Chapter 6 – Natural Selection Basics

Natural Selection

Haploid

Diploid, Sexual

Results for a Diallelic Locus

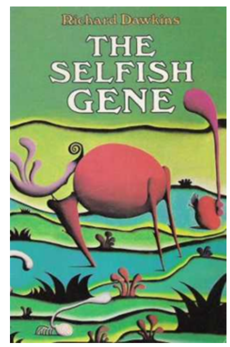
Fisher's Fundamental Theorem

Darwinian Selection

- evolution vs. natural selection?
- evolution
  - "descent with modification"
  - change in allele frequency within a population
    - mutation, drift, selection, gene flow
- natural selection
  - "survival of the fittest" ?
  - differential survival and reproduction (**fecundity**)
- selection is an automatic consequence, not some kind of mysterious, external "force"

Units (or Levels) of Selection

- genes, individuals, populations ?
  - in general, selection is at the level of the individual (phenotype) but it is the population that evolves
  - but see Dawkins, "*The Selfish Gene*"
- phenotypes versus genotypes?



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Although it is common to speak of an *allele* favored by natural selection, any change in allele frequencies is really caused by natural selection on *genotypes* due to their different-viability phenotypes. Alleles themselves do not have phenotypes nor fitness values in most types of natural selection (natural selection on gametes or haploid genomes are exceptions). The changing frequency of genotypes is what causes allele frequencies to change. Although two allele frequencies can be displayed with more economy than three genotype frequencies, it is critical not to forget that natural selection directly causes changes in genotype frequency and that change in allele frequencies is an indirect consequence.

Fitness

- What is fitness?
- fitness of a gene, genotype, individual?
- absolute versus relative fitness
  - the relative fitness of a genotype at a particular locus depends on complex interactions with the "genetic background" and the physical and ecological environment
- ~~selection produces adaptation~~
- adaptation is the automatic consequence of selection

Models of Natural Selection

- how do allele frequencies change over time ?
  - haploid/asexual versus diploid/sexual models
  - discrete generation versus continuous models

Selection in Haploid Organisms

- selection in asexual, haploid organisms depends only on relative population growth
  - competition between strains

Selection in Haploid Organisms

- strain A versus strain B
  - N_A, N_B - number of cells of each strain

$$N_{A(t+1)} = \lambda_A N_{A(t)}$$

$$N_{B(t+1)} = \lambda_B N_{B(t)}$$

  - if $\lambda_A \neq \lambda_B$, then the populations grow at different rates and the relative proportion of cell types changes over time

Selection in Haploid Organisms

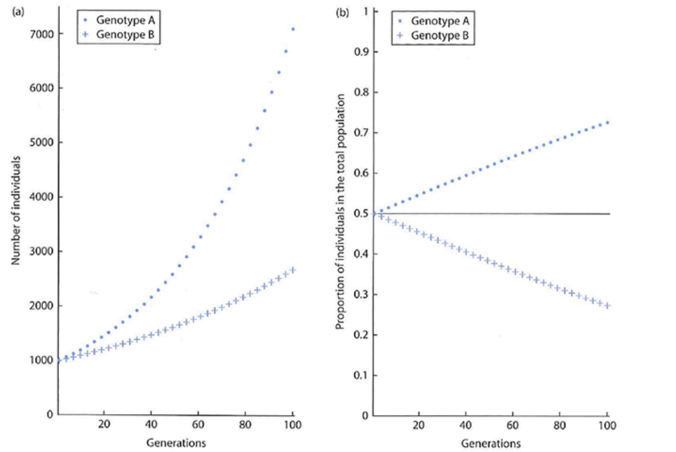

Figure 6.1 Population growth in two genotypes with clonal reproduction, starting out with equal numbers of individuals and therefore equal proportions in the total population. Genotype A grows 3% per generation ($\lambda = 1.03$) and genotype B grows 1% per generation ($\lambda = 1.01$). (a) Individuals of both genotypes increase in number over time. (b) Because the genotypes grow at different rates, their relative proportions in the total population change over time. The solid line shows the initial equal proportions. Eventually, genotype A will approach 100% and genotype B 0% of the total population. Values are plotted for every third generation.

Selection in Haploid Organisms

- ratio of strain B to strain A over time:

$$\frac{N_{B(t)}}{N_{A(t)}} = \left(\frac{\lambda_B}{\lambda_A}\right)^t \frac{N_{B(t=0)}}{N_{A(t=0)}}$$

  - w = relative fitness of strain B to strain A
  - if $\lambda_B > \lambda_A$, then $w > 1$ and relative proportion of strain B cells increases indefinitely, approaching 1.0

Selection in Haploid Organisms

- What are we assuming so far?
  - ratio of growth rates remains the same over time
  - populations continue to grow indefinitely?
  - what happens when the population reaches the carrying capacity of the environment (K) or overshoots K and subsequently crashes?
- most models of selection ignore population size and consider only changes in proportions (allele frequencies)

$$\Delta p = p_{t+1} - p_t = \frac{p_t w_A}{p_t W_A + q_t w_B} - p_t$$

Selection in Diploid Organisms

- selection (differential success) can occur at any stage in the life cycle
  - viability selection
  - sexual selection
  - gametic selection
    - incl. meiotic drive, segregation distortion
  - fecundity selection
- selection on (the success of) a particular genotype may vary through the life cycle
  - in fact, it's likely – tradeoffs are pervasive!

Selection in Diploid Organisms

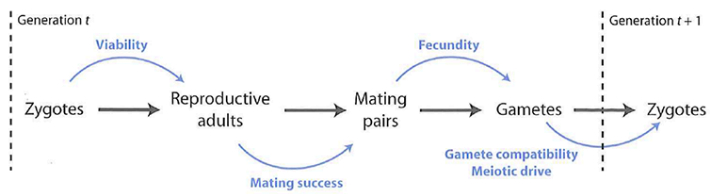

Figure 6.3 A diagram of the life cycle of organisms showing some points where differential survival and reproduction among genotypes can result in natural selection. Viability is the probability of survival from zygote to adult, mating success encompasses those traits influencing the chances of mating and the number of mates, and fecundity is the number of gametes and progeny zygotes produced by each mating pair. Gametic compatibility is the probability that gametes can successfully fuse to form a zygote whereas meiotic drive is any mechanism that causes bias in the frequency of alleles found in gametes. Most models of natural selection assume a single fitness component such as viability. In reality, all of these components of fitness can influence genotype frequencies simultaneously.

Model of Viability Selection

- start with basic HW assumptions
- add differences in viability for different genotypes
  - assume survival probabilities (viability selection) for different genotypes remain constant over time

Model of Viability Selection

- absolute fitness (survival probability) versus relative fitness (in comparison to reference genotype)

Ospreys

$$AA:0.75,\ Aa:0.75,\ aa:0.50$$

$$AA:1.0,\ Aa:1.0,\ aa:0.67$$

vs. Oysters

$$AA:0.00075,\ Aa:0.00075,\ aa:0.00050$$

$$AA:1.0,\ Aa:1.0,\ aa:0.67$$

Model of Viability Selection

- absolute fitness (survival probability) versus relative fitness (in comparison to reference genotype)
- outcome of selection depends on **relative fitness**
- survival probabilities likely to change with population size and environmental conditions, but it may be reasonable to assume that relative fitness remains ~constant

Table 6.2 Assumptions of the basic natural selection model with a diallelic locus.

- Genetic
  - Diploid individuals
  - One locus with two alleles
  - Obligate sexual reproduction
- Reproduction
  - Generations do not overlap
  - Mating is random
- Natural selection
  - Mechanism of natural selection is genotype-specific differences in survivorship (fitness) that lead to variable genotype-specific growth rates, termed viability selection
  - Fitness values are constants that do not vary with time, over space, or in the two sexes
- Population
  - Infinite population size so there is no genetic drift
  - No population structure
  - No gene flow
  - No mutation

Change in Allele Frequency w/ Viability Selection

- population size and composition at time = 0

$$p^2 N_1 + 2pqN_1 + q^2 N_1$$

- number of each genotype after selection given survival probabilities ℓ

$$\ell_{AA} p^2 N_1 + \ell_{Aa} 2pqN_1 + \ell_{aa} q^2 N_1$$

- new frequency of A allele in gametes

$$\frac{\ell_{AA} p^2 N_1 + \frac{1}{2}\left(\ell_{Aa} 2pqN_1\right)}{\ell_{AA} p^2 N_1 + \ell_{Aa} 2pqN_1 + \ell_{aa} q^2 N_1}$$

Change in Allele Frequency w/ Viability Selection

- new frequency of A allele in gametes

$$\frac{\ell_{AA}p^2N_1 + \frac{1}{2}\left(\ell_{Aa}2pqN_1\right)}{\ell_{AA}p^2N_1 + \ell_{Aa}2pqN_1 + \ell_{aa}q^2N_1}$$

$$\downarrow$$

$$\frac{\ell_{AA}p^2 + \ell_{Aa}pq}{\ell_{AA}p^2 + \ell_{Aa}2pq + \ell_{aa}q^2}$$

Change in Allele Frequency w/ Viability Selection

- replacing absolute fitness (ℓ) with relative fitness (w)…

$$p_{t+1} = p' = \frac{w_{Aa}pq + w_{AA}p^2}{w_{AA}p^2 + w_{Aa}2pq + w_{aa}q^2}$$

$$q_{t+1} = q' = \frac{w_{Aa}pq + w_{aa}q^2}{w_{AA}p^2 + w_{Aa}2pq + w_{aa}q^2} = \frac{w_{Aa}pq + w_{aa}q^2}{\overline{w}}$$

$$\Delta p = \frac{pq\left[q\left(w_{aa} - w_{Aa}\right) - p\left(w_{AA} - w_{Aa}\right)\right]}{\overline{w}}$$

General scenarios for 2 alleles

Table 6.4 The general categories of relative fitness values for viability selection at a diallelic locus. The variables *s* and *t* are used to represent the decrease in viability of a genotype compared to the maximum fitness of 1 ($1 - w_{xx} = s$). The degree of dominance of the A allele is represented by *h* with additive gene action (sometime called codominance) when $h = {}^1/_2$.

Category	Genotype-specific fitness		
	w_{AA}	w_{Aa}	w_{aa}
Selection against a recessive phenotype	1	1	$1 - s$
Selection against a dominant phenotype	$1 - s$	$1 - s$	1
General dominance (dominance coefficient $0 \leq h \leq 1$)	1	$1 - hs$	$1 - s$
Heterozygote disadvantage (underdominance for fitness)	1	$1 - s$	1
Heterozygote advantage (overdominance for fitness)	$1 - s$	1	$1 - t$