MULTI-LOCUS SELECTION & GENETIC HITCHHIKING

• Selection on two haploid loci

Genotype	AB	Ab	aB	Ab
Frequency	P_{AB}	P_{Ab}	P_{aB}	P_{ab}
Fitness	w_{AB}	w_{Ab}	w_{aB}	w_{ab}

– Recall…
- $p_A = P_{AB} + P_{Ab}, q_A = P_{aB} + P_{ab}, p_B = P_{AB} + P_{aB}, q_B = P_{Ab} + P_{ab}$
- $D = P_{AB}P_{ab} - P_{Ab}P_{aB}$
- $P_{AB} = p_A p_B + D, P_{Ab} = p_A q_B - D, P_{aB} = q_A p_B - D, P_{ab} = q_A q_B + D$

– After selection, $P_{ij}^* = P_{ij}\frac{w_{ij}}{\bar{w}}$ where $\bar{w} = P_{AB}w_{AB} + P_{Ab}w_{Ab} + P_{aB}w_{aB} + P_{ab}w_{ab}$

– After meiosis (recombination rate r) and random mating:

$P'_{AA} = P^*_{AA} - rD^*$

$P'_{Ab} = P^*_{Ab} + rD^*$

$P'_{aB} = P^*_{aB} + rD^*$

$P'_{ab} = P^*_{ab} - rD^*$

where $D^* = P^*_{AB}P^*_{ab} - P^*_{Ab}P^*_{aB}$

- These can be used to track evolution of haploid genotypes, allele frequencies, and the disequilibrium

  – For example, $p'_B = P'_{AB} + P'_{aB}$, $D' = P'_{AB}P'_{ab} - P'_{Ab}P'_{aB}$, etc.

• Genetic Hitchhiking

– Suppose that locus A only is subject to selection with selection coefficient s: $w_{AB} = w_{Ab} = 1, w_{aB} = w_{ab} = 1 - s$.

- Mean fitness is $\bar{w} = P_{AB} + P_{Ab} + P_{aB}(1-s) + P_{ab}(1-s) = 1 - sq_A$

– Locus B is neutral, but will it evolve?
- $\Delta p_B = p'_B - p_B = \left(P'_{AB} + P'_{aB}\right) - \left(P_{AB} + P_{aB}\right)$
- Note that $P'_{AB} + P'_{aB} = \left(P^*_{AB} - rD^*\right) + \left(P^*_{aB} + rD^*\right) = P^*_{AB} + P^*_{aB}$ so that $\Delta p_B = \left(P^*_{AB} - P_{AB}\right) + \left(P^*_{aB} - P_{aB}\right)$
- $P^*_{AB} - P_{AB} = \bar{w}^{-1}\left(P_{AB} - P_{AB}\bar{w}\right) = \bar{w}^{-1}P_{AB}\left[1 - \left(1 - sq_A\right)\right] = \bar{w}^{-1}sq_A P_{AB} = \bar{w}^{-1}sq_A\left(p_A p_B + D\right)$

- $P^{*}_{aB} - P_{aB} = \bar{w}^{-1}\left[P_{aB}\left(1-s\right) - P_{aB}\left(1-sq_A\right)\right] = -\bar{w}^{-1}P_{aB}s\left(1-q_A\right) = -\bar{w}^{-1}sp_AP_{aB} = -\bar{w}^{-1}sp_A\left(q_Ap_B - D\right)$
- Putting these together:

$$\Delta p_B = \bar{w}^{-1}s\left[\left(q_Ap_Ap_B + q_AD\right) - \left(p_Aq_Ap_B - p_AD\right)\right] = \bar{w}^{-1}sD\ .$$

– Already know $\Delta p_A = p_Aq_As/\bar{w}$ so can also write $\Delta p_B = D\Delta p_A/\left(p_Aq_A\right)$

– Punch Line: allele frequencies at neutral locus B will evolve in response to selection on locus A if $D \neq 0$

- Process dubbed "genetic hitchhiking" by J. Maynard Smith

– Selective sweep at one locus can affect levels of genetic variation at linked neutral marker loci

- J. Gillespie's term: "genetic draft"

– Selective sweeps happen more readily in large than in small populations—because genetic drift is weaker in large than small populations—so genetic draft should be more important in large than small populations.