

Chapter 10

Population Genetics and Random Evolution

10.1 Introduction

The following three chapters on the theory of evolution are based upon the prevailing neo-Darwinist interpretation of the theory. In short, genes are the principle determiners of traits, they are the main bringers of innovation, and they are the agents of inheritance of traits from one generation to the next. I need to point out that evolution theory itself continues to evolve. As a result, the basic neo-Darwinist model probably cannot explain all of the possibilities of evolution. I will address these issues more fully in chapter 12. Although the theory is becoming more sophisticated, there is no reason to reject neo-Darwinism altogether. It continues to represent a cohesive core of a maturing theory.

Having stated this caveat, I will focus on the core of modern evolution theory, neo-Darwinism. This form of the theory combines knowledge from ecology and genetics (and other fields too) to help explain the phenomenon of evolution. So, I will try to bring together the lessons from chapter ? (environmental stress) and chapter ? (innovation) to describe how evolutionary change happens. But first, what is evolution?

10.2 Evolution is how we describe the changes that happen to a species from one generation to the next

When a species undergoes a genetic change from one generation to the next, we call that genetic change an evolutionary result. The type of changes I am talking about can be big or small. Big evolutionary changes could include the development of a new adaptation, or the emergence of a new species. Small evolutionary changes mostly involve changing the frequencies of certain genetic alleles in the species.

The current chapter and the next emphasize the genetic perspective in the exposé of evolution theory. As we saw in chapter ??, genes code for the construction, operation and maintenance of an individual. And copies of genes can be passed on to offspring. A species can have several kinds of genes for each trait (different alleles). Evolution can be a simple

and random re-shuffling of the alleles. But evolution is more interesting when alleles are re-shuffled non-randomly, as we will see in the next chapter. Which leads me to reproduction and innovation.

The reproduction event is a crucial part of evolution because this is where innovations are admitted into the story. It is before and during reproduction that genetic innovations can arise such as by meiosis or with a new mutation. And it is after reproduction that innovations get their chance at the world. According to the theory, the huge diversity of life and the adaptations they possess are the result of the accumulation of small innovations over many generations. Genes can be re-shuffled and re-shuffled over and over. But the really interesting part of evolution is when new genes enter into the population and change it in helpful ways — the emergence of adaptations.

The ultimate goal of this chapter and the next is to understand how evolutionary change can lead to adaptations. But there is much more to evolution than just adaptations. As we will see below, evolution can take many forms that can lead in many different directions. Evolution is an inevitable consequence of robust biological properties and dynamic environmental circumstances. There are random circumstances and there are non-random circumstances. There are statistical realities and there are useful innovations. There are short-term consequences and there are long-term consequences. In fact, evolution is so big that it is impossible to grasp its full power in the space of a few chapters. So, I have tried to focus on those parts of the theory of evolution that will help us understand planetary biology — namely how evolution produces adaptations that assist in the colonization of the planet.

Be prepared to deal with a long story rich in detail. Much of what you will learn in these two chapters is about the mechanics of evolution. But please try to remember why we are studying evolution. The modern theory of evolution is the best explanation so far on how living things were able to colonize the planet.

They did it by developing special adaptations. Without special adaptations, it is unlikely that life could have come to inhabit all of the Earth's diverse environments.

The first purpose of this chapter is to present how the science of population genetics is very useful in helping to understand evolution. As we will see, the science of evolution largely is a blend of environmental circumstance (ecological circumstances) and genetics. The second purpose of this chapter is to discuss how random evolutionary results can occur. Then, in the next chapter we will focus on those environmental circumstances that specifically lead to adaptations — namely, non-random evolution, or evolution by selection.

10.3 Adaptations are one of the consequences of evolution

Before we immerse ourselves in evolution theory, let's quickly address what an adaptation is in the first place. An adaptation generally is defined as any evolutionarily-developed trait, that helps its bearer succeed in its particular environment. As we will see in the next chapter, adaptations are a consequence of evolution by selection. The type of environment powerfully influences the type of adaptations possible. Artificial environments yield artificial adaptations, natural environments give natural adaptations and sexual environments produce sexual adaptations. In terms of the dispersal of life on Earth, I am particularly interested in the development of *natural* adaptations that help different species survive in different kinds of natural environments. For example, the ability to store water is a natural adaptation that helps the barrel cactus survive dry, hot desert summers. The thick fur of the polar bear is a natural adaptation that helps it conserve heat on cold winter days (and cold summer days, for that matter).

10.4 An adaptation is a consequence of many generations of microevolution

Biologists can consider the products of evolutionary change on two basic levels: 1) macroevolution; and 2) microevolution. Macroevolution (macro means 'big') consists of large-scale changes that happen to a species. An adaptation generally represents a BIG change to the species — an example of *macroevolution*. How do adaptations develop? If evolution is a legitimate phenomenon, why don't we witness large-scale evolutionary change happening right now in our everyday world? Well, we will probably never directly observe the kind of big change that leads to a new species or a new organ like an eye. The thinking is

that if evolutionary change appears in small increments from generation-to-generation — then big changes would take many generations (an extension of biological uniformitarianism).

Neo-Darwinist evolution theory argues that in most cases adaptations don't suddenly appear fully refined. Instead, they are more likely the result of gradual accumulations of tiny innovations over many, many generations. Many small changes eventually add up to a big change. If this is correct, we should be able to witness small changes in a species. And we can. These small changes are examples of *microevolution* in action. So, although we cannot directly detect *macroevolutionary* change, we can observe evidence of small *microevolutionary* changes in a species. Constrained by these circumstances, evolutionary biologists must study macroevolution by indirect means. First, they study what causes microevolutionary results. Then, they apply this knowledge to help explain how big changes like adaptations could result following many generations of microevolution.

The point is that in order to fully understand how adaptations can arise, we need to see how small changes can happen to a species. Which means we must spend some time learning about microevolution. Evolutionary biologists study microevolution by investigating the changes in the genetic makeup of living populations. They use a science called population genetics.

10.5 Microevolution is studied by using a science called population genetics

I have described microevolution as the small changes in the genetic makeup of a species. Genetic change usually is tracked *quantitatively*, as the mathematical frequencies (proportions) of different alleles change. Biologists study these quantitative genetic changes using a science called population genetics.

Population genetics is a type of genetic science that tries to understand populations in terms of the statistical distribution of alleles. Remember that the word 'species' refers to a *kind* of living thing. The word 'population' refers to a group of interbreeding individuals of the same species that live in a given place, like a canyon or a whole mountain range. Members of a species may exist in different geographical pockets, each pocket being a separate population. So, individual populations can experience different degrees of separation. They can be completely isolated, as in the case of mountaintops or islands. They can be seasonally separated by snow-blocked or drought-blocked trails. Or populations can be hardly separated at all, existing loosely in different locations along a genetic gradient. Evolutionary biologists use

Panel 10.1

The term, “adapt”, has several confusing meanings in biology

People understandably get confused by unclear use of the word — ‘ADAPT’. This word is the verb form of ‘adaptation’, and biologists use it in two very different ways.

One meaning relates to evolution and changes in the nature of a trait. This called ‘evolutionary adaptation’. An evolutionary adaptation consists of the **information / instructions** for the installation, operation and maintenance of a body system or component. The hardware and software.

The other meaning of the word, adapt, refers to the physiological changes experienced by an **individual** during its lifetime. Physiology refers to the **operation** of the body. A ‘physiological adaptation’ is an instantaneous, moment-by-moment operational adjustment of the individual’s body. The operations.

It is easy to get these meanings mixed up. If you do, you will certainly misunderstand the theory of evolution. So I will try to clarify the difference. It is better not to think of the word ‘adaptation’ alone. Instead, think of it as two different terms: 1) physiological adaptation; and 2) evolutionary adaptation.

Physiological adaptation is when an individual undergoes an internal adjustment to its environment

Physiological adaptation is the kind of internal operational adjustment that an individual experiences on a moment-by-moment basis, usually in response to changing internal and external environmental conditions. For example, when you walk out of an air-conditioned office into a hot summer day, your body is faced with a stressful new environment — high heat. In **response**, your body physiologically adapts by producing more sweat. This will act to cool your body and prevent it from overheating. As the day gets cooler, your sweat production decreases.

In order to produce more sweat, your body does not undergo any kind of genetic change. For instance, if you move across country to a hot climate and perspire a lot for a few years, then bear a child, your child will not have an enhanced supply of sweat glands. But the ability to execute physiological changes like these is made possible by the suite of genes an individual is born with.

The **ability** to adapt physiologically is just another genetically-controlled trait in a suite of traits that individuals possess. If a given physiological trait helps the individual survive to reproduce, then the genes that produced the physiological trait will be passed-on to the next generation.

Let’s think about the snowshoe hare as an example (fig. 7?). The hare’s fur is brown in summer and changes to white in winter. The actual operation of changing fur color from brown to white is a **physiological** adaptation. However, this **ability** to change fur color is inherited, in the form of genes, from the individual hare’s parents. What is transferred from one generation to the next is the **genetic ability** (the software to build the fur color system) to engage physiological adaptations. Therefore, the improved **ability** to physiologically adapt is an example of an evolutionary adaptation. Think about it for a while.

Physiological adaptations:

- Are responses to the environment
- Do not involve any kind of genetic change
- Are not inheritable

Evolutionary Adaptation is when a species or population changes genetically over many generations

This is the kind of change that happens as a result of evolution by selection. It takes place over many generations. Evolutionary adaptation happens not to the individual (as does physiological adaptation), but to the species. It is a change in the genetic makeup of the species as a whole. The rate of change may be slow, as many

generations of survivors steadily define the genetic course of the species. Unlike physiological adaptation, evolutionary adaptation is not really a ‘response’ to changes in the environment. Instead, if the environment gradually changes, some individuals will survive to reproduce, others will not. The alleles that enabled survival will be passed on to following generations. If the same kind of environmental stress persists, the surviving alleles could become widespread in the species.

Evolutionary adaptations:

- Are NOT responses to the environment
- Are the result of genetic changes
- Are inheritable

Panel 10.1B The term, “species”, means a particular kind of living thing

The term “species” refers to a particular kind of organism. A species can be represented by living individuals (the species is extant) or the species may have no more living representatives (the species is extinct). The living representatives of a species can and do reproduce to make fertile offspring. For example, the house cats that roam your backyard are all living representatives of the species, **Felis catus**. The species, **Canus familiaris** describes the living dogs taunted by their catty neighbors. So, a species is a body of information that describes a type of living thing. Although the information itself is not alive, it can provide instructions for the development, operation and maintenance of a particular kind of living thing.

The environment can be populated with living representatives of a species for millions of years, even though individuals may have short life spans. The many generations of individuals maintain the legacy of the species. The species avoids extinction because of the constant introduction of new individuals following the process of reproduction.

Evolution is the result of genetic change that happens to a species from one generation-to-the-next.

An extant species is represented by living individuals

'Individual' is a self-defining term, but it is important to clearly and constantly make the distinction between the term, 'individual' and the term, 'species', when thinking about evolution. Evolution focuses on the overall change in the species over many generations of individuals. That is, change in the information content that

describes the type. The living individual has a role to play in contributing to evolutionary change. It turns out that the individual is the **agent** of change. We could simply think of each individual as a genetic experiment. At 'birth', each individual brings to the species a completely new and different combination of genetic traits to be 'tried-out' in the given environment.

It is very important to remember that evolution is not about changing the individual. The individual has no power to re-program its genetic code to better suit its environment. The individual contributes

to the change of its species only by surviving to reproduce and otherwise contributing to population dynamics such as through migration. That is the extent of the individual's role in evolution. The individual is the bearer of genes. The genes program the individual to survive. Those individuals who survive long enough to reproduce pass elements of their genetic programming to their offspring who try to do the same thing

Panel 10.2

An individual is made up of many traits

Individual organisms possess a suite of characteristics that help them to survive and reproduce. In the sciences of genetics and evolution, these characteristics are called 'traits' and they include the following types:

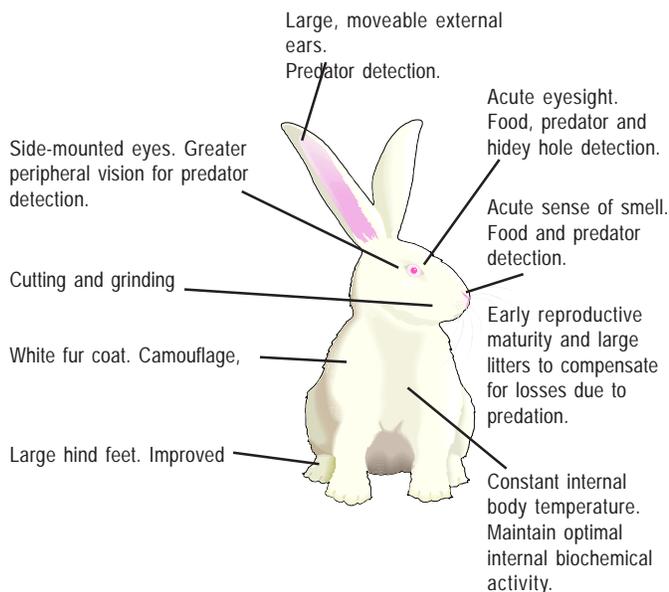
Physical: For example: general anatomy, sensory apparatus, size, thickness of fur, coloration, number of legs.

Behavioral: For example: feeding behaviors, predator avoidance behaviors, mating rituals

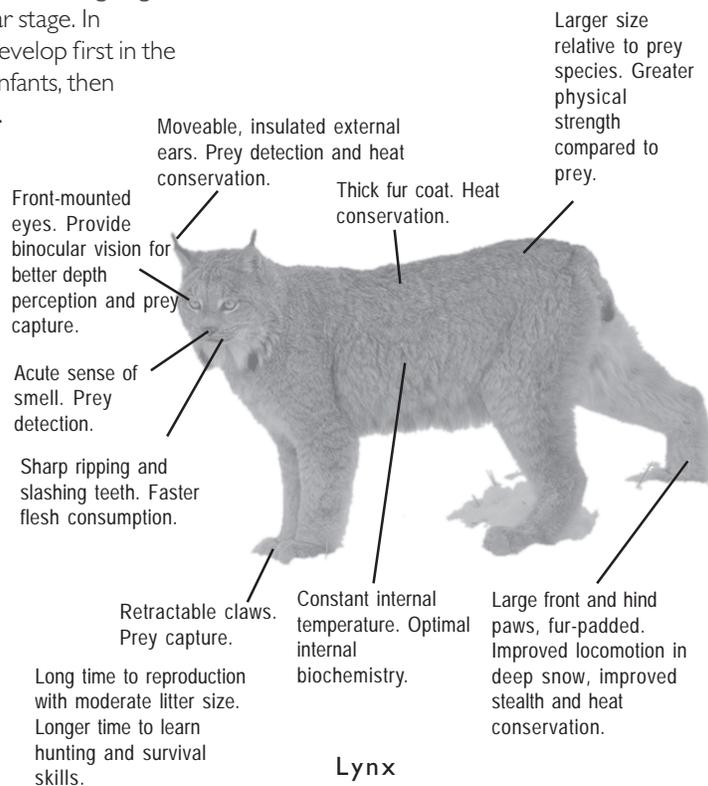
Physiological: A physiological trait is the ability to make internal adjustments in response to changes in the surrounding environment. For example: sweating in response to heat, shivering in response to cold, faster heart rate in response to increased physical activity.

Developmental: Development is the biological process in which a newly fertilized egg grows into a reproductive adult. Different species develop differently. For example, a butterfly emerges after first going through a caterpillar stage. In contrast, humans develop first in the womb, emerge as infants, then develop into adults.

Life history: Life history traits generally refer to the larger approaches used by individuals to balance the risks of survival with the demands of reproduction. For example: having a normally long life span vs. a short one; reproducing early vs. late in life; producing many offspring vs. few; surviving after reproduction vs. dying afterwards.



Rabbit



Lynx

techniques in genetics and ecology to investigate evolution on the population level. They work with small populations because it is more practical and more convenient than trying to include all members of a widely-distributed species. And, evolution tends to happen more vigorously on the level of the population anyway.

A population is a current, living manifestation of the species. Another way of thinking about 'population' is that a population is a pool of living things within which many of the genes of a species reside (the gene pool). A species evolves as the frequency of certain alleles (different varieties of a gene are referred to as *alleles*) increase or decrease in the population, or otherwise change, from generation-to-generation. As we will see, a population can experience genetic changes without involving other populations. But sometimes, the migration of individuals between different populations can cause genetic changes. The sections below describe just a few of the many ways genetic change can happen to populations.

10.6 You can't know the players without a program

Let's zoom out for a moment and look at the playing field from up in the blimp. From a big picture perspective, we can think about evolution as a consequence of two major happenings. Imagine you are watching a baseball game. The players move around the field for a while. Then they change sides. Once again there is more movement and a similar episode follows. Baseball is a game of activity and transition, activity and transition.

Now, back to evolution. It also is a system of activity and transition, activity and transition. First, there is the activity phase. This phase is when the living individuals of the population experience the streaming circumstances of their environment (the ecological element of the theory). As individuals die (an ecological phenomenon), the genetic makeup of the population changes slightly (the genetic element). I will refer to this ongoing form of genetic change as '**real time genetic change**'. This genetic change is not evolution yet. Then there is a transition phase like a change of innings. The transition phase is when the individuals in the population reproduce and pass copies of their genes to their offspring. If the real time genetic changes experienced by the population in one generation are reflected in the genetic makeup of the population after the next breeding season (the next generation, VOILA! An evolutionary result.

To recap, a baseball game evolves from one inning to the next. How the game evolves depends upon the experiences of the players during each of the innings. The population of players can change from one inning to the next. Bats stir the air, flies are caught and bases are found. In a somewhat similar manner, a

population evolves from one generation to the next. How the population evolves depends upon the experiences of the living individuals during each generation. The genetic makeup of the population can change from one generation to the next. Bats stir the air, flies are caught and caves are found.

10.7 Populations pulse through time

I want to present a model to help us visualize the life of populations. Then onto this model, I will overlay the various ecological circumstances that can result in different kinds of real time genetic change. Hopefully, you will be able to see how different kinds of ecological circumstances compare with each other and how they can contribute to an extremely complex variety of genetic outcomes. Reminder: Evolution theory is a synthesis of ecological theory and genetics theory. We use techniques in ecology and genetics to discover and interpret evolutionary results.

Our basic model is presented in figure ????. This drawing represents a living population over a period of time, between reproductive episodes — between breeding seasons. Starting on the left, the population is large because it is flush with new individuals just 'born' into the population. These new additions are not sexually mature. They must undergo growth and development before they have the abilities to pass their genetic information into the next generation. Since it takes time to develop into sexual maturity, these developing individuals are obliged to cope with their environment in the interim.

As you move to the right on the diagram (as time passes), the population gets smaller. The population shrinks because many individuals are unable to cope with the environmental stresses that inevitably confront them during their lives. So, individuals die from hunger, or thirst, or cold, or predation, or disease, or something else. Still, there are survivors who are alive when the next episode of reproduction happens — the next breeding season. Reproduction amongst the surviving and sexually mature members of the population produces a burst of new individuals and the population is big again.

If we follow this population through several reproductive events (several generations), a pattern begins to emerge. Population size pulses through time like the beat of a heart. Real time genetic change happens only to living individuals during each pulse. Following reproduction, the real time genetic change that a population experienced during one pulse is reflected in the starting genetic makeup of next pulse. Each pulse of the population can experience its own unique combination of real time genetic changes. At each new pulse, the population is genetically different from the pulse before.

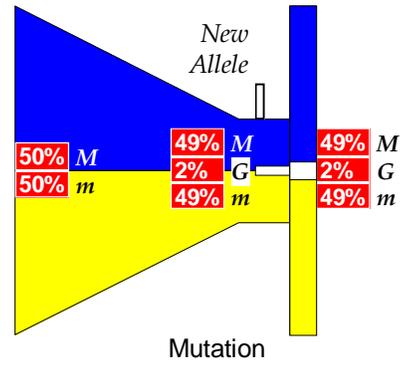
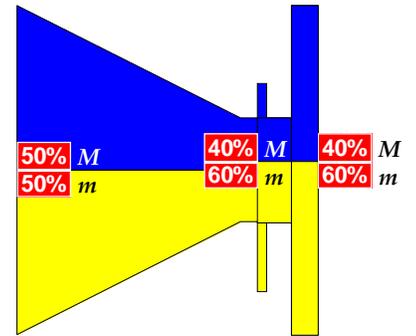
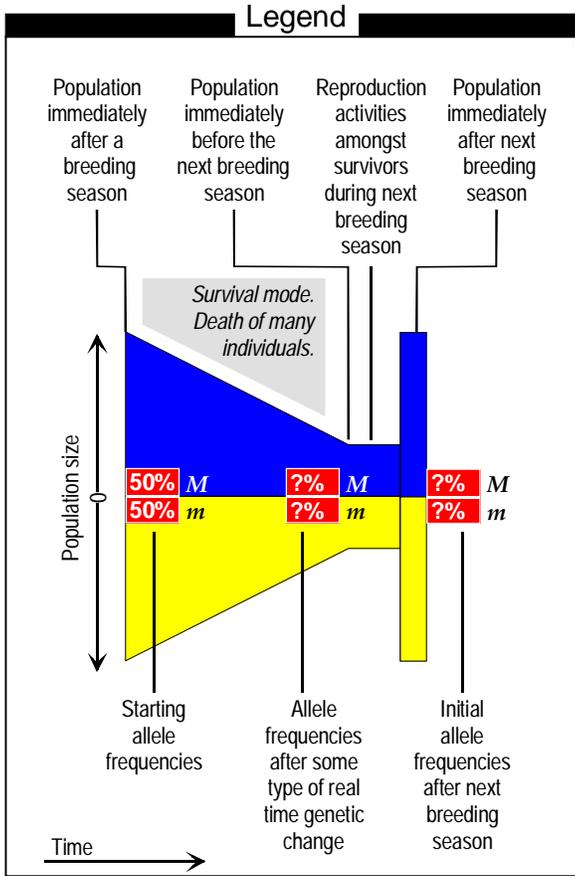
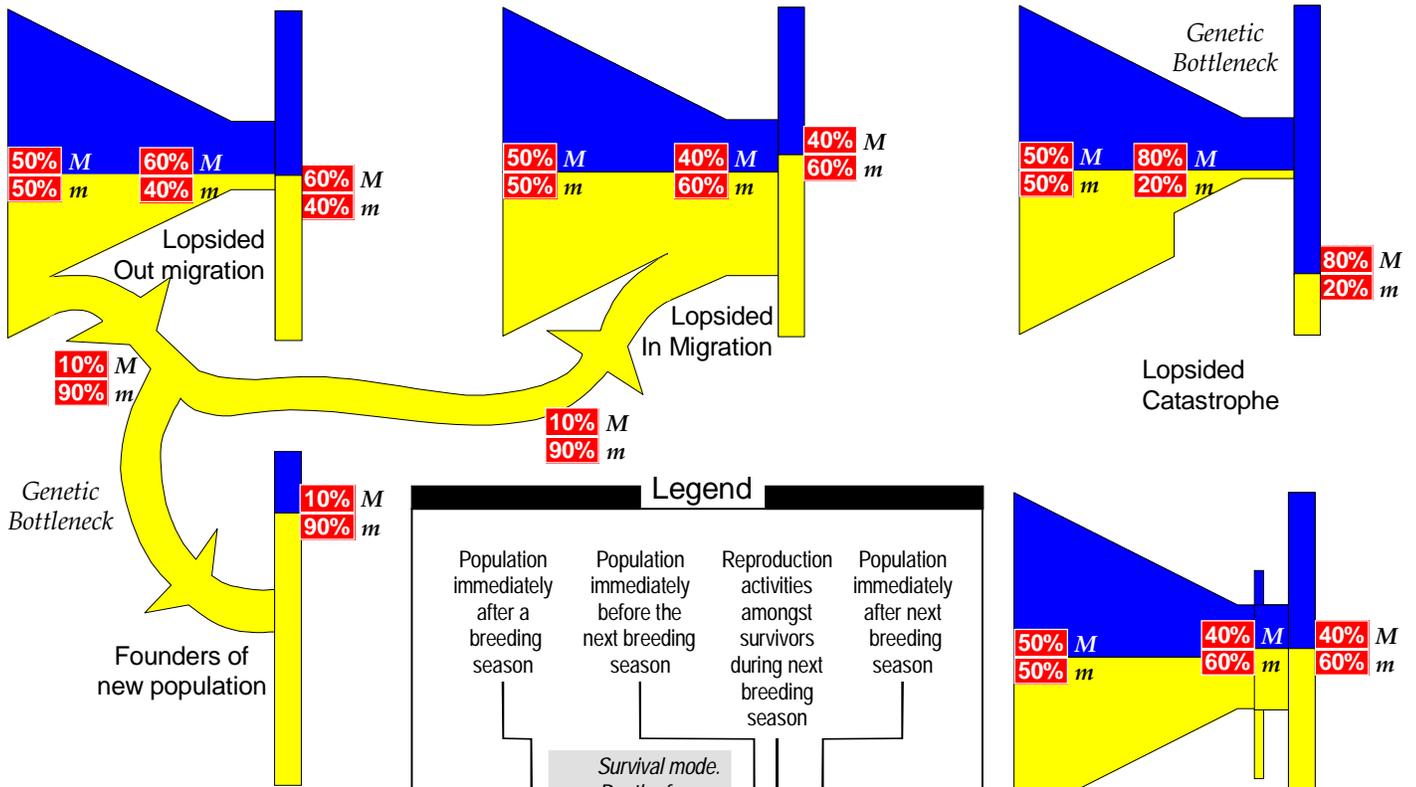
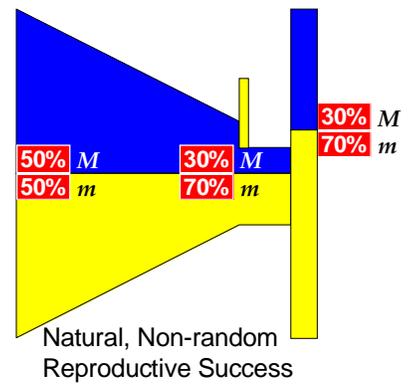
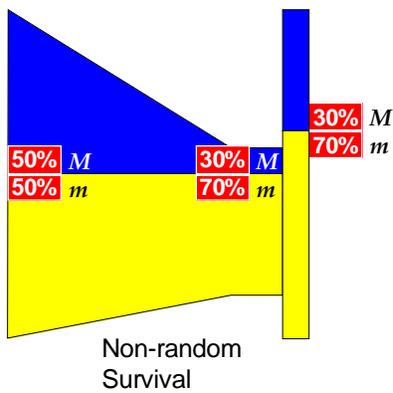
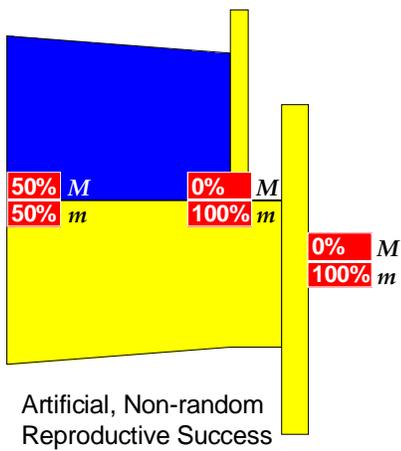


Figure 10.1. Population Pulse Model and different kinds of real time genetic change.



We interpret the genetic change that the population experiences from pulse-to-pulse (generation-to-generation) as an evolutionary result.

I will use this population pulse model as the common structure for all later discussions regarding real time genetic change. Each different mode of real time genetic change will influence the living population differently, therefore will influence the evolutionary result differently. So, let's examine some of the different kinds of real time genetic change. This is where the action is.

To standardize my discussion of evolution, I will present the different ways that living populations can experience real time genetic change. And within each category of real time genetic change, I will describe the kind of evolution that results.

10.8 Population genetics recognizes several causes for real time genetic change

Let me stress again that microevolution cannot happen unless there is at first some kind of real time change in the genetic makeup of the living population. The phenomenon of real time genetic change is any change in the proportional makeup of alleles of a living population — prior to reproduction. Populations can experience real time genetic change in a variety of ways, either from random ecological circumstances or non-random ecological circumstances. The following sections present the many different ways real time genetic change can happen to a population – as a result of random ecological circumstances (remember ecology, genetics).

Real time genetic change can happen to a population as a result of the following main ecological circumstances:

Different types of random real time genetic change

1. **Lopsided out-migration** - changes in the allele frequencies of the vacated population because of the movements of individuals out of the vacated population.
2. **Lopsided in-migration** - changes in the allele frequencies of the host population because of the movements of individuals into the host population.
3. **Lopsided catastrophes** - Catastrophes kill off many individuals, leaving a surviving population with a genetic profile that is different from the pre-catastrophe population.
4. **Random gamete production** - random copying of alleles during the production of sperm and egg cells results in statistical errors and deviations from the perfect expected outcome.

5. **Mutation** - changes in the gamete allele frequency because of the spontaneous synthesis of new and different alleles in the sex cells of a reproductively active individual.

Different types of non-random real time genetic change (next chapter)

1. **Artificial, non-random reproductive success** - change in allele frequencies because of non-random mating in an artificial environment created by the preferences of humans.
2. **Non-random survival** - changes in the allele frequency because the traits programmed by certain alleles perform better in the natural environment than traits programmed by other alleles.
3. **Natural, non-random reproductive success** - changes in the allele frequency because of a sexual environment in which certain traits are associated with greater mating success than others.

10.9 Random circumstances cause random change

I want to point out that real time genetic change can happen in several different ways. Remember that we are defining evolution as any change in the genetic makeup of a population from one generation to the next. Evolutionary change can appear over one generation or millions of generations. But evolutionary genetic change cannot arise without the reproduction of at least one new generation. If the results of real time genetic change are passed on to future generations, then we interpret this result as an evolutionary result. So, any ecological circumstance that can cause real time genetic changes in a population has the potential to produce evolutionary results. This is true even if the genetic changes seem haphazard and useless. In such cases, this is called random evolution.

First, a few words about random vs. non-random. When Darwin pondered his theory, he didn't think that evolution was the result of purely random circumstances. Why not? Darwin, like other naturalists before him, recognized that the features of organisms were not random. Instead, they were consistent with their environment. Darwin was confident that the environment was essential in helping to shape new adaptations. The environment was a consistent and non-random situation in which most individuals of a generation died before adulthood. To Darwin, evolution was tightly coupled to the environment. His theory was not about random happenings, because the environment was not random. Darwin's focus was on how *non-random* evolution as it led to adaptations. As Darwin saw it, the environment represents an element of some stability within which and to which species evolve

How influential are random ecological circumstances? That mostly depends on the size of the population. The general rule is that the smaller the population, the greater the influence of random ecological circumstances. The larger the population, the lesser the influence of random ecological circumstances.

There are many ecological circumstances that can produce random real time genetic change to a population. But I will discuss five that I think are very important.

10.10 Lopsided out migration can cause real time genetic changes in the vacated population

Let's consider 'lopsided out migration' as an ecological agent of real time genetic change. Out migration is when members of population permanently migrate away from their home population, and have no further interaction with it. A population's allele frequencies can change in real time as a result of individuals moving out of the area. Let's see how this works.

For this example, I have chosen the adorable and melodic Mountain Chickadee, a delicate little bird that graces high elevation forests with chatter and song. Our hypothetical Chickadee population occupies one mountain in a range of mountains. Other mountains have their own Chickadee populations as well. Let's track the relative abundance of two alleles, M and m , in our Chickadee population. As we start our investigation, the allele frequencies for the population as a whole are 50% M and 50% m . These allele frequencies can be influenced by lopsided out migration.

In this scenario, neither the M allele nor the m allele influence migration. Imagine that a large number of Chickadees leave their home population permanently. By chance, the leaving population has a greater proportion of m alleles than was typical for the pre-migration population. Their allele frequencies are lopsided toward more m alleles. This means that the vacated population has just been lopsidedly depleted of m alleles. After the migration, the allele frequencies of the home population has changed from 50% M and 50% m to 60% M and 40% m .

Let's sum up and clarify. I am calling this kind of real time genetic change, a 'lopsided out migration.' Out migration is an ecological phenomenon and is lopsided if the allele frequencies of the vacating population are different from the allele frequencies of the pre-migration home population. If these genetic changes are reflected in the home population after the next breeding season, then this result is an instance of 'evolution by lopsided out migration'.

10.11 Lopsided in-migration can cause real time genetic change to the host population

Let's consider 'lopsided in-migration' as an ecological agent for real time genetic change. In-migration is when individuals from outside populations join a given population. Imagine that our group of migrating Chickadees from our previous example now joins a different population on a neighboring mountain. By chance, these immigrants have low frequencies of the M allele and high frequencies of the m allele. Their allele frequencies are lopsided toward more m alleles. So they would then infuse the host population with a burst of m alleles. This could result in significant real time changes in the host population's allele frequencies. Let's say that the flow of new m alleles carried in by immigrants changes the host population's allele frequencies from its initial 50% M and 50% m to 40% M and 60% m . The host population has just experienced real time genetic change as a result of lopsided in migration.

Another radical form of in-migration is the establishment of a completely new population from a small number of immigrants — the founders. Of course this doesn't really change the genetic profile of any host population, because before the arrival of the founders, there was no host population. Because founding populations tend to be small, the allele frequencies in the founders are likely to be very different from the allele frequencies of their home population. So, in describing the peculiar and sometimes less diverse genetic profile of the new population, evolutionary biologists refer to this phenomenon as the *founder effect*.

The founding population has passed through a kind of genetic bottleneck. A genetic bottleneck can take on several forms. Generally, a genetic bottleneck is any ecological circumstance that results in a very small population where there was once a large population. Bottlenecks include catastrophes, diversions of small groups of out migrants as founders of new populations, or even a prolonged episode of hard times at home like drought or disease. The resulting small populations likely will have different allele frequencies and other genetic differences compared to the original large population from which it formed. So, genetic bottlenecks result in genetic peculiarities in the small populations that successfully pass through the bottleneck. This effect is called the *bottleneck effect*. The founder effect is just one specific kind of bottleneck effect.

Let's sum up and clarify. I am calling this kind of real time genetic change, a 'lopsided in-migration.' In-migration is lopsided if the allele frequencies of the entering population are different from the allele

Panel 10.3 Hardy-Weinberg equations

The Hardy-Weinberg equations gave biologists the statistical tools to tell if a population is: 1) in a state of genetic stability; or 2) in a state of genetic change? Let's begin by learning about the statistical behavior of genetically stable populations.

Genetically stable populations should be easy to recognize

By default, a population exists in a state of genetic stability when there is an absence of all sources of genetic change. That is, no natural selection, mutation, dispersal effects, non-random mating, or genetic drift. If these forces are absent, we should be able to recognize certain patterns in the population's genetic makeup. So, what are the genetic patterns we should expect to see?

In the 1920s, two scientists addressed this problem. Hardy and Weinberg saw that genetically stable populations can have many different proportions of the three traditional genotypes (*AA*, *Aa*, and *aa*, for example). That is, one genetically stable population could be composed of mostly homozygous dominants (Figure 8.?), while another genetically stable population could have a completely different mix of genotypes. It could have mostly homozygous recessives (Figure 8.?). The point is that there is no single **best**

genotype frequency that typifies genetically stable populations in general. Hardy and Weinberg based their claim on a statistical analysis of Mendelian genetics in large, sexually reproducing populations. The factor that determined the proportional mix of genotypes was the degree to which a particular allele was present or absent in the population - the **allele frequency**.

In genetically stable populations, allele frequencies tend to remain unchanged after many generations

For example, let's consider two alleles **A** (dominant) and **a** (recessive) in a genetically stable population. If in one generation the dominant allele **A** makes up only 20% of the alleles for a locus, and the recessive allele **a** makes up 80%, these alleles will be present in the offspring population in the same proportions. They will have the same allele frequencies.

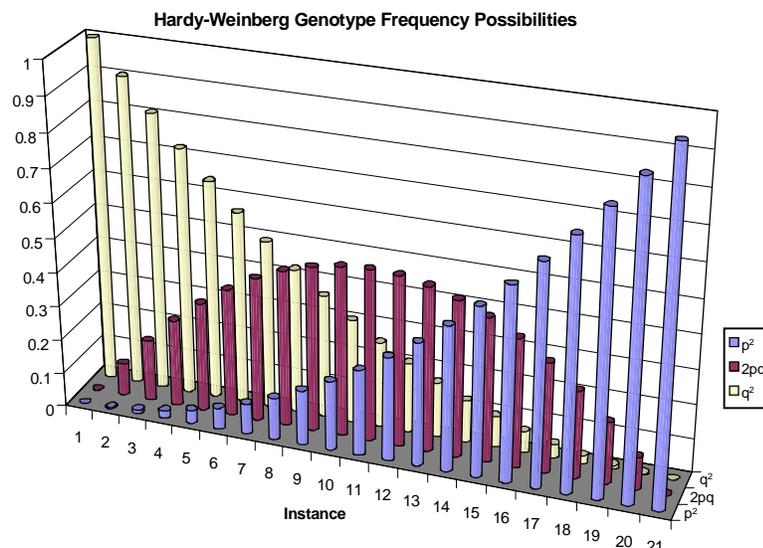
Hardy and Weinberg demonstrated mathematically that allele frequencies stay the same from generation-to-generation in genetically stable populations. This holds true even if each allele in the starting population is present in unequal amounts. If the frequency of allele **A** is 0.80 (80%) and the frequency for allele **a** is 0.20 (20%) in one generation, the allele frequencies will remain unchanged in the next generation and every generation thereafter. There is no tendency to even out allele frequencies in genetically stable

populations. Allele frequencies are conserved, even if the presence of one allele far outweighs the presence of the other.

A genetically stable population will gravitate toward fixed genotype frequencies

In addition, Hardy and Weinberg showed that a given combination of allele frequencies in one generation would produce a unique and predictable combination of **genotype frequencies** in the next generation, and every generation thereafter. That is, as long as the allele frequencies of the population don't change, they will always produce a predictable and unchanging mix of genotypes. This condition of genetic stability is referred to as the **Hardy-Weinberg equilibrium**. So, where is the pattern that will help us to spot genetically stable populations?

The Hardy-Weinberg equilibrium principle argues that each unique combination of allele frequencies in a population always produces its own unique combination of genotype frequencies in the next generation and each generation thereafter. This rule is the result of statistical probabilities for the assortment of alleles during gamete production, followed by sexual reproduction. For example, if one starting population had allele frequencies of 0.20 **A** and 0.80 **a**, it will produce the following genotype frequencies in the next generation and every generation thereafter: 0.04 *AA*, 0.32 *Aa*, and 0.64 *aa*.



On the other hand, if another population had allele frequencies of 0.80 **A** and 0.20 **a**, all following generations will have genotype frequencies of 0.64 **AA**, 0.32 **Aa**, and 0.04 **aa**. Hardy and Weinberg discovered a simple statistical method of predicting genotype frequencies in genetically stable populations by using known allele frequencies.

In genetically stable populations, each unique combination of allele frequencies results in a unique combination of genotype frequencies

Panel 7 ? shows a table and an accompanying graph with 21 different combinations of allele frequencies. Each unique combination of allele frequencies produces its own unique combination of genotype frequencies. There are three messages I want to get across here: 1) A genetically stable population, with unchanging allele frequencies will have only one possible combination of genotype frequencies; 2) Different genetically stable populations with different combinations of allele frequencies will have different combinations of genotype frequencies; and 3) For genetically stable populations, there

are statistical boundaries on the range of possible genotype frequency combinations. This is because of constraints on the assortment of alleles during reproduction. In other words, not all imaginable genotype frequency permutations are possible in genetically stable populations. Hardy and Weinberg addressed this statistical problem mathematically. We now recognize their solution as the famous Hardy-Weinberg equations.

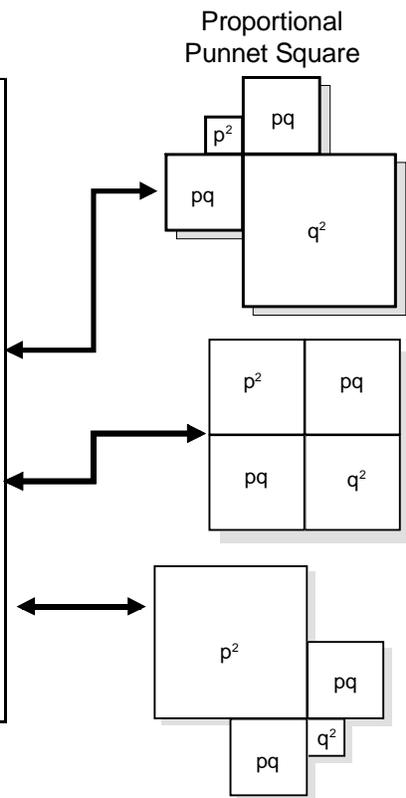
We can use the Hardy-Weinberg equations to check the genetic stability of populations

OK. So, get to the point. The point is that genetically stable populations have a predictable genetic profile that helps us easily recognize them at an instant in time. Biologists use the Hardy-Weinberg equations to tell if a population is genetically stable or not.

Here's how they do it. In order to check the genetic stability of a population, biologists must follow two major steps. First, they must determine the population's **actual genotype frequencies** and **actual allele frequencies**. They do this by performing traditional genetic test crosses

with live subjects from the population. Next, biologists plug the actual allele frequencies into the Hardy-Weinberg equations to calculate **the expected genotype frequencies** (p^2 , $2pq$, and q^2) that should be present in a genetically stable population. Then they compare the **expected** genotype frequencies with the **actual** genotype frequencies. If the actual genotype frequencies are different from the expected genotype frequencies, it means, without question, that the population is in a state of genetic change. Why this is so could become the basis for future investigation.

Allele Frequencies			Hardy-Weinberg Calculation					
Instance	Dominant Allele Frequency	Recessive Allele Frequency	Genotype Frequency for Homozygous Dominant	+	Genotype Frequency for Heterozygous	+	Genotype Frequency for Homozygous Recessive	Sum
	p	q	p^2		$2pq$		q^2	
1	0.00	1.00	0.0000	+	0.0000	+	1.0000	= 1
2	0.05	0.95	0.0025	+	0.0950	+	0.9025	= 1
3	0.10	0.90	0.0100	+	0.1800	+	0.8100	= 1
4	0.15	0.85	0.0225	+	0.2550	+	0.7225	= 1
5	0.20	0.80	0.0400	+	0.3200	+	0.6400	= 1
6	0.25	0.75	0.0625	+	0.3750	+	0.5625	= 1
7	0.30	0.70	0.0900	+	0.4200	+	0.4900	= 1
8	0.35	0.65	0.1225	+	0.4550	+	0.4225	= 1
9	0.40	0.60	0.1600	+	0.4800	+	0.3600	= 1
10	0.45	0.55	0.2025	+	0.4950	+	0.3025	= 1
11	0.50	0.50	0.2500	+	0.5000	+	0.2500	= 1
12	0.55	0.45	0.3025	+	0.4950	+	0.2025	= 1
13	0.60	0.40	0.3600	+	0.4800	+	0.1600	= 1
14	0.65	0.35	0.4225	+	0.4550	+	0.1225	= 1
15	0.70	0.30	0.4900	+	0.4200	+	0.0900	= 1
16	0.75	0.25	0.5625	+	0.3750	+	0.0625	= 1
17	0.80	0.20	0.6400	+	0.3200	+	0.0400	= 1
18	0.85	0.15	0.7225	+	0.2550	+	0.0225	= 1
19	0.90	0.10	0.8100	+	0.1800	+	0.0100	= 1
20	0.95	0.05	0.9025	+	0.0950	+	0.0025	= 1
21	1.00	0.00	1.0000	+	0.0000	+	0.0000	= 1



frequencies of the host population. If these genetic changes are reflected in the host population after the next breeding season, then this result is an instance of 'evolution by lopsided migration'.

10.12 Lopsided catastrophes change population allele frequencies

Let's consider environmental catastrophe as an ecological agent of real time genetic change. First of all, I will define a catastrophe as a kind of random and destructive environmental phenomenon. Many generations may pass between each instance of a catastrophe. In other words, catastrophes are so random and so infrequent that they are not part of a selective environment. There is no way to adapt evolutionarily to a catastrophe. Catastrophes are destructive intruders that disrupt the normal course of evolution by selection (next chapter). Examples of catastrophes include fires, floods, volcanic eruptions, mudslides, tornadoes, and even asteroid strikes. Survival usually is a matter of good luck.

Continuing on with the Mountain Chickadee as our hypothetical subject, neither the M allele nor the m allele influence nest site selection. So we would expect a random geographic distribution of M -carrying birds and m -carrying birds. This means some clumping. By pure chance a higher than expected proportion of MM Chickadees are clumped together in a small ravine. Then one night a large fire quickly blazes over the mountain, killing all the Chickadees there except the Chickadees in the ravine.

Before the fire, the allele frequencies for the whole population were M , 50% and m , 50%. After the fire the allele frequencies for the surviving population were M , 60% and m , 40%. By virtue of luckily surviving the fire in greater numbers, the proportion of M alleles in the population increased from 50% to 60%. This fire is an example of a lopsided catastrophe because it killed more of one kind of allele (m) than the other (M). I call this a lopsided catastrophe because the allele frequencies of the surviving population differs from the allele frequencies of the pre-catastrophe population.

Catastrophes can create another type of genetic bottleneck. The population that successfully passed through the bottleneck had allele frequencies that were different from frequencies of the original population overall. In the case of our Chickadees, a random fire produced the bottleneck.

Let's sum up and clarify. I am calling this kind of real time genetic change, a 'lopsided catastrophe.' A catastrophe is lopsided if the allele frequencies of the surviving population are different from the allele

frequencies of the pre-catastrophe population. If these genetic changes are reflected in the home population after the next breeding season, then this result is an instance of 'evolution by lopsided catastrophe'.

10.13 Random gamete production: Random deviations in gametic allele frequencies can result in a kind of evolution called 'genetic drift'

Let's consider random gamete production as an ecological agent of real time genetic change. The cold, hard mathematics of the Punnett square and the Hardy-Weinberg equations are somewhat misleading. Still, we use them to make predictions about the next generation. But what we expect is not always what we get. Here is the reason. Population genetics is a statistical phenomenon and the production of each new generation is subject to a peculiar statistical phenomenon — chance. Randomness influences each round of egg and sperm production, or gamete combination such that *actual* results will differ slightly from the results expected by an ideal Hardy-Weinberg prediction.

For example, imagine you are making popcorn. But this is special popcorn. All of the kernels are identical except that some kernels make red popcorn and others make green popcorn (ugh!). Imagine that you start out with an exact mix of 100 red kernels and 100 green kernels. Start the popper and away they go. Now anyone who has ever popped popcorn knows that some of the kernels just don't get popped. This is purely bad luck on their part, random chance. For some random reason, these kernels just didn't get hot enough to pop, even though most others did. Being a scientist, you count the different colors of popped corn. Instead of the expected 100 red and 100 green pops, you got 87 red and 95 green. Because of randomness, the actual results deviated slightly from the expected results. All of the kernels had an equal ability, but some kernels just didn't get the chance to pop.

Now let's look at gamete formation. In a perfect world, the allele frequencies in all of the gametes in a population should be identical to the allele frequencies in the adult population from which they were formed. If the allele frequency for allele M is 0.3 in the adult population, then Hardy-Weinberg expects it also should be 0.3 in the sperms and eggs from this population. But because of randomness, the *actual* gametic allele frequencies will deviate from the *expected* gametic allele frequencies. And that deviation will show up in the allele frequencies of their offspring population. When it does, the population as a whole has just evolved.

There are two random statistical phenomena that influence the deviation of gametic allele frequencies: 1) the first influences the *size* of the deviation; 2) the second influences the *direction* of the deviation.

10.13.1 Deviation size is biggest in small populations

Let's address the issue of deviation size first. Statisticians and population biologists have worked out a way of estimating how much random deviation in allele frequencies we can expect from one generation to the next. The statistical tool they use is called 'standard error'. It turns out that standard error, and therefore the size of the deviation, gets bigger as the population size gets smaller.

I will give you an example without exposing all the calculations. Imagine two populations. Population 1 has 500,000 individuals and population 2 has only 50 individuals. Let's say that the allele frequencies are 0.5 for allele M and 0.5 for allele m , half and half. Random events during gamete formation will cause the gametic allele frequencies to deviate from that of the population that is producing the gametes. Randomness prevents perfect Hardy-Weinberg futures. That is, the actual results will deviate from the expected results. The size of the deviation is determined by calculating the standard error factor. For the large population, the standard error means we might get a deviation of only $\pm 0.1\%$ from the expected gametic allele frequencies — negligible. But for the small population, the standard error is much larger. We might get a $\pm 10\%$ deviation from expected gametic allele frequencies.

10.13.2 The deviation can randomly flip between two possible directions

Now let's think about the deviation *direction*. In this example, the deviation is between two parameters, M and m . So by pure chance, the deviation could go toward M or the deviation could go toward m . Two chance possibilities, like the toss of a coin. You know that if you flip a coin ten times, you could get a string of five heads in a row or more. Statisticians call such a run of luck a 'random walk.' See Panel ??? for more information on random walks. If random walks can happen while flipping a coin, they can happen to the gametic allele deviation too.

Let's stay with the small population for the moment and see how the deviation experiences a random walk. A deviation of $\pm 10\%$ would mean that the allele frequencies of the offspring population could deviate to either $0.45M$ and $0.55m$, or $0.55M$ and $0.45m$. Random chance means it could flip either way. Let's say it flips toward the ms ($0.45M$ and $0.55m$) and now we'll follow the population for a few generations. These gametic allele frequencies would be reflected in the offspring population. Then another round of gamete formation will occur. Assuming the same size population, the

standard error is about the same, $\pm 10\%$. Again, the deviation can flip either way. If the allele frequency deviation flips in favor of more M alleles, then we will get back nearly to the original starting point of $0.5M$ and $0.5m$. But if the deviation again flips toward more m alleles, then we end up with allele frequencies of $0.4M$ and $0.6m$ — farther away from the starting point. Let's assume that the deviation keeps flipping in the same direction. The next generation will be $0.35M$ and $0.65m$. The next, $0.3M$ and $0.7m$. A random walk of the deviation direction has rapidly and significantly changed the M and m allele frequencies in this small population.

You can see that should this random walk continue much longer, the M allele will disappear from the population and the m allele will become 'fixed.' But there is no reason the random walk can't stop and go in the other direction. Allele frequency deviations can flip back and forth while experiencing random walks of different lengths. However, the risk of allele extinction varies with an allele's changing frequency. The lower the allele frequency, the greater the chance of allele extinction. The higher the allele frequency, the lower the chance of allele extinction. Ask anyone who has ever sat down at a blackjack table with 20 bucks.

Let's sum up and clarify. I am calling this kind of real time genetic change, 'random gamete production.' If these genetic changes are reflected in the home population after the next breeding season, then this result is an instance of 'evolution by random gamete production'.

Remember that we actually have two random ecological/environmental phenomena that produce random gamete production. One random phenomenon influences the *size* of the deviation in gametic allele frequencies. The other random phenomenon influences which *direction* the deviation will go — either more Ms or more ms . In other words, the first random phenomenon determines how big a step to take. The second random phenomenon determines in which direction the step will be made.

Other authors, including Sewall Wright himself, have described evolution by random gamete production as one example of genetic drift.

10.14 Mutations are random changes in the DNA

Let's consider mutation as an ecological agent of real time genetic change. Mutations are described as changes in the DNA. As far as evolution goes, we are most interested in mutations that occur in the gametes (egg cells or sperm cells). Mutations are random events that can happen in several ways. They can have several different kinds of effects on the developing individual. Please refer to chapter ? for a more complete presentation regarding mutations.

Since mutations generally are rare individual events, their initial contribution to the population is more qualitative than quantitative. As a result, the appearance of a single mutation usually will cause a negligible quantitative impact on the population's genetic profile. But mutations bring new kinds of alleles to the population that then are subject to other types of real time genetic change including random gamete production, lopsided catastrophes, lopsided out-migration, lopsided in-migration, and selection.

Let's sum up and clarify. I am calling this kind of real time genetic change, a 'mutation.' If these genetic changes are reflected in the home population after the next breeding season, then this result is an instance of 'evolution by mutation'.

10.15 Random evolution alone does not lead to useful features

These are just a few ways in which ecological circumstances can bring about random real time genetic change in populations. And each flavor of random real time genetic change can result in its own kind of random evolutionary change. The point I want to make is that there are many ways to produce evolutionary results that have nothing to do with creating adaptations. Random evolutionary changes will occur, given the statistical realities of population genetics, random walks, the migratory movements of individuals, and occasional random environmental circumstances. But random evolutionary change alone will never lead to useful features we call adaptations. Random evolutionary change alone could never produce an eye or a flower. These features are so complicated that, if we were to rely on pure chance alone, it could take trillions and trillions of years to produce them — more time than is available to our Universe and dozens of its descendants. Therefore, it is absurd to consider complex life forms as products of random evolution. Which leads us to the idea of non-random evolution. To be continued in the next chapter.

Panel 10.4

A run of luck is an example of a statistical phenomenon called a random walk

A random walk is a phenomenon in which, because of randomness (chance), a set of events strays from the outcome expected by probability.

According to simple Mendelian genetics, if we know the genotypes for any two parents, we can predict the genotype frequencies of their offspring. The same is true for whole populations. We saw in Panel 8.7 that for a breeding population in which the allele frequencies are known, the Hardy-Weinberg equations can predict

the genotype frequencies of the next generation. In both cases, these are the frequencies we expect based on pure probability. As it turns out, because of random sampling during gamete formation, the **actual** outcome could be different from the **expected** outcome. If the actual outcome differs repeatedly from the expected frequency in favor of one allele over another, a random walk is in progress.

Random events are events that are unpredictable except in terms of probability. Probability is a statistical concept that quantifies the likelihood that a given event will happen. Probability also quantifies the expected mix of outcomes in a set of many events. For example, take out a coin and flip it in the air, catch it and look at the side facing up. This is one event — a random event at that. There are only two possible outcomes for this event (heads or tails). We can quantify the

statistical probability of each possible outcome. In this case, each possible outcome has an equal probability of actually happening. So, the probabilities are 50:50. Heads has a probability of 0.50, and tails has a probability of 0.50. In any single coin toss there is a 50% likelihood that it will turn up heads, and there is a 50% likelihood it will turn up tails. We can also use probability to determine the expected mix of outcomes for many coin toss events. In this case we can predict that out of 100 coin tosses, we expect 50 heads and 50 tails.

Here is where it gets a little tricky. Keep in mind that probabilities only establish the *likelihood* of a particular outcome of random events. They cannot determine or force any individual outcome of random events. Despite our statistical expectations, randomness can skew our actual results in a set of events.

Randomness means 'chance' or 'luck'. For example, I have just tossed a quarter in the air 10 times. This is a set of events. Probability predicts that I should have gotten 5 heads and 5 tails. But wait. I got 3 heads and 7 tails. What went wrong? Nothing. Each coin toss was a purely random event. My lopsided results are an example of what statisticians call a 'random walk'.

The term, random walk, describes how pure chance acts on a set of events, not just a single event. A random walk means a 'run of luck' in which a particular outcome happens in a set of events more frequently than probability predicts. Keep in mind that for coin tosses each event is completely independent of past and future events. That is, when I toss a coin, the probability for the outcome is always 50:50. Just because one toss is heads, it doesn't mean the next toss must be tails. Probability just quantifies the likelihood of each possible outcome each time I toss the coin. What I actually get is a result of randomness. Sometimes it seems like a run of good luck invalidates the idea of probability. But it doesn't — as long as the set of events is large.

Here is an example of a set of events we all can relate to. Most of us travel the same busy streets on the way to work or school. We are very familiar with all of the traffic lights along the way. Usually we experience a mixture of red lights and green lights (I'll ignore yellow lights for now). Do you remember the days when you got all red lights? (Do I ever!) Likewise, do you remember the days you got all green lights? (Oh happy day!) By the way, it had nothing to do with the harmonic wavelengths of your psychic aura. On such days of either all red lights or all green lights, you experienced a statistical phenomenon called a random walk. Despite your lopsided experience, the

probabilities for reds and greens that day were still 50:50. But because of randomness and the small set of events, your experience was very one-sided.

Does that mean that probability is worthless? No, lopsided experiences like those described above tend to even out as the set of events gets bigger. Random walks often meander back-and-forth from one side to the other. For example, some days you get mostly red lights, and some days you get mostly green lights. After a year, the number of signals encountered would be very large and the results would show an almost equal number of red lights and green lights.

The point I am trying to make is that random walks tend to show up in all sets of purely random events. Random walks can be small or big. The consequences of random walks are especially noticeable in small sets of events.

In the case of microevolution, random walks show up in reproductive genetics. Randomness causes the mix of genotypes of a new generation to stray from the mix predicted by Mendelian genetics and Hardy-Weinberg. If, for purely random reasons, one allele shows up in increasing frequency in many successive generations, a random walk is in progress.

Uniform distribution based upon probabilities of 50:50

Day	Traffic Signals										Red	Green
	1	2	3	4	5	6	7	8	9	10		
1		5	5
2		5	5
3		5	5
4		5	5
5		5	5
6		5	5
7		5	5
8		5	5
9		5	5
10		5	5
											50	50

Random distribution based upon probabilities of 50:50

Day	Traffic Signals										Red	Green
	1	2	3	4	5	6	7	8	9	10		
1		5	5
2		6	4
3				3	7
4		.		.		.					2	8
5		5	5
6	7	3
7		4	6
8			5	5
9	6	4
10	6	4
											49	51