Reproduction

In evolutionary terms, the white-tailed deer is a success. It has weathered ice ages and thaws, it has colonized mountain and swamp, and it thrives in the midst of the disturbances caused by the destructive invader of its world, man. One of the reasons for its success is its reproductive strategies: the whitetail can breed at an early age, select the best sires in a herd, produce more than one offspring per year, arrange for the young to be born at a favorable time of year, even alter the sex ratio within the herd to maintain a healthy population. In fact, the white-tailed deer is one of the most prolific mammals and the most productive deer species.

Whitetails reach puberty and breed at a very early age—but only under the right conditions. To reach puberty, a deer first has to obtain a critical body size, about 80 to 90 pounds for northern races of white-tailed deer and about 70 pounds for the smaller southern races. Up to 80 percent of the doe fawns in the midwestern farm belt reach puberty and breed at 6 to 8 months of age. In the southeastern United States, this number is generally much lower, with only 10 to 40 percent of doe fawns breeding in their first year under good range conditions.

Whether a doe reaches puberty in her first year of life depends on when she herself was born, and on the quality and quantity of food she eats in her first six months. In poorer habitat, such as the Florida pine flatwoods, deer do not reach puberty until they are 1 year of age or more. Good habitat, in and of itself, does not mean good nutrition, however: herd density can rapidly reach the point where quality forage is no longer available. The growth rate of fawns is slowed and puberty is delayed until their second year.

Biologists, then, often use fawn reproduction as an indicator of current range conditions. In well-managed deer herds, fawn reproduction is generally high, the one exception being the northern extremes of the white-tailed deer's range, where bitterly cold winters and deep snow make survival unlikely for offspring of inexperienced doe fawns. Researchers Ozoga and Verme found that even among supplementally fed deer in the upper peninsula of Michigan, fawn does did not carry fawns, whereas in the farmland of the lower peninsula more than 60 percent of the female fawns carried young.

Both protein and energy are important to the reproductive process and the onset of puberty. Protein is required for body growth; energy, in the form of carbohydrates and fats, appears particularly important to the production of female hormones. Researchers in Virginia demonstrated that female fawns on high-energy diets had higher levels of the hormone progesterone than fawns fed low-energy diets (different protein levels had no effect on progesterone values). These differences in hormonal levels relate directly to the female's ovary production and release of eggs and thus to the ability to breed.

DRAKE

The interplay of hormones prompts a rise in sexual energy among bucks and does. The rut is timed so that the fawns are born when weather and resources can best ensure their survival.

Male fawns respond to nutrition and time of birth in the same manner as their female counterparts. In general, the same proportion of each sex reaches puberty as fawns. Sexually mature male fawns have calcified antler "buttons." And, as with female fawns, this sign of sexual maturity usually appears long after the normal rut for adult deer. Thus, it would be rare for a buck actually to participate in the rut during his first year of life unless it was to breed a female fawn.

Timing

The ability to breed does not necessarily mean that a species can reproduce: for a population to remain stable or grow, the young animals must survive to adulthood and themselves begin to reproduce. The renewal of life for white-tailed deer depends on favorable birthing times. In most regions that whitetails inhabit, only certain periods of the year allow newborns and their mothers to thrive and survive. Unlike domestic farm animals, which breed year-round, deer require a restrictive breeding period, timed so that the resulting embryo will become a completely developed fawn and be born at a time that favors survival. The mechanism by which breeding takes place at just the right time of year is an ingenious adaptation.

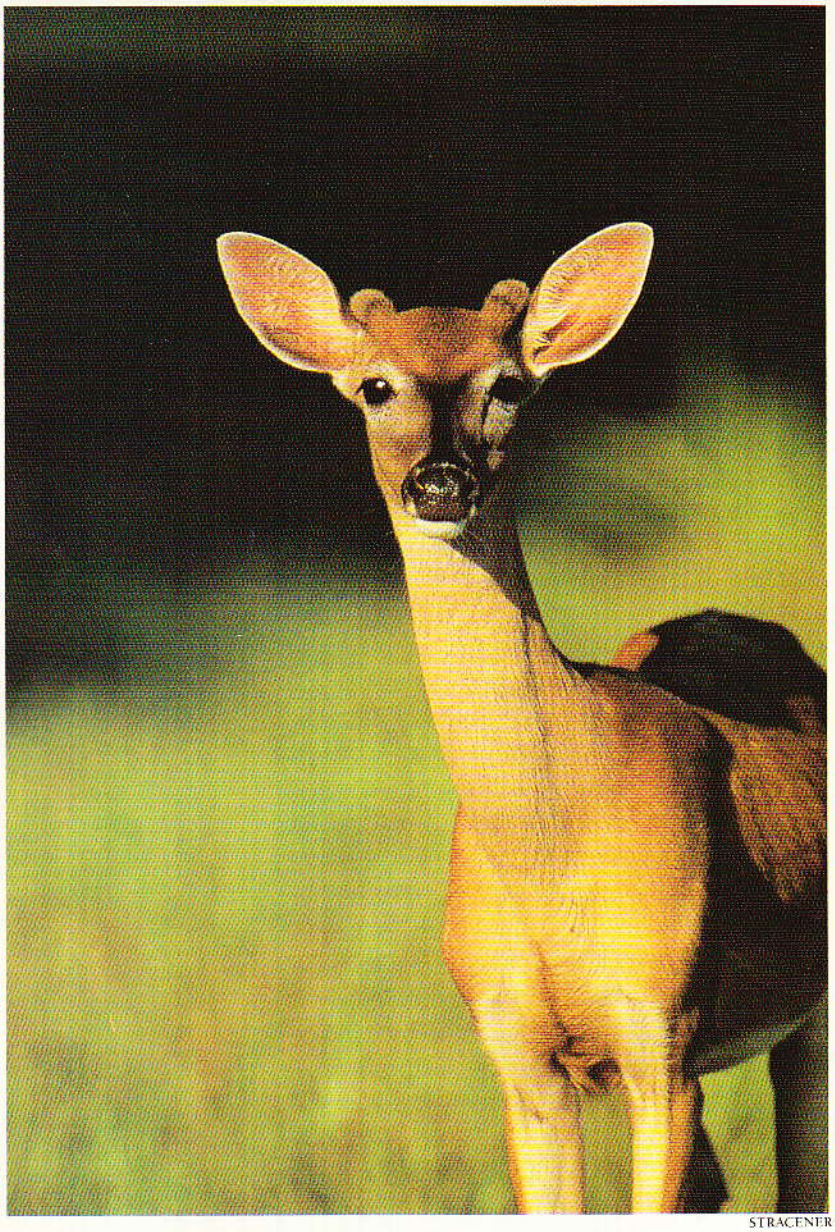
That the breeding of the white-tailed deer might be regulated by photoperiod was expounded in 1970 by McDowell, who observed a difference in timing between North and South: from mid-October to mid-December above the 36-degree latitude, and from the autumnal equinox (September 22) to the vernal equinox (March 21) in the South, between 28 and 36 degrees latitude.

What accounts for the different breeding seasons in North and South is the difference in the length of daylight: a deer, like other mammals in temperate zones, has in the brain a pineal gland, whose function is to measure photoreception and respond to changes in photoperiod. This small, pea-sized gland is regulated by the optic nerves from the eyes. (Indeed, the gland is itself embryologically developed from the same tissue from which eyes are.) In darkness, the pineal gland secretes a hormone called melatonin, which apparently regulates the repro-

ductive hormones produced by the pituitary gland. That melatonin can regulate breeding has been demonstrated by New Zealand researchers Barrell and Lapwood. These researchers were able to advance the breeding of red deer by more than a month through daily administration of melatonin.

The white-tailed deer is unique among deer species in that its range covers both tropical and temperate zones. Deer near the equator have been shown to breed during all months of the year. In Venezuela, Brokx found that white-tailed does not only bred at all times of the year but, unlike their northern cousins, also can breed again shortly after giving birth and thus can fawn more than once in a single year.

Most bucks reach sexual maturity as yearlings but even then cannot compete with larger rivals for does; this fawn buck's buttons reveal his immaturity.



STRACENER

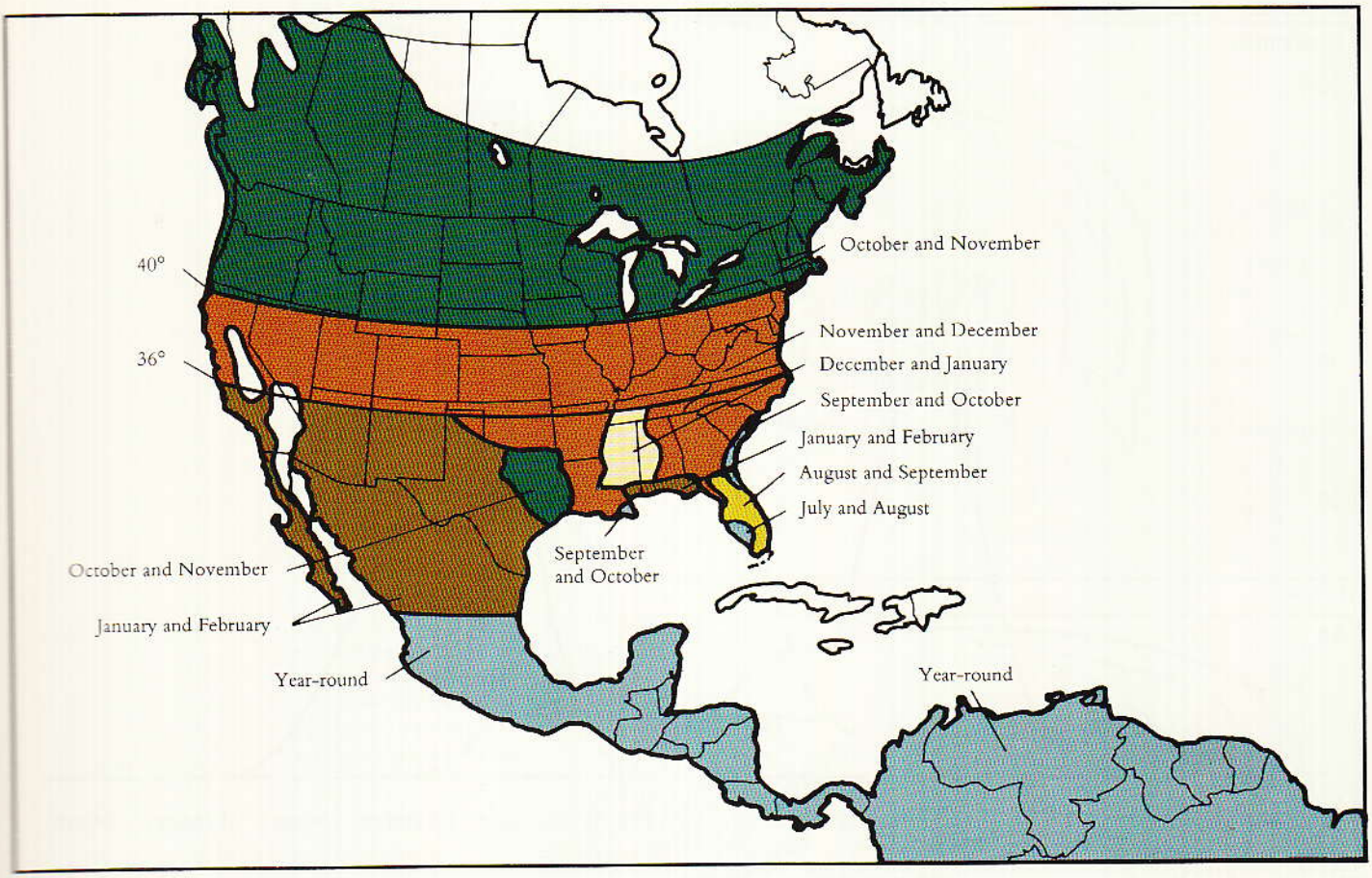
Although photoperiod appears to be the prime regulator of breeding timing, other factors may be at work. Consider the breeding records of deer at the same latitude: South Carolina deer breed starting in September, but Mississippi deer don't begin until November. That the rut is occurring at different times within the same latitudes suggests that photoperiod is not the only controller of breeding timing.

We now have evidence that genetics is likely involved with breeding timing. Deer transported from Michigan to Mississippi maintained the same October and November breeding dates that they had in the North, even as their native Mississippi penmates bred in late December and January. Crossbred offspring of Michigan and Mississippi deer bred over the whole range of both parents.

Though it is true that in the tropics whitetails can breed in every month of the year, it also is generally true that deer in any one locality are still somewhat synchronous in their breeding. Klein reported that in Honduras most whitetails breed between July and November. Deer in the Cocoa Beach area of Florida breed from the last of May through early December, with the peak around September 25. Near Labelle, Florida, just over a hundred miles south of Cocoa Beach, deer rut between mid-June and mid-September, with the peak rut near July 22. Why these tropical deer breed at such different times than northern deer is likely a result of different selection pressures. Perhaps biting insects or annual flooding has caused these populations to breed when they do. In any event, it appears likely that it is an interplay of photoperiod and genetics that regulates reproduction.

Nutrition has a small part in the timing of reproduction. From dietary studies conducted by Verme, we know that deer placed on low-quality diets breed later and have pregnancy periods four to six days longer than well-nourished does. Although nutrition is important to reproductive success and fawn survival, as a mechanism in the timing of breeding, it is very limited.

There is a myth among hunters that the timing of the rut also depends on the weather. Indeed, deer appear to be more



LLOYD

In North America the onset of the rut generally occurs later in the South than in the North. Actual dates are determined by local climate and have evolved so that newborn fawns are spared late-winter storms, spring floods, and hatches of biting insects.

active on cold or cool fall days than during an unseasonal heat wave. There is, however, no evidence of any correlation between breeding timing and weather conditions. Most likely, deer just feel better and are more active in cool weather. Displays of aggression, moreover, generally occur well before breeding begins. Like such physical changes as swollen necks and hard antlers, aggressive behavior helps bucks establish dominance rankings but does not necessarily coincide with the peak of breeding.

Another factor that has been suggested as a regulator of breeding timing is the phenomenon called biostimulation. In theory, the presence of individuals in breeding condition stimulates other members of a group to breed at the same time. At present there is little evidence for this, but we still have a great deal to learn about the influence of pheromones and social factors on white-tailed deer behavior.

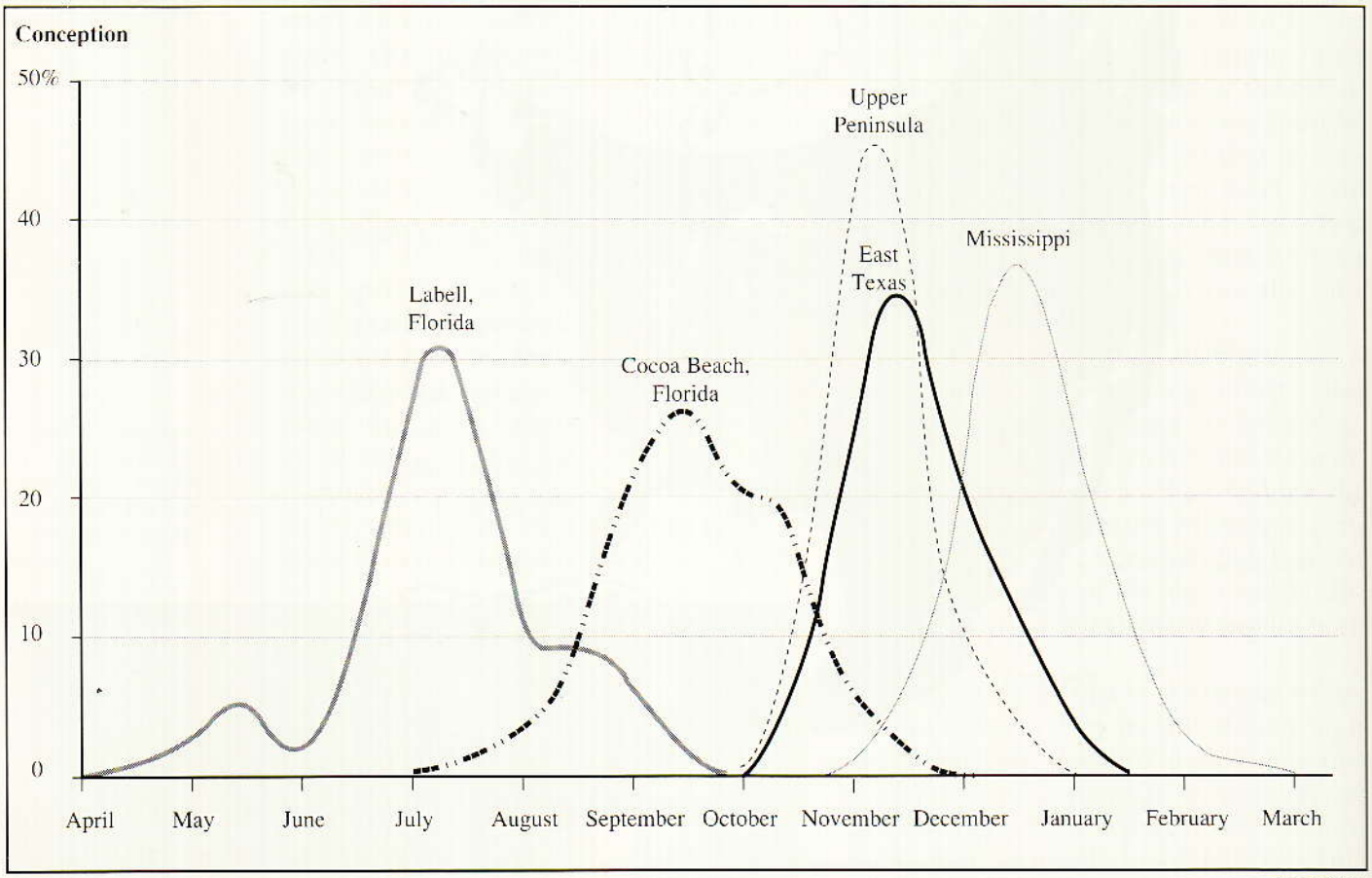
What is known to affect the breeding season of a deer herd is the ratio of does to bucks. Herds with more does than bucks have a prolonged breeding season and a later peak rut than herds with an approximately 1:1 sex ratio. Separate studies conducted in Mississippi by Jacobson and in South Carolina by Guynn have demonstrated that as a high doe-to-buck ratio returns to a balanced sex ratio, the breeding period shifts from later to earlier, with the peak of the rut occurring two to three weeks earlier than it was with an unbalanced sex ratio.

The Rut

The rut is initiated by a sequence of hormonal changes in both male and female deer. This begins with melatonin stimulation of the so-called reproductive clock. The

SMITH

A doe's readiness to breed—and her ability to bear more than one fawn—depends on age and good nutrition. Some fawn does are bred during their first fall, but they rarely bear twins.



ZIEGENFUSS

Although the two Florida populations of deer live only about 100 miles apart, they have dramatically different peak breeding periods. Similarly, the Mississippi and East Texas deer are in the same latitude yet breed at different times. Deer in the Upper Peninsula of Michigan have the most synchronous breeding, probably because fawns born only a few weeks too early or too late will have little chance of survival.

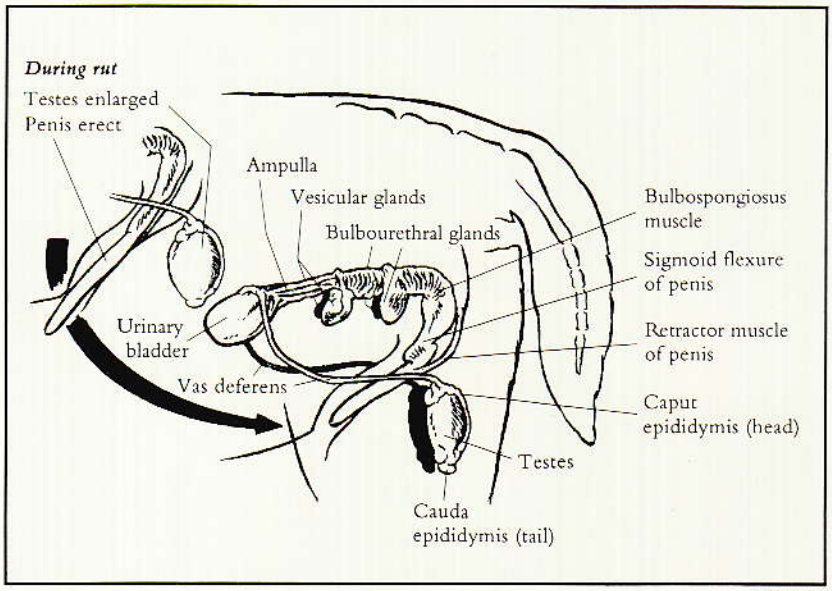
exact mechanism is not known, but the end result is that three hormones are produced by the pituitary, a gland in the brain. These hormones are follicle-stimulating hormone (FSH), luteinizing hormone (LH), and lactogenic hormone, also called prolactin (LTH). In bucks LH initiates the production of the hormone testosterone by the testes. Testosterone and FSH together allow the manufacture of sperm. Testosterone is also responsible for many of the changes that bucks undergo in preparation for breeding, both physical and behavioral, from the hardening of the antlers and the sloughing off of velvet to aggressive challenges and antler rubs. LTH appears to act synergistically with the other hormones to increase the amount of testosterone.

The same three pituitary hormones in the female have different functions and produce different results. In does, FSH causes growth of follicles in the ovary and stimulates production of the hormone estrogen by the ovaries. Estrogen in turn causes increased development of the female sex organs and prepares the uterus for receiving the eggs. It also contributes to secondary sex characteristics and behavioral changes, causing the doe to become restless and to seek out bucks for mating. The time when the female is receptive to mating is referred to as estrus, a period that in the white-tailed deer normally lasts about 24 hours.

Shortly after the level of FSH begins to increase, there is an increase and then a surge of LH, the luteinizing hormone. This further stimulates the follicles, which contain the developing eggs, to grow rapidly and rupture, releasing the eggs. No one knows for sure precisely when this occurs, but researchers' best guess is that the eggs are released about 10 to 20 hours after the doe first allows a buck to mount her. This means that fertilization of the eggs occurs within the oviduct, well before they reach the uterus.

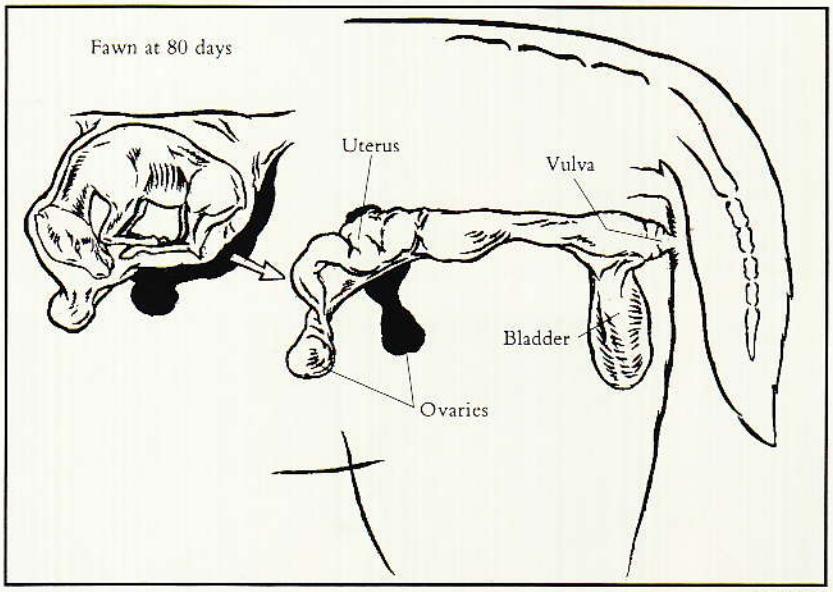
Once the follicle containing an egg has ruptured, it actually becomes a gland, known as the corpus luteum. The release of LH and LTH by the pituitary causes this gland to secrete the female hormone progesterone. The most important function of pro-

For most of the year the testes are well protected by the body wall; only during the rut do they enlarge.



BESENGER

The horned uterus of the whitetail doe enables her to bear, as a rule, two fawns. Triplets and quadruplets are possible, too, if one or both parts of the uterus carry twins.



BESENGER

gesterone is to prepare the uterus for implantation by the egg. If the egg is fertilized, it produces a hormone, called chorionic gonadotropin, that maintains production of progesterone by the corpus luteum and fosters the early stages of pregnancy.

Without the hormonal signal from a fertilized egg, the uterus instead secretes a hormone called prostaglandin. Prostaglandin has many functions, but at this stage of reproduction it causes the corpus luteum to regress and the uterus to return to normal so that the estrous cycle can begin all over again. The whole sequence of events takes from 22 to 28 days.

If a doe is not bred on her first estrus, then, or if for some reason the embryo does not implant in the uterus, she will again come into estrus 22 to 28 days after the first cycle. White-tailed deer that do not conceive have been documented to go through as many as six estrous cycles in a single breeding season.

For bucks, the pituitary and testes are most important to reproductive success. But there are four accessory organs involved in the male reproductive function: the epididymis, the seminal vesicles, the prostate gland, and cowper's glands. These organs show seasonal changes in the white-tailed deer and are their largest and most active during the peak of breeding.

The epididymis is where sperm mature to their fertile state. Seminal vesicles secrete a

number of substances, including amino acids and sugars, that provide nutrients for the sperm. They also secrete small quantities of prostaglandin, which causes uterine contractions and helps propel the sperm toward the oviduct where fertilization occurs. The prostate secretes a milky fluid during ejaculation that helps neutralize the acid environment of the vagina and therefore increase sperm motility and survivability. Cowper's glands, also referred to as bubo urethrae glands, supply mucus to the urethra and lubrication that aids in ejaculation.

Gestation and Birth

The white-tailed deer has a gestation period of about 200 days, during which nutrition is critical to the survival of both fawn and doe. Up to a point, does deplete their own body reserves to provide nutrients for the growing fetus. Fetal death and reabsorption, however, are common among deer in overpopulated range.

In preparation for fawning, does begin to avoid contact with other members of their social group. Just before giving birth, a doe may shift her home range to an area outside of the normal home range or at its edge, according to Bartush and Lewis's study of whitetails in Oklahoma. Does have a marked fidelity to their birthing sites, returning to the same area to give birth from one year to the next.

Among captive deer, a period of restlessness and pacing signals the beginning of the birth process. This is particularly true of first-time mothers. A doe nearing labor generally shows enlarged and swollen mammary glands. She also adopts a peculiar walk; her tail is extended out and down, but with a fishhook-shaped crook. She seeks out a secluded area to give birth.

As with other mammals, labor begins with the bursting of the water sac. Labor often lasts a long time—twelve or more hours has been clocked in captive does—but deer are known to be able to stop the labor process if disturbed. After birth, the doe chews off the umbilical cord and eats the afterbirth. Whether she does so for nutritional purposes or to make it more difficult for predators to find the birth site is only conjecture, but both guesses are reasonable explanations for this behavior.

The doe immediately licks her fawn dry and establishes the bonding that lets her distinguish her fawn from others. She nurses it shortly after birth and remains with or near it for the first twenty-four hours. Does with twins may move the fawns to separate bedding areas within a few hours of birth. Bartush and Lewis found that the distance between the beds used by sibling fawns increased each day for the first eight days of life. This separation of twin fawns presumably increases the chance of survival for one: a predator that finds one fawn is not likely to find the other.

Fawn Mortality

Body weight at birth is critical to the fawns' survival. Except for the subspecies of small whitetails, like Key deer, fawns with body weights less than 5 pounds have little chance for survival. The normal birth weight for a healthy fawn is 6 to 9 pounds; fawns 12 pounds or more are not too unusual.

The mother's nutrition affects maternal behavior. Abandonment of the young is

The gravid doe needs highly nutritious food. Undernourished does may abort their fetuses, or the unborn fawns may be reabsorbed into their mothers' bodies.

BINEGAR

Having eaten the afterbirth, the doe licks her fawn dry and waits for it to stand and begin to nurse. Her winter coat has not yet finished molting.

SMITH

common in undernourished deer herds, particularly by first-time mothers. In a study conducted by Langenau and Lerg in Michigan, 27 percent of the mothers on low-quality diets abandoned their fawns, versus only 2 percent abandonment rate for well-fed does.

The biggest danger for fawns in poor habitats is predation. An astounding mortality rate of 80 percent has been recorded for some areas, generally in overpopulated range and areas that lack protective escape cover. In the brush country of southern Texas and the prairies of Oklahoma, for example, coyotes are effective predators of fawns because they can observe a doe going to her young from a distance. Protective ground cover to conceal fawns is important: In overpopulated range, much of the protective cover that would otherwise shield fawns has been eaten by the deer themselves. In healthy deer populations, fawn survival is usually high in most forested regions of the country, even when predators are numerous, because such habitats have bushy understories that provide escape cover.

Some fawns succumb to disease. Although high mortality can occur among captive deer under crowded conditions because of diseases or parasites, in wild populations disease does not take a high toll on well-nourished fawns. Bacterial diseases, screwworm flies, stomach worms, lung worms, and ticks can cause problems though.

SMITH

Poor cover and inexperienced or undernourished mothers can leave fawns vulnerable to predation.

A variety of bacterial diseases can affect newborns, but the most serious are those that cause diarrhea. Salmonella outbreaks in captive deer facilities have resulted in the death of nearly all fawns. With wild deer, bacterial diseases among fawns are less significant because contagious spread is unlikely. Screwworms occur only in Latin American countries and occasionally in the border region of Texas and Mexico; they have been controlled in the United States. Screwworms can be a serious problem because the flies deposit their eggs on the newborn's umbilical cord, where the larvae can gain entry to the body. Stomach worms and lung worms take their toll on stunted and undernourished fawns and are most likely to be a problem in overpopulated range. Tick parasitism can be a significant mortality factor in some areas. One Oklahoma study attributed 37 percent of fawn losses to tick parasitism in the post-oak region. A combination of high deer density and hot, humid oak forests seems to favor the ticks, which can kill fawns by causing them to lose blood and by spreading secondary infections.

Accidents take an incidental number of young animals. Fawns may break legs and necks when they run into fences and other obstructions. Hay mowers, farm machinery, and automobiles probably account for most accidental deaths of fawns. Flooding may be a significant mortality factor for some white-tailed deer fawns in river bottoms and swampland areas.

Though the dieoffs that cause great crashes in deer population are certainly dramatic, they are the exception. The interplay of factors that can maintain a healthy population is more subtle. Reproduction and fawn mortality are the two most important factors. High reproduction and low fawn mortality generally characterize healthy deer populations, whereas just the opposite is true in overpopulated herds

Fecundity

The doe with her gamboling twin fawns is a common sight. Triplets are not rare, and even quadruplets are born on occasion. Whether a doe has one fawn or four depends on a complex of factors—age is one.

A fawn doe, if she conceives, generally gives birth to just one offspring. For most of the country, yearling does average 1.5 to 1.6 offspring per pregnancy, and adult does, 1.7 to 1.8.

Habitat has an effect on fertility of the white-tailed deer, too. Does from the midwestern farm country generally have the highest fertility rates, and those from the sandy forests of the South's coastal plains, the lowest. The difference is nutrition. Deer herds that are in balance with the area's forage have the highest reproductive rates, whereas few fawns are produced on overstocked ranges. Both energy and protein are important. Does given high-energy diets before the breeding season have a much higher incidence of twin and triplet births than those on low-energy diets; protein is critical to growth and survival of the fetus and also the mother's nutritional well-being.

The last factor that may bear on fertility is genetics. The subject has been well researched for domestic animals; in sheep, genetics can be very important in determining reproductive rates. Comparatively little is known about the role of genetics in reproduction in white-tailed deer, but genetics may explain regional differences in fertility rates. Tropical does rarely have twins, for example, but can have more than one fawn a year and may breed as early as a month after the last fawns were born. Poor soil fertility and lower nutritional quality of plants in the tropics would make it difficult for a doe to get sufficient protein to support twin fetuses, even under the best of conditions. Thus, it is reasonable to assume that these populations would evolve genetic controls of reproductive rates to match their environment.

Sex Ratios of Fawns

Whitetails, as populations, have the ability to change the sex ratios of their offspring under different nutritional conditions. Look at the facts, all well documented by several researchers:

- Well-nourished white-tailed deer have a higher number of female offspring than male offspring.
- Poorly nourished deer and herds on overpopulated range produce more males.
- Fawn does conceive more male fetuses.
- Maiden yearling does on high-quality diets have a high proportion of female offspring.
- Maiden yearling does on low-quality diets produce more males.
- Well-nourished captive does with single births have higher numbers of female offspring.
- Well-nourished captive does with twin offspring run close to equal sex ratios.
- Well-nourished captive does with triplet offspring have a higher proportion of males.

The basis for all these differences, researchers suspect, may be female hormonal levels at conception. These hormones cause higher probability of one sex or the other because they affect the uterine environment and thus the relative motility of sperm. It is the sperm cell that determines the sex of offspring depending on X or Y chromosome presence. Perhaps these hormones cause changes in acidity within the uterus, which make the X-chromosome sperm swim faster or slower and thus reach the ova earlier or later than the Y-chromosome sperm.

Breeding timing and social factors may also be involved. Ozoga and Verme first proposed that deer bred early in their estrous cycle would conceive more females, and deer bred late in their cycle would have more male fawns. This same mechanism can help explain how social factors can affect offspring sex ratios. In herds with more does than bucks, the dominant adult does could be

A pair of healthy young fawns indicates that their mother is of prime age and has been eating a high-quality diet. The doe keeps her offspring free of any odors that might attract predators.

NAGLE

BRAUD / DEMBINSKY PHOTO

Mutual grooming helps forge a strong bond between mother and young and thus improves the fawn's chances for survival.

expected to breed earlier in their estrous cycle than subordinate and yearling does. The does that were bred later in their estrous cycle would produce more male offspring, and thus deer herds with high buck mortality and low buck-to-doe ratios could be expected to produce more male than female offspring.

These changes in sex ratios enable white-tailed deer herds to adapt to changing environmental conditions. In good times, a high percentage of female births allows the herd to increase rapidly. When the population grows too large, or range conditions are poor, more males are born, slowing the growth of the herd.

From an evolutionary perspective, a doe may have the best chance of making a genetic contribution to the herd if her first fawn is male. If she survives her first year, it may then be best to have female fawns; because females have a lower mortality rate, they have a greater probability of reproducing. Males, however, if they survive to maturity, can sire many more offspring than females. Therefore, for a doe 2 years old or older, it might be best to have an equal proportion of male and female offspring to ensure the passage of her genes to subsequent generations.

–Harry A. Jacobson