#### **Quantitative Genetics - Review**

- many independent additive loci normal distribution
- selection acts on the standing genetic variance
  - small changes in allelic frequencies
  - constant variance (but changing linkage!)

$$z = x + e$$

phenotypic additive environment value genetic etc. value  $\overline{e} = 0$ x and e are independent and normally distributed

• mean phenotype of the offspring: 
$$\frac{x_{mother} + x_{father}}{2}$$

• mean phenotype in the next generation = = mean x of parents after selection =  $\overline{x}_s$ 



$$\Delta \overline{z} = \overline{x}_s - \overline{z} = \overline{x}_s - \overline{x} = h^2 [\overline{z}_s - \overline{z}]$$
$$h^2 = \frac{COV(x,z)}{V(z)} = \frac{V(x)}{V(z)}$$

# **Frequency dependent selection:** $W(z,\overline{z})$

$$\Delta \overline{z} = h^2 (\overline{z}_s - \overline{z})$$
  

$$\overline{z}_s = \int z p_s(z) dz,$$
  

$$p_s(z) dz = \frac{W(z, \overline{z}) p(z) dz}{\int W(z', \overline{z}) p(z') dz'}$$

$$\Delta \overline{z} = \frac{V(x)}{V(z)} \left[ \frac{\int z W(z, \overline{z}) p(z) dz}{\overline{W}} - \overline{z} \right] = \frac{V(x)}{V(z)} \frac{\int (z - \overline{z}) W(z, \overline{z}) p(z) dz}{\overline{W}}$$

• Taylor-expansion:

$$W(z,\overline{z}) = W(\overline{z},\overline{z}) + \frac{\partial W}{\partial z}(z-\overline{z}) + \frac{1}{2}\frac{\partial^2 W}{\partial z^2}(z-\overline{z})^2 + \frac{1}{6}\frac{\partial^3 W}{\partial z^3}(z-\overline{z})^3 + \dots$$
$$\Delta \overline{z} = \frac{V(x)}{V(z)}\frac{1}{\overline{W}} \left[ 0 + \frac{\partial W}{\partial z}V(z) + 0 + \frac{1}{6}\left(3V^2(z)\right)\frac{\partial^3 W}{\partial z^3} + \dots \right]$$

• Assume small 
$$V(z)$$
:  $\Delta \overline{z} = \frac{V(x)}{\overline{W}} \frac{\partial W(z,\overline{z})}{\partial z}\Big|_{z=\overline{z}}$ 

**Quantitative Genetics (with separate species):** 

$$\Delta \overline{z}_i = V_{Ai} \frac{\partial W(z; \overline{z}_1, \dots, \overline{z}_n)}{\partial z} \bigg|_{z=\overline{z}_i}$$

**Canonical Equation of Mutation-Limited Evolution:** 

$$\frac{dx_i}{dt} = \frac{1}{2} \mu_i \sigma_i^2 \hat{N}_i(x_1, \dots, x_n) \frac{\partial s_{x_1, \dots, x_n}(y)}{\partial y} \bigg|_{y=x_i}$$

#### **Disruptive Selection on a Multilocus Trait under Random Mating**



Figure 1: a) Evolutionary branching in the individual-based as exual model: at the branching point  $x_0 = 0$ , the population splits into two morphs. Three insets show fitness functions (continuous curves) generated by the ecological interactions at different points in time (indicated by horizontal dotted lines). Selection changes from directional to disruptive when evolution reaches  $x_0$ . The resource distribution K(x) has its maximum at  $x_0$  and is shown for comparison (dashed curve).

b) Same as a) but with multilocus genetics for the ecological character and random mating. Shading represents phenotype distributions (5 diploid and diallelic loci result in 11 possible phenotypes). Despite disruptive selection at the branching point (see insets), branching does not occur.

Dieckmann & Doebeli (1999)

### **Reproductive Isolation - Speciation**

- Sexual selection: two reproductively isolated species Ecological trait diverges under disruptive selection
- Mating is assortative by the ecological trait (e.g. size)
- Assortativeness by a neutral marker trait must be in linkage disequilibrium with the ecological trait strong selection required to overcome recombination
- Spatially subdivided populations: isolation by habitat choice

#### How to deal with multilocus genetics?

- *n* loci (often haploid with recombination), two alleles
- Iterate genotype frequencies: 2<sup>n</sup> genotypes!
- Hypergeometric model: phenotype frequencies can be iterated (*n*+1) assumes free recombination equal effects in all loci (phenotype = # of "+" alleles) equal allele frequencies across loci within each phenotype linkage equilibrium within each phenotype
- Quasi-linkage equilibrium: allele frequencies can be iterated assumes weak selection

## I. Mate choice based on the ecological trait



Dieckmann & Doebeli (1999)



#### II. Mate choice based on a neutral marker trait

Dieckmann & Doebeli (1999)