Natural Selection

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Selection

Selection is a bias in survival and/or reproduction: when one allele is better than another.

Charles Darwin's big idea. (Also Alfred Russell Wallace.)

The only evolutionary force capable of producing adaption.

Main job: removing harmful mutations.

Can produce rapid change in allele frequencies.

Basic model

A locus with two alleles, A_1 and A_2, with relative frequencies in some generation are p and $q \equiv 1 - p$.

Genotype A_iA_j has "fitness" w_{ij}. Think of this as a probability of survival. Selection also works through fertility, but the algebra is different.

Genotype	A_1A_1	A_1A_2	A_2A_2
Freq. before selection	p^2	$2pq$	q^2
Fitness	w_{11}	w_{12}	w_{22}
Freq. after selection	$p^2 w_{11}/\bar{w}$	$2pqw_{12}/\bar{w}$	$q^2 w_{22}/\bar{w}$

Where $q = 1 - p$

and $\bar{w} = p^2 w_{11} + 2pqw_{12} + q^2 w_{22}$

After one generation of selection:

$$p' = \frac{p^2 w_{11} + pq w_{12}}{\bar{w}}$$

where p' is the allele frequency among offspring.

Rate of change:

$$\begin{aligned}
\Delta p &= p' - p \\
&= \frac{pq}{\bar{w}} \big[p(w_{11} - w_{12}) + q(w_{12} - w_{22}) \big]
\end{aligned}$$

Implications

$$\Delta p = \frac{pq}{\bar{w}}[p(w_{11} - w_{12}) + q(w_{12} - w_{22})]$$

1. Response to selection is slow when either allele is rare, because then pq is small.
2. Response is slow when a recessive allele is rare. In this case, $w_{12} = w_{22}$, and $\Delta p \propto p^2$.
3. Response is slow when a dominant allele is common.
4. A rare allele spreads if its heterozygote is fitter than the common homozygote, because if p is small, $\Delta p \propto w_{12} - w_{22}$.

Implications

$$\Delta p = \frac{pq}{\bar{w}}[p(w_{11} - w_{12}) + q(w_{12} - w_{22})]$$

5. If the heterozygote has intermediate fitness, then one allele will increase to fixation.
6. If the heterozygote has the highest fitness, then A_1 evolves toward an intermediate equilibrium.

Wright's equation

Sewall Wright noticed that the formula for Δp, the quantity in square brackets is half $d\bar{w}/dp$:

$$\Delta p = \frac{pq}{2\bar{w}} \cdot \frac{d\bar{w}}{dp}$$

This implies that selection pushes a population "uphill": in a direction that increases mean fitness.

This is why selection explains adaptation.

Selection plus Mutation

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All that matters is *relative* fitness

The frequency, p', of A_1 among offspring is

$$p' = \frac{p^2 w_{11} + pqw_{12}}{\bar{w}}, \quad \text{where}$$

$$\bar{w} = p^2 w_{11} + 2pqw_{12} + q^2 w_{22} \quad \text{is mean fitness.}$$

If we multiply all fitnesses by some constant, K, nothing changes,

$$p' = \frac{p^2 K w_{11} + pqKw_{12}}{K\bar{w}}$$

because the constant cancels.

Reformulating fitness

Old notation	w_{11}	w_{12}	w_{22}
New notation	1	$1 - hs$	$1 - s$

Here, s is the selective disadvantage of A_2A_2, and h measures dominance. $h = 1/2$ if effects are additive, $h = 1$ if A_2 is recessive, and $h = 0$ if A_2 is dominant.

$$\begin{aligned}\Delta p &= \frac{pq}{\bar{w}}\left[p(w_{11} - w_{12}) + q(w_{12} - w_{22})\right] \\ &= \frac{pqs[ph + q(1-h)]}{\bar{w}}\end{aligned}$$

where

$$\bar{w} = 1 - 2pqhs - q^2 s$$

Mutation and selection

$$\Delta p = \frac{pqs[ph + q(1-h)]}{\bar{w}} \approx qhs$$

if $q \approx 0$, $p \approx 1$, and $\bar{w} \approx 1$.