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MOVEMENTS, POPULATIONS, AND BEHAVIOR OF DEER ON A WESTERN MONTANA WINTER RANGE

by

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INTRODUCTION

Wild ranging herds of Rocky Mountain mule deer (Odocoileus hemionus hemionus [Rafinesque]) typically inhabit terrain that is subject to yearly inundations of deep snow. Deep snow cover forces the animals to lower elevations where the environment is more nearly optimum, but the area is greatly restricted (Dixon, 1934; Olsen, 1938; deNio, 1938; Aldous, 1945; Fowle, 1950; Leopold, Riney, McCain, Tevis, 1951). Olsen (1938) states that winter range is the principal limiting factor of big game herds.

The winter range of the Rattlesnake Creek mule deer herd is located in the low foothills and mountain ridges that descend into Missoula Valley from Stuart Peak. This area is located approximately six miles north of the University of Montana campus.

In view of the need for knowledge of the relationship of Rocky Mountain mule deer to their winter range, and the proximity of the area to the University, a long term project was initiated in 1957 to study this herd. Several aspects of the life of the herd have been investigated. K. L. White studied its summer range ecology in 1958.

In the fall of 1960, D. A. Klebenow began a study of the ecology and productivity of the winter range. E. D. Bailey in 1960 investigated the behavior of the herd on its winter range and suggested that deer movements on the winter range were initiated by a time-oriented stimulus. In the winter of 1960, this present study was begun to investigate the movements, populations, and behavior of the Rattlesnake Creek mule deer herd on its winter range. Data were collected each winter, November through April, from 1960 to 1962. The study was established to achieve the following objectives:

1. To observe the deer populations on the winter range, to note dates of migration into and out of the area, and to define the size and composition of the herd.

2. To describe the grouping relationships among the deer on this winter range.

3. To observe the local movements of deer, and to attempt to determine their causes.

4. To test the hypothesis that the main winter range movements of this herd were correlated with calendar time.

LITERATURE REVIEW

History

Primitive history. Sometime between the middle Miocene and late Pleistocene, some one to fifteen million years ago, a small species of primitive deer successfully crossed the land bridge from Asia, and established itself in the western hemisphere (McLean, 1940; Taylor, 1956).

The members of the genus *Odocoileus* are believed to be descendants of these first successful colonizers. Other genera of the deer family (Cervidae), notably *Rangifer*, *Alces*, and *Cervus*, are believed to arise from stock which migrated to this continent at a later date. These late arrivals are correspondingly more closely related in structure to their counterparts in the Old World (Taylor, 1956).

Phylogenetically, deer of the genus *Odocoileus* are related to other genera of the family Cervidae by their common possession of antlers and dermal glands and lack of upper incisiform teeth (McLean, 1940; Schwartz and Schwartz, 1959).

The initial cervid migrants to this continent must have spread over a large portion of its emerging surface. Barriers to distribution developed, causing populations to become isolated. Isolation led to divergent lines of evolution. The groups which survived this process comprise two well defined species, the white-tailed deer (*Odocoileus virginianus*) and the mule deer (*Odocoileus hemionus*). These two species have become further diversified. There are 30 recognized sub-species of *Odocoileus virginianus*, and 11 sub-species of *Odocoileus hemionus*

(Taylor, 1956). It is the opinion of Taylor (1956) that the black-tailed deer Odocoileus hemionus columbianus is a race proceeding toward specific isolation.

During the Pleistocene period a particular race of mule deer evolved in the steep foothills and mountains of the West. This was the Rocky Mountain mule deer (O. h. hemionus), which spread into areas uncovered when the glaciers withdrew and thus became the most widely distributed of the races of mule deer. It inhabited the bulk of the western segment of the continent, from Great Slave Lake in the Northwest Territory to the Mogollon Rim in Arizona, and from the lakes of northeastern Minnesota to the summit of the Sierra Nevada-Cascade Range and the fjords of the Coast Range. It currently has the widest distribution of any sub-species of large game animal in North America. Its climatic tolerance has few parallels among mammals (Cowan, 1936; Taylor, 1956).

Mackenzie, making some of the first travels into the Rocky Mountain range of the mule deer, recorded it at the "Great Falls" on the Peace River in 1792 (Taylor, 1956). Trapper and adventurer Charles Le Raye was held captive by the Sioux Indians from 1801 to 1812. While with the Indians on the Big Sioux River in South Dakota, he kept a journal, including observations of the Rocky Mountain mule deer. From this journal, in 1817, C. S. Rafinesque described the species which is now designated O. h. hemionus (Rafinesque). No type specimen was designated (Cowan, 1936).

In 1803, the Lewis and Clark expedition began exploration of the Northwest. They were the first white men to inspect the Upper Missouri, observe the confluence of the Clark Fork and Bitterroot Rivers, and to cross Missoula valley, where their camps were pitched in 1805 and 1806 (White, 1958). During this intermountain travel, the expedition observed and hunted the mule deer (Russell, 1932; Koch, 1941; White, 1958). The journals of Lewis and Clark noted that the floors of the Missoula and Bitterroot valleys abounded with game. Big horn sheep (Ovis canadensis), elk (Cervus canadensis), deer (Odocoileus), and wild horses all utilized these alluvial plains (Koch, 1941; White, 1958). The dense mountain forest was another story, and the journals report game scarcity on the trail over Lolo pass and into the valleys of the Salmon River (Koch, 1941).

Following the same route, Alexander Ross camped at the mouth of Rattlesnake Creek on the Clark Fork River in 1823 and noted abundance of game in the area. In 1842, St. Mary's Mission was built in the Bitterroot Valley and white settlements soon became established (White, 1958).

Modern history. The white settlers began to modify the environment to their special uses. Taylor (1956) writes of the pressure that was placed on some deer populations by the frontiersmen and market hunters. However, this exploitation did not seem to affect the populations of Rocky Mountain mule deer to the extent that it did the white-tailed deer of the eastern and midwestern areas or the coastal mule deer.

All deer populations, however, decreased over the nation, in some areas reaching dangerously low levels in the late nineteenth century. Effective conservation began about 1900; refuges were formed and seasons completely closed (Gabrielson, 1943; Taylor, 1956). The trend reversed and high local populations of deer built up; many of them overutilized their preferred forage plants (Leopold, Sowls, and Spencer, 1947). A realization of the need for reliable biological information on which to base sound deer conservation measures ultimately followed.

Life History

Biology. A Rocky Mountain mule deer begins its existence at fertilization in the fall season of the year during the breeding season, or "rut." The occurrence of the rut varies with latitude (Taylor, 1956). Robinette and Gashwiler (1950) state that in Utah the rut begins in late October and ends in late January. The peak of activity is between November 20 and December 2. White (1958) reports that in 1957 the Rattlesnake herd bred during the period November 8 to December 18.

Conception by fawns is suggested as being rare in mule deer (Dasmann and Taber, 1956). Robinette and Gashwiler (1950) found that yearlings commonly breed; 57 percent of yearlings were pregnant in Utah mule deer compared to 85 percent of all older does.

Yearling males are sexually mature, but rarely breed, as they must compete with older dominant males for the opportunity to reproduce (Robinette and Gashwiler, 1950).

The nutritive quality of the deer range is directly related to fertility levels of the herds. Fecundity is highest on the areas of most fertile soils and most abundant high nutrient plants (Cheatum and Severinghaus, 1950; Taber, 1953, 1956).

Although it has been found that in yearling does the peak of pituitary gonadotrophic potency is earlier than that in adults (Grieser and Browman, 1956), it has also been found that the yearlings actually breed later (Taber, 1956; White, 1958). Possibly they pass through one estrus period without conception.

The growing embryo is carried by the doe during the winter period of great environmental stress. As a result, the body reserves of the doe may be depleted by the demands of the fetus. Normal fawns, therefore, are often produced by does in very poor condition (Taylor, 1956).

In late winter and early spring, the deer move off wintering areas and back toward summer range (Russell, 1932; Dixon, 1934). Gestation averages 202 days and fawning normally occurs in late May, June, and early July (Dixon, 1934; Robinette and Gashwiler, 1950; White, 1958). Taber (1953) found that fawning in black-tailed populations varied from April to June depending on plant phenology. Abortion of fetuses after conception is thought to be negligible and the ovulation rate is therefore reflected in the current fawn crop (Taber, 1953; Robinette, _et al._, 1957).

Preceding actual parturition, the females become territorial (Dasmann and Taber, 1956). After birth, association of the fawn with the doe permits the fawn to learn habits that will adapt it to its environment (Russell, 1932; Darling, 1937; Bailey, 1960).

As in most mammals, secondary sex ratio in mule deer is unbalanced toward males. Robinette, _et al._ (1957) found fetuses to average 111 males to 100 females and new-born fawns 114 males to 100 females.

Taber and Dasmann (1954) found a higher proportional mortality among male fawns than among female fawns. These authors suggest that under poor range conditions, male fawns suffer higher morality rates.

However, mortality is more nearly equal on good range.

Hunting pressure together with possible higher male fawn mortality are probably the cause of adult sex ratios, which typically show a high proportion of females. Ratios of 1:3.5 to 1:7.4 males to females with a maximum of 1:14 are reported (McLean, 1940; Interstate Deer Herd Comm., 1949; Taylor, 1956).

The biological potential of wild deer herds seems adequate to meet the extremes of stress placed on them. Dixon (1934) states that in an area of 1,000 square miles, when 22,214 deer were removed to combat hoof and mouth disease, populations rebuilt to substantial levels in ten years.

Investigators working with the Jawbone deer herd of California report that natural mortality may, on occasion, remove large portions of that herd, yet in a short period the reproductive capacity of the animals replaces the removed numbers (Leopold, et al., 1951). The magnitude of this potential may range as high as 60 percent net productivity (Taylor, 1956).

In autumn deer begin to move from the extensive summer range to the restricted wintering area. Fawns presumably learn the traditional migration route and winter range by following older deer.

Movement. Literature on movements will be reviewed in two parts: 1) Migratory Movements, and 2) Non-migratory Movements. Home range sizes and associated movements will be reviewed as non-migratory movements.

On any particular range, the environmental conditions change seasonally and annually; deer respond by moving (Edwards and Ritcey, 1956; Woodbury, 1956).

Dixon (1934) states that movements are necessary for animals to obtain livelihood. Burt (1943) defined a home range as applied to mammals as "that area traversed by the individual in its normal activity of food gathering, mating, and caring for young."

Migratory movements. The annual migrations of mule deer from summer to winter ranges were noted by the early explorers and settlers of the mountainous West (Russell, 1932; Dixon, 1934).

Russell's work on migration in Yellowstone and Yosemite National Parks is the earliest study on such deer behavior which is now accepted as commonplace (Russell, 1932). The annual beginning of migration seems to be as variable as the seasons in different latitudes. The downward movement to winter range may continue until late in January (Edwards, 1942). White (1958) states that the Rattlesnake herd begins its migration in November. The consensus is that while the migration away from the summer ranges occurs during the late fall and early winter, the exact timing depends on local conditions (Russell, 1932; Dixon, 1934).

Snow is the common factor on all ranges where migrations occur. It is obvious that deer cannot survive in areas of deep snow. Drops in temperature, early snow squalls, and storms in high mountains are coincident with restlessness among deer which inhabit these areas. Fall migration begins as these deer drift to lower elevations.

Russell's (1932) study of migration in Yosemite and Yellowstone National Parks showed annual temperatures varied at the times migrations were initiated. This variance apparently ruled out temperature as a stimulus to migration.

Snow is repeatedly suggested in the literature as a cause or or stimulus of migration. Russell (1932) writes that snow storms are the most decisive factor in initiating migration from the summer range in Yellowstone and Yosemite. Edwards (1956) suggests that snow depth is inversely proportional to ungulate abundance and thus has been a selective factor in creating migrations. Many authors suggest that snow depth with resulting interference with foraging and activity cause migrations (Dixon, 1934; McLean, 1940; Rasmussen, 1941; Edwards, 1942; Dasmann, 1953; Dasmann and Taber, 1956; Pruitt, 1960).

Edwards and Ritcey (1956) point out that temperature may be the basic cause of deer migrations; temperature is often related to snow depth. They also state that moose migrations fluctuate with temperature changes and snow thaw or accumulation rates. They conclude that migration is basically dependent on temperature.

Closely related species are shown to respond to weather factors in much the same way as deer. Elk, moose, and caribou, in many respects, parallel the reactions of deer (Brazada, 1953; Edwards and Ritcey, 1956; Knowlton, 1960; Picton, 1960; Pruitt, 1960). Anderson (1954) points out that elk begin movement at six to ten inches of snow depth. He also states that storms initiate movement and succeeding storms increase this activity.

Several authors have reported stimuli which could cause migratory behavior. Reports are rather frequent of deer seeming to begin migrations before an unseen approaching snow storm (Russell, 1932; McLean, 1940). Other authors only suggest responses unexplained by environmental lacks (Rasmussen, 1941). Day length is suggested as a learned stimulus in an imprinted stimulus-response complex association (Bailey, 1960).

Internal physiological rhythms are also mentioned (Russell, 1932).

In synopsis, the general opinion is that the physical depth or quality of snow is the factor causing migratory movement. The actual stimulus remains an unknown factor which may vary with the locality, but in some way must be related to yearly conditions of weather and snow depth.

The annual migration of deer herds sometimes involves extreme elevation changes and long distances. Mule deer are known to summer as high as 12,750 feet (Dixon, 1934). In Yellowstone and Yosemite National Parks the deer range to 10,000 and 11,000 feet. These same animals make an annual climb and descent of 5,000 to 6,000 feet in elevation (Russell, 1932). Range changes may involve travels of up to 50 to 150 miles (Russell, 1932; Dixon, 1934; Gruell, 1958).

Gruell (1958) found that although suitable winter range was available close to summer range, some deer moved across six and seven major divides and traveled 81 to 96 miles in the process of reaching their wintering areas. Ashcraft (1961) reported that of deer tagged on California summer ranges, only two moved down drainage, the others were scattered over seven different winter ranges. This last study shows that deer herds apparently mix on summer ranges and sort out to move to ancestral winter ranges. In contrast, it was found in Utah that the majority of the deer tagged on a winter range spent the summer in the same drainage area (Doman and Rasmussen, 1944).

Mule deer return in successive years to the same winter range with reasonable reliability. Individuals may even return to the exact meadow or location (Cliff, 1939; Gruell, 1958). This return is repeated to the extent that in some areas deep migration trails are cut into the soil in favored locations (Interstate Deer Herd Comm., 1949; Leopold _et al._, 1951; Taylor, 1956).

The stresses of migration and distance do not affect all herds of mule deer. In areas where the majority of animals make the twice yearly trip, a few animals never leave the winter ranges (Russell, 1932; Cowan, 1936; Darling, 1937). On some ranges, entire herds do not migrate. This occurs predominately in southern regions of dry, warm climate (Clark, 1953). The black-tailed deer as a race is generally non-migratory, because most of its range is snow free (Dasmann, 1953; Zwickel, Jones and Brent, 1953).

Non-migratory movements. All deer herds also exhibit movements that are not directly connected with migrations. These movements will be discussed as non-migratory. Migratory deer have definite movement patterns while they are on winter and summer ranges, while non-migratory deer exhibit well-defined home ranges that are small in area compared with the large acreages covered by migratory herds.

The black-tailed deer of California are reported to have a sex-age difference in home range areas. Adult males occupy the largest area, with other groups inhabiting smaller home ranges (Dasmann, 1953).

Mule deer of the Southwest have home ranges varying from 9.3 to 1.3 square miles (Clark, 1953). White-tailed deer are reported to have home ranges correlated with habitat type. These animals travel greater distances in open prairie and deciduous-type habitat than they do in coniferous-type habitat. Movements vary from 9.7 to 5.1 miles, respectively (Carlsen and Farmes, 1957).

All required environmental factors are present within a deer's home range, but deer will move out of their home range to adapt to changing environmental factors or stress. Weather conditions appear to be the major cause of such movement (Dasmann, 1953).

In some cases, within a limited home range, animals will seek out the area of most nearly optimum temperature (Taber and Dasmann, 1958). In some regions, during winter, south and southeast slopes are most optimum and are utilized at these times (Cook and Hamilton, 1942; Shanks and Norris, 1950; Bailey, 1960; Welch, 1960).

When excessive stress occurs, the deer may be forced to leave familiar range and extend their movements into less familiar areas. Even in non-migratory herds, snow may necessitate a range shift. This type of movement is not an annual occurrence and seems to be related to the severity of the stress. Hamerstrom and Blake (1939) found that in mild winters not all concentration areas were used and animal groups were not as consistent in composition as during severe weather. Deer moved out of concentrations earlier and more rapidly in a mild period. It was suggested that temperature was a stimulus, not a cause, as the deer spent most of the winter in swamps, where temperatures were colder than those of other habitat types (Hamerstrom and Blake, 1939). Concentrations are apparent adaptations to increasing stress from snow conditions (Hamerstrom and Blake, 1939; Marston, 1942). When the environmental factors become less severe, deer will return toward the formerly-used range (Hamerstrom and Blake, 1939). At those times, deer may return to northern aspects (Welch, 1960).

Factors other than snow may cause movement outside the normal home range. In dry areas, the quantity of available free water directly influences movements (Clark, 1953; Welch, 1960). Harassment of deer by men and dogs are reported to cause temporary movement away from home ranges (Clark, 1953; Dasmann, 1953; Progulski and Baskett, 1958; Welch, 1960).

Some permanent dispersal movements from familiar areas will occasionally occur. Yearling females sometimes move off alone to unfamiliar areas to give birth and in this way establish new home ranges. Yearling males may desert the social group, join all-male groups, and establish new home ranges (Darling, 1937; Dasmann and Taber, 1956; Bailey, 1960).

Dispersals cause intermingling of populations. When intermixing occurs on summer ranges of migratory herds, new social groups may form and may establish new or changed migration routes (Bailey, 1960; Ashcraft, 1961).

Dasmann (1953) states that deer become familiar with the locations of all normal requirements of life in the area in which they are born. The animals may adjust to changes in these factors, but usually remain in familiar areas.

Winter range. The goal of the annual fall movements is the relative security of the winter range. Deer arrive on these special areas over a period of several months (Edwards, 1942).

Habitual use of winter range has evolved in most mule deer herds. In summer the herds range extensively, but winter snows force them into concentrated areas where movement is possible and food accessible (Dixon, 1934; DeNio, 1938; Olsen, 1938; Aldous, 1945; Fowle, 1950).

The densely populated winter range is the first area to show over-utilization of forage when ungulate numbers become excessive (Aldous, 1945). As a direct result of over-utilization of winter range forage, large die-offs will occur in ungulate populations (Leopold *et al.*, 1947). Available winter range is then the key factor in determining ungulate population size.

The over-population, over-utilization, population decrease sequence was first recognized on the Kaibab Plateau in Arizona (Rasmussen, 1941; Leopold *et al.*, 1947). The history of the Kaibab and its deer herd is now a classic example in modern game management. The plateau is largely isolated due to topographic features. Local predators were severely reduced in numbers and hunting of deer was restricted from 1906 until 1923. The unchecked population, estimated in 1906 at 4,000 deer, increased to 100,000 by 1925. Damage to forage and winter range was first noted in 1918. Hunting was finally permitted on the plateau in 1924 to reduce the deer population, but thousands of deer had already died of malnutrition and related causes (Rasmussen, 1941).

The damage had already been done to the range, and by 1930 the plateau would support only 10,000 deer. This population was considerably below the original carrying capacity of the range. These facts focused national attention on the problems and effects of maladjusted ungulate populations (Rasmussen, 1941).

Robinette *et al.* (1952) state that it is inevitable that deer herds suffer losses, yet large die-offs differ from ordinary winter mortality. The large die-offs follow population irruptions and mortality is caused by deterioration of the winter range due to damage which occurs during the peak of the population irruption.

There are two important causative factors in winter deer losses: snow depth and lack of forage. Ungulate population declines are correlated with the years of deep snows. Abundant populations are correlated with light snow periods. These years tend to occur in groups. Edwards (1956) also states that on an understocked range there is less tendency for deep snows to affect the population.

Severinghaus (1947) supports Edwards' findings and reports that winter mortality in white-tailed deer in New York varied from year to year with the severity of the winter. According to this report, low temperatures did not cause mortality. Snow depth of over 20 inches was the cause of the higher mortality.

The basis for the 20-inch limit seemed to be that adult deer measured 20-22 inches to the chest, and fawns measured 18-19 inches. Snow which was deeper than 20-22 inches would greatly impede movement and cause increased expenditure of energy. Fluffy snow also causes deer to flounder and then weaken rapidly. It is suggested that deep snow must last five weeks to affect the animals, as even deer in poor condition are reported to maintain themselves for three to four weeks. Snows late in the year caused the highest mortality (Severinghaus, 1947).

The second of the two factors is range over-utilization or deterioration. In areas of warm environment, at relatively low altitude, cold temperatures are rare yet mortality still occurs. These losses are caused by range deterioration and overuse aggravated by livestock grazing on the range. The first spectacular losses occurred in such mild environments in 1937 (Kelsall, 1955).

Hanson and McCulloch (1955) report that Arizona mule deer are subjected to losses throughout the year. Drought is the causative factor as it reduces free water and abundance of forage.

Several authors concur with the suggestion that winter losses are due to a condition of poor forage quality compounded by increased energy requirements during heavy snows (Aldous et al., 1938; DeNio, 1938; Edwards, 1942; Doman and Rasmussen, 1944; Fowle, 1950; Robinette et al., 1950). Cold weather and persistent snow aggravate food shortage by impeding movements and increasing energy requirements. Further, quantity and availability of winter food are critical. Weather only contributes by rendering the animals vulnerable to malnutrition (Fowle, 1950).

In Utah, few deer reportedly died during hard winters until 1935-1936. These years of deep snow forced large herds into small areas. Large die-offs occurred four times. However, during the years in which the die-offs occurred, snow was not sufficiently deep to be the cause of the extreme mortality. It was suggested that one year of extreme overuse of the winter range during a severe winter adversely affected browse production for several years thereafter. Weather was then only a predisposing factor in mortality, in that it forced the concentrations on over-used range and resulting malnutrition. Mortality was attributed to poor quality of forage and not to the quantity that was available (Doman and Rasmussen, 1944). In years of severe winters, losses almost doubled when compared to moderate years. The mortality varied inversely with forage supply on the study units. During the most severe winters mortality rates increased only 1 to 3 percent on the study units that had an adequate supply of browse.

From these findings it is apparent that the causes reported to be responsible for losses vary with the locality. However, the literature shows that all areas have a common factor responsible for mortality, and that is weather and its effect on forage supply. In regions where deep snow covers all of the range, the snow is directly responsible for unavailable food. In other regions with large areas of low-altitude range that is either clear of snow or has shallow cover, the snow forces the animals into the winter range, and there overpopulation leads to excessive range use and consequent malnutrition.

Winter losses of ungulates rarely are equal in all age and sex classes. The young are universally most vulnerable to environmental stresses. Of all age classes, fawns show winter mortality several times that of older animals (Doman and Rasmussen, 1944; Robinette et al., 1957).

Taber and Dasmann (1954) report that male fawns are more subject to mortality than female fawns under all range conditions. Yearling animals also are more subject to mortality than adults (Robinette et al., 1957).

In the Northwest, big game populations are proportional to quantity and quality of available winter food supply (DeNio, 1938). A major problem exists for deer herds in acquiring the proper nutrition. The quality of the forage is variable throughout the year and studies of seasonal nutritive content changes in forage are voluminous; only a few authors are noted here (Hart, Guilbert, and Goss, 1932; Cook, Stoddard, and Harris, 1956; Halls, Hale, and Knox, 1957; Robertson and Torell, 1958). Hellmers (1940) has shown that the trend is toward a reduction of nutritive value throughout the winter. Other authors suggest low protein levels as the major cause of mortality (Dassman and Taber, 1956;

McEwen et al., 1957). It is also reported that species of plants which are unpalatable to deer are normally only lightly utilized. In severe winters, greater use is made of these species and malnutrition results. Deer shift species utilization because preferred species are unavailable (Harris, 1945; Hill, 1946).

The general quality of the browse of an area is directly dependent upon soil fertility. The browse can only be as good as the basic soil potential (Mitchell and Hosley, 1936; Albrecht, 1958).

Several workers have found that a deer consumes a given amount of forage per day regardless of the quality of the browse. The amount is stated by A. A. Nichol (Palmer, 1944) as being 2.35 lbs. air-dried weight per 100 lbs. of live weight per day. Colorado workers used the number of 5.0 lbs. air-dried weight per deer per day (Palmer, 1944).

On the mule deer ranges of the West, the herds move onto the foothills and south exposures in winter (DeNio, 1938). In Utah these ranges are below 5,000 feet elevation, and the southern exposures are clear of snow in winter except directly after snowfall (Robinette et al., 1952). Montana winter ranges are similar; herds concentrate on south and southwest exposed foothill ridges at low elevations (Carter, 1951; Bailey, 1960).

The density of populations on these winter ranges vary from year to year and seems to be dependent upon weather conditions, particularly snow accumulation. The Interstate deer herd concentrates in direct relation to the severity of the winter. In mild winters, many deer are observed outside the recognized concentration ranges (Interstate Deer Herd Comm., 1949).

When snows do come to these normally open ranges, the deer modify their habits until the areas clear (Dixon, 1934; DeNio, 1938). These conditions, if prolonged, may force the animals into the valley floors that were the original winter range (Koch, 1941; White, 1958). Today, valley land is largely denied to herds due to fencing and farming operations (Edwards, 1942).

The white-tailed deer of the north central and northeastern regions face a totally different set of circumstances in both weather and topography, but likewise exhibit an example of behavior modified to meet environmental changes. In northern New York winters typically have a deep and continuous snow cover over entire ranges. In this area the deer congregate in swamps (Marston, 1942).

Deer congregations in swamps is the classic form of yarding in which the deer establish networks of trails in a small area. These trails allow movement and browsing where snow depths would make such movement difficult. The yarding behavior and use of swamp habitat types are an example of maximum adjustment to adverse conditions and best use of the environment available (Cook and Hamilton, 1942).

However, another situation exists in nearby central New York. Here the climate is milder and there is less snow. In this region deer congregate on steep south and southeast slopes where the ground is clear of snow. These slopes are 20 degrees or steeper. The sun's rays are twice as intense on the slopes as they are on level or north sloping topography. The south slopes are sheltered from prevailing winds, and deer congregate on these slopes with no preference shown for cover type (Cook and Hamilton, 1942; Webb, 1948).

On the two adjacent winter ranges in New York, the local deer herds have evolved different adaptive patterns to meet adverse winter environmental conditions which are markedly different. Each adaptive behavior pattern of winter range selection and use makes use of the habitat available to efficiently reduce the stress of the winter environment. On the northern range, swamp cover-type offers the best habitat to lessen stress. On the central ranges south slope topography offers the best habitat to lessen the stress. Cook and Hamilton (1942) state that both types of adaptive behavior, in its own region, is the best solution to lessen the stress of adverse winter environmental conditions.

Deer herds are also sensitive to yearly conditions as well as regional conditions. In years of deep and long snow cover, the deer of northern New York gather early, move little, and move back to summer areas only when snow melts. In years of little snow they concentrate less (Hamerstrom and Blake, 1939; Cook and Hamilton, 1942).

Carter (1951) found that game herds on Montana winter ranges were specific in the topography and cover type utilized to adjust to winter conditions. Mule deer were found to select long ridges of open exposure. White-tailed deer were more sensitive to snow depth and selected short ridges broken by cover interspersion.

The onset of the winter season necessitates either a range shift or a long migration for the majority of deer herds. The weather conditions associated with this period are the cause for such range changes. The adaptation that is inherent in such range changes is toward the best habitat available under the circumstances. This adaptation is performed in different ways in different regions and localities. The best available habitat is usually in short supply and the result may be local over-population. The rigors of the environment, over-population, poor forage quality, and other factors combine to cause winter mortality. These losses may be extreme. When populations decline, it is usually the old and young age classes that bear the brunt of the fluctuations.

Behavior

Behavior has been defined as the activity of an entire organism (Scott, 1956).

Social organization.

Social relationships of individuals comprise the more complex whole that is social organization. Scott (1956) states that social relationship is regular and repeatable behavior between two or more individuals.

A consistent fact of the social organization of deer is the matriarchal social system (Darling, 1937; Buss and Harbert, 1950; Clark, 1953; Linsdale and Tomich, 1953; Delap, 1957).

The female and her young constitute the basic unit of the population. Through constant association with the female, the young learn by imitation, the behavior patterns of the female. Only rarely does a dominance-submissive relationship exist between a female and her current offspring (Darling, 1937; Clark, 1953).

The females isolate themselves during birth and for a few weeks thereafter. Gradually they will tolerate closer association of their young of the previous year and other deer. A family group will then be formed, and is composed of a female and all of her female offspring, each with its own fawn (Russell, 1932; Darling, 1937; Cook and Hamilton, 1942; Linsdale and Tomich, 1953; Dasmann and Taber, 1956; Bailey, 1960).

These groups may form into larger units until herd-like groups occur. Such groups most commonly occur in numbers of 6 to 15 animals. Maximum herd sizes are thought to be 55 to 70 animals (Russell, 1932; Cook and Hamilton, 1942).

Most commonly, male ungulates remain either solitary, or in all male groups (Russell, 1932; Dixon, 1934; Cook and Hamilton, 1942; Clark, 1953; Linsdale and Tomich, 1953). These male groups are especially noticeable from early spring to late fall (Russell, 1932). The relationship of the males within these groups seems amiable, but not well organized. The organization consists of mere association rather than dependence or cooperation (Dixon, 1934; Darling, 1937). Even during the rut, males do not assume a leadership roll over the females or herds. In this period, the males are reported to desert the group when under stress (Clark, 1953).

Young sub-adult animals face a crisis in their relationship to the social group as a whole. The sub-adult age is one of adjustment from a life of dependence to a life of independence (Altmann, 1958; deVos , 1960). During the fall rut, the secure association of the fawn is first challenged by the breeding males. By the second fall the competition of new fawns and increased sexual competition with the mother will cause the young animal to become independent (Darling, 1937; Clark, 1953; Linsdale and Tomich, 1953; Robinette _et al._, 1957; Altmann, 1953, 1960; deVos, 1960). This relationship of growing independence is apparent early in young males, and may account for high mortality in this group (Clark, 1953; Taber and Dasmann, 1954; Robinette _et al._, 1957;

Bailey, 1960). This association between male fawns and the family groups may fluctuate, and young males may rejoin female groups for short periods. During winter concentrations, all sexes are intermixed to a greater degree (Russell, 1932; Dixon, 1934; Cook and Hamilton, 1942; Linsdale and Tomich, 1953).

Conflict. Conflict is the agonistic behavior described by Scott (1956). Conflict is any behavior of conflict or fighting, and can only occur in organisms capable of fighting.

Conflict may be observed between all age groups and sexes of deer. The common concept of conflict is the fighting of males during the rut. Actually, males are quite congenial except during this period, and even then most fighting is limited to pushing (Linsdale and Tomich, 1953; Dixon, 1934). Older males exert dominance over younger males. Antler shape and size are factors deciding social rank (Darling, 1937; Woodbury, 1941; Hediger, 1955.

It has been reported that adult males are the most dominant animals in any conflict situation (Linsdale and Tomich, 1953; Browman and Hudson, 1957; Bailey, 1960). However, Buss and Harbert (1950) report that adult females can successfully defend themselves in conflict with males.

Within adult female groups and mixed female-fawn groups, the oldest doe is the dominant animal (Darling, 1937; Linsdale and Tomich, 1953). Adult doe groups form the usual dominant-submissive pattern, and the most dominant animal usually is the leader (Darling, 1937; Bailey, 1960).

The youngest members of the social groups are usually the least dominant individuals. This continued subordinate relationship may act as a selective factor against the young, causing their high mortality (Robinette *et al.*, 1957; Altmann, 1960; Bailey, 1960).

Intraspecific conflict is apparent, especially in relation to predators. Male animals are reported to defend a social group from predators (Clark, 1953). Buss and Harbert (1950) report that a group of deer trampled a bothersome dog.

Linsdale and Tomich (1953) report that adult females with fawns are actively aggressive toward bobcats (*Lynx rufus*). Most commonly flight is stimulated by the posture and behavior of the predator (Bailey, 1960; Fuller, 1960). Altmann (1958) states that group size influences flight tendency; solitary animals show greater flight tendency than do animals in groups. Peripherally located groups have a greater flight tendency than do central groups. Hunting season increases the flight tendency in all ungulates.

Activity and bedding. Deer respond to different cover types by different general activity levels. Dense cover types result in less movement of animals (Robinson, 1960). In some areas, considerable night activity is observed, especially during very hot weather (Clark, 1953).

Bedding sites are directly correlated with temperature. In extremely cold periods, deer remain bedded down all day (Cook and Hamilton, 1942). Generally, deer bed down from late morning to early evening. Such behavior is infectious and shared by the group (Darling, 1937; Browman and Hudson, 1957; Bailey, 1960; Robinson, 1960). Fawns were found to feed for longer periods during the day and not to remain bedded down as long as adults (Bailey, 1960). Winds may be a factor in causing animals to seek shelter or to bed down (Dasmann and Taber, 1956; Bailey, 1960; deVos, 1960; Robinson, 1960).

Learning and imprinting. Altmann (1956, 1958) states that the doe-fawn relationship is important to survival. A leader-follower relationship exists between the doe and fawn and lasts beyond the weaning period. This leader-follower complex is especially important in establishing the migratory patterns of the mother in the young (Bailey, 1960). The formation of social groups and the cohesion of these groups is dependent upon the associations learned by the young fawn from its parent.

Finally, it appears that the ultimate condition of an animal after environmental stress is largely dependent upon its social status (Bailey, 1960; Robinson, 1960). Individual animals with the highest social dominance may best meet a selective situation.

STUDY AREA

Location. The study area is located approximately 6½ miles north-northeast of the University of Montana campus at Missoula, Montana. It is situated in Missoula County, Montana, Sections 23, 24, 25, and 26 of Township 14 North, Range 19 West (Figure 1).

Wallman Ridge (also locally called Strawberry Ridge) comprises the major portion of the winter range study area. This land form is bounded on the west-northwest by Spring Gulch, on the south-southeast by Rattlesnake Creek, and on the northeast by Frazer Creek (Figure 2).

Topography. The topography of the study area is relatively steep. Wallman Ridge rises from the 4,000 foot elevation of the valley floor, at an angle of approximately 30°, to an elevation of 4,500 feet. This elevation is relatively constant for the length of the ridge. At the northeastern end of the study area, the topography makes a steep ascent to 5,500 feet.

From the high point of 5,500 feet elevation, the ridge line joins several others and enters a ridge complex which turns north, culminating at Stuart Peak at an elevation of 7,945 feet.

The land form of the study area shows evidence of several types of geophysical changes. According to Alden (1953), the ridges and valleys to the north of the study area were sculptured by mountain glaciation.

A terminal moraine is present at the northeastern edge of the study area near the junction of Frazer and Rattlesnake creeks. Ancient Lake

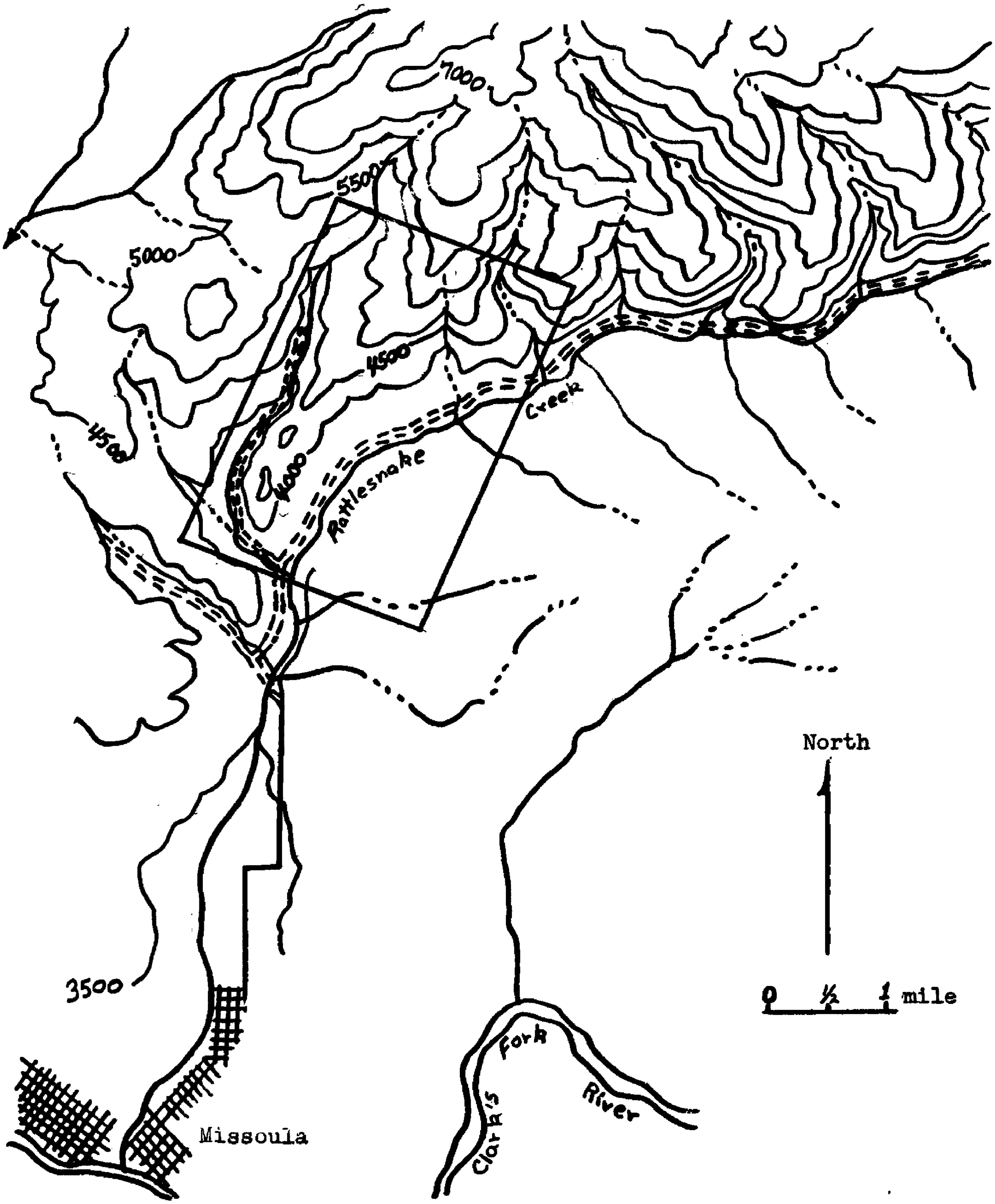


FIGURE 1. Rattlesnake Creek Drainage in the vicinity of the study area. Outlined portion contains the study area. Based on a portion of U.S.G.S. map of Bonner Quadrangle.

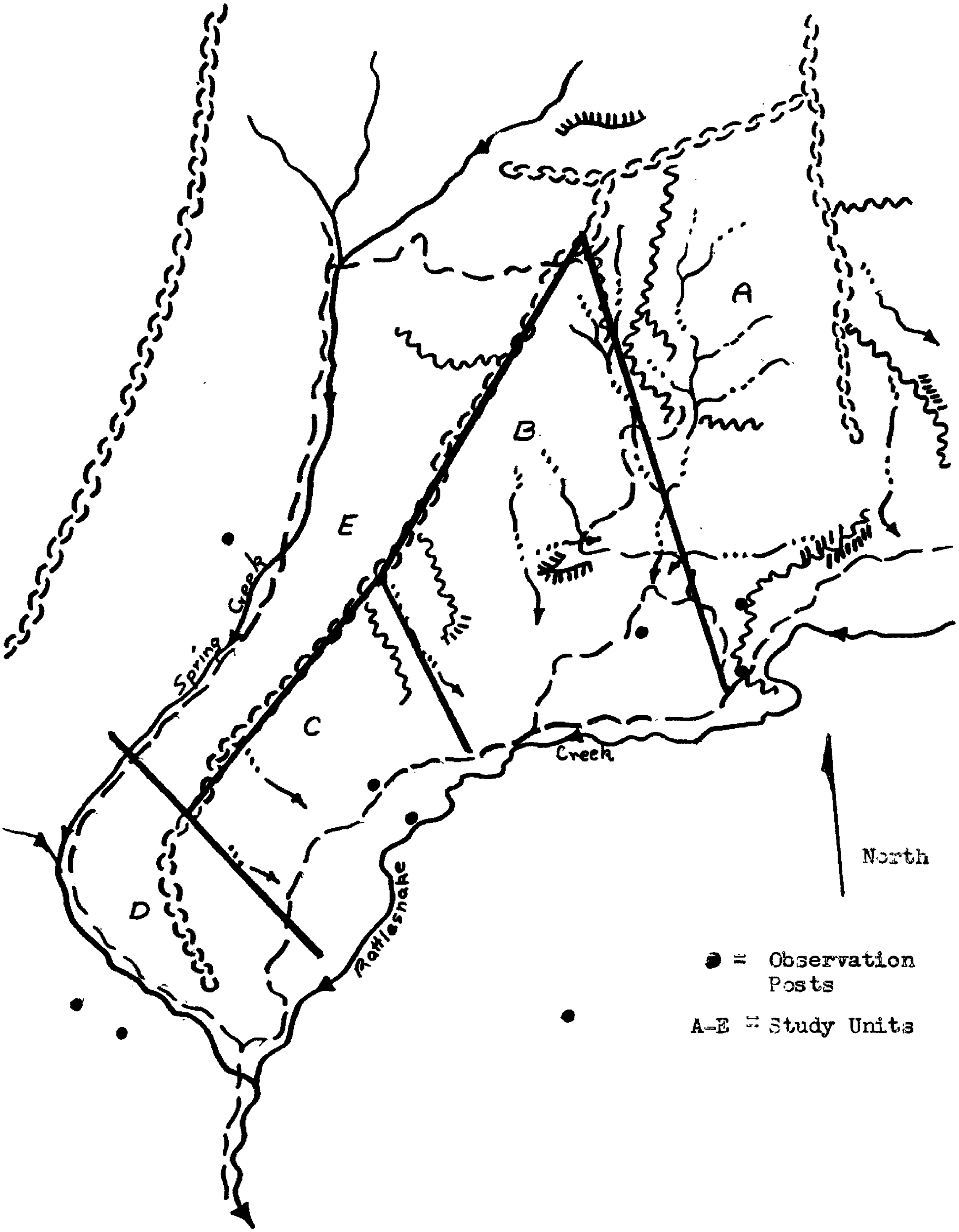


FIGURE 2. Wallman Ridge winter range study area. Based on 1955 Soil Conservation Service aerial photographs.

Missoula is believed to have extended northward to the base of this southern glacier and once inundated a portion of the present winter range.

In the upper portions of the study area, the steep topography is accentuated by rock outcrops and exposed slopes of loose sliding rock.

Vegetation. A previous study of the ecology and productivity of this winter range defines the flora present on the study area. The following description of the vegetation is taken from Klebenow's (1962) work.

The primary plant association is *Pseudotsuga taxifolia*/*Physocarpus malvaceus* with the drier sites supporting a *Pinus ponderosa*/*Physocarpus malvaceus* association (Daubenmire, 1952).

According to White (1958) and Klebenow (1962), the major portion of the study area was burned in 1919. This was the last known fire on the drainage. Succession is now proceeding and the browse types are giving way to the encroaching timber as the area moves toward climax timber type (Klebenow, 1962).

Most predominant browse species are snowbrush (*Ceanothus velutinus*) and ninebark (*Physocarpus malvaceus*), with other important shrub species being serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana* var. *demissa*), snowberry (*Symphoricarpos albus*), and spiraea (*Spiraea betulifolia* var. *lucida*). The grass and herbaceous plant classes are dominated by elk sedge (*Carex geyeri*) and blue bunch wheatgrass (*Agropyron spicatum*). Klebenow (1962) has compiled a plant list for the winter range study area.

The northwestern slope of Wallman Ridge designated as Unit E

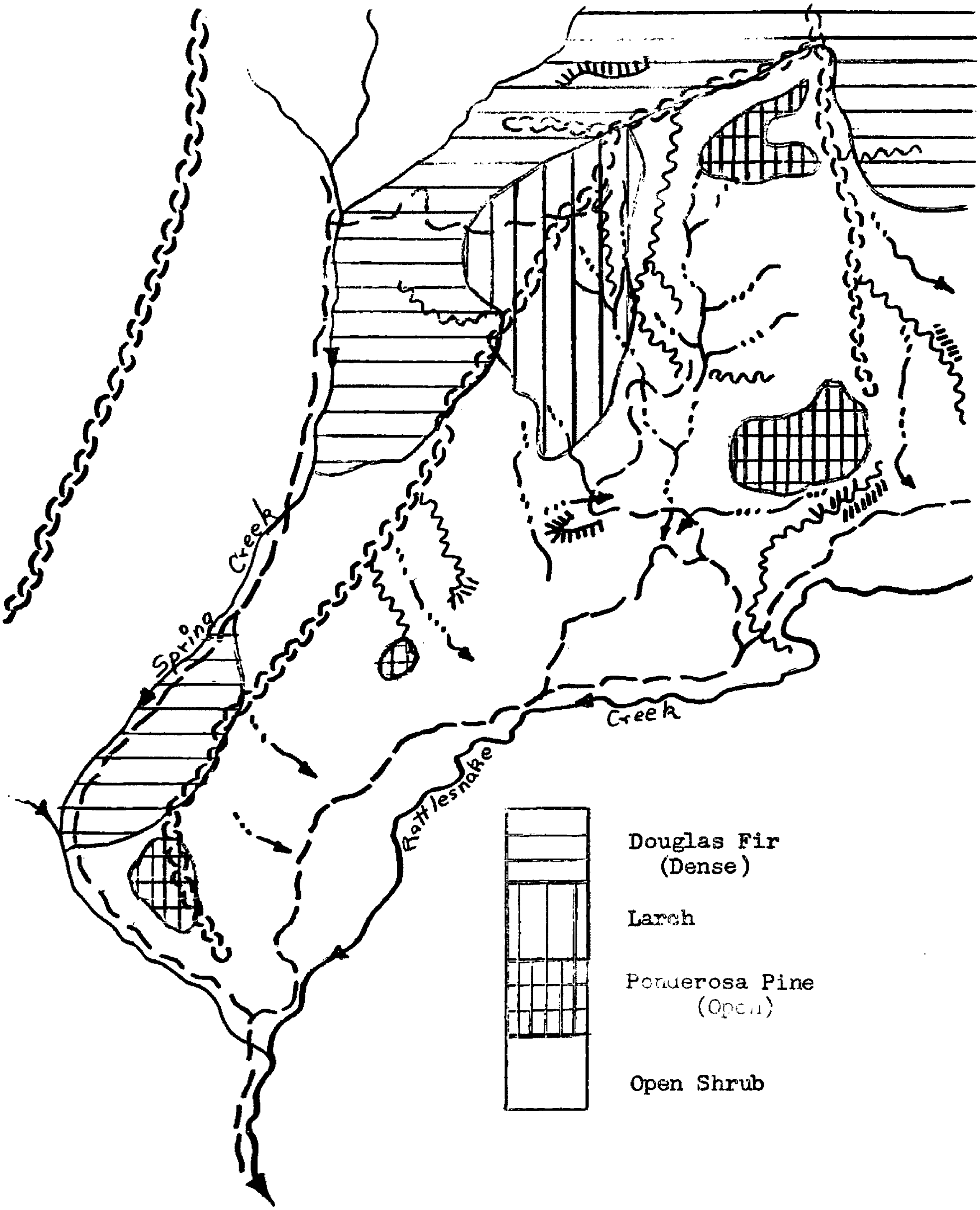


FIGURE 3. Distribution of woody vegetation on the study area.

(Figure 2 and Figure 3) is one of the more heavily timbered portions of the study area. This unit is dominated by Douglas-fir reproduction. Open and brushy areas are largely confined to the center and upper portions of the Unit.

Climate. Weather data were gathered from two sources: The U. S. Department of Commerce, Weather Bureau, Missoula County Airport, Missoula, Montana, which is located approximately 10 air miles southwest, and the Stuart Peak snow course which is located approximately 5 miles northwest of the study area. The study area is intermediate between these two extremes.

Precipitation at the airport ranges between 12 and 15 inches annually. The average from 1905 to 1961 was 13.86 inches. Rainfall accounts for most of the precipitation; May and June are the wettest months, approximately 2 inches of rain falls each month.

Approximately 5 inches of the total precipitation arrives as snow, between the months of November and April. Mean snowfall is 38 inches. In contrast with the weather station data taken at elevation 3,190 feet, the approximate average snow depth on the Stuart Peak snow course, 3½ miles north of the study area at 7,400 feet elevation, is 70-80 inches of which 30 inches is water (Codd and Farnes, 1962).

On the study area slope exposure modifies the effect of effective moisture and especially affects accumulated snow depths. Steep south and southwest exposed slopes are dry sites and are snow free for most of the winter.

Generally, the temperatures on the study area during the winter months have a wide range. Low temperatures of -23°F were recorded during

December, January and February (Figure 4). Between the cold periods, temperatures fluctuate into the high 30's and 40's. Warming trends in late March and April may result in high temperatures of 70-80^{o}F.

During the winter and early spring, cloudy periods of several days are common. Temperature inversions cause persistent cloud layers to form. During these periods, however, the study area may be cloudless. Air currents from the higher mountain elevations cause fluctuating cloud movements in and out of the main Rattlesnake Valley.

Winds are usually from the south-southwest, especially during warming trends in early spring. During periods of storm and in stationary weather, air movement is largely down valley from the high elevations.

History. White (1958) has described the early use of the study region by both the Indians and white settlers. According to this author, in the early 1900's there were several homesteads in the valleys bordering the study area. At the present time these homesteads are not farmed and the land is mostly owned by the Montana Power Company. The U. S. Forest Service is the other major land owner in the drainage.

According to White (1958), portions of Wallman Ridge were logged by select cut of western larch and Douglas-fir. In 1956, the bulk of Unit A was likewise subject to select cut (Bailey, 1960). Skid roads from this operation still penetrate the unit and make access to this portion of the study area an easier task.

During the summer months, logging trucks daily used the valley roads coming from the current cutting areas in the upper Rattlesnake drainage to the north. Easy access and proximity to the City of Missoula result in rather heavy use for recreational purposes. From spring to fall, the area is subject to a wide range of recreational use. Hiking, camping, target shooting, horseback riding, picnicking, sledding, cross-country skiing, parking, and hunting are all practiced during these periods.

According to White (1958), hunting was restricted to a buck only season until 1951, and either sex hunting began in 1952. During 1957, the first two-deer bag limit began. Hunting seasons during this period extended from October 20 to November 21. White (1958) estimated that in 1958, 40 white-tailed deer, 60 mule deer and 15 elk were killed in the drainage. In this season, 237 hunters checked through the temporary check station. The large proportion of these hunters were road hunters who drove through the area every evening after work (White, 1958).

In the 1960 and 1961 hunting seasons, hunting dates were approximately the same as White described. In 1961, the limit on deer was lowered to one animal, either sex.

It is believed that harvest of the herd which spends the winter on Wallman Ridge is light (White, 1958; Bailey, 1960; Klebenow, 1962). Klebenow (1962) reports that the ages of the kills reported by White (1958) indicate a light harvest, and further suggests that in view of decreasing range quality and area the wintering herd should be more heavily harvested. However, data obtained during this present study when compared with previous evidence (Bailey, 1960) indicates that hunter kill may be more substantial than supposed (see Discussion).

METHODS

A preliminary survey of the proposed study area was made in October of 1960. After a review of the previous work and findings of Bailey (1960), objectives were formed (see Introduction). To fulfill these objectives, the following methods were used or devised.

Observation. Binoculars and a spotting scope were necessary for observation of the animals from distances of 100 yards to $1\frac{1}{4}$ miles. The binoculars were 9 x 35 power and were used to locate the deer; then the 20-30x spotting scope was used to classify the animals, and to observe behavior and markings.

The study area boundaries lay between Spring Creek and Rattlesnake Creek, ending in the south at the junction of these two creeks and in the north at Frazer Creek (Figure 2). The study area was divided into five units (Figure 2).

To facilitate observation, six observation posts were chosen (Figure 2). The posts were chosen for a commanding view, maximum angle of view of the ridge top and proximity to the ridge. In 1961-62, a more flexible placement was used. In Unit A, it was found that if during an observation period no deer were observed, movement of the post to one or more alternate positions usually revealed deer in small pockets previously hidden.

After a few weeks' experience, it was found that the best observations were obtained from one hour before sunrise, until three hours after sunrise (Dasmann and Taber, 1956; Bailey, 1960). Afternoon observations were also taken, but the morning periods yielded better data.

Four or five days of each week were spent in observation. Saturdays and Sundays were usually spent on all-day trips through the area.

Recordings. Maps of the area, drawn from aerial photographs obtained from the Montana State Forestry Department, were mimeographed and used to note location of snares (see below), groups of deer, or movements.

In addition, dates and times of observation, weather conditions, numbers, sexes, ages, and groups of deer were recorded in a field notebook. Patterns of behavior were also noted. The criteria established by Dasmann and Taber (1956) were used to determine the sex and age of animals under observation.

Sketch maps were drawn on the spot whenever the mimeographs proved inadequate. These sketches were always keyed to identifiable landmarks.

Marking and snaring. Since the beginning of intensive study of large land mammals, methods of marking large numbers of such animals have been sought. Such a device should be cheaply constructed and, ideally, the animal should mark itself. This avoids constant maintenance of equipment by workers.

Ashcraft and Reese (1957) report the use of a catch and hold snare. Various authors have shown construction of ear and neck markers to distinguish individual animals (Progulske, 1957; Taber and Dasmann, 1958; Bailey, 1960; Arnold, 1962).

Automatic paint guns were developed by Clover (1954). However, the paint did not remain on the marked animal's hair for a sufficient period (Clover, 1954; deVos, 1957; Bailey, 1960; White, 1960).

Romanov (1956), Bailey (1960), and Arnold (1962) suggest the use of a break-away snare marker. Such a break-away device is one in which the animal becomes entangled in a snare. After the device locks securely, it is released and the animal is freed with a marking collar around its neck.

Due to the relative failure of the snare developed for the previous study (Bailey, 1960), it was decided that a new model needed to be devised and tested.

Several different modifications of the basic design were used throughout the period; however, the essentials remained the same. A 26-inch collar of cloth encased elastic shock chord formed the basis. A 3/4-inch steel ring was fastened to one end. A catch fashioned of No. 18 piano wire and formed in the shape of a broadhead arrow (with spring release sides) was attached to the opposite end of the collar. To the collar were attached various combinations of colored ½ x 12-inch plastic marking tape (see Appendix A).

To close the loop, 4 feet of No. 8 gauge soft galvanized wire was attached to the arrow point and run through the ring. The set of the snare was arranged at a narrow site along a deer trail. The snare was placed 26 inches from the ground or trail surface and the distant end was looped loosely around a nail or tied loop of fish line, attached to a tree. The snare was held upright by loops of light thread tied to branches. The soft wire was then filed three-fourths of the way through at a distance of 3 inches from the catch.

Unfortunately, no observed success was achieved with this model during the study period. During 1960-61, 62 snares were placed in the study area. Deer moving through the set sites, however, were not becoming snared. On the few occasions when snares closed successfully, they fell or were pulled off of the animal within 200 yards. In 1961-62, the improved model described was tested with 23 snares set. Indications were somewhat better. Six snares were disturbed and disappeared. One was later found 1-2/3 miles from the set site, but none were observed on animals, and it was assumed that they dropped off or were pulled or rubbed off. The weakness may lie in the stretchable rubber collar.

An attempt was made to use the natural markings method of noting individual animals as described by Bailey (1960) and White (1958). Repeated observations of animals noted in this way were few. It is assumed that this fact was due to lighting conditions and obstruction of the observer's view by brush. For all practical purposes, no animals were individually identifiable.

Weather data. Notations of weather conditions on the study area were made as mentioned under Recordings. In addition, weather data compiled by the Weather Bureau, Missoula County Airport, were used. Comparison of these data with that of Bailey (1960), which were taken on the study area, showed enough correlation to establish trends in conditions.

Snowshoe trips. Three trips were taken during the period of 1960-61 into the upper elevations of the drainage to observe snow conditions. Some of this area was designated by White (1958) as the summer range for portions of the deer herd under study. One of these trips in

March, 1961, encompassed Spring Creek, Stuart Peak, High Falls Creek, and Middle Rattlesnake Creek. During these trips, the paramount impression was of an area devoid of animal life. Small mammals and large predators do winter in this upper area but the 10-15 feet of snow cover is too deep for ungulates. Only in the middle reaches of Spring Creek and lower elevations of Middle Rattlesnake Canyon was there any sign of ungulate presence, and these traces were few and seemingly wandering.

Air surveillance. In February, 1962, an aerial trip was made over the study area. The ground covered by the low level flight included the study area (in detail), and the Rattlesnake Canyon and all the tributary valleys of the Upper Rattlesnake Creek drainage. It had been previously suggested that current logging operations in the valleys of the Upper Rattlesnake Creek might provide slash cuttings of such quality as to concentrate deer and cause them to remain past normal migration times. Sudden storms might trap the deer in these areas, but no deer were seen in this snowy canyon; only the tracks of mountain goat were noted along rocky ledges.

Simultaneous observations. Due to the difficulty of one man obtaining adequate observations on an area of this extent and the impossibility of 100 percent coverage, it was suggested that a group of men observing all aspects of the area at one time might aid in establishing population levels and counts from which trends could be estimated. Beginning in February, 1961, three counts of this sort were made during the study year. The participants numbered from four to six. In 1961-62, the group observations were begun in December with four men. The last such count was in February, 1962, with nine persons cooperating. Data obtained in this way are especially valuable in making estimates of population size, as practically the entire population of the study area was included in such an observation period.

RESULTS

Deer herds as natural living animal groups are greatly affected in their movements, groupings, and behavior patterns by weather conditions and other environmental factors (Leopold et al., 1947; Fowle, 1950; Edwards and Ritcey, 1956; Woodbury, 1956; Bailey, 1960).

Weather

Local conditions. A comparison of weather conditions during the 1960-61 and 1961-62 winters exhibits two markedly different sets of weather data (Figure 4).

Temperature: The general picture of winter temperatures on the study area shows that a cooling trend begins in November and continues throughout December into January. A warming trend begins in February or March and increases throughout April.

During the study period, minimum temperatures rarely were recorded above freezing, and the lowest minimum temperatures occurred in January each year. Large fluctuations between months were apparent in maximum temperatures.

The temperature pattern seems similar for both study years; however, a detailed comparison of the data reveals several pertinent contrasts in temperature.

1. All months during the winter of 1961-62 were colder than the corresponding months the previous winter.

2. Maximum temperatures during November 1961 were considerably

lower than maximum temperatures during November 1960. The lower maximum temperatures allowed snow to accumulate.

3. In 1961-62 there were two periods of extreme cold. The first cold period occurred in early December 1961; the second occurred in mid-January 1962.

4. A general warming trend began in February 1961 and continued into April 1961; however, in 1962 a general warming trend did not begin until March.

Snow: Snow depth is correlated with temperature conditions and snowfall. Snowfall was not equal for both winters (Figure 4, Table 1).

In general, more snow fell in 1961-62 than in the preceding year. The important difference between the periods, however, is not the total snowfall but the period during which it fell. During 1960-61 snow fell periodically throughout the winter, but did not accumulate due to periods of warm temperatures between the snowfalls. No snow fell for four weeks during January 1961 and temperatures were relatively high; as a result critical snow depths did not occur.

A large amount of snow fell during November 1961, and due to low temperatures it failed to melt. Snow continued to fall in large amounts throughout December 1961 and January 1962. Low temperatures in January 1962 caused most of the snow to accumulate. The crucial snow condition of the season occurred during January 1962. By the end of January the study area had a deep snow cover; the effect of this on the deer was to severely limit their optimum range and to place them under increasing physical stress.

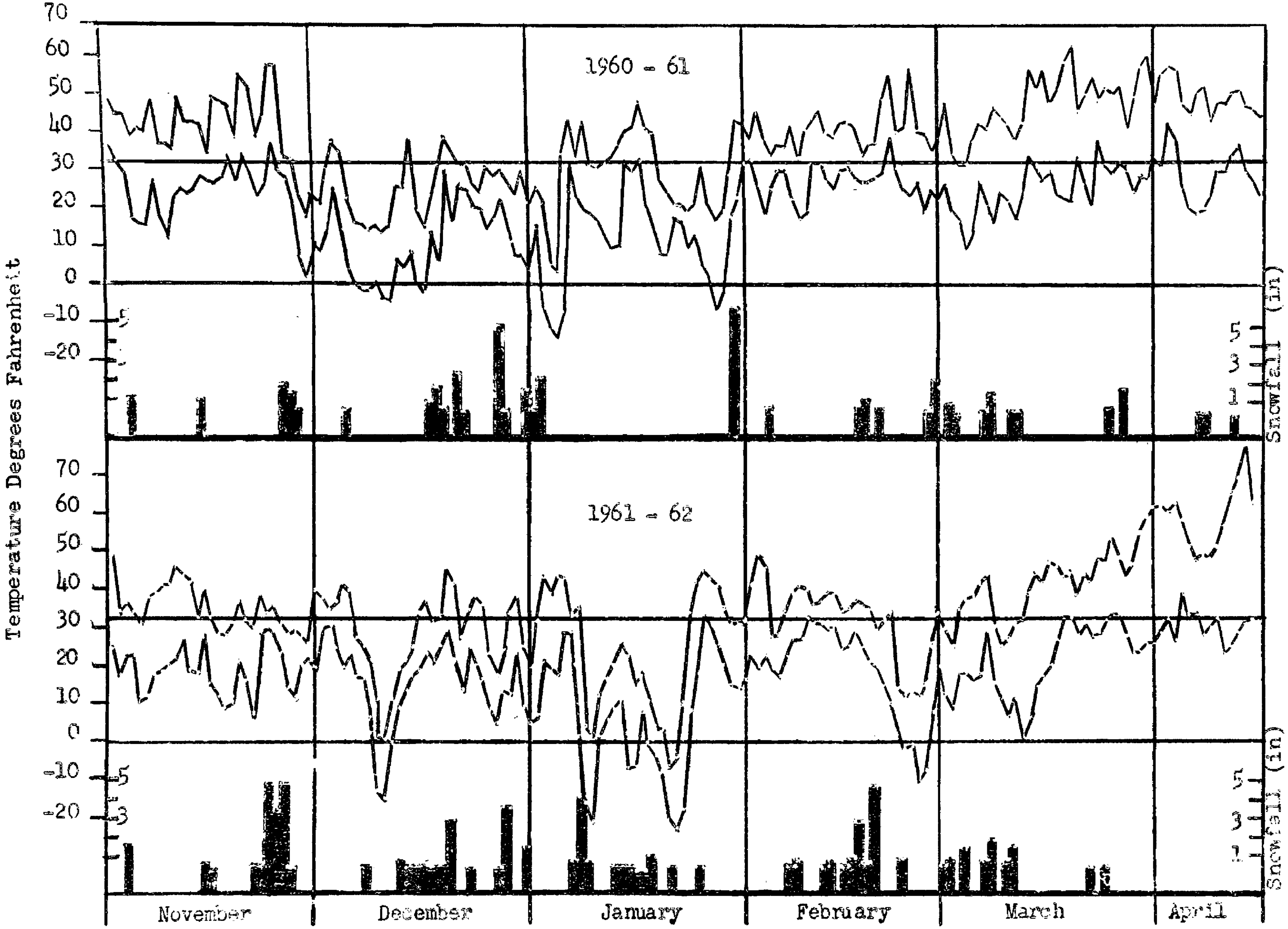


FIGURE 4. Daily minimum, maximum temperatures and snow fall at Missoula County Airport. 1960 - 61 and 1961 - 62. Figures compiled from U. S. Weather Bureau data.

TABLE I

SNOWFALL AT MISSOULA AIRPORT IN INCHES

	1960-61	1961-62
November	5.1	15.1
December	11.7	11.3
January	7.9	10.0
February	3.3	10.4
March	5.2	6.9
April	4.7	0.0
Total	37.9	53.7

Study area conditions. The study area, located in the first ridges leading to the main mountain formations, is influenced by cold air drainage from these higher regions. Heavy cold air moves down from the high mountains and flows into the valleys, displacing lighter warm air which rises. During general warming periods, the foothills tend to retain snow cover longer and remain colder than the valley floor.

The same cold air drainage causes a build up of cold air in the valley. When warm air moves into the region and flows over the valley, cloud covers form where the two air masses meet; this remains for several days.

Comparison of U. S. Weather Bureau data with that recorded by Bailey (1960) shows close correlations at extremely low temperatures and wide discrepancies at high temperatures. Apparently warming trends affect the valley floor temperatures drastically, while cold air flowing against a thermal gradient maintains lower temperatures in the foothills. Continental cold air masses moving into the region flow over the whole area more equally, and minimum temperatures are closely correlated. In general, fluctuations are less extreme in the lower mountain areas than in either the valley floor or the high mountains.

Snow cover: A marked response to the composite of local conditions is seen in a comparison of snow accumulation on the study units between the two seasons (Figure 5).

Conditions during the 1960-61 season justify designating that season as an "open" winter. Low snow depths coupled with a warming trend in mid-December allowed south and southeast exposures to clear. The mild January weather again allowed clearing. Snow remained on north slopes in only three units of the study area. One deep snow during January delayed this snow-melt for only a few days. By mid-February, four units (A, B, C, D) of the study area had only spotty snow cover. Snow remained only in pockets and on north exposures. The four units became completely clear of snow on all exposures by late February. Snow depths accumulated over 1.5 feet on the study area during 1960-61 only in restricted areas. March snows formed a shallow cover which lasted a few days, and by mid-March all four units (A, B, C, D) were again cleared of snow.

The 1961-62 season was completely different (Figure 5). The deep snows of November and early December remained throughout the warming trend in mid-December. Cold stabilized the snow cover for long periods.

The extended cold in mid-January, coupled with snows during this

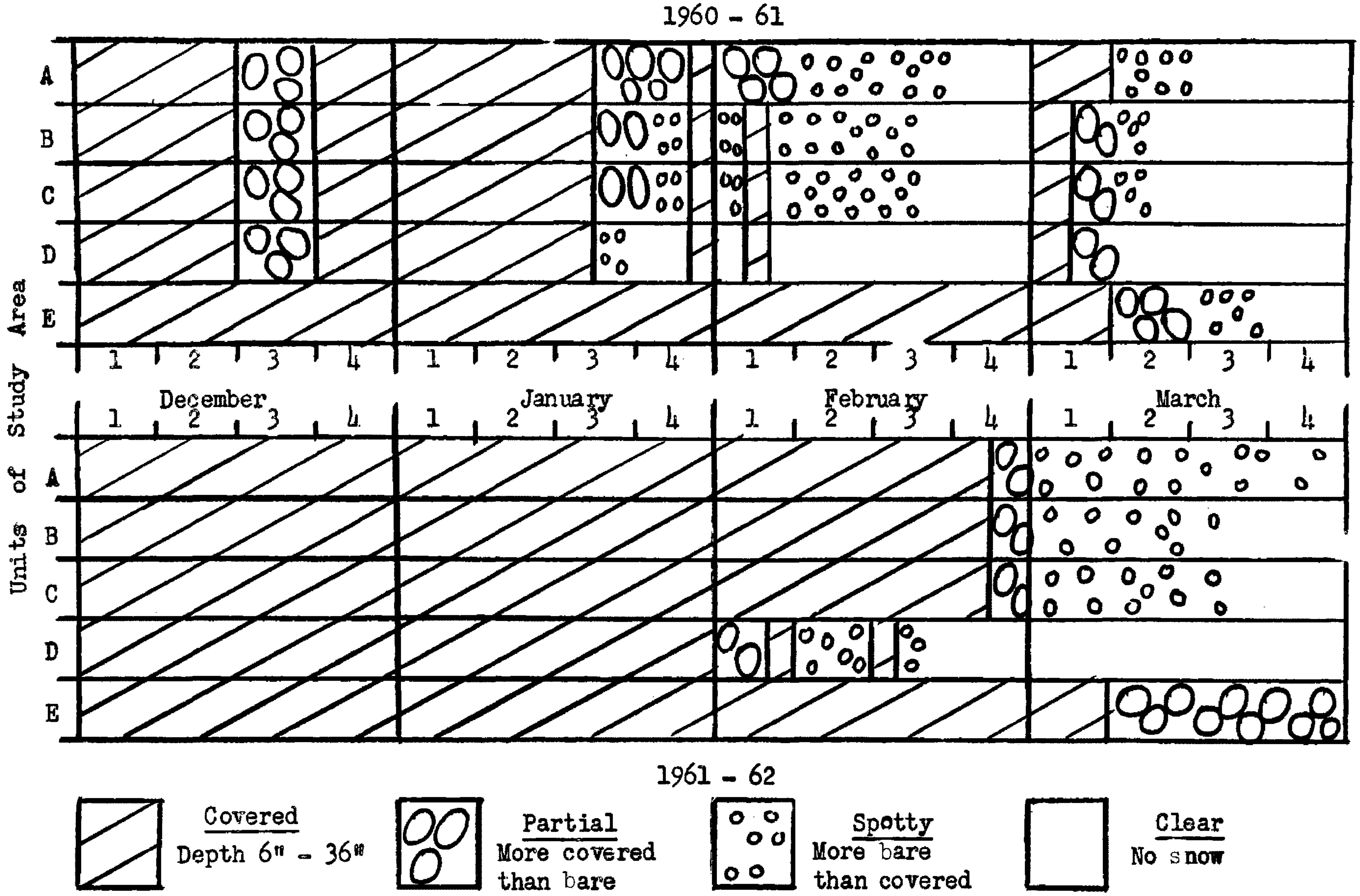


FIGURE 5. Snow cover on the study area during 1960-61 and 1961-62.

time, was the major deciding factor in forming the snow cover of the season. Two weeks of accumulating snows followed by a week of stationary conditions left the area deep in fresh, soft snow. Depths reached 3 feet on the ridge top and in the valley of Spring Creek. Levels of 2 to 2.5 feet were common throughout Units A, B, C and E.

February was a month of fluctuating snow depths. During this time, the first unit began clearing. By the end of the month, four units were clearing. This trend continued through March and by the last of the month all units were completely clear of snow cover.

The units of the study area must be considered separately in an analysis of results. The differences in snow cover on the study units stem from differences in exposure and snowmelt, since snowfall is apparently much the same on all sites. Slope exposure strongly affects maximum temperatures (Shanks and Norris, 1950). Cook and Hamilton (1942) state that the sun's rays are twice as intense on south slopes as they are on level ground. As a result, the units differ greatly in snow cover throughout the year (Figure 5). Important factors of this picture of snow cover are outlined below:

Unit A--This unit has a south-southwest exposure; is located furthest up the valley; it is the highest of the units. In 1960-61, this area began clearing in December, the snows of mid-January did not last long and the area became completely clear in late February (Figure 5). In 1961-62, in contrast, this unit remained snow covered until late in February and did not clear until April. Even during this period, however, the extreme southern end of the unit was never covered except for a few days at a time. This clear area comprised only a few acres.

Unit B--This unit has a southeast exposure and a lower elevation than Unit A. It clears of snow cover a few days prior to Unit A.

Unit C--This unit has a more southeastern exposure and is lower in elevation. It is the second unit to show clearing, and is similar to Unit B. In 1960-61, it began clearing in December, again in mid-January, and was completely clear by mid-February. In 1961-62, the unit remained covered until late February and was completely clear in mid-March.

Unit D--This area has a south-southwest exposure and accumulates the least snow cover of all units. Some areas on this unit clear within a few days after a snow. In 1960-61, this unit completely cleared in mid-January. In 1961-62, the unit began clearing in early February and became completely clear in mid-February. In both years Unit D cleared of snow before all other units.

Unit E--This unit is exposed to the northwest and, as a result, has the deepest and most persistent snow cover. The unit shows clearing only by mid-March and does not become completely clear until the end of March or mid-April.

There appears to be a direct correlation between altitude, exposure to the sun, and snow depths.

Snow surface conditions: Pruitt (1960) states that snow surface conditions and snow depths are important to ungulate populations. The condition of the snow surface is a result of temperature, snowfall, and wind. Warm daytime temperatures cause the snow surface to melt, freezing nighttime temperatures then cause a heavy crust; the texture of the snow becomes hard, granular, and icy. The thickness of the crust is proportional to length and intensity of the warm period. A heavy crust may be covered by fresh snow or may form a cover over soft snow if melting is incomplete.

The condition of the cover surface was quite similar during both study years (Figure 6). Both were typified by long periods of melting and resulting heavy crusts in the night and morning, with the snow becoming soft throughout the day. The snow surface conditions observed during this study were only rarely dense enough to support the weight of an adult deer.

The one major difference was apparent during the month of January 1962. A period of cold and deep snows left a condition of heavy crust covered by more than 12 inches of soft snow. A melting period late in the month formed a crust on the surface. In early February, a cold wave caused a heavy crust on the surface of 24 inches of snow.

General considerations. The outstanding differences in environment between the two years seem to depend on temperature and snowfall. In 1960-61, fluctuating cold and warm periods occurred, and snows were so interspaced in these periods that little snow accumulated. The result of all factors was an "open" winter in which snow depth did not exceed 15 inches and slopes cleared early.

In 1961-62 early November storms deposited a deep base of snow. Continued heavy snows in December and January added to this base. A thaw in late January and following cold periods developed a heavy crust over 24 inches of snow. Due to deep snow and low temperatures, slopes did not clear until March.

Bailey (1960) in his work with the Rattlesnake deer herd, could

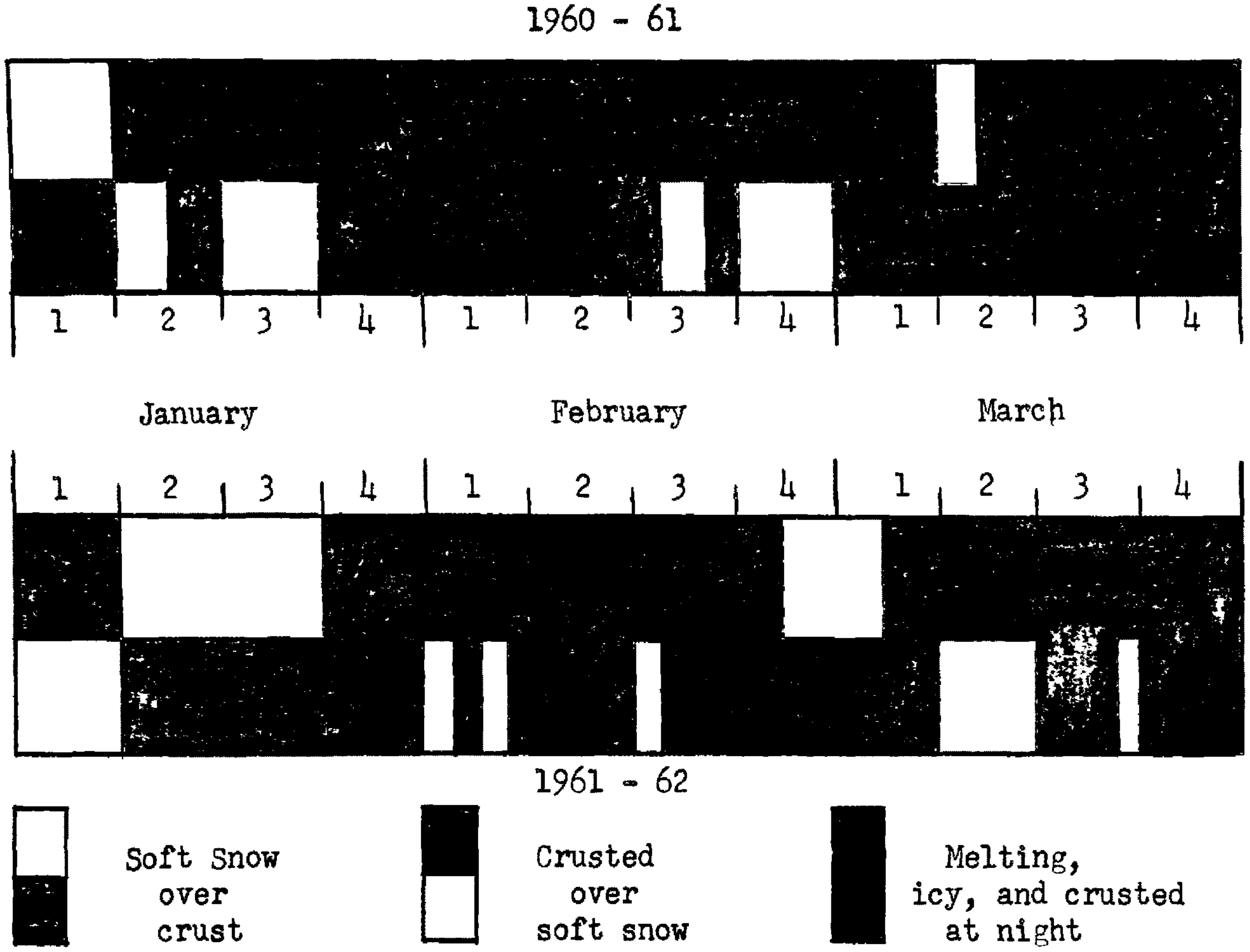


FIGURE 6. Snow surface conditions on the Wallman Ridge winter range during 1960 - 61 and 1961 - 62.

find no correlation of deer activity with temperature, and this factor was not investigated during the present study. Bailey (1960), Darling (1937) and Linsdale and Tomich (1953) found humidity to make deer inactive.

Wind was a factor during 1961-62. Several days of high winds occurred during the January cold period. In these periods fewer numbers of deer were observed and it is assumed that they had moved into the timber. However, single day periods of wind did not seem to affect the populations or their movements. Rain occurred frequently throughout 1960-61; this did not seem to affect the animals.

Populations

Numbers. The populations of deer observed on the study area varied during the study period. A few deer are resident there (Figure 7). In October, 1960, five mule deer were observed in the upper regions of the study area. In July, 1961, four mule deer were seen in the same area. An estimated maximum of ten animals comprises the non-migratory population.

From these low population levels, herd numbers steadily build until maximums are reached in February and March. In 1961, a maximum of 80 animals was observed on the study area on February 26. During the 1961-62 period, a maximum of 132 animals was counted on March 17.

Maximum observations at two periods during each month were graphed (Figure 7). These maximum observations are believed to approximate the true population.

However, there is a possibility that the January and early February

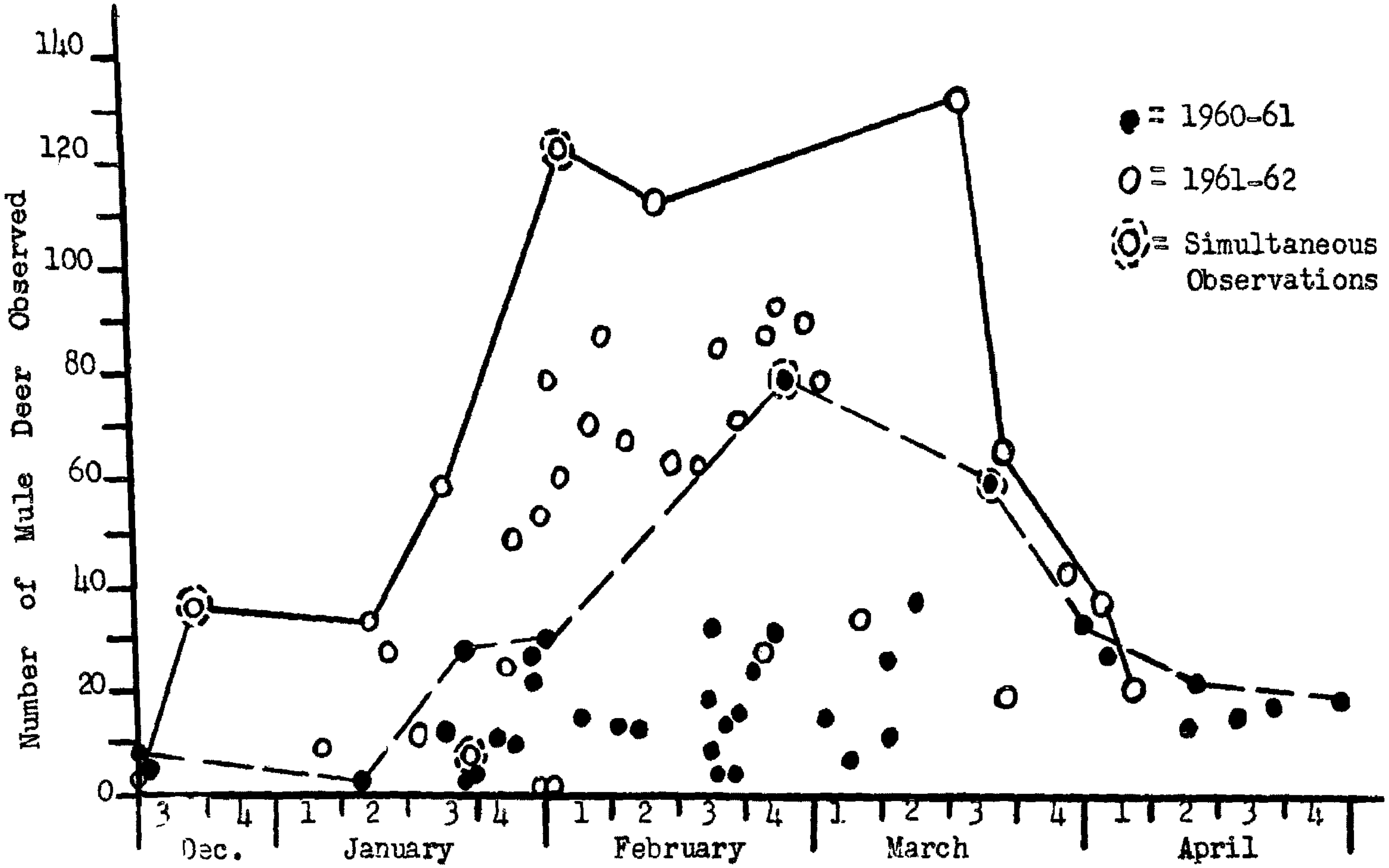


FIGURE 7. A comparison of Mule deer populations on the Wallman Ridge winter range during 1960-61 and 1961-62. Connecting lines represent bi-monthly population trends.

counts for 1961 may be underestimates. During this period, Unit E was not explored. Simultaneous counts in late February on all units, including Unit E, produced the maximum numbers which approximate the total wintering mule deer herd using the study area.

The mule deer population wintering on the study area was larger in 1961-62 than in 1960-61. During this second year of study, more accurate population estimates were made because of the investigator's experience and familiarity with the study area. However, the differences observed between the two years were undoubtedly due to actual population levels rather than observational error. It seems apparent that the numbers of animals using the winter range in 1961-62 were at least 50 percent greater than populations of the preceding year, and resulted from deer forced by more severe weather onto the study area from surrounding less optimum areas.

Composition of populations. Any consideration of populations of animals is incomplete without an analysis of the sex and age composition of the population. The composition of the study population was derived by totaling the sex and age observations for two week periods. Rarely were all observed animals classified. Observation samples of deer groups were taken when large herds of animals were present.

An attempt was made to use the classifications of Dasmann and Taber (1956) to separate the animals into sex and age groups. However, the yearling population was not analyzed separately. After repeated attempts at observation, it was found that consistent results were not obtainable because the long distances and poor light conditions, as well as the near adult size of the animals at this season of the year, introduced large errors in judgment. Bailey (1960) also encountered this same difficulty.

The percentage of male mule deer using this winter area was approximately 29 percent of the population. The percentage was stable throughout each winter (Figure 8) and was similar for both study periods (Table II).

TABLE II

AVERAGE WINTER RANGE POPULATION PERCENT COMPOSITION BY AGE AND SEX

	1960-61	1961-62
Males	29.7	28.4
Females	46.5	42.0
Fawns	23.8	29.6

The female composition, on the other hand, varied between the two periods, but was relatively stable throughout each year. One exception was a low level of females in early April, 1962. It is possible that this shift represented a partial movement of females from the area, coincident with migration and approaching birth of fawns. This period was typified by high temperatures with snow clearing in the upper drainage areas. In general, the proportion of females in the population is approximately 44 percent of the herd. This figure includes yearling animals. The proportion of fawns (the third category) in the population averaged 24 percent in 1960-61 and 30 percent in 1961-62 (Table II, Figure 8).

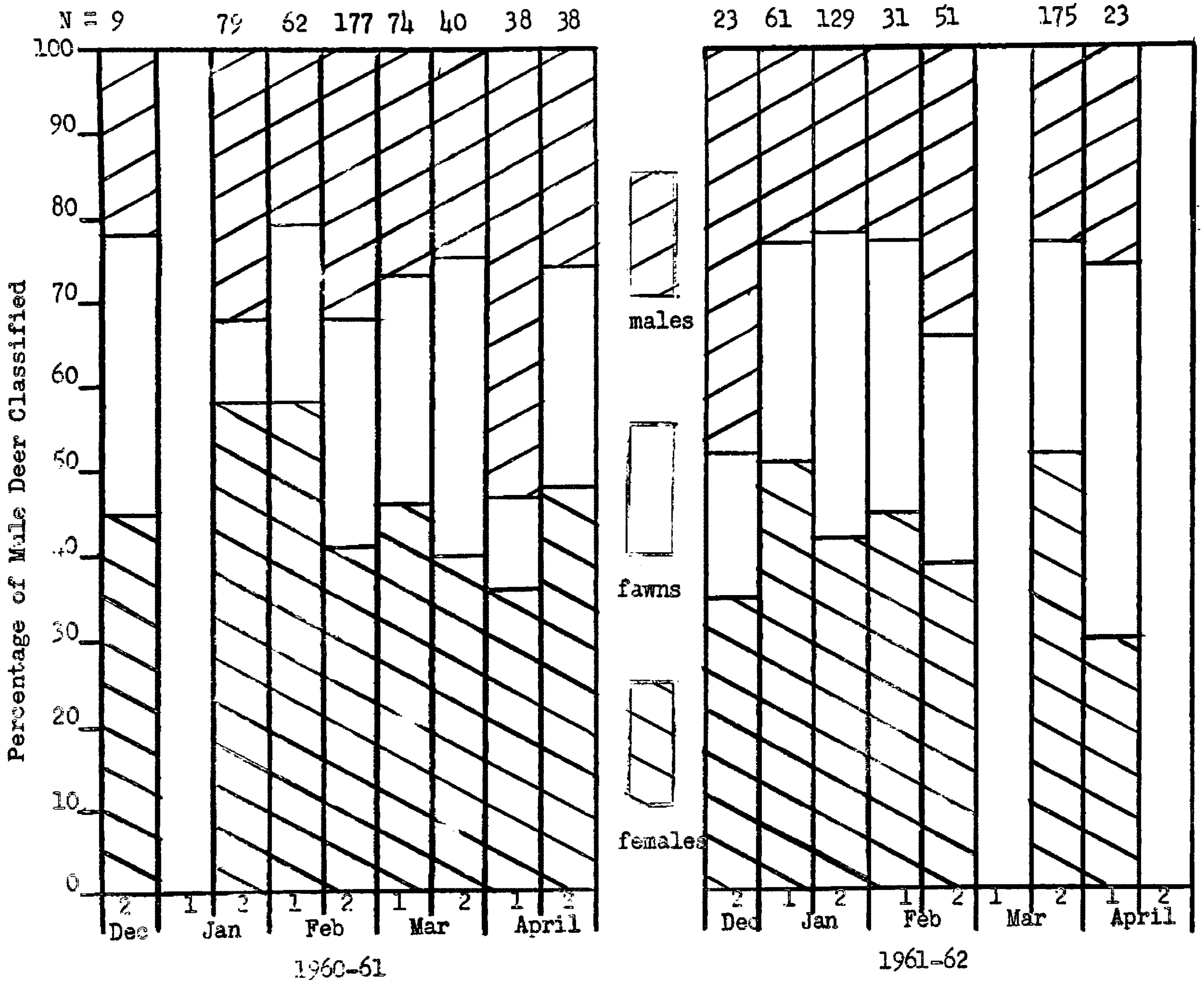


FIGURE 8. Sex and age composition of the mule deer population during 1960-61 and 1961-62

There appears to be no observational evidence of severe winter mortality in the herd during the study period. Only four carcasses were found in the two years; three of these were adult animals. Even though the second of the two study years presented deep snow conditions, mortality was lower than that reported by Bailey (1960) who found 12 carcasses on the study area from 1958 to 1960. He reported that a major portion of deaths were in the fawn age group. The differences in mortality from year to year are further discussed below (see Behavior; Predators).

Groupings. During the study period animals observed were categorized by sex, age, and number of animals in each group. A group was considered by the observer to be a single unit if the distance between members of the unit was less than the distance to surrounding individuals or units.

Sizes of groups: Group size was categorized as follows: 1, 2, 3-5, 6-8 and 9+ animals. This classification is derived to include most common combinations of association. Single animals of both sexes are common. Groups of 2 animals include male pairs or females with fawns or yearlings. Groups of 3-5 include male groups; females with fawns, yearlings, and possibly two year old females with fawns. The higher numbers represent combination of these groups.

Animals in groups of 3-5 were most common (Table III, Figure 9). However, this relationship was not constant throughout the study period. On the winter range mule deer have a cycle of group size, as follows: high frequency of small groups and single animals in the late fall; increasing frequency of larger groups during February and March; a return

TABLE III

PERCENT FREQUENCY OF MULE DEER GROUPS OBSERVED ON STUDY AREA DURING BIMONTHLY PERIODS

	Group Size													
	1960-61							1961-62						
Period	1	2	3-5	6-8	9+	n	$\bar{x}$*	1	2	3-5	6-8	9+	n	$\bar{x}$*
Dec. 2	50	17	33	0	0	6	2.0	28	18	36	09	09	11	2.54
Jan. 1	--	--	--	--	--	--	---	15	23	23	16	23	13	2.07
2	26	26	35	10	03	39	2.38	19	27	45	07	02	61	3.13
Feb. 1	12	20	44	12	12	16	2.93	14	16	27	11	32	44	3.31
2	19	11	43	21	06	48.	2.85	09	14	20	18	39	44	3.86
Mar. 1	21	08	46	21	04	23	3.00	41	10	24	10	15	29	2.44
2	25	0	12	44	19	16	3.31	15	24	40	15	06	54	2.72
Apr. 1	41	13	36	05	05	22	2.18	45	30	15	10	0	20	1.90
2	30	25	45	0	0	20	2.15	--	--	--	--	--	--	---
$\bar{x}$	26	15	37	14	06			23	20	29	12	16		

*= Relative Mean; Groups 1, 2, 3-5, 6-8, 9+ were weighted 1, 2, 3, 4, 5, respectively.

n = Number of groups classified.

to high frequency of small groups in the spring (Figures 9 and 10).

This annual grouping cycle is caused by weather conditions on the winter range (Figure 4). The 1960-61 season was typified by the greatest number of single animals and a high frequency of small groups. Occurrence of the 9+ category was sporadic and infrequent. Groups of 3-5 were prevalent throughout January and February. Late March found a shift to

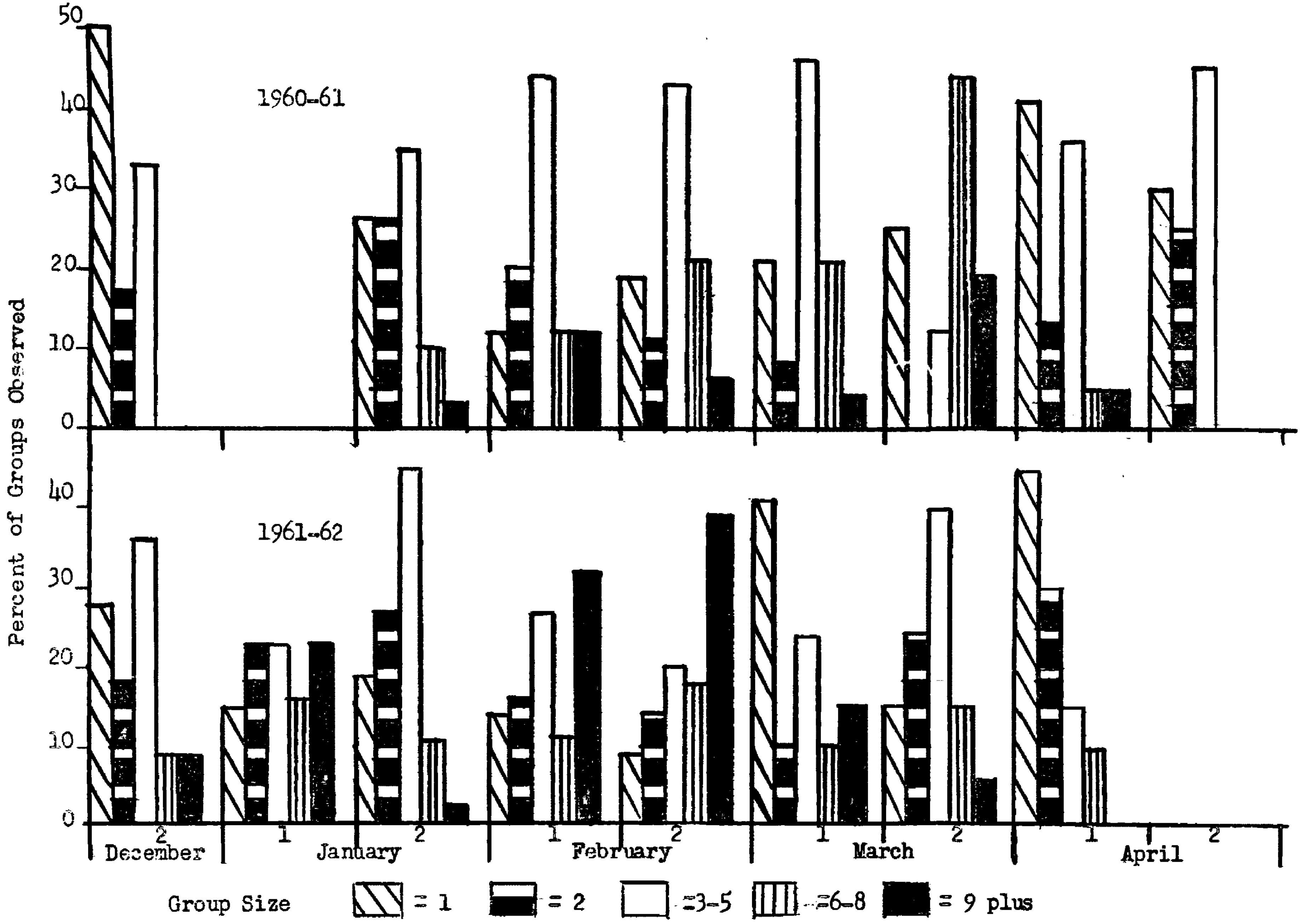
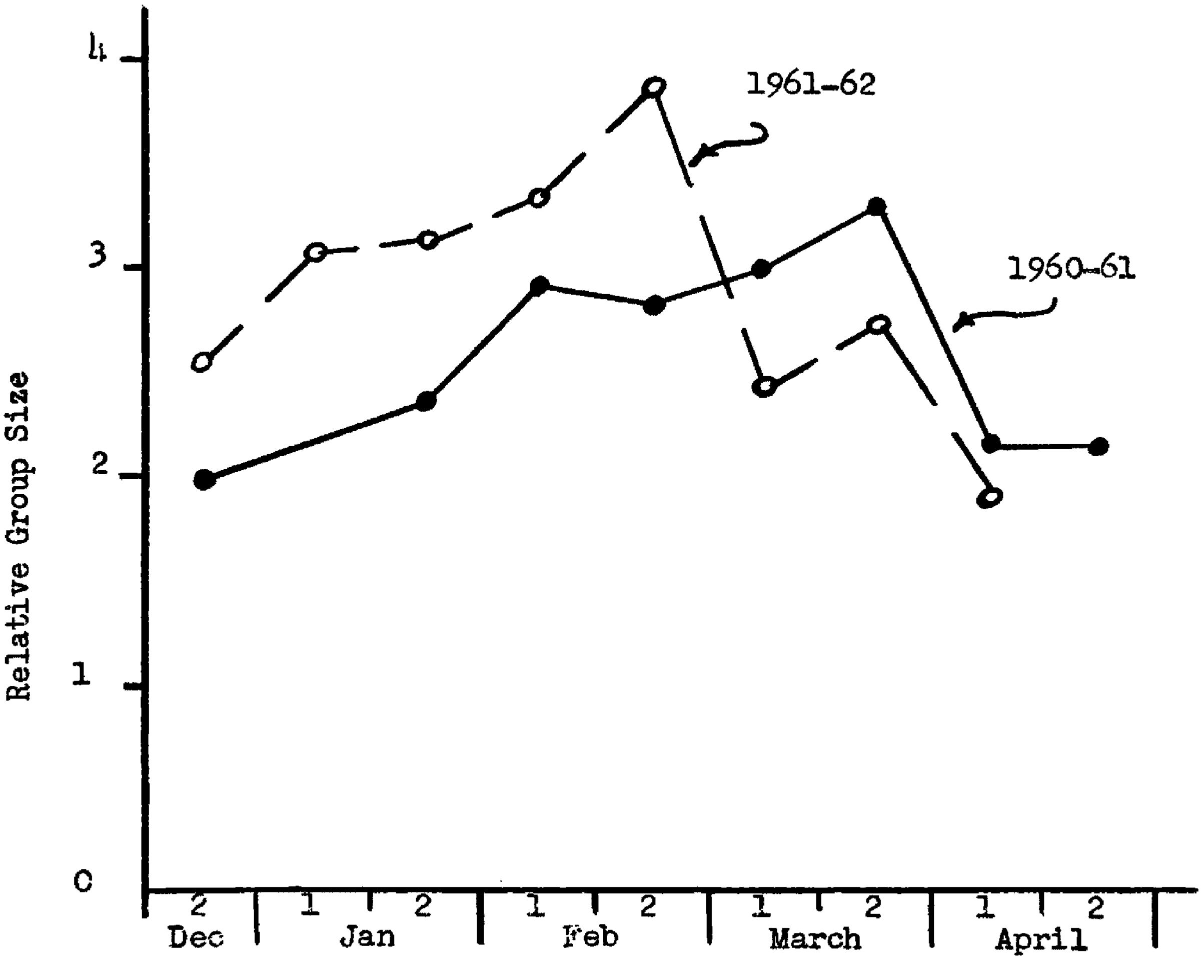


FIGURE 9. Observed frequency of mule deer groups.



Weighted Group Sizes

1 = 1   3 = 3-5
2 = 2   4 = 6-8
5 = 9 plus

FIGURE 10. A comparison of relative average sizes of mule deer groups during 1960-61 and 1961-62.

groups of 6-8 and larger. Groups of 3-5 were high in frequency for the remainder of the year.

In contrast, 1961-62 was typified by fewer small groups and few single animals. The important point is the high frequency of groups of 9 or more. The latter classification was prevalent throughout February and March. After the peak occurrence of larger groups in February, an abrupt shift to single animals was apparent (this factor might indicate a reaction to long periods of close association). The increased frequency in 1961-62 of large groups may be due to restricted optimum range rather than choice association.

Composition of groups: The preferred grouping of animals into sex and age classes is reflected in the group size. Relationship of animals within the groups is an important factor determining association:

1. Male segment. Male deer tend to be found alone or in all-male groups. Of all male animals observed, the largest proportion are found in association with other males (Figures 11 and 12). The occurrence of single males varies throughout the year and between study years (Figures 11 and 12). The total percentage of all single males to all groups observed was relatively constant, although lower during 1961-62. The observation of single males, like the occurrence of small groups, appears inverse to the severity of the weather conditions.

Single males decreased steadily during 1961-62 until the peak occurrence of large groups. Then single males were again sighted more frequently. The decrease in lone male occurrence during late March and April appears to be due to beginnings of migrations.

2. Family segment. Female animals were rarely observed alone

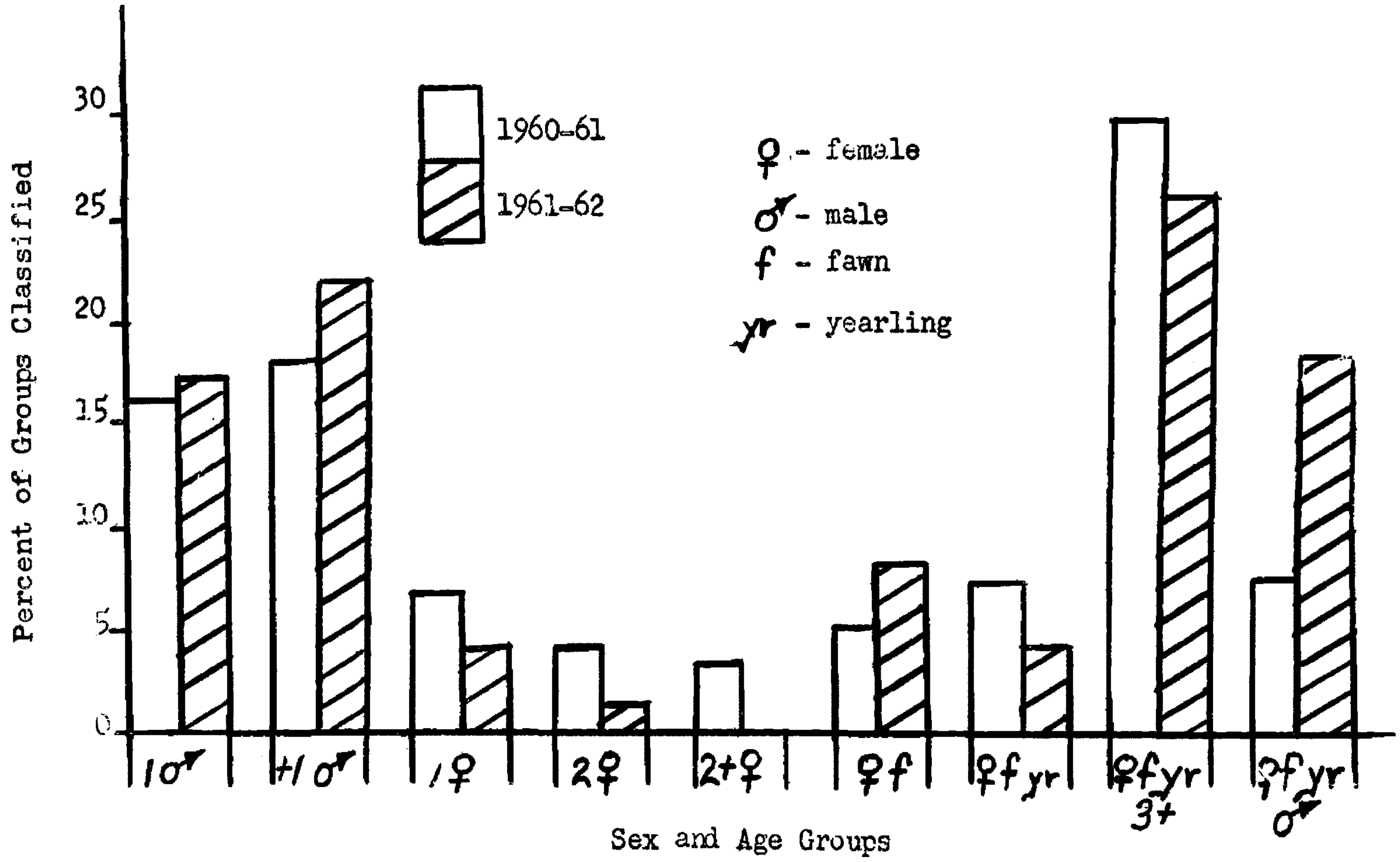


FIGURE 11. Percent frequency by age and sex of mule deer groups observed.

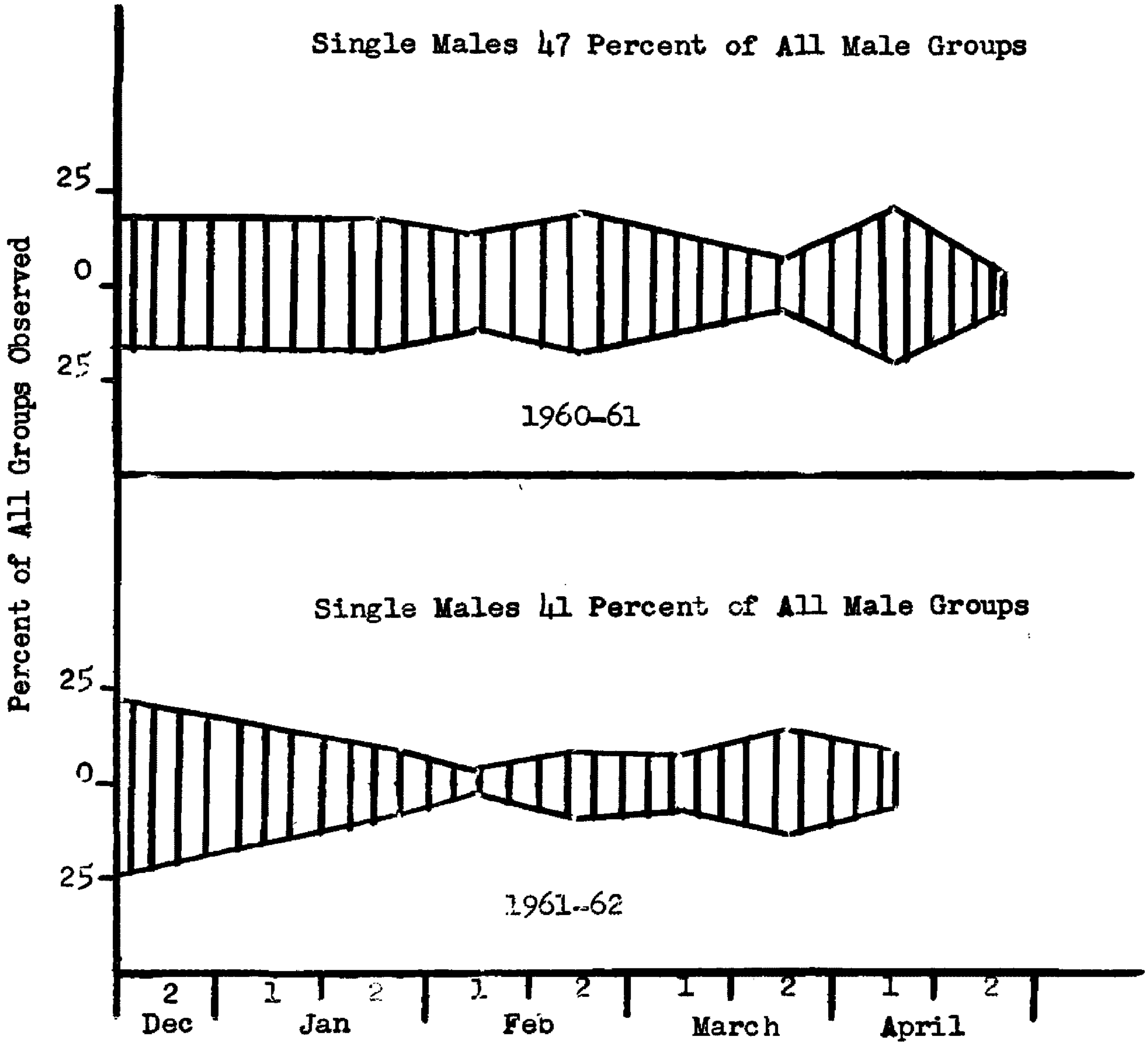


FIGURE 12. Percent frequency of single male and all male mule deer groups observed on the study area during 1960-61 and 1961-62.

or in all female groups (Figure 11). Occurrence of female-fawn or female-fawn yearling groups also were infrequent. Females were most frequently observed in groups composed of two or more females with accompanying fawns and yearlings. The exact composition of this group was highly variable, but was never composed of all females, all fawns, or all yearlings. This grouping appears to be the family association described by Bailey (1960).

Within these large fluctuating family groups, the association of a female and her fawn of the year was always apparent. The group moved together and remained in close association, yet the female-fawn relationship seemed to be a unit or group within a group. Rarely did the fawn move any great distance away from the female. It ate, played, bedded, and moved in close association with the doe. In flight situations, it moved in imitation of its parent. From observation, it is concluded that the fawn-doe group is the strongest, most basic association.

Late in the winter season, the attachment of the male fawn to the doe decreases in strength. Male fawns associating with all male groups were first observed in February 1962. These animals seemed to be accepted and at least tolerated in the male society.

Adult male animals are occasionally observed mixed with the larger family groups. The occurrence of groups with males and females was correlated with the buildup of large units of 9+ in size. This frequency of occurrence of mixed groups appears inversely proportional to observation of single males.

In mule deer the family group of three to five females and fawns is the most common group. Male mule deer are either solitary or associate most often with other males. Under stress and decreasing optimum winter range, large intermixed groups will form, due to physical association and not due to innate behavior. These large intermixed groups will dissolve as soon as the optimum range increases.

Movements

Migratory movements. A good analysis of migratory movements of large land mammals necessitates marking of sample individuals. Marking of animals on this study failed. As a result, analysis of migratory movements must be indirect.

The population changes on the area throughout the year apparently are due to migratory movements. The resident population of ten animals increases to 80-132 animals within two months' time. Two months after peak populations, the numbers of animals on the area return to pre-winter levels (Figure 7). No single period can be designated as the definite migratory period. Movements down to the winter area occurred throughout December and early January, and movements back to summer range occurred throughout late March and April.

The location of the summer range of this herd is a matter of conjecture. White (1958) stated that the mountain slopes of the Upper Rattlesnake Creek and Stuart Peak area constitutes the summer range for part of this herd. Bailey (1960) also supported this statement. The reasoning remains logical but unsupported.

However, local terrain features make access to this winter area a natural feature for animals spending the summer at higher elevations above this range. No well defined trails or observed movements suggest migration routes that would cross the drainage basin and begin in any other topographic features.

Non-migratory movements. Once the animals arrive on the winter range, they exhibit shifts in areas of utilization which are of a local nature. Observations of animals and groups were plotted on maps of the study area. These data were used to construct population tables of animal numbers on the various study units (Table IV).

The animal population within study units followed the general pattern of the population curve for the whole study area. Yet, within the study units, local shifts in utilization are quite abrupt. Such a shift between areas may necessitate a move of only a few hundred yards or a quarter of a mile. Use of the various units was observed to change between months and years (Table IV).

Populations on Unit A remained relatively constant throughout the months and maintained levels of approximately 20 animals in both years.

Populations on Unit B were consistently high during 1960-61, especially throughout January, late February and early March. During 1961-62, this unit was only lightly utilized. The clearing of snow in mid-March brought a sharp increase of population in this unit.

Unit C populations also varied between years. In 1960-61, high population levels were observed through January, then an unexplained drop occurred. Late February numbers were high and then decreased throughout March and April. The 1961-62 year was quite different: few animals were noted on Unit C until February. During the late part of the month, populations on this unit were very high and continued so

TABLE IV

MAXIMUM NUMBERS OF MULE DEER OBSERVED ON STUDY UNITS AT WEEKLY INTERVALS*

Weeks		1960-61					1961-62				
		Units					Units				
		A	B	C	D	E	A	B	C	D	E
Dec.	3	9	0	0	0	0	1	5	7	0	23
	4	-	-	-	-	-	-	-	-	-	-
Jan.	1	-	-	-	-	-	8	1	0	0	0
	2	2	0	0	0	0	27	0	0	0	33
	3	12	3	15	0	0	16	0	0	0	43
	4	19	9	18	0	0	23	0	7	0	49
Feb.	1	0	6	27	0	9	21	2	25	76	0
	2	13	0	0	0	0	16	0	26	71	0
	3	18	10	7	8	7	21	0	47	48	0
	4	27	25	15	7	15	15	0	75	80	0
Mar.	1	0	15	0	0	0	11	0	66	0	0
	2	25	11	1	0	8	-	-	-	-	-
	3	26	0	0	6	28	8	42	77	5	0
	4	19	13	0	0	0	18	12	12	0	0
Apr.	1	5	0	0	0	23	15	0	13	0	6
	2	6	7	0	0	18	-	-	-	-	-
	3	16	6	0	0	15	-	-	-	-	-
	4	4	6	9	0	0	-	-	-	-	-

*Maximum number observed during any single observation period.

until mid-March. The spring migration then reduced the study area population.

Unit D was the most widely variable in population numbers. This southwesterly exposed unit is a relatively small area, but remains clear of snow throughout most of the winter. In 1960-61 only a few small groups of deer were observed on this unit. The succeeding year was quite different. Beginning on February 1, populations jumped rapidly within a two-day period. During the first week of February, approximately 80 percent of all deer on the study area were observed in this unit. This extreme concentration lasted for seven days. However, populations continued high on this unit until the first week of March when the population rapidly dropped.

Bailey (1960) found that from March 2 to March 15, 1959, during a period of deep snow, the bulk of the deer herd was observed in the area now designated Unit D, and that in 1959-60, a winter of light snow, the deer herd did not move into Unit D.

Numbers of deer on Unit E seem to be inverse to the numbers on Units B and C. The animals utilized Unit E early in the season until they either shifted to Unit D suddenly, or slowly moved onto Units C and B. In the early part of 1960-61 no observations were made on this unit. However, it seems probable that this unit supported deer populations throughout December and January 1960-61.

A comprehensive comparison of areas of utilization may be obtained from maps on which observation locations are plotted (Figures 13, 14, 15, 16, 17).

Special note should be taken of observations in Unit A. During the winter of 1961-62, these animals were observed largely on the far southern extension of the unit. These sightings were made at low elevations a few hundred feet above the valley floor. Only in early spring, after the clearing period, did the animals move into the higher sections of the unit. During 1960-61 deer utilized the whole unit.

A subtle shift may be noted in Unit A during the 1960-61 season.

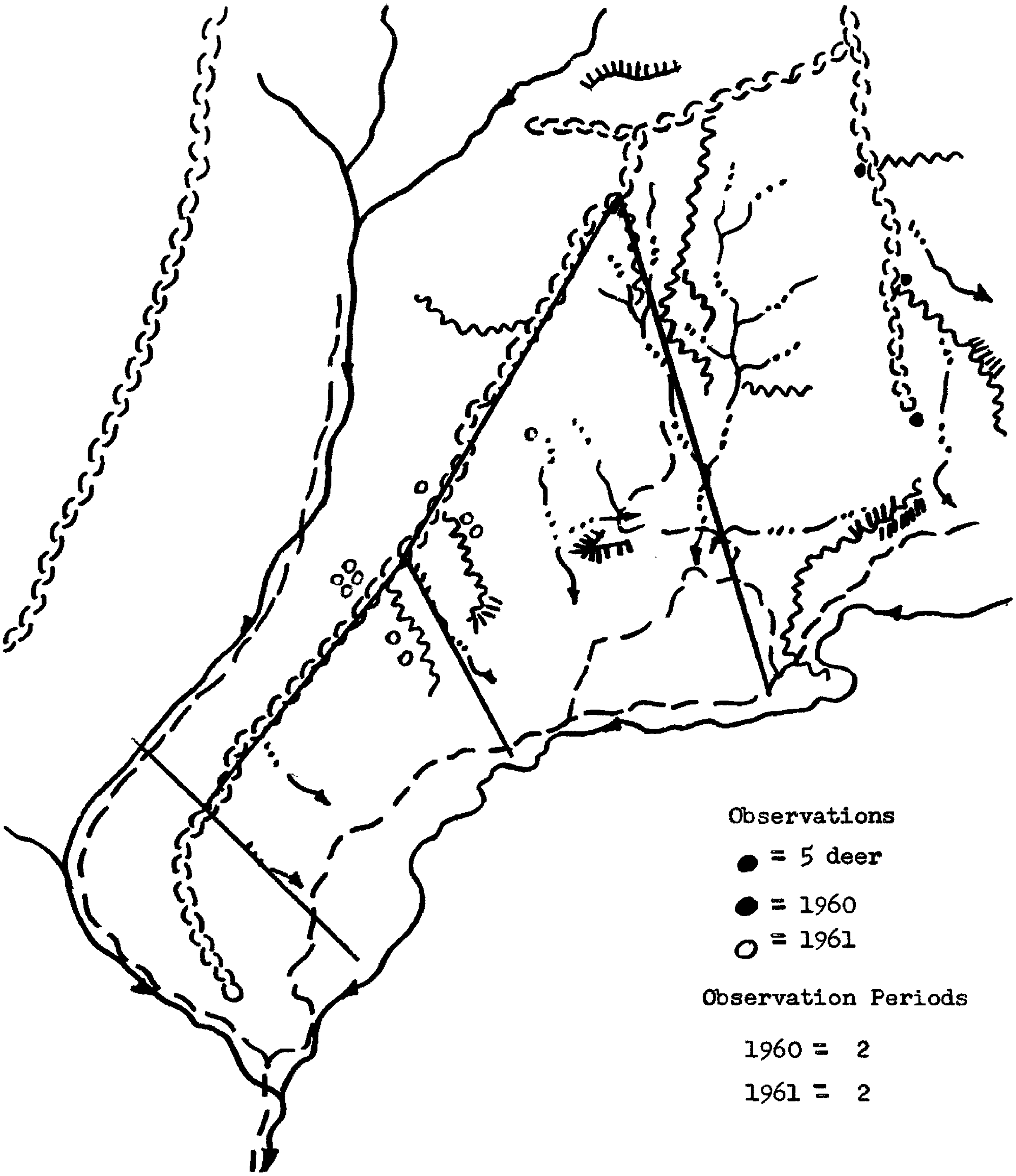


FIGURE 13. Observed mule deer distribution on the study area during December 1960 and 1961.

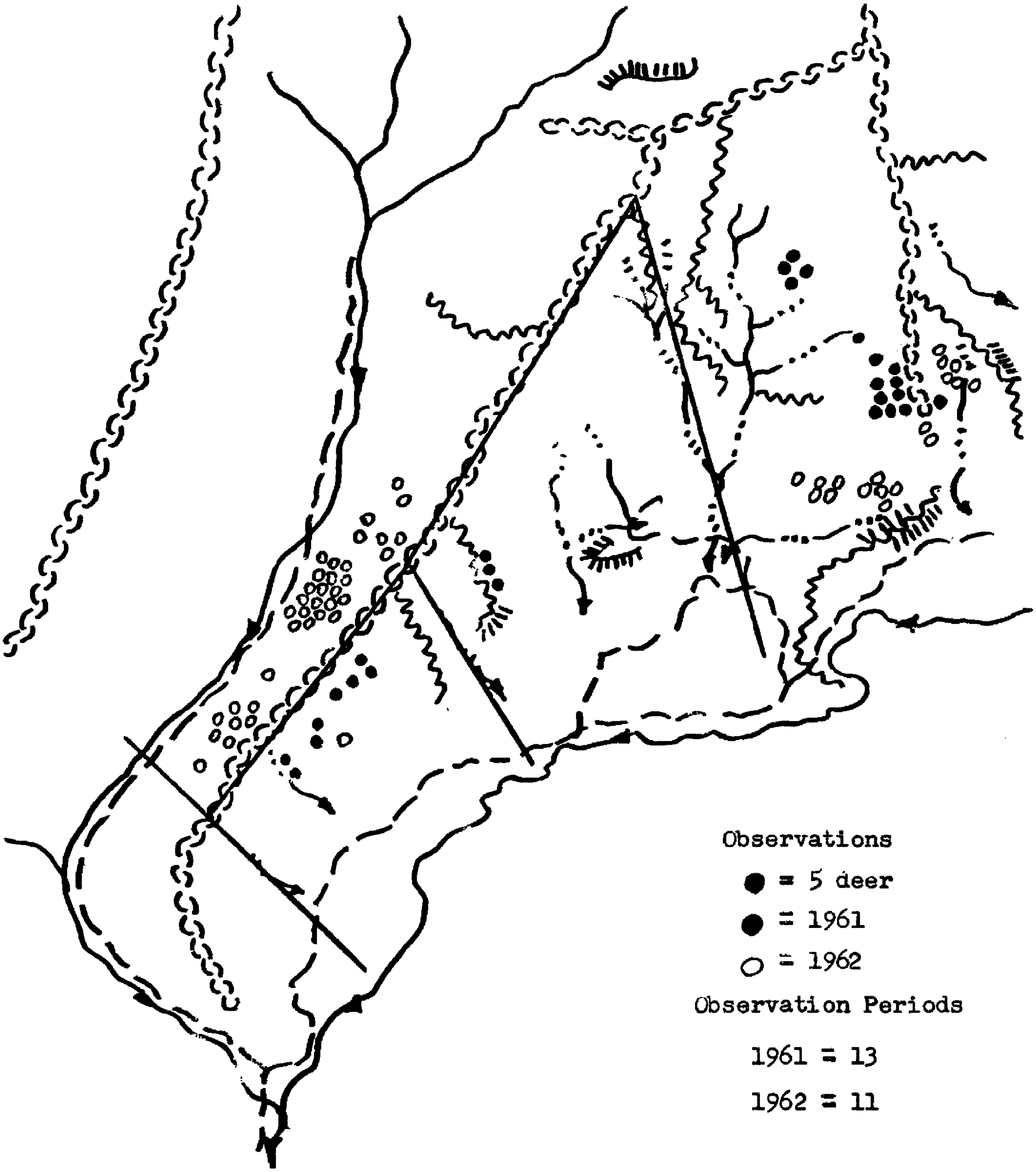


FIGURE 14. Observed mule deer distribution on the study area during January 1961 and 1962.

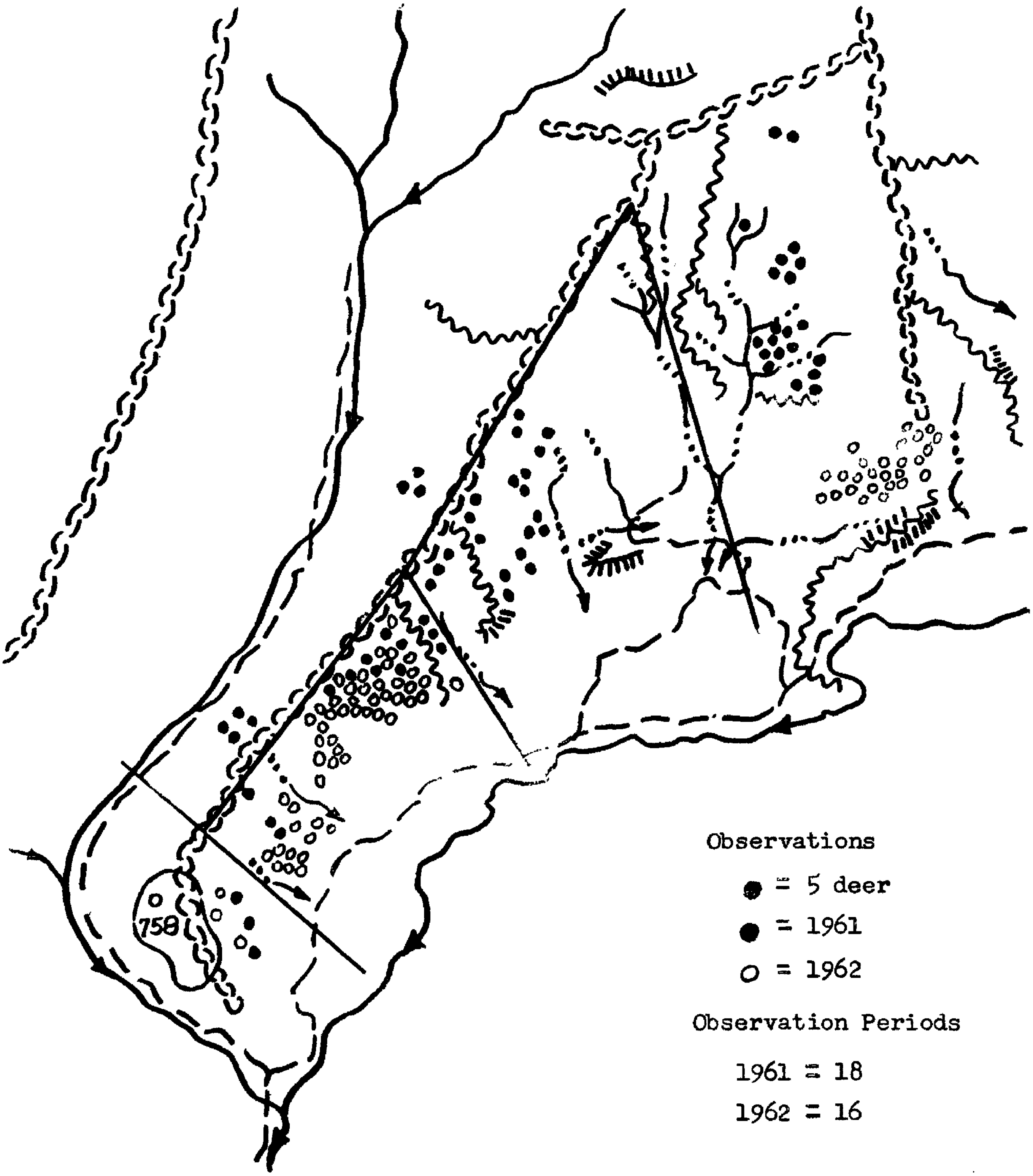


FIGURE 15. Observed mule deer distribution on the study area during February 1961 and 1962.

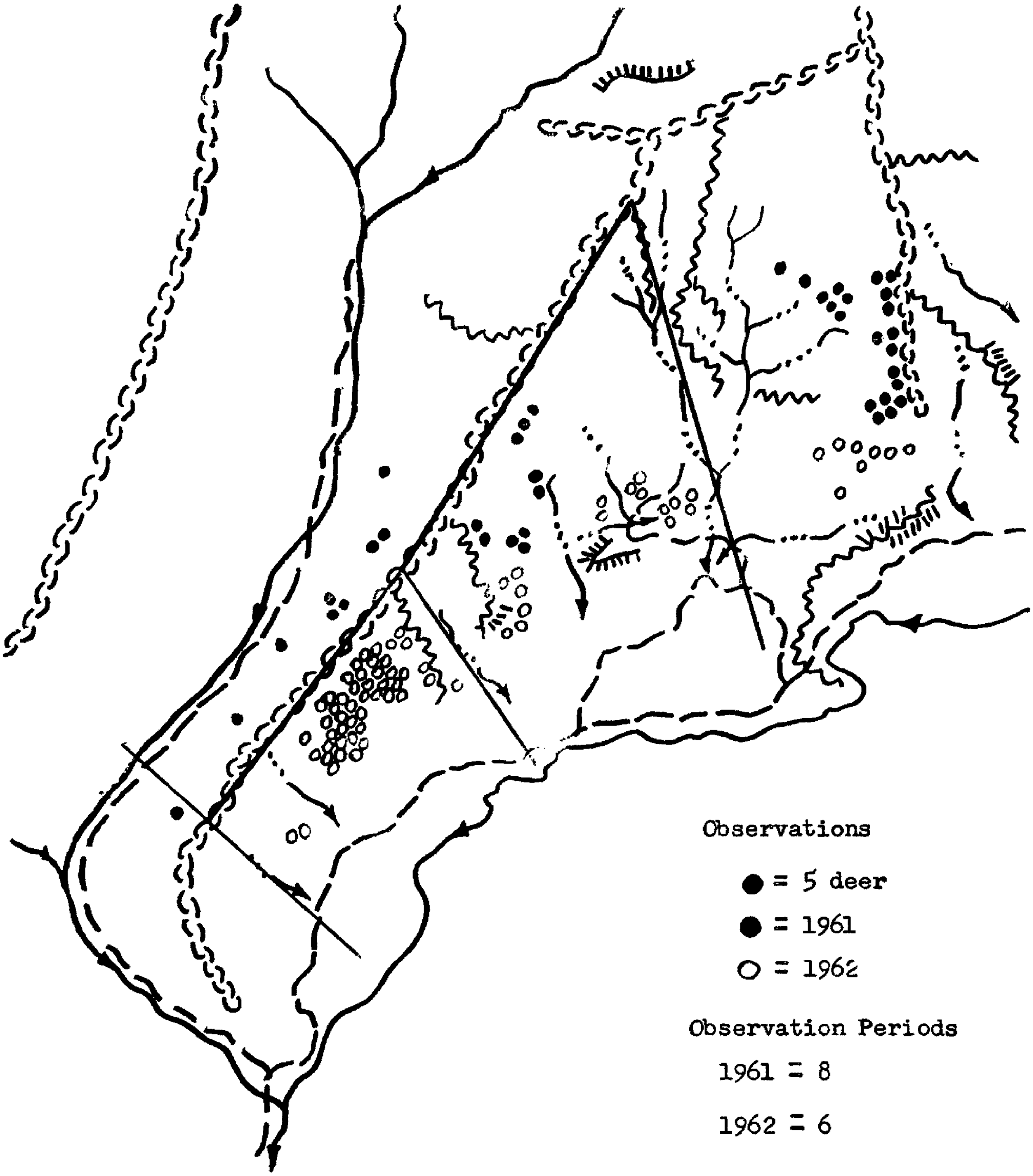


FIGURE 16. Observed mule deer distribution on the study area during March 1961 and 1962.

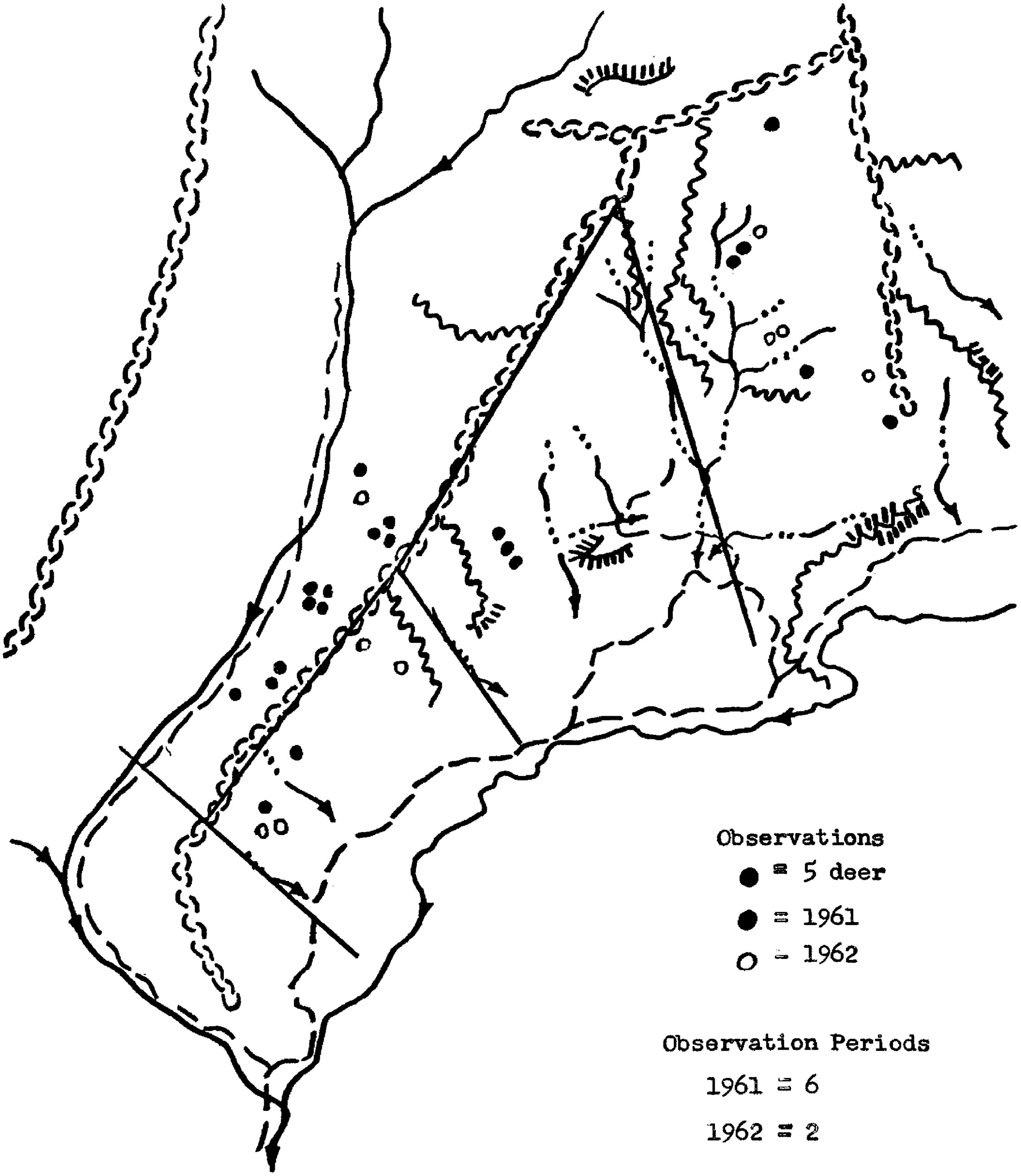


FIGURE 17. Observed mule deer distribution on the study area during April 1961 and 1962.

Early winter observations were plotted along the ridge line (Figures 13, 14). Mid-winter observations were concentrated low in the drainage (Figure 15). Early spring sightings were again high on the ridge (Figure 16).

In Unit B the area was utilized throughout the year in 1960-61. In 1961-62, however, sightings were not made on the unit until March and then at low level. No observations were recorded high on this unit during this period (Figures 13, 14, 15, 16, 17).

In Unit C populations tended to concentrate high during February 1961, and low during February 1962. Few observations were made on the unit during March 1961 (Figures 14, 15).

Populations on Unit D vary from zero to very high (Figures 13, 14, 15, 16, 17).

Behavior

General. Previous work by Bailey (1960) described the behavior of the Rattlesnake Creek mule deer herd during the winters of 1958 and 1959. Additional observations were noted during this present study and comparisons are made between the two sets of data.

Individual behavior. Individual behavior is behavior of the single organism without relationship to other organisms. Behavior such as browsing, self grooming, bedding, and individual flight are cases of individual behavior.

Bedding and feeding. Deer observed on the winter range spent the early morning hours browsing. Deer began to bed down within one hour after sunrise. Similar findings were made by Darling (1937) and

Browman and Hudson (1957). On days of very cold temperatures, deer remained in beds from very first light to late morning.

Beds were situated where the resting animal had a view of the terrain below and lateral to its position. Bailey (1960) likewise mentioned this tendency. On steep slopes, it seems impossible for the animal to lie with its feet stretched uphill or tucked underneath it so that its back is toward the downhill side. On several occasions, in steep terrain, animals were approached quite closely from above without initiating flight. The ears of the resting animals were noted to be constantly on the move, shifting and changing position together or independently at each sound. When startled, these animals jumped upright and attempted to identify the intruder before taking flight.

Beds were usually situated at the base of clumps of vegetation or beside fallen logs. This arrangement tended to shield the animal from view from above. There were occasional exceptions. One example was an adult doe observed lying flat, neck outstretched, completely in the open on a patch of snow.

Animals remained in beds throughout the day with occasional periods of feeding. Fawns were noted to feed more frequently and for longer periods at a time than adults. Male animals tended to feed less and to bed down for longer periods.

Feeding in late afternoon seemed to be sporadic. Few consistent observations of groups or numbers were obtainable during the late afternoon periods.

Grooming: After rising from occupied beds, deer were observed to groom themselves before beginning to browse. The animals usually stretched and then began a prolonged period of licking or grooming their legs and posterior portions.

Irritability: Generally, as observed in this study, deer herds showed little irritability. One incident, however, was noted in which irritability seemed to figure. In early February, 1962, when there were high deer populations on Unit D, activity of the observer in the valley below and noise caused by the Jeep elicited little response from the animals. These animals were approximately 300 yards from the site of disturbance. Late in the month, this same population showed an increased tendency to be disturbed. Sounds of the vehicle below caused the animals to move into positions hidden from the valley floor.

This change in tolerance of intruders may have been a result of increased irritability. Irritability may have increased due to crowding of the deer herd onto Unit D. Crowding has been shown to increase irritability (Dasmann and Taber, 1956).

Taber, White, and Smith (1960) found that the annual cycle of physical condition of adult female mule deer in the Rattlesnake herd (which comprise the major portion of the herd and its group leadership) began to decline during the winter and reached a low point in May.

It is possible that as the physical condition of the animals reached a low point, thresholds of irritability likewise became lower. Altmann (1958) reports that flight distances increased for elk on poor range but not for elk on good range. Poor animal condition and high population density both contributed to increase the irritability of the mule deer herd.

In contrast, during the period of apparent high irritability, groups of 16 and more animals were seen to feed on the same vegetative clump at the same time. These animals were standing shoulder to shoulder to obtain access to the available browse. No conflict was observed. It may be that at the specific time of these observations the drive to obtain food was powerful enough to dominate any increased irritation due to population density.

Antler shedding: Wislocki (1943) demonstrated that antler shedding in white-tailed deer was begun by a decline in production of testosterone, a hormone secreted by the testis. Bailey (1960) stated that antler shedding in the Rattlesnake herd was completed by the third week of February.

During the present study, the dates of antler shedding were not similar (Figure 18). In 1961, the first antlerless male was seen on January 27. The last male with antlers was observed on March 11. In contrast, in 1962 the first antlerless male was observed on January 5; the last male with antlers was seen on January 28.

Dixon (1934) and Taylor (1956) state that antler loss is closely associated with physical vigor, that a mature deer in good condition sheds antlers early, while a poorly nourished animal may not shed antlers until March or April.

Klebenow (1962) reports that browse production on the study area was not significantly different between 1960-61 and 1961-62. However, weather conditions were different during this period. Minimum temperatures were lower during the second period (Figure 4) and there were greater depths of accumulated snow during the second period (Figures 4, 5).

The low temperature and deep snows during the 1961-62 period could

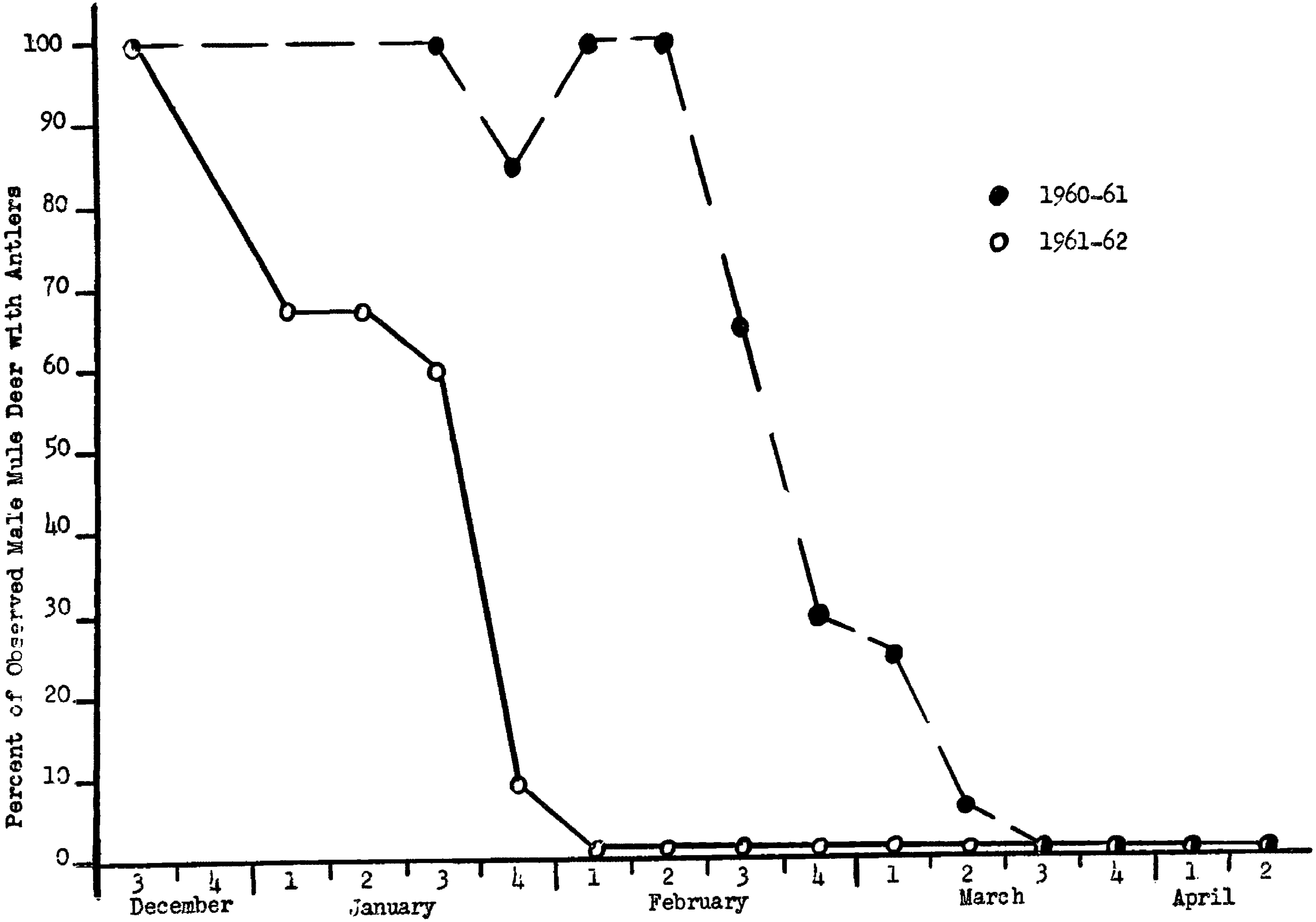


FIGURE 18. Percent of male mule deer with antlers at weekly periods during 1960-61 and 1961-62.

have been the cause of a low level of physical condition among the males compared to the better condition of males during the previous milder winter. From these facts it would seem that males of the Rattlesnake herd should have lost their antlers later in the second year than the first, due to more severe winter conditions and poor physical condition. This did not occur, because antlers were lost at an earlier date the second year. No cause could be found for the discrepancy in antler shedding dates.

Linsdale and Tomich (1953) report that there is no progressive weakening of antler attachment, but that antlers are shed suddenly, usually dropping to the ground within a few feet of one another. These authors report that deer may place pressure on the antlers without loosening the attachment resulting that day but the following day the antlers may fall off without pressure.

It was frequently observed, however, that some mule deer of the Rattlesnake herd retained one antler after losing the other. While under observation, none of the animals retaining one antler were seen shedding the remaining beam. Remaining antlers in these instances were apparently retained for longer periods than Linsdale and Tomich (1953) reported. Taylor (1956) reports that male mule deer were observed carrying single beam antlers for three weeks after loss of the first beam.

Bailey (1960) states that antlers were a major badge of social prestige. Woodbury (1941) and Hediger (1955) also report that antler size is a deciding factor of dominance among males. Bailey (1960) reports that animals with large antlers, who ranked high in the social order, lost status when they shed their antlers. Lesser ranking animals retaining antlers were raised in social rank.

Social behavior. Behavior which may be termed social involves relationships and interaction among members of the same species. It is defined by Scott (1956) as regular and repeatable behavior among two or more individuals of one species.

Dominance: Most animal societies tend to form a definite social order. Browman and Hudson (1957) and Bailey (1960) report that mule deer societies form a social order in which dominance occurs in the following sequence: adult males, yearling males, adult females, yearling females, and fawns.

Conflict of some sort is one method of exerting dominance. When a deer resorts to conflict to exert dominance over another deer, the dominant deer will usually approach the subordinate deer and will extend its neck out and downward while striking out and downward with a front leg or hoof. Conflict was observed between all age and sex classes, but was most rare among males. Bailey (1960) reported that the dominant animal always approached the subordinate animal from the rear; however, during the present study deer were seen to approach from front, rear, and from the side when exerting dominance.

On two occasions antler conflict was observed between males. One incident was observed as follows: Four male deer browsing on a ridge crest were seen on January 27, 1961. One animal with a large set of antlers with 5-4 points was fighting with a smaller animal with 2-1 points. This conflict resembled play in its level of activity: actions were slow and deliberate, and the animals did not seem to be using their full strength. The deer pushed and twisted with their heads, occasionally their antlers became interlocked. The 2-1 animal soon withdrew and began to browse (see Sexual Behavior--Displacement). The 5-4 animal approached and nudged 2-1 with his nose, 2-1 then turned and entered the conflict again. After a few moments, 2-1 again withdrew. At this time a new animal with 3-4 points approached and began a conflict with 5-4. Animal 2-1 moved to a hornless male nearby. The animal 0-0 placed his forehead between the antlers of 2-1 and began pushing. The 0-0 animal exercised care to avoid the antlers of 2-1. After a few short withdrawals, the conflict resumed when 0-0 placed his forehead between the antlers of 2-1. When 2-1 twisted his head, the antlers hooked 0-0 and he pulled back. Animal 2-1 finally withdrew.

In the conflict reported, the male animals with the largest sets of antlers were dominant in each contest. Large males were seen to dominate yearling males even though both were antlerless. Some of these conflicts involved no fighting; instead dominance was exerted by posture. Young subordinate animals always yielded when confronted with an aggressive pose.

Darling (1937) reports that in red deer herds, dominance is dependent on antler shape rather than size. Woodbury (1941) and Hediger (1955) reported that antler size decides dominance. Bailey (1960) stated that antler size was "a major badge of social prestige," but that "the largest animal was normally the dominant one while all were carrying antlers."

It appears that antler size is the major deciding factor in dominance ranking; however, size and age of individual animals likewise are factors affecting dominance.

Linsdale and Tomich (1953) report that adult females have shown aggressive activity toward young males and have dominated them. Buss and Harbert (1950) also state that adult females were seen to be dominant over males during conflict.

During the present study, one incident was noted in which an adult female exerted dominance over a male. No incidence was noted of yearling males dominating over adult females. It seems probable that on occasion an adult female, especially one of high dominance rank, may exert dominance over young adult males.

Dominance is not always asserted by direct conflict as the dominant animals seem to be recognized as dominant by the subordinate animals. Dominant animals by closely approaching subordinate animals will cause subordinate animals to yield a contested position.

Leadership: Scott (1956) termed leadership as alelomimetic behavior which is behavior of the same act with mutual stimulation, but in varying degrees. Leadership differs from dominance in that it is not directed at a subordinate animal and does not require conflict. Allee (1938) states that leadership does not necessarily follow the established dominance relationship. This factor is apparent when male reaction to leadership is observed. Darling (1937) considers the male an egocentric. This term well describes the male mule deer's actions, since he appears independent, aloof and self centered.

Six opportunities occurred during this study to observe flight after a disturbance in mixed groups of deer. In no instances, when male animals were grouped with females and fawns, did the male animals lead the flight. The males sometimes remained as members of the group during flight and occupied a central position in the group. The alternative male reaction was to separate from the group and take flight alone. If several males formed a sub-group within a larger mixed group, these males would usually separate from the main group and take flight as an all male unit. Bailey (1960) reports this same pattern of male mule deer behavior.

This leadership behavior pattern has been observed among males of other cervid species: black-tailed deer (Linsdale and Tomich, 1953), elk (Altmann, 1956), and red deer (Darling, 1937). It appears that independent male behavior during flight or male subordination to female leadership during flight is a behavior pattern common among several cervids.

Grouping: The tendency of deer to form social groups of various composition and size has been discussed in another section (see Populations). Grouping of male animals is readily noticeable. These animals, although remaining in proximity to each other, do not seem to maintain as close an attachment as the family groups do. Young males are tolerated in male social gatherings. Male groups may contain yearling males and male fawns late in the winter season. The male fawns feed and bed down with the adult male groups and are apparently accepted into the group relationship.

Mutual grooming: Mutual grooming occurs when two animals simultaneously or alternately lick each other's body. This behavior was seen at various times throughout the day, but not during high levels of browsing activity. Linsdale and Tomich (1953) found that mutual grooming occurred among deer of all classes. Similarly, mutual grooming occurred among all classes during the present study; also, it was found that most of the grooming was confined to the head and neck of the deer, the remainder of the body being groomed occasionally.

Learning: The relationship of learning and imprinting and its place in deer survival was discussed by Bailey (1960).

A significant incident occurred during the present study. A herd of deer was disturbed in Unit A. These animals, led by an adult doe, included 17 females, 5 adult males and 5 fawns. Their flight in fresh snow took them away from the study area and toward the north and east across a drainage and onto an opposing slope. Examination of the fresh tracks revealed that the deer followed an existing trail. This old trail was impossible for the deer to distinguish due to snow cover of two feet. Landmarks aided the observer in identifying the fresh trail to within two feet of the location of a deeply cut trail noted on a previous trip through the area. It was apparent that the location of this easy access route was known, at least to the lead animal.

Deer were also observed to walk precisely in the tracks of leading animals. Deer tracks were likewise noted in the observer's foot prints. It appears that the animals are aware that travel is easier on packed surfaces than on fresh or crusted surface.

It appears that these behavior patterns may be derived and maintained in a species or herd through natural selection. Bailey (1960) stated that most learning had a definite survival value, especially those behavior patterns which fixed escape route and located areas of cover in the memory of members of local herds. Dasmann (1953) states that all required environmental factors are present within a deer's home range and that location of these factors is learned by the individual animal.

The habit of following in the steps of larger or leading animals could influence survival during periods of deep snows or heavy crust. Under heavy crust conditions, fresh deer trails frequently showed blood splatterings in the snow, apparently caused by the crust cutting the animals' legs. Continued cutting about the legs might decrease an animal's chances for survival if the animal were under heavy stress.

Sexual behavior: Incidents of sexual behavior were observed on the study area in 1961, on January 27, and February 3. It is doubtful that either case of this behavior was initiated by normal sexual drives. On January 27, an adult male, with his head and neck outstretched, ears back and walking stiffly, approached an adult female (typical mating pose described by Taylor, 1956; Broman and Hudson, 1957). The female moved away and the male pursued, walking stiffly, neck extended. The female finally bounded away and the male gave up the chase.

The second observation was made on February 3, when a male fawn mounted an adult female. The behavior seemed to be complete for the male, culminating with a copulatory move. The male dropped to the ground, the female then began licking the male around the head. He responded by mounting again, but quickly dropped to the ground.

White (1958) states that the breeding season of the Rattlesnake herd occurs between November 8 and December 18. In 1961, the shedding of antlers had just begun during the fourth week of January. According to Wislock's (1943) hypothesis, general levels of testicular activity in a herd would be near the low point at the time of antler drop. Therefore, it seems doubtful that this was normal rutting activity, but instead was an example of displacement behavior. Displacement behavior, according to Tinbergen (1953) and Thorpe (1956), is an unrelated response which occurs due to two opposing and equal responses being elicited by some stimulus. Bailey (1960) observed a male mule deer mounting another male and termed it displacement behavior. Due to the season of the year, it is improbable that the apparent sexual behavior in the deer herd has any origin other than displacement behavior, yet the original stimulus is unknown.

Interspecific Behavior. Interspecific behavior is any behavior which takes place between two species.

Predators: The deer on the Wallman Ridge study area are disturbed frequently by a variety of predators. The most significant in extent of harassment is the coyote (Canis latrans).

Throughout the winter periods, coyotes were observed hunting over most of the study area, frequently in groups of three. Howling by these animals was common in early morning and late evening hours. The deer were only slightly disturbed by this sound, but occasionally a deer would stop browsing and strike an alert pose when hearing a coyote howl. The tendency of the deer to ignore the local coyotes continued even when the coyote groups approached within 100 feet of the herds. Bailey (1960) reports observing coyotes to walk within a few feet of browsing deer without disturbing them.

In contrast, an excellent example of the coyote's hunting technique was seen when three of these animals attacked a group of feeding deer. The coyotes were first observed hunting below the deer in heavy brush and logs. One coyote slipped forward in a crouched position, head extended toward the deer, then stopped. The next animal then moved forward. They approached the deer in this alternate manner. Finally, one of the coyotes made a sudden dash at a male deer feeding separately in dense vegetation. The herd of 27 deer became frightened and ran uphill in a group, for a distance of approximately 200 yards. The coyotes cut the single animal off from escape uphill and attempted to run it downhill. One coyote ran above the deer and the other behind. The deer gradually worked its way uphill, finally leaping a fallen log. The coyote could not follow and had to run around the obstacle. This maneuver allowed the deer to escape.

After another 100 yards, the deer stopped and turned on the coyote. By this time it had moved close to the other herd members and perhaps received psychological security from their presence. The coyote immediately skidded to a halt and retreated a short distance. The deer advanced, head low, feet spread wide and forward. The coyote made two more dashes at the deer but was met with striking front hooves. Another male deer moved toward the site of conflict and the coyotes retreated a few hundred yards.

While the coyotes remained in the vicinity, the whole herd of animals watched them. Even when the coyotes sat down and pointedly looked away, down the valley, the deer remained alert.

Bailey (1960) reported a similar incident of coyote-deer behavior. He stated that the seated pose or posture of the coyote served to frighten or alert the deer in the same manner as an aggressive or attack pose.

No coyote kills were found on the study area during the two year period but it is known that these animals do sometimes prey successfully on the wintering herds. Bailey (1960) estimated that 12 deer were killed by coyotes on the winter range in 1958-59; four known coyote kills were located in 1959-60. Bailey (1960) suggests that approximately one-half the annual fawn crop is removed by coyotes. During the years of the present study, however, coyote predation during the winter was negligible.

In October, 1962, a predator hunter claimed that he killed 15 to 25 coyotes in the vicinity of Wallman Ridge in 1961-62. He claimed to have killed 40 coyotes in the Rattlesnake Creek drainage that same year. If this kill figure is accurate, it could explain the decline in coyote predation from 1959 to 1962, since this man began hunting in the area in 1959 or 1960.

The reaction of deer to domestic dogs is quite different from their behavior toward coyotes. On one occasion, a domestic dog barked four times on the ridge top in Unit E. Immediately all of the deer located in Unit E became frightened and ran singly or in groups into the timber to the northeast. At no time were dogs seen pursuing the deer, yet the move covered a distance of approximately one mile.

Man is a persistent user of this area. During the fall hunting season, he preys to some extent upon this herd. White (1958) estimated that 70 and 60 mule deer were removed from the upper Rattlesnake Creek drainage in 1957 and 1958, respectively, by hunters.

Deer do not recognize the sight of man "per se" as a potential enemy. When being disturbed by the observer, the animals would resume feeding if the intruder did not move. When the observer moved, the animals took flight.

Shooting, target practice, hiking, horseback riding, and skiing are recreational activities occurring on the study area. The road in the valley floor is used heavily during spring and fall. On one warm day after a long cold period, seven cars were seen on a 1.5 mile stretch of road. If disturbances reach high levels, the deer tend to move into cover or across a ridge away from the intruders; otherwise, deer ignore the slight disturbance unless directly approached. In one instance, a man using a predator call was seen on the ridge face; the deer which had been browsing walked swiftly from the ridge.

Some poaching is done on the study area from time to time. Evidence of a deer being dragged from the upper part of Unit A was found in December, 1960. The carcass of a yearling buck which had been sounded by a small caliber weapon was found in May, 1961.

Mule deer-white-tailed deer: White-tailed deer are known to use the study area throughout the summer months. They also were observed on the winter range while it was occupied by the migrant mule deer herd. There was a significant difference between the two study years in numbers of white-tailed deer observed on the area during the winter months (Figure 19). In 1960-61, white-tailed deer were seen from mid-January to late March. Maximum numbers observed during this period were 25 animals during the third week of February and 42 during the third week of March. More commonly, groups of 3 and 11 were observed. Most frequent observations were made in Unit C and lower parts of Unit B. Occasional observations were made in Unit E (Figure 2).

During the 1961-62 season, few white-tailed deer were seen. Eight animals were observed in December, none in January, four in February, one

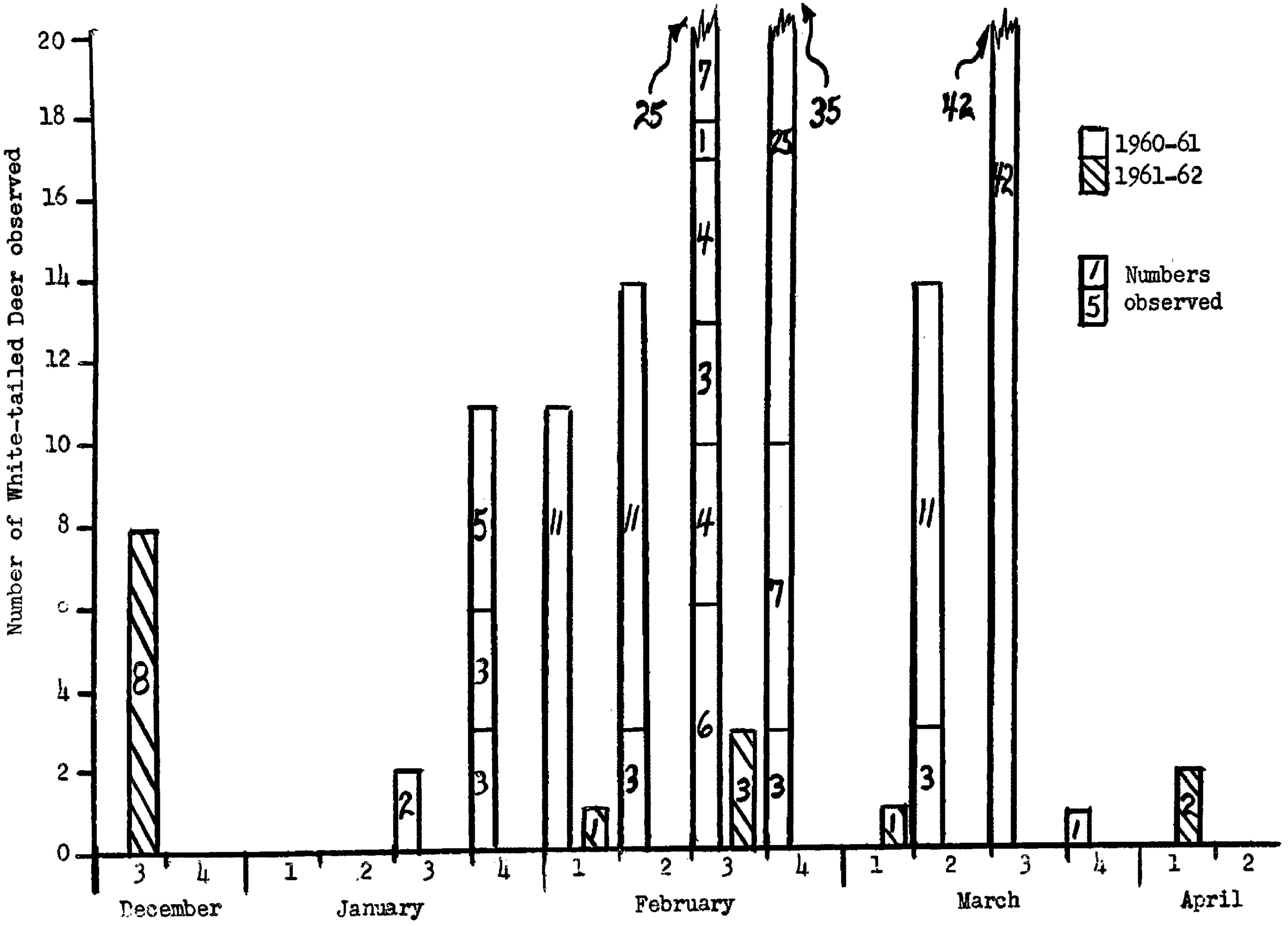


FIGURE 19. Number of White-tailed deer observed on the study area during 1960-61 and 1961-62.

in March and two in April. Most December observations were in Unit E and a few in Unit C. One animal was seen in Unit D in February.

The cause for the change in the white-tailed deer population is not readily apparent. Since mule deer and white-tailed deer are members of the same genus and have similar food habits, conflict might arise between the species so that one might dominate the other. Case (1938) reports that elk dominate mule deer on Idaho winter ranges. Elk also were observed to be dominant over white-tailed deer in one instance (see Deer-elk). Populations of mule deer were highest during the second year of the study (Figure 7), at the time when populations of white-tailed deer were lowest. The rise in number of mule deer on the study area possibly could account for the decrease in number of white-tailed deer. It would seem, however, that if this were true, incidence of conflict between the two species would be more common than it was. Bailey (1960) reported five instances when white-tailed deer and mule deer groups were close enough together so that tolerance and intolerance could be observed. On only one instance did intolerance occur, and that happened when a white-tailed deer closely approached a mule deer. During the present study the two species were observed in close proximity on three occasions and no intolerant behavior was seen. During a fourth observation a lone female white-tailed deer was seen browsing near a large group of mule deer. She appeared more excited than the other deer; within five to ten minutes she moved into cover away from the mule deer herd. White-tailed deer were usually found to maintain their groups apart from mule deer groups, and no specific instance of intolerance was observed which could support the conclusion that mule deer exert specific dominance over white-tailed deer.

It is possible, however, that interspecific domination is present without outright conflict being apparent. Once dominance has been established by a species or individual, negative conditioning to this dominance occurs in subordinate species or individuals. The subordinate member of the dominant-subordinate relationship responds to the dominant member by removing itself from the vicinity to lessen the stress which it is experiencing. If this pattern is established, the subordinate member will rarely come into direct contact or conflict with the dominant member, as its response to the dominant member is to move away to avoid repeating the stress which it experienced previously. I suggest if the white-tailed deer were negatively conditioned to mule deer (i.e., subordinate to them) interspecific dominance might occur without conflict, but no investigation has been done to confirm this relationship.

The abrupt change in observed white-tailed deer populations on the winter range indicates a more specific causative basis than increased populations of mule deer account for. Carter (1951) found a definite difference in white-tailed deer and mule deer winter range. He found that the winter range limits were set by snow depths and that white-tailed deer utilized range that had snow depths of 12-15 inches. The white-tailed deer were more selective as to cover type, preferring ponderosa pine cover with escape cover and water close by.

Deep snow remains as a possible explanation for white-tailed deer population declines during the present study. The second year, when populations of white-tailed deer were low, weather conditions were more severe than the previous year (Figures 4, 5, 6; also see Weather). The severe weather caused deep snow conditions on the study area (Figure 5). The hypothesis that white-tailed deer use mule deer winter range in an inverse relationship with snow depth is further supported by detailed comparisons of data from 1960-61. Maximum observations of white-tailed deer were obtained in the fourth week of February and third week of March (Figure 19). These dates coincide with dates when the slopes of the winter range were becoming clear of snow cover (Figure 5). Populations of mule deer were at their highest during the same periods of maximum populations of white-tailed deer (Figure 7).

It was observed that white-tailed deer maintained separate grouping relationships from mule deer populations; when white-tailed deer were on the slopes of the winter range, mule deer could not be seen in the same unit or section of a unit. It is possible that dominance relations between these two deer species caused the observed segregation. There is evidence, however, that weather factors, snow depths, and snow surface conditions are the causes for changes in the white-tailed deer usage of the mule deer winter range.

Deer-elk: Elk were observed on the study area for short periods during both years. On February 13, 1961, a group of elk comprised of two cows and two calves appeared on the winter range. No mule deer were occupying the area at the time, but white-tailed deer were browsing in Unit C when the elk, moving northeast, appeared on the ridge top. The group of deer struck an alert pose and then, ahead of the elk, walked swiftly up ridge and to the northeast, while the elk moved slowly along the ridge and into the timber.

In 1962, elk were observed on the area on March 29. Again there were two cows and two calves. Reports were received that the animals had been on the area in Unit A and Unit B for two days. A mule deer doe was seen browsing within 200 yards of the elk when they appeared. This deer stood watching the elk for a long period and finally resumed feeding, striking an alert pose only occasionally. Presence of the elk on the study area appeared to be a disturbing influence to the deer herds; however, elk rarely appeared on the winter range.

DISCUSSION

Populations. Populations of free ranging ungulates are dynamic systems, the numbers of which are constantly modified by the environment (Dixon, 1934; Leopold, et al., 1947; Edwards, 1956; Taylor, 1956).

Mule deer populations on the Rattlesnake winter range have remained relatively stable in composition during the 1960-62 study period. The wintering herd was found to contain an average of 29 percent male animals throughout the period. The proportion of fawns to the population, however, was less constant. The larger proportion of fawns during the second study year requires discussion. If the 1960-61 mild winter resulted in greater fawn survival, then the yearling population in 1961-62 would have been larger than expected. A large yearling population added to a normal adult female population should cause the 1961 fawn crop to appear proportionally small. But instead of being smaller, the fawn crop was larger.

A possible explanation is the increased movement of animals onto this wintering area as reflected in the increase in total population. It is possible that this increase in animals was proportionately greater in females with fawns than other classifications.

Another possible reason for the increase in fawns would be a significantly higher rate of conception, birth, and survival of fawns. The mild winter of 1960-61 might have allowed the pregnant females to leave the winter range in better condition than would have been possible after a severe winter. Summer conditions may have allowed greater survival of fawns until fall.

White (1958) reports that summer doe-fawn ratios were lower than doe-fetus ratios and proposed significant mortality immediately following parturition. If this mortality indeed occurred (whatever its form), it is possible that it operated at a lower level than usual in 1961, allowing a higher percentage of fawns to reach winter range.

There were also indications during the present study that high mortality is affecting this herd at some time other than on the winter range. In 1960-61, winter mortality was negligible; the majority of the fawn crop survived the winter. This greater survival rate should have caused a decreased percentage composition of fawns the following year, as twelve month old females rarely give birth (Dasmann and Taber, 1956). As previously stated, the fawn percentage classification was greater the second year, which indicates that there was a loss of a large segment of the 1960-61 fawn crop at some time after they left the winter range in 1961.

Significant numbers of animals could have been removed by hunters. White (1958) reported that hunters killed approximately 65 mule deer in the drainage of Rattlesnake Creek. However, most of this kill presumably did not come from the herd which wintered on Wallman Ridge, since their summer range was at an elevation too rugged and high to be easily reached by hunters.

Possibly the hunter harvest of the Wallman Ridge herd was greater than has been supposed. If approximately 20 percent of the herd was removed each year and coyote predation likewise took a toll each year, the discrepancy in population composition would be accounted for.

The movements and population dynamics of the Wallman Ridge mule deer herd are in need of further investigation to fully illuminate the fate of fawns after leaving the winter range.

Movements. Animal activity is correlated with seeking physical comfort (Woodbury, 1956). Edwards and Ritcey (1956) state that ungulate movements are an attempt to improve their situation. Such activity may develop into pure migratory movements or may become movements of non-migratory nature and local in extent.

To produce a movement, there must first exist an environmental condition which is detrimental to comfort or survival. Detrimental environmental conditions are ultimately derived from present or past conditions of weather. Fowle (1950) states that all factors contributing to decreased deer populations are insignificant when compared to weather related factors. Leopold et al. (1947) also state that deer populations are cumulative in numbers and are controlled by weather.

Several authors have reported studies that, when compared, show that different weather factors cause ungulate mortality and ungulate movements in different regions of the country (Severinghaus, 1947; Taylor and Hahn, 1947; Clark, 1953; Hanson and McCulloch, 1955; Dasmann and Taber, 1956; Edwards, 1956; McEwen et al., 1957; Welch, 1960).

In northern regions where winter snows are often deep and persistent, snow depth is the selective factor for deer survival. The amount and quality of snowfall is dependent on the total weather picture. Weather causes snow, which changes availability of forage, which changes metabolic balance, which may cause death. These factors are all interdependent, but the physical presence of snow remains the selective factor for deer survival.

Snow is the primary cause for ungulate movement (Russell, 1932; Severinghaus, 1947; Dasmann, 1953; Edwards, 1956; Edwards and Ritcey, 1956; Pruitt, 1960). Where snow does not exist, or falls in small amounts, other factors become causative for movement behavior (Clark, 1953; Dasmann, 1953; Taber and Dasmann, 1958; Welch, 1960). In the Rocky Mountain mule deer range, the presence of snow on the ground is the primary factor which is detrimental to survival (Russell, 1932).

Migratory movements. The species of deer which inhabits the uplands of the Rocky Mountain region have responded to deep snow conditions by developing a migratory pattern of behavior.

In areas where the weather is considered "mild" and does not fluctuate widely in severity, there is no annual migration (Clark, 1953; Dasmann, 1953; Zwickel *et al*., 1953). If conditions which make certain areas uninhabitable existed at all times, it is obvious that no ungulates would inhabit these regions. It is then the cyclic nature of weather conditions which allows use of some areas and also forces migrations away from them.

As behavior responses to environmental stimuli develop, a learning complex is established (Bailey, 1960). The stimulus-response association is present in all learning (Scott, 1958). Each succeeding generation of deer learns by imitating or following adults. In this way the migration response and the use of particular areas as winter ranges or refuges from inhospitable conditions are perpetuated.

The movement response is well known; it remains for the individual stimulus to be understood (Russell, 1932; Edwards and Ritcey, 1956). As previously stated, the gross yearly weather conditions are cyclic. The snow conditions over the bulk of the deer summer range are cyclic and predictable. The accumulated snows will be greater than is compatible with deer survival. The deer must migrate each year.

The stimulus for migration may justifiably be timed in correlation with a factor which is itself cyclic and related to weather cycles. Migratory responses to stimuli of an annual nature could be efficient adaptations, since they would remove all deer from the inhospitable area every year. Stimuli of this sort would be time oriented. Harker (1958) proposes that all organisms have an inherited cellular rhythm which allows the organisms to account for time. Brown (1959) does not agree and states that organisms respond to environmental stimuli to account for time and not to inherent cellular clocks. Russell (1932) suggests physiological rhythms as possible causes for movements. Browman and Sears (1956) and Grieser and Browman (1956) have shown the correlation of physiological rhythms with day length in mule deer. Bailey (1960) proposes the stimulus of day length for all deer movements. Harker (1958) also proposed that inherited rhythms may at times be overridden by environmental necessities. During the present study, little evidence was obtained to either substantiate or refute a hypothesis of time-oriented stimulus for migration.

Non-migratory winter range movements. The stimuli that produces non-migratory movements on the winter range appears to be a separate phenomenon from stimuli causing migration.

A hypothesis is proposed: that the Rattlesnake Creek mule deer are sensitive to stimuli which occur on the winter range and which directly affect the animals; that these stimuli are a product of weather conditions; that these stimuli are not time oriented, but occur at variable times within the major weather cycles; that these stimuli in the Rattlesnake Creek mule deer herd are snow depth and crust conditions; that the deer respond to these stimuli by moving to known areas where conditions are less severe, and that deer by moving to known optimum areas establish a stimulus-response complex which is learned.

Evidence from the literature and data collected during the long term project study of the Rattlesnake Creek mule deer winter range will support this hypothesis and is given below.

As previously stated, animals are thought to move to seek physical comfort (Woodbury, 1956) or to improve their environmental situation (Edwards and Ritcey, 1956). Factors which become limiting to survival would then cause movement and selection would develop movement behavior patterns.

What factors then have been found to cause movement or to affect survival? Dasmann and Taber (1958), working in an area of mild climate and little snow fall, found that deer would seek out areas of optimum temperatures. Several authors working in areas of moderate snowfall have found deer to move onto south and southeast sloping hillsides where due to higher temperatures the snow was not as deep (Cook and Hamilton, 1942; Shanks and Norris, 1950; Bailey, 1960).

Hamerstrom and Blake (1939), studying in areas where the whole range was covered by deep snows, found that deer congregated in "yard" areas where trampling of snow made movement easier. These authors likewise noted that in mild winters not all yarding areas were used.

Such changes in movements were thought to be adaptations to snow conditions (Hamerstrom and Blake, 1939; Marston, 1942).

Pruitt (1959, 1960), working with caribou, found that movements were caused by several factors, such as hardness, density, and thickness of snow cover. Each factor had a specific threshold of sensitivity which, when surpassed, initiated a movement response.

The movement response to a specific stimulus is not a rigid response, but rather a varied response depending on the stimulus strength and threshold level. Welch (1960) found that deer returned to areas where there were improved snow conditions even though such areas might previously have been uninhabitable. Cook and Hamilton (1942) found that deer in New York responded differently to deep snows, depending on the snow conditions and topography. These facts would indicate that deer are locally affected by environmental conditions and respond to these conditions in an adaptive way.

Dixon (1934) and DeNio (1938) likewise found that mule deer modified their habits to meet local conditions. The Interstate deer herd was also found to concentrate in direct relation to the severity of the winter, indicating a response to local conditions or stimuli (Interstate Deer Herd Comm., 1949).

Several authors have suggested that deer mortality is directly caused by snow depths (Russell, 1932; Dixon, 1934; Rasmussen, 1941; Severinghaus, 1947; Carter, 1951; Dasmann, 1953; Edwards, 1956; Pruitt, 1960). Severinghaus (1947) suggested specific thresholds of snow depth which, when passed, greatly increase mortality among white-tailed deer. He suggested a 20-inch snow depth threshold and added that fluffy snows or snows which lasted for five weeks or longer increased the severity of effects on deer populations.

Bailey (1960) found that the Rattlesnake mule deer formed scattered groups when snow depths were below 20 inches and were not crusted. When snow depths became greater than 20 inches and became crusted, large groups of deer were observed. These groups then formed into one or two large concentrations comprising the whole herd. The reverse form of grouping was apparent as snows cleared.

From the literature, it is apparent that: in regions where deep snows occur, these snows may become limiting to deer life; snow depths of greater than 20 inches are limiting; deer are sensitive to local environmental stimuli and may react to these stimuli through a spectrum of adaptive responses; crust and density of snow may become stimuli to movements; deer may respond to these stimuli by selective movement to modify the stress.

Data collected during the present winter range study further support the proposed hypothesis. Bailey (1960) has suggested that the Rattlesnake mule deer herd responded to a time-oriented stimulus initiating non-migratory movement. He proposed that the movement may be maintained by a secondary stimulus which is not necessarily time oriented. Bailey based his hypothesis partly on the fact that a major movement of the herd was observed to occur on nearly the same date two succeeding years.

Time is cyclic (i.e., the earth rotates and moves around the sun). Time as a single factor is not a primary motivating stimulus to movement. However, time can become a primary stimulus to movement if repeated secondary association occurs with some primary stimulus.

Crusted snow depths in excess of 20 inches have been shown to be the primary stimulus for movement. Crusted snow depths on the winter range do not occur in a cyclic pattern because weather conditions which cause snow to accumulate vary from year to year. Because time is cyclic and because the occurrence of crusted snow depths is not cyclic, time cannot be repeatedly associated with the crusted snow depths, so time in its own right cannot become a primary stimulus to movement.

Even though single factors of weather do form an annual weather cycle, the sum total of weather variables, which produce deep crusted snow depths and which directly affect deer survival, cause the timing of environmental conditions to be different each year.

In 1961-62, the various combinations of snowfall, snow quality, and periods of prolonged cooling or warming resulted in an accumulation of more than two feet of snow which became crusted. The previous year, slopes were clearing of snow during this same period. Given the same variables of snowfall, temperature, and the magnitude of other weather factors, no two years or even series of years will be enough alike in timing of conditions to become a cause for movement, around which a time-oriented factor could become an associated stimulus.

Bailey (1960) found that weather condition, snowfall, and ground snow cover differed greatly during his study also. But he suggested that a time-oriented stimulus caused deer to move from Unit A to Units B and C on or about February 17 of both years. In the present study, the deer utilizing Unit A seemed to be a separate population from the deer on the remainder of the range. This population remained relatively stable throughout each winter. Even during intense concentrations on Unit D on February 1-14, 1962, deer were also observed on Unit A. If this group were part of the larger herd, and both were sensitive to the same time-oriented stimulus, movement would have been simultaneous, as suggested by Bailey (1960). This did not occur; throughout the 1960-61 study period, deer were observed in Unit A, and no movement was observed from Unit A into other units.

In 1960-61, the deer did not form large groups in Units B and C as reported by Bailey (1960). They did not move to Unit D. In 1961-62, all animals moved to Unit D on February 1, 1961, except those in Unit A. Bailey observed movements to Unit D in late February, 1959. Therefore, there seems to be no rigid time pattern in the movements of the Rattlesnake mule deer.

The factors of snow depth and surface conditions are the primary stimuli for movement. These factors are related to weather conditions. They vary in time with local weather conditions.

Populations of deer on the study area reflect a non-rigid response to local stimuli. Populations were 50 percent larger the second year. The influx of more animals apparently came from portions of the same herd which had spent the previous, milder winter spread out over a larger area. Evidently, some of this herd moves onto the winter range only under the stimulus of deep crusted snow.

The movement and behavior of the Rattlesnake herd within the limits of the winter range is in response to local stimuli. In Unit A, animals were observed during 1960-61 moving over the major portion of the slope which was largely free of snow. Most of the snow on Unit A was confined to the ridge top. Early and late in the season more observations were made along the ridge tops while these areas were clearing of snow. In 1961-62, the deer confined their activity to the southern portion of the unit as the remainder of the unit was deep in snow most of the winter.

Utilization of Unit B was moderate and general in 1960-61. In this period the slope was largely clear of snow. In 1961-62, only the lower portion of this unit was utilized. The upper portions were deeply covered by snow during this period.

It appears that deer are discriminating in their response to stimuli; that the stimuli are local snow depth and crust conditions; that the deer respond to these stimuli by moving, perhaps only a few hundred yards, into areas where snow depths and crust conditions are below threshold levels.

Unit E exhibited the best example of threshold levels, and a primary local stimulus. By late January, 1962, Unit E had more than 24 inches of snow cover. There were 12 inches of soft powder snow over 12 inches with a crust. During this period, fawns were observed to flounder above their chests to obtain browse. The deer did not move a great deal, but spent most of the time bedded down or browsing close to established trails and trampled areas. The deer heavily utilized the snow shadow (Pruitt, 1960) area around trees and bushes. Even with these conditions existing, the herd of 47 to 57 animals remained on the unit.

The last three days of January were melting periods and crust formed on the soft snow every night. Within the last two days of the thaw, the entire group of animals moved from Unit E onto Unit D, which was clearing or just lightly covered by snow. This sudden movement from an area with crusted snow to a second area that was not snow covered indicates a sensitivity to crusted snow and a learned response to it, which results in movement to a more optimum environment.

Bailey (1960) likewise noted an instance about February 22, 1959, when identical conditions as those described above initiated a movement response which similarly caused the deer to move into Unit D.

From the accumulated data, it appears that snow 20 to 24 inches deep which becomes heavily crusted precipitates a movement of the Rattlesnake mule deer herd onto the southern (Unit D) portion of the winter range. This area is the optimum portion of the range at the time of movement.

Unit D was almost totally unused in 1959-60 (Bailey, 1960) and in 1960-61, at which time snow conditions in all areas were light and below threshold levels. The fact that this portion of the range was used in 1958-59 and 1961-62 (deep snow years) and unused in 1959-60 and 1960-61 (light snow years) indicates that deer respond to a certain snow depth and crust condition by moving into this area (Unit D). This movement is a learned response to the snow depth and crust stimuli, and the movement is maintained until the animals reach an area where snow conditions are sub-threshold.

The Rattlesnake mule deer do not move on their winter range in response to a time-oriented stimulus. Instead they respond to the stimulus of deep crusted snow which is caused by the fluctuating weather conditions during the winter period. The deer respond to the stimulus through an established stimulus-response complex which is learned by each new member of the herd as he follows and imitates older dominant deer.

SUMMARY

A study of the populations, movements, and behavior of Rocky Mountain mule deer was conducted on Wallman Ridge in the Rattlesnake Creek drainage during the winters of 1960-61 and 1961-62. The winter range study area was a Douglas-fir/ninebark seral which was burned in 1919. It is located approximately 6 miles northeast of Missoula, Montana.

Deer herds were observed throughout the two winters of the study. Size and composition of populations were obtained from visual counts. Numbers and composition of groups were noted, and movements and locations of animals were plotted on maps. Behavior was also observed and noted.

Attempts were made to develop a workable break-away snare marking device. Two models were field tested, without much success.

1. Weather conditions in the locality were different during the two years of the study period. The first winter was open; the second period had lower temperatures and deeper snows.

2. Conditions on the study area reflected the local weather. During the first year, slopes began clearing in January. In the second winter, slopes did not begin clearing until late February. Snow cover was deeper throughout the second period.

3. Unit D (Figure 2) of the study area was the first to clear of snow due to its south-southeast exposure. Unit E (Figure 2) retained its snow cover the longest.

4. During the first winter only a portion of the deer herd moved down to the area under observation; during the second winter the total herd moved onto the study area.

5. Composition of the herd remained relatively consistent during the two-year study period: Males 29.7 to 28.4 percent, females 46.5 to 42.0 percent, fawns 23.8 to 29.6 percent. The reason for the apparent increase in proportion of fawns is not known, but it may well have been due to a higher than average fawn survival the previous spring and summer.

6. The most frequent group size during the study was 3-5. During periods of decreasing available range due to snow conditions, large groups of 9+ animals were most prevalent. Single animals were most frequently observed early and late in the winter season.

7. Male animals were frequently observed associating in all male groups.

8. Males tended to join larger groups and groups of mixed sex and age during periods when range was restricted. This appeared to be due to chance association rather than choice.

9. The most prevalent family group was composed of 3-5 animals in combinations of females, fawns, and yearlings.

10. Migratory movements onto the winter range appeared to be a gradual movement extending from December until February each year. The reverse migration was similar, beginning in March each year. This migration is possibly stimulated by a time-oriented factor.

11. Non-migratory winter range movements were found to be stimulated by snow depth and crust conditions. The threshold for a movement

response was found to be snow depth which exceeded 20 inches and which was crusted. These non-migratory movements were not stimulated by a time-oriented factor.

12. Irritability among the herd was found to increase inverse to physical condition and parallel to population density.

13. Antler shedding was found to occur at an earlier date the second study winter.

14. Dominance in male deer was found to be correlated with antler size.

15. Coyote did not cause substantial winter mortality in the deer herd.

17. Populations of white-tailed deer on the study area were lower the second study year. Little evidence of conflict between mule deer and white-tailed deer was observed.

LITERATURE CITED

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Albrecht, William A. 1958. Soil fertility and animal health. Fred Hahne Printing Co., Webster City, Iowa. 232 p.

Alden, W. C. 1953. Physiography and glacial geology of western Montana and adjacent areas. U. S. Geol. Surv. Prof. Paper 231.

Aldous, C. M. 1945. A winter study of mule deer in Nevada. J. Wildl. Manag. 9(2):145-151.

Aldous, Shaler E., and Clarence F. Smith. 1938. Food habits of Minnesota deer as determined by stomach analysis. Trans. N. A. Wildl. Conf. 3:756-767.

Allee, W. C. 1938. The social life of animals. W. W. Norton and Co., Inc., New York. 287 p.

Altmann, Margaret. 1956. Patterns of social behavior in big game. Trans. N. A. Wildl. Conf. 21:538-544.

_______. 1958. The flight distance in free-ranging big game. J. Wildl. Manag. 22(2):207-209.

_______. 1958. Social integration of the moose calf. Anim. Behav. 6(3-4):155-159.

_______. 1960. The role of juvenile elk and moose in social dynamics of their species. Zoologica 45(1):35-39.

Anderson, Chester C. 1954. Migration studies of Jackson Hole's elk herd. Wyo. Wildl. 18(4):26-34.

Arnold, D. A. 1962. Personal communication, Cusino Wildl. Exp. Sta., Shingleton, Mich.

Ashcraft, Gordon C., Jr. 1961. Deer movement of the McCloud Flats herd. Calif. Fish Game 47(2):145-152.

_______, and Don Reese. 1957. An improved device for capturing deer. Calif. Fish Game 43(3):193-199.

Bailey, Edward D. 1960. Behavior of the Rattlesnake mule deer on their winter range. Unpub. M. S. thesis, Mont. State Univ., Missoula. 110 p.

Brazada, Arthur R. 1953. Elk migration patterns, and some of the factors affecting movement in the Gallatin River Drainage, Montana. J. Wildl. Manag. 17(1):9-23.

Browman, Ludvig G., and Howard S. Sears. 1956. Cyclic variation in the mule deer thymus. Proc. Soc. Exp. Biol. Med. 93(1):161-162.

________, and Paul Hudson. 1957. Observations on the behavior of penned mule deer. J. Mammol. 38(2):247-253.

Brown, Frank A., Jr. 1959. The rhythmic nature of animals and plants. Amer. Sci. 47(2):147-168.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammol. 24:346-352.

Buss, Irven O., and Frank H. Harbert. 1950. Relation of moon phases to the occurrence of mule deer at a Washington salt lick. J. Mammol. 31(4):426-429.

Carlsen, J. C., and R. F. Farmes. 1957. Movement of white-tailed deer, tagged in Minnesota. J. Wildl. Manag. 21(4):397-401.

Carter, R. L. 1951. An environmental analysis of winter game range in western Montana. Unpub. M. S. thesis, Mont. State Univ., Missoula. 103 p.

Case, George. 1938. The influence of elk on deer populations. Univ. Idaho Bull. 33(22):25-27.

Cheatum, E. L., and C. W. Severinghaus. 1950. Variations in fertility of white-tailed deer related to range condition. Trans. N. A. Wildl. Conf. 15:170-189.

Clark, E. D. 1953. A study of the behavior and movement of the Tucson mule deer. Unpub. M. S. thesis, Univ. of Ariz., Tucson. 111 p.

Cliff, Edward P. 1939. Relationship between elk and mule deer in the Blue Mountains of Oregon. Trans. N. A. Wildl. Conf. 4:560-569.

Clover, Melvin R. 1954. Deer marking devices. Calif. Fish Game 40(2): 175-181.

Codd, A. R., and P. E. Farnes. 1962. Federal-state-private cooperative snow surveys and water supply forecasts for Montana and northern Wyoming. Soil Conserv. Serv. and Mont. Agr. Exp. Sta., Bozeman. 17 p.

Cook, David B., and W. J. Hamilton, Jr. 1942. Winter habits of white-tailed deer in central New York. J. Wildl. Manag. 6(4):287-291.

Cook, C. Wayne, L. A. Stoddart, and Lorin E. Harris. 1956. Comparative nutritive value and palatability of some introduced and native forage plants for spring and summer grazing. Utah Agr. Exp. Sta. Bull. 385. 39 p.

Cowan, I. M. 1936. Distribution and variations in deer (Genus Odocoileus) of the Pacific Coastal Region of North America. Calif. Fish Game 22(3):155-246.

Darling, F. F. 1937. A herd of red deer. Oxford University Press, London. 215 p.

Dasmann, Raymond F. 1953. Factors influencing movement of non-migratory deer. Proc. Ann. Conf. Western Assoc. State Game Fish Comm. 33: 112-116.

_______, and Richard D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. J. Mammol. 37(2):143-164.

_______, and _____. 1956. Determining structure in Columbian black-tailed deer populations. J. Wildl. Manag. 20(1):78-83.

Daubenmire, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. 22(4):301-330.

Delap, Peter. 1957. Some notes on the social habits of the British deer. Proc. Zool. Soc. London 128(4):608-612.

DeNio. R. M. 1938. Elk and deer food and feeding habits. Trans. N. A. Wildl. Conf. 3:421-427.

deVos, A. 1957. Summer studies of moose in Ontario. Trans. N. A. Wildl. Conf. 21:510-525.

_______. 1960. Behavior of barren ground caribou on the calving grounds. J. Wildl. Manag. 24(3):250-258.

Dixon, J. S. 1934. A study of the life history and food habits of mule deer in California. Calif. Fish Game 20(3-4):182-282, 315-354.

Doman, Everett R., and D. I. Rasmussen. 1944. Supplemental winter feeding of mule deer in northern Utah. J. Wildl. Manag. 8(4):317-338.

Edwards, R. Y. 1956. Snow depths and ungulate abundance in the mountains of western Canada. J. Wildl. Manag. 20(2):159-168.

_______, and Ralph W. Ritcey. 1956. The migration of a moose herd. J. Mammol. 37(4):486-494.

Edwards, O. T. 1942. Winter deer range survey report, Malheur National Forest, Oregon. J. Wildl. Manag. 6(3):210-220.

Fowle, C. D. 1950. The "natural" control of deer populations. Conv. Int. Assn. Game, Fish and Conserv. Comm. 40:56-63.

Fuller, W. A. 1960. Behavior and social organization of the wild bison of Wood Buffalo National Park, Canada. Arctic 13(1):2-19.

Gabrielson, Ira N. 1943. Wildlife refuges. Macmillan Co., New York. 257 p.

Grieser, Kenneth C. and Ludvig Browman. 1956. Total gonadotrophic potency of mule deer pituitaries. Endocrinology 58(2):206-211.

Gruell, George. 1958. Results from four years of trapping and tagging deer in northeastern Nevada. Proc. Ann. Conf. Western Assoc. State Game Fish Comm. 38:179-183.

Halls, L. K., O. M. Hale and F. E. Knox. 1957. Seasonal variation in grazing use, nutritive content, and digestibility of wiregrass forage. Georgia Agr. Exp. Sta. Tech. Bull. N. S. 11. 28 p.

Hamerstrom, F. N., Jr., and James Blake. 1939. Winter movement and winter foods of white-tailed deer in central Wisconsin. J. Mammol. 20(2):206-215.

Hanson, William R., and Clay Y. McCulloch. 1955. Factors influencing mule deer on Arizona brush lands. Trans. N. A. Wildl. Conf. 20: 568-588.

Harker, Janet E. 1958. Diurnal rhythms in the animal kingdom. Biol. Revs. Camb. Philos. Soc. 33(1):1-52.

Harris, Dave. 1945. Symptoms of malnutrition in deer. J. Wildl. Manag. 9(4):319-322.

Hart, G. H., H. R. Guilbert, and H. Goss. 1932. Seasonal changes in the chemical composition of range forage and their relation to nutrition of animals. Univ. of Calif. Agr. Exp. Sta. Bull. 543. 61 p.

Hellmers, Henry. 1940. A study of monthly variations in the nutritive value of several natural winter deer foods. J. Wildl. Manag. 4(3): 315-325.

Hediger, H. 1955. Studies of the psychology and behavior of captive animals in zoos and circuses. Criterion Books, New York. 153 p.

Hill, Ralph. 1946. Palatability ratings of Black Hills plants for white-tailed deer. J. Wildl. Manag. 10(1):47-54.

Interstate Deer Herd Committee. 1949. Third progress report on the cooperative study of the Interstate deer herd and its range. Calif. Fish Game 35(2):115-134.

Kelsall, John P. 1955. Barren ground caribou movements in the Canadian Arctic. Trans. N. A. Wildl. Conf. 20:551-566.

Klebenow, D. A. 1962. Ecology and productivity of a mountain forest winter deer range, western Montana. Unpub. M. S. thesis, Mont. State Univ., Missoula. 93 p.

Knowlton, Frederick F. 1960. Food habits, movement, and populations of moose in the Gravelly Mountains, Montana. J. Wildl. Manag. 24(2):162-170.

Koch, Elers. 1941. Big game in Montana from early historical records. J. Wildl. Manag. 5(4):357-370.

Leopold, Aldo, Lyle K. Sowls, and David L. Spencer. 1947. A survey of over-populated deer ranges in the United States. J. Wildl. Manag. 11(2):162-176.

Leopold, A. Starker, Thane Riney, Randal McCain, and Lloyd Tevis, Jr. 1951. The Jawbone deer herd. Calif. Div. of Fish and Game. Game Bull. 4. 139 p.

Linsdale, Jean M., and P. Quentin Tomich. 1953. A herd of mule deer, Univ. of Calif. Press, Berkeley and Los Angeles. 567 p.

Marston, Merwin A. 1942. Winter behavior of deer in northwestern Maine. Unpub. M. S. thesis, Univ. of Maine, Orono.

McEwen, L. C., C. E. French, N. D. Magruder, R. W. Swift, and R. H. Ingram. 1957. Nutrient requirements of the white-tailed deer. Trans. N. A. Wildl. Conf. 22:119-132.

McLean, Donald D. 1940. The deer of California with particular reference to the Rocky Mountain mule deer. Calif. Fish Game 26(2):139-166.

Mitchell, H. L., and N. W. Hosley. 1936. Differential browsing by deer on plots variously fertilized. Black Rock Forest Papers, Mass. 1(5):24-27.

Olsen, Orange. 1938. Winter range as a limiting factor in big game management. Univ. Idaho Bull. 33(22):20-22.

Palmer, L. J. 1944. Food requirements of some Alaskan game mammals. J. Mammol. 25(1):49-54.

Picton, Harold D. 1960. Migration patterns of the Sun River elk herd, Montana. J. Wildl. Manag. 24(3):279-290.

Progulske, D. R. 1957. A collar for identification of big game. J. Wildl. Manag. 21(2):251-252.

_______, and Thomas S. Basket. 1958. Mobility of Missouri deer and their harassment by dogs. J. Wildl. Manag. 22(2):184-192.

Pruitt, Wm. O., Jr. 1959. Snow as a factor in the winter ecology of the barren ground caribou (Rangifer arcticus). Arctic 12(3):158-179.

_______. 1960. Animals in the snow. Scientific American 202:61.

Rasmussen, D. Irvin. 1941. Biotic communities of Kaibab Plateau, Arizona. Ecol. Monogr. 11(3):230-275.

Robertson, J. H., and Clark Torell. 1958. Phenology as related to chemical composition of plants and to cattle gains on summer ranges in Nevada. Nevada Agr. Exp. Sta. Bull. (Tech.) 197.

Robinson, William L. 1960. Test of shelter requirements of penned white-tailed deer. J. Wildl. Manag. 24(4):364-371.

Robinette, W. Leslie, and Jay S. Gashwiler. 1950. Breeding season, productivity and fawning period of the mule deer in Utah. J. Wildl. Manag. 14(4):457-469.

_______, Odell Julander, Jay S. Gashwiler, and Justin G. Smith. 1952. Winter mortality of mule deer in Utah in relation to range conditions. J. Wildl. Manag. 16(3):289-299.

_______, J. S. Gashwiler, J. B. Low, and D. A. Jones. 1957. Differential mortality by sex and age among mule deer. J. Wildl. Manag. 21(1):1-16.

Romanov, A. N. 1956. Avtomaticheskoye Kol"tsevaniye Dikikh Zhivotnykh I Perspektivy yego Primeneniya. Zoologicheskiy Zhurnal, 35, 12, Moscow, p. 1902.

Russell, C. P. 1932. Seasonal migrations of mule deer. Ecol. Monogr. 2:1-46.

Schwartz, Charles W., and Elizabeth R. Schwartz. 1959. Wild mammals of Missouri. Univ. of Mo. Press and Mo. Conserv. Comm., Columbia. 341 p.

Scott, J. P. 1956. The analysis of social organization in animals. Ecology 37(2):213-221.

_______. 1958. Animal behavior. Univ. of Chicago Press. 281 p.

Severinghaus, C. W. 1947. Relationship of weather to winter mortality and population levels among deer in the Adirondack Region of New York. Trans. N. A. Wildl. Conf. 12:212-223.

Shanks, Royal E., and Fred H. Norris. 1950. Microclimatic variation in a small valley in eastern Tennessee. Ecology 31(4):532-539.

Shelford, V. E. 1954. The antelope population and solar radiation. J. Mammol. 34(4):533-538.

Taber, Richard D. 1953. Production, mortality, and yield of black-tailed deer on Chaparral Range. Proc. Ann. Conf. Western Assoc. State Game Fish Comm. 33:128-131.

_______. 1956. Deer nutrition and population dynamics in the North Coast Range of California. Trans. N. A. Wildl. Conf. 21:159-172.

_______, and R. F. Dasmann. 1954. A sex difference in mortality in young Columbian black-tailed deer. J. Wildl. Manag. 18(3):309-315.

_______, and _______. 1958. The black-tailed deer of the Chaparral. Calif. Fish Game Bull. No. 8. 161 p.

_______, Keith L. White, and Norman S. Smith. 1960. The annual cycle of condition in the Rattlesnake, Montana mule deer. Proc. Mont. Acad. Sci. 19:72-79.

Taylor, Walter P., and Henry C. Hahn. 1947. Die-offs among the white-tailed deer in the Edwards Plateau of Texas. J. Wildl. Manag. 11(4):317-323.

_______, ed. 1956. The deer of North America. Stackpole Co., Harrisburg, Pa. 668 p.

Thorpe, W. H. 1956. Learning and instinct in animals. Harvard Univ. Press, Cambridge, Mass. 460 p.

Tinbergen, N. 1953. Social behavior in animals. Methuen and Co. Ltd., London, and John Wiley and Sons, Inc., New York. 150 p.

Webb, William L. 1948. Environmental analysis of a winter deer range. Trans. N. A. Wildl. Conf. 13:447-449.

Welch, Joseph M. 1960. Factors influencing movement of white-tailed deer of southern Arizona. Unpub. M. S. thesis, Univ. of Arizona, Tucson.

White, K. L. 1958. Summer range ecology of Rattlesnake Creek mule deer in the spruce-fir zone. Unpub. M. S. thesis, Mont. State Univ., Missoula. 95 p.

Wislocki, George B. 1943. Studies on growth of deer antlers. II. Seasonal changes in the male reproductive tract of the Virginia deer (Odocoileus virginianus borealis) with a discussion of the factors controlling the antler-gonad periodicity. Essays in biology in the honor of Herbert M. Evans. Univ. Calif. Press, Berkeley and Los Angeles. p. 629-653. (From Taylor, 1956).

Woodbury, A. M. 1941. Changing the "hook order" in cows. Ecology 22: 410-411.

______. 1956. Comfort for survival in nature and man. Vantage Press, New York. 104 p.

Zwickel, Fred, Gardiner Jones, and Homer Brent. 1953. Movement of Columbian black-tailed deer in the Willapa Hills area, Washington. Murrelet 34(3):41-46.

APPENDIX

APPENDIX A

MARKING SNARE