Non-Mendelian Inheritance

Many patterns of inheritance are more complex than those Gregor Mendel described.

Red, white, and pink snapdragons (*Antirrhinum majus*).

What happens when traits don’t follow simple Mendelian inheritance rules? Pink snapdragons are an example of how inheritance can be apparently blended when red and white snapdragons are crossed to form an intermediate trait in the heterozygous offspring.

John Kaprielian/Science Source.

Topics Covered in this Module

- Non-Mendelian Patterns of Inheritance

Major Objectives of this Module

- Give examples of non-Mendelian inheritance.
- Explain how dominance may follow complex patterns.
- Understand that most genes have multiple phenotypic effects.
- Relate environmental effects on phenotype.
Non-Mendelian Patterns of Inheritance

Gregor Mendel, working in the 1800s, contributed enormously to the modern understanding of genetics. He determined that a diploid organism inherits two copies of the same gene, called alleles, one from each parent. An allele coding for a dominant trait may hide the expression of an allele coding for a recessive trait; an organism can express the recessive phenotype only if the recessive allele is inherited from both parents. If one or both of the alleles coding for a dominant trait are present, the organism will show the dominant phenotype. Mendel also discovered that at least in some cases, the alleles of multiple genes were inherited independently from one another.

The Mendelian theory of inheritance makes a number of specific predictions. One is that offspring will express a trait that is inherited from either or both parents, but not a blend of those traits. In other words, one would predict from Mendel's findings that crossing a red flower and a white flower would produce either a red flower or a white flower but not a pink flower. But is it true that all traits involve only two possible outcomes? While this is true for some traits, such as human earwax, which is either wet (dominant) or dry (recessive), other traits once thought to be Mendelian, such as eye color, are now thought to be more complex. Likewise, rather than the discrete traits of Mendel's studies, where a trait could take one form or the other, many traits are continuous, such as human height and skin color, and these have more complex patterns of inheritance.

In fact, although Mendel's results are still very informative to modern genetics, we now know that inheritance of many traits can be extremely complex. For these genes, we say that they follow non-Mendelian inheritance. Mendel himself realized the likelihood of non-Mendelian inheritance when he looked at patterns of inheritance for characteristics of his pea plants that he did not explicitly consider in his experiments. But how exactly does non-Mendelian inheritance work?

Relationships between dominance and phenotype may be complex.

As Mendel found, crossing a true-breeding purple-flowered pea plant with a true-breeding white-flowered pea plant produces an entire generation of purple-flowered plants. The purple phenotype is completely dominant to the white phenotype. But the situation is different in carnations (Dianthus caryophyllus), which also come in many different colors. Crossing a true-breeding red carnation with a true-breeding white carnation produces a pink carnation (top left of Figure 1). How does this happen? Before Mendel developed his inheritance laws, a popular hypothesis held that parents' traits blended in their offspring. Is this what is happening in carnations?

One way to investigate this question is to cross those pink individuals from the F₁ generation and examine the color patterns from the F₂ generation (bottom right of Figure 1). The blending hypothesis would predict that crossing pink flowers would produce more pink flowers. But this isn't what happens. When pink F₁ carnations are crossed, the parental traits of red and white flowers can reappear in the F₂ generation.
This kind of inheritance pattern is called incomplete dominance. Neither the red trait (R allele) nor the white trait (r allele) is completely dominant in a heterozygous (Rr) individual. Having only one R allele in heterozygotes produces only enough pigment to make the plant's flowers pink, not enough to make them red. Flowers homozygous for the white allele (rr) produce no color pigment, which is why they are white. The reappearance of red and white flowers in the F₂ generation shows that flower color alleles remain separate, as Mendel predicted, and are segregated independently into gametes. The alleles recombine in the F₂ plants to create more variety in phenotypes than the theory of blended inheritance would predict. From this cross, on average, one-half of the offspring are pink (Rr), one-quarter are red (RR) and one-quarter are white (rr).

In incomplete dominance, the two alleles of a heterozygote show a partial effect on phenotype. Using the example above, the Rr heterozygote shows neither the white nor the red phenotypes but a partial red (pink) phenotype.

Figure 1: Carnation flower color demonstrating incomplete dominance in genetic inheritance.
Crossing true-breeding red (RR) and white (rr) carnations produces pink carnations in the F₁ generation. Crossing pink (Rr) flowers yields red, pink, and white flowers in an approximately 1:2:1 ratio.
© 2014 Nature Education All rights reserved.

Another type of inheritance that differs from simple Mendelian processes is called codominance, in which alleles combine to influence the phenotype of the organism. A well-known example of codominance is observed in the alleles underlying human blood types. In the early 1900s, Karl Landsteiner, an Austrian scientist, was trying to understand why blood transfusions were sometimes life saving but other times appeared to cause severe reactions.
and even death. In doing so, he recognized the variation in human blood types that we now categorize as the ABO blood group. Human red blood cells can carry molecules on their surface called antigens. For the ABO gene, there are two types, the A antigen and the B antigen. The immune system of individuals that have only one or the other of these antigens will not produce antibodies against the antigen their own blood contains. On the other hand, if the blood type with the alternative antigen is introduced, the antigen is recognized as "foreign" by the immune system, and antibodies are formed against it that cause cells to clump. Although many individuals have only the A antigen (type A) or the B antigen (type B), some have both A and B antigens (type AB) and some have no antigens (type O).

<table>
<thead>
<tr>
<th>Blood type</th>
<th>Genotype</th>
<th>Antigen on red blood cell</th>
<th>Red blood cell phenotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>P^A P^A or P^A P^O</td>
<td></td>
<td><img src="image1.png" alt="Image" /></td>
</tr>
<tr>
<td>B</td>
<td>P^B P^B or P^B P^O</td>
<td></td>
<td><img src="image2.png" alt="Image" /></td>
</tr>
<tr>
<td>AB</td>
<td>P^A P^B</td>
<td></td>
<td><img src="image3.png" alt="Image" /></td>
</tr>
<tr>
<td>O</td>
<td>P^O P^O</td>
<td></td>
<td><img src="image4.png" alt="Image" /></td>
</tr>
</tbody>
</table>

Table 1: Blood types and related genotypes.
The A and B alleles of human red blood cells code for specific antigens. The O allele does not code for any antigen.

© 2014 Nature Education All rights reserved.

Sometimes a heterozygote shows the partial effect of an allele that codes for a phenotype that is not completely dominant (incomplete dominance), and sometimes a heterozygote shows two different effects from two different alleles of the same gene (codominance). What else may happen? There are many other possibilities. For example, a heterozygote can express a phenotype that is more extreme than either parent, a phenomenon called overdominance. Plant breeders have long known that a hybrid cross of two (heterozygous) strains of crops can sometimes result in offspring that produce a higher yield than their true-breeding parents. The underlying genetic mechanisms behind this phenomenon, sometimes called heterosis, are still being investigated.

In 2010, researchers at the Hebrew University of Jerusalem and Cold Spring Harbor Laboratory identified a single gene that controls yield and shows overdominance in heterozygous tomato plants (Figure 2). In nature, the size and number of fruits a plant makes in any given time is constrained by the balance of immediate potential fitness gains by allocating resources to reproduction (production of fruits) versus longer term fitness gains by allocating resources to survivorship (production of leaves and storage of resources). In tomatoes, individuals with normal or wild-type alleles have genes that balance flower production and plant growth, but the researchers found a mutation in one of these genes that shifted the balance. Heterozygous individuals, with one functional copy of this gene, shifted away from growing leaves toward growing fruit and had a higher yield than the wild-type, which was homozygous for the non-mutant allele. However, plants that were homozygous for the mutant allele overproduced leaves and
allocated less to fruit production than the wild-type plants.

Figure 2: Overdominance in tomatoes.
The hybrid tomato plant in the middle has more and larger tomatoes than the wild-type plant on the left or the double mutant on the right.

© 2010 Nature Publishing Group

What happens when there are multiple alleles, but they can't all be expressed simultaneously? Many phenotypes are influenced by multiple allelic inheritance. For example, in the early 1900s, Thomas H. Morgan and Calvin Bridges discovered that a locus responsible for eye color in *Drosophila melanogaster* (fruit fly) had over one-hundred alleles. In this allelic series, eye colors range from complete absence of pigment in the white allele to a brick-red color in wild-type eyes.

Similarly, although many genes and environmental factors (e.g., temperature) can influence the timing of when pea plants flower, researchers have identified multiple alleles of a gene called LATE FLOWERING (*LF*) that play an important role in this timing. The alleles of this gene are *L* (later flowering), *L^f* (latest flowering) and *l^a* (earliest flowering). The influence of the four alleles on the timing of flowering shows an inheritance pattern called a dominance series: one allele is dominant over the other three, a second allele is dominant over two others, a third allele is dominant over one other, and the last allele is recessive to all others (Table 2).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Earliest flowering</th>
<th>Earlier flowering</th>
<th>Later flowering</th>
<th>Latest flowering</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L</em>/<em>L</em></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>l</em>/<em>l</em></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L^f</em>/<em>L^f</em></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>l^a</em>/<em>l^a</em></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L</em>/<em>l^a</em></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L</em>/<em>l</em></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><em>L</em>/<em>L</em></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><em>L</em>/<em>l^a</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
In many cases, it may be difficult to determine whether a trait is inherited in a dominant, incompletely dominant, codominant or overdominant way. For instance, in humans, Tay-Sachs disease behaves like a recessively inherited trait. If only one parent has one copy of the allele, no children will have the disease. If both parents are heterozygous for the allele, each child would have a 25% chance of having the disease. The associated gene, HEXA on chromosome 15, codes for the enzyme hexosaminidase A, which is involved in breaking down lipids in the brain. Without sufficient quantities of the enzyme, lipids build up in the brain even before birth, causing seizures, blindness and usually death before age 5. There are more than one-hundred known mutations on this gene, and these mutations are often found in populations of humans that had very lower numbers of individuals when they were founded. People who are "carriers" have one mutant allele and have no symptoms, although the enzyme activity is almost half of that expressed in homozygous individuals without any mutations. Carriers have just enough of the enzyme to clear their brains. On the scale of the organism, the mutant allele appears recessive because individuals are healthy. However, on the scale of the enzyme, the alleles show a pattern of incomplete dominance. In heterozygous Tay-Sachs carriers, the functional allele in carriers produces some enzyme but not as much as homozygous non-carriers make, similar to the way the red allele produces enough red pigment in heterozygous snapdragons to make them pink.

Most genes have multiple phenotypic effects.

Genes code for proteins, and most traits are a product of the complex interactions between multiple proteins. Gene products are also often strongly influenced by how other elements in the genome regulate their transcription. For example, in multicellular organisms, genes may be turned "on" or "off" in cells from different parts of the organism?

Sometimes, a single gene influences two or more apparently unrelated phenotypic traits. This phenomenon, called pleiotropy, was coined by the German geneticist Ludwig Plate in 1910. In a classic example, researchers in the 1930s noted that a dominant allele that caused birds' feathers to curl out ("frizzle") rather than lie flat on the body (Figure 3) was not the only phenotypic trait that differed between "normal" and "frizzled" chickens. The chickens with altered feathers were unable to regulate their body temperatures as effectively as those with normal feathers and as a result had higher rates of metabolism, blood flow and digestive capacity; these physiological differences also led to fewer eggs laid (Figure 3). Although there are certainly many genes involved in all of these traits, a simple allelic
variation in the gene that caused feathers to “frizzle” has a pleiotropic effect that alters a great many traits in the entire phenotype of the organism.

Figure 3: A chicken showing the dominant frizzle phenotype.

The expression of this dominant allele in chickens causes a phenotype with disheveled feathers. This gene has a number of pleiotropic effects that influence many other traits in chickens with this allele. 

WilleeCole Photography/Shutterstock.

In Tay-Sachs disease, one dysfunctional enzyme results in many serious effects that have one root cause: the accumulation of lipids in the brain. Phenylketonuria, or PKU, is an inherited disorder caused by mutations in a single gene (the \( P A H \) gene) that has pleiotropic effects. The gene codes for an enzyme called phenylalanine hydroxylase, which is necessary to metabolize the amino acid phenylalanine and convert it into tyrosine. Untreated PKU leads to a buildup of phenylalanine in the brain, which competes with other amino acids that are essential for normal brain function. At the same time, this gene has a pleiotropic effect by reducing the level of tyrosine, which is involved in the production of melanin (an important pigment in skin and hair), causing individuals with the disease to have light skin and hair. If both parents are carriers, there is a 25% chance of a child inheriting both abnormal alleles and, consequently, developing the disease. The disease is detectable in newborns, and symptoms can be largely avoided with careful regulation of diet (Figure 4).
Another gene known to have pleiotropic effects in humans is fibrillin-1, which codes for a connective tissue protein. Marfan syndrome is caused by a dominant mutation in the fibrillin-1 gene. People with Marfan syndrome are usually tall and thin with long arms and legs, and they are also at increased risk for heart disease and eye problems. The symptoms may be treated individually, and people with Marfan syndrome may have normal life spans.

In pleiotropy, the expression of one gene has multiple phenotypic effects. There are also many cases where two or more genes can interact to influence a phenotype. Epistasis and polygenic inheritance are two different ways in which multiple genes can influence phenotype. In epistasis, the product of one gene masks or changes the expected phenotype of one or more other genes. In polygenic inheritance, multiple genes influence the expression of a trait that is usually quantitatively variable (e.g., human height).

Epistatic interactions among genes involve some genes modifying the effect of other genes on an organism's phenotype. Coat color in many mammals, including several domesticated species such as dogs, cats and sheep, represents a classic example of epistatic interactions among two or more genes. Epistasis among genes that influence the production of color pigments can lead to the great varieties of coat color phenotypes observed in these species. The specific genes involved have alleles that reduce, enhance, mask or otherwise change the phenotype expressed by alleles for other genes. Consider guinea pigs, whose fur can have many different colors, patterns and lengths as a result of interactions among many different genes. One important interaction is in the two genes that determine coat color. One of these two genes influences the production of melanin, a dark pigment in the hair and skin of many mammals, while the other gene influences the deposition of melanin. Depending on the alleles present for these two genes, one of three fur colors will result: black, brown or white (Figure 5). For the gene that determines how much melanin is deposited in the fur of guinea pigs, there are two alleles: the dominant \( B \) allele, which codes for a large amount of melanin to be deposited, resulting in black fur, and the recessive \( b \) allele, which codes for a moderate amount of melanin to be deposited, resulting in brown fur. However, the other gene, which determines whether melanin is produced at all will interact with the first gene to determine coat color. In this case, the dominant \( C \) allele codes for the production of melanin, while the recessive \( c \) allele does not code for any pigment. Thus, individuals with the genotypes \( CCBB \), \( CcBB \), \( CCBb \), and \( CcBb \) will have black fur, and individuals with the genotypes \( CCbb \) and \( Ccbb \) will have
brown fur. However, because an individual that is homozygous for the c allele will produce no melanin at all, its phenotype will be white (albino) regardless of the genotype of the gene that determines how much melanin is deposited. Here, we say that the gene that determines whether melanin is produced (C or c) can epistatically modify the gene that determines how much melanin is deposited on the fur (B or b).

© 2014 Nature Education All rights reserved.

As Mendel demonstrated, in a dihybrid cross (such as AaBb x AaBb), two traits that segregate independently will show a 9:3:3:1 phenotypic ratio. Nine-sixteenths of the offspring will show both dominant traits, 3/16 will show one dominant trait, 3/16 will show the other dominant trait, and 1/16 will show both recessive traits. If a dihybrid cross, however, consistently results in a different ratio than this predicted ratio, one possible explanation is that the genes for the two traits are interacting through epistasis. Guinea pig fur color consistently shows a 9:3:4 ratio. Thus, the phenotypic ratio is consistent with epistasis. However, there are many other types of epistatic interactions between genes that can lead to other phenotypic ratios depending on the nature of their interaction.

**Test Yourself**

How many genotypes result from the cross presented in Figure 5? And how many phenotypes result?

Certain varieties of summer squash come in three shapes: disk-shaped, sphere-shaped and long. The phenotypic ratios generated by dihybrid
crosses suggest that two genes contribute to squash shape, and one doesn’t simply mask the other as in recessive epistasis (Figure 6). What may be determined from the results of this cross?

![Summer squash shapes](image)

**Figure 6: Summer squash shapes.**
Phenotypic results of a dihybrid cross show that two genes interact to determine squash shape and yield a new sphere-shaped phenotype in the F₂ generation, in addition to producing modified dihybrid ratios.

© 2013 Nature Education All rights reserved.

**Test Yourself**

What phenotypic ratio does this dihybrid cross show? What is the genotype of the long squash? What are the genotypes of the sphere-shaped squashes?

The type of epistasis in this squash is called **duplicate interaction**. The gene pairs interact, and both influence fruit shape. A dominant allele at either locus generates a sphere-shaped fruit. In the absence of dominant alleles, the fruit is long. However, if the dominant alleles for both genes (A and B) are present, the fruit displays a flattened, disc shape (as the parent).

A large number of traits vary continuously, rather than being characterized by a few qualitatively distinct types (e.g., round or wrinkled seeds). Many traits that vary along a continuum are the result of polygenic inheritance, in which multiple genes influence the phenotypic trait. Human skin color is a classic example that varies from very light to very dark and is controlled by several genes, including those that determine the production of melanin pigments (Figure 7).
Figure 7: Parents and children may have skin color that varies along a continuum.

Human skin color is a polygenically inherited trait that is influenced by several genes. 

Courtesy of Carl Zitsman/USFWS.

While many polygenic traits are influenced by the complex interactions of many genes and the traits vary continuously, human eye color is a somewhat simpler example that can be roughly predicted using our standard tools, such as a Punnett square. Many people think human eye color is a simple Mendelian trait, although we've known for a long time that it is much more complicated. In fact, eye color can be extremely variable and involves many alleles of several genes that influence pigmentation in many parts of the iris. However, we can still categorize eyes into a few basic types: light brown, dark brown, light blue or green, and dark blue or green. And we can make some predictions about the inheritance of these basic types. For simplicity's sake, we can explore this problem by examining the influence of two important genes. Each of these genes influences the production of a pigment that has a yellow-brown color. One gene codes for the pigment in the first layer of the iris, and the other codes for the pigment in the second layer of the iris. None of the alleles for these genes has dominance. In the first iris layer, an individual with the \textit{AA} genotype produces lots of the pigment, a heterozygous individual (\textit{Aa}) produces moderate amounts of the pigment, and an individual with the \textit{aa} genotype produces no pigment. Likewise, in the second layer, an individual with the \textit{BB} genotype produces lots of pigment, a heterozygous individual (\textit{Bb}) produces moderate amounts of pigment, and an individual with the \textit{bb} genotype produces no pigment. If we overlay the pigments in these two layers, we can see how these two genes combine to influence the phenotype, with the \textit{AABB} genotype producing the darkest brown eye color, and the \textit{aabb} genotype producing the lightest blue eye color. The children of two people who were heterozygous at every gene for eye color (\textit{AaBb}) could show any of five distinct eye color phenotypes (Figure 8).
Parents that are heterozygous for alleles coding for eye color could have children whose eye color ranges from the darkest shade of brown to the lightest shade of blue. However, these parents are more likely to have children whose eye color is similar to theirs.

The environment may affect phenotype.
What else affects skin color? One obvious factor is how much time a person has spent in the Sun. Multifactorial characteristics are influenced by multiple genetic factors as well as the environment in which the organisms lives. In fact, these environmental factors are extremely important in determining a wide variety of phenotypic traits and can include diet, climate, illness and stress. In psychology, the question of "nature versus nurture" in determining human behaviors embodies the question of the role of genes versus environment. Are our behaviors innate qualities that are the products of our genes and millions of years of evolution; that is, does "nature" predominate? Or, do our experiences over the course of our lifetimes determine how we behave; that is, does "nurture" predominate? In biology,
we know that nature and nurture — genes and environment — typically interact in complex ways to determine the phenotypes of a great many traits of most organisms. For example, a plant grown in dry soil may develop a very different root system than one grown in wet soil. Likewise, people raised at high elevations (and low oxygen) have a variety of traits that allow them to use oxygen more efficiently. Some snails and small aquatic crustaceans can alter the shape of their bodies as they grow when they smell a predator nearby to reduce the likelihood of being consumed.

Even though environment can influence the phenotype of an organism, there is a normal range of phenotypes that are not typically exceeded. For instance, human height varies based on both environment (nutrition) and genetics, but not many people are shorter than 4½ feet or taller than 7 feet. The range of phenotypic possibilities when environmental conditions change is called the norm of reaction. Some types of hydrangeas, for example, may have flowers that are blue, pink or purple depending on the pH and levels of aluminum in the soil in which they grow (Figure 9). A hydrangea plant's flowers will be blue in low pH (acidic soil), but the same plant's flowers will be pink in higher pH (alkaline) soil. Some human characteristics have a narrow norm of reaction, such as blood type. Others have a wide norm of reaction, such as the volume of red blood cells, which varies depending on factors including physical fitness and the elevation a person lives at.

**Figure 9: Hydrangea macrophylla flower color depends on soil pH.**

The flowers of these two *Hydrangea macrophylla* shrubs differ in color as a result of the underlying soil pH. Plants in more acidic soil have blue flowers, while those in more neutral soil have pink flowers.

Alan L. Detrick/Science Source.

**Future perspectives.**

Recent research has revealed additional inheritance patterns that are still not well understood. For instance, in 2005, researchers at Purdue University showed that *Arabidopsis thaliana*, which are small flowering plants in the mustard family, are able to express genes coding for a dominant trait that neither of their parents carried. For several different genes, approximately 10% of the plants in a generation showed the ancestral wild-type phenotype instead of the parents' recessive phenotype — far more than random mutations could account for. The scientists hypothesized that the plants were using ancestral RNA templates outside their genomes to modify their DNA. Other researchers responded to the article by suggesting alternative hypotheses. Perhaps the templates were DNA fragments called "reverting sequences"
instead of RNA. Perhaps genes from a previous generation of wild-type spores entered embryo sacs weakened by mutations. However the process works, genetic information from their ancestors may help plants survive mutations that would otherwise have doomed them.

**Genetic testing and inherited diseases.**

As discussed earlier, Tay-Sachs is a neurodegenerative disease that cannot be treated and is usually fatal before a child reaches the age of 5. If each parent has one recessive copy of the mutated allele, their children have a 25% chance of having the disease. Although anyone may carry Tay-Sachs, it is most common among Ashkenazi Jews; in this population, about 1 in 27 adults is a carrier. A couple who both have Ashkenazi Jewish heritage may want to have genetic testing so that they may determine whether they are carriers. Parents who carry a mutation in the gene may have the mother’s amniotic fluid tested early in pregnancy to determine whether the child will have Tay-Sachs. Some parents make the difficult decision to terminate an affected fetus instead of giving birth to a child who will suffer and die in early childhood. The professionals who help people assess their risk of developing or passing on a disease are genetic counselors. In 2010, genetic testing was available for over 2,000 alleles that cause disease.

Genetic testing may be used to determine:

- whether a person's symptoms are caused by an inherited disease
- whether a child or adult with no current symptoms will develop a disease, such as PKU or Huntington's disease
- whether a person has a higher than usual risk of developing a disease, such as breast cancer
- how likely prospective parents are to have children with a genetic disorder, such as Tay-Sachs, cystic fibrosis, or Duchenne muscular dystrophy
- whether an embryo is affected by a genetic disorder or a chromosomal disorder, such as Down syndrome

Genetic counselors help people decide whether they want genetic testing and then how to interpret the information the tests provide. These counselors usually have master's degrees in genetic counseling and backgrounds in genetics, psychology, public health, nursing and/or social work.
Summary

**OBJECTIVE**

Give examples of non-Mendelian inheritance.

Mendelian inheritance patterns explain how some traits are inherited, but not all traits. Incomplete dominance, codominance, overdominance, and the influence of multiple alleles on the same trait are all exceptions to the Mendelian pattern of inheritance.

**OBJECTIVE**

Explain how dominance may follow complex patterns.

Sets of alleles, variations of one gene, may influence phenotypes in different ways and phenotypes may have different degrees of dominance. In overdominance, hybrid offspring show a more extreme phenotype, such as higher fruit yield, than either homozygous parent. Multiple alleles may also take effect in a dominance series, with certain alleles coding for traits that are dominant over the traits coded for by other alleles.

**OBJECTIVE**

Understand that most genes have multiple phenotypic effects.

Most genes have multiple phenotypic effects. In several diseases, including phenylketonuria, the loss of one important protein causes numerous symptoms. Multiple genes may interact to determine one characteristic, either modifying or masking each other. For instance, in yellow labs, alleles coding for the recessive coat pigmentation phenotype mask the expression of alleles coding for coat color.

**OBJECTIVE**

Relate environmental effects on phenotype.

A variety of environmental factors can affect an organism’s phenotype. For instance, extended periods in the Sun can alter human skin color, and soil acidity dictates the flower color of some Hydrangeas.

Key Terms

**codominance** Each allele affects the phenotype in a distinct way.

**duplicate interaction** Complete dominance at both gene pairs.

**epistasis** Genes that interact to mask or change the effect of each other.

**incomplete dominance** One allele is not able to completely mask the other allele.

**multifactorial** Traits that are influenced by both multiple genetic and environmental factors.

**non-Mendelian inheritance** Genes that do not follow Mendelian patterns of inheritance.

**norm of reaction** Range of phenotypic possibilities for a trait in response to changing environmental factors.

**overdominance** Heterozygotes exhibit more extreme phenotypes than either parent.

**pleiotropy** Single gene with multiple phenotypic effects.

**polygenic inheritance**
Phenotypic trait that is determined by more than one gene.
Test Your Knowledge

1. Why does crossing true-breeding red and white snapdragons result in pink offspring?
   - The allele that codes for the red pigment trait has incomplete dominance.
   - The alleles that code for the red and white trait are on the same chromosome.
   - Parents’ traits blend in their offspring.
   - The allele that codes for the white color trait prevents expression of the gene that codes for the red color trait.
   - White flower color is a recessive trait.

2. Which of these inheritance patterns involves interaction of more than one gene?
   - codominance
   - pleiotropy
   - environmental effects
   - epistasis
   - incomplete dominance

3. What happens in overdominance?
   - The hybrid has a more extreme phenotype than either parent.
   - Both participating alleles show an additive effect on the phenotype.
   - One gene has multiple phenotypic effects.
   - One gene prevents the other from exerting any effect.
   - Each relevant allele contributes independently to the phenotype.

4. Which of the following factors affects how many blood cells a person has?
   - contracting an infection
   - the person’s genes
   - moving to a high altitude
   - training for a triathlon
   - All answers are correct.

5. Marfan syndrome is associated with tall height and a high risk of heart and eye problems. How does mutation of one gene cause all these symptoms?
   - Each symptom is a result of high blood pressure.
   - The gene codes for a connective tissue protein used in many parts of the body.
   - The gene codes for an enzyme that catalyzes many different reactions.
   - Multiple alleles create a variety of phenotypes through incomplete dominance.
   - The mutation up-regulates transcription of several genes.

6. The growth factor bone morphogenetic protein-4 (BMP-4) was first identified as a bone-forming factor by its ability to form bone tissue when injected into muscle. However, it has since been found to also play important roles in neural development and the formation of a large variety of tissues. Mutations in the BMP-4 gene are therefore expected to cause a wide range of abnormalities. Which term best describes this phenomenon?
   - pleiotropy
   - overdominance
incomplete dominance
- dominance series
- duplicate interaction

IN THIS MODULE
- Non-Mendelian Patterns of Inheritance
- Summary
- Test Your Knowledge

PRIMARY LITERATURE
Aneuploids may not be so abnormal
Aneuploidy confers quantitative proteome changes and phenotypic variation in budding yeast.
View | Download