14
Non-Mendelian Genetics

Learning Objectives

In this chapter, you will learn:

- ➜ Linked Genes
- ➜ Multiple Gene Inheritance
- ➜ Nonnuclear Inheritance
- ➜ Phenotype = Genotype + Environment

Overview

The inheritance of many traits do not follow the laws of Mendelian genetics. When the observed ratios of phenotypes in the offspring do not follow the ratios predicted by the Punnett squares and Mendelian laws, it may be the result of linked genes, multiple genes coding for the phenotype, nonnuclear inheritance, or even the effects of the environment on the phenotype, all of which will be discussed in this chapter.

Linked Genes

As discussed in Chapter 12, genes that are close together on the same chromosome are said to be linked. Since **linked genes** are on the same chromosome (which is a long piece of DNA), they tend to be inherited together more often than unlinked genes (which are on separate chromosomes).

During prophase I of meiosis, genetic recombination may occur between linked genes. The farther apart two linked genes are on a chromosome, the more likely a genetic recombination event will occur because there is more space in which recombination can happen. The closer together two linked genes are on a chromosome, the less likely a genetic recombination event will occur. Recombination frequencies can be used to create genetic maps that show the distance between genes on a chromosome, as shown in Table 14.1 and Figure 14.1. The distance between genes is measured in **map units**. A recombination frequency of 10% between two genes would place those two genes 10 map units apart. A recombination frequency of 25% between two genes would place those two genes 25 map units apart.

Table 14.1 Genes and Recombination Frequencies

Genes	Recombination Frequency
A and *B*	10%
B and *C*	15%
A and *C*	25%

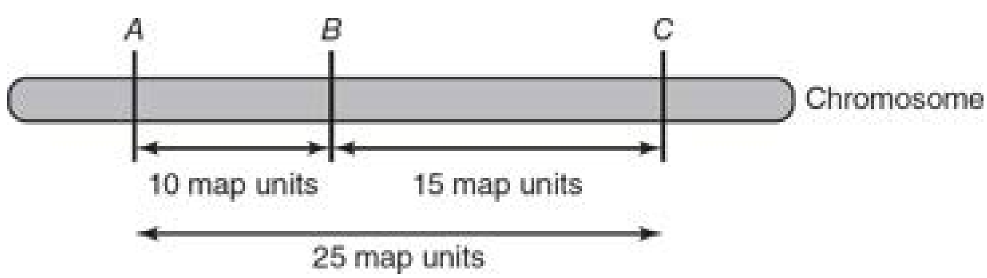


Figure 14.1 Genetic Map from Recombination Frequencies

Sex-Linked Genes

Most genes are located on **autosomes**, chromosomes that are not directly involved in sex determination. Males and females are equally likely to inherit genes located on autosomes. **Sex chromosomes** are involved in sex determination, and genes on sex chromosomes have different inheritance patterns than genes on autosomes.

A special case of linked genes are sex-linked genes. **Sex-linked genes** are genes that are located on sex chromosomes. Sex chromosomes are nonhomologous in humans; females typically have two X chromosomes, and males have one X and one Y chromosome. For this reason, traits that are coded for by sex-linked recessive alleles are more likely to be expressed in males since males have only one X chromosome. Females could also express a sex-linked recessive trait, but since females have two X chromosomes, a female would need to inherit the allele for the trait from both parents in order to express it. When looking at a pedigree that shows more males with the trait than females, it is likely the trait is coded for by a gene that is located on a sex chromosome, as shown in Figure 14.2.

TIP

Remember, in pedigrees, squares typically represent males and circles represent females. Shaded figures usually represent individuals who possess the trait.

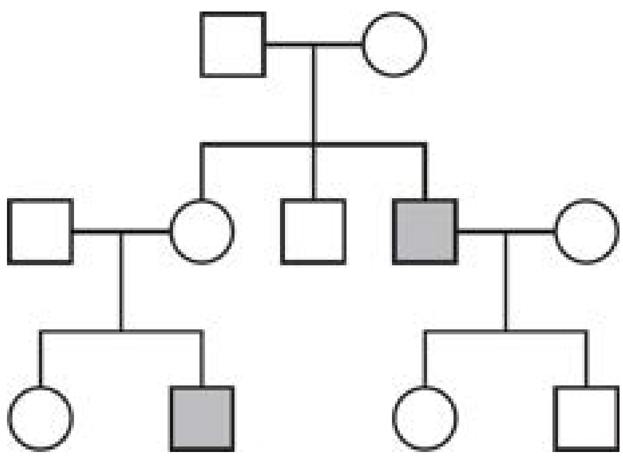


Figure 14.2 Pedigree for a Sex-Linked Trait

Examples of sex-linked recessive traits in humans include hemophilia and color blindness.

There are sex-linked dominant traits in humans, but these are very rare. If a male has a sex-linked dominant trait, all of his daughters will inherit the trait because all females inherit an X chromosome from their father. If a female has a sex-linked dominant trait, both her sons and daughters will have a 50% chance of inheriting the trait.

Multiple Gene Inheritance

Some traits are produced by multiple genes acting together to produce the phenotype. Because more than one gene is involved in producing the trait, these traits would not follow the ratios predicted by Mendelian laws. Some examples of traits that are produced by multiple genes are height and eye color. For example, say height in a plant is determined by three genes (*A, B*, and *C*), and each dominant allele present in the three genes has an additive effect on the plant's height. The more dominant alleles a plant inherits, the taller the plant will be. A plant with the genotype *AABBCC* would be very tall, while a plant with the genotype *aabbcc* would be very short. A plant with the genotype *AaBbCc* would have a height in the middle of the range. Note that many different genotypes (i.e., *AAbbCc* or *AaBBcc* or *aaBbCC*) would result in a plant with a height in the middle of the range.

Nonnuclear Inheritance

As discussed in Chapter 5, mitochondria and chloroplasts have their own DNA separate from nuclear DNA. Genes on mitochondrial or chloroplast DNA do not follow the inheritance patterns seen in genes located on nuclear DNA.

During gamete formation, the eggs produced in animals and the ovules produced in plants are much, much larger than the sperm (in animals) or pollen (in plants) that are produced. Since the eggs and ovules are larger, they contribute far more mitochondria and mitochondrial DNA (mtDNA) than the sperm or pollen do. In plants, the ovules also contribute more chloroplast DNA (cpDNA) than the pollen do. For this reason, traits on nonnuclear DNA in the mitochondria or chloroplast demonstrate maternal inheritance. Figure 14.3 shows a pedigree that illustrates an example of maternal inheritance. Note that the trait can be passed from mother to either her sons or her daughters. Males with the trait do not pass it on to their offspring.

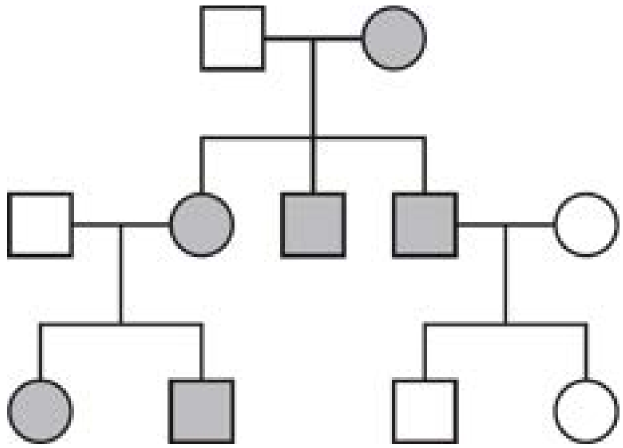


Figure 14.3 Pedigree Showing Nonnuclear Maternal Inheritance

> It is important to note the difference between nonnuclear maternal inheritance and sex-linked inheritance. In sex-linked inheritance, sex-linked genes are located on a sex chromosome (usually the X chromosome) in the nucleus and can be inherited from either fathers or mothers. In nonnuclear inheritance, genes are located in the mitochondria or the chloroplast and can only be inherited from the mother.

Phenotype = Genotype + Environment

The environment can affect gene expression and the resulting phenotype of an organism. For example, in the flowers of the hydrangea plant, a basic soil pH results in flowers with a pink color, while an acidic pH results in blue flowers. In humans, exposure to ultraviolet light can stimulate the expression of genes involved in the production of melanin. This ability of the same genotypes to produce different phenotypes in response to different environmental factors is called **phenotypic plasticity**.

Practice Questions

Multiple-Choice

1. Two genes that are close together on the same chromosome are said to be _______ and are _______ likely to be inherited together than _______ genes.

   (A) linked; less; unlinked
   (B) linked; more; unlinked
   (C) unlinked; less; linked
   (D) unlinked; more; linked

2. Sex-linked recessive traits in humans are _______ likely to be expressed in _______.

   (A) less; males
   (B) more; females
   (C) more; males
   (D) equally; both males and females

3. An example of a trait that involves multiple gene inheritance in plants is seed size. If seed size involves three genes (*A*, *B*, and *C*), in which each dominant allele contributes to increased seed size, which of the following genotypes would result in the smallest seed?

   (A) *AABBCC*
   (B) *AaBBCc*
   (C) *AaBbCC*
   (D) *AaBbCc*

4. Which of the following statements best explains the difference between nonnuclear inheritance and sex-linked inheritance?

   (A) Females may pass on nonnuclear and sex-linked traits to both their sons and daughters, but only their sons may pass on nonnuclear traits to the next generation.

(B) Females may pass on nonnuclear and sex-linked traits to both their sons and daughters, but only their daughters may pass on nonnuclear traits to the next generation.

(C) Females may pass on sex-linked traits to their offspring, but they cannot pass on nonnuclear traits to their offspring.

(D) Females may pass on nonnuclear traits to their offspring, but they cannot pass on sex-linked traits to their offspring.

5. Two snowshoe hares (a type of rabbit) have the same genotype. During the winter, the hare that lives outdoors in the cold has white fur, but the hare that lives in a climate-controlled and warm environment has brown fur. This is an example of _______.

(A) sex-linkage

(B) multiple gene inheritance

(C) nonnuclear inheritance

(D) phenotypic plasticity

6. In *Drosophila* (fruit flies), females have two XX chromosomes, and males have one X chromosome and one Y chromosome. The eye color gene is located on the X chromosome, and the red-eyed allele is dominant to the white-eyed allele. A heterozygous, red-eyed female is mated with a white-eyed male. Which of the following is the most likely result in their offspring?

(A) All females are red-eyed, and all males are white-eyed.

(B) All females are red-eyed, 50% of males are red-eyed, and 50% of males are white-eyed.

(C) 50% of females are red-eyed, 50% of females are white-eyed, and all males are white-eyed.

(D) 50% of both sexes are red-eyed, and 50% of both sexes are white-eyed.

7. Sex determination in birds follows the ZW system, where males have two copies of the Z chromosome (ZZ) and females are heterozygous (ZW). A male bird (who is heterozygous for a trait on the Z chromosome) is mated with a female bird (who expresses the recessive phenotype for that trait). Which of the following best describes their most likely offspring?

   (A) 25% males with the dominant phenotype, 25% males with the recessive phenotype, 25% females with the dominant phenotype, and 25% females with the recessive phenotype
   (B) all males with the dominant phenotype and all females with the recessive phenotype
   (C) 25% males with the dominant phenotype, 25% males with the recessive phenotype, and 50% females with the recessive phenotype
   (D) 50% males with the dominant phenotype, 25% females with the dominant phenotype, and 25% females with the recessive phenotype

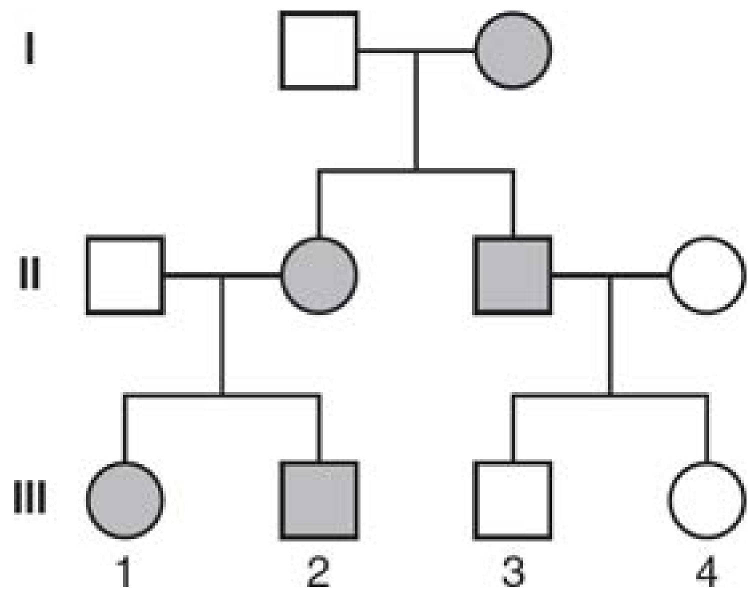
8. Cats with two X chromosomes are female, and cats with one X and one Y chromosome are male. The gene for fur color in cats is on the X chromosome: X^B is the black allele and X^o is the orange allele. Cats who are heterozygous express the calico phenotype, with patches of black fur and patches of orange fur. A female calico cat is mated with a black male cat. Which of the following best describes the predicted ratios of their offspring?

   (A) $\frac{1}{2}$ of the offspring would be female calico cats, and $\frac{1}{2}$ of the offspring would be male black cats.
   (B) $\frac{1}{4}$ of the offspring would be female black cats, $\frac{1}{4}$ of the offspring would be female calico cats, $\frac{1}{4}$ of the offspring would be male black cats, and $\frac{1}{4}$ of the offspring would be male orange cats.
   (C) $\frac{1}{2}$ of the offspring would be female black cats, and $\frac{1}{2}$ of the offspring would be male calico cats.

(D) $\frac{1}{2}$ of the offspring would be female black cats, $\frac{1}{4}$ of the offspring would be male black cats, and $\frac{1}{4}$ of the offspring would be male orange cats.

Questions 9 and 10

Refer to the figure, which shows a pedigree of an inherited trait.



9. Based on this pedigree, which of the following most likely describes the inheritance of this trait?

(A) autosomal dominant
(B) autosomal recessive
(C) sex-linked recessive
(D) mitochondrial inheritance

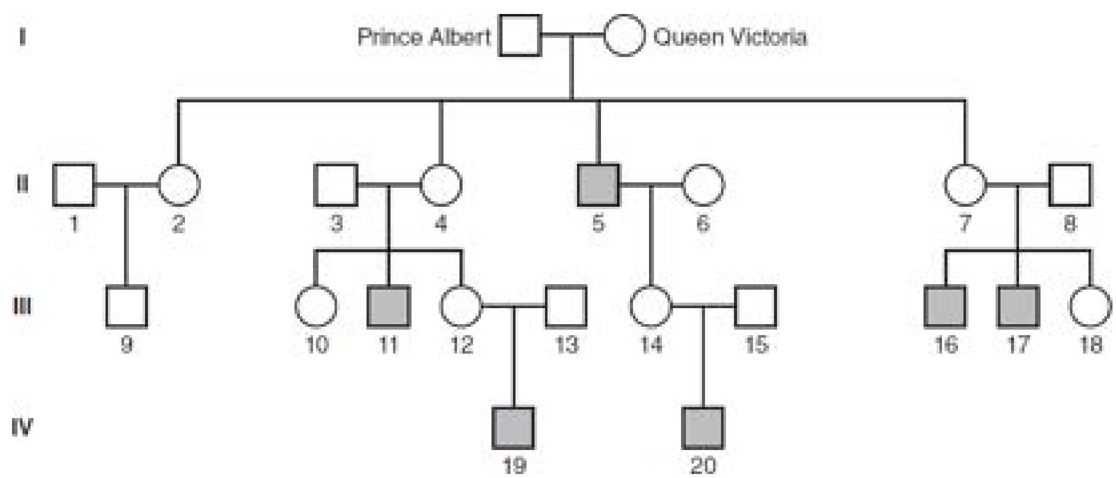
10. If individual III-3 has a child with a woman who does not have the allele, what is the most likely probability that their child will have the trait?

(A) 0%

(B) 25%
(C) 50%
(D) 100%

Short Free-Response

11. Hemophilia is a sex-linked recessive disorder on the X chromosome. The following figure shows a portion of a pedigree of the descendants of Queen Victoria of England. Individuals with hemophilia are indicated by shading.



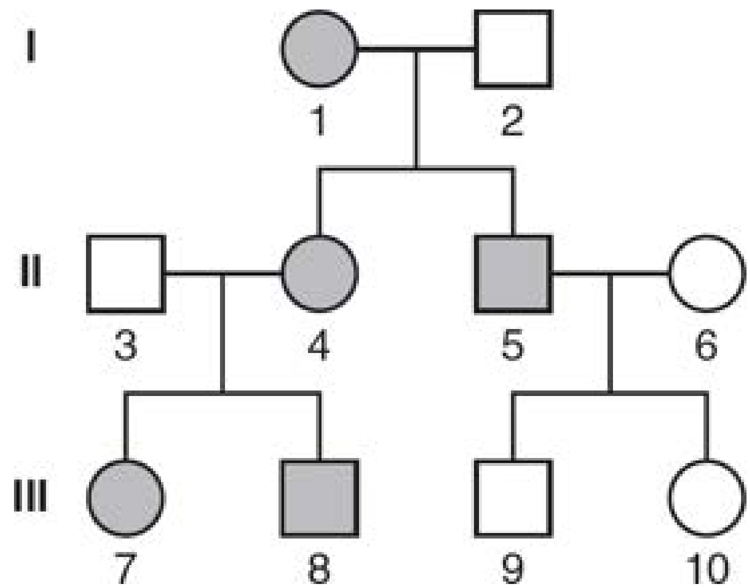
(a) **Describe** the genotype of individual 4 in generation II. **Justify** your answer with evidence from the pedigree.

(b) What is the genotype of individual 14 in generation III? **Explain** how you know her genotype.

(c) Create a Punnett square that **represents** the possible genotypes of the offspring of individuals 7 and 8 in generation II.

(d) **Explain** why the offspring of two closely related individuals are more likely to express recessive traits.

12. This pedigree shows the inheritance of a trait in three generations of a family.



(a) **Describe** a likely mode of inheritance of this trait. Use evidence from the pedigree to **justify** your answer.

(b) **Explain** how a pedigree for a trait that is recessive would look different from a pedigree for a trait that is dominant.

(c) A student makes a claim that this pedigree indicates the trait is inherited through mitochondrial DNA. **Evaluate** this claim using evidence from the pedigree.

(d) **Explain** why the pattern of inheritance of an autosomal dominant trait is different from the pattern of inheritance of a mitochondrial trait.

Long Free-Response

13. In *Drosophila* (fruit flies), eye color is on the X chromosome. Male flies have an X and a Y chromosome, and female flies have two X chromosomes.

(a) A red-eyed male fly is mated with a white-eyed female fly. All the resulting female offspring have red eyes, and all the resulting male offspring have white eyes. **Explain** which trait, red eyes or white eyes, is dominant and why. **Draw** a Punnett square to support your answer.

(b) Scientists have discovered that white-eyed flies have a mutation in the enzyme TRY 2,3-dioxygenase (TDO2). TDO2 mutations prevent the accumulation of kynurenine, a compound associated with aging. White-eyed flies and red-eyed flies were raised under identical conditions, and the mean life span of both type of flies was recorded. **Identify** the independent variable and the dependent variable in that experiment.

(c) The data from the experiment described in part (b) are shown in the following table.

Phenotype	Mean Life Span in Days (± 2SEM*)
White-eyed flies	42.8 (± 5.8)
Red-eyed flies	29.1 (± 4.9)

*Standard Error of the Mean

Evaluate the data to determine whether or not there is likely a statistically significant difference in the life spans of white-eyed and red-eyed flies based on this experiment.

(d) A nondisjunction event in meiosis leads to the production of a heterozygous red-eyed male fly with two X chromosomes and one Y chromosome. **Predict** the possible offspring from a mating between this male and a white-eyed female, and **justify** your answer.

Answer Explanations

Multiple-Choice

1. **(B)** Genes that are close together on the same chromosome are *linked* and are *more* likely to be inherited together (since they are close together on the same piece of DNA) than *unlinked* genes. Choice (A) is incorrect because linked genes are more, not less, likely to be inherited together. Choices (C) and (D) are incorrect because unlinked genes may be either on separate chromosomes or far apart on the same chromosome.

2. **(C)** Sex-linked genes are *more* likely to be expressed in *males* since males have only one X chromosome. Choice (A) is incorrect because sex-linked genes are more likely, not less likely, to be expressed in males. Females have two X chromosomes, so a sex-linked recessive trait is less likely to be expressed in females because a female would have to inherit two copies of the allele while a male would only have to inherit one copy of the allele for it to be expressed. Thus, choices (B) and (D) are both incorrect.

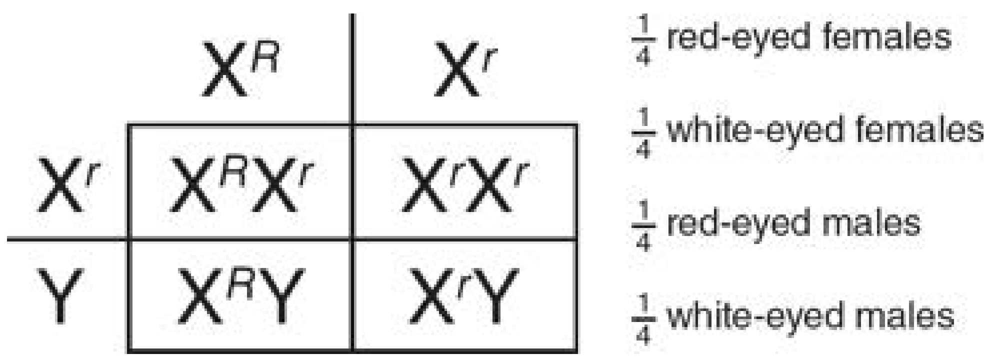
3. **(D)** *AaBbCc* has the least number of dominant alleles (three) out of all the answer choices given. So the additive effect of the alleles in that genotype would be the least, and this genotype would result in the smallest seed. Since each dominant allele contributes to increased seed size, choice (A) is incorrect because it has the highest number of dominant alleles out of all the answer choices given. So it would produce the largest seeds. Choices (B) and (C) are incorrect because they both have four dominant alleles, so they both would produce larger seeds than choice (D).

4. **(B)** Females may pass on sex-linked traits to the next generation through their X chromosomes and nonnuclear traits through their mitochondrial DNA. Since mitochondrial DNA is passed on through eggs and not sperm, males cannot pass on nonnuclear traits to the next generation, but females may pass on nonnuclear traits to the next generation. Therefore,

the only true statement is choice (B), and choices (A), (C), and (D) are incorrect.

5. **(D)** Phenotypic plasticity describes the ability of two individuals with the same genotype to produce different phenotypes, depending on the different environmental factors that affect each individual. Choice (A) is incorrect because sex-linkage involves traits found on the sex chromosomes. Multiple gene inheritance refers to multiple genes contributing to an individual's phenotype, so choice (B) is incorrect. Nonnuclear inheritance refers to traits coded for by genes outside of the nucleus (in the mitochondria or chloroplast), so choice (C) is incorrect.

6. **(D)** A heterozygous, red-eyed female fly would have the genotype X^RX^r, and a white-eyed male fly would have the X^r Y genotype. The Punnett square for this cross is shown in the following figure.



The most likely result would be 50% of both sexes would have red eyes and 50% of both sexes would have white eyes.

7. **(A)** The figure that follows shows the Punnett square for the cross between a heterozygous male and a female with the recessive trait. So $\frac{1}{4}$ of the offspring would be males with the dominant phenotype, $\frac{1}{4}$ would be males with the recessive phenotype, $\frac{1}{4}$ would be females with the dominant phenotype, and $\frac{1}{4}$ would be females with the recessive phenotype.

	Z^A	Z^a
Z^a	Z^AZ^a	Z^aZ^a
W	Z^AW	Z^aW

$\frac{1}{4}$ males with dominant phenotype

$\frac{1}{4}$ males with recessive phenotype

$\frac{1}{4}$ females with dominant phenotype

$\frac{1}{4}$ females with recessive phenotype

8. **(B)** As shown in the figure, $\frac{1}{4}$ of the offspring would be black female cats, $\frac{1}{4}$ would be calico female cats, $\frac{1}{4}$ would be black male cats, and $\frac{1}{4}$ would be orange male cats.

	X^B	X^O
X^B	X^BX^B	X^BX^O
Y	X^BY	X^OY

$\frac{1}{4}$ black female cats

$\frac{1}{4}$ calico female cats

$\frac{1}{4}$ black male cats

$\frac{1}{4}$ orange male cats

9. **(D)** Both females and males are affected, but only females appear to be able to pass the trait on to the next generation—these are hallmarks of mitochondrial inheritance. Autosomal traits are equally likely in both sexes, so choices (A) and (B) are incorrect. Sex-linked traits are more likely to appear in males than females, so choice (C) is incorrect.

10. **(A)** This is most likely a mitochondrial trait (see the explanation for Question 9). Individual III-3 does not have the trait, so he does not carry the allele. Even if he did carry the allele, males cannot pass on mitochondrial traits to the next generation. If he has a child with a woman who also does not have the allele, there is 0% chance of them having a child with the trait since neither of them have the allele for the trait. Choices (B), (C), and (D) are incorrect because if the woman does not have the allele for a mitochondrial trait, her offspring will not have the allele for the trait.

Short Free-Response

11. (a) Individual II-4 is a heterozygous carrier of the hemophilia allele (X^HX^h) because she does not have hemophilia but she does have a male offspring who does have hemophilia.

(b) Individual III-14 is a heterozygous carrier of the hemophilia allele (X^HX^h) because her father has hemophilia and all females inherit an X chromosome from their father. It is also clear that she is a heterozygous carrier because she does not have hemophilia but she does have a male offspring who does have hemophilia.

(c)

		Individual 7	
		X^H	X^h
Individual 8	X^H	X^HX^H	X^HX^h
	Y	X^HY	X^hY

(d) Closely related individuals are more likely to share the same alleles. If two closely related individuals share the same recessive alleles, their offspring would be more likely to express that recessive trait than two individuals who are not as closely related and do not have the same recessive alleles.

12. (a) Because the trait is expressed in every generation, it could be an autosomal dominant trait. Since both sexes can express the trait but only females can pass the trait to the next generation, the mode of inheritance could be mitochondrial (nonnuclear).

(b) If a trait is dominant, it will usually appear in every generation in a pedigree. Recessive traits will appear in offspring but do not necessarily appear in the parents because the parents may be unaffected heterozygous carriers of the trait.

(c) Mitochondrial DNA is passed on from mother to offspring. The egg is thousands of times larger than the sperm, so during fertilization, the zygote inherits its mitochondria from the mother. Mothers will pass on mitochondrial DNA to all of their offspring, but their sons will not pass it on to the next generation. This is exactly what is shown in the three generations of this pedigree.

(d) Autosomal dominant traits can be passed on to the next generation by either males or females. Mitochondrial traits can only be passed on to the next generation by females.

Long Free-Response

13. (a) Females inherit one X chromosome from their male parent and one from their female parent. Since all of the females produced from the cross have the same phenotype as their male parent (red eyes), red eyes must be dominant to white eyes. Males inherit their only X chromosome from their female parent, so all of the males have the white-eyed phenotype. The results of the cross are shown in the following figure.

	X^R	Y
X^r	X^RX^r	X^rY
X^r	X^RX^r	X^rY

(b) The independent variable is the color of the eyes (or the presence or absence of the TDO2 mutation). The dependent variable is the mean life span.

(c) There is likely a statistically significant difference if the 95% confidence intervals do NOT overlap. The lower limit of the 95% confidence interval for the mean life span of the white-eyed flies is 37 days (42.8 – 5.8). The upper limit of the 95% confidence interval for the mean life span of the red-eyed flies is 34 days (29.1 + 4.9). The 95% confidence intervals do not overlap, so there is likely a statistically significant difference in the life spans of the two groups of flies in this experiment.

(d) In this mating, $\frac{2}{3}$ of the females would have red eyes, $\frac{1}{3}$ of the females would have white eyes, $\frac{2}{3}$ of the males would have white eyes, and $\frac{1}{3}$ of the males would have red eyes, as shown in the figure.

	Possible Gametes from X^RX^rY					
Possible Gamete from X^rX^r	X^RX^r	X^RY	X^rY	X^R	X^r	Y
X^r	$X^RX^rX^r$	X^RX^rY	X^rX^rY	X^RX^r	X^rX^r	X^rY
Phenotypes	Red-eyed female (with 3 X chromosomes)	Red-eyed male (with 2 X chromosomes)	White-eyed male (with 2 X chromosomes)	Red-eyed female	White-eyed female	White-eyed male