Genetic Drift

Among the nonselective mechanisms of evolution, there is one that is absolutely random. That mechanism is genetic drift. Genetic drift does not lead to adaptation, but it does lead to changes in allele frequencies. In the Hardy-Weinberg model, genetic drift results from violation of the assumption of infinite population size.

1. **A Model of Genetic Drift**
    a. To see how genetic drift works, imagine an ideal population similar to the ones we have worked with before, but finite – in fact, small in size. As usual, we will focus on a single locus with two alleles, A_1 and A_2. Imagine that in the present generation's gene pool, allele A_1 is at frequency 0.6 and allele A_2 is at frequency 0.4. We will let the gametes in this gene pool combine at random to make exactly 10 zygotes. These 10 zygotes will constitute the entire population for the next generation.
    b. We can simulate the production of ten zygotes from our gene pool with a physical model. A bag containing 100 beads represents the gene pool. Sixty of the beads are blue, representing allele A_1; forty of the beads are white, representing allele A_2. We make each zygote by shaking the bag, closing your eyes, and drawing out beads. First, we draw a bead to represent the egg, note its genotype, and return it to the bag. Then we draw a bead to represent the sperm, note its genotype, and return it to the bag. We are drawing beads from a bag as we write. The genotypes of the 10 zygotes are:

    A_2A_1 A_1A_1 A_1A_1 A_1A_1 A_2A_2
    A_1A_1 A_2A_2 A_1A_2 A_1A_1 A_1A_1

    Counting the genotypes, we have A_1A_1 at a frequency of 0.6, A_1A_2 at a frequency of 0.2, and A_2A_2 at a frequency of 0.2. Counting the alleles, we see that when these zygotes grow up and reproduce, the frequency of allele A_1 in the new gene pool will be 0.7 and the frequency of allele A_2 will be 0.3.
    c. We have completed one turn of the life cycle of our model population. Nothing much seems to have happened, but note that both conclusions of the Hardy-Weinberg equilibrium principle have been violated. The allele frequencies have changed from one generation to the next, and we cannot calculate the genotype frequencies by multiplying the allele frequencies. The reason our population has failed to conform to the Hardy-Weinberg principle is simply that the population is small. In a small population, chance events produce outcomes that differ from theoretical expectations. The chance events in our simulated population were the draws of beads from the bag to make zygotes. We picked blue beads and white beads not in their exact predicted ratio of 0.6 and 0.4, but in a ratio that just happened to be a bit richer in blue beads and a bit poorer in white beads. This kind of random discrepancy between theoretical expectations and actual results is called sampling error. Sampling error in the production of zygotes from a gene pool is genetic drift. Because it is nothing more than cumulative effect of random events, genetic drift cannot produce adaptation. But it can, as we have seen, cause allele frequencies to change. Blind luck is, by itself, a mechanism of evolution.
    d. Sometimes it is difficult to see the difference between genetic drift and natural selection. In our model small population, copies of allele A_1 were more successful at getting into the next generation than copies of allele A_2. Differential reproductive

success is selection, is it not? In this case, it is not. If it had been selection, the differential success of alleles in our model population would have been explicable in terms of the phenotype the alleles confer on the individuals that carry them. Individuals with one or two copies of A_1 might have been better at surviving, finding food, or attracting mates. However, individuals carrying copies of allele A_1 were none of these things. They were just lucky; their alleles happened to get drawn from the gene pool more often. Selection is differential reproductive success that happens for a reason. Genetic drift is differential reproductive success that just happens!

e. Another way to see that genetic drift is different from selection is to recognize that the genotype and allele frequencies among our 10 zygotes could easily have been different from what they turned out to be. To illustrate this, we can repeat the exercise drawing beads from our bag to make 10 zygotes. This time, the genotypes of the zygotes are:

A_1A_1 A_1A_1 A_1A_1 A_2A_1 A_1A_2

A_2A_2 A_1A_2 A_1A_1 A_2A_1 A_2A_2

Among this set of zygotes the genotype frequencies are 0.4 for A_1A_1, 0.4 for A_1A_2, and 0.2 for A_2A_2. The allele frequencies are 0.6 for A_1 and 0.4 for A_2. Repeating the exercise a third time produces these zygotes:

A_1A_1 A_1A_1 A_1A_1 A_1A_2 A_1A_1

A_1A_2 A_2A_1 A_2A_2 A_2A_2 A_2A_2

Now the genotype frequencies are 0.4 for A_1A_1, 0.3 for A_1A_2, and 0.3 for A_2A_2, and the allele frequencies are 0.55 for A_1 and 0.45 for A_2.

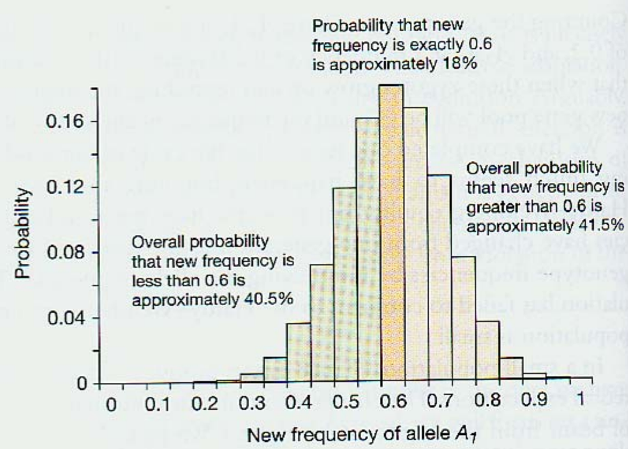

Figure 6.11 The range of possible outcomes in our model population of ten mice This graph shows the possible outcomes, and the probability of each, when we make 10 zygotes by drawing alleles from a gene pool in which alleles A_1 and A_2 have frequencies of 0.6 and 0.4. The single most probable outcome is that the allele frequencies will remain unchanged. However, the chance of this happening is only about 18%.

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2. Genetic Drift and Population Size

a. Genetic drift is fundamentally the result of finite population size. If we draw beads from our bag to make a population of more than 10 zygotes, the allele frequencies among the zygotes will get closer to the values predicted by the Hardy-Weinberg equilibrium principle. Drawing beads out of a bag quickly becomes tedious, so we used a computer to simulate drawing gametes to make not just 10, but 250 zygotes. As the computer draws each gamete, it gave a running report of the frequency of A_1 among the zygotes it had made so far. At first, this running allele frequency fluctuated widely. As the cumulative number of zygotes made increased, the frequency of the allele A_1 in the new generation bounced around less and less, gradually settling toward the expected value of 0.6. This simple computer simulation demonstrates that sampling error diminishes as sample size increases. If we kept drawing gametes forever to make an infinitely large population of zygotes, the frequency of allele A_1 among the zygotes would be exactly 0.6. Genetic drift is a powerful evolutionary mechanism in small populations, but its power declines in larger populations!

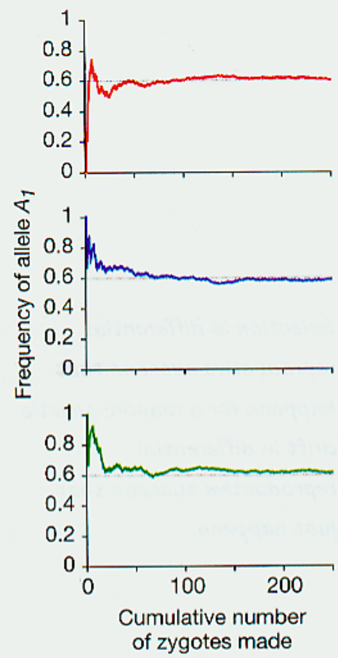

Figure 6.12 A simulation of drawing alleles from a gene pool, run three times At first the new frequency of allele A_1 fluctuates considerably, in a unique trajectory for each run. As the number of zygotes made increases, however, the new frequency of A_1 settles toward the expected value of 0.6.

3. The Founder Effect

a. If we want to observe genetic drift in nature, the best place to look is in small populations. Populations are often small when the have just been founded by a group pf individuals that have moved, or been moved, to a new location. The allele frequencies in the new population are likely, simply by chance, to be different than they are in the source population. This is called the founder effect. The founder effect is a direct result of sampling error. For example, if 25 different alleles are present at a single locus in a continental population of insects, but just 10 individuals are on a log that rafts to a remote island, the probability is aero that the new island will contain all of the alleles present on the continent. If, by chance, any of the founding individuals are homozygous, allele frequencies in the new population will have shifted even more dramatically. In any founder event, some degree of random genetic differentiation is almost certain between old and new populations. In other words, the founding of a new population by a small group of individuals typically represents not only the establishment of a new population but also the instantaneous evolution of differences between the new population and the old population.

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4. Random Fixation of Alleles and the Loss of Heterozygosity

a. We have seen that genetic drift can produce substantial change in the allele frequencies in a single generation. Drift is even more powerful as a mechanism of evolution when its effects are compounded over many generations. We can investigate the cumulative effects of genetic drift with the same physical model we used before: blue and white beads in a bag!

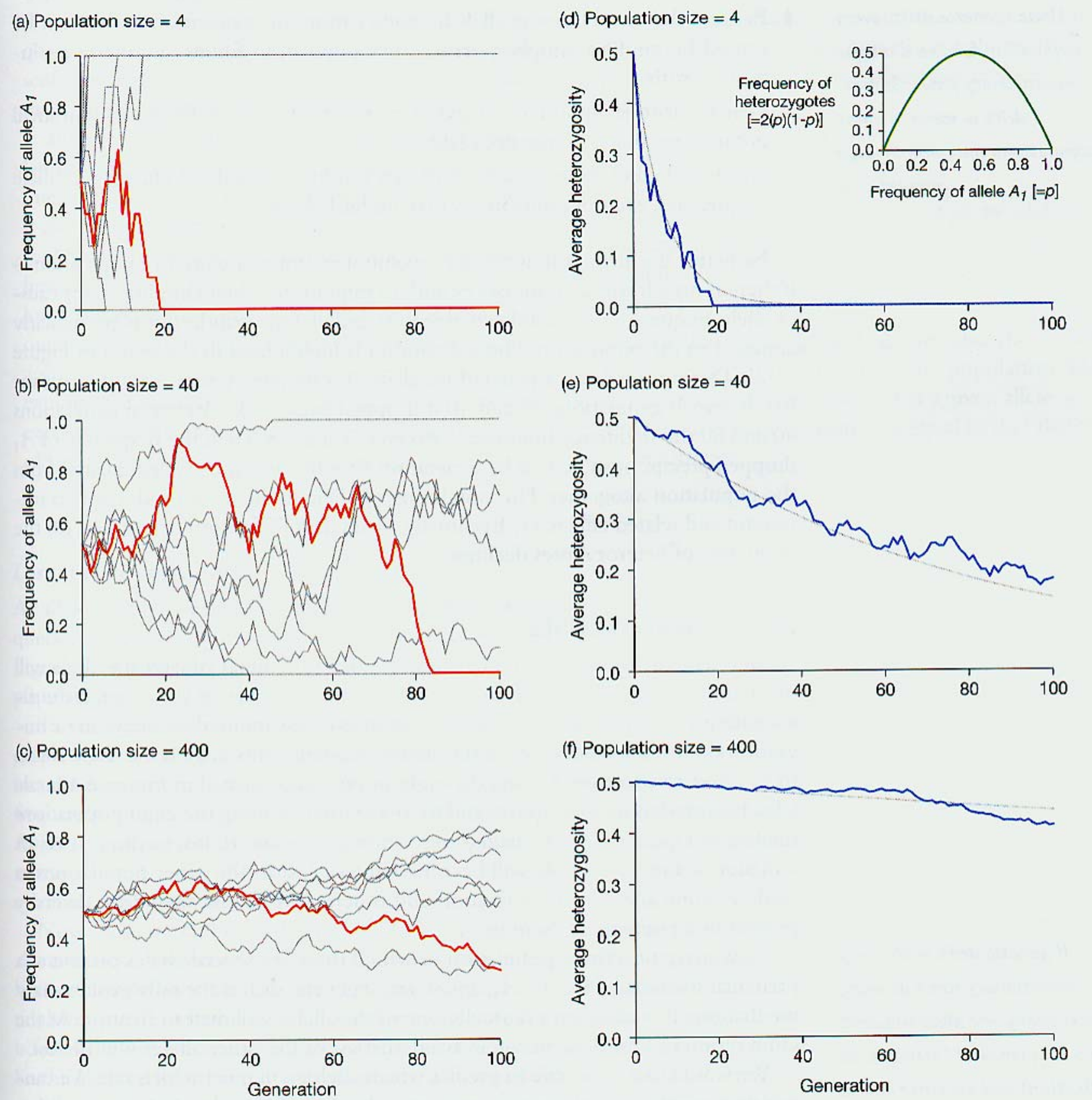

Figure 6.13 Simulations of genetic drift in populations of different sizes Plots (a), (b), and (c) show the frequency of allele A_1 over 100 generations. Eight populations are tracked in each plot, with one population highlighted in red. Plots (d), (e), and (f) show the average frequency of heterozygotes over 100 generations in the same sets of simulated populations. The gray curves represent the rate of decline predicted by theory. The inset in plot (d) shows the frequency of heterozygotes in a population, calculated as $2(p)(1 - p)$, as a function of p, the frequency of allele A_1. Collectively, the graphs in this figure show that genetic drift leads to random fixation of alleles and loss of heterozygosity, and that drift is a more powerful force of evolution in small populations.