

In this unit, we'll look at the evolutionary consequences of violating the remaining 3 assumptions of H-W: no migration, infinite population size, and random mating

Notes for this chapter:

1. Go over the review questions at the end of the chapter. Develop one or more hypotheses for the pattern in question 2.
2. Read the introductory material on the Greater Prairie Chicken on your own.
3. Skip the sections on the rate of evolution by drift; empirical research on inbreeding in malaria parasites; and the general analysis of inbreeding.

Topic outline:

I. Migration

- A. Migration as an evolutionary force*
- B. Case study I: water snakes of Lake Erie*
- C. Case study II: red bladder campion*
- D. Summary*

II. Genetic drift

- A. Drift = a random change in allele frequency due to small population size*
- B. Drift leads to the founder effect in natural populations*
- C. The effects of drift are magnified when compounded over many generations*
- D. Case studies*
- E. Summary*

III. Non-random mating

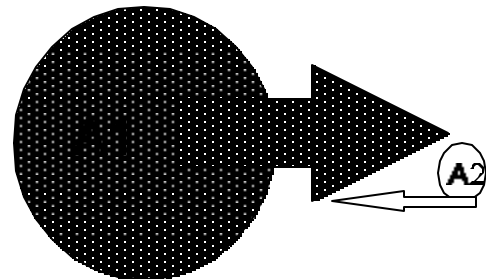
- A. Non-random mating takes several forms*
- B. Non-random mating may result in inbreeding*
- C. Inbreeding depression is one evolutionary consequence of inbreeding*
- D. Summary*

IV. Putting it all together: Greater Prairie Chickens, revisited

I. Migration

A. Migration as an evolutionary force

1. In evolutionary biology, **migration** = the movement of alleles = **gene flow**
2. We'll use only the simplest case to examine migration: the one-island model (fig. 6.4)
 - a. imagine two populations:
 - i. one large mainland population and one small island population
 - ii. each population has a different allele for a locus (e.g., mainland = A1; island = A2)
 - b. because mainland population is so large relative to island, migration from mainland to island will swamp migration from island to mainland – gene flow will be effectively unidirectional, from mainland to island
 - c. process of migration will clearly change allele frequencies on island: A1 will increase and A2 will decrease
 - d. over time, result will be that allele frequencies on island become same as those on mainland



B. Case study I: water snakes of Lake Erie – selection and migration can “oppose” each other, resulting in a different pattern than if either acted alone

1. Background:

- a. snakes = *Nerodia sipedon*; live on both mainland around Lake Erie and on the islands in the lake (fig. 6.6).
- b. Snakes vary in appearance from strongly banded to unbanded (fig. 6.6)
- c. Color pattern roughly consequence of a single locus with 2 alleles – banded is dominant over unbanded

2. The pattern
 - a. Almost all mainland snakes are banded
 - b. on islands, most snakes are unbanded or intermediate (fig 6.7)
 - c. migration from mainland to islands relatively frequent; little or none from islands to mainland
 - d. so would expect to get a higher frequency of banded island snakes than actually found – why?
 3. Selection seems to be “opposing” migration:
 - a. on islands, snakes bask on limestone shelves
 - b. young, unbanded snakes are more cryptic on limestone shelves than are young, banded snakes
 - c. unbanded snakes have higher survival on islands than do banded snakes
 - d. result = polymorphism among populations maintained by
 - i. migration bringing banded alleles onto islands
 - ii. selection “weeding them out”
- C. Case study II: The effect of migration homogenizes red bladder campion populations
1. Giles and Goudet studied plants on islands in a Swedish archipelago
 - a. islands vary in age
 - b. plants are early colonizers (early successional species)
 - c. when populations established, migration (gene flow) among islands is common
 - d. eventually, plants are outcompeted by late successional species
 2. Predicted that effects of migration on gene flow would be most apparent in populations of intermediate age:
 - a. young populations would be genetically variable because of founder effects (more on this shortly)
 - b. over time, migration would homogenize populations

- c. as succession proceeded, older populations would represent ~ random collections of few individuals, so expected higher levels of variation in older populations
3. tested by analyzing genotypes at six loci; results matched predictions (fig. 6.9): variation was highest in youngest and oldest populations, and lowest in populations of intermediate age

D. Summary:

1. main effect of migration = homogenizing allele frequencies among populations, preventing genetic divergence among populations
2. migration can also help maintain variation within populations if it is balanced by selection

II. Genetic drift

A. Drift = a random change in allele frequency due to small population size

1. Thought experiment:
 - a. start with a small population
 - i. $p = A1 = .60$
 - ii. $q = A2 = .40$
 - b. Assume all assumptions of H-W are met EXCEPT the assumption of infinitely large population size – what will happen with allele frequencies in the next generation if we limit population size to 10 individuals?
 - c. Can't use the "standard" process of using Punnett square with allele frequencies included
 - i. that process is actually a way of determining what the average result will be given extremely large populations
 - ii. because we don't have extremely large populations, we need to simulate by performing "random draws" of alleles based on their frequency (like pulling marbles out of a bag)
 - iii. use computer to generate outcomes

- d. Result = instead of a single outcome, get a range of outcomes with different probabilities (fig. 6.11):
 - i. most frequent outcome = allele frequencies stay the same – but frequency of this outcome is only 18%!
 - ii. all other outcomes give us allele frequencies that are different from those of parental generation
 - e. i.e., all other outcomes give us an evolutionary change over time
2. Statistical principles behind thought experiment:
 - a. Any time we have a random process, we expect to get slight differences between actual results and those predicted based on probability
 - i. i.e., coin tosses should result in 50% heads; 50% tails,
 - ii. but we aren't surprised if, out of 4 tosses, we got 3 heads and 1 tail
 - b. Those random differences between expected and predicted results = sampling error
 - c. Sampling error increases when the number of trials decreases – i.e., we'd be much more surprised if, out of 1000 tosses, we got 750 heads and 250 tails
 3. Genetic drift = deviation of a population from Hardy-Weinberg expectations due to sampling error
 - a. because it results in a change in allele frequency over time, it results in evolutionary change
 - b. because the change in allele frequency is due strictly to random chance (not due to any particular feature of the genotype or phenotype), drift does not result in adaptive change
 - i. remember that adaptive change is due to selection
 - ii. and selection is based on non-random survival and reproduction
 - c. because drift is a result of sampling error, its effects will be stronger in small populations than in large populations (and effects should increase as

population size decreases)

B. Drift leads to the founder effect in natural populations

1. The founder effect occurs when a new population (on, e.g., a newly-formed island) is founded by a small, random subset of some source population
 - a. because few individuals are founders, they are unlikely to have the same number and frequency of alleles as found in source population – so the population they found will differ from source population, even when no differences in selection pressure exist
 - b. because founders represent random subset of source population, and because subsequent differences are due to chance alone, the differences between new and source populations are due to drift
2. Examples of founder effect (read details on your own – pp. 167-8):
 - a. Relatively high frequency of Ellis-van Creveld syndrome (rare form of dwarfism) among Amish in eastern Pennsylvania
 - b. differences between populations of large ground finches on Daphne Major vs. other islands in Galápagos

C. The effects of drift are magnified when compounded over many generations

1. The effects of drift over time are easiest to demonstrate using computer simulations – fig. 6.13
 - a. one gene with two alleles, A1 and A2 (as usual)
 - b. 3 population sizes: 4, 40, 400
 - c. for each size, 8 populations allowed to mate at random with no migration or selection for 100 generations
 - d. for each population, graphs show
 - i. frequency of A1
 - ii. frequency of heterozygotes (= average heterozygosity)
2. Results show five important patterns:
 - a. because fluctuations in allele frequency are caused by (random) sampling

error, every population follows unique evolutionary trajectory

- b. in every population, tendency is for one of the two alleles to become fixed (or to move toward fixation – i.e., to be the only allele present)
 - i. note that which allele is fixed should be a function of starting frequency
 - ii. so if frequency of each allele = 50%, then $\frac{1}{2}$ of populations should tend toward fixation of A1 and $\frac{1}{2}$ toward fixation of A2
 - c. in every population, trend toward fixation of one allele is accompanied by a decrease in average heterozygosity (= increase in homozygosity)
 - d. over time, drift can produce significant evolutionary change even in relatively large populations
 - e. the effects noted in a-c, though, are much more dramatic in small than in large populations
3. Note that these findings have major conservation implications!!
- D. Case studies (read details on your own – pp. 172-177)
1. Experimental study of drift in fruit flies
 - a. Buri (1956) established 107 populations, each starting with 16 flies (8 male, 8 female) heterozygous for one body color allele
 - b. every generation selected 8 adults of each sex at random to breed for next generation
 - c. continued for 19 generations
 - d. predictions: over time, should see
 - i. fixation of one of the two body color alleles in each population, with each fixed in $\sim \frac{1}{2}$ of populations
 - ii. decrease in heterozygosity in all populations
 - e. results conformed to predictions (fig. 6.14, 6.15)
 2. Drift in Ozark collared lizards
 - a. Collared lizards are desert species that were established in Ozarks during extended dry, hot period $\sim 8,000 - 4,000$ years ago

- b. because of subsequent environmental change and own habitat requirements, populations are currently limited to scattered, small "island" remnants of desert habitats = glades
- c. Tempelton et al. predicted that, because populations on glades are small, should show evidence of drift
 - i. screened lizards for genotypes at several loci
 - ii. predicted pattern of
 - a) single genotype within populations (because drift fixes one allele at each locus)
 - b) variation in genotypes among populations (because which allele is fixed is random)
 - iii. results conformed to predictions: fig. 6.16

E. Summary

1. Drift = non-adaptive mechanism of evolution
2. Results from sampling error leading to changes in allele frequencies over time
3. major consequence = loss of genetic variability within populations due to
 - a. fixation of alleles
 - b. loss of heterozygosity
4. effects increase with decreasing population size

III. Non-random mating

A. Non-random mating takes several forms

1. types of non-random mating include (but aren't limited to)
 - a. mating based on distance – e.g., mating with nearest neighbor
 - b. mating based on phenotype – e.g.'s include
 - i. positive assortative mating = mate with partner of phenotype most similar to own
 - ii. negative assortative mating = mating with partner of phenotype most different from own

- iii. mating based on phenotype frequency
 - iv. mate choice based on size, ornamentation, etc. (sexual selection)
 - c. selfing (including parthenogenesis, etc., in animals)
2. Non-random mating is almost certainly the rule rather than the exception!
- B. Several forms of non-random mating may result in **inbreeding** = mating with near relatives
- 1. inbreeding doesn't change allele frequencies, so technically doesn't lead to evolutionary change
 - 2. inbreeding does change genotype frequencies, with potentially important evolutionary consequences
 - a. specifically, it increases homozygosity (and decreases heterozygosity) =
 - i. increases the number of loci at which the average individual is homozygous
 - ii. increases the proportion of individuals homozygous for an individual locus in the population
 - b. increase in homozygosity is one of the most important consequences of inbreeding . . .
- C. Inbreeding depression is one evolutionary consequence of inbreeding
- 1. An increase in homozygosity means an increase in the chances that an individual will be homozygous for deleterious recessive alleles
 - 2. This results in **inbreeding depression** = decrease in average fitness of individuals in a population
 - 3. Inbreeding depression has been documented widely in numerous plants and animals – e.g.:
 - a. in humans, infant mortality is ~ 4% greater among children of first cousins than among children of unrelated parents (fig. 6.22)
 - b. in great tits, inbreeding increases egg failure rate (fig. 6.24)
 - 4. Experimental studies of inbreeding depression in angiosperms (good model

systems) reveal three broad patterns that may be generally applicable to a wide variety of organisms:

- a. the effects of inbreeding are often most severe when plants are under some kind of environmental stress – e.g.
 - i. grown outdoors vs. greenhouses
 - ii. grown in competition with other plants
 - iii. subject to insect pests
- b. effects of inbreeding often show up in later stages of the lifecycle – presumably because maternal influence (e.g., energy reserves provided to seeds) has diminished
- c. the degree of inbreeding depression varies among plant families – some show large negative effects, some show little effect, some actually show enhanced performance

D. Summary

1. Forms of non-random mating that result in inbreeding don't alter allele frequencies, so they're not mechanisms of evolutionary change
2. Because inbreeding does alter genotype frequencies, it can have major evolutionary consequences, such as inbreeding depression

IV. Putting it all together: Greater Prairie Chickens, revisited

- A. Why is Illinois greater prairie chicken in decline, even though reserves have been established and populations protected? Westemeier et al. have proposed multi-part hypothesis:
 1. destruction of prairie reduced population size
 2. destruction of habitat also fragmented populations – by 1980's, populations consisted of few individuals “stranded” on small “islands” of prairie embedded in “seas” of farmland
 3. fragmentation of populations reduced migration/gene flow among populations, leading to genetic drift

4. drift led to inbreeding depression
 - a. as population size drops, inbreeding inevitable, leading to an increase in the number of individuals homozygous for deleterious recessive alleles
 - b. as population size declines, deleterious mutations are more likely to become fixed due to drift
5. from here, populations enter positive feedback loop (“mutational meltdown”; “extinction vortex”):
 - a. as inbreeding depression increases, population size drops
 - b. as population size drops, effect of drift increases – more deleterious mutations become fixed
 - c. as more deleterious mutations become fixed, inbreeding depression increases
 - d. etc.

B. Tested hypothesis:

1. Used data from long-term study of Jasper population to document inbreeding depression (fig. 6.25): found steady decline in hatching success beginning in 1970's
2. Looked for “genetic signature” of drift:
 - a. two patterns predicted:
 - i. less genetic variability in Jasper population than in larger populations elsewhere
 - ii. decline in genetic variability in Jasper population over time
 - b. both were found:
 - i. Illinois birds have much less genetic variability than birds in other areas
 - ii. comparison with DNA from museum specimens from 1930's and 1960's showed significant decline in genetic variability over time (note importance of museum specimens!!!!)
3. Used hypothesis to develop conservation strategy – specifically, increase gene

flow by “transplanting” individuals from other areas to Illinois populations

- a. hatching rate has increased from 40% to 90%
 - b. seems to be working!
- C. Note that this is a classic conservation scenario – it applies to far more than just this species.