}} - fA];
\Delta fB = FullSimplify[fB_{\text{Sel}} - fB];
\Delta fE = FullSimplify[fE_{\text{Sel}} - fE];
\Delta fF = FullSimplify[fF_{\text{Sel}} - fF];

(* \Delta fC = FullSimplify[fC_{\text{Sel}} - fC]; *)

(* Check: do genotype freqs after selection sum to one? *)
FullSimplify[fA_{\text{Sel}} + fB_{\text{Sel}}]
FullSimplify[fE_{\text{Sel}} + fF_{\text{Sel}}]

Out[113]= 1

Out[114]= 1

```

# Analysis

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

```
In[115]:= invasionOfUnlinkedModeifier =
  FullSimplify[ $\bar{W} \Delta fF / fF$  /. randomHaps /. D → 0 /. sum2one /. minormod] /.
   fF → 0 (*this assumes no LD and random mating*)
Out[115]=  $-(-1 + fB) fB ((-1 + 2 fB) hs - fB s) \epsilon$ 

(*With some rearrangement,
invasionOfUnlinkedModeifier=  $-\epsilon fA fB (fB s + (fA - fB) hs)$ )
So long as sh<
s, [i.e. the driver does not have an underdominant effect on fitness] this is
guaranteed to be positive when  $\epsilon$  is negative [i.e. the modifier dampens drive]*)
```

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

```
In[126]:= fixationOfUnlinkedModeifier = FullSimplify[
  FullSimplify[ $\bar{W} \Delta fF / (1 - fF)$  /. randomHaps /. D → 0 /. sum2one /. minormod] /.
   fF → 1]
(*this assumes no LD and random mating*)
Out[126]=  $(-1 + fB) fB (hs - 2 fB hs + fB s) \epsilon$ 

(*With some rearrangement,
fixationOfUnlinkedModeifier=  $-\epsilon fA fB (fB s + hs(1 - 2 fB))$ )
So long as sh<
s, [i.e. the driver does not have an underdominant effect on fitness]
this is guaranteed to be positive when  $\epsilon$  is
negative [i.e. the modifier dampens drive]*)

In[127]:= FullSimplify[fixationOfUnlinkedModeifier - (- $\epsilon fA fB (fB s + hs(1 - 2 fB))$ ) /.
  sum2one]
Out[127]= 0
```