**Evolutionary quantitative genetics and one-locus population genetics**

- Most evolutionary problems involve questions about phenotypic means
- **Goal**: determine how selection causes *evolutionary* change in the mean of a quantitative character.
- **Aside**: Quantitative vs. Qualitative Traits

- Back to our main story...election on a trait such as body size
  
  - body size of individual is denoted $z$
  
  - mean body size in a population: $\bar{z}$
  
  - Suppose selection alters allele frequencies at loci that affect $z$
  
  - Consider the effect on body size of one specific locus, $i$

  - In general, to determine how much $\bar{z}$ changes, one needs to determine:
    1) how selection changes $p_i$ at all loci affecting $\bar{z}$
    2) how changes in $p_i$ combine to change $\bar{z}$.

  ![Graph](image)

  - We'll focus on the effects of one of the loci that affects $\bar{z}$

  - The phenotype of an individual depends on:
    1) its genotype at locus $i$
    2) its genotype at other loci that affect the trait
    3) its environmental experience

  - lump 2 & 3 into a single factor, $c$

  - Can think of an individual's phenotype as $z = a_{jk} + c$

  VI-1
The average phenotype can similarly be broken down into the average contribution of locus \( i \) and the average over other loci and environmental effects: \( \bar{z} = \bar{a} + \bar{c} \)

Consider the effect of a change in \( p^{(i)} \) on \( \bar{z} \) (holding all other loci constant)

\[
\Delta \bar{z}^{(i)} = \bar{z}(p^{(i)} + \Delta p^{(i)}) - \bar{z}(p^{(i)})
\]

\[
\approx \frac{\partial \bar{z}}{\partial p^{(i)}} \Delta p^{(i)}
\]

\[(\text{drop } i)\]

\[
\approx \frac{\partial \bar{z}}{\partial p} \left[ \frac{1}{2} p(1-p) \frac{d \ln w}{d \bar{z}} \right] \quad (\text{term in brackets is just our old friend})
\]

\[
\approx \frac{\partial \bar{z}}{\partial p} \left[ \frac{1}{2} p(1-p) \frac{\partial \bar{z}}{\partial \bar{z}} \frac{d \ln w}{d \bar{z}} \right] \quad (\text{using the "chain rule"})
\]

or \( \Delta \bar{z}^{(i)} = \frac{1}{2} pq \left( \frac{\partial \bar{z}}{\partial p} \right)^2 \frac{d \ln w}{d \bar{z}} \) (form emphasizes the dependency of fitness \( w \) on phenotype \( z \))

What is \( \frac{\partial \bar{z}}{\partial p} ? \)

\[
\frac{\partial \bar{z}}{\partial p} = \frac{d}{dp} (\bar{a} + \bar{c})
\]

\[
= \frac{d}{dp} \left( p^2 a_{11} + 2pq a_{12} + q^2 a_{22} + \bar{c} \right) \quad (\text{assuming H-W})
\]

\[
= 2pa_{11} + 2qa_{12} - 2pa_{12} - 2qa_{22} + 0
\]
– So, putting all the pieces together:

\[
\Delta z_i^{(i)} = \frac{1}{2} \times pq \times 4 \left( p a_{11} + q a_{12} - p a_{12} - q a_{22} \right)^2 \frac{d \ln w}{d \zeta}
\]

or

\[
\Delta z_i^{(i)} \approx G_i^{(i)} \beta
\]

where \( G_i^{(i)} = 2 pq \left[ (p a_{11} + q a_{12}) - (p a_{12} + q a_{22}) \right]^2 \) and \( \beta = \frac{d \ln w}{d \zeta} \).

– What is \( \beta \)?

• Called the selection gradient
• It is a measure of the strength of selection acting on a trait:

– What is \( G^{(i)} \)?

• It is an extremely important quantity called the additive genetic variance contributed by locus \( i \)

• Why "additive"?

– Dominance Variance

• Consider the total amount of variation in \( z \) due to variation at locus \( i \):

\[
\text{var}(z^{(i)}) = \text{var}(a_{jk} + c) = \text{var}(a_{jk}) \text{ since we have fixed } c.
\]

– So, \( \text{var}(z^{(i)}) = \text{var}(a_{jk}) = E(a_{jk}^2) - [E(a_{jk})]^2 \)

(assuming H-W equilibrium) \( = (p^2 a_{11}^2 + 2 pq a_{12}^2 + q^2 a_{22}^2) - (p^2 a_{11} + 2 pq a_{12} + q^2 a_{22})^2 \)

(after a lot of tedious algebra) \( = G^{(i)} + \left\{ 2 pq \left[ a_{12} - \frac{a_{11} + a_{22}}{2} \right] \right\}^2 \)

\( = G^{(i)} + D^{(i)} \)

where \( D^{(i)} = \left\{ 2 pq \left[ a_{12} - \frac{a_{11} + a_{22}}{2} \right] \right\}^2 \).
• What is $D^{(i)}$?
  – It’s called the **dominance variance** contributed by locus $i$.
    
    • Note: $D^{(i)}$ is never negative and has units of $z^2$
    
    – Why "dominance"?
    
    – Relationship between $G^{(i)}$ and $D^{(i)}$
    
    • Case 1: **No Dominance**
    
    • Case 2: **Symmetric Overdominance**
    
    – What about other loci that contribute to the traits?
    
    • Generally difficult (recall complications of 2-locus population genetics) to understand;
    
    • Assuming linkage equilibrium for all loci contributing to a trait:
      
      $$
      \Delta \bar{z} = \Delta \bar{z}^{(1)} + \Delta \bar{z}^{(2)} + \Delta \bar{z}^{(3)} + \ldots
      = \left[ G^{(1)} + G^{(2)} + G^{(3)} + \ldots \right] \beta
      = \left[ \sum_{i=1}^{n} G^{(i)} \right] \beta \text{ or (recall that } \beta \text{ reflects how a change in mean phenotype changes mean population fitness: it doesn't care what the cause of the change in phenotype is.)}
      $$
      
      $$\Delta \bar{z} = G\beta$$
    
    – This is the central equation of quantitative genetics
    
    – Note its similarity to the equation for selection at one locus.
    
    – Note that it’s written in several other ways
    
    • Important Message: It’s not the total phenotypic variance nor even the total *genotypic* variance that determines how fast a population mean evolve in response to selection
    
    – Total genotypic variance = $G + D$ (where $D = D^{(1)} + D^{(2)} + \ldots = \sum_{i=1}^{n} D^{(i)}$)
    
    • In general, there’s between-locus genetic "interaction" variance as well.
– Total phenotypic variance = $G + D + E$ (also written $V_P = V_A + V_D + V_E$)

  • $E$ is the variance that's due to environmental effects.

  • A few quibbles with “heritability”