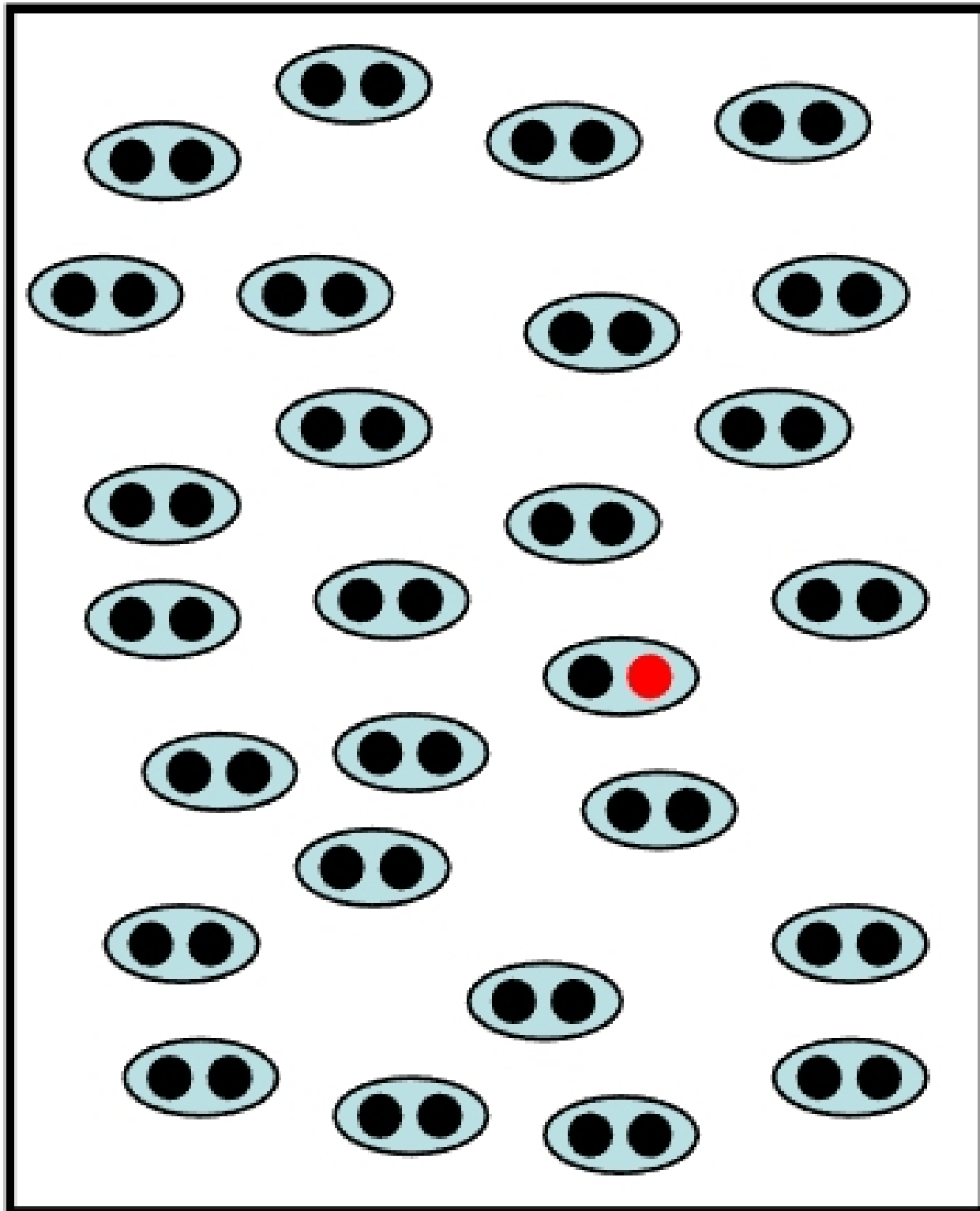


Adaptive fixations

In the beginning ...

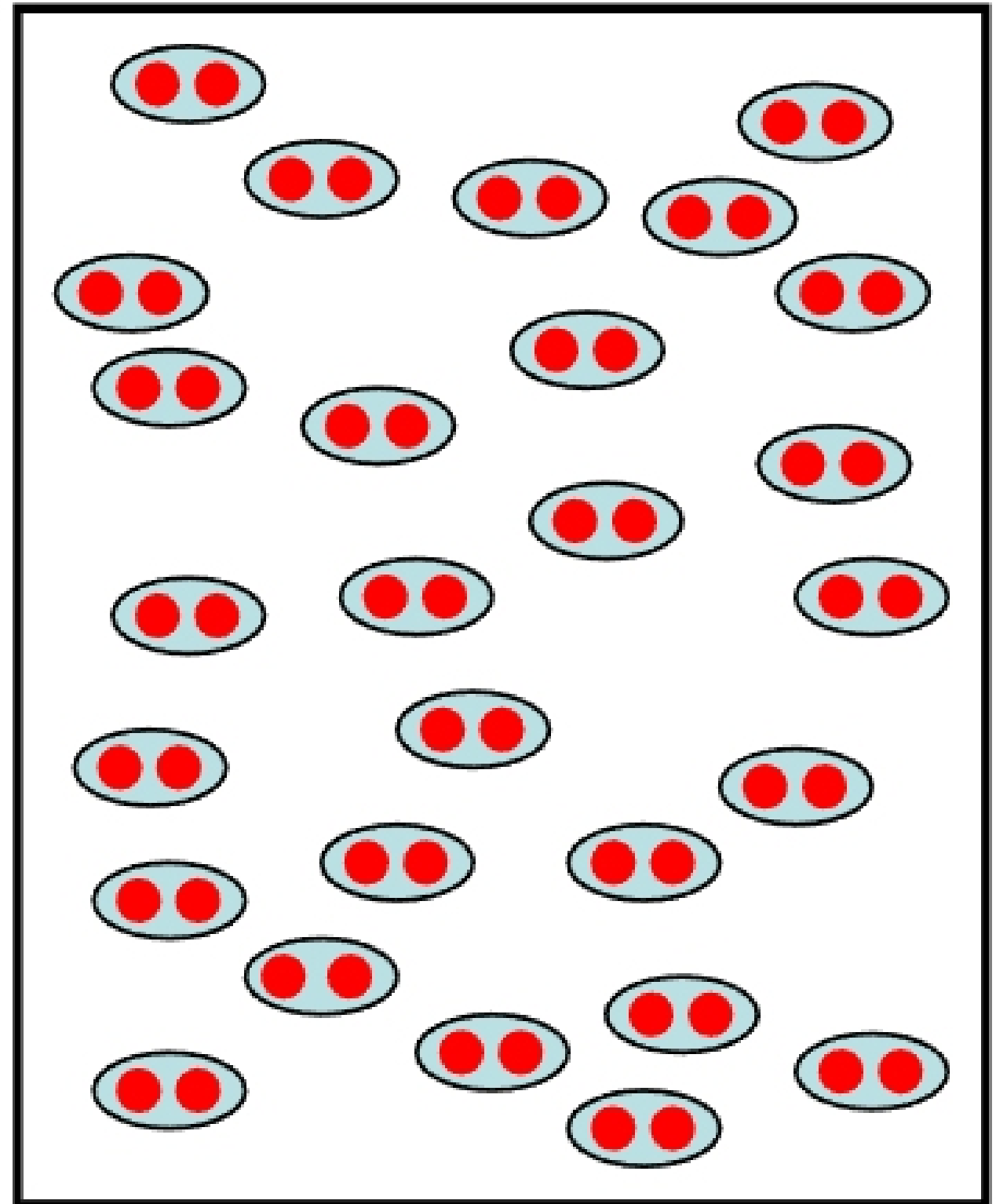
$$p = 1/2N$$



... then after substitution

What's the chance this happens?

If neutral? If beneficial?



How selection biases drift

Intuition suggests that if the random allele frequency change caused by drift is much larger than the directional change caused by selection, then drift might overpower selection and allow deleterious mutations to fix in the population.

In 1962, Motoo Kimura showed that

$$P_{\text{fix}} = (1 - e^{-4Ns q}) / (1 - e^{-4Ns})$$

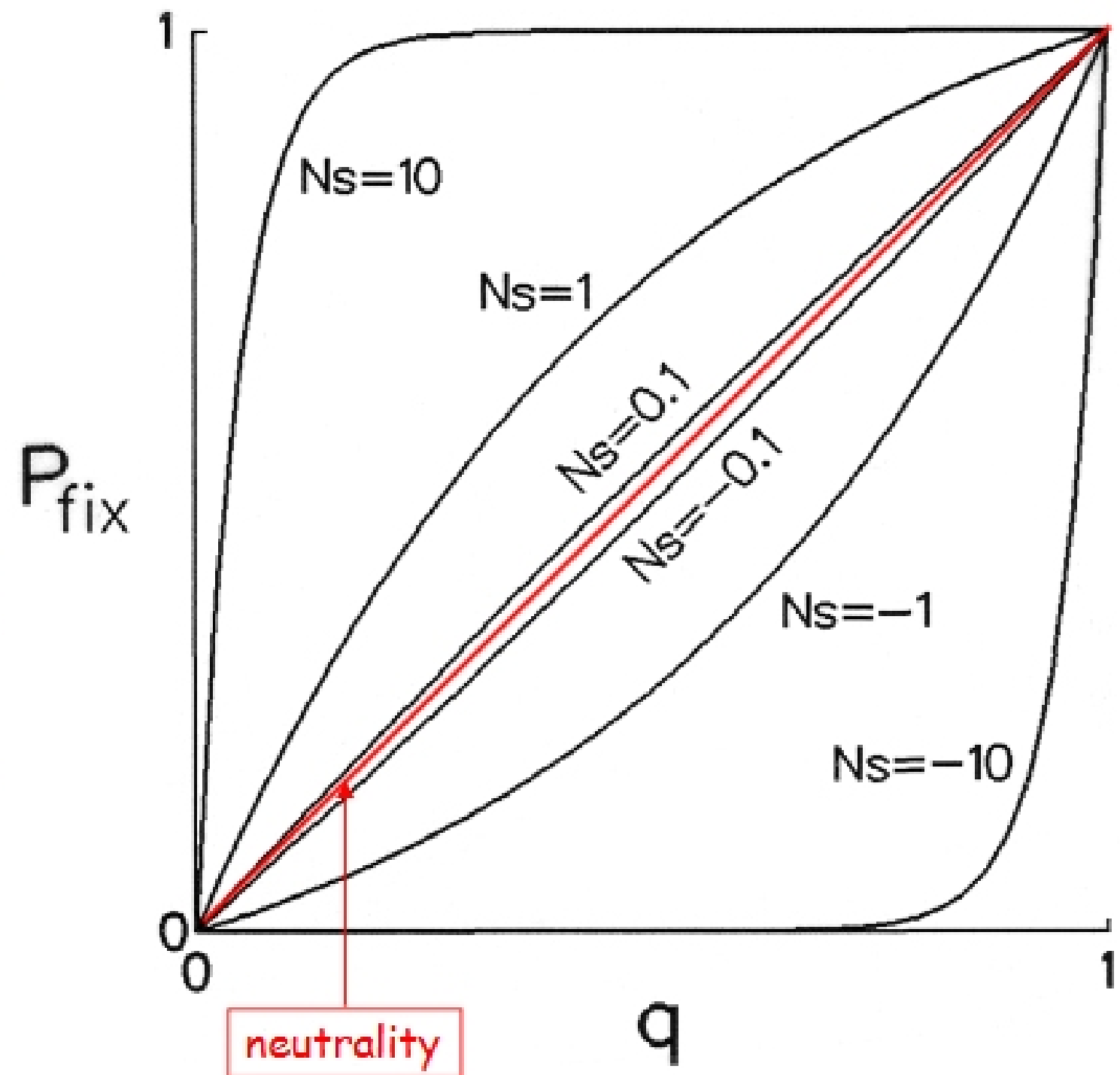
where the fitnesses of the **AA**, **Aa** and **aa** genotypes are 1, $1+s$, and $1+2s$, and q is the current frequency of **a**.

Note that the population size (N) and the selection coefficient (s) always appear as their product, and never separately.

When $s = 0$ (**neutrality**), then the probability that **a** will ultimately fix is simply its present frequency, q .

When $Ns > 1$ in absolute value, then *selection* tends to determine the outcome.

But when $Ns < 1$ the alleles act almost as if they are neutral, *regardless of s* .



Thus *small fitness differences* will determine the evolutionary fates of alleles in *larger populations*, but *larger fitness differences* are required to overcome drift in *smaller populations*.

Movies of drift versus selection (N , s , and the fates of mutations)

Each panel shows 100 allele-frequency histories for a given N , s , and initial frequency q_0 .

Each history runs for 1000 generations or until fixation occurs.

Within each row of three panels, the population sizes are 25, 250, and 2500.

$$W(A_1A_1) = 1, \quad W(A_1A_2) = 1 - \frac{1}{2}s, \quad \text{and} \quad W(A_2A_2) = 1 - s.$$

The first set of cases (below) is a neutral "control" for the experiments in subsequent slides.

$$s = 0, \quad q_0 = \frac{1}{2} \quad (\text{neutral case, pure drift})$$

