Evolutionary quantitative genetics and one-locus population genetics

READING: Nielsen & Slatkin pp. 215–230

• Most "interesting" evolutionary problems involve questions about phenotypic means

• <u>Goal</u>: determine how selection causes *evolutionary* change in the mean of a quantitative character.

• <u>Aside</u>: Quantitative vs. Qualitative Traits

• Back to our main story.... selection on a trait such as body size

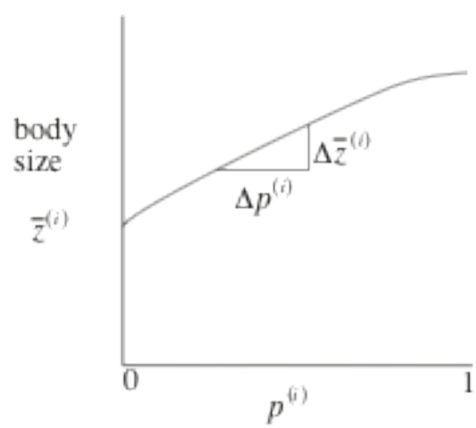
– body size of individual is denoted z

– 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 $\bar{z}$.

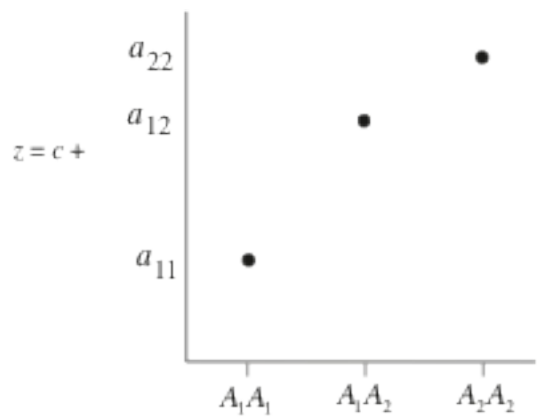


– We'll focus on the effects of one of the loci that affects $\bar{z}$

• 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 $z = a_{jk} + c$



• 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):

$$\Delta\bar{z}^{(i)} = \bar{z}\left(p^{(i)} + \Delta p^{(i)}\right) - \bar{z}\left(p^{(i)}\right) \approx \frac{d\bar{z}}{dp}\Delta p^{(i)}$$

(*drop i*) $= \frac{d\bar{z}}{dp}\left[\frac{1}{2}p(1-p)\frac{d\ln\bar{w}}{dp}\right]$

(*term in brackets is just our old friend the adaptive topography*)

(*using the chain rule)* $= \frac{d\bar{z}}{dp}\left[\frac{1}{2}p(1-p)\frac{d\ln\bar{w}}{d\bar{z}}\frac{d\bar{z}}{dp}\right]$

- Summarizing: $\Delta\bar{z}^{(i)} \approx \frac{1}{2}\left(\frac{d\bar{z}}{dp}\right)^2 p(1-p)\frac{d\ln\bar{w}}{d\bar{z}}$

(*This form emphasizes how mean fitness depends on mean phenotype*)

• What is $\frac{d\bar{z}}{dp}$?

$$\frac{d\bar{z}}{dp} = \frac{d}{dp}(\bar{a} + \bar{c}) = \frac{d}{dp}(p^2a_{11} + 2pqa_{12} + q^2a_{22} + \bar{c})$$
$$= 2pa_{11} + 2qa_{12} - 2pa_{12} + 2qa_{22} + 0$$
$$= 2(pa_{11} + qa_{12} - pa_{12} + qa_{22})$$

Putting these pieces together:

$$\Delta\bar{z}^{(i)} = \frac{1}{2}\times pq\times 4(pa_{11} + qa_{12} - pa_{12} + qa_{22})^2$$

or

$$\Delta\bar{z}^{(i)} = G^{(i)}\beta$$

where

$$G^{(i)} = 2pq[(pa_{11} + qa_{12}) - (pa_{12} + qa_{22})]^2$$

and

$$\beta = \frac{d \ln \overline{w}}{d\bar{z}}$$

- What is β ?

  - called the **selection gradient**
  - measures the strength of "directional" selection acting on a trait *z*

- What is $G^{(i)}$?

  - It is a centrally important quantity called the **additive genetic variance** contributed by locus *i*

  - Why "additive"?

- Dominance Variance

  - Consider total variation in *z* due to variation at locus *i*:

    var($z^{(i)}$) = var(a_{jk} + c) = var(a_{ji}) since assume *c* is fixed.

    So, var($z^{(i)}$) = var(a_{ji}) = $E\left(a_{jk}^2\right) - \left[E\left(a_{jk}\right)\right]^2$

    (*assuming HW equilibrium*)
    $= (p^2a_{11}^2 + 2pqa_{12}^2 + q^2a_{22}^2) - (p^2a_{11} + 2pqa_{12} + q^2a_{22})^2 =$

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

    where $\left\{D^{(i)} = 2pq\left[a_{12} - \frac{a_{11}+a_{22}}{2}\right]\right\}^2$

  - $D^{(i)}$ is called the **dominance variance** contributed by locus *i*

  - Why "dominance"?

- Relationship between additive and dominance Variance

- Case 1: no dominance
- Case 2: symmetric over-dominance

• What about other loci that contribute to variation in the trait?

- Generally difficult (recall complications of 2-locus population genetics) to understand

- Assuming linkage equilibrium among all loci contributing to variation in the trait:

$$\Delta\bar{z} = \Delta\bar{z}^{(1)} + \Delta\bar{z}^{(2)} + \cdots + \Delta\bar{z}^{(k)} = \left[G^{(1)} + G^{(2)} + \cdots + G^{(k)}\right]\beta = \left[\sum_{i=1}^{k} G^{(i)}\right]\beta$$

If we define $G = \sum_{i=1}^{k} G^{(i)}$, then

$$\boxed{\Delta\bar{z} = G\beta}$$

- This is a version of the **breeder’s equation**, which is *the* central equation of quantitative genetics

- Note its similarity to the equation of selection at one locus

- A more traditional form of the breeder’s equation is $R = h^2 S$
  - $R = \Delta\bar{z}$ is the “response to selection”

  - S = the “selection differential” = difference between the means of the breeders and the population

  - h^2 is the “heritability” = G/P where P is the total (“phenotypic”) variability in z due to all genetic and environmental causes

  - This implies that $S = P\beta$

  - $P = G + D + E$ where $D = \sum_{i=1}^{k} D^{(i)}$ to the total “dominance variance” and E is the variation due to “environmental” effects (including genetic interactions besides dominance, such as epistatis)

  - Important: only G determines the response to selection since additive effects are the only “predictable” components of genetic variation.

    - Note that additive, dominance variances change as allele frequencies change.