

The rut

A dominance fight between mature whitetail bucks is truly awesome. With impressive speed, agility, and strength, the two animals battle each other. The clash of their antlers rings in the forest, and their racks rattle as they twist and push. Finally one buck retreats and the victor stands panting, his breath condensing in the chill air.

Such scenes occur only when males are in rut—the peak of breeding condition. Their antlers are polished and hard, and high levels of the male sex hormone testosterone course through their blood. Bucks' breeding capability may not be limited to the period during which they have hard antlers, however. On rare occasions bucks in prerut, with late velvet, and bucks in postrut that have shed antlers have been observed copulating with estrous does; it is not certain that they have sufficient sperm to father offspring.

The rut includes the normal breeding period, which, at least in temperate climates, is most intense near the middle of the hard-antler period. We think of the rut as when bucks are doing things associated with readiness to mate, such as rubbing and scraping. These occur to some extent throughout the entire period of hard antler. But the peak of the rut is determined by the time when most does come into estrus, or heat. The bucks stay ready to breed over several months, but their swollen necks and deeply stained tarsal glands bespeak the peak of rutting condition just as or just before large numbers of does

start coming into heat. The chase that follows—"running," as some hunters refer to the courtship phase—is the result of does' coming into estrus.

Intensive breeding activity may last as little as two weeks or can be spread out over a much longer period. Each doe's heat lasts only twenty-four to thirty-six hours, although she will cycle again if not bred. Research at the University of Georgia by Knox, White, and others found that a doe that is not bred may cycle as many as eight times over a seven-month period. In a population with enough mature bucks, however, most does are bred during their first heat.

In temperate climates the rut usually occurs during the fall. Day length, or photoperiod, is the most important trigger initiating reproductive activity and related physical changes in both does and bucks. A portion of the brain called the pineal gland responds to photoperiod changes and acts like a chemical clock. Differential secretion of the hormone melatonin from the pineal initiates a chain of events in other glands within the deer's body, such as the hypothalamus, the pituitary, and finally the reproductive organs themselves.

Whitetails are referred to as short-day breeders because their cycle is usually activated by decreasing day length in the late summer or fall. Nevertheless, the timing of the phases of a whitetail's reproductive cycle varies in different parts of its geographic range. Near the equator, for example, where



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Because not all females come into estrus at the same time, the dominant buck in an area can breed the majority of does

day length changes little, Branan and Marchinton have seen whitetail bucks in every stage of antler development throughout most of the year.

Whitetails' reproductive cycle has become adapted so that fawns are born at the time most conducive to their survival. In northern areas this results in late spring or early summer births, when ample food is available from new plant growth. These relatively early births enable the fawns to grow large before they must face the harsh winter. In parts of the southern United States and in Central and South America, the breeding season varies greatly from area to area and may even be spread out over much of the year. Breeding in areas without extremely cold weather is influenced by other, more subtle factors that affect fawns' survival, such as seasonal rains, droughts, and food sources. For convenience this chapter will generally refer to the timing of rutting activities typical of the northern and central United States, as well as some southern areas. Even within small areas, however, there can be minor differences in timing

caused by the density, structure, and social organization of the population or by other environmental factors.

LEADING UP TO THE RUT

The rut consists of a number of phases extending over several months. The progression of events begins with the formation of bachelor groups.

Though female groups tend to be closely related by maternal descent, bucks usually associate with unrelated individuals. Older bucks spend a long, quiet spring and summer in bachelor groups. During this time, they recover from the loss of physical condition caused by the enormous effort expended during the previous rut and the rigors of winter, and they grow a new set of antlers. Early summer to midsummer is an especially quiet time for bucks. "Male bonding" may be too anthropomorphic a description, but they do spend this time learning about each other.

Membership in buck groups is constantly shifting. In late spring or early summer, when yearlings of both sexes are driven out

of family groups, they often try to associate with the older bucks. They may be tolerated but are frequently driven away for no apparent reason. Perhaps because of this, male and female yearlings are often seen together in exclusive yearling groups during the summer. By early fall, yearling does are no longer found with buck groups, and aggression toward yearling bucks by members of older buck groups is less apparent.

McCullough and other researchers have presented evidence that bachelor groups live in different areas than the does. They also may fill different niches and occupy poorer habitats if good ones are in short supply. This behavior could be a natural selection advantage, because bucks can maximize the survival of their offspring by relinquishing the best habitats to them and their dams during this critical phase of the fawns' survival and development.

While in bachelor groups during the spring and summer, bucks' testicles are small and the production of testosterone, the most important sexual hormone, is very low. As the summer nears an end, the testes begin to enlarge and the spermatogonia lining the seminiferous tubules start the process of producing sperm. The Leydig cells increase in size and begin to manufacture testosterone. Rising levels of testosterone in the blood slow antler growth and start the hardening process. Around September 1 the antler's velvet covering is shed. In 1977 Hirth observed that loss of velvet is likely to occur first among older animals. Older bucks also experience earlier and higher peaks in testosterone levels, according to Miller and others.

As the bucks lose their velvet, they enter a time often referred to as the prerut. The entire process of removal rarely requires more than one or two days. A few bucks have been observed eating their velvet; Hamilton reported seeing one buck eat the velvet from another penned deer, but it is not known if this is common in the wild.

Even before the velvet is completely gone, bucks begin to test their new weapons on trees and bushes. The new antlers, particularly those of mature animals, are adorned with prominent pearling—many small bumps usually found near the bases but sometimes extending well up the main



BRYAN

beams. These are useful in removing tree bark but will become smoother as rubbing and sparring wear them down.

Now the bucks have these wonderful polished antlers on their heads and a rapidly rising concentration of testosterone in their bodies. A transformation in behavior occurs.

ESTABLISHING A HIERARCHY

During the rut, the social organization of bucks can best be described as a dominance hierarchy in which the highest-ranked individual is the one most likely to do the breeding. Animal A is dominant over all others, animal B is dominant over all others except A, and so forth. Since this phenomenon was

With swollen neck and stained tarsals, the buck trails does that are approaching estrus. Chemicals in their urine alert him to their readiness.

By the time bucks are in hard antler, their breeding hierarchy is well established. The smaller males will nevertheless seek to breed if the dominant buck is with one doe while another comes into heat.



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Bucks often engage in the highly ritualized act of sparring. One animal invites another to spar by lowering his antlers. Carefully locking antlers to avoid injury, they twist necks; disengagement follows. The smaller buck then licks the dominant animal's face and forehead, possibly to memorize his scents.



described first in poultry, it has also been called a pecking order. Hierarchies occasionally can be nonlinear and become more of a web or matrix—for example, animal C may be dominant over animal D, and D over E, but E dominates C. This is not often the case among whitetail bucks, however. If there are sufficient numbers of bucks in the population with a good range of ages, they will have established hierarchies by the breeding season, and usually a clear dominant type will emerge in a particular area.

Some animals organize themselves by territories, with each territorial male controlling and breeding females that occupy or enter his area. According to Marchinton and Atkeson in 1985, whitetails basically follow a social hierarchical ranking, but there seems to be a spatial element at times. Those authors suspect that the site of an encounter between two high-ranking bucks can have a bearing on the outcome and determine which gets to breed the doe.

It is during the prerut, after velvet has been shed from antlers, that bucks begin to spar with each other. Townsend and others in 1973 pointed out that the function of sparring seems to be to establish a well-defined hierarchy among bucks. Sparring is not to be confused with fighting. True dominance fights may come later, but for now the buck is simply comparing his antlers and strength with those of others. He does this by touching his antlers to another buck's and pushing almost casually or playfully. Marchinton and Hirth observed that sparring matches often begin when one buck lowers his antlers toward another. If the second buck accepts the challenge, the two engage antlers in what can best be described as a pushing match. The smaller of the two bucks is likely to be pushed backward.

Both bucks learn something about their proper place in the dominance hierarchy from this experience. These authors also noted that "small bucks often challenge larger bucks only to be forced into a hasty retreat. On other occasions, larger bucks will tolerate the challenges of small bucks, often standing still while yearlings push at them with all their strength." Sparring matches may last for several minutes. Contests between bucks of the same size, when the outcome is in doubt, are likely to become more serious. Younger bucks spend more time sparring than do older animals and may continue even into the breeding season. Older, clearly dominant animals seem to be more secure in their hierarchial positions.

Before the actual engagement of antlers in a sparring match, it is common for the subordinate buck to groom the face and forehead of the larger buck. Forand and Marchinton in a 1989 study speculated that the subordinate may be licking the forehead gland and memorizing the smell of the adversary. This would not only aid in recognizing the larger animal in the future but also allow identification of the animal's dominance areas, which are marked by his signposts, or rubs.

What physical attributes and behavior are characteristic of dominant bucks? Certainly age is a factor. Bucks reach physical maturity around 5 years of age. Where there are few bucks older than yearlings in a population, clearly formed hierarchies may not occur. Where older bucks are present, the most mature individuals are likely to be dominant until they begin to deteriorate physically as a result of advanced age, debilitating injury, or disease. When old age becomes a negative factor varies. Some bucks may be over the hill at 6 or 7 years, but others can maintain



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dominance well into their teens. The caliber of competition from younger bucks certainly plays a role.

Other important factors involved in achieving dominance are body size and strength and antler size. Antlers are pretty good indicators of overall body size and health. They serve as symbols of the buck's age and physical condition in addition to being weapons. Geist has noted that antler size itself can be intimidating to smaller bucks.

Occasionally smaller bucks or those with lesser antler development become dominants, but this is not especially common, Hirth pointed out in 1973. Studies at the University of Georgia suggest that testosterone levels play a role in the aggressiveness of bucks. Dominant bucks usually have high concentrations of this hormone in their blood. There is evidence that winning sparring matches or dominance fights may increase the production of testosterone by the winner and decrease it in the loser. It is not altogether clear, however, whether being dominant results in higher levels of testosterone or whether high levels of testosterone cause bucks to be more aggressive and achieve higher rank. There is scientific evidence to support both theories.

DOMINANCE FIGHTS

Early in the rut, dominant bucks are fairly tolerant of subordinates, but when does begin to come into heat, the hierarchy becomes more rigidly enforced. How does a dominant buck express his position behaviorally? Aggressive intentions, Thomas and others pointed out in 1965, are expressed by stereotypical postures. The lowest level of threat is a direct stare with the ears laid back along the neck. Often this is all that is neces-

sary to cause a subordinate to retreat. If the subordinate does not leave, the dominant buck erects his body hair, making himself appear larger and darker—in short, very formidable. He advances or sidles slowly toward and around the other buck with a deliberate, stiff-legged gait. A vocalization described by Atkeson, Marchinton, and Miller as the grunt-snort-wheeze is sometimes produced in these situations. This is considered to be the most threatening sound a whitetail buck makes. If the other buck does not retreat or assume a subordi-

Small, young bucks frequently spar with much larger rivals. Once into the breeding season, while the dominant animals are mating, these low-ranking bucks continue sparring among themselves.



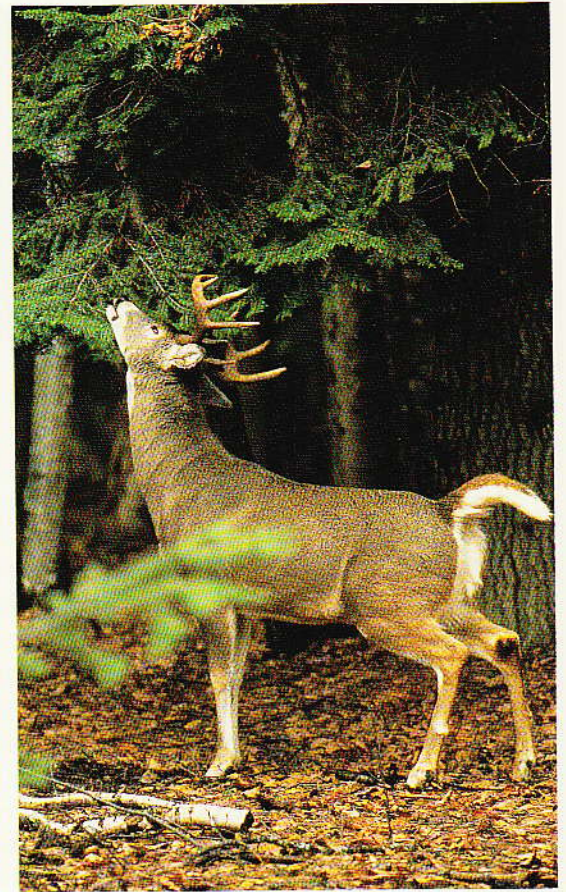
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Erect hair, darkened coat, ears laid back, hard stare: a buck approaches a challenger in a dominance display.

In herd species, like bison, males and females consort all year long; among whitetails the sexes are separate for most of the year and the forest habitat precludes large aggregations and visual communication. The whitetail buck must therefore advertise his status by scent marking—in this case with the preorbital gland—and the hemlock serves as his signpost.



nate posture, the dominant animal threatens with his antlers. Unless the bucks are very closely matched, the lesser one usually yields. If neither yields, a dominance fight likely ensues.

Dominance fights generally do not last more than thirty seconds, but they sometimes go much longer before a winner is established. Injury to one of the combatants is not the inevitable outcome. Usually one of the bucks withdraws quickly without being harmed.

Nevertheless, injuries do occur—a broken antler tine, a broken antler main beam, a puncture wound. These may not be serious, but fatalities have been observed. Sometimes even the winning animal may receive head wounds that become infected, forming brain abscesses that result in death months later. A number of these cases have been reported by Nettles and Davidson at the Southeastern Cooperative Wildlife Disease Study laboratories.

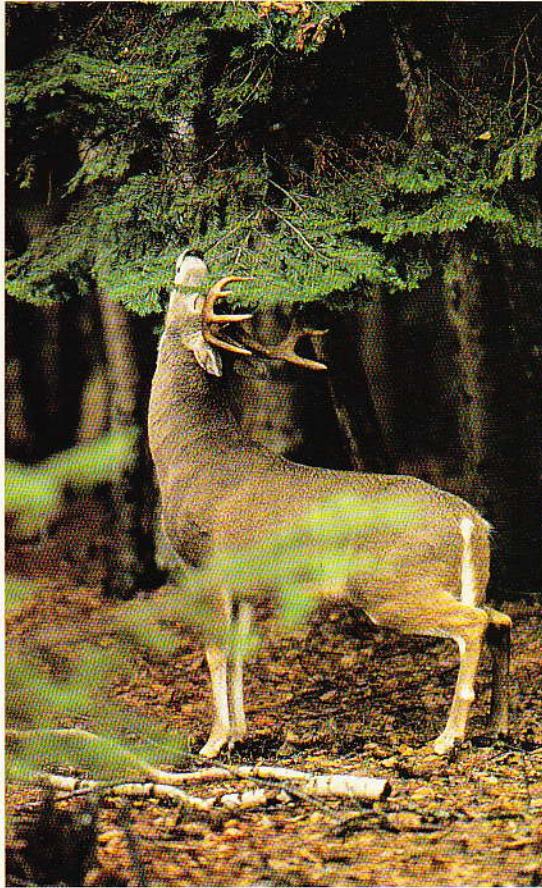
On fairly rare occasions, large, evenly matched bucks' antlers become locked together so tightly that they cannot disengage

and both bucks perish from starvation or predation. Instances have been recorded in which one of the locked animals remained alive even after his adversary was partially consumed by coyotes or other predators. Bucks staggering around with the head of another buck locked onto their antlers have been observed.

SIGNPOSTING

Because mature bucks and does tend to remain separate from each other except during actual courtship and breeding—a process that usually lasts only a few days—some sort of signposting or advertising *in absentia* is necessary for social communication. To accomplish this, whitetails have developed an elaborate system of licking branches, rubbing, and scraping.

Licking branches. Throughout the sexually quiescent spring-summer period, when their new antlers are growing, bucks communicate with one another using an olfactory language. This is done through communal licking of branches. How these branches are selected is not clear, but they often are the



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same ones under which scrapes are made during the rut. They are most likely to be branches that are located over a trail or along the edge of a field and that are slightly above the buck's head when he is in a normal walking position. Bucks seem to prefer to reach up, and sometimes they actually stand on their hind legs to mark a branch. Rearing up on the hind legs is more likely to happen where branches of the proper form and right height are in short supply or where long-term use of a site has eliminated suitable lower branches.

Marking involves mouthing the branch and sometimes rubbing it with the forehead or preorbital glands. At the same time, bucks apparently smell and taste marks already there. Many bucks may use the same licking branch. Outside the rut, at least, no proprietary tendencies are evident, and there is communal use of the licking branch by all bucks in the area. The function of year-round licking of branches is not fully understood, but buck behavior suggests that it communicates identities and status and may facilitate social bonding.

Rubbing. Bucks begin rubbing as the velvet is being shed. Twenty-five years ago it was assumed by scientists and hunters alike that the primary purposes of rubbing were to remove velvet and build up neck muscles for fighting. But intensive studies of rubbing by Moore and Marchinton, beginning in the late 1960s, revealed that its function was far more than that. Rubbing during and shortly after velvet removal is rather violent and likely to break branches and destroy bushes. Though rubbing probably does serve to strengthen neck muscles and may help remove velvet, testing out the new weapons is likely a more important function.

As the rut progresses, rubs change to the more typical, highly visible signpost type, in which the buck uses his antlers to tear the bark of bushes, saplings, or trees, exposing the lighter-colored wood underneath. He then anoints the exposed wood with scent from his forehead gland. He may stop periodically to carefully lick his handiwork. These rubs obviously have important communicative functions: the buck is passing on information for other deer to read, through

After using his antlers to rub off the bark, the buck deposits scents from his preorbital gland. Both bucks and does will read the signs, but the tree itself reveals something of the buck's age: older and larger animals select larger trees.



scent, rub appearance, and the sound of his making the rubs. The scent on rubs remains detectable for several weeks, as Moore and Marchinton demonstrated with trained dogs.

These early signpost rubs, Ozoga and Verme pointed out, are usually made by the more mature bucks; yearling bucks make only about half as many rubs during the breeding season as older animals.

There is a distinct relationship between a buck's age and the size of the rub. Older bucks are likely to rub much larger trees. A typical yearling rarely rubs bush stems or saplings larger than about 5 centimeters (2 inches) in diameter, but a fully mature buck may rub pole trees 15 centimeters (6 inches) or larger. There have been observations of rubbed trees exceeding 30 centimeters (1 foot) in diameter. The larger trees used by mature bucks seem to have special scent communication functions, as bucks may repeatedly return to them. Recently Woods and others, using automatic cameras, demonstrated that not only bucks but also does come to inspect these larger rubs. Much of the activity is late at night, however, and so is usually unobserved by humans. Smaller rubs are much less frequently rerubbed, although does occasionally do inspect them. Buck and doe behavior associated with the large rubs suggests that older bucks are depositing some important information on them and that they play major roles in the sociobiological functioning of the herd.

What kind of bushes and trees do bucks select for rubbing? Proper growth form is important; limbs very low on the bole prevent easy access by the buck. Bucks seem to prefer aromatic trees, such as cedar or sassafras, when available. These may draw attention to or enhance the scents the buck leaves on the tree.

Scraping. Another very important and obviously complex signpost made primarily by bucks is the scrape. Scraping has been observed from July through March but is usually done when the bucks are in hard antler. Several researchers have found that only mature, dominant males produce significant numbers of scrapes. Scraping by dominant bucks is most intense just before the peak of breeding; subordinates, if they scrape at all, are more likely to begin later. Once does begin to come into heat in large numbers, dominant bucks no longer need to advertise their availability, as they are fully occupied handling their breeding duties. There is some evidence that scraping activity picks up again after the peak of rut.

The full scrape sequence is a combination of overhead branch marking, pawing, and urination. A scrape involves several scent sources and probably has multiple functions as a signpost communication system. Scraping behavior typically begins with a buck walking under a limb hanging just above his head. He sometimes rubs it with his forehead gland or his preorbital gland, rattles it with his antlers, or does both. He then takes



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a twig into his mouth and moistens it with saliva. By doing so, he also may detect chemicals left by other deer.

After the overhead limb is marked, the buck normally paws away the leaves below it; the area cleared varies, but a 3-foot-diameter circle is common. The buck then steps forward and urinates on the bare soil. This usually involves urinating onto the tarsal glands while rubbing them together, a behavior known as rub-urination. The urine of a mature buck leaves a persistent odor and may stain the soil dark even after it has dried. It appears that the urine of bucks, especially mature or socially dominant ones, has special qualities that enhance its communicative significance.

Does sometimes approach scrapes, and the scents they perceive may play a role in priming their reproductive cycles. Also, as Moore and Marchinton reported, does apparently leave "calling cards" in the form of scent when they are approaching receptivity. Clear documentation as to how this is done is still lacking, but urination in or near the scrape is thought to be involved.

Subordinate bucks may create fewer scrapes because of behavioral or pheromonal suppression by dominants. Subordinates often approach scrapes and mark the overhanging limbs just as they lick branches during the summer. Young bucks are unlikely to perform the full scrape sequence if there are adults around, however. Furthermore, when does coming into heat are nearby, or for

other reasons known only to deer, a dominant buck sometimes does not tolerate even a subordinate's presence near a scrape. The lesser buck may be repulsed by a hard look or aggressively chased away from the scrape.

It is apparent that signposting is an extremely complex scent communication system with important functions within the deer herd; even though a great deal has been learned about signposting behavior since the 1960s, its mysteries still are not completely unraveled.

COURTSHIP AND BREEDING

Many aspects of reproductive behavior among animals are directed toward ensuring their survival as a species. As the does approach estrus and the bucks sort themselves out for breeding rights, signposts help deer become aware of each other and identify hierarchical status, conveying pheromones that prime reproductive processes in both sexes and providing information about possible sexual partners.

Who seeks out whom when the breeding season arrives? It depends. Probably the sex in the minority is courted more aggressively. Bucks do most of the seeking when the number of males is adequate, and they may move about in search of receptive does. There is evidence that some males become superdominants, or floaters, and travel over thousands of acres. Because of their physical superiority, they can intimidate bucks wherever they go. On the other hand, if mature

To scrape, the buck first marks an overhead branch with his forehead gland or preorbital gland (or both) and licks it to pick up scents from other bucks. He then clears a circle in the forest floor and urinates, rubbing his hind legs together so that chemicals from his tarsal glands are captured by the flow. The scrape holds the buck's scents for passersby. He periodically returns to determine whether any does approaching estrus have urinated near the spot.



bucks are in short supply, does may leave their normal range to seek a mate. A doe is aided in her search by the bucks' signpost advertising. These excursions in search of a mate may last only a day or two, but if she is not successful, she will likely try again in about four weeks when she cycles back into heat.

It is likely that does are selective in choosing mates when choices are available but not if the number of bucks is small. Ozoga suggests that a doe is more receptive when courted by a male of approximately the same age. There is evidence that when given a choice, an adult doe selects mature bucks over yearlings or precocial fawns. She sometimes accomplishes this by leading her younger suitors to a dominant male, who then displaces the lesser bucks in the courtship chase.

The whole process of chasing and courtship is a very visible one that exposes participants to risk from predators, both human and otherwise. This is the only time of year when white-tailed deer, particularly bucks, forsake cover and put themselves into vulnerable positions. Given the obvious selective disadvantage, why doesn't such behavior get bred out of the population? The reason is that it also provides very strong *positive* selective values. It allows the doe to be bred by the most physically superior buck in the area. She dashes around—in anthropomorphic terms, making quite a spectacle of herself—so that the local bucks become aware of her impending receptivity and join her entourage, at least until they are displaced by the largest buck. This competition among suitors usually assures that her offspring will be sired by the best buck she can find.

Dominant bucks will probably breed any doe, but they too may be selective if there is

more than one doe in heat at the same place and time. Subordinate bucks are able to breed does when the dominant buck is not present, which can happen when several does cycle simultaneously. In other words, being dominant may not give a buck exclusive breeding rights, only first choice.

As the breeding season gets close, bucks begin checking does for signs of estrus. A doe nearing estrus telegraphs this by certain behaviors and by changes in her chemical cues, or pheromones. Does practice a special coquetry. They run from an approaching buck but not so far or so fast that he cannot find them. Sometimes several bucks join in, but if the doe is very close to estrus, usually the most dominant is first in the line of pursuing suitors.

A doe thus being chased often stops to urinate, apparently to provide the chasing buck with a pheromonal message about her reproductive status, to prime his reproductive processes, or both. The buck approaches the spot where she urinated and performs flehmen behavior, whereby he draws chemicals from her urine into the vomeronasal organ receptacles located on the roof of his mouth just inside the upper lip. If she is not nearing estrus, he may break off pursuit and search for another doe. Young bucks are less able to discriminate and are more likely to harass does that are not ready or even close to being ready to breed. Older, more experienced bucks waste little time with a doe that is not close to breeding.

Courtship or chasing of a doe approaching estrus may last a day or two and usually involves running circles several hundred meters in diameter. When the doe allows the buck to come near, breeding is imminent. Brown and Hirth noted that males employ a tentative low-stretch posture in virtually all



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close approaches to females in or coming into estrus. The buck's head is lowered so that it is even with or below the line of his back. He usually moves his tail from side to side or flips it rapidly up and down.

The time when a doe is receptive is coordinated with ovulation so that eggs are available for fertilization by the buck's sperm. When she is physiologically ready for conception, she allows the buck to catch her. Warren and others reported that the buck licks her urogenital region or proceeds directly to chin-resting behavior, in which he presses his chin on the doe's rump. This seems to immobilize her. At this point the chase is over and she allows him to mount. Sometimes mounting proceeds without the chin rest, but it does seem to be an important behavioral cue. One way to determine whether a captive doe is in heat is for the human observer to place a firm hand on the top of her rump. If a doe responds by assuming the breeding stance, she is in heat.

In mounting, the buck slides his chin along the doe's back while straddling her with his forelegs. She may run out from under him on his first attempt, but more than likely intromission of the penis occurs. Intromission is quickly followed by the pelvic thrust, which can be violent. Both of the buck's hind legs sometimes leave the ground while he clasps the doe tightly with his forelegs. His entire weight may be placed on the doe, which drives her forward and down. She may even be knocked to the ground if the buck is very large or if she is small. The entire process from mounting to disengagement usually lasts only fifteen seconds or less.

Following copulation, the doe often exhibits a hump-backed postcopulatory stance. The tail may also be raised, giving her

what has been described by Hamilton as a "Halloween cat" appearance. The position is associated with contractions in the abdominal region. Warren and others observed repeated contractions of the vulva, and sometimes after several breedings, fluids dripped from it. This behavior may facilitate movement of the sperm to the egg or eggs.

After the first breeding, the buck tends the doe and often is observed licking his preputial area. The pair may or may not copulate again over the next several hours or even a day. While tending, the buck threatens others that approach by body postures, the grunt-snort-wheeze vocalization, and some-

To test her readiness to breed, or perhaps prepare himself for copulation, the buck licks the doe's fresh urine and, with a set of muscle contractions that produce the lip-curl grimace, transfers the material into his vomeronasal organ.



FRANZ

When the doe is finally ready to be bred, she stands and allows the buck to lick her urogenital region. He slides his forelegs along her flanks, enters her, and climaxes with a leaping thrust.



times rubbing his antlers on nearby bushes. When his right to the doe is seriously challenged, a dominance fight will occur. Such a fight is an all-out struggle that can result in injury or, on rare occasions, death of one or both adversaries.

When mature bucks are not present in the population or at least the immediate area, yearlings assume breeding duties. It is not clear whether they have as well-defined dominance hierarchies or are as defensive toward other bucks. Presumably the larger, more physically capable yearlings do most of the breeding. No documentation of this is available, however.

Just how many does a buck breeds in a season would certainly vary, depending on many factors. Severinghaus and Cheatum reported a situation in which twenty-one does were left in a pen, and a small buck with very small antlers was accidentally left with them. Nineteen of the does became pregnant. Obviously this buck did not have any competition, nor did he have to search for receptive does.

The rut is stressful to breeding bucks. They eat little during its peak and lose up to 25 percent of their body weight before it is over. This places them in a difficult situation as they enter the winter. Supplies of body fat may be exhausted just when the bucks need energy to get them through the winter. This is why the long, quiet summer is so important to bucks: it is the time when they replenish their reserves and grow their antlers. For bucks younger than 5½ years, it is also the time for physical growth. Marchinton and Miller have suggested that bucks may grow larger if they do not become breeders before their growth is complete—which can happen only if adult bucks are available for breeding duties.

Good breeding-season success depends on the food supply in summer and early fall. High-energy foods, such as berries during summer and acorns during fall, are critical. It is also important that populations be maintained at reasonably low levels and have balanced sex and age ratios. Wildlife biologists have sought to determine the harvest levels that can maintain herds in proper balance in the absence of natural predators. The concept of quality herd management, popularized by Brothers and Ray, is a good effort.

The length and intensity of the breeding season vary according to area and the characteristics of the herd. It is likely to be short and intense in the north and longer and less intense near the equator. The sex ratio and ages of bucks and does also seem to be factors. If the number of bucks, particularly older ones in the herd, is inadequate, some does may cycle late or not get bred during their first cycle. They may continue to come into heat for six months or more if they do not conceive during their first heat periods. But if enough mature bucks are present, breeding of adult does is essentially over in about three weeks. Fawn does that are large and fit enough to breed may come into heat later, thus stretching out the breeding season a little.

THE RUT ENDS

Bucks' sexual interest in the late season is affected by many things. After most does are bred, younger bucks that were not allowed to breed during the main part of the season may become more active and assertive in the search for any does that remain unbred. Miller and others noted that the testosterone levels and therefore sexual interest of young bucks go up after the larger bucks' activity begins to wane. Forand and March-



inton found that where the does come into heat over a long period and breeding effort is of lower intensity, the most dominant bucks stay active and maintain high levels of testosterone well into the winter or until all does are bred. But if breeding is very intense, they may burn out early, allowing younger bucks to breed.

Falling testosterone levels eventually precipitate antler drop. Poor nutrition or a highly intensive, stressful rut can cause early drops. In the Northern Hemisphere, bucks often lose their antlers before January, and most have lost them by mid-April. Regrowth is likely to begin in early May. Preparations for the next rut begin with the initiation of new antler growth, and the buck's annual cycle starts again.

—R. Larry Marchinton and Karl V. Miller



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