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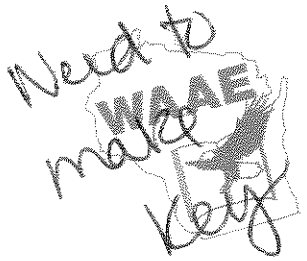
8 Genetics

Careers in Agriculture
The Sky's the Limit



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Key Terms

Additive gene action
Alleles
Aneuploidy
Animal breeding
Artificial selection
Autosomes
Biotechnology
Centromere
Chromosome
Codominance
Crossbreeding
Deoxyribonucleic acid (DNA)
Diploid
DNA polymerase
DNA replication
Dominant
Epistasis
Expression
Gametes
Gametogenesis
Gene
Gene frequency
Genetic drift
Genetic engineering
Genome
Genotype
Genotypic frequency
Haploid
Heritability
Heterosis
Heterozygous
Homologous chromosomes
Homozygous
Inbreeding
Inbreeding depression
Incomplete dominance
Inheritance
Multiple alleles
Mutations
Natural selection
Nucleotide
Outbreeding
Phenotypic frequency
Polymerization
Polyploidy
Population genetics
Principle of independent assortment
Principle of segregation
Purines and pyrimidines
Qualitative traits
Quantitative traits
Recessive
Ribonucleic acid (RNA)
Ribosomes
Selection
Selection differential
Sex-influenced inheritance
Sex-limited traits
Sex-linked inheritance
Somatic cells
Testcross
Transcription
Transfer RNA (tRNA)
Transgenic
Translation
Trisomy

Learning Objectives

After you have studied this chapter, you should be able to:

- Explain the role that genetics plays in animal production.
- Describe the location of genes within a cell.
- Explain the process of cellular division with relation to the replication of cells containing a full complement of genetic information.
- Explain the process of cellular division that ultimately produces cells containing only half of the genetic information.
- Describe how variation in traits is passed from parent to offspring.
- Describe how gene frequencies change in a population.
- Explain the concept of relationship between individuals.
- Describe several systems of mating individuals.
- Summarize the implications of genetic engineering, the promise it holds for future animal production, and the opportunities that animals will have to provide even greater benefits to humanity.

INTRODUCTION

Genetics can be termed the foundation of life, for without the ability to transfer genetic information from one generation to the next, existence would be impossible. In the nature versus nurture debate, genetics is the nature side. Inheritance takes place by the transmission of genes, in the form of chemical entities, from parent to offspring at the time of conception. During this transfer of molecular material, certain information is passed on to the offspring that is combined to form a blueprint of characteristics that will describe both the physical appearance and the molecular composition of the animal. An animal's genetic makeup, or **genotype**, sets the stage for disposition, coat type, coat color, speed, gait types, body composition, growth, reproduction, milk production, disease resistance, and other traits.

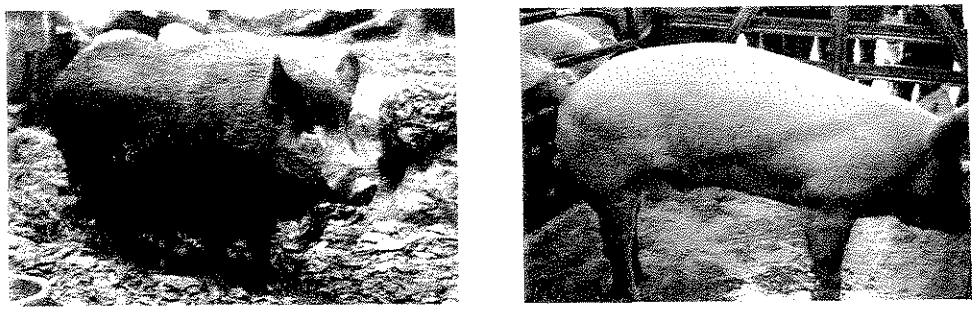
Genotype The genetic makeup of an organism.

A large part of how efficiently animal products can be produced is related to the genetic composition of the animal or herd of animals. The **expression** of the genotype into traits of economic importance provides the basis for the animal's worth when marketed. Because there are many ways to market an animal, it is important to produce animals with the necessary genotype for maximum value in the target market.

Expression Manifestation of a characteristic that is specified by a gene.

Within each major animal species, producer and consumer preferences set the pace for desired characteristics in the animals that are produced. From a livestock producer standpoint, efficiency of production might be the most important overall goal in regard to other traits, such as disposition, which also receive consideration because of the effect such traits have on the producer's ability to care for the animals. However, when viewing animals from a consumer's position, tenderness, flavor, color, and leanness might top the list of important characteristics. This is not to say that these characteristics don't overlap between the producer and the consumer, because they surely do. For instance, the consumer is interested in cost, which is related to efficiency of production. However, the priorities on each side are often different. In the companion species, there too may be differences in producer and consumer concerns. An elite breeder may strive to breed an international champion. The average consumer may just want a healthy dog with no major flaws and a good disposition that will be a good companion.

Applied genetics in animals is usually referred to as *animal breeding* (Figure 8–1). It is the science that helps in the quest to breed better animals. The practice of breeding and selection has led to remarkable changes in animal species. The wolf has been transformed into dogs as different as the Saint Bernard and the Chihuahua. The wild aurochs became the specialized milk, meat, or work breeds of modern cattle. The wild boar, the Red Junglefowl, the vicuña, the Siberian hamster, and several score



(a) (b)

Figure 8–1
The application of animal breeding and selection techniques has led to remarkable changes, such as arranging the genes of the wild boar (a) into those of the modern meat-type hog (b).

of other wild animals have been converted to the modern domestic species we know today. Interestingly, the greatest changes in domestic species through the practice of animal breeding occurred before the science was named, and before the scientific basis of inheritance was discovered. Dogs have been dogs rather than wolves for at least 10,000 years. **Deoxyribonucleic acid (DNA)**, the stuff genetic codes are made of, was determined to be the genetic material relatively recently, in 1952. However, research in **genetic engineering** has made possible advances that may come to dwarf those earlier accomplishments, and it will likely do so in the span of a few decades rather than a few millennia.

Deoxyribonucleic acid (DNA) Chemically, a complex molecule composed of nucleotides joined together with phosphate sugars. Chromosomes are large molecules of DNA.

Genetic engineering The term most frequently used to describe the technologies for moving genes from one species to another.

THE GENE

The nucleus of the cell contains the **chromosomes**. Chromosomes are large molecules composed of DNA and protein. Within these large molecules are smaller segments of DNA called **genes**. The genes contain the information that controls all of the biochemical processes of the cell. By controlling the biochemical processes of the cell, genes control the life processes. A gene is a segment of DNA that codes for a specific protein. These DNA molecules are in the shape of a double helix. DNA comprises chromosomes, which are found in pairs. It is this arrangement of genes, DNA, and chromosomes that provides the basis for inheritance (Figure 8–2).

Chromosome The DNA-containing structures in cells. Composed of segments called genes.

Gene A short segment of a chromosome. Genes direct the synthesis of proteins or perform regulatory functions.

Because genes are segments of DNA, we should look at the structure of DNA to determine the existence of genetic material. Deoxyribonucleic acid (DNA) consists of two strands comprised of alternating sequences of the sugar deoxyribose and phosphate bonds. At each sugar, there is a bridge of nitrogen **bases** composed of chemical compounds called **purines and pyrimidines**. The purines present in a DNA molecule are adenine (A) and guanine (G); the pyrimidines are thymine (T) and cytosine (C). The bridges are always combined, with adenine attaching to thymine and guanine with cytosine. The bases are attached with hydrogen bonds (Figure 8–3). The segment of deoxyribose, phosphate, and one of the bases is called a **nucleotide**. A gene is a segment of the double helix consisting of several nucleotides. These segments produce a genetic code that specifies the chemical composition of proteins, which ultimately are the end product of genetic expression. The entire genetic material of an animal is termed its **genome**.

Bases One of the four chemical units on the DNA molecule that form combinations that code for protein manufacture. The four bases are adenine (A), cytosine (C), guanine (G), and thymine (T).

Purines and pyrimidines Organic ring structures made up of more than one kind of atom (heterocyclic compounds). Purines and pyrimidines contain nitrogen in addition to carbon.

Nucleotide The building blocks of nucleic acids. Each nucleotide is composed of sugar, phosphate, and one of four nitrogen bases.

Genome The complete genetic material of an organism.

Genomes of organisms vary in size, with simpler organisms having genomes substantially smaller than those of complex multicellular organisms. Because chromosomes comprise the genome, there is an issue of how this genetic information is held in such small spaces. DNA segments can be of varying lengths, and this is important when they must be packed into small sections of the chromosome. DNA is supercoiled in such a way that it becomes very compact and is able to fit into extremely small sections of the chromosome. Imagine a DNA molecule that has ends attached in such a way as to produce a circle. Now imagine twisting this circle so it decreases in width by half, and now one circle is lying on top of the other. Picture a coiled garden hose that has been twisted in this manner. With each twist, the circumference of the circle decreases but gets deeper or thicker as the hose stacks up on top of itself. This same concept is true of supercoiled DNA. As this sequence progresses, the DNA molecules in a chromosome become much more compact and the chromosome shortens and thickens, thus becoming smaller in overall size.

There is some potential for variation in chromosome numbers because of the many processes that must first take place for inheritance to be possible. One such variation in chromosome numbers is called **polyploidy**. A polyploid individual has

Polyploidy Having more than two full sets of chromosomes.

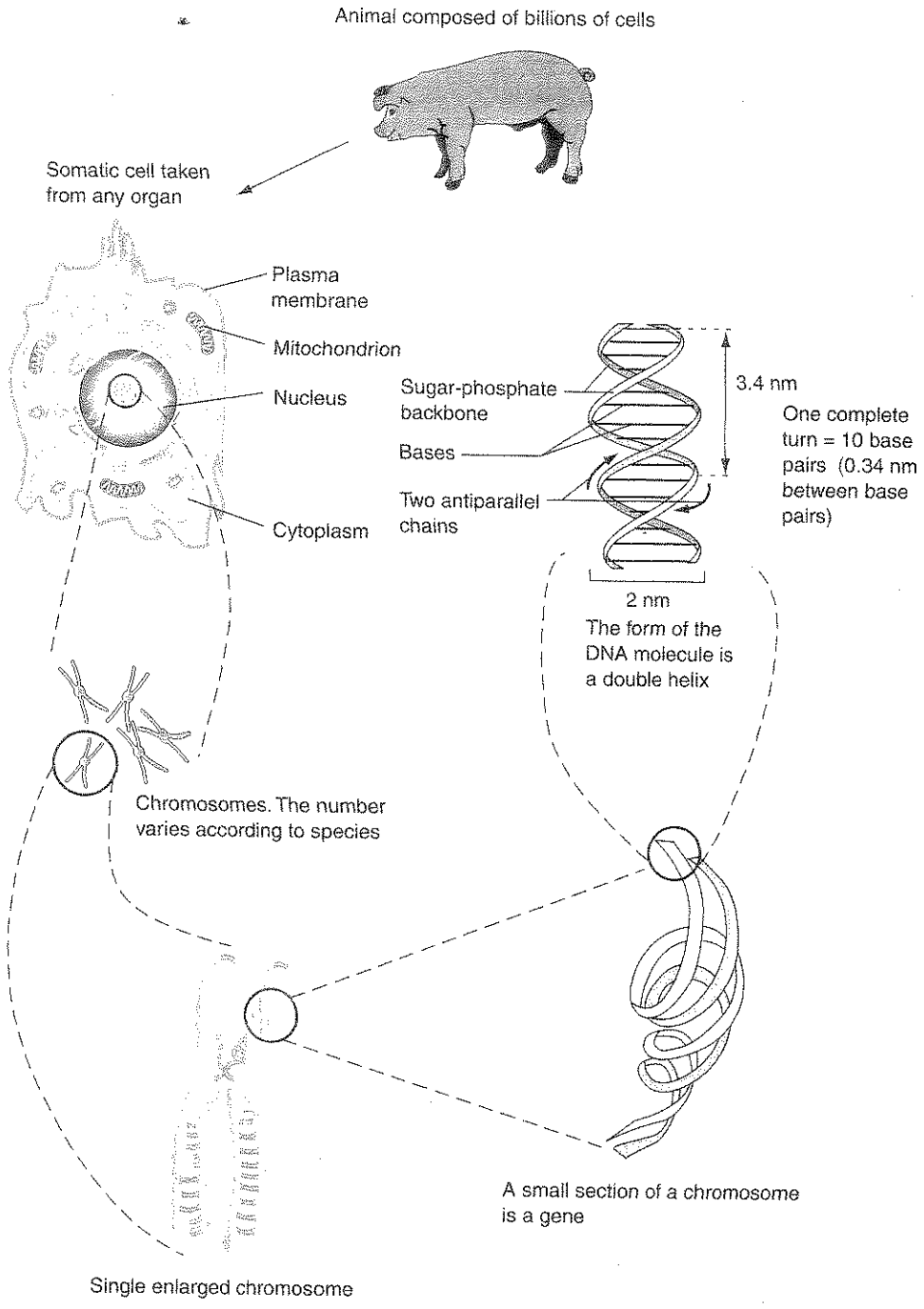


Figure 8–2
Location and structure of genetic material. (Source: Adapted from Alcamo, 1996, p. 10.)

more than two full sets of chromosomes. Polyploidy is very uncommon in vertebrates but quite widespread in plants. This is beneficial in some situations. Many times polyploidy causes failure of meiosis because there is more than one pairing partner for each chromosome and the result is just a few small seeds; for example, seedless watermelons.

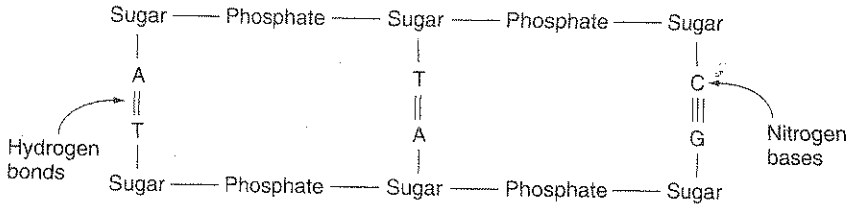


Figure 8–3
Chemical nature of DNA. This structure is the double helix form of DNA. A & T are joined with double hydrogen bonds; G & C are joined with triple hydrogen bonds.

Another example of variation is **aneuploidy**, in which there is variation in chromosome number with respect to individual chromosomes. If an organism is missing a chromosome ($2n - 1$), it is said to be **monosomic**. If an organism contains an extra chromosome ($2n + 1$), it is possible for development to be either normal or slightly abnormal. This is referred to as **trisomy**. Monosomies and trisomies are frequently lethal unless the affected chromosome is one of the smallest chromosomes. A common nonlethal example of trisomy is Down syndrome in humans, which is caused by trisomy of autosome number 21. Trisomy is often related to failure of the chromosomes to separate properly in meiosis, producing a gamete with two copies of the chromosome.

DNA is a sequence of base pairs (i.e., ATCG with TAGC) that represents the code for a specific gene. A sequence of four bases can be arranged in 256 different ways; therefore, it is easy to see how sequences of many more base pairs can be arranged in exponentially many more ways. This concept provides the complexity of DNA and thus the code for many different genes.

DNA replication is the process of making a copy of a DNA molecule. Replication must occur accurately so the daughter cell (the cell being produced) inherits the same information contained in the parent cell. This process of synthesizing DNA is carried out by unzipping the existing DNA strand between base pairs (i.e., unzipping between A-T and C-G) to expose each base. **DNA polymerase** is the enzyme that forms the sugar–phosphate bond between adjacent nucleotides in a chain. For DNA polymerase to act, an RNA primer must be present to which the DNA polymerase attaches to begin the replication process. The process of **polymerization** is carried out by DNA polymerase. More specifically, this consists of deoxynucleotides being added to the existing single strand of DNA, thereby producing a complete DNA molecule with matching base pairs and sequences just like the initial molecule. Thinking through this process, it is easy to visualize the splitting of a DNA molecule to produce two strands of DNA. Then the addition of nucleotides that complement the existing bases (i.e., ATGC) forms a complete DNA molecule. By starting with one DNA molecule, this process ultimately produces two identical molecules.

The next step is to look at how this genetic information is used to specify the type of molecule to be produced. DNA is located in the nucleus of the cell, but proteins are produced by **ribosomes** located in the cytoplasm. Because the purpose of the DNA is to serve as a template for the construction of a protein, the genetic message found in the DNA must be transported from within the nucleus out to the ribosome. **Ribonucleic acid (RNA)** molecules are fitted especially for this process. RNA molecules are built to complement the DNA. This process is known as **transcription**. DNA serves as a template and codes for the manufacture of RNA. Once a complementary RNA has been synthesized, it is processed to remove sections of base pairs from the primary transcript that are not part of the coding sequence for the specific protein needed. The end product of this processing is a **messenger RNA (mRNA)** that contains only the sequences of base pairs used to code for the specific protein. The DNA also codes for a second RNA called **transfer RNA (tRNA)**, which is used to collect the amino acids needed to build the protein. The mRNA leaves the nucleus and attaches to the ribosome, where it is used as the template to manufacture the protein. The tRNA moves into the cytoplasm and attaches to the amino acid for which each is coded. Next, the ribosomes move along the length of the mRNA and align with the tRNA, which brings the amino acids into the chain. As they are aligned, the amino acids chemically bond to each other. A chain of amino acid sequences is thus constructed. This process is known as **translation** of the mRNA code for the protein being built. When the tRNA comes to a three-base sequence for which it has no match, the process is complete. The resulting chain of amino acids is a protein. The protein is now ready to do its work in the cell.

Aneuploidy A condition in which an organism has a chromosome number that is not an exact multiple of the monoploid (m) number.

Monosomy The absence of one chromosome from an otherwise diploid cell.

Trisomy The presence of one extra chromosome in an otherwise diploid cell.

DNA replication The cellular process of making a copy of a DNA molecule.

DNA polymerase The enzyme that forms the sugar–phosphate bonds between adjacent nucleotides in a chain so that replication can occur.

Polymerization The process of building high molecular weight molecules by repeatedly chemically bonding the same compound to itself.

Ribosomes A component of cells that contain protein and tRNA. They synthesize proteins.

Ribonucleic acid (RNA) Long chains of phosphate, ribose sugar, and several bases.

Transcription In protein manufacture, the process of building RNA that is complementary to DNA.

Messenger RNA (mRNA) Nucleic acid that carries instructions to a ribosome for the synthesis of a particular protein.

Transfer RNA (tRNA) Molecules of RNA coded by DNA to bond with a specific amino acid. tRNA molecules "collect" the amino acids from the cytoplasm that the ribosomes use to manufacture proteins.

Translation In protein manufacture, the process of building an amino acid sequence according to the code specified by mRNA.

PRINCIPLES OF INHERITANCE

Alleles One of two or more alternative forms of a gene occupying corresponding sites (loci) on homologous chromosomes.

Homologous chromosomes Chromosomes having the same size and shape, occurring in pairs, and affecting the same traits.

Locus The specific location of a gene on a chromosome.

Homozygous When two genes of a pair are the same.

Heterozygous When two genes in a pair are not the same.

Inheritance The transfer of gene-containing chromosomes from parent to offspring.

Gametes The sperm from the male parent and the egg from the female parent.

Principle of segregation Mendel's first law; often called the law of segregation. The law states that when gametes are formed, the genes at a given locus separate so that each is incorporated into different gametes.

Principle of independent assortment Mendel's second law. It says that in the formation of gametes, separation of a pair of genes is independent of the separation of other pairs.

In 1866, Gregor Mendel discovered the principles of inheritance while working with garden peas. He sought to understand why peas were consistent within lines but different between lines. Our understanding of how traits are inherited has sprung from the simple experiments of this monk.

The various forms of a given gene are called **alleles**. Alleles affect the same trait, but each allele causes the production of a different protein and thus differences in the way the trait is expressed. Genes are located on molecules called chromosomes. Chromosomes that have the same size and shape and occur in pairs are called **homologous chromosomes**. Homologous chromosomes have genes that affect the same traits. The number of chromosomes containing the genetic information of an individual differs among species (Table 8–1). An animal that has matching alleles at a given point on the chromosome, or **locus**, is said to be **homozygous** (*AA*), and one with different alleles is **heterozygous** (*Aa*).

The method by which these alleles are passed on from one generation to the next is known as **inheritance**. Each parent produces reproductive cells called **gametes**, and within each gamete is a single allele for each gene. In the formation of these gametes, the parental alleles separate so that each gamete contains only half of the genetic code the parent possesses. Two important principles come into play at this point:

> The **principle of segregation** states that alleles separate so that only one (randomly chosen) is found in any particular gamete.
>
> The **principle of independent assortment** states that in the formation of gametes, separation of a pair of genes is independent of the separation of other pairs.

When the gametes combine to produce an individual, these alleles are brought together and coding for a protein begins. Any given gamete contains one allele for each gene in the genotype. A genotype is the entire genetic composition of the animal; however, genotype can also mean only the alleles of genes of interest to a particular situation.

The concept of sex determination is important in the formation of gametes. The male gametes are *sperm* and the female gametes are *eggs*. In mammals, female genotypes contain a pair of X chromosomes and males have an X and

Table 8–1
NUMBER OF CHROMOSOMES BY SPECIES

Species	Number of Chromosomes (2*n*)
Human	46
Cattle	60
Swine	38
Sheep	54
Goat	60
Horse	64
Chicken	78
Bison	60
Llama	74
Cat	38
Dog	78

Source: Compiled from Bourdon, 2000, and Van Vleck et al., 1987.

a Y chromosome. Thus a female can contribute only an X chromosome to her offspring; a male is capable of passing on either an X or a Y. The pairing of these sex chromosomes in the zygote ultimately determines the sex of an individual. In this situation, the male contributes the gamete that will determine the sex of the offspring. In the avian species, the female gamete contains pairs that do not match, making her the parent that passes on the chromosome that carries the information for sex differentiation; the male passes on gametes with only one type of sex chromosome.

Each normal body tissue cell, or **somatic cell**, of an individual has two sex chromosomes, or one pair. However, every somatic cell also has $(2n - 2)$ **autosomes**, which are simply all chromosomes other than sex chromosomes. In other words, for each somatic cell of an organism, such as a human, that has 46 chromosomes (23 pairs), two chromosomes (1 pair) are sex chromosomes and the other 44 chromosomes (22 pairs) are autosomes. Each gamete cell has one sex chromosome and $(n - 1)$ autosomes. In the human, a gamete contains 1 sex chromosome and 22 autosomes. A visual representation of the chromosomes of a species is called a *karyotype*. Karyotypes are put together by using pictures of individual chromosomes taken at metaphase (see following section). They are then arranged by chromosome number so that visual comparisons can be made (Figure 8–4).

Somatic cells All cells in the body other than gametes.

Autosomes All chromosomes other than the sex chromosomes.

The production of gametes is responsible for providing the means by which inheritance takes place. By applying the aforementioned principles, it is possible to understand how variation exists in a population. The principle of segregation, when combined with the principle of independent assortment, provides a means for randomization of alleles within the gametes.

Chromosomes occur in pairs in somatic cells. Thus a somatic cell contains a **diploid** $(2n)$ number of chromosomes. The germ cells, sperm and egg, contain only a **haploid** number (n). A chromosome can be thought of as long strands of genes. Chromosome size depends on how many genes are located on each respective chromosome. Another feature of the chromosome is the **centromere**, which can be located anywhere along the chromosome. The centromere serves as the point of attachment for the spindle fibers during cell division. The location of the chromosome is another feature that can be used to identify chromosomes. To understand the method by which somatic cells and gametes obtain their respective number of chromosomes, it is important to identify the different types of cell division.

Diploid Having two sets of chromosomes as opposed to the one set found in gametes.

Haploid A cell with half the usual number of chromosomes. Sex cells are haploid.

Centromere The region of a chromosome where spindle fibers attach.

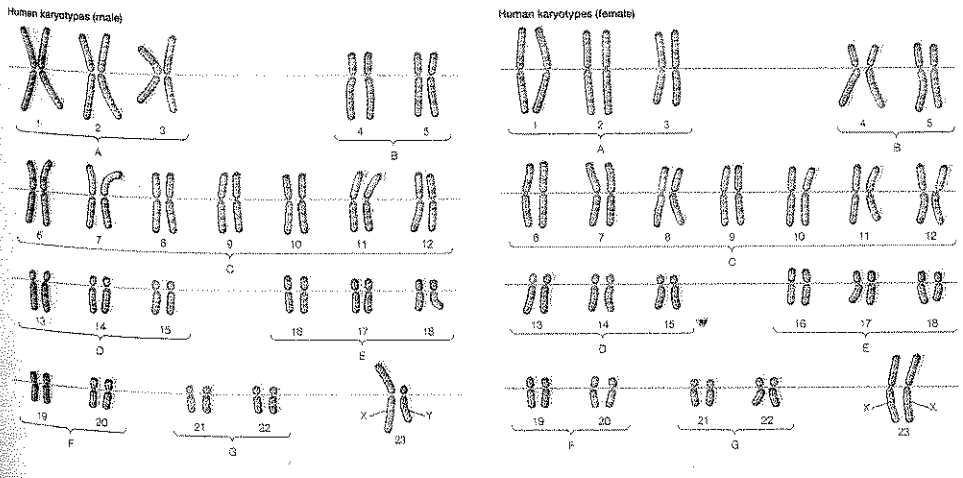


Figure 8–4
A false-color light micrograph of a normal human karyotype.

MITOSIS AND MEIOSIS

Mitosis

Mitosis The process of somatic cell division.

Mitosis is the process of somatic cell division (Figure 8–5). It occurs in normal body tissues and is responsible for the everyday maintenance of the body and for growth in young animals. Mitosis is really just replication of cells. A diploid cell undergoes division that allows the production of two diploid cells. This is a replicational process whereby a ($2n$) cell has produced a pair of matching ($2n$) cells.

Meiosis

Gametogenesis The formation of gametes.

Sperm The gamete from the male.

Oocyte The gamete from the female.

Meiosis The process that forms sex cells. Cells formed through meiosis have half the chromosomes of the parent cells.

Gametogenesis is the development of the sex cells, (i.e., **sperm** and **oocyte**). This is a reductional process ($2n$ to n) responsible for forming cells that contain half of the genetic message. The cell division that occurs in gametogenesis is called **meiosis** and consists of two divisional procedures (Figure 8–6). During the first division, one diploid cell ($2n$) divides into two haploid cells (n). The second division consists of a replication of each of the two haploid cells to produce four haploids. This process of gametogenesis is efficient in that one diploid cell divides and replicates in such a way as to produce four haploid cells. These are the cells passed on in the form of sperm or oocytes that, when combined, produce a cell with the full genetic complement of DNA.

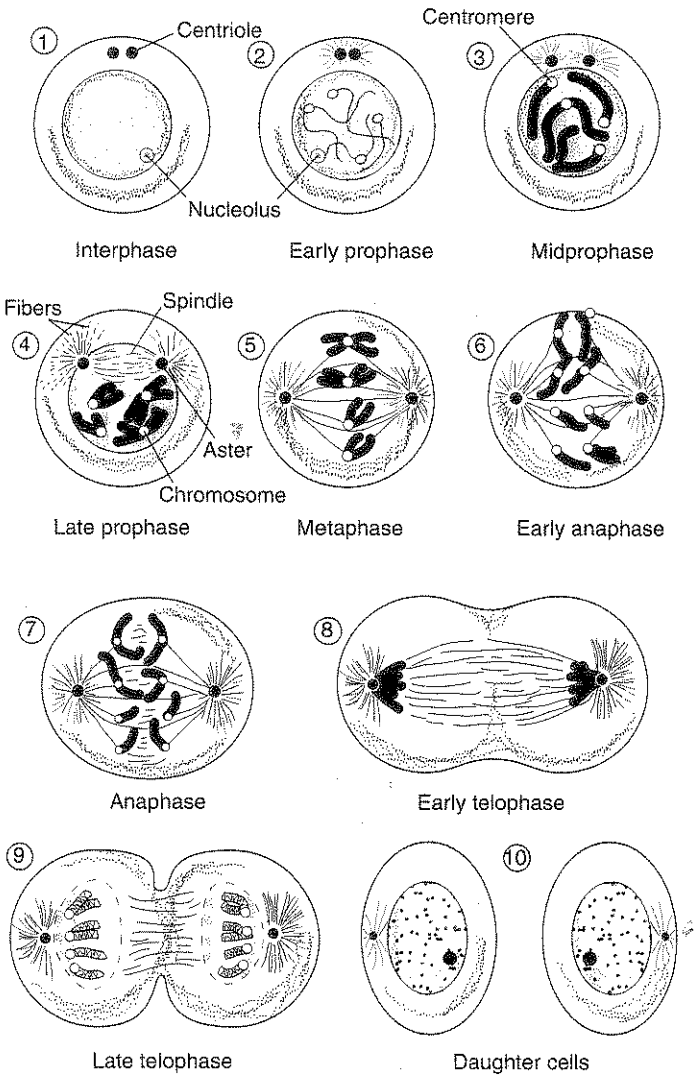


Figure 8–5
Mitosis (Source: Levine, 1980. Used with permission.)

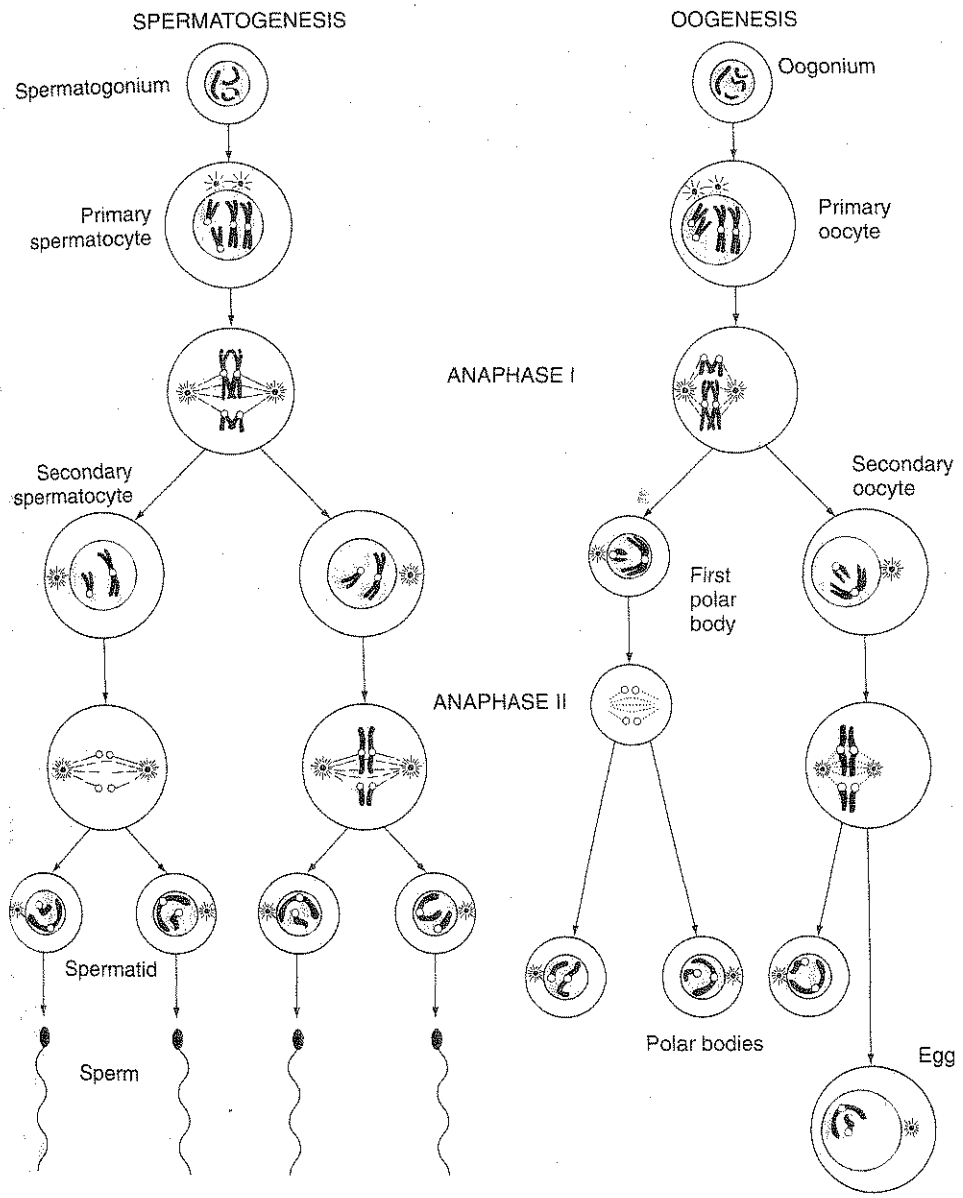


Figure 8–6
Meiosis (Source: Levine, 1980. Used with permission.)

GENE EXPRESSION

Dominant and Recessive Expression

Once the alleles have combined to determine the genetic makeup of an individual, the methods by which they become interpreted into traits, or are expressed, becomes important. **Dominant** alleles, signified by a capital letter (*A*, for example), express themselves over **recessive** alleles (*a*). For example, *R* stands for an allele that codes for black coat color, and *r* represents red coat color. If an individual receives *R* from each parent, then its genotype is *RR* and the phenotype, or physical appearance, is black. Likewise, an individual with an *Rr* genotype would also express a black coat color. In this case, the dominant allele masks the recessive and the phenotype is representative of the dominant allele. However, if an individual inherited an *r* allele from each parent, its genotype is *rr*, and the animal will express a red coat color. For the individual to have a phenotype representative of the recessive allele, both of the inherited alleles must be of the recessive form. This concept is illustrated in Figure 8–7.

Dominant One member of a gene pair is expressed to the exclusion of the other.

Recessive The member of a gene pair that is only expressed when the dominant allele is absent from the animal's genome.

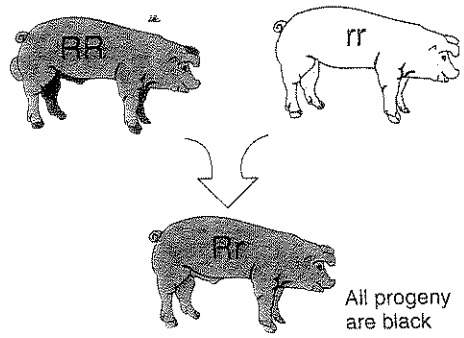
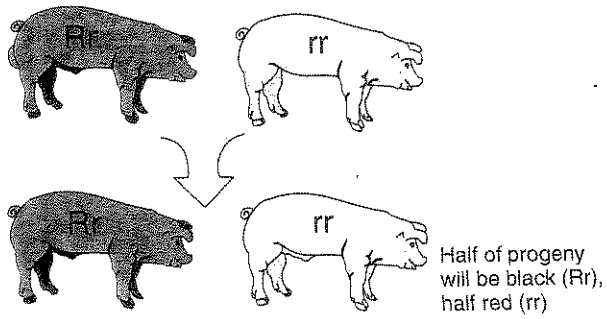


Figure 8–7
The behavior of simple dominant and recessive traits.

R represents black and r represents red. All progeny are black because the R gene each received from the sire masks the expression of r.



In this mating half the offspring receive an rr and half receive Rr. Thus half the progeny are red and half are black.

RR is the homozygous dominant condition.
Rr is the heterozygous dominant condition.
rr is the homozygous recessive condition.

Codominance

An exception to the rule of dominance occurs when neither allele masks the other and both are expressed in the phenotype. This situation is known as **codominance.** An example would be that of coat color in Shorthorn cattle. An animal that inherits one of each type of allele *RW* will express both red and white in its coat color to produce what is called a *roan color pattern.* This is illustrated in Figure 8–8.

Codominance Both alleles are expressed in the phenotype when present in the heterozygous state.

Incomplete Dominance

Incomplete dominance is a situation in which no dominance exists and a heterozygous individual will appear as an intermediate between the two alleles. We can illustrate this with an example of coat color. Assume that a particular breed expresses incomplete dominance such that a heterozygote will produce a color that is neither white nor black but rather a smutty gray that is intermediate between white and black. The terms *incomplete dominance* and *codominance* are easy to confuse. To help remember, use the Shorthorn cattle example above. The roan color in the Shorthorn is produced from codominance. If Shorthorn color were instead inherited by incomplete dominance, the coat color would be pink.

Incomplete dominance Condition in the heterozygote where both genes are expressed in a way different from either homozygous condition.

Epistasis

The previous examples discussed inheritance of genes for which gene expression is a function of only that single pair of genes. However, many gene pairs act in concert with one another to produce gene expression. In such cases, the expression of one

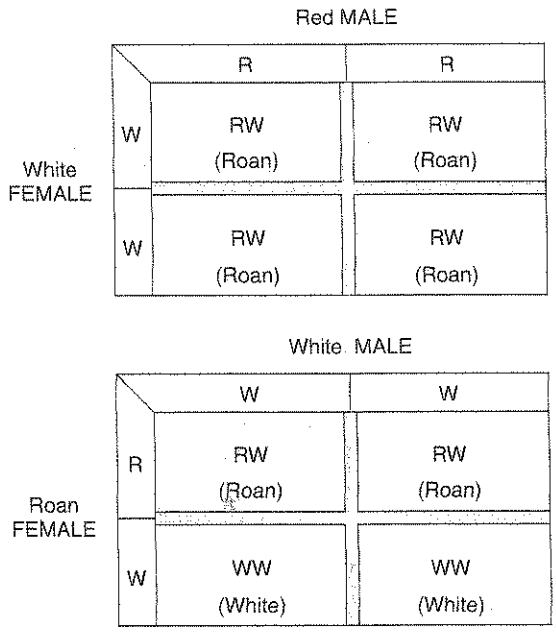


Figure 8–8
Codominance.

gene is influenced by the presence of another. This is known as **epistasis**, which is capable of causing the appearance of a dramatic departure from the principles of Mendelian inheritance. A gene may express a typical action when another specific gene is not present, but when this gene does exist and epistasis exists as well, the gene could have a totally different action. Coat color in many species is affected by epistasis. For example, horses either have black hair or they don't. This is controlled at the *E* locus. However, whether they have black hair all over their bodies or just on the **points** is controlled by the extension gene at another locus. Those with genotype *Ea* are black all over. Those with genotype *EA* are bay in color, which is typically some shade of reddish-brown body with black only on the points.

Epistasis Interaction among genes at different loci. The expression of genes at one locus depends on alleles present at one or more other loci.

Points Legs, mane, and tail.

Multiple Alleles

Remember that only two alleles can exist on each locus for an individual animal. However, there could be many alleles of a gene present in a population. This is known as a system of **multiple alleles**. A common example used to represent this concept is the A-B-O blood types in humans. Type A and type B are both dominant to type O, and types A and B are codominant to each other. In other words, if a person's genotype is *AA* or *AO*, he or she has the antigen A produced in his or her blood. Likewise, if the genotype is *BB* or *BO*, the antigen B is produced. If, however, the person has both the *A* and *B* alleles, codominance is in effect and the blood type is AB, in which both antigens are present in the blood. When the individual contains two alleles of the O blood group, the genotype is *OO*. In this case, no antigen is present in the blood.

Multiple alleles Genes with three or more alleles.

Testcrossing

It would be beneficial to be able to look at an animal and determine its genotype based on its phenotypic appearance. This would make the selection process much more efficient. It is not possible to do this when dominance is in effect. An animal that is homozygous recessive for a gene such as coat color could easily be identified because it has to have both alleles of the recessive gene. Therefore, it will express the recessive form in its phenotype. However, animals that phenotypically express the dominant form of the gene cannot be as easily identified genetically. An animal could

Testcross Mating with a fully recessive tester animal to determine if an individual is homozygous or heterozygous.

be heterozygous or homozygous dominant, either of which will express the dominant phenotype. For instances such as this, a **testcross** can determine whether the animal is homozygous or heterozygous. A testcross can be conducted by mating this individual to one with a homozygous recessive genotype, which can only contribute a recessive allele. If an offspring is produced with the recessive phenotype, then it must be homozygous recessive, which means the test animal is heterozygous. If all offspring are produced with the dominant phenotype, we can conclude the test animal is homozygous dominant, and the animal is considered to be "true breeding."

SEX-RELATED INHERITANCE

Sex-Linked Inheritance

Sex-linked inheritance Traits inherited on the X or Y chromosome and therefore inherited only when that respective chromosome is passed on.

Some genes are located only on the X or Y chromosome and therefore are inherited only when that respective chromosome is passed on. This is referred to as **sex-linked inheritance**. X and Y chromosomes are homologous to each other in certain regions. This means they contain the same, or nearly the same, genetic sequence. Sex-linked genes are those that reside in the nonhomologous portions of the X and Y chromosomes. *X*-linked genes reside in the nonhomologous area of the X chromosome and can be inherited through the acquisition of that chromosome. *X*-linked genes can be passed on to either male or female offspring because each has at least one X chromosome. For males, it is easy to determine the genotype from the phenotype for *X*-linked genes. The male has only one *X* chromosome, so the phenotype representative of X-linked genes is easily recognizable. For females, however, the genotype is more difficult to determine. Females have two X chromosomes, and the phenotype can be portrayed as either of those respective genes. *Y*-linked genes reside in the nonhomologous portion of the Y chromosome and are inherited only with that chromosome, meaning only males can have a phenotype representative of that gene.

Sex-Influenced Inheritance

Sex-influenced inheritance When the same genotype is expressed differently depending on the sex of the animal.

The genes for **sex-influenced inheritance** traits are carried on the autosomes. In sex-influenced inheritance, the phenotypes are not expressed in the same way in the two sexes. Let's examine an example of horns in sheep. In the male, the gene for horns (*H*) is dominant to the recessive form (*h*) for polledness. However, in females the *h* gene is dominant to *H*. In either case, when the genotype *HH* is present, the animals will have horns. Likewise, when either sex contains the *hh* genotype, no horns are present. In a case in which a male is heterozygous (*Hh*), horns will be present. However, if the heterozygous form of the gene is inherited in a female, she will be polled.

Sex-Limited Traits

Sex-limited traits Traits expressed in one sex or the other such as milk production in females. Both sexes carry genes for the trait.

Another example of sex-related inheritance is that of **sex-limited traits**. In this case, traits are unique to only one sex. Some examples are milk production, litter size, and egg production by females. Both sexes carry genes for these traits, but only one sex is capable of expression.

POPULATION GENETICS

Gene Frequency

Gene frequency The proportion of loci in a population that contain a particular allele.

Genotypic frequency The frequency with which a particular genotype occurs in a population.

Knowing how often genes occur in a population of animals is important to make genetic change. **Gene frequency** is defined as the proportion of loci in a population that contain a particular allele. Thus the **genotypic frequency** can be defined as how often a particular genotype occurs in a population. The proportion of individuals in

a population that express a particular phenotype is the **phenotypic frequency**. In a population of cattle in which half are horned and half are **polled**, the phenotypic frequency for polledness is 0.5, as is the frequency of horned cattle. Because many pairs of genes control most traits, it is important to expand these concepts of frequencies beyond just one pair of genes.

Phenotypic frequency The proportion of individuals in a population that express a particular phenotype.
Polled Having no horns.

Animal Breeding and Population Genetics

The study of how gene and genotypic frequencies change, and thus change genetic merit in a population, is called **population genetics**. The principles of genetics discussed previously affect not only the proportion of genes in an individual, but also the occurrence of these genes in a population. The science of using the principles of genetics to make improvement in a livestock species is **animal breeding**. Robert Bakewell is given credit for being the first animal breeder. He lived in Dishley, England, from 1726 to 1795. In his productive life as a stockman, he made significant improvements in the English Longhorn breed of cattle, the Leicester breed of sheep, and the Shire breed of horses. He practiced "breeding the best to the best," even when the animals were blood relatives. This is said to have scandalized some of his neighbors. However, others saw the merits of what he was doing and joined him in his efforts. As a result, the discipline of animal breeding was born.

Population genetics The study of how gene and genotypic frequencies change, and thus change genetic merit in a population.
Animal breeding The science of using the principles of genetics to make improvement in a livestock species.

Animal breeders seek to influence population genetics. In a population of animals, represented either by an entire breed or just a set of animals within that breed, various factors play a role in the type of animals produced. Genetic merit of the population is influenced by many interactions among genes, as well as the frequency of genes in the population. Production animal breeders must incorporate an understanding of the principles of genetics into their production practices to make the necessary genetic changes within their herd.

Mutation and Genetic Drift

To understand how gene frequencies remain stable and how they change from one generation to the next, we must define some ways in which change is made. **Mutations** are changes in the chemical composition of a gene that alter DNA. This causes the production of new alleles that can affect gene and genotypic frequencies. However, the frequency of mutations that directly affect phenotype in a population is very small. Another method by which gene frequencies change is **genetic drift**. This is a change in gene frequency owing to chance that cannot be controlled in direction, but can be controlled in amount by the size of the population. As the population gets larger, the amount of genetic drift decreases. Mutations and genetic drift cannot be used to cause genetic improvement, but direct changes in gene frequency can be accomplished using migration and selection.

Mutations Changes in the chemical composition of a gene.

Genetic drift A change in gene frequency of a small breeding population owing to chance.

Migration and Selection

Migration is the process of bringing new breeding stock into a population. Migration can be performed on a herd, a breed, or on an industrywide basis. Large changes in gene frequencies can be made quickly by this method. An important factor in migration is that the frequency of genes in the existing herd and the migrants must be different. Bringing a new sire into a population is a way to cause migration, but only if the sire's genotype is different from that of the existing population. When genotypes are very different, gene frequency can be changed quickly. **Selection** is the process of allowing some animals to be parents more than others. Selection can be expanded to include how many offspring each animal is allowed to produce and how long that animal stays in the breeding population. Two types of selection can occur.

Migration The process of bringing new breeding stock into a population.

Selection The process of allowing some animals to be parents more than others.

Figure 8–9
Through artificial selection, animals within a species have been developed into breeds as diverse as the Rottweiler and the Chihuahua. (Courtesy of Justin and Tamra Beard. Used with permission.)

Natural selection Selection based on factors that favor individuals better suited to living and reproducing in a given environment.

Natural selection is based on the fact that some animals are more suited and/or have more natural opportunity to be parents than are others. This fact is controlled by nature and can be illustrated in domestic animals using the example of a herd of cows that run with several bulls. Some bulls will sire more offspring than others will because of their aggressiveness, age, and reproductive ability. Thus in managed populations, natural selection is still a very important force. Wild populations are selected through natural selection exclusively.

Artificial selection The practice of choosing the animals in a population that will be allowed to reproduce.

The other type of selection, **artificial selection**, is controlled by the herd manager. Artificial selection is based on management decisions to allow certain animals more opportunity to mate and produce offspring than others. (In common usage, the term *artificial selection* is shortened to *selection*.) Selection involves culling less desirable animals and choosing superior replacements. Selection is a very valuable tool to the animal producer, but it has limitations as well. The effect of selection is limited by the rate at which offspring are produced or by the generation interval (Figure 8–9).

Now that an understanding of possible methods of changing gene frequency has been established, we can apply an important principle to reinforce this concept:

> The *Hardy-Weinberg law* states that in a large, random mating population where mutation, migration, and selection are nonexistent, gene and genotypic frequencies will remain stable from one generation to the next, and if there are two alleles with frequency of p_A and q_a, the genotypic frequencies are p_A^2 *AA*, $2p_Aq_a$ *Aa*, and q_a^2 *aa*.

Practically speaking, if the desired genetic merit of the herd has been achieved, no methods of selection, migration, or mutation are occurring, and the herd is large, then the gene frequencies will remain constant within that herd from one generation to the next.

Qualitative traits Those traits for which phenotypes such as coat color can be classified into groups.

Quantitative traits Those traits that are numerically measured and are usually controlled by many genes, each having a small effect, such as milk or egg production.

QUANTITY VERSUS QUALITY TRAITS

Qualitative and Quantitative Traits

Qualitative traits are those for which phenotypes can be classified into groups rather than numerically measured. Examples of such traits are coat color and the presence of horns. **Quantitative traits** are those that are numerically measured and usually

controlled by many genes, each having a small effect. One can rarely pinpoint the contribution of any particular gene to the quantitative phenotype of an animal. Most often, it is necessary to measure these traits with some kind of measuring tool. Evaluating the growth rate of pigs requires the use of scales, for example. Quantitative traits are influenced by the same types of gene action as qualitative traits are. If there is no dominance at a locus, it is referred to as **additive gene action**. Additive effects deal with individual genes, which allow for more efficient selection. For each individual gene, a representative effect on the trait occurs. For instance, if one A^+ represents a calf that is 2 lbs heavier at birth, then an animal with the genotype of A^+A^+ will be 4 lbs heavier than one with the alleles AA. Likewise, a calf with the genotype A^+A would be 2 lbs heavier than a calf with the genotype AA.

Additive gene action
When the total phenotypic effect is the sum of the individual effects of the alleles.

Just as the type of inheritance affects a specific trait, the environment in which the animal is raised has an effect on the expression of quantitative traits. The genetic merit is very valuable in producing animals with certain characteristics or animals that perform to certain levels. However, factors such as climate, management practices, and health determine whether the animal performs to its genetic potential. This nongenetic source of variation is one that must be considered when evaluating animals based on quantitative traits. Using this understanding, it is easy to realize that the phenotype is a result of the genotype and environmental interaction.

Heritability

Differences in the phenotypes of animals are due to genetics and environment. Only the additive genetic effects are inherited. The proportion of the difference in individuals that is due to additive gene effects is known as **heritability**. Practically speaking, heritability is a measure of the proportion of phenotypic variation that can be passed from parent to offspring. Heritability is thus used as an indicator of the amount of genetic progress that can be achieved by choosing superior parents. The range of values for heritabilities is from zero to one, and they can be thought of as percentages or proportions. Heritability estimates have been calculated for most important traits for the different livestock species and can be used to give an indication of how much progress can be made in traits from generation to generation.

Heritability A measure of the proportion of the phenotypic variation that is due to additive gene effects.

We can use an example of litter size here to demonstrate how heritability acts. Assume a group of sows is averaging 7 pigs per litter and a producer wishes to improve this number. For his next matings, he chooses boars and sows from litters averaging 11 pigs. The first step is to calculate a **selection differential**. This selection differential is the phenotypic advantage of those chosen to be parents. The selection differential here is 11 – 7, or 4 pigs. Now, assuming that the heritability of litter size is 0.10, we can expect only 10% of the 4-pig selection differential to be inherited, or 0.4 of a pig per litter. Thus, we would expect the litters from these selected parents to be 0.4 pigs bigger, or 7.4 pigs per litter compared to 7 pigs. This might not seem like much progress. However, litter size is a trait that is quite important from an economical standpoint and improvement of .4 pigs per litter would make a big difference in a large swine operation. It is easy to see that traits with higher heritability estimates can be selected with much greater efficiency. Lowly heritable traits don't express much change from generation to generation from selection.

Selection differential The phenotypic advantage of those chosen to be parents. The difference in the mean of those chosen to be parents and the mean of the population.

As a rule, carcass merit traits are considered to be highly heritable (0.4–0.6), which is encouraging because there is increased interest in, and demand for, specific carcass characteristics to meet today's market needs. This enthusiasm should be tempered by the knowledge that carcass traits are difficult to measure accurately in potential parents. Moderately heritable traits are those having heritabilities of 0.2–0.4. Growth traits are examples of moderately heritable traits and are selected for less progress when compared to carcass traits. Traits such as reproductive ability have low

heritabilities (0–0.2), which is unfortunate considering they are among the most economically important traits in animal production.

Through the process of making genetic improvement in a population, animals begin to share similarities in their genetic composition. The relationship between two animals can be thought of as the proportion of genes they are expected to have in common. Siblings or offspring that have at least one parent in common inherit some of their genes from that parent, and thus the brothers and sisters have some of those gene pairs in common. The relationship coefficient can range from 0–1 and is most often by a factor of half. The following is a list of common relationships:

	R
Full-sibs	0.5
Half-sibs	0.25
Parent-offspring	0.5
Grandparent-offspring	0.25
Great-grandparent	0.125
Great-great-grandparent	0.0625
First cousin	0.125

These values are an indication of how closely related the individuals are. Notice that the further back in the animal's pedigree a relative exists, the smaller the value of the relationship.

Systems of Mating

Inbreeding The mating of closely related individuals.

Inbreeding depression A loss or reduction in vigor, viability, or production that usually accompanies inbreeding.

Linebreeding Mating system in which the relationship of an individual is kept close to an outstanding ancestor by having the ancestor appear multiple times on both sides of the pedigree.

Inbreeding is the mating of closely related individuals (Figure 8–10). It is used to increase homozygosity for desired traits. When practiced in a herd, inbreeding decreases the variation in the genes existing in a herd or population. Individual animals will have more gene pairs in the homozygous state. As this happens, detrimental recessive genes also begin to express themselves because of the increase in homozygosity. Therefore, it is important to avoid high levels of inbreeding so that expression of bad recessive genes can be minimized, while allowing more expression of the good ones. Inbreeding causes a decline in performance that is called **inbreeding depression**.

Linebreeding is a form of inbreeding in which the purpose is to concentrate the genes of an outstanding ancestor in the linebred individuals. Linebreeding may result in mild inbreeding if the common ancestor appears at least three to four generations back in the pedigree. However, the inbreeding can be intense with parent offspring matings or after several generations of linebreeding to the same common ancestor. The adoption of modern genetic evaluations has replaced the practice of linebreeding in the livestock species. However, linebred pedigrees are relatively common in many companion animal species, especially in those bred for show ring type.

Figure 8–10
Historically, inbreeding has been practiced to fix the traits associated with breeds such as color and markings, horns, and production traits to produce animals with distinctive characteristics. Compare these distinctly different beef breeds: the Angus and the Brahman.
(Photos courtesy of Christy Collins, Inc. Used with permission.)

Outbreeding is the process of mating less closely related individuals when compared to the average of the population. This can be applied to animals in the population as well as animals as far out as another breed. The effect of this is directly opposite to that of inbreeding. This procedure produces individuals that have more heterozygous gene pairs. This increase in heterozygosity increases the vigor in the animals, which is termed **heterosis**, or hybrid vigor. Heterosis is defined as the superiority of an outbred individual relative to the average performance of the parent populations. Traits that are lowly heritable often show high levels of heterosis. Reproductive traits are a good example of a lowly heritable trait that shows high levels of heterosis. Moderately heritable traits show moderate levels of heterosis, such as the growth traits. Highly heritable traits show little heterosis. The amount of heterosis that is used can either be increased or decreased by the system of mating used.

Outbreeding The process of mating less closely related individuals when compared to the average of the population.

Heterosis The superiority of an outbred individual relative to the average performance of the parent populations included in the cross.

Crossbreeding, mating animals from different breeds, is a means of taking advantage of outbreeding. Each breed is generally more homozygous than the average of the population. By mating individuals from different breeds, a breeder can take advantage of the homozygocity of the parents to ensure heterozygocity in the offspring. The success of a crossbreeding program depends on the quality of the animals used in the system and whether or not their genetics complement each other. Therefore, it is essential to use breeds that complement each other well to strengthen the good traits and decrease expression of the bad ones. Reproductive traits benefit from crossbreeding systems. On average, crossbred females have more offspring (litter-bearing species) and have better mothering characteristics than the average of the two breeds used to produce them. Many times, breeders produce crossbred females and then mate them to a purebred sire of a third breed that excels in non-maternal traits such as feedlot performance or carcass characteristics to take full advantage of the heterosis in both the offspring and the dam, as well as the strengths of each of the breeds. Elaborate methods of controlled crossbreeding have been developed to capitalize on the advantages breeds can offer in outcrossing. In general, crossbred individuals tend to be more vigorous, fertile, and healthy, and grow faster than the average of parental stock that make up the cross.

Crossbreeding Mating animals of diverse genetic backgrounds (breeds) within a species.

Several different methods can be used to evaluate how much genetic contribution an animal will have in any breeding scheme. Methods are being applied to evaluate parents and determine an estimate of their genetic merit. This information can be used to get an idea of the additive genetic merit of an individual, and in selecting animals that have the opportunity to produce offspring that excel in the evaluated traits. These predictions of genetic merit are based on records of the individual's own performance as well as the performance of all relatives. Relatives that are more closely related to the animal being evaluated are more beneficial because they are more likely to contain similar genetic makeup. However, all related animals are useful because they share at least some common genes. Breeding values are covered in more detail in the next chapter.

BIOTECHNOLOGY AND GENETIC ENGINEERING

Genetics is an area of science that is contributing greatly to the overall advancements being made in **biotechnology**. In fact, the advances made in recombinant DNA technology, often called *genetic engineering*, have made it the most recognizable form of biotechnology being practiced today. It is common for people to think of biotechnology and genetic engineering as synonymous terms and not realize there are other areas of biotechnology.

Biotechnology A set of powerful tools that employ living organisms (or parts of organisms) to make or modify products, improve plants or animals, or develop microorganisms for specific uses.

Molecular biology has made it possible to identify the specific genes that control various characteristics. Worldwide, scientists are working to identify all of the

genes of humans and animals, as well as their actual DNA sequences. This mapping of the genome is one of the finest examples of shared information and cooperation in the history of science. Scientists in laboratories scattered to the corners of the earth communicate, contribute information to shared databases, and work together to untangle the mysteries of the genetic code. Once genes are located on the chromosome and the functions they control are identified, then more precise animal breeding practices can be employed. For example, a trait like meat tenderness, which cannot be measured directly on potential parents, may be influenced by a few genes with large effects and DNA markers could be used to identify those individuals that possess the favorable alleles associated with meat tenderness. Although conventional selection on performance characteristics would still be used, it could be enhanced through the inclusion of genetic markers obtained through DNA analysis. This is referred to as **marker-assisted selection**. Marker-assisted selection is currently being employed through several efforts in different types of livestock. For example, genomic information has been incorporated into predictions of genetic merit in dairy cattle since 2009. The American Angus Association now includes genomic information in its predictions of genetic merit. Various suppliers of swine and poultry breeding stock routinely include genomic information to enhance genetic improvement in their lines. In addition, inserting the genes from one animal into another can create new combinations of genes. This can even be done between species. This process of genetic modification creates a **transgenic** animal. These concepts are explored further in a later chapter.

Marker-assisted selection Selection for specific alleles using markers such as linked DNA sequences.

Transgenic An animal or plant that has had DNA from an external source inserted into its genetic code.

The benefits of this new form of genetic manipulation over conventional forms are multiple. In traditional breeding practices, many of the genes passed to the next generation are unknown. More individual genes and markers are being identified rapidly in all types of livestock that will allow precision breeding, which will ensure that good genes are passed on and undesirable ones excluded. Outcomes will be easier to predict. In transgenic animals, even less guesswork will be involved because the exact genetic information being transferred to create a transgenic animal will be known. The speed of genetic improvement will be increased because the genetics of a set of potential breeding animals can be mapped long before they even reach puberty. In traditional breeding schemes, identifying the genetics of an individual often has to wait for the birth and development of its offspring.

As exciting as the potentials are for improving livestock for production purposes, the area of greatest promise for gene manipulation and recombinant DNA technology is in a slightly different area. Genes can be inserted from animals of the same species. However, they can also be inserted from any species into another. Human genes can be inserted into bacteria or other species of animals. Fish genes can be inserted into pigs, and so on. Although several potential benefits can be envisioned from this procedure, one area holds incredible promise. Animals, microorganisms, and plants can be genetically manipulated to produce substances they otherwise could not produce. For example, bacteria now produce human insulin that is identical to the insulin produced by the human body. Prior to the commercial availability of this insulin, diabetics depended on the insulin of pigs and cattle, which was harvested as a slaughter by-product. Although life saving, this insulin was slightly different from that produced by humans. Now insulin-dependent diabetics can use the same insulin their bodies refuse to produce for them. Already, goats, sheep, and cows have been genetically manipulated to produce foreign proteins in their milk that have value in treating diseases. Most of these are protein products. The animals that produce these compounds are simply milked and the compound is purified. In this way, these transgenic animals can produce large quantities of therapeutic agents that are otherwise not available or are too expensive to produce. Many more of these applications are

expected in the very near future. Transgenic chickens will probably be producing a range of therapeutic medicinals in their eggs in the near future.

Gene mapping and, subsequently, improved selection, combined with the use of transgenics for specific genes, will provide benefits in other areas as well. Specific gene therapies will be developed for diseases in animals and humans. Obviously, these are being developed with humans as the highest priority. Scientists working in this field confidently predict the availability of several dozen such gene therapies within the decade. Animals can be genetically manipulated to produce strains that will serve as models for the study of various human diseases. It is also likely that animals can be transgenically altered to produce organs that do not trigger rejection reactions for transplant into humans. Animals will be selected through the use of mapping technology to be resistant to specific diseases, reducing or eliminating the need for vaccines, antibiotics, chemicals, and other means of disease control and prevention. Biotechnology is explored in greater detail in a subsequent chapter.

SUMMARY AND CONCLUSION

Genetics is the study of how DNA codes for the biochemical reactions of life. From a practical perspective, it is important to understand how to direct the genetics of the next generation so the genetic material of the animals produced causes them to have characteristics that are considered economically important. Cells in the body reproduce by two processes. Mitosis is the process used for the growth and maintenance of body tissue. Meiosis is the other process, which differs from mitosis in that the genetic material of an individual is halved before the cell reproduces itself. This process leads to a recombination of genetic material, half from each parent, when sperm and egg unite. Humans have been manipulating the genetic codes of some species for millennia. The organized effort of animal breeding began in the 18th century with the work of an English stockman named Robert Bakewell. Modern animal-breeding techniques have led us to organized efforts that help us manipulate the genetic code. These techniques include breeding relatives through inbreeding and linebreeding to fix certain genetic types, and outbreeding and crossbreeding to maximize heterozygosity. The tools of modern molecular biology are revolutionizing the science of genetics. What used to take generations to accomplish is now possible in one generation. In addition, animals, microorganisms, and plants are being genetically altered to provide a wide range of medicinal products for our benefit. This evolving area of science is perhaps the most promising area of scientific discovery being pursued today.

STUDY QUESTIONS

1. Define the term *gene*.
2. Draw a DNA molecule with four base pairs.
3. List the two types of nitrogen bases in a DNA molecule.
4. What kind of bond holds these bases together?
5. Describe what is meant by supercoiling of DNA.
6. What is the variation in chromosome numbers when more than one full set is present in an individual?
7. Down syndrome is an example of what type of chromosomal variation?
8. What is the process that takes place within the nucleus of a cell whereby a copy of a DNA molecule is formed from another?
9. What is an allele?
10. What is the difference between an animal that is homozygous for a gene and one that is heterozygous?
11. Describe the relationship between a gamete and a somatic cell with regard to the number of chromosomes in each.
12. What is the entire genetic composition of an individual referred to as?
13. List the two types of sex chromosomes.
14. Each somatic cell contains _____ autosomes, whereas the same cell contains _____ sex chromosomes.
15. Each gamete contains _____ autosomes and _____ sex chromosomes.

16. Describe in general terms the process of mitosis.
17. Describe in general terms the outcomes of meiosis.
18. Compare/contrast dominant and recessive alleles.
19. What is the physical appearance of an animal known as?
20. Describe an example of codominance and an example of incomplete dominance.
21. The blood types of humans serve as a good example of what kind of allelic situation?
22. Explain the concept of sex-linked inheritance with relation to the X and Y chromosomes.
23. When the sex of an individual determines how a gene is expressed in the phenotype, this is known as a _____ trait.
24. Milk production is an example of what kind of trait?
25. Define *population genetics.*
26. What does the term *gene frequency* describe?
27. What are four methods by which gene frequencies are changed in a population? Briefly describe each.
28. Compare natural selection with artificial selection.
29. What kind of gene action takes place in qualitative versus quantitative traits? Name an example trait for each type.
30. What is the major nongenetic source of variation discussed in this chapter? Give three examples.
31. Define *heritability.* What is the range for heritability values?
32. A trait that is lowly/highly (circle one) heritable for a given trait allows more genetic change for that trait from one generation to the next.
33. Give examples of high, moderate, and lowly heritable traits.
34. Describe the systems of mating discussed in this chapter.
35. What is biotechnology? Genetic engineering? How are they related?
36. Describe some of the potential benefits to humans of the manipulation of the genetic code.

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Author's Note: For the second, third, and fifth editions, Dr. David S. Buchanan, Professor, Animal Science, formerly of Oklahoma State University and now of North Dakota State University, reviewed this chapter. In addition, Dr. Buchanan contributed new material to the chapter with each review. For the fourth and fifth editions, Dr. Tony Seykora, Professor, Dairy Genetics, University of Minnesota, reviewed this chapter. Dr. Seykora contributed new material. The author gratefully acknowledges these contributions.

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