

11

INTRASPECIES INTERACTION

A social structure within a population cannot exist without some form of communication between organisms. The ability to communicate depends on both the signal that is sent by one organism and the receiving ability of another organism. This has been discussed in Chapter 2, with the term "operational environment" applied to the stimulus-response combination.

11-1 SENSORY PERCEPTION

The sensory perceptions of animals include sight, hearing, smell, taste, touch, and thermal perceptions. The neurological perception levels are very difficult to quantify, especially for taste and smell. There really is no way to quantify the strength of these associations directly, although the responses of animals to such things as chemicals can be tabulated. Sight and hearing are more easily quantified since light and sound energy can be described in terms of wavelengths, frequencies, loudness, and other units.

There is general agreement among natural-history writers that most wild animals have good vision. Most appear to exhibit some difficulty in detecting the presence of motionless objects, but moving objects are usually detected very easily. The lack of ability to detect motionless objects is partly credited to the apparent lack of color vision. In the absence of color there are fewer stimuli that help to distinguish an object from its surroundings. In analyzing sight capabilities, careful distinction must be made between what an animal can see and what the animal sees and responds to since visual detection may occur without an observed behavioral response.

Many wild animals are active at night, and it appears that their night vision is considerably better than that of a human. Deer tend to feed in the early morning and late evening, indicating that activity periods transcend changing light conditions. Their readiness to bound off a road into a stand of trees at night indicates some ability to see in very dim light; however, inasmuch as humans cannot see the animals as they move through the forest at night, it is difficult to determine the number of collisions with branches and other objects.

Some wild ruminants can apparently see objects at greater distances than others. Pronghorns, bighorn sheep, and mountain goats seem to possess keen vision for distance. Their habitat is generally more open, and vision for long distances is useful for increasing their ability to detect danger. Their visual capabilities may be an indicator of evolutionary development that relates visual ability to the selection of certain habitat characteristics.

Caribou spend much of their time in rather open country, but their eyesight is considered inferior to that of most game animals (Kelsall 1957). They have good ability to detect moving objects, however, and Kelsall reports instances in which caribou bands have fled when a single person was walking at distances of more than one-half mile from the band.

Deer have a keen sense of hearing. Many accounts are recorded in the literature that attribute an almost unbelievable hearing ability to deer. There are strong indications that deer distinguish between noises that are a regular part of their habitat and those that are a bit different from the usual. My personal observations have indicated that the chattering of squirrels, the noise of the wind, the creaking of branches, and the like are accepted by deer. Distant gun shots do not cause concern. A sharp snap of a twig, however, makes them instantly alert.

The mobility of the ears is a striking characteristic of deer. The direction in which either ear is pointed can be controlled independently of the other. When both ears are directed toward a sound, their ability to hear is enhanced by the directional effect of ear orientation.¹

The bugling of elk is a form of sound communication that is a fairly common practice among elk, even by cows at about the time of parturition (Murie 1951). Bugling by male elk is usually thought of as a challenge to a rival bull. Murie suggests that the rivalry may be exhibited in more meaningful ways than bugling. Male elk will bugle early in the rutting season with no effect on other male companions. This illustrates how the importance of a biological characteristic is dependent not only on the stimulus but also on the condition of the receiver.

Another means of communication between individual animals is touch. The muzzle and tongue are used to make contact with different parts of another animal, which is part of the behavior pattern of both young and mature animals. The mouth is also sensitive to the mechanical characteristics of forages. The hair coat is sensitive to pressure; the skin twitches to rid itself of flies. Peterson (1955) suggests that touch might enhance the ability of moose to locate submerged

¹Notice the orientation of the ears of the deer in the photograph facing page 1. The ears are oriented forward in some of the deer and backward in the others.

vegetation: "... moose were observed to swim out to deep water, then suddenly dive for a few seconds, perhaps become completely submerged, and come up with a mouthful of pond weed (*Potamogeton* sp.)." He speculates that moose can feel the plants with their legs.

The sense of touch may be particularly important for animals that are born blind. Members of the cat family, for example, live in a world of sounds, odors, and tactile reflexes before their eyes open. The cuddling of human infants in the first few days of life is important for their development.

Observation of the sensory capabilities of moose have led to a generalization that may apply to most big-game animals. The ears often serve to alert an animal, the eyes are used to investigate the disturbance, and the sense of smell is the most important means of detection (Peterson 1955). Severinghaus and Cheatum (1956) state it another way: "Deer depend first on scent, second on hearing, and last on sight."

The importance of smell is indicated by many writers, and it is a consideration of every big-game hunter. The olfactory capabilities of wild ruminants may seem relatively greater, to an observer, than they actually are, because the sense of smell is so poorly developed in man. Nevertheless, the ability of ruminants, as well as that of most other wild mammals, to detect odors is particularly well developed.

Kelsall (1957) has observed deer, moose, bear, and caribou as they were catching a human scent. The first three always reacted as if the scent of man meant danger, but the caribou seem to doubt the evidence of scent. Although deer have been reported to move downwind from the source of a scent in order to confirm it, Kelsall has observed caribou moving downwind and toward the source as if to confirm it by sight. He further states that large herds seem less concerned than small herds when the scent of man is present.

One indication of the importance of scent in the activity of an animal is the relative flight distance when a stimulus is received by different senses. Peterson (1955) relates the observation of Sheldon that "After being frightened by scent, moose go much farther without stopping than when frightened by sight." The flight behavior of big game is discussed in Chapter 12.

A recent study of pheromones in black-tailed deer (*Odocoileus hemionus columbianus*) by Müller-Schwarze (1971) has revealed a number of distinct functions related to the various glands. The pathways taken are shown in Figure 11-1. Note how the pheromones are transferred from one part to another of a single deer (hindleg rubbed on forehead), from a deer to another object such as a branch, and from one deer to another through the air.

Four scents are considered important by Müller-Schwarze in social communication of the black-tailed deer. The *tarsal scent* serves to identify sex, age, or type of an individual at a close distance. The *metatarsal scent* acts like an alarm pheromone over moderately large distances. When a deer rubs its head on branches, the scent of the forehead glands left on them marks home range. The interdigital gland leaves scent on the ground, although infrequent responses were observed in the black-tailed deer.

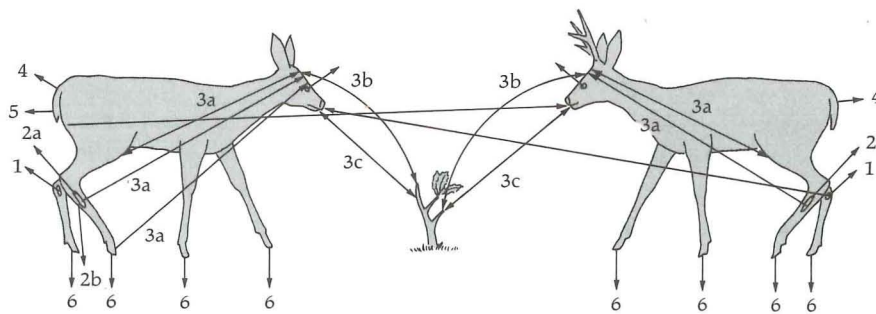


FIGURE 11-1. Pathways of social odors in black-tailed deer. Scents of tarsal organ (1), metatarsal gland (2a), tail (4) and urine (5) are transmitted through air. When the deer is reclining, the metatarsal gland touches ground (2b). The deer rubs hindleg over forehead (3a). Marked twigs are sniffed and liked (3c). Interdigital glands leave scent on ground (6). (From Müller-Schwarze 1971.)

Urine also provides olfactory information. Fawns urinate in their beds, and Müller-Schwarze observed that they did not use the same bed site again if the urine had been disturbed. Black-tailed fawns just two days old urinate on their hocks while rubbing their legs together; this habit continues through adulthood. It has also been observed in white-tailed deer. Black-tailed orphan fawns in captivity rub-urinated four times in 100 hours of observation, though none were observed by Müller-Schwarze in 300 hours of observation in the wild. Rub-urinating by a captive fawn living with its mother attracted the mother, indicating that it may be related to the separation of the doe and fawn. In adults, it appeared to serve to increase the distance between individuals.

Aggressiveness between males of many species of both birds and mammals can be observed. Pheasant (*Phasianus* sp.) males defend a "territory" against intrusion by other cocks. The females cross territorial lines and are courted by the resident male. No attempt seems to be made to herd the females or to retain a harem.

Ducks and geese establish territories during the breeding season too. Sowls (1955) discusses the home-range and territorial characteristics of several species. Home range is described simply as familiar area used by the birds. The defended territory is used exclusively by a single pair of one species. Hochbaum (1944) describes the territory as a place in which the paired drake and hen may be found day after day. It contains water, a loafing spot, nesting cover (adjacent or nearby), and food, and it is defended by the drake from intrusion by other sexually active birds of his own species. These territories are not strict geographical entities, however, inasmuch as they vary in size, they overlap, and there are differences in the degree of territoriality among birds.

Some species exhibit a social hierarchy within a group rather than a territorial separation of its members. The social order of Rio Grande turkeys (*Meleagris gallopavo*) on the Welder Wildlife Refuge near Corpus Christi, Texas, has been described by Watts and Stokes (1971). In the winter the males form flocks, in which the social status of the male is determined. Each male fights to establish

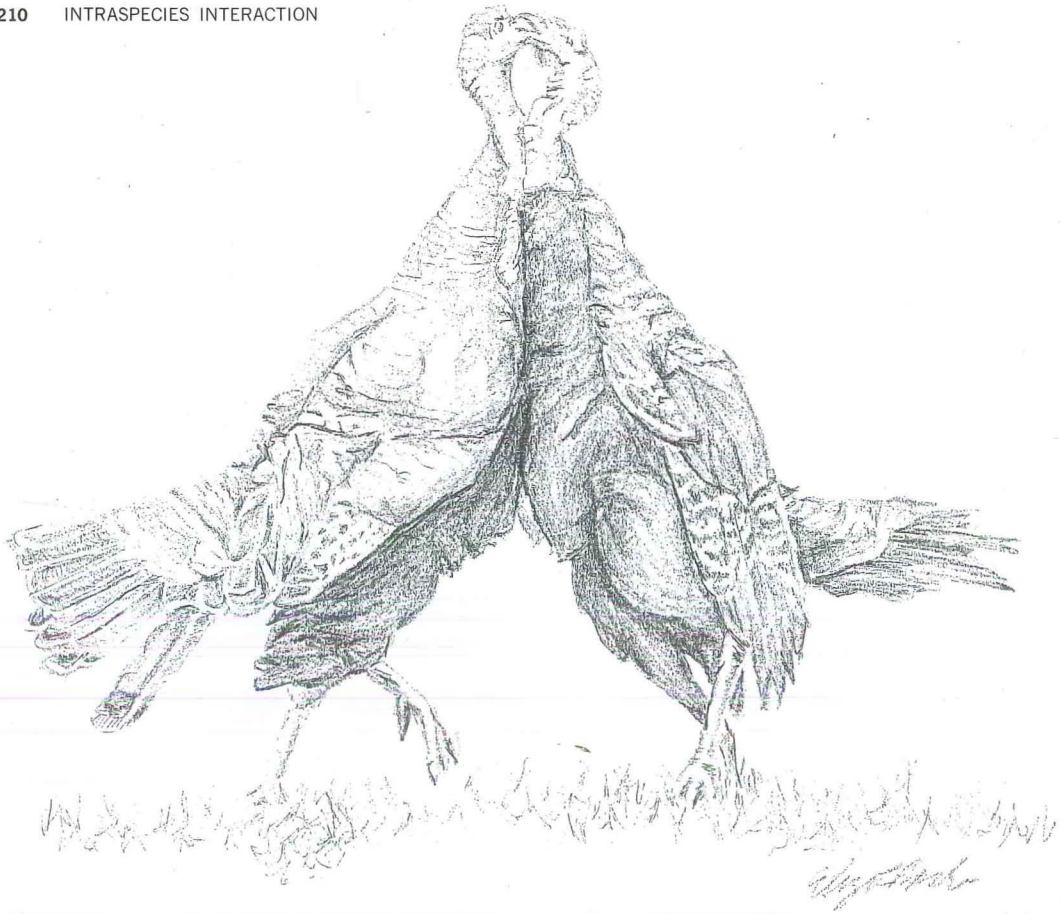


FIGURE 11-2. Wrestling match between juvenile wild turkeys, who are members of the same sibling group, is one of several forms of combat that eventually determine which male will dominate the other members of the group. The birds usually fight until exhausted. Dominant males at the Wedder Wildlife Refuge in Texas act as sires in the great majority of annual matings among the resident turkeys. (Adapted from "The Social Order of Turkeys" by C. Robert Watts and Allen W. Stokes.)

his position among his siblings first (Figure 11-2); then the entire group fights other sibling groups to determine its position among them. The winter flocks of males begin breaking up in February, with groups of sibling males courting the females. The dominant group moves about within the ranks of the females, and the subordinate groups follow along on the periphery of the female group. The dominant male in the dominant sibling group does nearly all of the mating with the hens! A complete copulation takes about four minutes, and subordinate males do not have time to fulfill the mating attempt before they are detected by the dominant male, who drives them off and completes the mating with the hen himself.

Male ruminants are generally aggressive during the breeding season. The presence of horns or antlers makes them potentially dangerous not only to man or to some other animal, but also to both male and female members of his own species. Rutting behavior includes two kinds of associations: (1) the aggressive

association between males and (2) the attraction between male and female during ovulation. The strength of these associations is marked, resulting in stronger interactions between individuals during the mating season than at any other time of the year.

One of the secondary sexual characteristics of members of the family *Cervidae* is the seasonal growth and shedding of antlers. Growth begins in later winter or early spring and accelerates during the summer. By August or September the velvet-covered antlers harden and the first signs of aggressive behavior begin to appear. Much has been written over the years about the "rubbing off of velvet," and the usual implication is that this is done in order to shed the velvet. Actually, the velvet on the antlers of white-tailed deer is shed in a matter of hours (Figure 11-3), and may not be accompanied by rubbing. The mutilation of small trees is an indication of an increase in aggressiveness that begins as the reproductive condition develops. Severinghaus and Cheatum (1956) reported that captive deer at the Delmar Laboratory exhibited aggressive behavior toward fences, trees, or any other resistant object as the neck muscles harden. This also serves to mark the territory, which Müller-Schwarze has described for black-tailed deer.

During the rut, male deer also paw and dig up a circular patch of ground a few feet in diameter, which results in the formation of a "scrape." These scrapes may also have some value as markers for a buck's territory, or at least for informing the other members of the population, both male and female, that an

FIGURE 11-3. Male white-tailed deer with velvet coming off.



area is being used by the buck. Bronson (cited by Severinghaus and Cheatum 1956) reports that white-tailed bucks urinate in the pawed-up ground and roll or wallow in it, leaving scent indications as well.

The scrapes or wallows of white-tailed bucks have their counterparts in the wallows made by moose and elk bulls. Peterson (1955) records accounts of natural historians who have observed moose bulls dig a wallow with their front feet, urinate in it, and roll in it. Bull elk also dig wallows, using their antlers as well as their front feet to tear up the sod. Bugling may occur while the bull is lying in a wallow (Murie 1951).

Male ruminants are generally polygamous, servicing as many females as possible during the breeding season. The sexual readiness of the male coincides with that of the female, although the latter has an estrous cycle that results in a readiness to stand at intervals of several days until fertilization occurs. Limits imposed on the number that can be serviced include both the number of receptive females and the energy of the male for repeated copulation. Observations of penned deer at Delmar, New York, and at the BioThermal Laboratory at Cornell University show that the female will stand for more than one buck. As a male becomes spent from repeated servicing, a second male will copulate successfully. These observations may not be strictly applicable to wild conditions, but they do indicate the potential of deer for repeated copulation.

Martinka (1969) describes the social relationships of elk from calving through the end of the breeding season, including calving in the first part of June, aggregation for two months following calving, dispersal prior to the breeding season, breeding in September and October, and reaggregation following breeding and on through the winter. Bull elk maintain control of a harem of cows during the breeding season. This social organization may not result in highly organized reproductive behavior, however, since subdominant bulls may breed with the cows when the harem bull is occupied with defensive behavior.

The approach of parturition does not seem to trigger special preparations by the white-tailed doe. Severinghaus and Cheatum (1956) describe several types of parturition sites that have been observed, including open fields, snow patches, and nicely sheltered insect-free sites. It would be easy to become anthropomorphic about the care with which a doe selects a place for giving birth, but it is apparently a matter of convenience, occurring wherever the mother happens to be at the time.

Barren-ground caribou cows seem to move with a sense of purpose prior to calving (Kelsall 1957). As calving time approaches they assume the leadership of the spring migration. When they reach the calving grounds, they tend to scatter widely and move slowly. The geographic location of calving grounds seems to vary, but it is evident that certain calving grounds are favored year after year even by widely separated herds.

The parental care of a fawn or calf begins immediately after birth. The mother licks the newborn, and although this is often said to be a cleaning process that may have nutritional benefits for the mother, the tactile stimuli very likely have an influence on the imprinting process. Not only does the newborn see its mother, but to feel the mother's gentle licking reinforces the relationship.

Barren-ground caribou calves are considered more precocious than the young of other ungulates, inasmuch as they may walk and run for several miles within an hour and one-half after birth (Kelsall 1957). Only two calves, each less than 4 hours old, were captured out of many hundreds seen, according to Kelsall. He also reports that calves less than 12 hours old will jump off an ice shelf and swim easily.

An interesting observation reported by Kelsall indicates the strength of the imprinting instinct in the caribou. The birth of a calf was observed and the calf was ear-tagged a short time after birth. The cow fled as the observers approached the calf. After handling the calf, the observers could not get away without the calf's following them. It was necessary to roll it on its side behind a boulder and dash away. The cow returned later and located the calf, apparently by accident. This account is similar to the explanation sometimes given by persons who have picked up white-tailed deer fawns that "the fawn followed us because it was lost." It is very likely a case of successful imprinting shortly after birth.

Imprinting has been observed in birds, too. It was recognized by Lorenz (1937) when he demonstrated that young geese and ducks become attached to whatever living creature they are first exposed to. Since that time, experiments have shown that ducks can be successfully imprinted to other species, man, and even mechanical objects (Figure 11-4).

11-2 PROTECTIVE BEHAVIOR AND FAMILY TIES

The protective instincts of the ruminant mother have been observed by many naturalists. In general, their accounts indicate that the female will actively defend her young against aggressors, whether of the same species or of another species. Peterson (1955), for example, relates an account of a bull moose coming between a cow and her calf, only to be driven off by the cow. Moose have been known to charge humans that were disturbing their young, but deer, elk, and caribou tend to step aside when human intruders appear.

The forefeet are often used for defense, and a blow from the hooves of deer or elk can cause serious injury. Several accounts of dogs having been killed by the hooves of elk are recorded in Murie (1951). Severinghaus and Cheatum (1956)

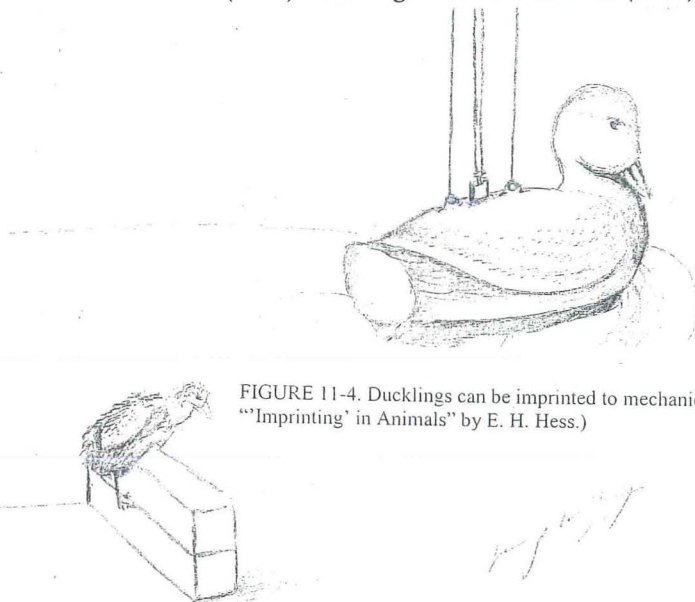


FIGURE 11-4. Ducklings can be imprinted to mechanical objects. (Adapted from "Imprinting" in Animals" by E. H. Hess.)

report that a Conservation Department employee observed a white-tailed doe chasing a red fox, striking at it with its front hooves as it ran.

The strength of family ties in wild ruminants is difficult to assess because of the few instances in which several generations have been tagged for field identification. It appears to be generally true that males are seldom a part of a family group; the bond between mother and young is much stronger. Further, the association between mother and young deteriorates during the breeding season. Nursing usually stops altogether, although the young may remain in close proximity to the mother. Moose cows seem to tolerate the presence of their previous young for a longer time than deer do, the young remaining until driven out by the pregnant moose cow just prior to calving.

The longer period of social attachment between mother and young for moose compared with deer is probably a reflection of the earlier breeding age of deer. Female white-tailed fawns can breed at the age of six months if they have been on a high nutritional plane, so they are capable of giving birth to their first young at the age of about one year. Moose do not reach sexual maturity until they are over a year old, and many do not breed until they are over two years old. This is also true for elk. Thus the completion of the weaning process, both nutritionally and socially, seems to be related to the sexual development of the young, but it is influenced to some extent by the reproductive condition of the mother.

11-3 MOVEMENT PATTERNS

The home range of any wild animal depends both on its behavioral characteristics, especially toward members of its own species, and on the physical and chemical characteristics of the habitat. Behavioral characteristics are difficult to quantify. Their effects can be measured, and some of them may be related to the density of the population. Seasonal changes occur in the reproductive condition of the animals and in the physical and chemical characteristics of the habitat.

The sizes of the home ranges of different wild ruminants vary widely. Some ruminants are migratory, while others remain in the same general area throughout the year or even for their entire lives. White-tailed deer seem to have one of the smallest home ranges of all the wild ruminants. The summer range of each individual is about one square mile, with little tendency for the animals to group together at that time. The doe and her fawn(s) form a family unit that is very close-knit both socially and nutritionally. They remain in close nutritional association until weaning and in social association until parturition approaches. Since the young of the previous year may have their own fawns if the range is in good condition, the tendency for separation of the doe and fawn is reinforced by parental instincts in both age groups.

Male white-tailed deer are quiescent during the summer. The antlers are developing, and the males seem content to forage, rest, and escape the flies and other insects that can be very bothersome. Relatively few observations of bucks in velvet are reported; they seem to be quite inconspicuous.

Seasonal movements of white-tailed deer vary considerably. Deer tagged in Minnesota have been relocated forty miles from the original site of tagging

(Blankenship 1957). Hawkins, Klimstra, and Autry (1971) observed that yearling bucks dispersed most widely from original trapping sites, with November being the principal time of dispersal.

White-tailed deer sometimes move several miles to a winter area of concentration. The triggering mechanism for the gregarious behavior is unknown. It is possible that reduced visibility causes deer to gather into groups (Moen 1966). Observers in prairie and agricultural habitats report that winter herds did form in certain areas, but up to 30% of the population remained dispersed throughout the winter (Sparrowe and Springer 1970). Some observers relate the yarding instinct to cold weather, high winds, or snow. The number of deer in a winter concentration area seems to be related to snow conditions inasmuch as deer may disperse during the winter if snow conditions do not inhibit travel. Large deer herds can be seen in late winter in many areas.

The daily activity patterns of white-tailed deer in Illinois were studied with the aid of radio telemetry (Montgomery 1963). The deer were active for 1 to 2 hours before sunset and continued to be active for an hour or so after sunset. Progressively more deer bedded until the peak of bedding occurred just before dawn in the summer. In the winter, with long nights, the peak of bedding occurred about 4 hours after sunset, following the activity period, with another bedding period before dawn. Undisturbed deer frequently bedded near their food supply. This was also observed by the author in Western Minnesota [(Moen 1966) and unpublished data] where the deer bedded in open fields near standing corn. Subzero temperatures did not cause the animals to bed in more sheltered areas.

Mule deer migrate between summer and winter ranges. The fall migration from the summer range at high elevations to the winter range at lower elevations seems to be coupled with a combination of weather factors. Storms and an accumulation of snow seem to be closely associated with the fall migration in some areas. The spring migration to higher elevations follows the snowline.

Elk are migratory and have a tendency to herd. Annual behavior patterns vary from the calving period when the cows are more or less scattered, through summer groups that become progressively larger and have a greater variety of individuals as the summer progresses, fall groups that are partly determined by the ability of the bull to maintain a harem, and winter herds that can include several hundred animals or more, depending on the winter range. The home range occupied by these different groups changes with time. In general, the area covered by elk is larger than that used by white-tailed or mule deer. This is reasonable because both the individual animal and the herd size is generally larger for elk.

The size of the home range of moose has been discussed by several writers and summarized in Peterson (1955). He suggests that an individual animal will likely remain within a radius of 2 to 10 miles for an entire lifetime, but that ecological conditions have an effect on the actual size of the home range for a given individual. It is fairly clear that moose are not migratory, and there seems to be little indication of territoriality. The fact that the animal has a large home range reduces the need for territorial instincts since the number of contacts with other members of the same species is small.

The widest-ranging and most gregarious of the wild ruminants is the barren-ground caribou. Caribou use forested winter ranges and barren-ground summer ranges. Kelsall (1960) describes the movement of one large herd over a period of 17 months. The daily and seasonal movements of the herd cover many miles, with individuals in a constant state of flux as they assemble, disperse, and reassemble in different locations with different individuals. Individual animals may shift from one herd to another as they travel, with some of the separations caused by reproductive conditions. Nonherding females and the males may travel farther during the calving season, with animals of all ages rejoining in herds for the autumn migration.

Snow seems to have a major influence on the movements of caribou. The animals move from areas of high snow density to low snow density, from high snow hardness to low snow hardness, and from greater to lesser snow depths. Wind is of considerable importance when insects bother the animals; Kelsall noted that the caribou took advantage of the wind to escape harassment. After the insect season, a pronounced dispersal was observed, with the herd spread over an area of 50,000 square miles in August. This dispersal included calves as well. Family ties were broken and new herds were formed as the animals herded up for movements to the winter range.

11-4 FEEDING BEHAVIOR

Wild ruminants forage for their food, combining this behavior with an alertness that is necessary for survival in the wild. Since they can feed at will, they do not reach the appetite levels of domestic ruminants from which feed is withheld until a certain time. However, daily feeding patterns for wild ruminants are fairly regular. Generally speaking, the animals feed actively in the early morning and in the evening. Feeding periods for white-tailed deer have been observed at noon or shortly thereafter, and there are also one or two feeding periods during the night.

Wild ruminants do not seem to be dependent on the availability of open water at all times. Snow is used as a substitute in the winter. During spring and summer, ingested forage is usually succulent and water requirements are partially satisfied by succulent vegetation. In addition, the vegetation is often covered by dew. The drinking periods seem to coincide generally with the daily feeding and activity cycle.

After eating and drinking, a ruminant usually lies down and ruminates. The food is regurgitated and chewed over again while the animal remains alert. Within groups of white-tailed deer, individuals usually lie in different orientations so that the group as a whole can see in all directions.

11-5 REST

The question of whether wild ruminants sleep has been debated often, but the answer seems fairly clear if the problem of semantics is avoided. If sleep is considered to be a resting mode with a marked reduction in alertness, then

white-tailed deer "sleep." This conclusion is based on my own field observations in which deer were seen placing their heads alongside their bodies and remaining unalert. Measurements of physiological parameters by telemetry have shown that the deer do indeed become unalert and sleep, especially in cold weather.

Murie (1951) describes an instance in which he walked up on a male Alaskan caribou that was resting quietly, its head drooping lower and lower until an antler rested on the ground. On another occasion a sleeping female caribou was actually captured and tied with a rope. He did not observe sleep in elk, but suggests that it probably occurs.

11-6 PLAY

Young animals play at times; this seems to be a normal part of the life of wild ruminants. Play activity in black-tailed deer was observed to decrease as the density of the population increased (Dasmann and Taber 1956). This may be an indication of social stress within the population. White-tailed fawns at the Bio-Thermal laboratory often start running in late afternoon, tearing around recklessly until they are panting heavily. Collisions do occur, but their agility is remarkable. Murie (1951) describes play activity in elk. A shallow pond is enjoyed by all ages, and erratic running has been observed in elk cows as well as calves.

11-7 SOCIAL ORDER

Social order in wild populations has been recognized by behaviorists for some time. The article by Watts and Stokes (1971) on wild turkeys in Texas is a lucid account of a very rigid social structure. The social structure of the Rio Grande turkey at the Welder Refuge is more rigid than that of the Eastern wild turkey inhabiting the Atlantic coastal states. Behavioral differences may be attributed to habitat differences; the authors suggest that habits of game birds of North America indicate that woodland species such as the ruffed grouse and spruce grouse are widely dispersed except during the mating season, while grassland brush inhabitants such as the prairie chicken, sharp-tailed grouse, and sage grouse live in large flocks. "The Welder turkeys . . . follow the grassland pattern of social organization, whereas the Eastern wild turkey, living in woodlands, favors small social units." Welty (1962) discusses various aspects of social behavior in birds, including songs, territoriality, and reproductive behavior. Social order in ruminants is well defined, particularly at certain times of the year.

DOMINANCE PATTERNS. The social structure of a deer herd is generally dominated by the adult doe. Family groups at the Crab Orchard National Wildlife Refuge are generally matriarchal, with the most common group consisting of an adult doe, her yearling daughter, and two fawns belonging to the older doe (Hawkins and Klimstra 1970). Doe dominance at feeding sites has been observed many times by several investigators, and often a larger number of does are trapped during

winter trapping operations because the dominant doe moves into the trap first to feed. A study in Maine, designed to expose the effects of different types of cover on the physical condition of deer, showed that the final condition of an individual deer seemed related to its position of dominance in the pen.

There are seasonal differences in the dominance pattern. Adult bucks exert a physical dominance during the breeding season. Male deer tend to form groups after the breeding season is over. This is apparently related to the reduction in the reproductive condition of the deer. It does not appear to be related to the time of the antler drop. Males in western Minnesota held their antlers well into March, but groups of 3 to 7 were common from January through the rest of the winter (Moen, unpublished data).

Elk tend to be more gregarious, and the social structure of a herd does not seem to be quite as separated as that of deer. The bulls assume a position of dominance during the breeding season, at least within their own sex group. Moose are quite independent and have little tendency to congregate. The size of the animal, with its concomitant high requirement for food, precludes the possibility of herding unless the animal migrates to new feeding areas as elk do.

Deer fawns are often thought of as physiologically inadequate to survive severe winters, but this may be due to their subdominant behavioral position. Verme (1965) states that "... exposure to icy gales can be fatal to nearly famished, completely unprotected fawns. A similar exposure of well-fed animals had little effect on their physical condition." He also states that deer often behave as though inadequate protection from bad weather is a greater peril than a lack of proper food. These observed responses of deer suggest that a very basic analysis of their energy exchange, such as that described in Chapters 6, 13, and 14, may provide a physiological basis for analyzing deer behavior in the winter.

11-8 RADIO TELEMETRY AND BEHAVIORAL ANALYSES

The description of behavioral characteristics has been greatly enhanced in the last decade by the use of radio telemetry. One of the earliest reports on the use of radio transmitters to locate free-ranging animals (woodchucks, *Marmota monox*, in this case) was published in 1958 by Le Munyan et al. Marshall (1962) used a radio-positioning technique for determining certain aspects of the activities of porcupines (*Erethizon dorsatum*). Both daytime and nighttime activities were observed using radio telemetry. Marshall and Kupa (1963) discuss the development of radio-telemetry techniques for ruffed grouse (*Bonasa umbellus*) studies, pointing out the potential of this approach for the analysis of an animal's reactions to weather conditions, food supplies, cover conditions, and other ecological considerations. Additional accounts of early work in bio-telemetry may be found in Slater (1963); species studied and described there include grizzly bears, woodchucks, porcupines, ruffed grouse, fish, monkeys, birds, insects, reptiles, and others. Additional references may be found in *BioScience* (1965; vol. 15).

An automatic radio-tracking system was developed at the Cedar Creek Natural History Area, University of Minnesota (Cochran et al. 1965), permitting continual

surveillance of the locations of animals. Signal characteristics can be interpreted to reveal something about their activity and behavior. This was used to advantage by Marshall (1965) when the movements of ruffed grouse caused the antenna to "whip," which resulted in corresponding changes in pitch in the audio signal. Observations of birds carrying transmitters permitted the field biologists on the project to equate signal variations with resting, walking, running, flying, feeding, and drumming activities. Loop antennae in collars show less signal variation than whip antennae, but many activities can still be determined from signal characteristics.

Radio telemetry systems can be designed to perform specific functions, including positioning by triangulation (Cochran et al. 1965), activity determination by signal interpretation, bioelectric potentials such as electrocardiograms and electroencephalograms (Mackay 1968), and physical factors associated with the animals such as sounds, light intensity, pressure, and many others.

Commercial instrumentation designed for the transmission of physiological data from humans can often be adapted to wild species. Equipment is currently being used on white-tailed deer to transmit heart rates and breathing rates. Close attention is paid to the activity and behavior of the deer during tests so that the signal can be interpreted properly (Moen and Jacobsen, unpublished data).

The suggestion that radio telemetry equipment be used in an ecological study often leads to the conclusion that the experimental work is now easier and less demanding inasmuch as the investigator can sit back and receive the data by remote means. Actually, quite the opposite is true. Radio telemetry permits much more efficient work in the field by providing a clue to an animal's location or physiological condition. Observations become much more meaningful, and the time spent in the field increases rather than decreases. So many new insights can be gained from field work with the aid of radio telemetry that the investigator tends to enjoy it much more, too!

A good example of the usefulness of radio telemetry is shown by the work of Mech et al. (1971) on the timber wolf. This wide-ranging animal is difficult to study because of its habits and life-style. Very fruitful studies of wolves have been conducted at Isle Royal National Park where the island naturally limits their range. On the mainland, radio telemetry becomes even more useful because of the greater possible variation in movement.

Their study in Minnesota combined visual observation with radio-locations. Visual sightings did not always result in day-to-day identification because most of the wolves were the same color. Five wolves carried transmitters emitting different frequencies, permitting individual recognition. Directional receiving antennae were attached to the wing struts of an airplane, permitting the investigator to locate the wolf by maneuvering the plane within visual sighting distance. The five wolves were located within time spans of 47 to 84 days before technical problems resulted in loss of signal.

Between 9:00 A.M. and 6:00 P.M., the wolves spent 62% of the time resting, 28% traveling, and 10% feeding. Resting was observed most often about noon. The wolves ranged several miles on most days, with the longest recorded straight-line

distance between two locations being 12.8 miles. This is an underestimation of the actual distance traveled, of course. The winter range of the five wolves bearing transmitters varied considerably. Some stayed in a relatively small area most of the winter while others moved to different areas. About 8% of the wolves were observed alone, with 92% of them sighted in a group.

The use of radio telemetry with aircraft tracking and observation is efficient if an animal such as a wolf, which may travel several miles a day is being studied. The technique is obviously limited to daylight hours, and it is also expensive. The cost per unit of information gained may be low, however.

Another study using radio telemetry techniques is described in Schneider, Mech, and Tester (1971), who used an automatic radio tracking system (Cochran et al. 1965) for tracking racoons (*Procyon lotor*). This resulted in a significant amount of information that could not be obtained by direct observation since the racoon is chiefly a nocturnal animal. The activity of the racoon was divided into three major phases: (1) from the end of winter dormancy until parturition; (2) from parturition until the cubs could travel with their mother; and (3) from the beginning of cub travel until winter denning. A fourth phase, covering the denning period, should also be recognized.

The telemetry technique was particularly successful in the racoon study because the young could be radio tagged, resulting in information on the social characteristics of the family group. An interesting aspect was the presence of temporary cub-cub and adult-cub liaisons that were repeatedly formed and dissolved. As the time for winter denning approached, however, the strength of the family bond began to increase. Family members bedded together more often, and in the last few days before denning they moved as a family unit. The entire family denned for the winter in the same tree or in a group of trees that were close together.

Recent advances in instrumentation make it possible to study free-ranging animals in much more detail than before. The student of analytical ecology should not feel that the use of instruments is necessary for successful ecological analyses, however. The significant part of any scientific investigation is the analysis of data and the use of the data in discovering ecological interactions. Work out these relationships through the use of simple models that depict the roles of several principal characters in the ecological theatre, whether they are insects, song birds, predators, game birds, or any other organism. As these relationships are worked out within the fundamental framework of matter and energy interactions, more use can be made of the ecological details that can be obtained with the aid of advanced instrumentation.

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IDEAS FOR CONSIDERATION

What energy and matter limitations are imposed on an animal that are reflected in its home-range or territorial characteristics? What is the relative importance of energy and matter compared with intraspecific interactions? Does food limit the size of the home range? Does the size of the home range vary in relation to the abundance of food? If food is plentiful, what minimum size can be tolerated in terms of intraspecific relationships? What seasonal variation in size is there in relation to variation in the abundance of food? How do the home ranges of predators depend on the abundance of prey?

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