SHIFTING BALANCE THEORY

Remember the sickle cell case? Inbreeding changed the adaptive topography, leading to selection to a higher fitness peak.

Here we want to consider peak shifts without changing the adaptive surface.

We do it in the context of an argument between R.A. Fisher and Sewel Wright.

Fisher's view

1. Populations are large and panmictic*.
   a) Hence genetic drift and inbreeding are of little importance.
   b) Selection operates on the average additive effect of alleles.

"... I believe that N must usually be the total population of the planet."

2. The population is conceived to contain all the genetic combinations possible, with frequencies appropriate to their actual probabilities of occurrence in all environmental circumstances.
WRIGHT'S VIEW

Populations are subdivided into demes

A. INBREEDING AND DRIFT CANNOT BE IGNORED

B. Selection operates on combination of alleles w/in demes. Epistasis CANNOT BE IGNORED.
First effective population size, $N_e$

**Effect of sex ratio on $N_e$**

$$N_e = \frac{4N_m N_f}{N_m + N_f}$$

For 200 cows and 2 bulls, we get

$$\frac{4(2)(200)}{200 + 2} = 7.92$$

2. Effect of variation among families in offspring production

$$N_e = \frac{N-1}{\sqrt{\frac{V_o}{E(0)^2}} + \frac{1}{E(0)}}$$

where $V_o = \text{var in offspring number}$ and $E(0) = \text{mean # offspring}$

From M.J. Wade's paper on course web site

Drift is important when

$$s < \frac{1}{N_e}$$
SHIFTING BALANCE

PHASE I - Genetic drift allows movement around peaks, possibly into valleys.

PHASE II - Demes that cross adaptive valleys can be "drawn" by selection up adjacent peaks.

PHASE III - Interdemic selection - demes at higher fitness peaks export more migrants. Migrants from high fitness demes into low fitness demes can aid the crossing of fitness valleys.