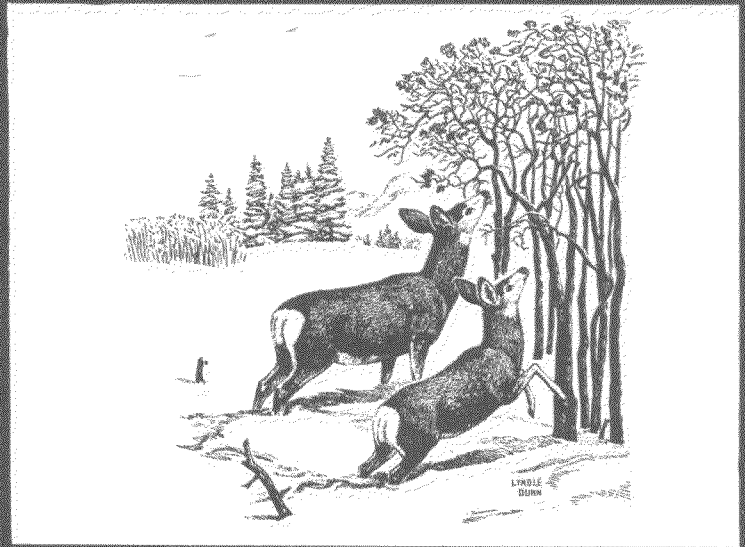


SPECIAL REPORT NUMBER 7 August 1966

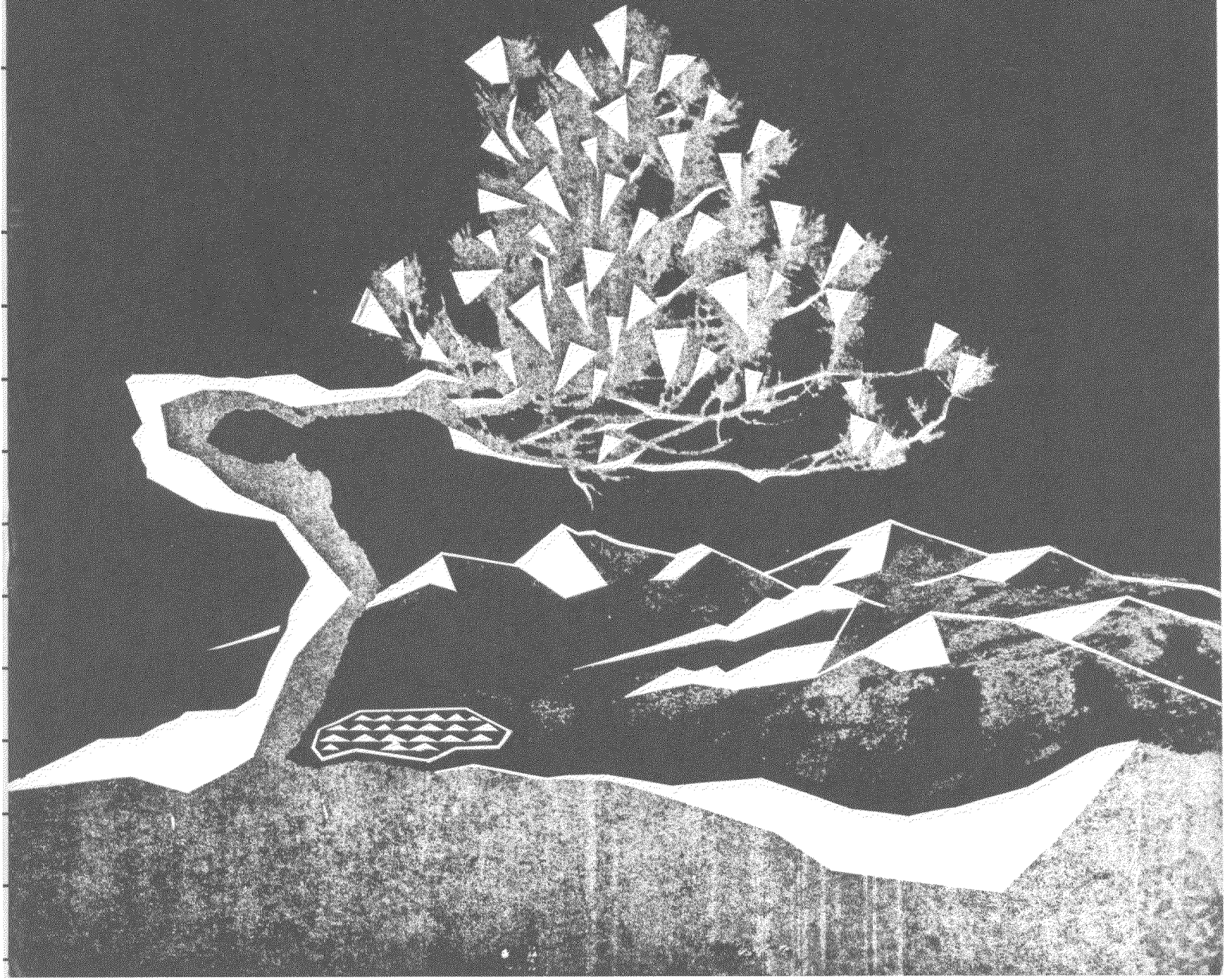
A LITERATURE REVIEW
ON BEHAVIOR OF
MULE DEER

by
MICHAEL J. DORRANCE



STATE OF COLORADO

DEPARTMENT OF GAME, FISH, AND PARKS
GAME RESEARCH DIVISION
AND
COOPERATIVE WILDLIFE RESEARCH UNIT



A Literature Review on Behavior of Mule Deer

by
Michael J. Dorrance

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State Publication Code GFP-R-S-7

Price \$1.00

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A contribution of the Colorado Cooperative Wildlife Research Unit and the Game Research Branch, Colorado Game, Fish and Parks Department, Federal Aid in Wildlife Restoration Project W-105-R

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Foreword

Big game hunting, as most of us have known it, will become more restrictive in future years. This will not be due to any shortcomings or negligence on the part of present game management in terms of overharvesting, but rather to the almost inevitable result of a combination of factors. These include an increasing human population, of which a possibly larger percentage may have more time for recreation such as hunting; an ever-decreasing quantity and quality of big game range, particularly the all-important and limiting winter range; and a necessarily reduced big game animal population to be sustained by this shrinking and deteriorating range.

It will then become necessary to manage big game on a much more refined approach than has been employed. Definite herd, range or hunting areas must be delimited based on intimate knowledge of the game species involved, as well as their habitat, and the impact of the hunting public on them. At this time harvesting will be restricted to allow the removal of a specific number of animals, and further, to the removal of designated individuals by sex, and possibly age. It is obvious that present data are not available in the detail necessary for such finite management, nor has it been necessary to manage on this basis heretofore.

Research is usually predicated on the needs of management, therefore, by the time that management realizes certain needs for immediate application, research many times produces results in a belated manner. It is for this reason that all research cannot be termed as "applied," but demands that a certain amount of "pure" research be conducted to supply background data to be available at the time it becomes needed.

Studies such as this one by Michael J. Dorrance on the behavioral aspects of mule deer will become applied at such a future time that a more intensive deer management program becomes necessary. It represents the initiation of consideration of behavior and social structure of mule deer herds in game management practices, and is one facet of the complex job of obtaining the data required for more refined management.

The implications of such a study are: (1) that hunting success may be increased by knowledge of particular herd habits in the use of cover and terrain; (2) numbers and sex of animals to be removed may be specified by knowledge of social structure and resultant potential productivity, and (3) areas of customary use may be rehabilitated by revegetation, fertilization or control of competitive foraging.

Dorrance's exhaustive research in the available literature, and the review presented here, mark a beginning in a field of future management on which relatively little has been done. This review was a preliminary phase of his original field work on the subject, and fulfills part of the requirements toward his Master of Science degree. Mr. Dorrance, as well as the agencies and individuals concerned with this publication, should be commended.

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A Literature Review on Behavior of Mule Deer

Introduction

Mule deer and black-tailed deer, Odocoileus hemionus, are natives to North America. The species originated from a primitive deer that is believed to have come from Asia. The mule deer evolved in the rugged badlands and mountains of the West. As pointed out by Cowan (1956b), mule deer are mammals of open forests and broken brushland on steep and rugged terrain.

Odocoileus hemionus is composed of 11 subspecies whose ranges extend from Great Slave Lake in the north to Tiburon Island and Cape San Lucas in the south; and from western Minnesota in the east to the Pacific coast on the west (Fig. 1; Hall and Kelson, 1959).

The subspecies, O. h. columbianus (Richardson) and O. h. sitkensis (Merriam), have the common name of black-tailed deer. The other nine subspecies are grouped under the common name of mule deer. Cowan (1956b, p. 339) listed the following common and scientific names for the 11 subspecies:

Rocky Mountain mule deer	<u>O. h. hemionus</u> (Rafinesque)
California mule deer	<u>O. h. californicus</u> (Caton)
Southern mule deer	<u>O. h. fuliginatus</u> Cowan
Peninsula mule deer	<u>O. h. peninsulae</u> (Lydekker)
Inyo mule deer	<u>O. h. inyoensis</u> Cowan
Burro deer	<u>O. h. eremicus</u> (Mearns)
Tiburon Island mule deer	<u>O. h. sheldoni</u> Goldman
Desert mule deer	<u>O. h. crooki</u> (Mearns)
Columbian black-tailed deer	<u>O. h. columbianus</u> (Richardson)
Sitka deer	<u>O. h. sitkensis</u> Merriam
Cedros Island deer	<u>O. h. cerrosensis</u> Merriam

Many people regard the black-tailed deer and mule deer as two separate species. However, Cowan (1956b, p. 339) stated:

"A detailed study had led the writer to conclude that these two races [O. h. columbianus and O. h. sitkensis] actually constitute a species in the making, partially segregated from the other races of blacktail by the peculiarities of their distribution and migratory behavior, but not yet differentiated to the specific level by the development of psychological, physiological or structural barriers to interbreeding."

The black-tailed deer and mule deer are, as yet, given only subspecies distinction. Behavior differences at the subspecies level were not apparent from the literature reviewed, with the exception of the description of aggressive behavior by Cowan and Geist (1961). For these reasons, I have not distinguished between the behavior of the black-tailed deer group and the mule deer group in this presentation.

The behavior studies herein included are concerned primarily with three subspecies. Clark (1953), Einarsen (1956), Browman and Hudson (1957), Bailey (1960), and Loveless (1964) were concerned with O. h. hemionus. Dixon (1934) and Cronemiller and Bartholemew (1950) studied O. h. californicus. Cowan (1945 and 1956a), Linsdale and Tomich (1953), Dasmann and Taber (1956a), Golley (1957), Taber and Dasmann (1958), and Anderson (1959) studied O. h. columbianus. It is worth noting that Linsdale and Tomich's (1953) book, A Herd of Mule Deer, is actually concerned with O. h. columbianus.

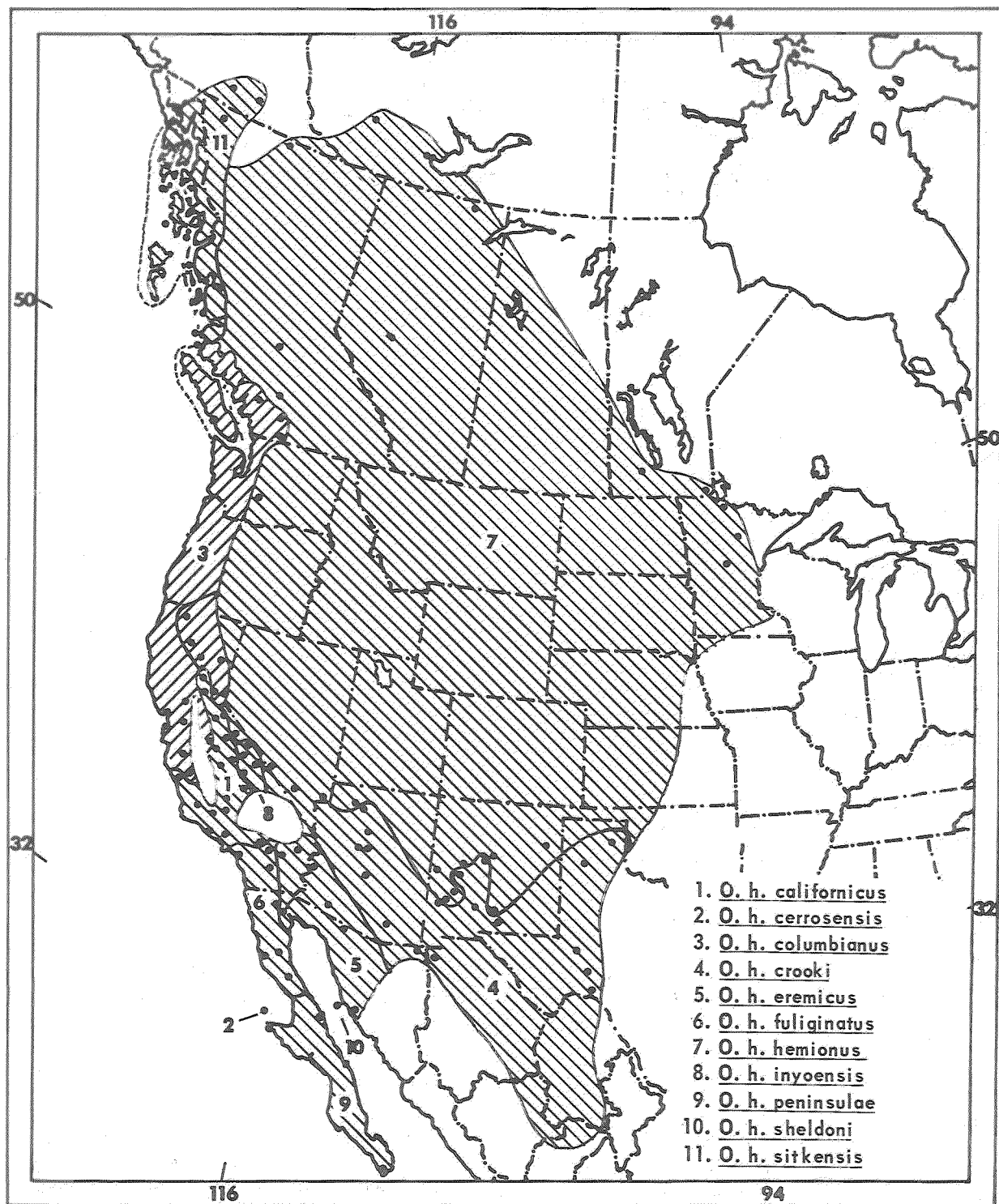


Fig. 1. Distribution of subspecies of *Odocoileus hemionus*. Map adapted from Hall and Kelson, 1959, for *Dama hemionus*. Nomenclature from Cowan, 1956b.

Daily Activity

Feeding Behavior

Deer may break off vegetation either with an upward or downward motion of the head when they are grazing. The cheek teeth can be used to sever woody vegetation (Cowan, 1945; Linsdale and Tomich, 1953). The lips are used to bring food into the mouth, while the tongue moves the food around. Deer commonly ingest twigs as large as 1/8 inch in diameter (Linsdale and Tomich, 1953).

Bailey (1960) described the feeding habits of deer in Montana on the winter range. Deer cover little distance while feeding and tend to move from one bush to another. An animal usually starts to feed in the vicinity of its bed soon after it gets up. Occasionally the first bites are taken without moving, but usually the deer will take two or three steps before feeding. Feeding behavior tends to be stereotyped. For example, a deer will feed on one shrub for several minutes and then will move to another. A second deer often follows the first for two or three stops.

Feeding activity tends to be infectious. Fawns often continue feeding while adults rest. Two or three fawns may feed near a resting adult. The adult may get up and start to feed and then another may get up and start to feed. The reaction may spread throughout the group. The completeness of the reaction probably is determined by how long the group has been resting (Bailey, 1960).

Cowan (1945) observed on Vancouver Island that deer prefer to feed with their front feet higher than their back feet. This results in heavier utilization of shrubs on the downhill side. Deer also seem to prefer hillsides to flat areas. Deer do not force their way into clumps of brush. Rather, they tend to feed around the margins. They avoid thorn-bearing plants and, according to Cowan (1945), also dislike seed heads of grass. Dixon (1934) and Cowan (1945) found that deer were able to tell good acorns from hollow ones and suggested that deer used their sense of smell to distinguish between them.

The most common feeding times are at dawn and dusk (Cowan, 1945; Swank, 1958; Taber and Dasmann, 1958). In summer the feeding periods are well defined as the combined factors of insects and heat often force deer to seek shelter during the daylight hours (Cowan, 1945). Deer were observed feeding at all hours of the day during the winter, although they were more active early in the morning and late in the evening than at other times of the day or night (Rieck, 1952; Swank, 1958).

Generally, the members of a group rest from mid-day to about one hour before dusk, at which time feeding becomes general. Cronemiller and Bartholomew (1950) reported that deer are not active during mid-day in the spring. However, pregnant does require more food and consequently spend more time feeding the few weeks before parturition (Cowan, 1945). Bailey (1960) found that deer on winter range in Montana feed from before daylight until between 9:30 and 11:30 AM. They then rest until they start to feed again between 2:00 and 4:00 PM, and continue to feed until after dark. Fawns feed longer than adults. Nearly every day, some fawns feed straight through the rest period.

Anderson (1959) found that deer in Oregon are active at night during the first four hours after sunset and the last hour before sunrise during the spring and summer. The number of deer that are active gradually decreases during the first four hours after sunset.

Resting Behavior

Deer examine a site thoroughly before bedding. They often lower their nose as if to smell the ground and search the site with their eyes. Less care is taken in choosing a bed on open ground than on litter, sticks, or stones. Deer paw the ground to scrape away loose litter or snow before bedding. Deer seldom paw at open grassy ground (Linsdale and Tomich, 1953).

Bailey (1960), while working on Montana winter range, found that each bedding period is initiated by some member of the group. Adult bucks are the first to lie down although bedding activity can be initiated by any member of a group. The resting response spreads outward from the resting animals toward the periphery of the herd. The speed and completeness of a resting response increases with the time a group has been feeding.

The pattern formed by a group of deer when bedding is random except as governed by the site. Deer facing in different directions provide better lookouts than several facing the same direction (Linsdale and Tomich, 1953).

Linsdale and Tomich (1953, p. 359) give a detailed description of deer at rest as follows:

"Deer ordinarily rest with the forelegs flexed beneath the chest, with the head up and slightly to one side, and with one hind leg exposed along the same side. In the time of resting, however,

they may assume a variety of attitudes by shifting the ears, head, and forelegs, or, less commonly, the entire body. Resting deer are not purposefully alert to their surroundings, but they rely on the involuntary function of the senses for information. A deer at rest in the daytime may occasionally lay its head back on a flank or hind leg and doze. The eyes are not fully open; the lids droop more or less, but sometimes open wide and then gradually close again. This is apparently as close to sleep as deer ever come."

During the winter, beds are located at the base of a tree or bush on the downhill side and parallel to the contour so the animal's body is level. Beds are located with a view of the slope below whenever possible (Bailey, 1960). Deer prefer a bed of dry leaves in a sheltered area to a bed in the snow (Dixon, 1934). Swank (1958) stated that in Arizona daytime beds are located in dense cover but without apparent choice as to site.

Dixon (1934) found that moonlight affects the choice of bed sites at night. Deer are inclined to bed in open, grassy meadows during dark nights but stay back in the trees during moonlit nights. Deer seek sunny spots to bed and change locations with changing shadows during cold weather (Dixon, 1934; Loveless, 1964). Bailey (1960) found that strong winds cause deer to pick sheltered bed sites. Deer may change beds when the wind changes on windy days.

Beds of deer conform closely to the size and shape of their bodies. With continuous use, beds gradually are worked deep into the litter. The scraping of leaves and soil to the downhill side produces a level floor on steep slopes (Linsdale and Tomich, 1953).

Deer apparently bed in the same general area each day and may use the same bed for several days in succession (Cowan, 1956a). Dixon (1934) felt that frequent interchange of beds by young deer had a direct bearing on the transfer of ticks from one deer to another.

There is general agreement among authors that deer have a major rest period during the middle of the day. Cronmiller and Bartholomew (1950) stated that deer generally rest from mid-day to about one hour before dusk during the winter in California. Clark (1953) stated that the heat of day in Arizona apparently caused deer to seek shade where they rest until late afternoon or early evening.

Linsdale and Tomich (1953) recorded 300 observations of completed rest intervals. The average length of rest for the 300 observations was 47 minutes. Approximately 94% of the rest periods were from 1 to 90 minutes long. Shorter rest periods 1 to 20 minutes long made up 26% of the total. There was a tendency for rest periods to become longer from January to mid-summer and then steadily decline until autumn.

Cud Chewing

A deer chews its cud through the rest period. Ordinarily the animal lies down but sometimes it stands. Linsdale and Tomich (1953, p. 430) described cud chewing as follows:

"A cud ball in regurgitation is clearly evident as a swelling that moves rapidly up the neck. Chewing begins immediately and continues until the food is swallowed. Swallowing is not perceptible, but there is a pause of a few seconds before the next cud ball rises. The deer holds its head slightly above the shoulder level as it chews cud. When the animal is chewing while at rest, its head is never laid out on the ground. The deer appears unalert as it chews. Its ears may droop nearly to the horizontal, or they may be held back. The forehead slopes at a moderate angle toward the ground. The eyes may be partly closed if the deer is relaxed."

Browman and Hudson (1957) observed that only 32% of 1465 observations on bedded deer showed cud chewing. Does averaged 54 chews per cud with a range of 47 to 62 chews per cud.

Use of Water

Deer are capable of attaining their moisture requirement from snow and seldom drink free water on the snow-covered portion of their range. Highly succulent vegetation also will relieve the necessity to drink. However, free water is required during the heat of the summer (Cowan, 1956a).

Swank (1958) reported that the peak of watering activity in Arizona was soon after sunrise and at sunset, with evenings preferred. Clark (1953) stated that deer in Arizona do most of their drinking after dark.

Home Range

Dasmann and Taber (1956a) gave an excellent discussion of home range, mobility, and territoriality in the non-migratory deer in the north coast range of California. The home range is an area normally occupied by a deer in feeding, resting, and escape activities. Maps of home ranges must be general, for a home range consists of a series of small feeding, bedding, watering, and escape areas connected by travel lanes. For this reason, the size and shape of a home range is variable.

Dasmann and Taber found that in California adult does occupied a home range with a maximum diameter of 700 to 1400 yards. An area 250 yards in radius within the home range accounted for 72% of all observations of adult does. The home range was contracted in winter for many does. Adult bucks were more mobile than does. A large percent of the home ranges fell within the 900 to 1400 yard diameter class. Only 53% of the sightings of bucks on their home ranges fell within an area 250 yards in radius. The home range of yearling males resembled that of does. Yearling females and fawns usually had the same home range as their mother and still associated with her. Similar observations were made by Linsdale and Tomich (1953).

Studies by Leopold, Riney, McCain, and Tevis (1951) of the migratory Jawbone deer herd in California showed that the winter home range of bucks averaged approximately 760 yards in diameter with a minimum of 300 yards and a maximum of 1800 yards. Does and fawns had an average winter home range of 320 yards in diameter with a maximum of 900 yards. The home range in summer averaged about twice that in winter.

Deer apparently have larger home ranges in Arizona. Clark (1953) found that the average home range for yearlings was 4.5 square miles with a maximum of 9.3 square miles and a minimum of 1.3 square miles. In the Arizona brushlands, Hanson and McCulloch (1955) found that the average home range was about 2 miles in diameter.

Deer will take advantage of a new food supply within their home range but will not move out of their home range to a new food supply (Taber and Dasmann, 1958).

Movement

Daily travel may be restricted to an area as small as 100 yards in diameter or may take in the entire home range (Dasmann and Taber, 1956a). Clark (1953) observed that pregnant does seldom moved over one-quarter mile from water. Hanson and McCulloch (1955) found that the daily cruising radius averaged nearly 1 mile. Deer frequently were observed to move 1/2 mile during a feeding period and up to 1 mile in flight.

Indirect evidence suggests that young deer may disperse to new areas although many may settle close to where they were reared (Dasmann and Taber, 1956a).

Migratory deer move to the same summer and winter range year after year (Leopold, et al., 1951). This also was observed on the winter range by Zalunardo (1955) and on the summer range by Siglin (1965).

Effects of Weather

Wind.--Loveless (1964) stated that wind velocity or direction apparently induced little reaction in deer in Colorado except during very cold weather. There seemed to be a tendency toward increased activity on days when winds were gusty. Deer sought sheltered places on days when temperature was low (15 F and lower) and wind velocity was high (25 mph and more). Bailey (1960) found that wind had no apparent effect upon feeding deer. However, beds were located in sheltered places if the wind was strong. Deer often moved to another sheltered location if the wind changed after they had bedded.

Rain.--Deer sometimes feed in open areas during light rain, but steady rain usually forces deer to take cover where they remain until the rain subsides (Linsdale and Tomich, 1953). Moderately heavy rain will keep deer in their beds the first day, but on the second consecutive day deer will be feeding even in heavy rain (Cowan, 1956a). Rieck (1952) stated that deer which are forced out of cover to feed walk stiffly about continually shaking the water from their bodies and flicking their tails from side to side in apparent discomfort. Bailey (1960) reported that rain apparently has little effect on deer on Montana winter range. Anderson (1959) observed a conspicuous lack of activity on nights following rainy days in Oregon.

Snow.--Loveless (1964) found that deer in Colorado showed no discernible reaction during snow storms. However, deer were rarely observed in exposed situations during heavy snow storms accompanied by high winds and temperatures below 10 F. Loveless (1964, p. 424) stated:

"Depth of ground-surface snow induced perhaps more response in deer than any other weather element with the possible exception of interacting air temperature and atmospheric moisture. Locations intensively used by deer, viz., south- and east-facing shrub types and open-timber shrub-understory types, had significantly ($\leq .05$) less surface snows than the other exposures compared."

Bailey (1960) observed that snow had little influence on daily activity.

Ground surface snow of 10 to 12 inches impeded deer movement, particularly yearlings. Depths of 20 to 24 inches essentially precluded use of an area (Loveless, 1964). Rieck (1952) observed that deer did not make definite trails in only 1 or 2 feet of snow in Oregon. They propelled themselves through deep snow by a series of leaps, covering approximately 50 to 150 feet at a time in this manner. They also walked in small creeks to

avoid floundering in deep snow. Sudden heavy snow storms caused deer in western Oregon to move from ridge tops into the canyons and then into brush or timber stands.

Loveless (1964) stated that excessive snow depths were apparently associated with the deer's tendency to concentrate. During periods of heavy snow, deer were observed in groups larger than ordinarily observed. Cowan (1956a) postulated that this tendency to gather under snow conditions may be a deep-seated trait of behavior which offers the advantage of numbers in establishing trails in deep snow.

Temperature. --Deer respond noticeably to fluctuations in temperature, particularly sudden increases or decreases. Evidence suggests that deer move from location to location on the winter range to seek the most "comfortable" temperature. In Colorado, this appeared to be about 15 to 45 F (Loveless, 1964). Taber and Dasmann (1958) stated that the favorite temperature of deer in the northern coast range of California appears to be between 55 and 65 F. Linsdale and Tomich (1953) stated that the lack of an extensive system of sweat glands which facilitates loss of heat, forces deer into the shade when the air temperature in the open areas goes above 80 F. In summer, activity is reduced in the early morning when the minimum temperature drops below 45 to 50 F.

Perhaps the "comfort" zone of deer varies considerably in different parts of the range as deer become acclimated to different temperature gradients.

Anderson (1959) found that night activity was greatest following days with high maximum temperature, and Loveless (1964) stated that nocturnal activity appeared to be reduced during extremely cold periods.

Linsdale and Tomich (1953) observed that deer erected the body hair as a means of insulating the body against cold. The hair was elevated at about 40 F and lower. This reaction was not exhibited during short periods of cold early in the morning in summer. Rather, this response occurred during the winter when the entire day remained cold.

Deer also will clamp their tail tightly against their body in response to cold (Linsdale and Tomich, 1953).

Relative Humidity. --Relative humidity is an artificial ratio and as such does not exist in the environment. Relative humidity shows a negative correlation with air temperature with a given air mass. Therefore, if animal behavior is associated with one element it must be associated with the other (Loveless, 1964).

Deer activity was reduced during periods of high temperature and low humidity, but deer activity increased during periods of low temperature and high humidity. However, low temperatures (25 F and below) and low humidity (20% and below) also were associated with a decrease in activity (Loveless, 1964). Similar results were obtained by Linsdale and Tomich (1953). However, Bailey (1960) found that deer in Montana rested a shorter time on days with low relative humidity than during days of high relative humidity. No obvious relationship was observed between temperature and activity. In Oregon, deer were most active on nights following days with low relative humidity (Anderson, 1959).

Light. --Loveless (1964) observed that on particularly cold days (0 F and below) deer sought direct sunlight. Under these conditions deer chose bedding sites located in the direct sunlight and moved to sunny locations with the changing shadows. During warm spring days (45 F and above) deer avoided direct sunlight by moving into the shadows and continually altered their positions to remain in the shadows. Similar reactions were observed by Dixon (1934) and Linsdale and Tomich (1953).

Taber and Dasmann (1958) reported that in early morning during the summer deer tended to follow the line of shade down the hillside. However, Loveless (1964) on winter range observed deer feeding immediately about the "sunshadow" on exposed aspects.

Buss (1950) and Anderson (1959) observed that activity was significantly greater during bright moonlit nights than during dark nights.

Individual Behavior

Gaits

Linsdale and Tomich (1953) recognized four natural gaits in deer movements, walking, trotting, galloping and bounding. Deer do not maintain one gait for long except when they are walking and then they make frequent stops. Deer move almost constantly when they are not bedded. They employ an ambling walk when feeding, but use a much faster pace in moving from one place to another when no feeding takes place. Steps are long and quick if walking is involved in aggression (Bailey, 1960). A stilted walk in which the body swings forward with each step is characteristic of an animal not yet aware of the cause of its fears (Linsdale and Tomich, 1953).

The trot is used in withdrawing from danger or when crossing open spaces (Linsdale and Tomich, 1953). Bailey (1960) stated that the trot is frequently used before a deer starts bounding and again after it stops bounding.

Bounding is used in sudden retreats and for clearing obstacles (Linsdale and Tomich, 1953). Deer occasionally use the bounding gait in descending very steep slopes (Bailey, 1960). Dixon (1934) stated that bounding temporarily gives deer a better vantage point from which to view a pursuer.

Linsdale and Tomich (1953) stated that a slow run, which is a kind of a gallop, is the most frequent gait of deer that are hurried but not frightened. Stragglers often gallop to catch up to a group.

Grooming

Deer groom themselves by licking, mouthing, or biting and by scratching with a hind foot (Linsdale and Tomich, 1953). Deer nearly always lick themselves on the hind legs or stretch after rising from a bed (Bailey, 1960). A deer dresses its coat by licking with firm strokes and gradually progresses upward on the body. A deer can reach its shoulders, forelegs, flanks, hips, loins, perineal region, and tail with the tongue (Linsdale and Tomich, 1953).

The head, neck, shoulder, and less commonly, the back are attended by mutual grooming. Does groom the entire body of small fawns with the exception of their underparts. Adults also tend to neglect their underparts. Deer bite at the neck and shoulders of other deer and chew small objects that may be ectoparasites (Linsdale and Tomich,

1953). Bailey (1960) did not observe mutual grooming between sexes. It most commonly was observed between a doe and fawn but also occurred between two males or two females.

Linsdale and Tomich (1953) stated that scratching is limited to self grooming. The hind foot is used in grooming the head and neck. The growing antlers may be used for grooming the perineum but hard antlers were never observed to be used for this purpose. Biting is used to relieve itching, to smooth or clean the hair, and to dress the base of the tail.

Deer frequently shake their ears and head in an effort to drive off flies. The skin can be vibrated by means of subcutaneous muscles (Linsdale and Tomich, 1953).

Senses

One sense is rarely used alone, but the sense of smell is used extensively by deer to verify something seen or heard (Bailey, 1960). Deer are able to discover the general direction from which scent arises, for they will retreat from an alarming scent without seeing its source (Linsdale and Tomich, 1953). Deer regularly find food by the sense of smell.

Hearing is well developed in deer and they possess a sharp directional sense for sounds. They generally try to supplement listening with other senses (Linsdale and Tomich, 1953). Clark (1953) observed that a dull noise often causes deer to investigate while a sharp noise or the sound of rolling rocks causes immediate departure. Riney (1951) found that deer apparently are able to recognize the familiar sounds in their environment. The distress cries of birds or the zone of silence around an intruder will cause deer to become alert.

Vision is less acute than hearing and is variable in usefulness. An undisturbed deer does not search for strange objects in its environment. Foraging deer select the general area by sight and then use the sense of smell to find food at close range. Deer recognize others of their species and other animals at a distance by sight (Linsdale and Tomich, 1953). However, Dixon (1934) believed that does are not capable of recognizing their fawns by sight alone. Deer are most sensitive to movement (Cowan, 1956a). A deer will follow a moving object by moving its head rather than its eyes (Linsdale and Tomich, 1953).

Elimination

Deer regularly void waste products at any time of day or night. Ordinarily they defecate after rising from a long rest and then urinate a few minutes later. In this interval of time, the animal usually has moved several yards from its bed.

A deer may defecate when walking, standing, or feeding, usually without modifying its activity. In defecation the tail is raised to a position which is almost vertical. The terminal 2 inches generally are raised 20 to 45 degrees less than the rest of the tail. After defecation, the tail slowly sinks to its relaxed, pendant position.

Deer interrupt feeding or traveling to deposit urine. Both females and males assume a squatting position with the back slightly bowed and slanted at a 45 degree angle. The tail is raised but not so high as in defecation. The end of the tail is not bent downward. Females usually raise the tail higher than males. Both sexes urinate on the tarsal glands by assuming a slight crouch with the feet close together (Linsdale and Tomich, 1953).

Head Bobbing

Linsdale and Tomich (1953) stated that deer sometimes bob their heads in response to a strange object or unidentified possible danger. The head is quickly lowered from well above shoulder level to near shoulder level and then rapidly returned.

They believed that deer do this in an effort to cause the object to move.

A deer may move its head from side to side when studying an unidentified object. The head is moved as much as 6 inches to one side, a frozen position is assumed for several seconds, and then the head is moved back to center or to the other side. This action may be repeated several times. Obtaining a view from several different angles may aid recognition (Dixon, 1934; Linsdale and Tomich, 1953).

Displacement Activity

Displacement activity is the performance of an action, often incomplete or imperfectly oriented which is the result of side-tracking of energy (Tinbergen, 1953).

Bailey (1960) observed the following two types of displacement activity: One displacement activity normally took the form of feeding. Usually a few stems were nipped off and eaten. Sometimes the twigs only were mouthed. This type of feeding was characterized by assuming the alert position at intervals of only a few minutes. It was observed to be precipitated by a man moving slowly toward the deer, by a wind change which caused deer to move from their beds, and by the howl of a coyote. The second displacement activity was observed when something startled a group of deer and one buck mounted another for a few seconds.

Intraspecific Behavior

Leadership

Linsdale and Tomich (1953), Dasmann and Taber (1956), and Bailey (1960) reported that an adult doe always led the family group. Bailey (1960) stated that a doe without fawns never was found to be the leader. However, in Arizona Clark (1953) observed that in mid-July yearling groups occasionally were accompanied by an adult buck or an adult doe without fawns. In these cases, the adult appeared to be the leader.

The leader determines the direction of movement and the travel route (Bailey, 1960). Unfamiliar situations are investigated by the leader. Taber and Dasmann (1958) most commonly caught adult does in single deer traps because the does were the first to investigate and enter the trap. In an organized retreat, deer form a single file with the leader at the head. If a group is startled, organization breaks down and the animals retreat without following the leader (Bailey, 1960).

Clark (1953) stated that one individual in each group acted as a rear guard. While other members of the group fed and moved about, this deer was more interested in watching in the direction in which they had just come. If the herd moved over a ridge, the sentinel stood for as long as 5 minutes watching the trail over which they had just traveled. No other author reported this behavior for mule deer although similar behavior was observed in red deer by Darling (1937).

No leadership was apparent in groups containing only bucks (Dasmann and Taber, 1956a; Bailey, 1960). The first buck to detect danger may flee without alerting the remainder of the group. These groups do not always hold together in common flight (Dasmann and Taber, 1956a).

Dominance

Dominance is determined largely by sex and age class. Bailey (1960) observed deer on winter range in Montana and found adult bucks dominant over adult does and yearlings. Yearling males are dominant over most adult does and all younger females. Fawns always are in a subordinate position. Adult males never were observed to drive fawns from food or resting places. Browman and Hudson (1957) made similar observations on penned deer.

Linsdale and Tomich (1953) found no clear conflict between adult bucks and does although occasional encounters between yearling bucks and adult does were observed. Minor encounters be-

tween fawns and yearlings were observed, but usually did not extend beyond the stages of threat, bluff, and withdrawal. Does were observed to protect small fawns from injury by yearlings but by midsummer does ignored attacks upon their young.

Dominance is displayed either with a threat or an attack. A threat may take several forms; tossing the head, standing still and lowering the ears, lowering the ears and extending the head toward the animal at shoulder level, or advancing a few steps or lunging forward. The attack involves striking with one or both feet. Sometimes the threat is accompanied by a series of throaty grunts. Distance between animals is an important factor in determining whether or not one deer will attack another. However, this distance may vary from a few inches to several yards (Linsdale and Tomich, 1953).

Dominance in buck groups is determined largely by size, with the largest the most dominant. Bucks that shed their antlers are dominated by smaller bucks that still carry their antlers. When all bucks lose their antlers the social order returns to what it was before the antlers dropped (Bailey, 1960). In family groups, the lead doe also is the dominant animal, even over yearling males (Linsdale and Tomich, 1953; Dasmann and Taber, 1956a; Bailey, 1960).

Displays of dominance have prominent seasonal aspects. Displays most commonly occur when does drive yearlings away prior to fawning, when maternal groups merge in the fall, and when bucks meet during the rut. At other times, tolerance is the general rule (Linsdale and Tomich, 1953). Dasmann and Taber (1956a) found dominance to be linked with territorial behavior in does during the summer. Does protected their territory from invasion by surrounding does. Dasmann and Taber (1956a) also found that conflict increased with deer density.

Bailey (1960) observed that animals of high status had first choice of food and beds. However, subordinates did not wait for dominant animals to feed or to bed. The claiming of the feeding or bedding spot usually was done without assuming the aggressive pose. The dominant animal ordinarily walked up behind a subordinate and struck once with a front foot without rearing. A second blow followed if the first had no effect. The subordinate then left the feeding or bedding spot. Bailey (1960) speculated that survival potential varies directly with social status. Since fawns were found lowest in dominance, they had the

smallest chance for survival. Bailey (1960) found no connection between dominance and leadership, and established feeding or resting territories.

Play

Play is displayed predominantly by fawns, although yearlings and adult does participate occasionally. Adult bucks ordinarily do not play. Play is prominent in groups of deer which are feeding during mornings and evenings (Linsdale and Tomich, 1953). Anderson (1959) observed that deer appear to spend considerably more time playing on nights after cloudy or rainy weather. Play usually lasts from one to three minutes and then stops suddenly. The more active part of play usually does not exceed two minutes (Linsdale and Tomich, 1953). Play usually takes the form of active scampering and jumping about by individuals or games of chasing and "tag" involving two or more deer (Dasmann and Taber, 1956a).

Dasmann and Taber (1956a) found that play decreased as density of animals increased. They believed that play probably indicated an excess of energy. Linsdale and Tomich (1953) stated that play appeared to serve as practice for later and more serious encounters with predators. The need for activity by fawns may be a reason for the frequent occurrence of play among them. Fawns are restricted to a rather small sphere of activity by their dependence upon the doe. Vigorous exercise in a small area tends to develop into game-like activities.

Communication

Linsdale and Tomich (1953 p. 99) stated that:

"Any mark or movement by a deer that arouses some other animal to action is a signal. There are possibilities for signaling in tail position, tail switching, ear position, hair bristling, stance, and movement. Motion is not necessary, but it makes the sign more effective."

Bailey (1960) stated that the chief form of communication in deer appeared to be the pose, aspect, or posture of other deer. Linsdale and Tomich (1953) found that the response to movement by other deer seemed to be general rather than specific for each type of movement.

The alert position with the head raised, neck erect and motionless, and ears cupped forward, will alert individuals near by. However, the stance of the individual that is first alerted does not communicate to other deer the direction of the cause of alarm (Linsdale and Tomich, 1953; Bailey, 1960). The attention of the deer tends to be focused toward whatever direction they are facing before they become alert. The intensity of the alarm

wanes more quickly in deer that have not determined the initial source of disturbance (Bailey, 1960).

Linsdale and Tomich (1953, p. 102) stated that:

"Raising the hairs on the sacrum conveys a message to other deer. We have not seen how this causes a response. Possibly it is useful mainly as a threat and often only incidentally occurs along with other accompaniments of excitement."

The position of the tail may serve as a means of communication. Tail switching of an involuntary nature is frequent among feeding deer and commonly takes place when activity changes. The position of the tail may induce a response in other deer during aggressive movements or play (Linsdale and Tomich, 1953).

The threat pose, with neck stretched forward and level with the back, ears laid back along the neck, mouth open or closed, and front feet spread apart, will induce a specific response in deer. Subordinate animals readily associate this position with aggression (Linsdale and Tomich, 1953; Bailey, 1960).

Sudden movement may serve as a type of communication among deer. A deer rising suddenly from its bed will cause others to become alert. Trotting and bounding also will cause alarm among other deer (Linsdale and Tomich, 1953). The strength of the flight stimulus resulting from a bounding deer decreases with distance. Deer closest to a bounding deer may run a short distance. Deer further away become alert and walk a few steps, and deer still further away only become alert (Bailey, 1960). The stiff-legged walk of an alarmed individual also will cause an associated group of deer to become alert.

Scent may serve as a possible means of communication. However, there is no way at present to ascertain the many occasions in which it could be used.

Sound frequently accompanies visual signals. Deer remain within a relatively limited area in one day. Therefore, there is little need to convey signals to distant animals. Most sounds and signals are effective only at close range.

The snort is produced by expelling air through closed nostrils, causing them to vibrate and is a common sound to the deer hunter. It is frequently given by deer before retreating or when approaching suspected danger (Linsdale and Tomich, 1953). Cowan and Geist (1961) described the snort as it is used in aggressive behavior of *Odocoileus*

hemionus hemionus, O. h. sitkensis and O. h. columbianus. In its simplest form, the snort is used in aggression by all three races as a buck circles his opponent. However, Rieck (1952) stated that the Columbian black-tailed deer in western Oregon has no sound comparable to the loud snort of the white-tailed deer. Linsdale and Tomich (1953) believed that deer use the snort in some cases to test the nature of unidentified objects. The snort could startle animals enough to cause them to move. They also stated that the snort may serve as a warning to other deer.

Clark (1953) described three main classes of vocalization: the bark, snort, and bleat. He stated that the first two were used as warning calls to other deer in the vicinity. This would indicate deer made an effort to convey the presence of danger to other deer.

Linsdale and Tomich (1953) stated that deer respond to snorting on some occasions by becoming alert or departing. Snorting is closely associated with wariness. Does readily snort, but bucks are more likely to retreat without vocalization.

Several authors (Dixon, 1934; Rieck, 1952; Clark, 1953; Linsdale and Tomich, 1953; Cowan, 1956a; Einarsen, 1956) have observed does calling their fawns. Dixon (1934) found that does may call their fawns from hiding by using a note that is just loud enough to carry the few yards from the doe to the hidden fawn. Vocal communication between the does and fawns continue as long as they remain together.

Linsdale and Tomich (1953) reported that fawns produce a soft one-syllable bleat with the mouth closed and a louder two-syllable bleat with the mouth open.

After fawns have gained noticeable initiative in wandering with their mothers, they frequently become lost. A lost fawn will bleat and can be heard for considerable distance. In her gradual movement while feeding, the doe sometimes is unaware that her fawn has strayed. In such cases, the doe pays no attention to the bleating even if it is close. Evidently a fawn's bleat has no individual characteristics. However, if a group is scattered suddenly, the doe quickly will call her fawn or answer their "mewing" (Linsdale and Tomich, 1953). The reaction of the doe to the calling of a fawn is evidenced by the ability to attract nursing does with a deer call (Benson, 1948; Diem, 1954). Diem used a call which closely imitated the sound of a bleating fawn. A doe quickly would leave the area if a call was used when fawns were not in her presence. If fawns were present the doe would trot off only a short distance or she might even advance toward

the caller. She would act irritated by stamping her feet and switching her tail. Benson (1948) was able to call does but not bucks. Does were excited by the distress element in the call, although the call did not resemble the bleat of a fawn.

Lindzey (1943) described the call of a captive fawn as an "eep" which was audible for about 1/4 mile. When frightened this call developed in a squeal similar to, but more throaty than that of a wounded rabbit.

Deer are capable of uttering grunts of varying intensity. These are used in several different situations. During the rut a buck may sometimes use his voice to frighten a competing male away from a doe (Dixon, 1934). Linsdale and Tomich (1953) reported that bucks in breeding condition utter repeated, low, short, strained bleats. An enraged deer may make a grunting bellow or bark at the height of an aggressive movement. The sound seems to be a threat or expression of rage.

When mortally wounded, deer often emit a high-pitched scream (Dixon, 1934; Cahalane, 1947). Deer give a variety of sounds if trapped and handled by man. They may moan, bleat in a high pitch, or bellow with rage (Cowan, 1956a).

Clark (1953) described a bark in deer that is similar to the short bark of a dog. This call frequently was noted when deer were surprised. One or more deer emitted the short bark at intervals of 5 to 10 seconds. As soon as the deer were able to discern the cause of alarm the calling ceased and the deer immediately left the area. This is very similar to the description of the bark of the red deer given by Darling (1937).

Deer may be alerted by the sound of another deer bounding away. An alerted deer may stamp one or both front feet upon the ground. The forefoot is raised slowly and then brought down sharply. This by itself has little effect upon other members of the group although it may serve as an animator. Stamping may be accompanied by snorting. Possibly stamping is an expression of impatience. Stamping both feet together is a movement of aggressive defense or threat and resembles an attack which is climaxed by striking with both feet (Linsdale and Tomich, 1953).

Communication may be interspecific as well as intraspecific. Riney (1951a) found that a sudden change in the activity of birds could cause a response in deer. The silence that often surrounds intruders could cause deer to become alert. When birds returned to normal behavior with their accompanying sounds, the deer also returned to normal, undisturbed activity. However, the reaction of deer to the sounds of birds varied from

mild curiosity to headlong flight and changed with individuals, sex and age classes, and seasons.

Sociality

After reviewing the literature, it appears that the deer of North America can be arranged in the following order from most to least social: Barren-ground caribou, elk, mule deer, white-tailed deer, and moose. Dasmann and Taber (1956a) stated that deer which characteristically inhabit dense cover usually form small groups or are solitary. Herds are typical of species that inhabit open areas of grassland or tundra.

Linsdale and Tomich (1953, p. 168-169) stated that:

"Mule deer have a marked propensity to assemble into groups. However, under certain circumstances, they show an opposite tendency toward solitary existence. Their proneness to congregate, or not, at any given time, is the result of the relative strength of these opposite traits. Thus, their gregariousness is modified seasonally as well as for reasons of age and sex. We commonly see a deer alone, but if we watch one for several hours, we see that it comes near to others. Does with small young are often by themselves, and they ordinarily forage independently while the fawns rest. Older bucks are likely to be solitary at any time of year. They may occasionally encounter other deer, but not as close associates. Aloofness from other deer, however, is not a prominent characteristic of the males."

At the end of winter and beginning of spring the family group commonly consists of one or two yearlings, one or two fawns and a doe. The yearling bucks often are the first to leave the female. They drift off and join a buck group. Yearling does leave the group between mid-winter and spring (Dasmann and Taber, 1956a).

The doe rarely demonstrates intolerance toward her last year's fawns in the few weeks before parturition although just prior to parturition the doe will turn on her fawns and attempt to drive them off (Linsdale and Tomich, 1953; Cowan, 1956a). Yearlings frequently act confused at these attacks. The doe is persistent in her attacks and finally is left to herself.

After being driven off by their mother, yearlings frequently join other pregnant does until they again are driven off. Yearlings also may appear singly, in couples, or in small bands (Linsdale and Tomich, 1953). Yearling black-tailed deer of the northwestern United States characteristically form

pairs and can be seen throughout the summer and as late as the onset of the rut. Cowan (1956a) presented data which indicated that the members of these pairs may not be limited strictly to twins.

Linsdale and Tomich (1953) found that the doe and new-born fawns remain by themselves for the first few weeks. During this time they may encounter other deer and sometimes will mingle with them. Does appear to be tolerant of one another but will not tolerate yearlings near their fawns. However, Taber and Dasmann (1958) stated that pregnant does and does with fawns are antagonistic toward each other.

As summer progresses, the does gradually allow the yearlings to run freely with them and their fawns (Linsdale and Tomich, 1953; Dasmann and Taber, 1956a). In some groups, the yearling bucks still are subject to antagonism, but in others they are accepted readily (Dasmann and Taber, 1956a).

In the fall and winter, deer become more social, forming large groups of various sizes. In Montana, deer arrived on the winter range in two general types of groups: an adult doe with her fawns, or one to three does with their fawns plus one to five yearlings. Bucks older than yearlings were absent from these groups. Adult bucks formed their own groups of between four and six animals, although they often remained solitary. Occasionally an adult buck would join a family group. Resident deer tended to form bands apart from the migratory deer (Bailey, 1960). Linsdale and Tomich (1953) found similar behavior during the winter in non-migratory deer in California. Several maternal groups temporarily joined into evening feeding groups that often contained 10 to 20 animals. These groups maintained an all-day association in the winter and spring which became almost permanent. Similar associations were observed by Dixon (1934) in California.

In Montana, feeding groups merged to form large bands numbering up to 100 animals towards the end of the winter (Bailey, 1960). Bailey's data indicated that the wintering groups were relatively stable. Individuals seldom shifted from one group to another although groups merged to form larger groups. Dasmann and Taber (1956a) found that several family groups banded together to feed. This was most common in the spring. These groups bore superficial resemblance to a social herd but each small unit maintained its integrity. Conflict often resulted between groups. At the end of each feeding period, each group frequently went its own way without reference to the activity of the others. As previously stated, the family group gradually breaks up in the spring and the cycle is started over again.

Male sociality is different enough to warrant separate consideration. In summer, two or three males may travel together, although most are solitary. Males temporarily may join a family group at any season of the year. Bucks commonly are found with does during the breeding season (Dasmann and Taber, 1956a).

Bailey (1960) found that bucks on the winter range in Montana formed groups of four to six animals although bucks often remained solitary or joined family groups for one to several days. Clark (1953) made similar observations in Arizona. Cowan (1956a) stated that the normal size of the groups of bucks was from two to four individuals but varied from two to eight. The bucks in a group bedded and moved together during all seasons. Even during the period of the rut, large, swollen-necked bucks in the same groups can be observed picking ticks off each other, and according to Cowan, 1956a, most of the fighting is between bucks of different groups. Rieck (1952), however, stated that bucks have solitary habits but occasionally can be seen in groups of one to three. Usually bucks of the same size and age class were observed together. Large males were observed to guard their territory from intrusion by smaller males; however, it was not clear how Rieck defined territory.

Young bucks occasionally leave the family group in the spring as they approach one year of age, but more commonly, bucks leave the family group a year later (Dasmann and Taber, 1956a).

Pre-fawning Behavior

Linsdale and Tomich (1953) observed that heavy does can be very active and are capable of leaping fences. When alarmed a pregnant doe generally will withdraw at a steady trot. However, Dixon (1934) found that does far advanced in pregnancy were much more sedate and did not bound about as they might at other times of the year. Golley (1957) found this period to begin in captive deer about one month prior to fawning. Clark (1953) reported that does move very slowly and would move faster than a walk only under the severest stimulus. In Arizona pregnant does seldom moved further than one-quarter mile from water in the period just prior to parturition (Clark, 1953).

Fawning Behavior

Linsdale and Tomich (1953) stated that does usually retire from open areas and move into thick cover to give birth. They frequently seek a place that is brushy or wooded. This often is the place where they rest. Dasmann and Taber (1956a) and Lindzey (1943) made similar observations. Einarsen (1956) stated that does prefer a place of concealment on the margins of meadows or open glades. Dixon (1934) found considerable variation

in fawning sites in California. In Sequoia National Park deer often selected an area near the base of a giant sequoia (*Sequoia gigantea*). In San Diego County, deer frequently were found to give birth under or near some brushy thicket or even in a rock pile.

Golley (1957) made observations of 11 does while they gave birth. Six gave birth in the morning, one at noon, and four in the evening. Three captive does on Saltspring Island, British Columbia, gave birth at 9 AM, 11 AM, and 4 PM (Cowan, 1956a). Einarsen (1956) stated that many fawns found in the forenoon were still wet if they were less than a day old. This would mean that young often are born in the morning.

Post-fawning Behavior

Golley (1957) found that does spent considerable time licking and cleaning their fawns the first day after birth. This cleaning activity continued throughout early life.

Although fawns were not observed to begin nursing immediately after birth, they did make feeble attempts to find the udder of the mother (Golley, 1957). Dixon (1934) observed a doe with a fawn he thought to be less than one and one-half hours old. The fawn was wet and too weak to walk. The fawn dragged its hind legs feebly as it tried to crawl about. Linsdale and Tomich (1953) stated that newborn captive fawns crawled and aggressively attempted to nurse. The doe lay down beside the fawn for the first nursing, but thereafter the doe and fawn stood. Dixon (1934) believed that the prone nursing position provided greater safety for both the doe and fawn.

Fawns are able to move about a few hours after birth, but generally lie quietly. They readily follow the doe to new sites the first few days after birth. It appeared to be regular practice for does to lead the fawns to different parts of their feeding area (Linsdale and Tomich, 1953).

Golley (1957) found does definitely antagonistic toward fawns other than their own in a captive herd. However, Linsdale and Tomich (1953) stated that does usually ignored strange fawns. This behavioral difference might be the result of the change from natural conditions to captive conditions or it might be a subspecies difference.

Fawns escape detection and pursuit when young by crouching in the grass with their necks outstretched and remaining motionless. However, they normally lie with their head turned back and resting on their body (Dixon, 1934).

It is wholly the duty of the doe to remember the location of the concealed fawn for the first few

days. The fawn exhibits little initiative in finding its mother. However, fawns remain in almost the exact spot in which they are left for the first few days. Fawns will come to a doe when she approaches to within 60 to 80 feet of the hiding place at the age of 3 or 4 weeks. By the time fawns are 5 or 6 weeks old they may go to a doe when she is as far as 150 yards away. The doe takes no part in concealing the fawn, although she may lead the fawn from open ground after the nursing period (Linsdale and Tomich, 1953) and may call the fawn from concealment by using a low bleat. Vocal communication is not necessary at all times. A doe returning to her fawns may signal them from concealment by her presence and her attitude. In approaching fawns, a doe almost always walks slowly and hesitantly with her ears forward and her neck extended horizontally. Strange deer passing the fawns cause no response from them, possibly because of a different manner of movement. As the fawns become older and increasingly more alert to the approach of the doe, they often go to her voluntarily (Linsdale and Tomich, 1953).

A doe with more than one fawn ordinarily does not hide them together. They may be from a few feet to several hundred feet apart (Dixon, 1934; Einarsen, 1956). Fawns remain hidden for only 1 or 2 days after birth. After 3 to 5 days the fawns constantly remain with the doe and seldom does the doe bed further than 30 feet from her fawns (Clark, 1953).

The doe and her fawns run in different directions when flushed and the fawns hide at the first opportunity (Cowan, 1956a). Clark (1953) found the doe may utter a bleat when flushed. This may have been a sign for the fawns to escape. He observed that fawns run uphill if possible.

When a person is near a hidden fawn, the behavior of the doe indicates its presence. The doe does not retreat far. The doe will not attack a man near its fawns but will maintain a close watch and will exhibit extreme agitation (Linsdale and Tomich, 1953).

The fawn frequently walks in between its mother's forelegs and nurses with its tail to the doe's head. The action of a fawn nursing is similar to that of a domestic calf. There is frequent stimulation of the udder by the nudging and butting action of the muzzle of the fawn. Twins show no antagonism toward each other when nursing. The fawn approaches a doe with its tail raised stiffly vertical. Sometimes the fawn's tail moves from side to side. This may serve as a signal to another fawn that is not aware of the opportunity to nurse.

The doe shows considerable interest in the nursing fawn during the first few weeks but later merely stands quietly. The fawn voluntarily terminates the nursing period during the first few weeks but thereafter the doe leaps away from the fawn to end the nursing interval (Linsdale and Tomich, 1953).

Cowan (1956a) observed that fawns were nursed only at night or at least not until early evening during the first week. However, Linsdale and Tomich (1953) stated that fawns nursed regularly 1 to 3 hours after daybreak, although nursing could take place at any time with the possible exception of the late part of the night (Fig. 2, p. 15). Fawns are nursed at irregular intervals. Linsdale and Tomich (1953) found that in 14 observations, the average time between nursing periods was 276 minutes. The longest interval was 461 minutes and the shortest was 95 minutes. Clark (1953) stated that fawns nursed every few minutes after they were old enough to follow the doe as she moved about and browsed.

Einarsen (1956) found that nursing periods are quite long with each taking from 4 to 15 minutes. However, Linsdale and Tomich (1953) observed that nursing sometimes lasts only a few seconds and at other times may be drawn out over nearly an hour through several periods of nursing (Fig. 3, p. 15). The longest nursing periods occur when the fawn is small. Nursing periods gradually shorten as weaning approaches. Possibly the difference noted between Einarsen (1956) and Linsdale and Tomich (1953) resulted from different observation techniques.

Weaning takes place at approximately 2 to 2 1/2 months of age (Dixon, 1934; Clark, 1953; Taber and Dasmann, 1958). The does do not stand still when the fawns try to nurse at this time. Dixon (1934) believed that failure to wean is detrimental to both the doe and fawn in that they enter the winter in poor condition and are more prone to winter kill.

Cowan (1956a) stated that a 48-hour-old fawn was observed nibbling on grass. However, it is unlikely that any appreciable quantity of vegetation is taken during the first three or four weeks. Einarsen (1956) reported that captive fawns sample green vegetation at 15 to 20 days of age. Fawns take green food regularly and chew their cuds long before they lose interest in nursing. Clark (1953) found that fawns take green vegetation at 2 weeks of age and hard food such as mast and seedy fruit after 1 month.

Dasmann and Taber (1956a) stated that fawns were inexperienced at searching for good food. They sampled a wider range of plant species than did adults. This could be a handicap on poor range

since their diet is not the best and they are poor competitors with adults.

Taber and Dasmann (1954) reported higher mortality in male fawns than female fawns in California. This mortality resulted from starvation, accidents, and predation. They attributed the difference in mortality to greater curiosity, activity, and independence in male fawns. This independent behavior often caused them to investigate situations without waiting for experienced leadership from their mother.

Territorial Behavior

Dasmann and Taber (1956a) believed that territorial behavior was present in black-tailed does in California. Also, Graf (1956) indicated a belief that black-tailed bucks exhibit territoriality. Dasmann and Taber (1956a) observed that the centers of activity for adult does with fawns were

spaced evenly and were separated by at least 150 yards. The principal reason for the spacing appeared to be mutual antagonism. They found that the frequency of association between adult does increased in late winter and early spring and territorial behavior disappeared until the birth of new fawns. The centers of activity for adult bucks showed a tendency toward aggregation. No territorial behavior was observed in bucks. However, Graf (1956) suggested possible territorial behavior of bucks in Washington. He believed that the primary purpose of antler rubbing was the construction of sign posts and these represented an expression of territoriality.

Rutting Behavior

Linsdale and Tomich (1953) concluded that the sexual season represents a brief terminal phase of the whole hypophyseal-gonadal cycle. They believed it is initiated by the increasing daylight of

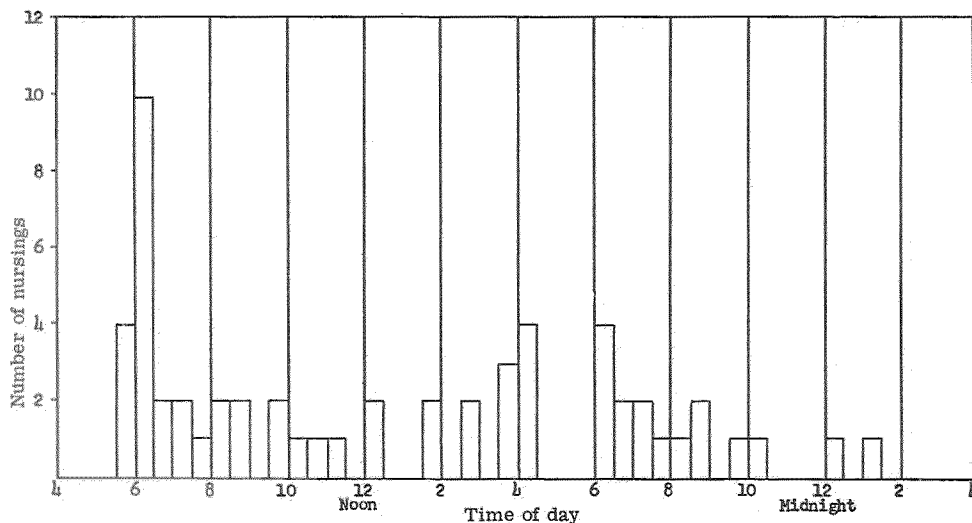


Fig. 2. Time of day by half hours at which 57 nursing periods began, in the 24-hour period and for all months (Linsdale and Tomich, 1953, p. 539).

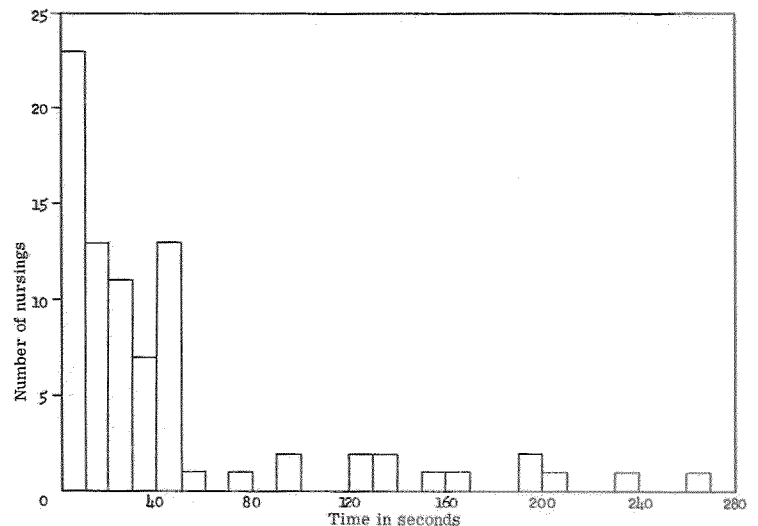


Fig. 3. Lengths in seconds of 84 nursing periods by 10-second classes (Linsdale and Tomich, 1953, p. 540).

spring and early summer. The fall rut comes in conditions of diminishing light. Cowan (1956a) stated that field observations indicate breeding activity is initiated by climatic conditions in the spring of the year.

The initial stage of the rut is marked by loss of wariness in adult bucks and they frequently appear agitated and anxious (Linsdale and Tomich, 1953). Bucks urinate on their tarsal glands and rub them together at all seasons of the year but this habit increases in frequency during the rut (Linsdale and Tomich, 1953; Cowan, 1956a; Browman and Hudson, 1957). Linsdale and Tomich (1953) believed that urinating on the tarsals constitutes a type of threat during the rut that is not conveyed at other seasons. This activity usually took place in the presence of other bucks, yearlings, or fawns.

Bucks "test" fresh urine of the doe during the rut. They smell or lick fresh urine, raise their head, elevate and wrinkle their muzzle, and slowly wave their head from side to side (Linsdale and Tomich, 1953; Cowan, 1956a; Browman and Hudson, 1957; Golley, 1957).

Linsdale and Tomich (1953) found the most characteristic display of a buck in the presence of a doe is a sudden depression of the head as the buck starts toward or when the buck faces a doe. The buck suddenly raises his head to shoulder level or above when he stops after walking towards a doe. He immediately bobs his head back to shoulder level.

Bucks beat and twist small limbs and bushes with their antlers early in the fall. Cowan and Geist (1961) believed the most important prerequisite for sham-fighting to be a yielding object. Seldom were antlers used against heavy stumps, stones, or large tree trunks. Dixon (1934) observed an adult buck chew off strands of velvet hanging from his antlers. Linsdale and Tomich (1953) found that bucks continue to polish their antlers long after the velvet is removed. Bucks also rub the basal parts of their antlers against limbs or small trees. Thrashing and rubbing take place at the same time. They believed that antler rubbing may provide practice for later contests between bucks, although antler rubbing may have become so formalized as to be engaged in for its own sake. Dixon (1934) suggested that saplings regularly used for antler rubbing by a number of bucks may serve as "intelligence posts" similar to bear trees.

Cowan and Geist (1961) described the aggressive behavior of three races of Odocoileus hemionus. Preliminary to actual contact, a buck would

crouch, lick its nose, circle, snort, and finally rush its opponent.

Linsdale and Tomich (1953) stated that combat does not usually develop beyond the stage of sparring. More often, it develops into a pushing contest with each opponent attempting to throw the other off balance and push him backwards. Dixon (1934) believed that the object of sparring is to push the opponent backward and cause him to bend his neck. The sharp terminal points of the aggressor's antlers then project far enough beyond the opponent's guard to gouge his eyes, ears, and neck. He stated that antagonistic behavior among bucks ceases as soon as the rut is over and fighting stops before the antlers drop. However, Linsdale and Tomich (1953) found that contests occur after the breeding season, although the most serious fights take place at the height of the breeding season. Several authors (Linsdale and Tomich, 1953; Cowan, 1956a; Taber and Dasmann, 1958) are of the opinion that violent battles are rare, with serious injury occurring infrequently. Linsdale and Tomich (1953) believed that contests result in a better distribution of bucks. They stated that the dominance of one male over another has little effect on determining which bucks do the breeding. Dixon (1934), however, believed that the dominance hierarchy established by the contests is important in determining which bucks do the breeding. Taber and Dasmann (1958) concluded that contests appeared to be a matter of mutual enjoyment and probably have the effect of building the rutting condition of the bucks.

Linsdale and Tomich (1953, p. 506) stated that:

"The use of the antlers is a prominent part of this breeding behavior. It has developed in different ways in different members of the deer family. What we actually see in the examples noted may be the results of considerable modification from habits established early in the history of this species or its relatives. At present the deer use their antlers to establish precedence over other males."

Bucks may remain in their home range or may wander considerably during the rut (Taber and Dasmann, 1958). Linsdale and Tomich (1953) believed that bucks may stay in an area for a few days and then disappear for as long as two weeks before appearing again. Bucks usually do not go back to the same place every year so does are not bred by the same buck every year.

Bucks start to make aggressive advances toward does within a week after they lose their wariness. The does are at first unprepared for the bucks and ignore them until touched. The does are startled by the buck's approach, but quickly be-

come wary and move off when approached by a buck. Chases at first consist of short spurts after the doe. The halting, broken pursuits are rarely faster than a slow walk. The doe leads the buck in a broken circle, frequently changing directions and stopping. Chases become more intense as the season advances, but the slow pursuit of the does continues throughout the season. The running flight of the doe from the buck does not come until the peak of the breeding season (Linsdale and Tomich, 1953). Dixon (1934) stated that the doe is singled out and followed closely when she reaches the pre-estrus period. This may be from 2 to 5 days prior to actual mating. Bucks are apparently able to determine the condition of a doe by the scent of her urine and rely heavily on scent when following a doe (Golley, 1957; Linsdale and Tomich, 1953).

Descriptions of voice in bucks during the breeding season range from a low bleat uttered at frequent intervals to a loud bellow. Bucks are apparently capable of a wide range of sounds during the rut.

Bucks frequently give voice when pursuing a doe (Linsdale and Tomich, 1953). Dixon (1934) reported that a buck sometimes will use his voice to frighten a competing male away from a doe.

Dixon (1934) believed that 90% of the breeding was done by dominant bucks in Sequoia National Park. This would indicate that yearling bucks do not take part in the rut. Taber and Dasmann (1958, p. 36) stated that "The yearling bucks appear to take no interest in the rut, but this does not mean that they would not be capable of breeding." In opposition to this opinion Linsdale and Tomich (1953) found that yearling bucks are frequently active in the pursuit of does and the females respond to them as they would adult bucks. Brown (1961) observed that yearling bucks displayed considerable interest in does during the rut. He believed yearling bucks were capable of breeding if given the opportunity.

Temperature may affect rutting activity. Cold tends to increase rutting activity. Extremely warm days may reduce activity so as to make the rut

scarcely discernible (Linsdale and Tomich, 1953).

Contrary to popular belief, bucks do not gather a harem (Linsdale and Tomich, 1953; Cowan, 1956a; Taber and Dasmann, 1958). Several authors (Dixon, 1934; Cowan, 1956a; Einarsen, 1956) are of the opinion that most breeding takes place at night. However, Linsdale and Tomich (1953) stated that breeding takes place most commonly during hours that deer are normally active. This would be during evenings and mornings. There is a tendency toward all-day activity as the rutting season progresses.

The decline and termination of the rut is somewhat the reverse of the onset. Bucks regain their wariness. They still may chase does, but do this less frequently and persistently. At the end of the rut the antlers begin to fall (Linsdale and Tomich, 1953).

Cowan (1956a) described the rutting behavior of a captive doe at Beaconhill Park. One of the earliest indications of approaching estrus was an increase in the frequency of urination. The doe urinated every 1 or 2 minutes immediately prior to the period of reception and in the presence of a male. An increase in activity, climaxed by a period of running at a fast trot, accompanied the period of frequent urination. The result of this activity was a more effectively marked trail covering a greater area which increased the chances for contact.

Does may have three or four estrus cycles in one season. These periods recur at approximately 3 to 4 weeks but last only a few hours. This would mean that close attendance by bucks is necessary to insure conception (Linsdale and Tomich, 1953).

There is general agreement that does will breed at approximately 18 months (Linsdale and Tomich, 1953; Swank, 1958; Taber and Dasmann, 1958). However, the amount and quality of food has considerable influence on the per cent of does that conceive, particularly in the yearling class (Cowan, 1956a; Swank, 1958; Taber and Dasmann, 1958). Taber (1953) found that yearling does ordinarily breed about a month later than adult does.

Interspecific Behavior

Deer-man Relations

Deer are inherently wary of large mammals and strange objects in their surrounding. Fear of man is largely overcome by constant close association, particularly if man does not disturb the deer. Deer show considerable variation in their response to approach by man. This variation may be caused by past experience, physical conditions of the environment, or individual differences resulting from sex, age, and season (Linsdale and Tomich, 1953).

An alert deer tends to be perfectly still before it moves. The deer will study the cause of disturbance and wait for it to act. Impatience or fear may finally drive the deer to action. The most common reaction toward an intruder is immediate flight in a stiff-legged bound for 10 to 20 leaps. The deer may then stop and watch the intruder for a period of time before walking or trotting out of sight (Clark, 1953). Deer express a general lack of concern toward the sound of rifle shots (Linsdale and Tomich, 1953) and, according to Dasmann and Taber (1956a), will not be driven from an area by the activity of hunters.

Deer-coyote Relations

Several authors (Dixon, 1934; Murie, 1940; Linsdale and Tomich, 1953; Bailey, 1960) have observed deer chasing coyotes. One or several deer were noted to run after coyotes and strike at them with their front feet. At other times, coyotes may

chase deer. Cahalane (1947) gave an excellent detailed description of several coyotes killing a doe. Bailey (1960) observed a pack of coyotes waiting near the periphery of a group of feeding deer. The coyotes rushed in behind a deer when it moved from the herd and attempted to drive the deer into deeper snow. They continued to harass the deer until it was weakened by loss of blood and fatigue. When the coyotes singled out one deer, the remainder of the group of deer ran uphill and formed very tight groups of two to seven animals and looked back. Similar formations have been observed by Linsdale and Tomich (1953).

Deer have been observed becoming attentive but otherwise undisturbed by coyotes howling one-quarter mile away (Cowan, 1956a). In one case, a coyote howl precipitated displacement feeding by deer on the winter range (Bailey, 1960).

Deer-bird Relations

Magpies have been observed sitting on the back or lower neck of deer and, presumably, feeding on ectoparasites. Deer showed little annoyance except when the birds picked around the region of the eye, nose, or base of the tail (Riney, 1951a; Linsdale and Tomich, 1953; Browman and Hudson, 1957; Bailey, 1960).

The influence of birds' songs and warning calls as an aid to location of possible danger to deer has already been described (see p. 7).

Summary

Daily activity primarily consists of a feeding period in the morning, a resting period during the middle of the day, and another feeding period in late afternoon and evening. During the winter, deer may be observed feeding during all hours of the day. Daily activity may be modified by weather conditions.

Deer have a home range which consists of a series of small feeding, bedding, watering, and escape areas connected by travel lanes. Daily travel may be restricted to a small area or may take in the entire home range.

Deer have four natural gaits: walking, trotting, galloping, and bounding. Seldom do deer remain in one gait for extended periods of time.

Deer groom themselves by licking, mouthing, biting, and scratching and it is common for them to groom each other.

One sense is rarely used alone, but the sense of smell is used extensively to verify something heard or seen. Vision is the least acute of the senses and is variable in usefulness.

Defecation may occur when walking, standing, or feeding. Both bucks and does assume the squatting position to urinate.

The most stable social unit is the family group: a doe and fawns, or a doe, fawns, and yearlings. Several families may band together in a feeding group during the winter. Offspring may leave the family in the spring as they approach 1 year of age or they may remain with the family until they are almost 2. Bucks may be solitary or in groups of two to eight at any time of the year.

Leadership always is assumed by an adult doe. No leadership is apparent in groups containing only bucks.

Dominance is determined largely by sex and age class with the largest animals being the most dominant. Bucks are dominant over does; does are

dominant over yearling does; yearlings are dominant over fawns.

Play is displayed predominantly by fawns although yearlings and adult does will participate occasionally. Play usually takes the form of active scampering and jumping about or games of chasing and "tag" involving two or more deer.

The chief form of communication in deer appears to be the pose, aspect, or posture; although deer will respond to vocal stimuli.

A pregnant doe drives off her yearlings and moves away by herself about 1 or 2 weeks before parturition. Deer usually retire from the open areas and move into thick cover to give birth.

Fawns spend the first few days alone and hidden. As they grow older, they spend more time following the doe. The doe may lie beside her fawns for the first nursing but after the fawns are strong enough to stand, the doe remains standing. The nursing period and the time interval between periods are variable. The longest nursing periods take place when the fawns are small. Weaning occurs at approximately 2 to 2 1/2 months of age. Fawns regularly take green food and chew their cuds long before they lose interest in nursing.

Territorial behavior in deer has been suggested by Dasmann and Taber (1956a) and Graf (1956).

The initial stage of the rut is marked by loss of wariness in bucks. Antler rubbing and combat between bucks are prominent parts of the rut. Close attendance of the does by bucks is necessary to insure conception. Does breed at approximately 18 months of age, although this may be altered by environmental conditions.

Deer are inherently wary of large mammals and strange objects in their surroundings. Fear of man can be overcome largely by constant close association, particularly if man does not disturb the deer. Deer have been observed at times to chase coyotes, while at other times coyotes have been observed chasing deer.

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Acknowledgments

This literature review was sponsored by the Colorado Cooperative Wildlife Research Unit which is supported by the Colorado Game, Fish and Parks Department, the Bureau of Sport Fisheries and Wildlife, the Wildlife Management Institute, and Colorado State University.

Deep appreciation is extended to my Major Professor, Dr. Douglas L. Gilbert, Associate Professor, Department of Forest Recreation and Wildlife Conservation, who gave valuable guidance and assistance throughout the study, particularly with administrative problems in the early portion of the study and with critical review of this manuscript. Deep appreciation is also extended Dr. Fred A. Glover, Leader, Colorado Cooperative Wildlife Research Unit, for guidance and encouragement throughout the study.

Thanks are extended the members of my graduate committee, Mr. Richard N. Denney, Assistant Game Manager, Colorado Game, Fish and Parks Department; Dr. Robert R. Lechleitner, Associate Professor, Department of Zoology; and Dr. Harold W. Steinhoff, Professor, Department of Forest Recreation and Wildlife Conservation, for the critical review of this manuscript.

I am deeply indebted to Mr. Dean E. Medin, Associate Wildlife Researcher, Colorado Game, Fish and Parks Department and Leader, Federal Aid in Fish and Wildlife Restoration Project W-105-R, who offered valuable advice and assistance throughout the study and never failed to stimulate thought.

Others aided in portions of the study and their efforts are acknowledged with thanks. These people include; Allen E. Anderson, Gary L. Brown, R. Bruce Gill, Charles M. Loveless, O. Doyle Markham and Vincent H. Reid.

Michael J. Dorrance