Deer talk: sounds, smells, and postures

The white-tailed deer is often called elusive, secretive, silent, wary. Descriptions like these give the impression that deer lack a complex communications system. This is far from the truth. Research by behavioral scientists is just beginning to open the doors to this animal's elaborate social communications system.

In addition to vocal signals, whitetails also use chemical and visual signs to relay information, which makes their communications system difficult to decipher. In fact, vocal communication appears to play only a minor role in the day-to-day life of the whitetail. Deciphering the other forms of communication requires intensive and detailed observation of behavior, along with sophisticated analytical equipment.

Whitetails are social creatures, living in either matriarchal or bachelor groups for much of the year. Within these groups, deer use a variety of signals to communicate with one another, including a number of vocalizations, body language, and chemical signals. The signals are often very subtle, and because they are used to communicate among members of a group, they generally are effective for only a short distance.

A different strategy is required for communication among individuals that are not members of a particular group. Whitetails live in an environment that is often thickly vegetated; therefore, neither visual displays nor vocal signals would be effective for more than a short distance. Instead, they use a system of scent communication that involves placing "signposts" throughout their range. These signposts relay information on the identity of deer in an area, including their sex, dominance status, and reproductive condition. Signposts are very important in the breeding behavior of whitetails. During the rut, rubs and scrapes communicate dominance status among bucks and also advertise the buck's availability to potential mates.

Vocal Communication

As early as 1926, Newsom recognized that whitetails produce a variety of vocalizations. Later, in 1937, Seton also described some of their vocal expressions. It was not until the 1980s, however, that the vocal repertoire of whitetails was recorded and characterized. This was done by Richardson and coworkers in Mississippi as well as by Atkeson and associates in Georgia.

Using sensitive recording equipment along with detailed observations, these two groups recorded a variety of sounds produced by deer. The Mississippi group distinguished seven vocalizations; the Georgia team recorded twelve. This variation generally reflects differences in the interpretation of the sounds recorded.

Alarm and distress calls. The snort is probably the most widely recognized of the whitetail's calls. It is not actually a call but a sound that results from air being forcibly passed through the nasal passages. Snorts are

Vocalizations are a small part of deer communication. The threatening grunt-snort-wheeze may precede a dominance fight.

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given in two distinct situations: when startled at close range, a whitetail often gives a single, very short, explosive snort at the moment it begins its escape. When a deer detects danger at a relatively safe distance, it often will produce a series of slightly longer snorts. Hirth and McCullough found that members of doe groups are much more likely to snort than members of buck groups. They suggested that these snorts serve to alert other related members of their group.

The bawl is a very intense call given only by deer in extreme distress, such as when injured or restrained. Deer of all ages may bawl, with the pitch decreasing as the deer grows older. Bawls by fawns may elicit defense by the dam. Smith in 1987 reported that fawn bawls elicited aggressive assaults in 30 to 87 percent of the instances he observed. He suggested that the differences in the tendency to defend the fawn were related to the physical condition of the mother.

Agonistic calls. Agonistic, or aggressive, calls consist of a low, guttural grunt, with other elements added as the intensity of the encounter increases. The lowest-intensity call is the low grunt alone. It is given by both bucks and does during all seasons of the year. The low grunt coupled with other visual signals such as the "head-high" or "head-low" threat is often used to displace a lower-ranking individual.

In more intense encounters, one to four short, rapid snorts are added to the low grunt. During the rut, bucks often give the grunt-snort during dominance interactions with other bucks. Females also occasionally give this call.

The grunt-snort-wheeze, produced only by males during the rut, consists of the grunt-snort coupled with a drawn-out wheezing expulsion of air through pinched nostrils. It is the most threatening call produced by bucks and often precedes a dominance fight.

Maternal and neonatal calls. The maternal grunt is a low-intensity grunt that can be heard for only a short distance. This call is given by the female while she is approaching a fawn's bedding area. The fawn responds to the maternal grunt by leaving its bed, moving toward the dam, and often nursing. When fawns become old enough to travel with their mothers, the does often use the maternal grunt to maintain cohesiveness among the family group.

Fawns often produce a high-pitched mew in response to the maternal grunt. The mew is used to solicit attention from the mother. The fawn bleat, similar to the mew, is a more demanding care-soliciting vocalization. The bleat is a more intense call—whereas the mew can be heard for only a short distance, the bleat can be heard by humans up to 100 yards away. The intensity of the bleat is directly related to the degree of need—hunger, thirst, social contact—of the fawn. Fawns also bleat when disturbed from their bedding sites, often bringing nursing does to investigate. Fawn bleats have been used successfully by both deer researchers and hunters to attract does. The successfulness of this technique decreases during late summer as fawns grow older.

During suckling or while searching for a nipple, fawns give a brief, low-intensity nursing whine. Richardson and coworkers sug-

gested that the nursing whine may help identify the fawn, reaffirm the maternal bond, transmit pleasure, and solicit additional attention. In response, the dam may provide continued or intensified comfort and security by grooming or additional nursing.

Mating calls. Two sounds are produced by males during courtship: the tending grunt and the flehmen-sniff. Only the tending grunt can be classified as a vocalization, however. This low, guttural call is made by rutting males, most commonly while tending a doe in heat, but also frequently while traveling in search of females. Tending grunts seem to be made most often by mature, dominant males and rarely by younger bucks.

The flehmen-sniff is a sound produced infrequently by rutting males while performing flehmen, or lip curl. This behavior is associated with the buck's investigation of urine via the specialized vomeronasal organ. The flehmen-sniff appears to be merely a by-product of this action and most likely has no communicative function.

Contact call. The contact call is occasionally made when an individual becomes separated from a group. This call is similar to the low grunt and the maternal grunt but is longer and has higher tonality and intensity, along with varying inflection. The contact call has thus far been reported only from females.

Visual Displays

Social groups of deer use a number of visual cues to communicate with other members of the group. Most of these signals are very subtle and often go unnoticed by the human observer. They are readily observed by other deer, however, and are used to convey a variety of information, such as dominance status, aggressive intent, and alarm. They are also used in courtship displays and in interactions between mother and neonate.

Aggressive intent. Other than overt attacks, whitetails use two types of visual displays to communicate aggressive potential in an attempt to dominate or master another individual. Threats signal an intent toward overt aggression, whereas dominance displays serve more to intimidate or challenge a potential rival.

CUMMINGS / DEMBINSKY PHOTO

A doe uses a grunt to maintain the cohesiveness of her family group. Recognizing the sound of its mother, the fawn draws near.

The lowest form of threat is the ear drop, in which the ears are laid back along the neck; this is coupled with a direct stare by the aggressor. More-aggressive postures have been defined by Hirth as the "head-high" and the "head-low" threats. The head-high posture signals the aggressor's willingness to rear onto its hind legs and flail the recipient with its front legs. This threat is used most commonly by does throughout the year and by bucks while their antlers are in velvet. The head-low threat signals an intent to chase and strike the opponent with a foreleg. During the breeding season, males also use this threat to indicate a willingness to use

Failure to acknowledge the dominance of a matriarch is met with an aggressive behavior: the doe lays back her ears and fixes the challenger with a hard stare. This signals that she will rise and strike at the challenger with her sharp front hooves.

STRACENER

KINNEY

Deer exhibit extremes of aggression and submission, from this buck's threatening ear-drop and stare to the ultimate posture of appeasement, the crouch.

REZENDES

their now hardened, polished, and tested antlers as weapons.

In contrast to threats, dominance displays draw attention and advertise status. These displays are used almost exclusively by males during the breeding season and are always accompanied by threatening postures.

A dominance display by a mature whitetail is a sight to behold. When displaying to an unfamiliar potential rival, the buck assumes a dominance posture: the ears are laid back along the neck, the eyes are held wide open, and all of the deer's hair stands on end. This piloerection helps make the buck look darker and larger to his rival. In a dominance display, the preorbital gland and the nostrils are commonly flared open. Beads of moisture appear on the buck's muzzle, and there often is noticeable drooling.

Dominance displays include not only visual signals but also vocal and chemical cues. A buck will often thrash a bush with his antlers, rub-urinate, or make a scrape. A grunt-snort or a grunt-snort-wheeze signals his willingness to carry this interaction toward further aggression.

During dominance displays, a mature buck approaches a rival at an angle with a slow, stiff-legged gait. This behavior, called sidling, allows the buck to display his body size and his antlers simultaneously without making himself unduly vulnerable to attack. Most encounters end at this point, with the smaller buck assuming a submissive posture or retreating. A vicious dominance fight may erupt if the two bucks are similarly matched, however.

Courtship displays. The communicative displays associated with courtship and breeding have been described in detail by Warren and coworkers in 1978 and by Brown and Hirth in 1979. During estrus, females are not known to display any overt visual signal to the male indicating their reproductive status and willingness to breed. Estrous advertisement appears rather to be largely an olfactory cue.

Alarm displays. When they detect danger or potential danger, whitetails use a series of visual displays in addition to the snort. The most conspicuous is the tail flag, from which the species gets its name.

WALLNER

Deer signal alarm by stamping the forefoot. In addition to that visual sign, there may be a chemical one as well: the interdigital gland is thought to release a scent that can alert nearby deer to the threat.

Upon encountering an unknown object, a whitetail assumes an alert posture. The head is held erect, and ears are cupped forward in the direction of the stimulus. Depending on the degree of alarm, the tail may be held partially or fully erect to expose its white underside and the white rump patch. This display alerts other members of the group, who likewise assume an alert posture. If the danger is not identified, the deer may either retreat with a bounding, tail-flagging gait or further investigate the unknown object. Whitetails are curious animals and often will not flee until the object of concern is identified. Apparently, deer do not have very good depth perception; thus they will move toward or parallel to the object or will move their heads from side to side to get a glimpse from another angle.

Accompanying this investigation, a deer often will stamp one or alternating forefeet. This stamping might function to urge a potential predator to move and reveal itself, or to release scent from the interdigital gland as a further warning to other group members, or both.

Unless surprised at close range or greatly alarmed, whitetails expose their "flags" when fleeing. Contrary to popular opinion, bucks and does flag with approximately equal frequency when alarmed. In a study conducted on the George Reserve in Michigan by Hirth and McCullough, buck groups flagged in 91 percent of the encounters with humans, whereas doe groups flagged in 95 percent of encounters.

But why would an individual expose a conspicuous white tail patch to a predator? Wouldn't this make it easier for the predator to pursue the animal and thereby decrease the deer's chances of survival? Perhaps the most logical explanation of the causes and consequences of tail flagging was presented by Hirth and McCullough in 1977. Many species of ungulates have conspicuous rump patches. In general, social species living in relatively open habitats, such as the elk *(Cervus elaphus)*, have white patches that are not hidden by the tails. In contrast, many solitary species that live in dense vegetation, such as the musk deer *(Moschus moschiferus)*, have no conspicuous rump patch at all. Apparently, the white rump patches have evolved among gregarious species as a means of maintaining group cohesiveness. Whitetails fall between these two extremes—they are social animals that live in heavily vegetated habitats. Therefore, they have evolved an "on-again, off-again" rump patch. At most times the patch is concealed beneath the tail, and they can rely on their camouflage coloration to avoid predation, but when they are discovered they can use the tail flag to maintain the cohesiveness of the social group while fleeing. Whether they flag or snort in the presence of danger depends on the closeness of the threat.

Groups of bucks or does may react differently to intruders under different circumstances. If danger is detected early, either visually or by scent, and there is a chance to escape undetected, members of buck groups and doe groups respond in very different ways. Does likely will snort to warn other group members about the possible danger. Since doe groups tend to be closely related, it is to their advantage to risk detection to warn their relatives and thereby "maximize their inclusive fitness," or help ensure the

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As a social species that depends on camouflage, the whitetail needs a visual signal that can be turned on and off. The white flag enables fleeing deer to keep together; once the animals are safe in cover, the brown top side of the tail blends into the forest.

survival of related individuals. In contrast, a buck often retreats without warning other members of his group—since buck groups are composed of unrelated individuals, there is no advantage to such a warning. Rather, it is to a buck's advantage to retreat and let the others in the group become potential prey.

If a potential predator is spotted at a more intermediate range, when an escape would certainly be detected, buck and doe groups act similarly. The members of the group flee with tail-flagging and possibly snorting. Tail-flagging may work to confuse the predator, but more important, it helps maintain group cohesion. By staying in a group, each individual reduces its chance of falling prey. In addition, the combined senses of several animals make the group more difficult to approach than a solitary individual.

If an individual is surprised at close range and the danger is severe, buck and doe groups again react similarly, with an explosive scramble for escape. This retreat may or may not be preceded by a loud snort but is rarely accompanied by tail-flagging.

Scent Communication

Though deciphering the information deer relay through vocal and visual signals is not an easy task, attempting to understand how deer use chemical signals for communicating is by far the most difficult area of investigation. Although detailed studies have not been conducted, it appears safe to say that a deer's sense of smell is many magnitudes greater than our own. Only very recently have scientists developed equipment and techniques that can detect compounds with a sensitivity similar to the deer's nose. Even with this sophisticated equipment, however, we are not able to get inside a deer's head to determine exactly what types of information are being relayed by these scents. Instead we have to rely on observations of the deer's behavior and make subjective estimates of the significance of these odors. This is an imprecise technique at best and is open for errors of interpretation. Nevertheless, our understanding of the significance of chemical cues in the behavioral ecology of deer is growing.

Chemical signals that relay information among animals are called pheromones. This term was originally coined to describe chemical sex attractants in insects but has since been expanded to include any chemical produced by one individual that transfers information to another member of the same species; some researchers reserve *pheromone* for insects and use *chemical signals* when referring to mammals. Whatever the terminology, these signals include releaser pheromones, which evoke an immediate behavioral response; priming pheromones, which result in a physiological response; and informer pheromones, which relay information but generally do not result in a behavioral or physiological response.

Sources of communicative odors in deer include specialized skin glands, the urine, vaginal secretions, and possibly saliva. Researchers have identified at least eight areas of a deer's body that have specialized development of glandular tissues likely to be involved in scent communication.

The interdigital glands are well developed in white-tailed deer. Although their significance has never been positively identified, these glands presumably are used in marking a trail while a deer walks. Other than a preliminary investigation by Atkeson in 1983, little work has been done on the function or chemistry of the interdigital. Atkeson found that the secretions of the interdigital contained a number of volatile components, including acetic, butyric, isobutyric, propionic, and isovaleric acids. These compounds have different volatilities, evaporat-

ing at different rates, and therefore the odor of a deer's track likely would change as the track ages.

Although the metatarsal of the black-tailed deer has been shown to produce an alarm scent, several investigators have been unable to demonstrate any functions of this gland in white-tailed deer. Perhaps this gland functions primarily as a sensory organ, as suggested by Quay in 1959. Other investigators suggest that this gland is an evolutionary remnant and has no function.

The tarsal gland is undoubtedly the most important source of chemical information to deer. Whitetails obtain information on individual identity, dominance position, physical condition, and reproductive status from odors arising from this gland. The tarsal of females appears to be used primarily for individual identification. Does frequently sniff the tarsals of others in their social group, and fawns use this scent to identify their mothers.

Though the sebaceous and sudoriferous glands underlying the tarsal may contribute to the odor of the gland, the primary source of information likely comes from urine. The enlarged sebaceous glands underlying the tarsal tuft secrete a fatty material that adheres to the tarsal hairs. During a behavior called rub-urination, deer urinate on their tarsal hairs. The fatty material then selectively retains fat-soluble compounds from the urine.

Deer of both sexes and all classes frequently urinate onto their tarsal glands. Sawyer found that throughout the year, does rub-urinated an average of 1.2 times every day and urinated in a normal posture eight to nine times per day. The rub-urination occurred most commonly at night, shortly after the doe rose from her nocturnal bed. After rub-urination, the doe invariably licks excess urine from the tarsal.

Bucks also frequently rub-urinate throughout the year, and during the rut, mature, dominant males may urinate exclusively in this posture. These males no longer lick the excess from their tarsals, and the resultant staining of the tarsal and lower leg is well known to most hunters.

Little work on the chemical composition of the odors arising from the tarsal has been conducted, though at least one active component of the black-tailed deer's tarsal scent has been identified. No compound identified yet from the whitetail's tarsal has been demonstrated to be important for communication. Atkeson in 1983 and Silverstein in 1971 investigated the odors from the tarsal gland, and both identified ortho-cresol and meta-cresol, along with other compounds. Some preliminary data indicate that there are considerable individual differences in the composition of the volatile compounds in the urine of male deer. Although these compounds have not yet been identified, the presence and concentrations of several of them appear to be directly related to the age and dominance status of the male. Some of these compounds are found only in the urine of the dominant males during the breeding season. Thus there must be differences in the odor of urine among bucks, differences that reflect each animal's dominance and reproductive status. These odors are transferred to the tarsal gland during rub-urination and, along with odors from the bacterial decomposition of other urinary compounds, contribute to the particular odor of a rutting buck.

The forehead area of the whitetail contains a large number of sudoriferous glands and is used in signpost marking. These glandular areas are found in both males and females, but the glands are most active in dominant males during the rut. Scent from the forehead gland is used to mark antler rubs during the breeding season. Females have been

Bucks rub-urinate more often than females. The urine flows over the tarsal glands, taking with it chemicals that are significant to other deer.

WERNER

A buck leaves messages on twigs and hanging vines, depositing chemicals from the preorbital gland or the forehead gland. The rival buck licks the message, enhancing its scent with his saliva. Does, too, check messages.

WERNER

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shown to respond to these rubs and may mark them with their own foreheads.

Bucks also mark overhanging branches throughout the year. These appear to be communal marking areas, as many bucks will use the same branches. The source of the scent left on these branches is difficult to determine, although the forehead is likely one contributor and the preorbital gland and saliva possibly are others.

Many overhanging branches become scrape sites during the breeding season. While only a dominant buck undergoes the entire scrape sequence, many bucks may continue to use the overhanging branch. Therefore, the branch appears to be important to bucks for identifying other males in an area, while the full scrape is a display of dominance by a particular buck.

Communication of estrus. How does a doe let a buck know that she is in heat and willing to be bred? Probably no other question pertaining to deer behavior has been asked more often and debated more intensely. Although it is certain that some form of chemical communication is involved, we are still unsure of the exact mechanism used. The pieces of the puzzle are starting to fall into place, however, and we have a good guess of how it is done.

To understand how reproductive information is communicated among deer, it is first necessary to look at how a deer perceives chemical signals. Like most mammals (except primates and humans), deer have two distinct means through which to receive chemical information: the main olfactory system and the vomeronasal organ. The main olfactory system receives airborne chemicals through the nose. Inspired air passes through the nose and over the olfactory epithelium, where nerve fibers pick up olfactory information and transmit it to the main olfactory bulb of the brain. In the olfactory bulb, these nerve fibers communicate with other nerve fibers, which then transmit the olfactory information to various parts of the brain. There, information is processed and decisions or behavioral responses are made.

The little-known vomeronasal organ has an opening near the center of the roof of a

deer's mouth. The organ's primary purpose appears to be analysis of other deer's urine. During the reproductive season, males respond to the urine of females using a stereotypical behavior called flehmen (a German term meaning "lip curl"). After taking a small amount of urine into his mouth, the buck opens his mouth slightly, curls his upper lip, and closes his nostrils; this pumps some urine into the vomeronasal organ for analysis.

The neural impulses, or information, obtained here do not go to the same parts of the brain as information obtained through the main olfactory system. Rather, information from the vomeronasal organ travels through the accessory olfactory system, in which nerves are connected via a single synapse in the accessory olfactory bulb to a part of the brain called the amygdala, which in turn has direct connections to the hypothalamus. This is important, since the hypothalamus is the part of the brain that controls the reproductive physiology through the production of hormones. Thus, information from the vomeronasal organ can affect the deer's reproductive physiology, but it does not appear to play a major role in regulating the deer's direct behavioral response.

Another difference between these two systems, the nose and the vomeronasal organ, is that the main olfactory system appears to be used to analyze smaller, more volatile, airborne molecules and the vomeronasal system to analyze larger, less volatile molecules that are in solution in some liquid, such as urine.

Why should an animal have two such systems? What part does each of these systems play in the ecology of deer?

Although no direct experimentation has been done with deer, experiments have been conducted on related animals, such as sheep and goats, to determine the roles of these two systems. Judging from behavior alone, one might conclude that the buck determines a doe's readiness to be bred by analyzing her urine via the vomeronasal organ. Yet in experiments with sheep, if sensory input from the vomeronasal organ is blocked, a ram still has no difficulty in telling ewes in heat from ewes that are not in heat. Conversely, if the main olfactory system is blocked, the ram cannot discriminate estrous ewes. Thus it appears that the chemical signal that indicates estrus is a volatile compound that is picked up through the nose, not through the vomeronasal organ.

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Even when she is not in heat, a doe's urine speaks to other deer, advising them of her range boundaries.

A series of experiments at the University of Georgia strongly suggests that reproductive information is relayed the same way in whitetails. Tests of estrous urine and estrous vaginal secretions have shown that urine is most likely not the main route that a buck uses to identify a doe in heat. Rather, it is volatile secretions from the reproductive tract of females in heat that cause bucks to pursue and court females.

If bucks use their main olfactory system to determine when a doe is ready to breed, then what is the purpose of the vomeronasal system? Findings here are much more speculative. Some researchers have suggested that flehmen of doe urine and subsequent vomeronasal analysis is used to determine whether the doe is *approaching* estrus. This is based on data showing that bucks tend to flehmen urine from does not yet in heat more often than from does already in heat.

The nonvolatile chemicals in a doe's urine are not perceptible to even a deer's keen sense of smell; the buck uses his vomeronasal organ to examine them.

KINNEY

We believe, however, that flehmen is used for a much more important but perhaps more subtle purpose. Since the vomeronasal system is connected to the part of the brain that controls reproductive physiology, a male's analysis of urine through this system likely serves to prime that physiology and thereby ensure that he reaches peak reproductive condition at the same time as do the females.

The primary cue that triggers the onset of the deer's breeding season is change in day length. Certain parts of the deer's brain mediate the response to this cue through a complex system that ultimately affects the hypothalamus—the reproductive control center of the brain. The result is a window of opportunity during which the deer is reproductively active. Since the vomeronasal system also leads to the hypothalamus, it likely helps fine-tune the breeding system to ensure that males and females are in reproductive synchrony. Evidence from other animals indicates that vomeronasal stimulation causes the hypothalamus to release hormones that affect the animals' reproductive capacity. Whether this occurs in deer awaits additional experimental evidence.

—Karl V. Miller and R. Larry Marchinton