46

Animal Reproduction

▲ **Figure 46.1 How can each of these sea slugs be both male and female?**

KEY CONCEPTS

- **46.1** Both asexual and sexual reproduction occur in the animal kingdom
- **46.2** Fertilization depends on mechanisms that bring together sperm and eggs of the same species
- **46.3** Reproductive organs produce and transport gametes
- **46.4** The interplay of tropic and sex hormones regulates mammalian reproduction
- **46.5** In placental mammals, an embryo develops fully within the mother's uterus

OVERVIEW

Pairing Up for Sexual Reproduction

The sea slugs, or nudibranchs (*Nembrotha rutilans*), in **Figure 46.1** are mating. If not disturbed, these marine molluscs may remain joined for hours. Sperm will be transferred and will fertilize eggs. A few weeks later, sexual reproduction will be complete. New individuals will hatch, but which parent is the mother? The answer is simple yet probably unexpected: both. In fact, each sea slug produces eggs *and* sperm.

As humans, we tend to think of reproduction in terms of the mating of males and females and the fusion of sperm and eggs. Animal reproduction, however, takes many forms. In some species, individuals change their sex during their lifetime; in other species, such as sea slugs, an individual is both male and female. There are animals that can fertilize their own eggs, as well as others that can reproduce without any form of sex. For certain species, such as honeybees, only a few individuals within a large population reproduce.

A population outlives its members only by reproduction, the generation of new individuals from existing ones. In this chapter, we will compare the diverse reproductive mechanisms that have evolved in the animal kingdom. We will then examine details of mammalian reproduction, particularly that of humans. We will focus on the physiology of reproduction mostly from the parents' perspective, deferring the details of embryonic development until the next chapter.

CONCEPT 46.1

Both asexual and sexual reproduction occur in the animal kingdom

There are two modes of animal reproduction—sexual and asexual. In **sexual reproduction**, the fusion of haploid gametes forms a diploid cell, the **zygote**. The animal that develops from a zygote can in turn give rise to gametes by meiosis (see Figure 13.8). The female gamete, the **egg**, is a large, nonmotile cell. The male gamete, the **sperm**, is generally a much smaller, motile cell. **Asexual reproduction** is the generation of new individuals without the fusion of egg and sperm. In most asexual animals, reproduction relies entirely on mitotic cell division.

For the vast majority of animals, reproduction is primarily or exclusively sexual. However, there are species that have a primarily asexual mode of reproduction, including a few all-female species for which reproduction is exclusively asexual. These include the microscopic bdelloid rotifer (see p. 677), as well as certain species of whiptail lizard (*Aspidoscelis*), which we will discuss shortly.

Mechanisms of Asexual Reproduction

Several forms of asexual reproduction are found only among invertebrates. One of these is **fission**, the separation of a parent organism into two individuals of approximately equal size **(Figure 46.2)**. Also common among invertebrates is **budding**, in which new individuals arise from outgrowths of existing ones (see Figure 13.2). In stony corals, for example, buds form and remain attached to the parent. The eventual result is a

▲ **Figure 46.2 Asexual reproduction of a sea anemone (*Anthopleura elegantissima*).** The large individual in the center of this photograph is undergoing fission, a type of asexual reproduction. Two smaller individuals will form as the parent divides approximately in half. Each offspring will be a genetic copy of the parent.

colony more than 1 m across, consisting of thousands of connected individuals. In another form of asexual reproduction, some invertebrates, including certain sponges, release specialized groups of cells that can grow into new individuals.

Another process of asexual reproduction involves two steps: *fragmentation*, the breaking of the body into several pieces, followed by *regeneration*, the regrowth of lost body parts. If more than one piece grows and develops into a complete animal, the net effect is reproduction. For example, certain annelid worms can split their body into several fragments, each regenerating a complete worm in less than a week. Numerous sponges, cnidarians, bristle worms, and sea squirts also reproduce by fragmentation and regeneration.

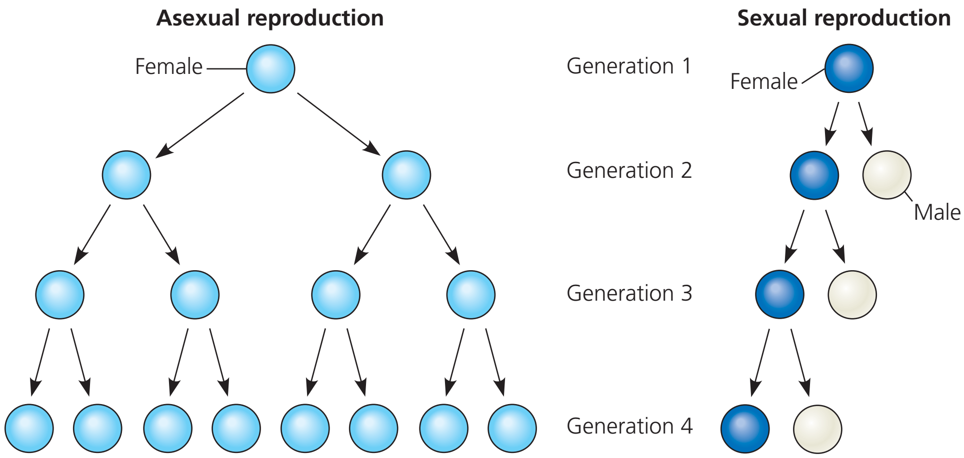
Parthenogenesis is asexual reproduction in which an egg develops without being fertilized. Among invertebrates, parthenogenesis occurs in certain species of bees, wasps, and ants. The progeny can be either haploid or diploid. If haploid, the offspring develop into adults that produce eggs or sperm without meiosis. In the case of honeybees, males (drones) are fertile haploid adults that arise by parthenogenesis. (In contrast, female honeybees, including both the sterile workers and the fertile queens, are diploid adults that develop from fertilized eggs.) Among vertebrates, parthenogenesis has been observed in about one in every thousand species. Recently, zookeepers discovered parthenogenesis in the Komodo dragon and in a species of hammerhead shark. In both cases, females had been kept completely isolated from males of their species but nevertheless produced offspring.

Sexual Reproduction: An Evolutionary Enigma

EVOLUTION Sex must enhance reproductive success or survival because it would otherwise rapidly disappear. To see why, consider an animal population in which half the females reproduce sexually and half reproduce asexually **(Figure 46.3)**. We'll assume that the number of offspring per female is a constant, two in this case. The two offspring of an asexual female will both be daughters that will each give birth to two more reproductive daughters. In contrast, half of a sexual female's offspring will be male. The number of sexual offspring will remain the same at each generation, because both a male and a female are required to reproduce. Thus, the asexual condition will increase in frequency at each generation. Yet despite this "twofold cost," sex is maintained even in animal species that can also reproduce asexually.

What advantage does sex provide? The answer remains elusive. Most hypotheses focus on the unique combinations of parental genes formed during meiotic recombination and fertilization. By producing offspring of varied genotypes, sexual reproduction may enhance the reproductive success of parents when environmental factors, such as pathogens, change relatively rapidly. In contrast, asexual reproduction is expected to be most advantageous in stable, favorable environments because it perpetuates successful genotypes faithfully and precisely.

There are a number of reasons why the unique gene combinations formed during sexual reproduction might be advantageous. One is that beneficial gene combinations arising through recombination might speed up adaptation. Although this idea appears straightforward, the theoretical advantage is significant only when the rate of beneficial mutations is high and population size is small. Another idea is that the shuffling of genes during sexual reproduction might allow a population to rid itself of sets of harmful genes



▲ **Figure 46.3 The "reproductive handicap" of sex.** These diagrams contrast the reproductive output of females (blue spheres) over four generations for asexual versus sexual reproduction, assuming two surviving offspring per female. The asexual population rapidly outgrows the sexual one.

more readily. Experiments to test these and other hypotheses are ongoing in many laboratories.

Reproductive Cycles

Most animals exhibit cycles in reproductive activity, often related to changing seasons. In this way, animals conserve resources, reproducing only when sufficient energy sources or stores are available and when environmental conditions favor the survival of offspring. For example, ewes (female sheep) have a reproductive cycle lasting 15–17 days. **Ovulation**, the release of mature eggs, occurs at the midpoint of each cycle. A ewe's cycle generally occurs only during fall and early winter, and the length of any resulting pregnancy is 5 months. Thus, most lambs are born in the early spring, when their chances of survival are optimal. Reproductive cycles are controlled by hormones, which in turn are regulated by environmental cues. Common environmental cues are changes in day length, seasonal temperature, rainfall, and lunar cycles.

Because seasonal temperature is often an important cue for reproduction, climate change can decrease reproductive success. Researchers in Denmark have demonstrated just such an effect on caribou (wild reindeer). In spring, caribou migrate to calving grounds to eat sprouting green plants, give birth, and care for their new calves **(Figure 46.4)**. Changes in the length of daylight trigger the migration, while the seasonal rise in temperature that thaws the tundra causes plants to sprout. Prior to 1993, the arrival of the caribou at the calving grounds coincided with the brief period during which the plants were nutritious and digestible. Between 1993 and 2006, average spring temperatures in the calving grounds increased by more than 4°C, and the plants now sprout two weeks earlier. Since the length of daylight is unaffected by climate change, the timing of the caribou migration has not changed. The result is a timing mismatch between new plant growth and caribou birthing. Without adequate nutrition for the nursing females, production of caribou offspring has declined by 75%.

▲ **Figure 46.4 Caribou (*Rangifer tarandus*) mother and calf.** As a result of warming due to global climate change, the number of caribou offspring in a West Greenland study site has fallen fourfold.

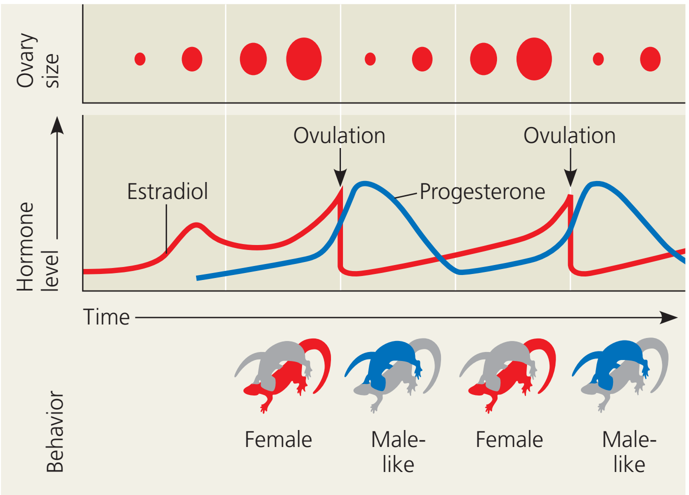
Reproductive cycles are also found among animals that can reproduce both sexually and asexually. Consider, for instance, the water flea (genus *Daphnia*). A *Daphnia* female can produce eggs of two types. One type of egg requires fertilization to develop, but the other type does not and develops instead by parthenogenesis. Asexual reproduction occurs when environmental conditions are favorable, whereas sexual reproduction occurs during times of environmental stress. As a result, the switch between sexual and asexual reproduction is roughly linked to season.

A very different type of reproductive cycle is found among animals that only reproduce asexually. Several genera of fishes, amphibians, and reptiles engage in a complex form of parthenogenesis that involves the doubling of chromosomes after meiosis, producing diploid offspring. Among these are about 15 species of whiptail lizards in the genus *Aspidoscelis*. There are no males, but courtship and mating behaviors are typical of sexual species of the same genus. During the breeding season, one female of each mating pair mimics a male **(Figure 46.5a)**. Each member of the pair alternates roles two or three times during the season. An individual adopts female behavior prior to ovulation, when the level of the female sex hormone estradiol is high, then switches to male-like behavior after ovulation, when the level of progesterone is highest **(Figure 46.5b)**. Ovulation is more likely to occur if the individual is mounted during the critical time of the hormone cycle; isolated lizards lay fewer eggs than those that go through the motions of sex. These observations support the hypothesis that these parthenogenetic lizards evolved from species having two sexes and still require certain sexual stimuli for maximum reproductive success.

Variation in Patterns of Sexual Reproduction

For many animals, finding a partner for sexual reproduction can be challenging. Adaptations that arose during the evolution of some species meet this challenge in a novel way—by blurring the strict distinction between male and female. One such adaptation arose among sessile (stationary) animals, such as barnacles; burrowing animals, such as clams; and some parasites, including tapeworms. Lacking locomotion, these animals have a very limited opportunity to find a mate. An evolutionary solution to this problem is **hermaphroditism**, in which each individual has both male and female reproductive systems (the term *hermaphrodite* merges the names Hermes and Aphrodite, a Greek god and goddess). Because each hermaphrodite reproduces as both a male and a female, *any* two individuals can mate. Each animal donates and receives sperm during mating, as the sea slugs in Figure 46.1 are doing. In some species, hermaphrodites are

(a) Both lizards in this photograph are *A. uniparens* females. The one on top is playing the role of a male. Every two or three weeks during the breeding season, individuals switch sex roles.



(b) The sexual behavior of *A. uniparens* is correlated with the cycle of ovulation mediated by sex hormones. As the blood level of estradiol rises, the ovaries grow, and the lizard behaves as a female. After ovulation, the estradiol level drops abruptly, and the progesterone level rises; these hormone levels correlate with male-like behavior.

▲ **Figure 46.5 Sexual behavior in parthenogenetic lizards.** The desert-grassland whiptail lizard (*Aspidoscelis uniparens*) is an all-female species. These reptiles reproduce by parthenogenesis, the development of an unfertilized egg. Nevertheless, ovulation is stimulated by mating behavior.

also capable of self-fertilization, allowing a form of sexual reproduction that doesn't require any partner.

The bluehead wrasse (*Thalassoma bifasciatum*), a coral reef fish, provides a well-studied example of a quite different variation in sexual reproduction. These wrasses live in harems, each consisting of a single male and several females. When the lone male dies, the opportunity for sexual reproduction would appear lost. Instead, a female wrasse undergoes sex reversal, a change in sex. Within a week, the transformed individual is producing sperm instead of eggs. Scientists have observed that it is the largest (and usually oldest) female in the harem that undergoes sex reversal. What advantage did this offer in the evolution of this wrasse? Because it is the male that defends a harem against intruders, a larger size may be more important for males than females in ensuring successful reproduction.

Certain oyster species also undergo sex reversal. In this case, individuals reproduce as males and then later as females, when their size is greatest. Since the number of gametes produced generally increases with size much more for females than for males, sex reversal in this direction maximizes gamete production. The result is enhanced reproductive success: Because oysters are sedentary animals and release their gametes into the surrounding water rather than mating directly, releasing more gametes tends to result in more offspring.

CONCEPT CHECK 46.1

1. Compare and contrast the outcomes of asexual and sexual reproduction.
2. Parthenogenesis is the most common form of asexual reproduction in animals that at other times reproduce sexually. What characteristic of parthenogenesis might explain this observation?
3. **WHAT IF?** If a hermaphrodite self-fertilizes, will the offspring be identical to the parent? Explain.
4. **MAKE CONNECTIONS** What examples of plant reproduction are most similar to asexual reproduction in animals? (See Concept 38.2, p. 812.)

For suggested answers, see Appendix A.

CONCEPT 46.2

Fertilization depends on mechanisms that bring together sperm and eggs of the same species

The union of sperm and egg—**fertilization**—can be either external or internal. In species with **external fertilization**, the female releases eggs into the environment, where the male then fertilizes them. Other species have **internal fertilization**: Sperm are deposited in or near the female reproductive tract, and fertilization occurs within the tract. (We'll discuss the cellular and molecular details of fertilization in Chapter 47.)

A moist habitat is almost always required for external fertilization, both to prevent the gametes from drying out and to allow the sperm to swim to the eggs. Many aquatic invertebrates simply shed their eggs and sperm into the surroundings, and fertilization occurs without the parents making physical contact. However, timing is crucial to ensure that mature sperm and eggs encounter one another.

Among some species with external fertilization, individuals clustered in the same area release their gametes into the water at the same time, a process known as *spawning*. In some cases, chemical signals that one individual generates in releasing gametes trigger others to release gametes. In other cases, environmental cues, such as temperature or day length, cause a whole population to release gametes at one time. For example, the palolo worm, native to coral reefs of the South Pacific, times its spawning to both the season and the lunar cycle. In spring, when the moon is in its last quarter, palolo worms break in half, releasing tail segments engorged with sperm or eggs. These packets rise to the ocean surface and burst in such vast numbers that the sea appears milky with gametes. The sperm quickly fertilize the floating eggs, and within hours, the palolo's once-a-year reproductive frenzy is complete.

When external fertilization is not synchronous across a population, individuals may exhibit specific mating behaviors leading to the fertilization of the eggs of one female by one male **(Figure 46.6)**. Such "courtship" behavior has two important benefits: It allows mate choice (see Chapter 23) and, by triggering the release of both sperm and eggs, increases the probability of successful fertilization.

Internal fertilization is an adaptation that enables sperm to reach an egg efficiently, even when the environment is dry. It typically requires cooperative behavior that leads to copulation, as well as sophisticated and compatible reproductive systems. The male copulatory organ delivers sperm, and the female reproductive tract often has receptacles for storage and delivery of sperm to mature eggs.

No matter how fertilization occurs, the mating animals may make use of *pheromones*, chemicals released by one organism that can influence the physiology and behavior of other individuals of the same species. Pheromones are small, volatile or water-soluble molecules that disperse into the environment and, like hormones, are active in tiny amounts (see Chapter 45). Many pheromones function as mate attractants, enabling some female insects to be detected by males from as far away as a mile. (We will discuss mating behavior and pheromones further in Chapter 51.)

▲ **Figure 46.6 External fertilization.** Many species of amphibians reproduce by external fertilization. In most of these species, behavioral adaptations ensure that a male is present when the female releases eggs. Here, a female frog (on bottom) has released a mass of eggs in response to being clasped by a male. The male released sperm (not visible) at the same time, and external fertilization has already occurred in the water.

Ensuring the Survival of Offspring

Comparing internal and external fertilization across many species reveals that internal fertilization is typically associated with the production of fewer gametes but the survival of a higher fraction of zygotes. Better zygote survival is due in part to the fact that eggs fertilized internally are sheltered from potential predators. However, internal fertilization is also more often associated with mechanisms that provide greater protection of the embryos and parental care of the young. For example, the internally fertilized eggs of many species of terrestrial animals exhibit adaptations that protect against water loss and physical damage during their external development. In the case of birds and other reptiles, as well as monotremes (egg-laying mammals), the zygotes consist of eggs with calcium- and protein-containing shells and several internal membranes (see Figure 34.25). In contrast, the fertilized eggs of fishes and amphibians have only a gelatinous coat and lack internal membranes.

Rather than secreting a protective eggshell, some animals retain the embryo for a portion of its development within the female's reproductive tract. Embryos of marsupial mammals, such as kangaroos and opossums, spend only a short period in the uterus; the embryos then crawl out and complete fetal development attached to a mammary gland in the mother's pouch. However, embryos of eutherian (placental) mammals, such as humans, remain in the uterus throughout fetal development. There they are nourished by the mother's blood supply through a temporary organ, the placenta. The embryos of some fishes and sharks also complete development internally, although typically the embryo and mother in such species lack a connection dedicated to nutrient exchange.

When a baby eagle hatches out of an egg or when a human is born, the newborn is not yet capable of independent existence. Instead, adult birds feed their young and mammals nurse their offspring. Parental care is in fact much more widespread than you might suspect. For example, there are many invertebrates that provide parental care **(Figure 46.7)**. Among vertebrates, the gastric brooding frogs (genus *Rheobatrachus*) of Australia provided a particularly unusual example prior to their extinction in the 1980s. During reproduction, the female frog would carry the tadpoles in her stomach until they underwent metamorphosis and hopped out of her mouth as young frogs.

Gamete Production and Delivery

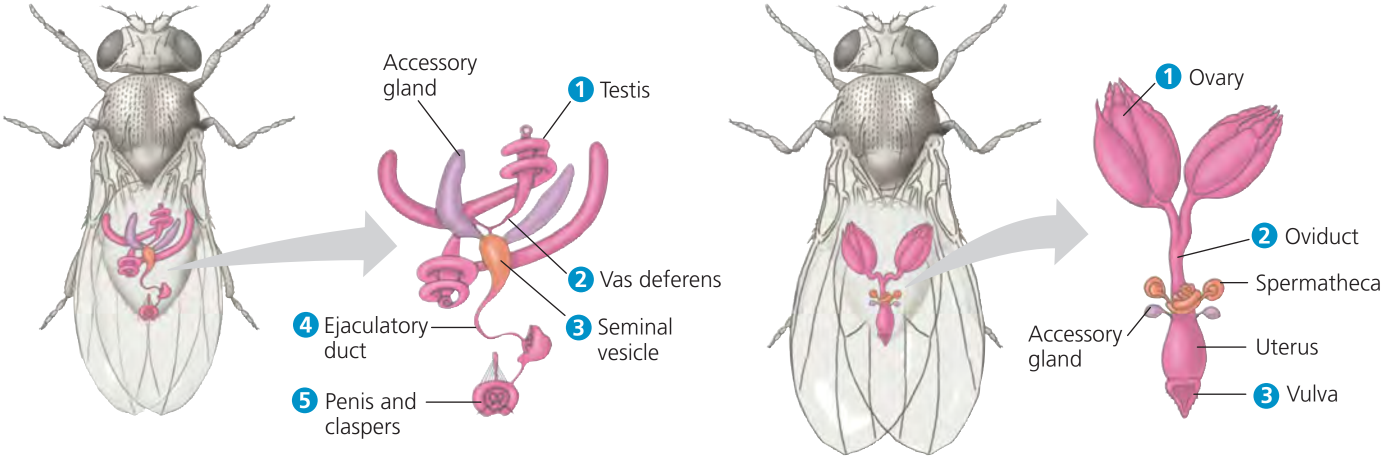
Sexual reproduction in animals relies on sets of cells that are precursors for eggs and sperm. A group of cells dedicated to this purpose is often established very early in the formation of the embryo and remains in an inactive state while the body plan

▲ **Figure 46.7 Parental care in an invertebrate.** Compared with many other insects, giant water bugs of the genus *Belostoma* produce relatively few offspring, but offer much greater parental protection. Following internal fertilization, the female glues her fertilized eggs to the back of the male (shown here). The male carries them for days, frequently fanning water over them to keep the eggs moist, aerated, and free of parasites.

develops. Cycles of growth and mitosis then increase, or *amplify*, the number of cells available for making eggs or sperm.

In producing gametes from the amplified precursor cells and making them available for fertilization, animals employ a variety of reproductive systems. The simplest systems do not even include discrete **gonads**, the organs that produce gametes in most animals. The palolo and most other polychaete worms (phylum Annelida) have separate sexes but do not have distinct gonads; rather, the eggs and sperm develop from undifferentiated cells lining the coelom (body cavity). As the gametes mature, they are released from the body wall and fill the coelom. Depending on the species, mature gametes may be shed through the excretory opening, or the swelling mass of eggs may split a portion of the body open, spilling the eggs into the environment.

More elaborate reproductive systems include sets of accessory tubes and glands that carry, nourish, and protect the gametes and sometimes the developing embryos. Most insect species, for example, have separate sexes with complex reproductive systems **(Figure 46.8)**. In the males, sperm develop in a pair of testes and are passed along a coiled duct to two seminal vesicles for storage. During mating, sperm are ejaculated into the female reproductive system. There, eggs develop in a pair of ovaries and are conveyed through ducts to the uterus. Eggs are fertilized in the uterus and then expelled for development outside the body. In many insect species, the female reproductive system includes one or more **spermathecae** (singular, spermatheca), sacs in which sperm may be stored for extended periods, a year or more in some species. Because the female releases male gametes from the spermatheca only in response to the appropriate stimuli, fertilization occurs



(a) Male fruit fly. Sperm form in the testes, pass through the sperm ducts (vas deferens), and are stored in the seminal vesicles. The male ejaculates sperm along with fluid from the accessory glands. (Males of some species of insects and other arthropods have appendages called claspers that grasp the female during copulation.)

(b) Female fruit fly. Eggs develop in the ovaries and then travel through the oviducts to the uterus. After mating, sperm are stored in the spermathecae, which are connected to the uterus by short ducts. The female uses a stored sperm to fertilize each egg as it enters the uterus before she passes the egg out through the vulva.

▲ **Figure 46.8 Insect reproductive anatomy.** Circled numbers indicate sequences of sperm and egg movement.

under conditions likely to be well suited to embryonic development. Even more complex reproductive systems can be found in some animals whose body plans are otherwise fairly simple, such as parasitic flatworms.

The basic plans of all vertebrate reproductive systems are quite similar, but there are some important variations. In many nonmammalian vertebrates, the digestive, excretory, and reproductive systems have a common opening to the outside, the **cloaca**, a structure that was probably also present in the ancestors of all vertebrates. In contrast, mammals generally lack a cloaca and have a separate opening for the digestive tract. In addition, most female mammals have separate openings for the excretory and reproductive systems. Among most vertebrates, the uterus is partly or completely divided into two chambers. However, in humans and other mammals that produce only one or a few young at a time, as well as in birds and many snakes, the uterus is a single structure. Male reproductive systems differ mainly in the copulatory organs. Many nonmammalian vertebrates, including all reptiles and amphibians, lack a well-developed penis and instead ejaculate sperm by turning the cloaca inside out.

Although fertilization involves the union of a single egg and sperm, animals often mate with more than one member of the other sex. Indeed, monogamy, the sustained sexual partnership of two individuals, is relatively rare among animals, including most mammals. Mechanisms have evolved, however, that enhance the reproductive success of a male with a particular female and diminish the chance of that female mating successfully with another partner. For example, some male insects transfer secretions that make a female less receptive to courtship, thereby reducing the likelihood of her mating again.

Can females also influence the relative reproductive success of their mates? This question intrigued two scientific collaborators working in Europe. Studying female fruit flies that copulated with one male and then another, the researchers traced the fate of sperm transferred in the first mating. As shown in **Figure 46.9**, they found that female fruit flies play a major role in determining the reproductive outcome of multiple matings. Nevertheless, the processes by which gametes and individuals compete during reproduction are only partly understood and remain a vibrant research area.

CONCEPT CHECK 46.2

1. How does internal fertilization facilitate life on land?
2. What mechanisms have evolved in animals with (a) external fertilization and (b) internal fertilization that help ensure that offspring survive to adulthood?
3. **MAKE CONNECTIONS** What are the shared and distinct functions of the uterus of an insect and the ovary of a flowering plant? (See Figure 38.6, p. 806.)

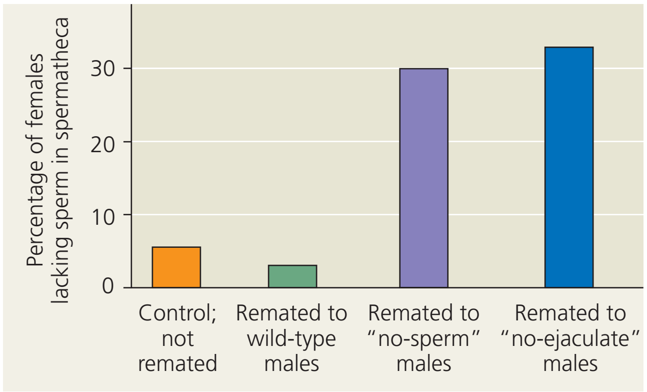
For suggested answers, see Appendix A.

▼ Figure 46.9 **INQUIRY**

Why is sperm usage biased when female fruit flies mate twice?

EXPERIMENT When a female fruit fly mates twice, 80% of the offspring result from the second mating. Scientists had postulated that ejaculate from the second mating displaces stored sperm. To test this hypothesis, Rhonda Snook, at the University of Sheffield, and David Hosken, at the University of Zurich, used mutant males with altered reproductive systems. "No-ejaculate" males mate, but do not transfer sperm or fluid to females. "No-sperm" males mate and ejaculate, but make no sperm. The researchers allowed females to mate with wild-type males and then mate with wild-type males, no-sperm males, or no-ejaculate males. As a control, some females were mated only once. The scientists then dissected each female under a microscope and recorded whether sperm were absent from the spermatheca, the major sperm storage organ.

RESULTS



CONCLUSION Because remating reduces sperm storage when no sperm or fluids are transferred, the hypothesis that ejaculate from a second mating displaces stored sperm is incorrect. Instead, it appears that females sometimes get rid of stored sperm in response to remating. This might represent a way for females to replace stored sperm, possibly of diminished fitness, with fresh sperm.

SOURCE R. R. Snook and D. J. Hosken, Sperm death and dumping in *Drosophila*, *Nature* 428:939–941 (2004).

WHAT IF? Suppose males in the first mating had a mutant allele for the dominant trait of smaller eyes. What fraction of the females would produce some offspring with smaller eyes?

CONCEPT 46.3

Reproductive organs produce and transport gametes

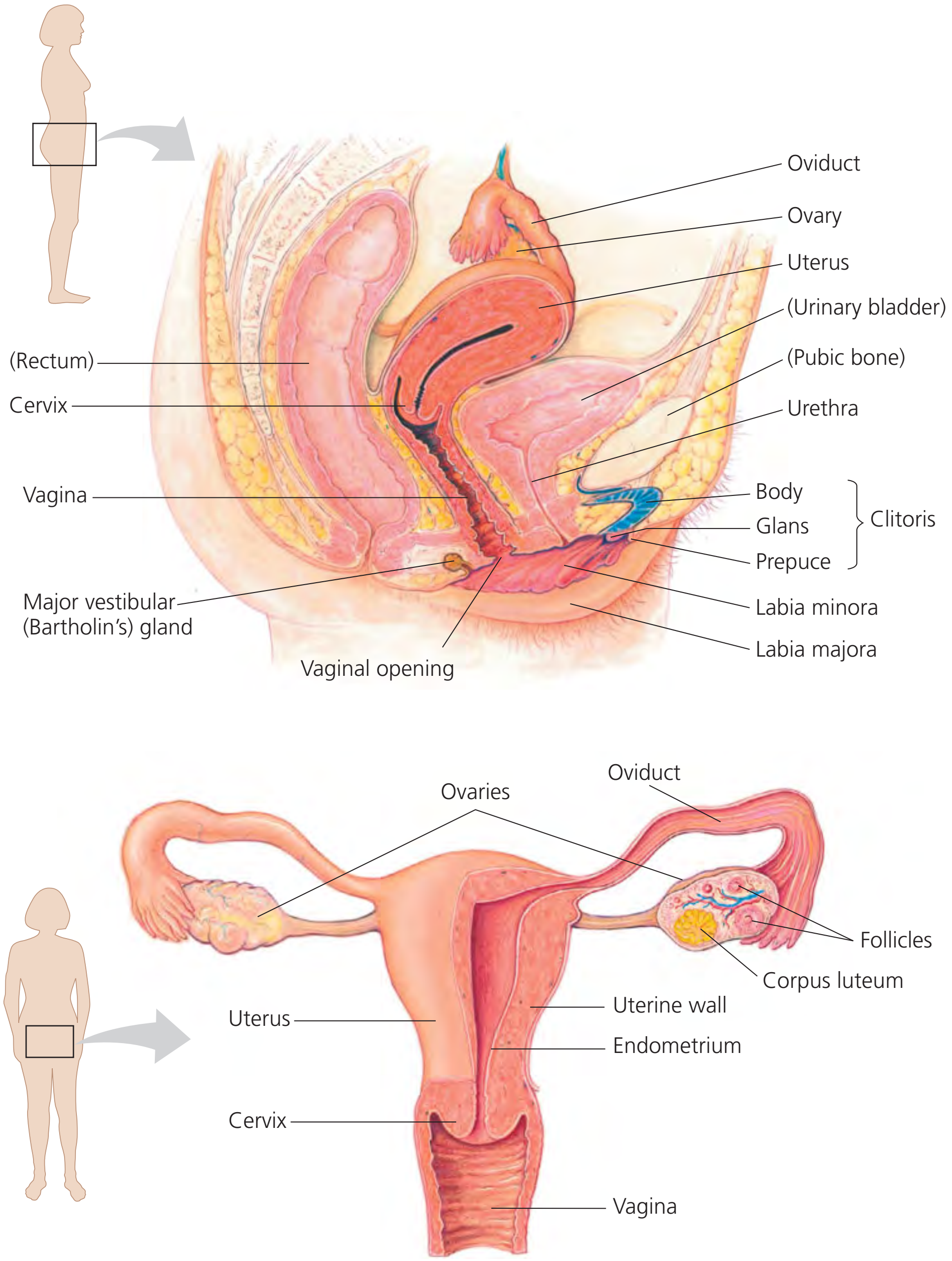
Having surveyed some of the general features of animal reproduction, we will focus the rest of the chapter on humans, beginning with the anatomy of the reproductive system in each sex.

Female Reproductive Anatomy

The female's external reproductive structures are the clitoris and two sets of labia, which surround the clitoris and vaginal opening. The internal organs are the gonads, which produce both eggs and reproductive hormones, and a system of ducts and chambers, which receive and carry gametes and house the embryo and fetus **(Figure 46.10)**.

Ovaries

The female gonads are a pair of ovaries that flank the uterus and are held in place in the abdominal cavity by ligaments. The outer layer of each ovary is packed with **follicles**, each consisting of an **oocyte**, a partially developed egg, surrounded by a group of support cells. The surrounding cells nourish and protect the oocyte during much of the formation and development of an egg. Although at birth the ovaries together contain about 1–2 million follicles, only about 500 follicles fully mature between puberty and menopause. During a typical 4-week menstrual cycle, one follicle matures and expels its egg, a process called ovulation. Prior to ovulation, cells of the follicle produce the primary female sex hormone, estradiol (a type of estrogen). After ovulation, the residual follicular tissue grows within the ovary, forming a mass called the **corpus luteum** ("yellow body"). The corpus luteum secretes additional estradiol, as well as progesterone, a hormone that helps maintain the uterine lining during pregnancy. If the egg cell is not fertilized, the corpus luteum degenerates, and a new follicle matures during the next cycle.



▲ **Figure 46.10 Reproductive anatomy of the human female.** Some nonreproductive structures are labeled in parentheses for orientation purposes.

Oviducts and Uterus

An **oviduct**, or fallopian tube, extends from the uterus toward each ovary. The dimensions of this tube vary along its length, with the inside diameter near the uterus being as narrow as a human hair. At ovulation, the egg is released into the abdominal cavity near the funnel-like opening of the oviduct. Cilia on the epithelial lining of the duct help collect the egg by drawing fluid from the body cavity into the oviduct. Together with wave-like contractions of the oviduct, the cilia convey the egg down the duct to the **uterus**, also known as the womb. The uterus is a thick, muscular organ that can expand during pregnancy to accommodate a 4-kg fetus. The inner lining of the uterus, the **endometrium**, is richly supplied with blood vessels. The neck of the uterus, called the **cervix**, opens into the vagina.

Vagina and Vulva

The **vagina** is a muscular but elastic chamber that is the site for insertion of the penis and deposition of sperm during copulation. The vagina, which also serves as the birth canal through which a baby is born, opens to the outside at the **vulva**, the collective term for the external female genitalia.

A pair of thick, fatty ridges, the **labia majora**, encloses and protects the rest of the vulva. The vaginal opening and the separate opening of the urethra are located within a cavity bordered by a pair of slender skin folds, the **labia minora**. A thin piece of tissue called the **hymen** partly covers the vaginal opening in humans at birth and usually until sexual intercourse or vigorous physical activity ruptures it. Located at the top of the labia minora, the **clitoris** consists of erectile tissue supporting a rounded **glans**, or head, covered by a small hood of skin, the **prepuce**. During sexual arousal, the clitoris, vagina, and labia minora all engorge with blood and enlarge. Richly supplied with nerve endings, the clitoris is one of the most sensitive points of sexual stimulation. Sexual arousal also induces the vestibular glands near the vaginal opening to secrete lubricating mucus, thereby facilitating intercourse.

Mammary Glands

The **mammary glands** are present in both sexes, but they normally produce milk only in females. Though not part of the reproductive system, the female mammary glands are important to reproduction. Within the glands, small sacs of epithelial tissue secrete milk, which drains into a series of ducts that open at the nipple. The breasts contain connective and fatty (adipose) tissue in addition to the mammary glands. Because the low level of estradiol in males limits the development of the fat deposits, male breasts usually remain small.

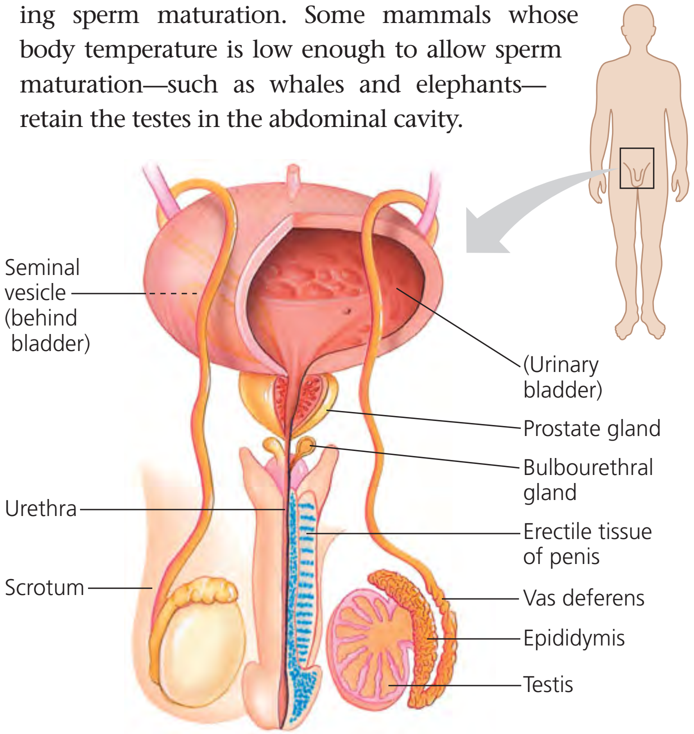
Male Reproductive Anatomy

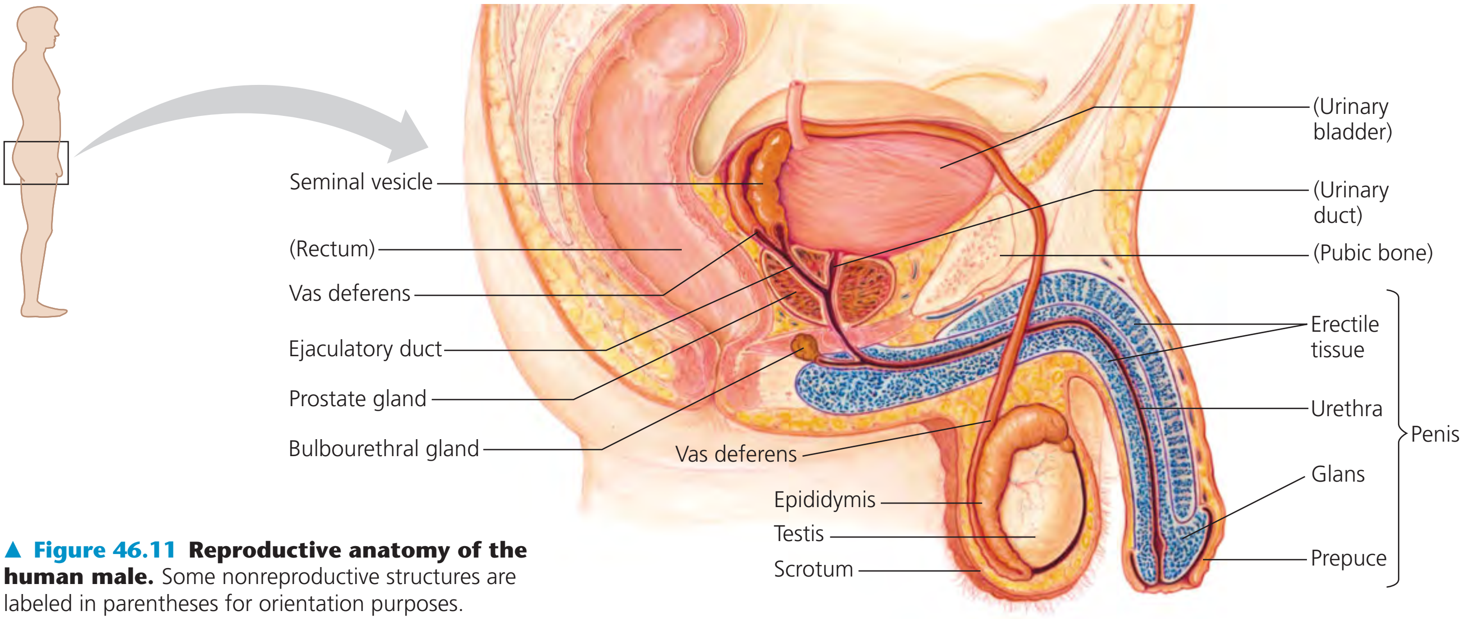
The human male's external reproductive organs are the scrotum and penis. The internal reproductive organs consist of gonads that produce both sperm and reproductive hormones, accessory glands that secrete products essential to sperm movement, and ducts that carry the sperm and glandular secretions **(Figure 46.11)**.

Testes

The male gonads, or **testes** (singular, *testis*), produce sperm in highly coiled tubes called **seminiferous tubules**. The **Leydig cells**, scattered in connective tissue between the tubules, produce testosterone and other androgens (see Chapter 45).

Most mammals produce sperm properly only when the testes are cooler than normal body temperature. In humans and many other mammals, the **scrotum**, a fold of the body wall, maintains testis temperature about 2°C below that of the rest of the body. The testes develop in the abdominal cavity and descend into the scrotum just before birth (a testis within a scrotum is a *testicle*). In many rodents, the testes are drawn back into the cavity between breeding seasons, interrupting sperm maturation. Some mammals whose body temperature is low enough to allow sperm maturation—such as whales and elephants—retain the testes in the abdominal cavity.





▲ **Figure 46.11 Reproductive anatomy of the human male.** Some nonreproductive structures are labeled in parentheses for orientation purposes.

Ducts

From the seminiferous tubules of a testis, the sperm pass into the coiled duct of an **epididymis**. In humans, it takes 3 weeks for sperm to pass through this 6-m-long duct. During this passage through the epididymis, the sperm complete maturation and become motile, although they acquire the ability to fertilize an egg only upon exposure to the chemical environment of the female reproductive system. During **ejaculation**, the sperm are propelled from each epididymis through a muscular duct, the **vas deferens**. Each vas deferens (one from each epididymis) extends around and behind the urinary bladder, where it joins a duct from the seminal vesicle, forming a short **ejaculatory duct**. The ejaculatory ducts open into the **urethra**, the outlet tube for both the excretory system and the reproductive system. The urethra runs through the penis and opens to the outside at the tip of the penis.

Accessory Glands

Three sets of accessory glands—the seminal vesicles, the prostate gland, and the bulbourethral glands—produce secretions that combine with sperm to form **semen**, the fluid that is ejaculated. Two **seminal vesicles** contribute about 60% of the volume of semen. The fluid from the seminal vesicles is thick, yellowish, and alkaline. It contains mucus, the sugar fructose (which provides most of the sperm's energy), a coagulating enzyme, ascorbic acid, and local regulators called prostaglandins (see Chapter 45).

The **prostate gland** secretes its products directly into the urethra through several small ducts. This fluid is thin and milky; it contains anticoagulant enzymes and citrate (a sperm nutrient). The prostate gland is the source of some of the most common medical problems of men over age 40. Benign (noncancerous) enlargement of the prostate occurs in more than half of all men in this age-group and in almost all men over 70. In addition, prostate cancer, which most often afflicts men 65 and older, is one of the most common human cancers.

The *bulbourethral glands* are a pair of small glands along the urethra below the prostate. Before ejaculation, they secrete clear mucus that neutralizes any acidic urine remaining in the urethra. Bulbourethral fluid also carries some sperm released before ejaculation, which is one reason for the high failure rate of the withdrawal method of birth control (coitus interruptus).

Penis

The human **penis** contains the urethra, as well as three cylinders of spongy erectile tissue. During sexual arousal, the erectile tissue, which is derived from modified veins and capillaries, fills with blood from the arteries. As this tissue fills, the increasing pressure seals off the veins that drain the penis, causing it to engorge with blood. The resulting erection enables the penis to be inserted into the vagina. Alcohol consumption, certain drugs, emotional issues, and aging all can cause a temporary inability to achieve an erection (erectile dysfunction). For individuals with long-term erectile dysfunction, drugs such as Viagra promote the vasodilating action of the local regulator nitric oxide (NO; see Chapter 45); the resulting relaxation of smooth muscles in the blood vessels of the penis enhances blood flow into the erectile tissues. Although all mammals rely on penile erection for mating, the penis of rodents, raccoons, walruses, whales, and several other mammals also contains a bone, the baculum, which probably further stiffens the penis for mating.

The main shaft of the penis is covered by relatively thick skin. The head, or glans, of the penis has a much thinner covering and is consequently more sensitive to stimulation. The human glans is covered by a fold of skin called the prepuce, or foreskin, which is removed if a male is circumcised.

Gametogenesis

Many of the differences in reproductive anatomy between males and females reflect the distinct structures and functions of the two types of gametes. Sperm are small and motile and must pass from the male to the female. In contrast, eggs, which provide the initial food stores for the embryo, are typically much larger and carry out their function within the female reproductive system. There they must mature in synchrony with the tissues that will support the embryo. Reflecting these differences, egg development and sperm development involve different patterns of meiotic division. We will highlight these differences as we explore **gametogenesis**, the production of gametes.

Spermatogenesis, the formation and development of sperm, is continuous and prolific in adult males. To produce hundreds of millions of sperm each day, cell division and maturation occur throughout the seminiferous tubules coiled within the two testes. For a single sperm, the process takes about 7 weeks from start to finish.

Oogenesis, the development of mature oocytes (eggs), is a prolonged process in the human female. Immature eggs form in the ovary of the female embryo but do not complete their development until years, and often decades, later.

Spermatogenesis differs from oogenesis in three significant ways. First, only in spermatogenesis do all four products of meiosis develop into mature gametes. In oogenesis, cytokinesis during meiosis is unequal, with almost all the cytoplasm segregated to a single daughter cell. This large cell is destined to become the egg; the other products of meiosis, smaller cells called polar bodies, degenerate. Second, spermatogenesis occurs throughout adolescence and adulthood. During oogenesis in human females, mitotic divisions are thought to be complete before birth, and the production of mature gametes ceases at about age 50. Third, spermatogenesis produces mature sperm from precursor cells in a continuous sequence, whereas oogenesis has long interruptions. **Figure 46.12**, on the next two pages, compares and contrasts the steps and organization of spermatogenesis and oogenesis in humans.

▼ **Figure 46.12**

Exploring Human Gametogenesis

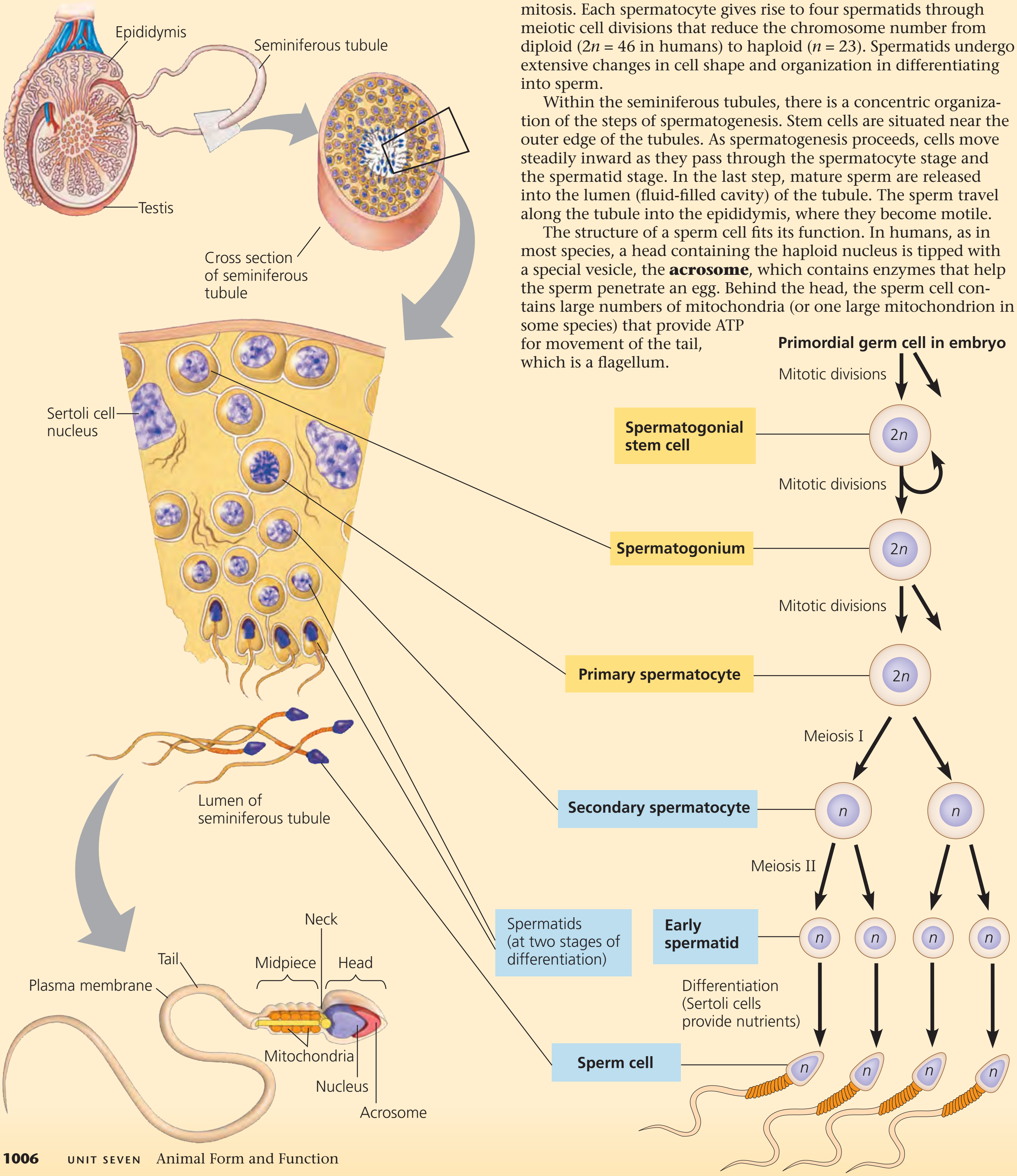
Spermatogenesis

These drawings correlate the mitotic and meiotic divisions in sperm development with the microscopic structure of seminiferous tubules.

The initial or *primordial* germ cells of the embryonic testes divide and differentiate into stem cells that divide mitotically to form **spermatogonia**, which in turn generate spermatocytes, also by mitosis. Each spermatocyte gives rise to four spermatids through meiotic cell divisions that reduce the chromosome number from diploid ($2n = 46$ in humans) to haploid ($n = 23$). Spermatids undergo extensive changes in cell shape and organization in differentiating into sperm.

Within the seminiferous tubules, there is a concentric organization of the steps of spermatogenesis. Stem cells are situated near the outer edge of the tubules. As spermatogenesis proceeds, cells move steadily inward as they pass through the spermatocyte stage and the spermatid stage. In the last step, mature sperm are released into the lumen (fluid-filled cavity) of the tubule. The sperm travel along the tubule into the epididymis, where they become motile.

The structure of a sperm cell fits its function. In humans, as in most species, a head containing the haploid nucleus is tipped with a special vesicle, the **acrosome**, which contains enzymes that help the sperm penetrate an egg. Behind the head, the sperm cell contains large numbers of mitochondria (or one large mitochondrion in some species) that provide ATP for movement of the tail, which is a flagellum.

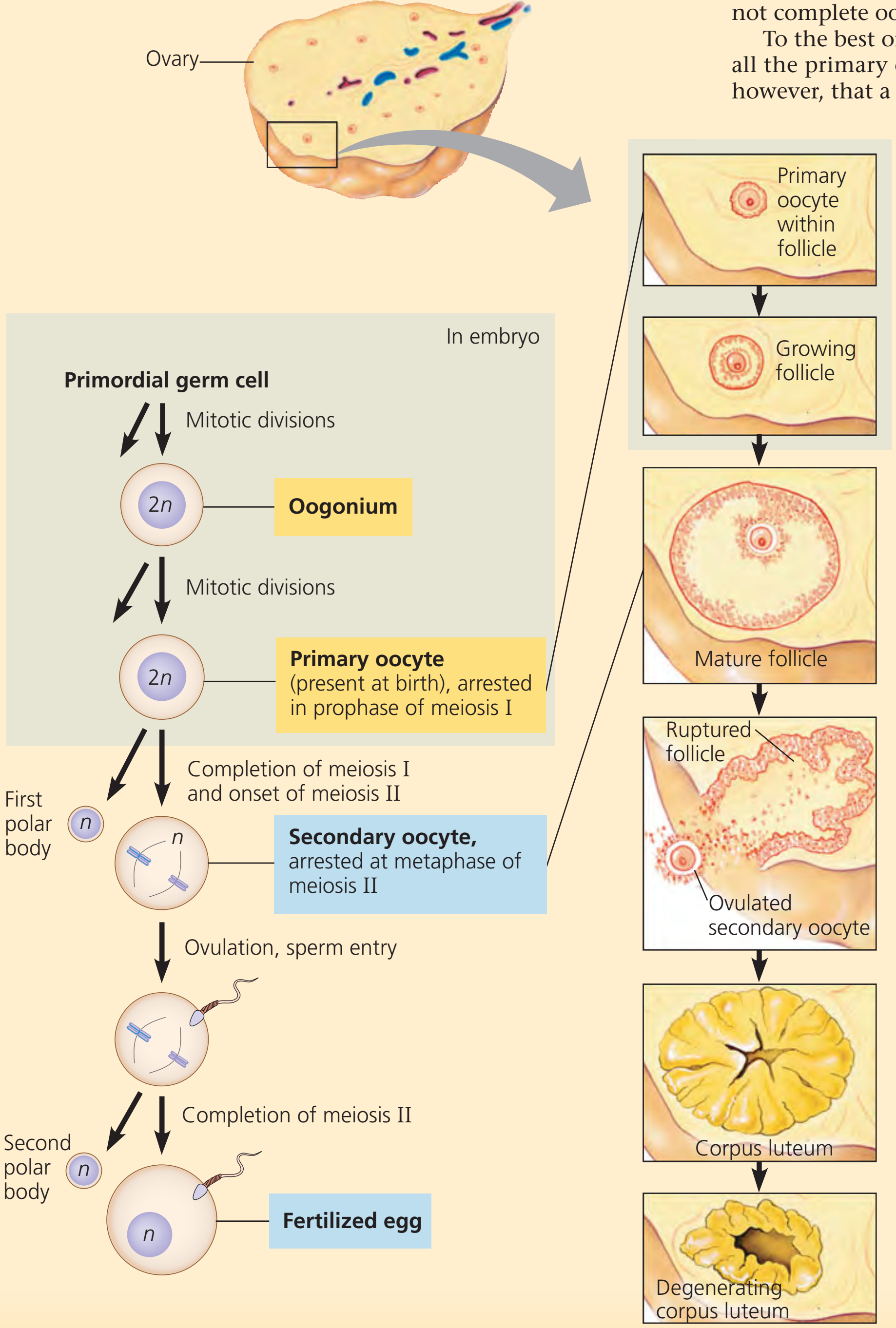


Oogenesis

Oogenesis begins in the female embryo with the production of **oogonia** from primordial germ cells. The oogonia divide by mitosis to form cells that begin meiosis, but stop the process at prophase I before birth. These developmentally arrested cells, called **primary oocytes**, each reside within a small follicle, a cavity lined with protective cells. Beginning at puberty, follicle-stimulating hormone (FSH) periodically stimulates a small group offollicles to resume growth and development. Typically, only one follicle fully matures each month, with its primary oocyte completing meiosis I. The second meiotic division begins, but stops at metaphase. Thus arrested in meiosis II, the **secondary oocyte** is released at ovulation, when its follicle breaks open. Only if a sperm penetrates the oocyte does meiosis II resume. (In other animal species, the sperm may enter the oocyte at the same stage, earlier, or later.) Each of the two meiotic divisions involves unequal cytokinesis, with the smaller cells becoming polar bodies that eventually degenerate (the first polar body may or may not divide again). Thus, the functional product of complete oogenesis is a single mature egg already containing a sperm head; fertilization is defined strictly as the fusion of the haploid nuclei of the sperm and secondary oocyte, although we often use it loosely to mean the entry of the sperm head into the egg.

The ruptured follicle left behind after ovulation develops into the corpus luteum. If the released oocyte is not fertilized and does not complete oogenesis, the corpus luteum degenerates.

To the best of our current knowledge, women are born with all the primary oocytes they will ever have. It is worth noting, however, that a similar conclusion regarding most other mammals was overturned by the discovery in 2004 of multiplying oogonia in the ovaries of adult mice that develop into oocytes. If the same turned out to be true of humans, it might be that the marked decline in fertility that occurs as women age results from both a depletion of oogonia and the degeneration of aging oocytes.



WHAT IF? Suppose you are analyzing the DNA from the polar bodies formed during human oogenesis. If the mother has a mutation in a known disease gene, would analyzing the polar body DNA allow you to infer whether the mutation is present in the mature oocyte? Explain.

CONCEPT CHECK 46.3

1. Why might using a hot tub frequently make it harder for a couple to conceive a child?
2. Oogenesis is often described as the production of a haploid egg by meiosis; but in some animals, including humans, this is not an entirely accurate description. Explain.
3. **WHAT IF?** If each vas deferens in a male was surgically sealed off, what changes would you expect in sexual response and ejaculate composition?

For suggested answers, see Appendix A.

CONCEPT 46.4

The interplay of tropic and sex hormones regulates mammalian reproduction

In both male and female humans, the coordinated actions of hormones from the hypothalamus, anterior pituitary, and gonads govern reproduction. The hypothalamus secretes gonadotropin-releasing hormone (GnRH), which then directs the anterior pituitary to secrete the gonadotropins, follicle-stimulating hormone (FSH) and luteinizing hormone (LH) (see Figure 45.16). These two hormones regulate gametogenesis directly, by targeting tissues in the gonads, as well as indirectly, by regulating sex hormone production. The principal sex hormones are steroid hormones: in males, androgens, especially testosterone; in females, estrogens, especially estradiol, and progesterone. Like the gonadotropins, the sex hormones regulate gametogenesis both directly and indirectly.

Sex hormones serve many functions in addition to promoting gamete production. In many vertebrates, androgens are responsible for male vocalizations, such as the territorial songs of birds and the mating calls of frogs. During development of the human embryo, androgens promote the appearance of the primary sex characteristics of males, the structures directly involved in reproduction. These include the seminal vesicles and associated ducts, as well as external reproductive anatomy. At puberty, sex hormones in both males and females induce formation of secondary sex characteristics, the physical and behavioral features that are not directly related to the reproductive system. In males, androgens cause the voice to deepen, facial and pubic hair to develop, and muscles to grow (by stimulating protein synthesis). Androgens also promote specific sexual behaviors and sex drive, as well as an increase in general aggressiveness. Estrogens similarly have multiple effects in females. At puberty, estradiol stimulates breast and pubic hair development. Estradiol also influences female sexual behavior, induces fat deposition in the breasts and hips, increases water retention, and alters calcium metabolism.

Hormonal Control of Female Reproductive Cycles

Upon reaching sexual maturity, human males carry out gametogenesis continuously, whereas human females produce gametes in cycles. Ovulation occurs only after the endometrium (lining of the uterus) has started to thicken and develop a rich blood supply, preparing the uterus for the possible implantation of an embryo. If pregnancy does not occur, the uterine lining is sloughed off, and another cycle begins. The cyclic shedding of the blood-rich endometrium from the uterus, a process that occurs in a flow through the cervix and vagina, is called **menstruation**.

There are two closely linked reproductive cycles in human females. Changes in the uterus define the **menstrual cycle**, also called the **uterine cycle**. Menstrual cycles average 28 days (although cycles vary, ranging from about 20 to 40 days). The cyclic events in the ovaries define the **ovarian cycle**. Hormone activity links the two cycles to one another, synchronizing ovarian follicle growth and ovulation with the establishment of a uterine lining that can support embryonic development.

Let's examine the reproductive cycle of the human female **(Figure 46.13)**.

The Ovarian Cycle

The reproductive cycle begins ① with the release from the hypothalamus of GnRH, which stimulates the anterior pituitary to ② secrete small amounts of FSH and LH. ③ Follicle-stimulating hormone (as its name implies) stimulates follicle growth, aided by LH, and ④ the cells of the growing follicles start to make estradiol. There is a slow rise in estradiol secreted during most of the **follicular phase**, the part of the ovarian cycle during which follicles grow and oocytes mature. (Several follicles begin to grow with each cycle, but usually only one matures; the others disintegrate.) The low levels of estradiol inhibit secretion of the pituitary hormones, keeping the levels of FSH and LH relatively low. During this portion of the cycle, regulation of the hormones controlling reproduction closely parallels the regulation observed in males.

⑤ When estradiol secretion by the growing follicle begins to rise steeply, ⑥ the FSH and LH levels increase markedly. Whereas a low level of estradiol inhibits the secretion of pituitary gonadotropins, a high concentration has the opposite effect: It stimulates gonadotropin secretion by acting on the hypothalamus to increase its output of GnRH. The effect is greater for LH because the high concentration of estradiol increases the GnRH sensitivity of LH-releasing cells in the pituitary. In addition, follicles respond more strongly to LH at this stage because more of their cells have receptors for this hormone.

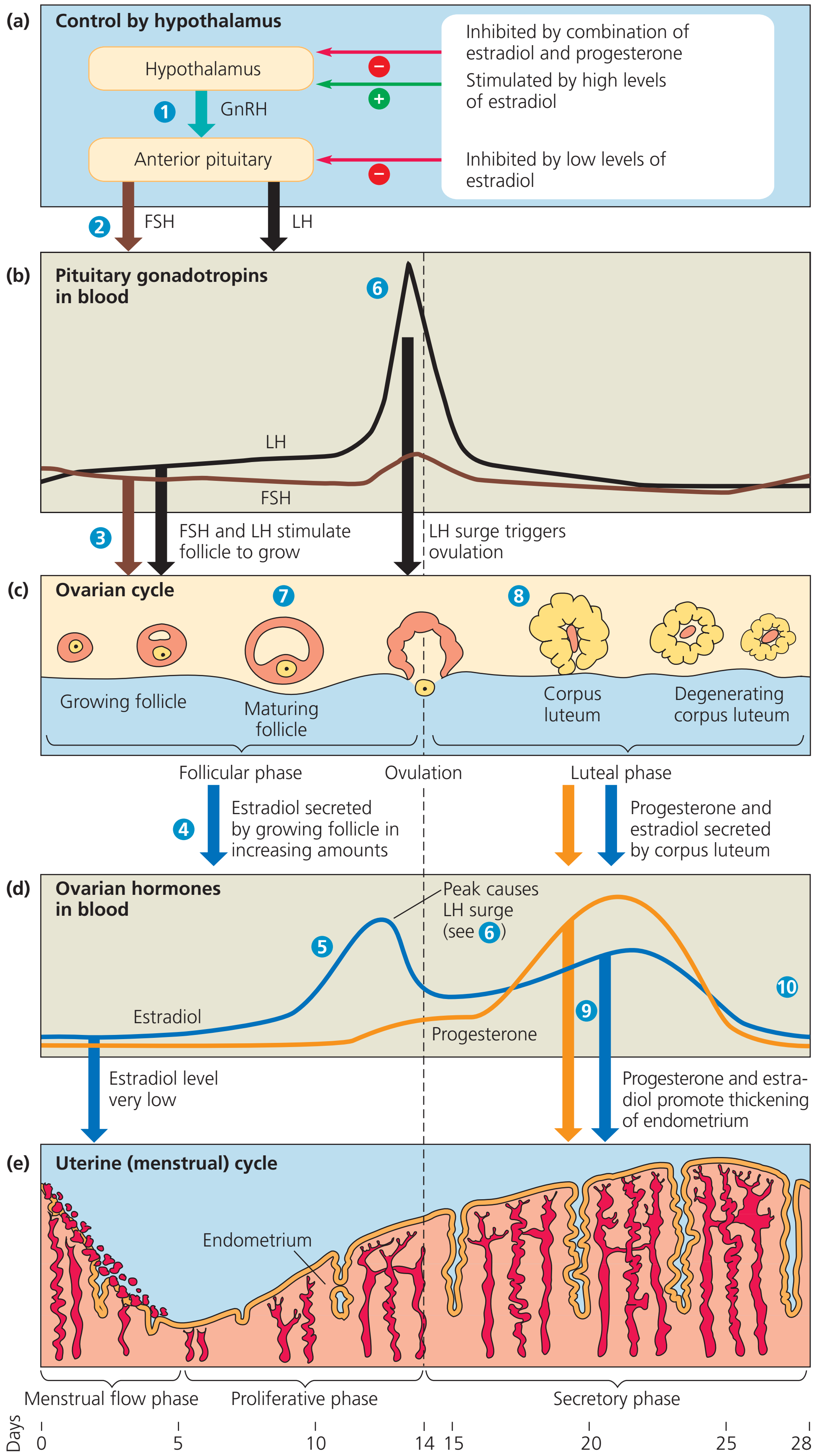
The increase in LH concentration caused by increased estradiol secretion from the growing follicle is an example of positive feedback. The result is final maturation of the follicle. ⑦ The maturing follicle, containing a fluid-filled cavity, enlarges, forming a bulge near the surface of the ovary. The follicular phase ends at ovulation, about a day after the LH surge. In response to the peak in LH levels, the follicle and adjacent wall of the ovary rupture, releasing the secondary oocyte. There is sometimes a distinctive pain in the lower abdomen at or near the time of ovulation; this pain is felt on the left or right side, corresponding to whichever ovary has matured a follicle during that cycle.

The **luteal phase** of the ovarian cycle follows ovulation. ⑧ LH stimulates the follicular tissue left behind in the ovary to transform into a corpus luteum, a glandular structure. Under continued stimulation by LH, the corpus luteum secretes progesterone and estradiol. As progesterone and estradiol levels rise, the combination of these steroid hormones exerts negative feedback on the hypothalamus and pituitary, reducing the secretion of LH and FSH to very low levels. This negative feedback prevents another egg from maturing when a pregnancy may already be under way.

Near the end of the luteal phase, low gonadotropin levels cause the corpus luteum to disintegrate, triggering a sharp decline in estradiol and progesterone concentrations. The decreasing levels of ovarian steroid hormones liberate the hypothalamus and pituitary from the negative-feedback effect of these hormones. The pituitary can then begin to secrete enough FSH to stimulate the growth of new follicles in the ovary, initiating the next ovarian cycle.

The Uterine (Menstrual) Cycle

Prior to ovulation, ovarian steroid hormones stimulate the uterus to prepare for support of an embryo. Estradiol secreted in increasing amounts by growing follicles signals the endometrium to thicken. In this way, the follicular phase of the ovarian cycle is coordinated with the **proliferative phase** of the uterine cycle. After ovulation, ⑨ estradiol and



▲ **Figure 46.13 The reproductive cycle of the human female.** This figure shows how **(c)** the ovarian cycle and **(e)** the uterine (menstrual) cycle are regulated by changing hormone levels in the blood, depicted in parts **(a)**, **(b)**, and **(d)**. The time scale at the bottom of the figure applies to parts **(b)–(e)**.

progesterone secreted by the corpus luteum stimulate continued development and maintenance of the uterine lining, including enlargement of arteries and growth of endometrial glands. These glands secrete a nutrient fluid that can sustain an early embryo even before it implants in the uterine lining. Thus, the luteal phase of the ovarian cycle is coordinated with what is called the **secretory phase** of the uterine cycle.

Upon disintegration of the corpus luteum, the rapid drop ⑩ in ovarian hormone levels causes arteries in the endometrium to constrict. Deprived of its circulation, much of the uterine lining disintegrates, and the uterus, in response to prostaglandin secretion, contracts. Small blood vessels in the endometrium constrict, releasing blood that is shed along with endometrial tissue and fluid. The result is menstruation—the **menstrual flow phase** of the uterine cycle. During menstruation, which usually persists for a few days, a new group of ovarian follicles begin to grow. By convention, the first day of menstruation is designated day 1 of the new uterine (and ovarian) cycle.

Overall, the hormonal cycles in females coordinate egg maturation and release with changes in the uterus, the organ that must accommodate an embryo if the egg cell is fertilized. If an embryo has not implanted in the endometrium by the end of the secretory phase, a new menstrual flow commences, marking the start of the next cycle. Later in the chapter, you will learn about override mechanisms that prevent disintegration of the endometrium in pregnancy.

About 7% of women of reproductive age suffer from **endometriosis**, a disorder in which some cells of the uterine lining migrate to an abdominal location that is abnormal, or **ectopic** (from the Greek *ektopos*, away from a place). Having migrated to a location such as an oviduct, ovary, or large intestine, the ectopic tissue responds to hormones in the bloodstream. Like the uterine endometrium, the ectopic tissue swells and breaks down each ovarian cycle, resulting in pelvic pain and bleeding into the abdomen. Researchers have not yet determined why endometriosis occurs, but hormonal therapy or surgery can be used to lessen discomfort.

Menopause

After about 500 cycles, a woman undergoes **menopause**, the cessation of ovulation and menstruation. Menopause usually occurs between the ages of 46 and 54. During this interval, the ovaries lose their responsiveness to FSH and LH, resulting in a decline in estradiol production.

Menopause is an unusual phenomenon. In most other species, females and males retain their reproductive capacity throughout life. Is there an evolutionary explanation for menopause? One intriguing hypothesis proposes that during early human evolution, undergoing menopause after bearing several children allowed a mother to provide better care for her children and grandchildren, thereby increasing the survival of individuals who share much of her genetic makeup.

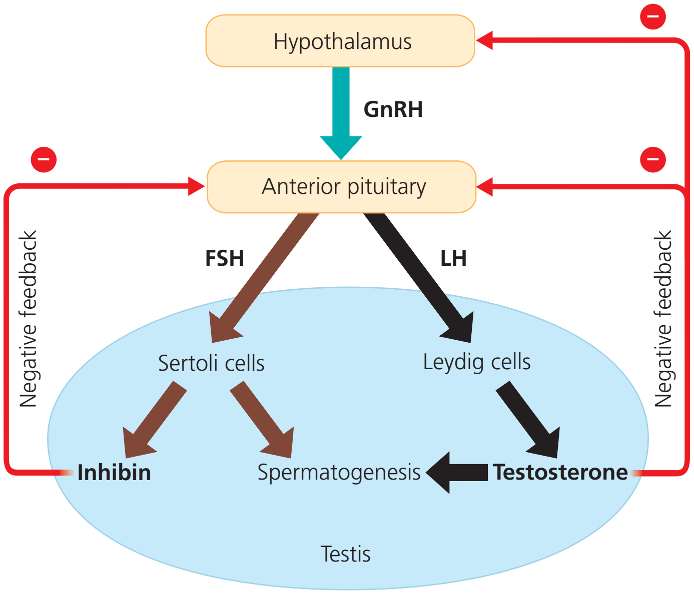
Menstrual Versus Estrous Cycles

In all female mammals, the endometrium thickens before ovulation, but only humans and some other primates have menstrual cycles. Other mammals have **estrous cycles**, in which in the absence of a pregnancy, the uterus reabsorbs the endometrium and no extensive fluid flow occurs. Whereas human females may engage in sexual activity throughout the menstrual cycle, mammals with estrous cycles usually copulate only during the period surrounding ovulation. This period, called estrus (from the Latin *oestrus*, frenzy, passion), is the only time the female is receptive to mating. It is often called "heat," and the female's temperature does increase slightly.

The length and frequency of estrous cycles vary widely among mammals. Bears and wolves have one estrous cycle per year; elephants have several. Rats have estrous cycles throughout the year, each lasting only 5 days.

Hormonal Control of the Male Reproductive System

In males, the FSH and LH secreted in response to GnRH are both required for normal spermatogenesis. Each acts on a distinct type of cell in the testis (**Figure 46.14**). FSH promotes the activity of Sertoli cells. Within the seminiferous tubules, these cells nourish developing sperm (see Figure 46.12). LH regulates Leydig cells, located in the interstitial space between



▲ **Figure 46.14 Hormonal control of the testes.** Gonadotropin-releasing hormone (GnRH) from the hypothalamus stimulates the anterior pituitary to secrete follicle-stimulating hormone (FSH) and luteinizing hormone (LH). FSH acts on Sertoli cells, which nourish developing sperm. LH acts on Leydig cells, which produce androgens, chiefly testosterone. Negative feedback by testosterone on the hypothalamus and anterior pituitary regulates blood levels of GnRH, LH, and FSH. FSH secretion is also subject to negative feedback by a hormone called inhibin, secreted by Sertoli cells.

the seminiferous tubules. In response to LH, Leydig cells secrete testosterone and other androgens, which promote spermatogenesis in the tubules. Both androgen secretion and spermatogenesis occur continuously from puberty onward.

Two negative-feedback mechanisms control sex hormone production in males (see Figure 46.14). Testosterone regulates blood levels of GnRH, FSH, and LH through inhibitory effects on the hypothalamus and anterior pituitary. In addition, **inhibin**, a hormone that in males is produced by Sertoli cells, acts on the anterior pituitary gland to reduce FSH secretion. Together, these negative-feedback circuits maintain androgen production at optimal levels.

Human Sexual Response

Whereas there is a wealth of information regarding the hormonal regulation of human oogenesis and spermatogenesis, comparable data regarding sexual desire and responses are scanty. Testosterone, prolactin, and oxytocin each appear to influence sexual function in males and females, but their precise roles have yet to be defined. Instead, the study of human sexual response has largely focused on the physiological changes associated with sexual activity.

As mentioned earlier, many animals exhibit elaborate mating behavior. The arousal of sexual interest in humans is particularly complex, involving a variety of psychological as well as physical factors. Reproductive structures in the male and female that are quite different in appearance often serve similar functions, reflecting their shared developmental origin. For example, the same embryonic tissues give rise to the glans of the penis and the clitoris, the scrotum and the labia majora, and the skin on the penis and the labia minora.

The general pattern of human sexual response is similar in males and females. Two types of physiological reactions predominate in both sexes: **vasocongestion**, the filling of a tissue with blood, and **myotonia**, increased muscle tension. Both skeletal and smooth muscle may show sustained or rhythmic contractions, including those associated with orgasm.

The sexual response cycle can be divided into four phases: excitement, plateau, orgasm, and resolution. An important function of the excitement phase is to prepare the vagina and penis for **coitus** (sexual intercourse). During this phase, vasocongestion is particularly evident in erection of the penis and clitoris; enlargement of the testicles, labia, and breasts; and vaginal lubrication. Myotonia may occur, resulting in nipple erection or tension of the arms and legs.

In the plateau phase, these responses continue as a result of direct stimulation of the genitalia. In females, the outer third of the vagina becomes vasocongested, while the inner two-thirds slightly expands. This change, coupled with the elevation of the uterus, forms a depression for receiving sperm at the back of the vagina. Breathing increases and heart rate rises, sometimes to 150 beats per minute—not only in response to the physical effort of sexual activity, but also as an involuntary response to stimulation of the autonomic nervous system (see Figure 49.8).

Orgasm is characterized by rhythmic, involuntary contractions of the reproductive structures in both sexes. Male orgasm has two stages. The first, emission, occurs when the glands and ducts of the reproductive tract contract, forcing semen into the urethra. Expulsion, or ejaculation, occurs when the urethra contracts and the semen is expelled. During female orgasm, the uterus and outer vagina contract, but the inner two-thirds of the vagina does not. Orgasm is the shortest phase of the sexual response cycle, usually lasting only a few seconds. In both sexes, contractions occur at about 0.8-second intervals and may also involve the anal sphincter and several abdominal muscles.

The resolution phase completes the cycle and reverses the responses of the earlier stages. Vasocongested organs return to their normal size and color, and muscles relax. Most of the changes of resolution are completed within 5 minutes, but some may take as long as an hour. Following orgasm, the male typically enters a refractory period, lasting anywhere from a few minutes to hours, during which erection and orgasm cannot be achieved. Females do not have a refractory period, making possible multiple orgasms within a short period of time.

CONCEPT CHECK 46.4

1. FSH and LH get their names from events of the female reproductive cycle, but they also function in males. How are their functions in females and males similar?
2. How does an estrous cycle differ from a menstrual cycle, and in what animals are the two types of cycles found?
3. **WHAT IF?** If a human female begins taking estradiol and progesterone immediately after the start of a new menstrual cycle, how will ovulation be affected? Explain.
4. **MAKE CONNECTIONS** A coordination of developmental events is characteristic of the reproductive cycles of a human female and an enveloped RNA virus (see Figure 19.7, p. 388). What is the nature of the coordination in each of these cycles?

For suggested answers, see Appendix A.

CONCEPT 46.5

In placental mammals, an embryo develops fully within the mother's uterus

Having surveyed the ovarian and uterine cycles of human females, we turn now to reproduction itself, beginning with the events that transform an egg into a developing embryo.

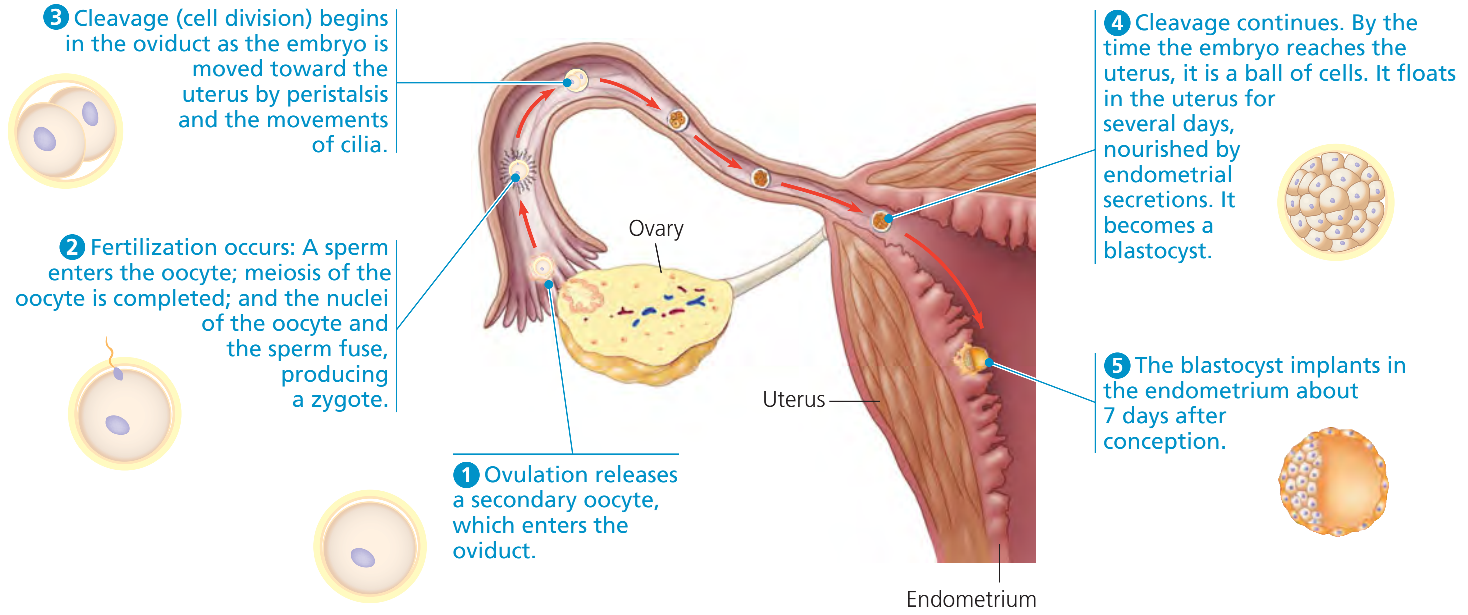
Conception, Embryonic Development, and Birth

During human copulation, 2–5 mL of semen is transferred, with 70–130 million sperm in each milliliter. The alkalinity of the semen helps neutralize the acidic environment of the vagina, protecting the sperm and increasing their motility. When first ejaculated, the semen coagulates, which may serve to keep the ejaculate in place until sperm reach the cervix. Soon after, anticoagulants liquefy the semen, and the sperm begin swimming through the uterus and oviducts.

Fertilization—also called **conception** in humans—occurs when a sperm fuses with an egg (mature oocyte) in the oviduct **(Figure 46.15a)**. About 24 hours later, the resulting zygote begins dividing, a process called **cleavage**. After another 2–3 days, the embryo typically arrives at the uterus as a ball of 16 cells. By about 5 days after fertilization, cleavage has produced an embryonic stage called the **blastocyst**, a sphere of cells surrounding a central cavity.

Several days after blastocyst formation, the embryo implants into the endometrium **(Figure 46.15b)**. Only after implantation can an embryo develop into a fetus. The implanted embryo secretes hormones that signal its presence and regulate the mother's reproductive system. One embryonic hormone, **human chorionic gonadotropin (hCG)**, acts like pituitary LH in maintaining secretion of progesterone and estrogens by the corpus luteum through the first few months of pregnancy. In the absence of this hormonal override during pregnancy, the corpus luteum would deteriorate and progesterone levels would drop, resulting in menstruation and loss of the embryo. Levels of hCG in the maternal blood are so high that some is excreted in the urine, where its presence is the basis of many early pregnancy tests.

The condition of carrying one or more embryos in the uterus is called **pregnancy**, or **gestation**. Human pregnancy averages 266 days (38 weeks) from fertilization of the egg, or 40 weeks from the start of the last menstrual cycle. Duration of pregnancy in other placental mammals correlates with body size and the maturity of the young at birth. Many rodents have gestation periods of about 21 days, whereas those of dogs are closer to 60 days. In cows, gestation averages 270 days (almost the same as in humans), while in elephants it lasts more than 600 days.



③ Cleavage (cell division) begins in the oviduct as the embryo is moved toward the uterus by peristalsis and the movements of cilia.

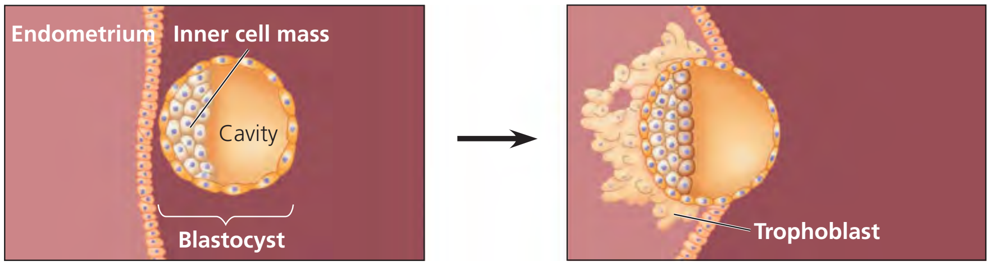
② Fertilization occurs: A sperm enters the oocyte; meiosis of the oocyte is completed; and the nuclei of the oocyte and the sperm fuse, producing a zygote.

① Ovulation releases a secondary oocyte, which enters the oviduct.

④ Cleavage continues. By the time the embryo reaches the uterus, it is a ball of cells. It floats in the uterus for several days, nourished by endometrial secretions. It becomes a blastocyst.

⑤ The blastocyst implants in the endometrium about 7 days after conception.

(a) From ovulation to implantation



(b) Implantation of blastocyst

▲ **Figure 46.15 Formation of the zygote and early postfertilization events.**

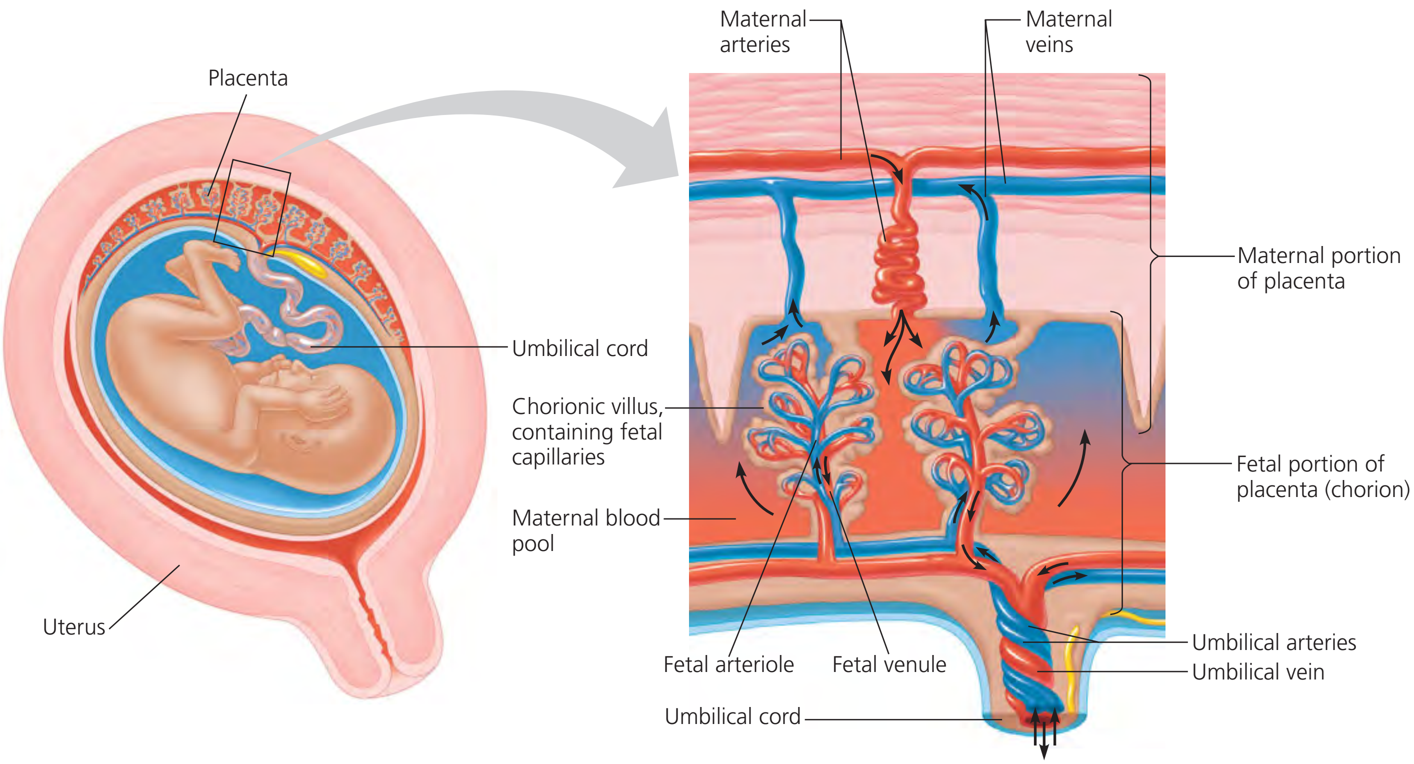
Not all fertilized eggs are capable of completing development. Many pregnancies terminate spontaneously as a result of chromosomal or developmental abnormalities. Much less often, a fertilized egg lodges in the oviduct (fallopian tube), resulting in a tubal, or ectopic, pregnancy. Such pregnancies cannot be sustained and may rupture the oviduct, resulting in serious internal bleeding. A number of conditions, including endometriosis, increase the likelihood of tubal pregnancy. Bacterial infections arising during childbirth, from medical procedures, or as a *sexually transmitted disease* (*STD*) can scar the oviduct, making ectopic pregnancy more likely.

STDs are the most significant preventable causes of infertility. For women who are between 15 and 24 years of age, approximately 700,000 cases of chlamydia and gonorrhea are reported annually in the United States. The number of women infected is actually significantly higher because most women with these STDs have no symptoms and are therefore unaware of their infection. Among women who remain untreated for either chlamydia or gonorrhea, up to 40% develop an inflammatory disorder that can lead to infertility or to potentially fatal ectopic pregnancies.

First Trimester

Human gestation can be divided for convenience into three **trimesters** of about three months each. The first trimester is the time of most radical change for both the mother and the embryo. Upon implantation, the endometrium grows over the blastocyst. Cells and tissues of the embryo begin to differentiate into specialized body structures. (You will learn much more about embryonic development in Chapter 47.)

During its first 2–4 weeks of development, the embryo obtains nutrients directly from the endometrium. Meanwhile, the outer layer of the blastocyst, called the **trophoblast**, grows outward and mingles with the endometrium, eventually helping form the **placenta**. This disk-shaped organ, containing both embryonic and maternal blood vessels, can weigh close to 1 kg. Material diffusing between the maternal and embryonic circulatory systems supplies nutrients, provides immune protection, exchanges respiratory gases, and disposes of metabolic wastes for the embryo. Blood from the embryo travels to the placenta through the arteries of the umbilical cord and returns via the umbilical vein **(Figure 46.16)**.



▲ **Figure 46.16 Placental circulation.** From the 4th week of development until birth, the placenta, a combination of maternal and embryonic tissues, transports nutrients, respiratory gases, and wastes between the embryo or fetus and the mother. Maternal blood enters the placenta in arteries, flows through blood pools in the endometrium, and leaves via veins. Embryonic or fetal blood, which remains in vessels, enters the placenta through arteries and passes through capillaries in finger-like chorionic villi, where oxygen and nutrients are acquired. As indicated in the drawing, the fetal (or embryonic) capillaries and villi project into the maternal portion of the placenta. Fetal blood leaves the placenta through veins leading back to the fetus. Materials are exchanged by diffusion, active transport, and selective absorption between the fetal capillary bed and the maternal blood pools.

? *In a rare genetic disorder, the absence of a particular enzyme leads to increased testosterone production. When the fetus has this disorder, the mother develops a male-like pattern of body hair during the pregnancy. Explain.*

(a) 5 weeks. Limb buds, eyes, the heart, the liver, and rudiments of all other organs have started to develop in the embryo, which is only about 1 cm long.

(b) 14 weeks. Growth and development of the offspring, now called a fetus, continue during the second trimester. This fetus is about 6 cm long.

(c) 20 weeks. Growth to nearly 20 cm in length requires adoption of the fetal position (head at knees) due to the limited space available.

▲ **Figure 46.17 Human fetal development.**

Splitting of the embryo during the first month of development can result in identical, or *monozygotic* (one-egg), twins. Fraternal, or *dizygotic*, twins arise in a very different way: Two follicles mature in a single cycle, followed by independent fertilization and implantation of two genetically distinct embryos.

The first trimester is the main period of **organogenesis**, the development of the body organs **(Figure 46.17)**. During organogenesis, the embryo is particularly susceptible to damage, such as from radiation or drugs, that can lead to birth defects. At 8 weeks, all the major structures of the adult are present in rudimentary form, and the embryo is called a **fetus**. The heart begins beating by the 4th week; a heartbeat can be detected at 8–10 weeks. At the end of the first trimester, the fetus, although well differentiated, is only 5 cm long.

Meanwhile, the mother is also undergoing rapid changes. High levels of progesterone initiate changes in her reproductive system: Increased mucus in the cervix forms a plug to protect against infection, the maternal part of the placenta grows, the uterus gets larger, and (by negative feedback on the hypothalamus and pituitary) ovulation and menstrual cycling stop. The breasts also enlarge rapidly and are often quite tender. About three-fourths of all pregnant women experience nausea, misleadingly called "morning sickness," during the first trimester.

The connection between mother and developing fetus via the placenta allows harmful as well as beneficial substances to pass between them. For this reason, consuming alcohol during pregnancy poses a major risk. Alcohol that reaches the developing central nervous system of the fetus can cause fetal alcohol syndrome, a disorder that can result in mental retardation and other serious birth defects. Similarly, smoking during pregnancy is associated with high risk of low birth weight and other health problems.

Second Trimester

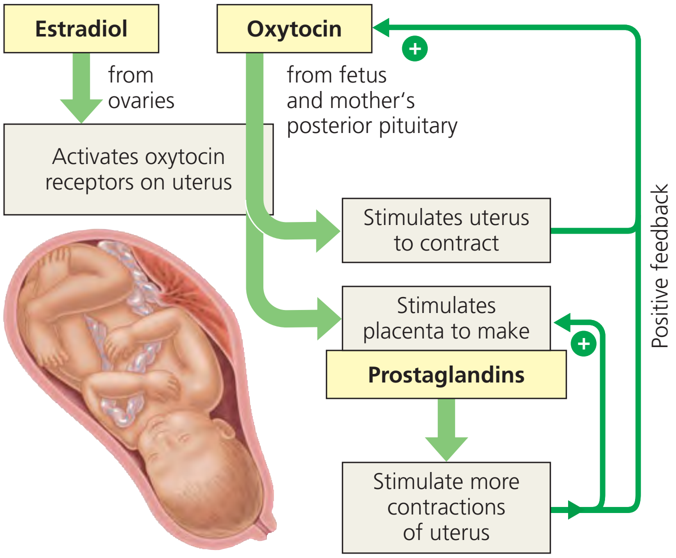
During the second trimester, the uterus grows enough for the pregnancy to become apparent. The fetus itself grows to about 30 cm in length and is very active. The mother may feel fetal movements as early as one month into the second trimester; fetal activity is typically visible through the abdominal wall one to two months later. Hormone levels stabilize as hCG declines; the corpus luteum deteriorates; and the placenta completely takes over the production of progesterone, the hormone that maintains the pregnancy.

Third Trimester

During the final trimester, the fetus grows to about 3–4 kg in weight and 50 cm in length. Fetal activity may decrease as the fetus fills the available space. As the fetus grows and the uterus expands around it, the mother's abdominal organs become compressed and displaced, leading to frequent urination and digestive blockages.

Childbirth begins with **labor**, a series of strong, rhythmic uterine contractions that push the fetus and placenta out of the body. Recent studies suggest that labor begins when the fully developed fetus produces hormones and certain lung proteins that initiate an inflammatory response (see Chapter 43) in the mother. However, further study is needed to determine if inflammation does in fact trigger labor.

Once labor begins, a complex interplay of local regulators (prostaglandins) and hormones (chiefly estradiol and oxytocin) induces and regulates further contractions of the uterus **(Figure 46.18)**. The action of oxytocin forms a positive-feedback loop (see Chapter 45), with uterine contractions stimulating secretion of oxytocin, which in turn stimulates further contractions.



▲ **Figure 46.18 Positive feedback in labor.**

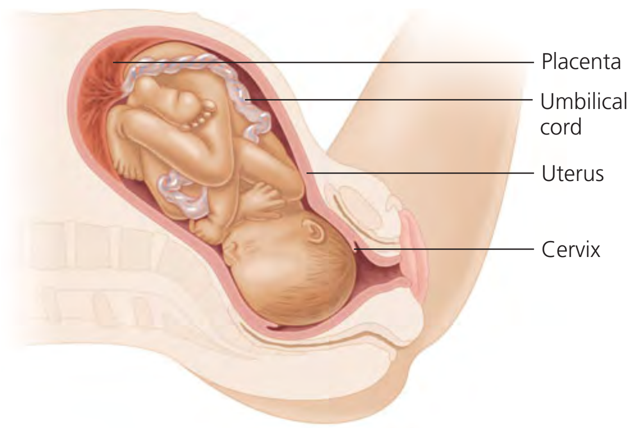
? *Predict the effect of a single dose of oxytocin on a pregnant woman at the end of 39 weeks gestation.*

Labor is typically described as having three stages (**Figure 46.19**). The first stage is the thinning and opening up (dilation) of the cervix. The second stage is the expulsion, or delivery, of the baby. Continuous strong contractions force the fetus out of the uterus and through the vagina. The final stage of labor is delivery of the placenta.

One aspect of postnatal care unique to mammals is **lactation**, the production of mother's milk. In response to suckling by the newborn, as well as changes in estradiol levels after birth, the hypothalamus signals the anterior pituitary to secrete prolactin, which stimulates the mammary glands to produce milk. Suckling also stimulates the secretion of oxytocin from the posterior pituitary, which triggers release of milk from the mammary glands (see Figure 45.15).

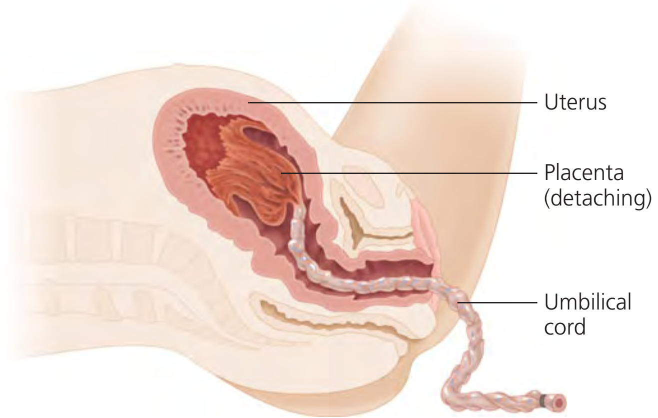
Maternal Immune Tolerance of the Embryo and Fetus

Pregnancy is an immunological puzzle. Half of the embryo's genes are inherited from the father; thus, many of the chemical markers present on the surface of the embryo are foreign to the mother. Why, then, does the mother not reject the embryo as a foreign body, as she would a tissue or organ graft from another person? One intriguing clue comes from the relationship between certain autoimmune disorders and pregnancy. For example, the symptoms of rheumatoid arthritis, an autoimmune disease of the joints, become less severe during pregnancy. Thus, the overall regulation of the immune system appears to be altered by the reproductive process. Sorting out these changes and how they might protect the developing fetus is an active area of research for immunologists.



① Dilation of the cervix

② Expulsion: delivery of the infant



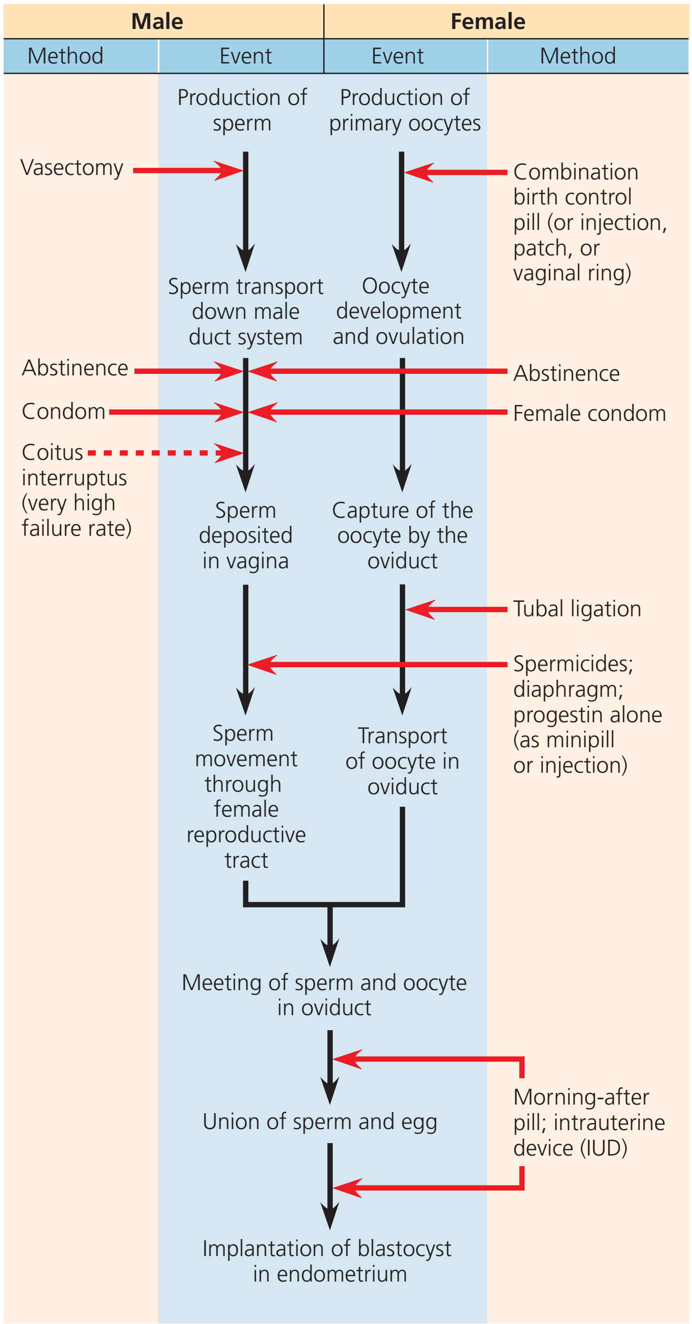
③ Delivery of the placenta

▲ **Figure 46.19 The three stages of labor.**

Contraception and Abortion

Contraception, the deliberate prevention of pregnancy, can be achieved in a number of ways. Some contraceptive methods prevent gamete development or release from female or male gonads; others prevent fertilization by keeping sperm and egg apart; and still others prevent implantation of an embryo. For complete information on contraceptive methods, you should consult a health-care provider. The following brief introduction to the biology of the most common methods and the corresponding diagram in **Figure 46.20** make no pretense of being a contraception manual.

Fertilization can be prevented by abstinence from sexual intercourse or by any of several barriers that keep live sperm from contacting the egg. Temporary abstinence, often called the **rhythm method** of birth control or **natural family planning**, depends on refraining from intercourse when conception is most likely. Because the egg can survive in the oviduct for 24–48 hours and sperm for up to 5 days, a couple practicing temporary abstinence should not engage in intercourse for a number of days before and after ovulation. The most effective methods for determining the time of ovulation combine several indicators, including changes in cervical mucus and body temperature during the menstrual cycle. Thus, natural family planning requires that the couple be knowledgeable about these physiological signs. Note that a pregnancy rate of 10–20% is typically reported for couples practicing natural family planning. (Pregnancy rate is the average number of women who become pregnant during a year for every 100 women using a particular pregnancy prevention method, expressed as a percentage.) Some couples use ovulation-timing methods to *increase* the probability of conception.



▲ **Figure 46.20 Mechanisms of several contraceptive methods.** Red arrows indicate where these methods, devices, or products interfere with events from the production of sperm and primary oocytes to an implanted, developing embryo.

As a method of preventing fertilization, *coitus interruptus*, or withdrawal (removal of the penis from the vagina before ejaculation), is unreliable. Sperm from a previous ejaculate may be transferred in secretions that precede ejaculation. Furthermore, a split-second lapse in timing or willpower can result in tens of millions of sperm being transferred before withdrawal.

The several barrier methods of contraception that block the sperm from meeting the egg have pregnancy rates of less than 10%. The **condom** is a thin, latex rubber or natural membrane sheath that fits over the penis to collect the semen. For sexually active individuals, latex condoms are the only contraceptives that are highly effective in preventing the spread of sexually transmitted diseases, including AIDS. (This protection is, however, not absolute.) Another common barrier device is the **diaphragm**, a dome-shaped rubber cap inserted into the upper portion of the vagina before intercourse. Both of these devices have lower pregnancy rates when used in conjunction with a spermicidal (sperm-killing) foam or jelly. Other barrier devices include the vaginal pouch, or "female condom."

Except for complete abstinence from sexual intercourse, the most effective means of birth control are sterilization, intrauterine devices (IUDs), and hormonal contraceptives. Sterilization (discussed later) is almost 100% effective. The IUD has a pregnancy rate of 1% or less and is the most commonly used reversible method of birth control outside the United States. Placed in the uterus by a doctor, the IUD interferes with fertilization and implantation. Hormonal contraceptives, most often in the form of **birth control pills**, also have pregnancy rates of 1% or less.

The most commonly prescribed birth control pills are a combination of a synthetic estrogen and a synthetic progestin (progesterone-like hormone). This combination mimics negative feedback in the ovarian cycle, stopping the release of GnRH by the hypothalamus and thus of FSH and LH by the pituitary. The prevention of LH release blocks ovulation. In addition, the inhibition of FSH secretion by the low dose of estrogens in the pills prevents follicles from developing. A similar combination of hormones is also available as an injection, as a ring inserted into the vagina, and as a skin patch. Combination birth control pills can also be used in high doses as "morning-after" pills. Taken within 3 days after unprotected intercourse, they prevent fertilization or implantation with an effectiveness of about 75%.

A different type of hormone-based contraceptive contains only progestin. Progestin causes thickening of a woman's cervical mucus so that it blocks sperm from entering the uterus. Progestin also decreases the frequency of ovulation and causes changes in the endometrium that may interfere with implantation if fertilization occurs. Progestin can be administered as injections that last for three months or as a tablet ("minipill") taken daily. Pregnancy rates for progestin treatment are very low.

Hormone-based contraceptives have both beneficial and harmful side effects. For women taking a combination pill, cardiovascular problems are the most serious concern. Women who regularly smoke cigarettes face a three to ten times greater risk of dying from cardiovascular disease if they also use oral contraceptives. Among nonsmokers, birth control pills slightly raise a woman's risk of abnormal blood clotting, high blood pressure, heart attack, and stroke. Although oral contraceptives increase the risk for these cardiovascular disorders, they eliminate the dangers of pregnancy; women on birth control pills have mortality rates about one-half those of pregnant women. Also, the pill decreases the risk of ovarian and endometrial cancers.

One elusive research goal has been a reversible chemical contraceptive for men. Recent strategies have focused on hormone combinations that suppress gonadotropin release and thereby block spermatogenesis. Testosterone included in such combinations has two desirable effects: inhibiting reproductive functions of the hypothalamus and pituitary and maintaining secondary sex characteristics. Although there have been some promising results, hormonal male contraceptives are still in the testing stage.

Sterilization is the permanent prevention of gamete production or release. **Tubal ligation** in women usually involves sealing shut or tying off (ligating) a section of each oviduct to prevent eggs from traveling into the uterus. Similarly, **vasectomy** in men is the cutting and tying off of each vas deferens to prevent sperm from entering the urethra. Both male and female sterilization procedures are relatively safe and free from harmful effects. Sex hormone secretion and sexual function are unaffected by both procedures, with no change in menstrual cycles in females or ejaculate volume in males. Although tubal ligation or vasectomy are considered permanent, both procedures can in many cases be reversed by microsurgery.

The termination of a pregnancy in progress is called **abortion**. Spontaneous abortion, or *miscarriage*, is very common; it occurs in as many as one-third of all pregnancies, often before the woman is even aware she is pregnant. In addition, each year about 850,000 women in the United States choose to have an abortion performed by a physician.

A drug called mifepristone, or RU486, can terminate a pregnancy nonsurgically within the first 7 weeks. RU486 blocks progesterone receptors in the uterus, thus preventing progesterone from maintaining the pregnancy. It is taken with a small amount of prostaglandin to induce uterine contractions.

Modern Reproductive Technologies

Recent scientific and technological advances have made it possible to address many reproductive problems, including genetic diseases and infertility.

Detecting Disorders During Pregnancy

Many genetic diseases and developmental problems can now be diagnosed while the fetus is in the uterus. Ultrasound imaging, which generates images using sound frequencies above the normal hearing range, is commonly used to analyze the fetus's size and condition. Amniocentesis and chorionic villus sampling are techniques in which a needle is used to obtain fetal cells from fluid or tissue surrounding the embryo; these cells then provide the basis for genetic analysis (see Figure 14.19). An alternative technique for obtaining fetal tissue relies on the fact that a few fetal blood cells leak across the placenta into the mother's bloodstream. A blood sample from the mother yields fetal cells that can be identified with specific antibodies (which bind to proteins on the surface of fetal cells) and then tested for genetic disorders.

Diagnosing genetic diseases in a fetus poses ethical questions. To date, almost all detectable disorders remain untreatable in the uterus, and many cannot be corrected even after birth. Parents may be faced with difficult decisions about whether to terminate a pregnancy or to raise a child who may have profound defects and a short life expectancy. These are complex issues that demand careful, informed thought and competent genetic counseling.

Treating Infertility

Infertility—an inability to conceive offspring—is quite common, affecting about one in ten couples both in the United States and worldwide. The causes of infertility are varied, and the likelihood of a reproductive defect is nearly the same for men and women. For women, however, the risk of reproductive difficulties, as well as genetic abnormalities of the fetus, increases steadily past age 35. Evidence suggests that the prolonged period of time oocytes spend in meiosis is largely responsible for this increased risk.

Reproductive technology can help with a number of fertility problems. Hormone therapy can sometimes increase sperm or egg production, and surgery can often correct ducts that have failed to form properly or have become blocked. Many infertile couples turn to **assisted reproductive technologies**, procedures that generally involve surgically removing eggs (secondary oocytes) from a woman's ovaries after hormonal stimulation, fertilizing the eggs, and returning early embryos to the woman's body. Unused eggs, sperm, and embryos are sometimes frozen for later pregnancy attempts.

The technique of ***in vitro* fertilization (IVF)** involves mixing oocytes and sperm in culture dishes. Fertilized eggs are incubated until they have formed at least eight cells and are then typically transferred to the woman's uterus for implantation. If mature sperm are defective, low in number (less than 20 million per milliliter of ejaculate), or even absent, fertility is often restored by a technique called **intracytoplasmic sperm injection (ICSI)**. In this form of IVF, the head of a spermatid or sperm is drawn up into a needle and injected directly into an oocyte to achieve fertilization.

Though costly, IVF procedures have enabled more than a million couples to conceive children. In some cases, these procedures are carried out with sperm or eggs from donors. To date, evidence indicates that abnormalities arising as a consequence of IVF procedures are rare.

By whatever means fertilization occurs, a developmental program follows that transforms the single-celled zygote into a multicellular organism. The mechanisms of this remarkable program of development in humans and other animals are the subject of Chapter 47.

CONCEPT CHECK 46.5

1. Why does testing for hCG (human chorionic gonadotropin) work as a pregnancy test early in pregnancy but not late in pregnancy? What is the function of hCG in pregnancy?
2. In what ways are tubal ligation and vasectomy similar?
3. **WHAT IF?** If a spermatid nucleus is used for ICSI, what steps of gametogenesis and conception are bypassed?

For suggested answers, see Appendix A.

46 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 46.1

Both asexual and sexual reproduction occur in the animal kingdom (pp. 996–999)

- Animals reproduce either asexually or sexually. **Sexual reproduction** requires the fusion of male and female gametes, forming a diploid **zygote**. **Asexual reproduction** is the production of offspring without gamete fusion. Fission, budding, fragmentation with regeneration, and **parthenogenesis** are mechanisms of asexual reproduction in various invertebrates. Facilitating selection for or against sets of genes may explain why sexual reproduction is widespread among animal species.
- Although most animals reproduce exclusively sexually or asexually, some alternate between the two. Variations on these two modes are made possible through parthenogenesis, **hermaphroditism**, and sex reversal. Hormones and environmental cues control reproductive cycles.

? *Would a pair of haploid offspring produced by parthenogenesis be genetically identical?*

CONCEPT 46.2

Fertilization depends on mechanisms that bring together sperm and eggs of the same species (pp. 999–1002)

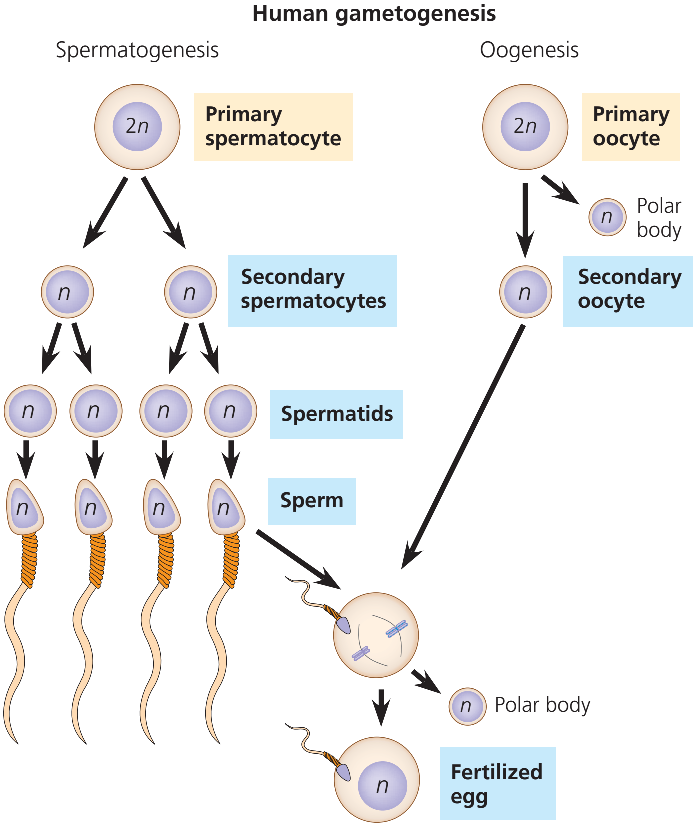
- Fertilization can occur externally or internally with regard to the mother's body. In either case, fertilization requires coordinated timing, which may be mediated by environmental cues, pheromones, or courtship behavior. Internal fertilization is typically often associated both with relatively fewer offspring and with greater protection of offspring by the parents. Systems for gamete production and delivery range from undifferentiated cells in the body cavity to complex **gonads** with accessory tubes and glands that carry and protect gametes and embryos. Although sexual reproduction involves a partnership, it also provides an opportunity for competition between individuals and between gametes.

? *Identify which of the following are unique to mammals: a female uterus and a male vas deferens, extended internal development, parental care of newborns.*

CONCEPT 46.3

Reproductive organs produce and transport gametes (pp. 1002–1008)

- The reproductive system of the human female consists principally of the **labia** and the **glans** of the **clitoris** externally and the **vagina**, **uterus**, **oviducts**, and **ovaries** internally. Eggs are produced in the ovaries and upon fertilization develop in the uterus. In males, sperm are produced in **testes**, which are suspended outside the body in the **scrotum**. Ducts extending from the scrotum connect the testes to internal accessory glands and to the opening of the **penis**. Both males and females have **mammary glands**, but milk production occurs only in females. During intercourse, males and females each experience the erection of certain body tissues due to **vasocongestion** and **myotonia**, culminating in **orgasm**.
- Gametogenesis, or gamete production, consists of **oogenesis** in females and **spermatogenesis** in males. Meiosis generates one large egg in oogenesis, but four sperm in spermatogenesis. In humans, sperm develop continuously, whereas oocyte maturation is discontinuous and cyclic.



? *How does the difference in size and cellular contents between sperm and eggs relate to their specific functions in reproduction?*

CONCEPT 46.4

The interplay of tropic and sex hormones regulates mammalian reproduction (pp. 1008–1011)

- In human males, androgens (chiefly testosterone) from the testes cause the development of primary and secondary sex characteristics. Androgen secretion and sperm production are both controlled by hypothalamic and pituitary hormones.
- In human females, cyclic secretion of GnRH from the hypothalamus and FSH and LH from the anterior pituitary orchestrates the reproductive cycle. FSH and LH bring about changes in the ovary and uterus via estrogens, primarily estradiol, and progesterone. The developing follicle and the corpus luteum also secrete hormones, with positive and negative feedback coordinating the uterine and ovarian cycles.
- **Estrous cycles** differ from **menstrual cycles** in that the endometrial lining is reabsorbed rather than shed and sexual receptivity is limited to a heat period.

? *Why do anabolic steroids lead to reduced sperm count?*

CONCEPT 46.5

In placental mammals, an embryo develops fully within the mother's uterus (pp. 1011–1018)

- After fertilization and the completion of meiosis in the oviduct, the zygote undergoes cleavage and develops into a blastocyst before implantation in the endometrium. All major organs start developing by 8 weeks. A pregnant woman's acceptance of her "foreign" offspring likely reflects partial suppression of the maternal immune response.
- Contraceptive methods may prevent release of mature gametes from the gonads, fertilization, or implantation of the embryo. Reproductive technologies can assist infertile couples by hormonal methods or *in vitro* fertilization and can also help detect problems before birth.

? *What route would oxygen in the mother's blood follow to arrive at a body cell of the fetus?*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Which of the following characterizes parthenogenesis?
   a. An individual may change its sex during its lifetime.
   b. Specialized groups of cells grow into new individuals.
   c. An organism is first a male and then a female.
   d. An egg develops without being fertilized.
   e. Both mates have male and female reproductive organs.

2. In male mammals, excretory and reproductive systems share
   a. the testes.
   b. the urethra.
   c. the seminal vesicle.
   d. the vas deferens.
   e. the prostate.

3. Which of the following is *not* properly paired?
   a. seminiferous tubule—cervix
   b. Sertoli cells—follicle cells
   c. testosterone—estradiol
   d. scrotum—labia majora
   e. vas deferens—oviduct

4. Peaks of LH and FSH production occur during
   a. the menstrual flow phase of the uterine cycle.
   b. the beginning of the follicular phase of the ovarian cycle.
   c. the period just before ovulation.
   d. the end of the luteal phase of the ovarian cycle.
   e. the secretory phase of the menstrual cycle.

5. During human gestation, rudiments of all organs develop
   a. in the first trimester.
   b. in the second trimester.
   c. in the third trimester.
   d. while the embryo is in the oviduct.
   e. during the blastocyst stage.

LEVEL 2: APPLICATION/ANALYSIS

6. Which of the following is a true statement?
   a. All mammals have menstrual cycles.
   b. The endometrial lining is shed in menstrual cycles but reabsorbed in estrous cycles.
   c. Estrous cycles are more frequent than menstrual cycles.
   d. Estrous cycles are not controlled by hormones.
   e. Ovulation occurs before the endometrium thickens in estrous cycles.

7. For which of the following is the number the same in spermatogenesis and oogenesis?
   a. interruptions in meiotic divisions
   b. functional gametes produced by meiosis
   c. meiotic divisions required to produce each gamete
   d. gametes produced in a given time period
   e. different cell types produced by meiosis

8. Which statement about human reproduction is false?
   a. Fertilization occurs in the oviduct.
   b. Effective hormonal contraceptives are currently available only for females.
   c. An oocyte completes meiosis after a sperm penetrates it.
   d. The earliest stages of spermatogenesis occur closest to the lumen of the seminiferous tubules.
   e. Spermatogenesis and oogenesis require different temperatures.

LEVEL 3: SYNTHESIS/EVALUATION

9. **DRAW IT** In human spermatogenesis, mitosis of a stem cell gives rise to one cell that remains a stem cell and one cell that becomes a spermatogonium. (a) Draw four rounds of mitosis for a stem cell, and label the daughter cells. (b) For one spermatogonium, draw the cells it would produce from one round of mitosis followed by meiosis. Label the cells, and label mitosis and meiosis. (c) What would happen if stem cells divided like spermatogonia?

10. **EVOLUTION CONNECTION**
Hermaphroditism is often found in animals that are fixed to a surface. Motile species are less often hermaphroditic. Why?

11. **SCIENTIFIC INQUIRY**
You discover a new egg-laying worm species. You dissect four adults and find both oocytes and sperm in each. Cells outside the gonad contain five chromosome pairs. Lacking genetic variants, how would you determine whether the worms can self-fertilize?

12. **WRITE ABOUT A THEME**
Energy Transfer In reproducing, animals transfer energy to their offspring. In a short essay (100–150 words), discuss how distinct investments of energy by females contribute to the reproductive success of a frog, a chicken, and a human.

For selected answers, see Appendix A.

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