Speciation in sympatry?

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Sympatric speciation

Sympatry: Random distribution of offspring mating sites in relation to mating sites of the parents.

Evolution of prezygotic isolation driven by evolution of association (LD) between loci under disruptive selection and loci causing assortment

Two problems:

1) Disruptive selection leads to elimination of genetic variation

2) Gene flow and recombination oppose divergence

When reproductive isolation
arises by substitution of different alleles in nascent species

Felsenstein 1982

DS locus:
BC: $(1+s)^2$
Bc, bC: 1+s
bc: 1

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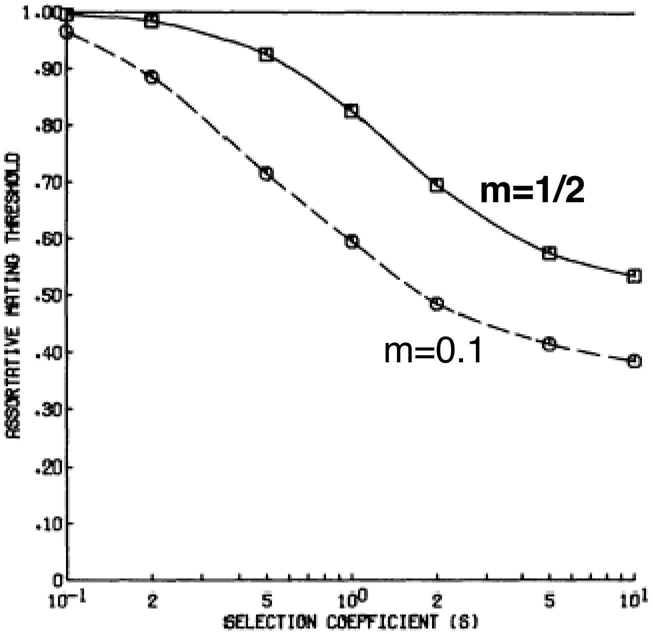
AM locus (prezygotic RI)
d assortative (aa, AA)
1-d random (Aa)

D-M incompatibility -> loss of fitness in F1 = $s^2/2$

FDS arises via separate density regulation in the two niches



Numerical solution – evolution of association between B&C locus

Felsenstein (1982) Skepticism towards Santa Rosalia, or why are there so few kinds of animals? Evolution 35: 124-138

Udovic 1980 / Gavrilets 2003, diploid model

DS locus:

1
BB, bb

1+s
Bb

AM locus
α assortative (aa-aa, AA-AA, Aa-Aa)
1- α random

Heterozygote disadvantage = s

FDS stabilizing DS locus

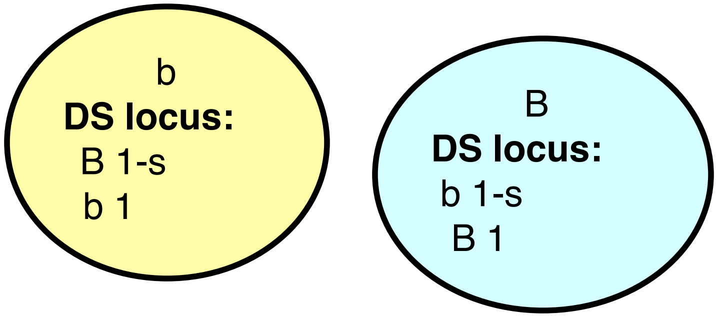
Association (LD) between DS locus and AM (prezygotic RI) loci evolves when

$$\alpha + s > 1$$

Gavrilets S (2003) Models of speciation: what we have learned in 40 years? Evolution 57: 2197-2215

Udovic D (1980) Frequency-dependent selection, disruptive selection, and the evolution of reproductive isolation. Am. Nat. 116: 621-641.

Haploid two locus model



b
DS locus:
B 1-s
b 1

B
DS locus:
b 1-s
B 1

AM locus
α assortative (a-a, A-A)
1- α random (a-A)

Heterozygote disadvantage = s

Fitnesses of zygotes = w(AM).w(DS)

	00	01	11
AM locus	**1**	**$1 - \alpha$**	**1**
DS locus	**1**	**1 – s**	**1**

Fitness effects of AM and DS loci are analogous

Haploid two locus model

b
DS locus:
B 1-s
b 1

B
DS locus:
b 1-s
B 1

AM locus
α assortative (a-a, A-A)
1- α random (a-A)

Heterozygote disadvantage = s

Fitnesses of zygotes = w(AM).w(DS)

	00	**01**	**11**
AM locus	$1 + \alpha\,(1/q_{AM} - 1)$	$1 - \alpha$	$1 + \alpha\,(1/p_{AM} - 1)$
DS locus	$1 + \beta\,(p_{DS} - q_{DS})$	$1 - s$	$1 + \beta\,(q_{DS} - p_{DS})$

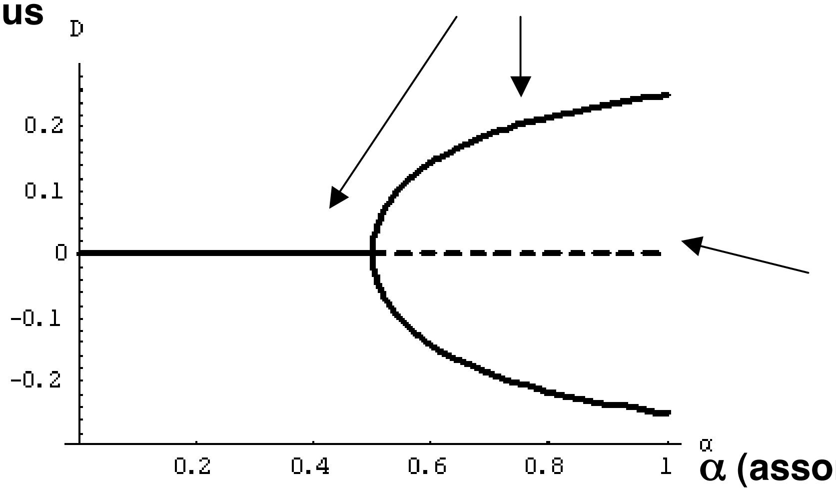
Frequency–dependent selection stabilizes density of both loci,

cost-free assortment

Evolution of association between AM and DS locus

Disequilibrium between AM and DS locus

stable equilibria



unstable equilibrium

α (assortment)

$$D = 0 \text{ or } \frac{\sqrt{s + \alpha - 1}}{4\sqrt{s\,\alpha}}$$

$s=0.5$

$D = 0$ is stable for $\alpha + s < 1$ and $\beta > s$.

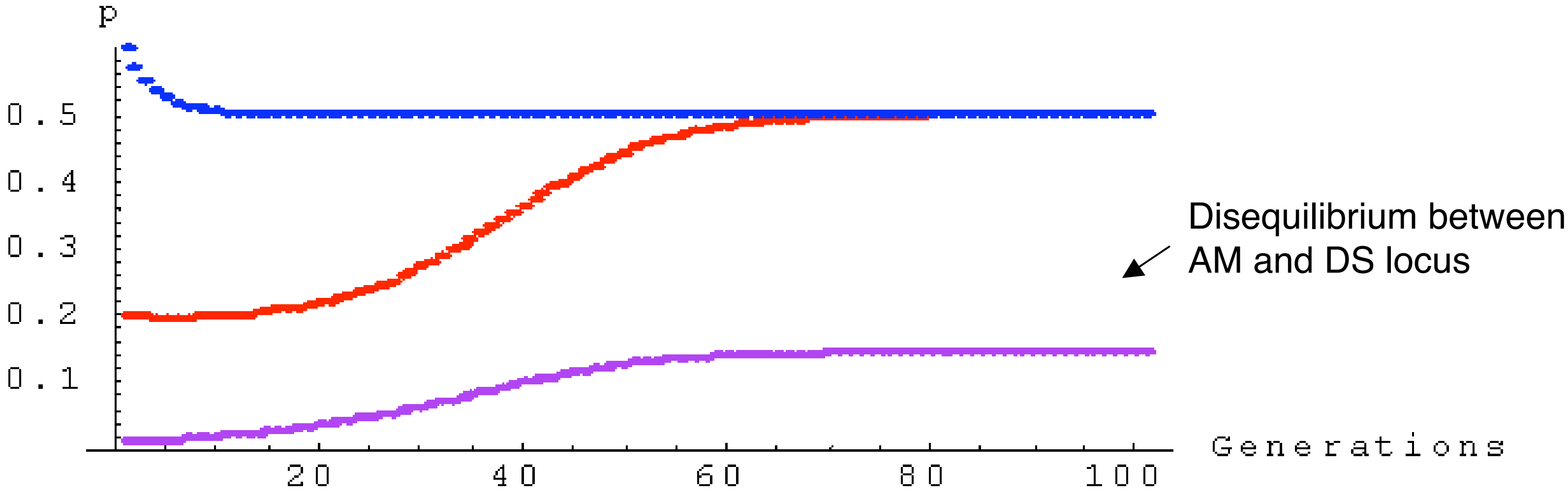
$D \neq 0$ is stable if $\alpha + s > 1$ and **$\beta > s(1- \alpha)/(1+ \alpha))$**

β .. degree of frequency-dependent selection (maintaining polymorphism)

2 locus (AM, DS) haploid model

Numerical solution: α=0.5, β=1, s=0.6.

Allele frequency of AM and DS locus



Disequilibrium between AM and DS locus

Both assortment and underdominant locus are stable, purple line shows disequilibrium.

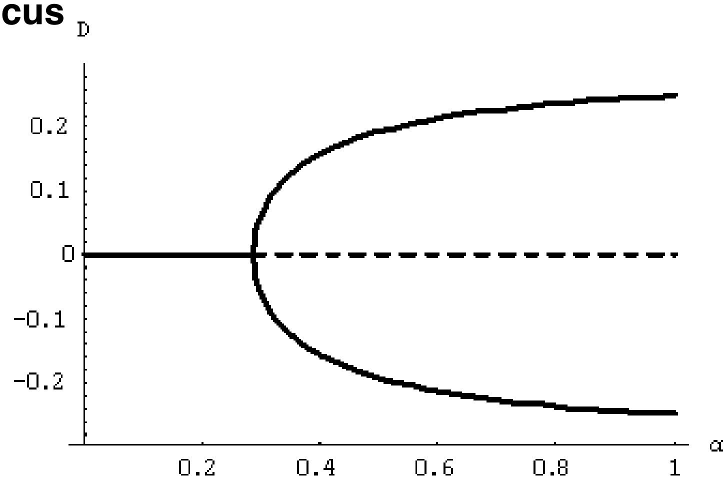
D $\neq$ 0 is stable if $\alpha + s > 1$ (and $\beta > s(1-\alpha)/(1+\alpha)$)

The initial disequilibrium has to be $\neq$ 0.

With linkage ($r<1/2$)

Disequilibrium evolves earlier (in relation to s, α).

Disequilibrium between AM and DS locus

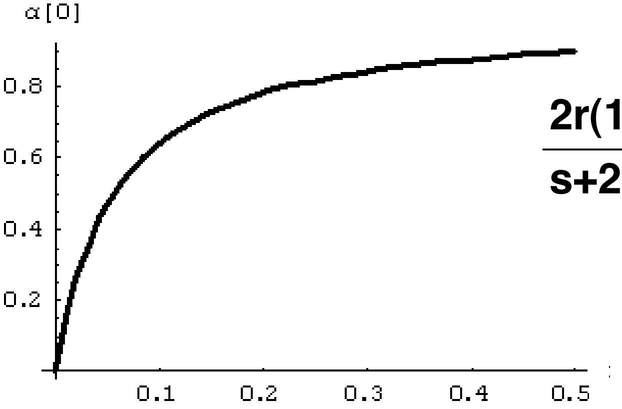


α (assortment)

($s=0.5$, $r=0.2$)

Threshold α ($s=0.1$)

α_0



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

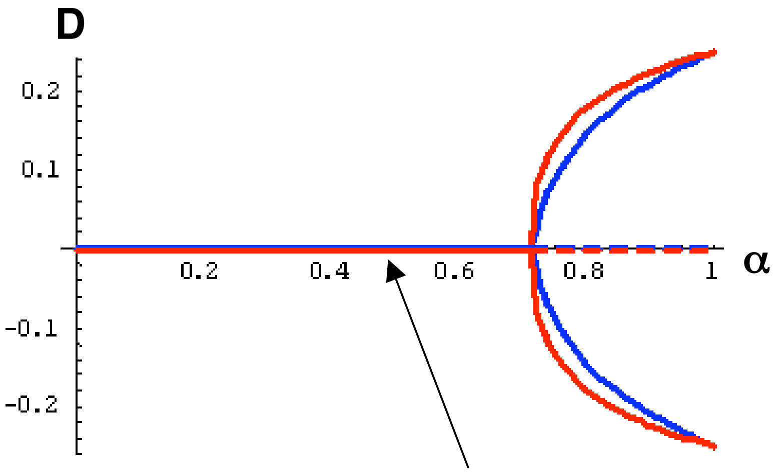
r

What happens with more loci?

3 locus (1 AM, 2 DS) haploid model

Additive model for disruptive selection loci –
double heterozygotes have fitness of 1-s, single heterozygotes of 1-s/2

Stability of disequilibria:



D ≠ 0 becomes stable for the two locus model.

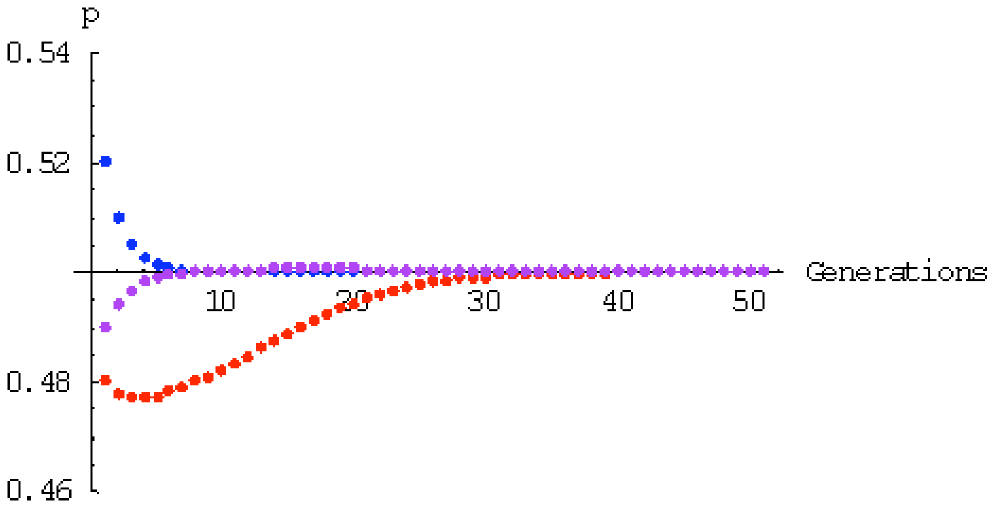
D=0 unstable for $\alpha > (3s-4)/(s-4)$, $s > 2\beta$.
($s=0.5$)

Stability of D ≠ 0 was tested only numerically.

Red line shows disequilibrium between DS loci, blue line D between AM and DS loci.
3rd order disequilibrium among all three loci is always zero.

Numerical solution : α=0.8, β=1, s=0.6 (Additive model for DS)

Allele frequency of AM and DS loci



Assortment and both underdominant loci are stable.

At least one of the initial disequilibria between DS and AM locus has to be ≠ 0.

TWO LOCI: $\alpha + s > 1$, FDS : $\beta > s(1-\alpha)/(1+\alpha)$

THREE LOCI: Evolution of stable nonzero disequilibria still possible though even less likely ($\alpha > (3s-4)/s-4$)

Linkage between the loci allows evolution of a stable system with $D \neq 0$ under less limiting conditions for α, s.

Direct analysis of more loci hardly feasible..

Symmetric model

Allelic effects of all loci are equivalent
Phenotype: #"1"

With n loci 2^n genotypes form n+1 classes,

3 loci: 000,001,010,100,011,101,110,111 -> 0, 1, 2, 3

Stability for

-phenotypic value $\lambda_{1,2,3}$

-discordant shifts in allelic frequencies keeping phenotype constant $\lambda_{4,5}$

-changes in LD λ_6

Barton & Shpak (2000) The stability of symmetric solutions to polygenic models. Theor. Pop. Biol. 57: 249-263

Doebeli (1996) A quantitative genetic competition model for sympatric speciation. J. Evol. Biol. 9: 893-909.

Fitness of phenotypes is both frequency and density dependent (no assortment)

$$W \sim K(z)\ \mathrm{Exp}[-\ \psi_{\mathbf{eff}}\ \mathbf{(z)}\ \mathbf{]}$$

ψ_{eff} ..effective density

- population density weighted by a frequency-dependent competition $G \sim N\ (z\text{-}z', \sigma_z)$

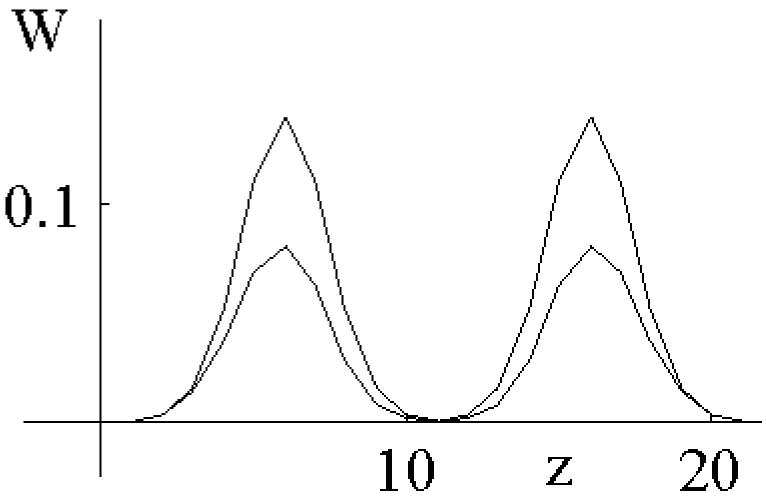
K.. carrying capacity $\sim N\ (\pm z_0, \sigma_k)$

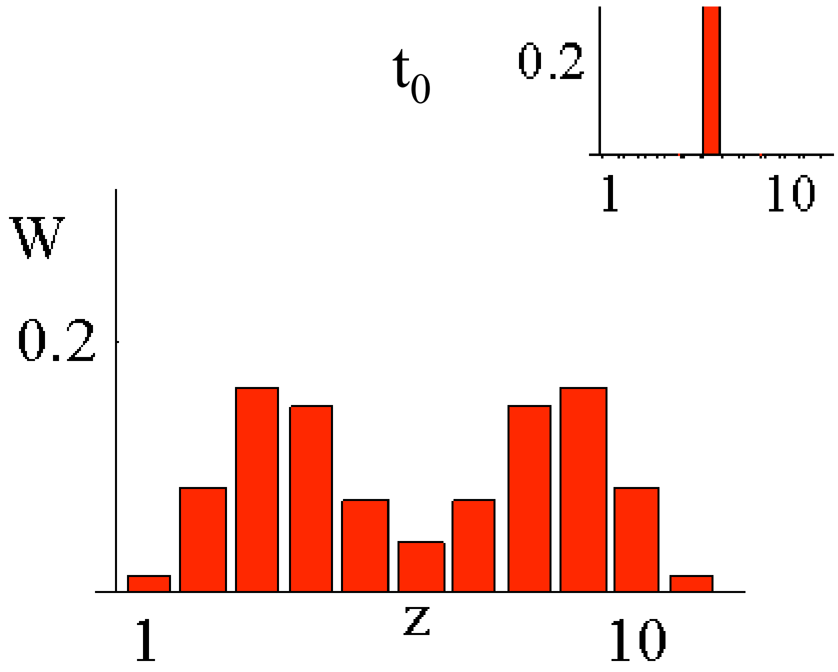
$$W = \left(\frac{N[i+j-z_0-L,\ V_k] + N[i+j-z_0-L,\ V_k]}{2}\right) \mathrm{Exp}\left[-\gamma \sum_{kk=0}^{2n} \phi_{kk}\ N\left[i+j-kk,\ \frac{1}{\beta}\right]\right]$$

Example for 10 loci –

With strong DS, distribution of phenotypes can be bimodal if stabilized by FDS.

(Even without assortment.)





$$W = \left(\frac{N[i+j-z_0-L,\ V_k] + N[i+j-z_0-L,\ V_k]}{2}\right) \mathrm{Exp}\left[-\gamma \sum_{kk=0}^{2n} \phi_{kk}\, N\left[i+j-kk,\ \frac{1}{\beta}\right]\right]$$

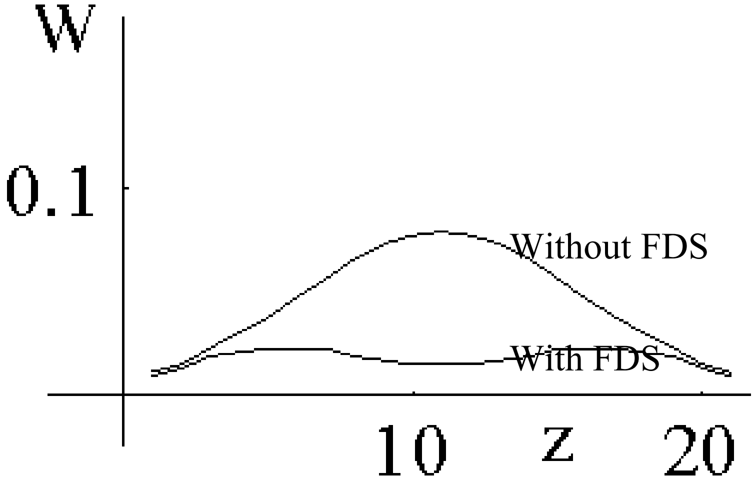
DS

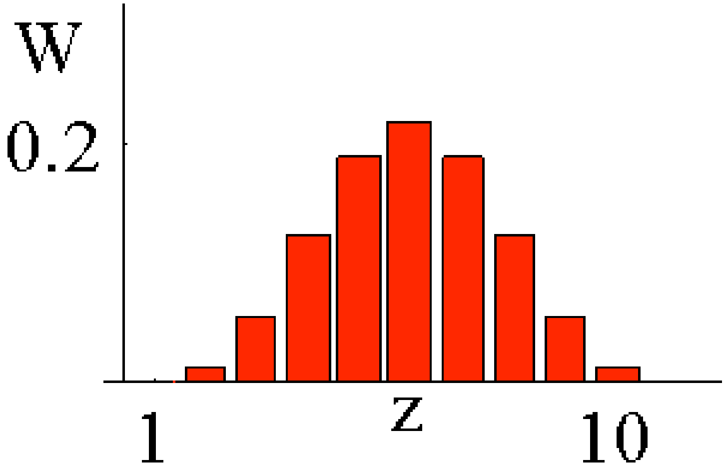
FDS

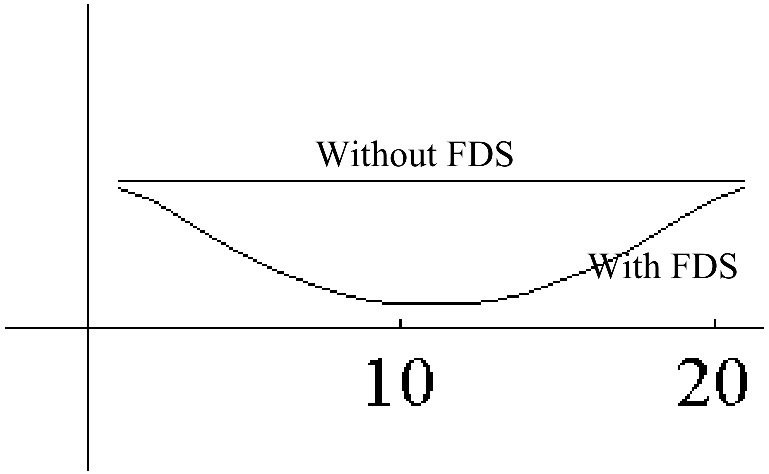
$z_0=10$, $L=5$, $V_k=2$, $V_c=3$, $\gamma=16$

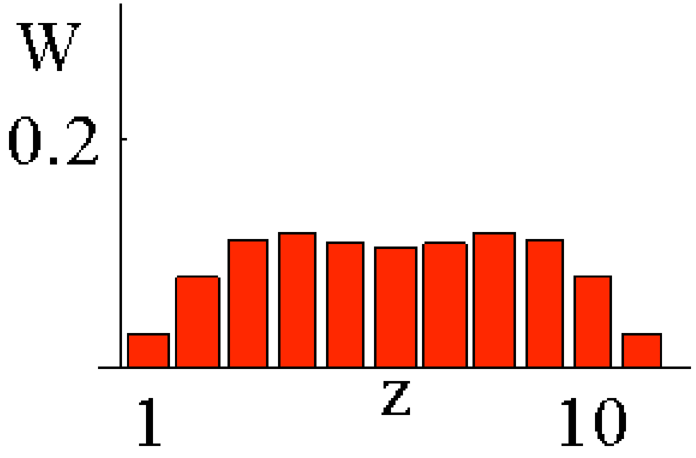
Example for 10 loci, stabilizing selection

(DS arising due to limits on trait range)









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