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THE MULE DEER
of
Mesa Verde
National Park

Edited by
Gary W. Mierau
and
John L. Schmidt

Mesa Verde National Park, Colorado
Mesa Verde Museum Association, Inc.

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Compiled from project reports by:

COOPER, WILLIAM D., M.S.; deceased, formerly Biologist, National Park Service, Capitol Reef National Park, Utah.

DILLINGER, KENNETH C., M.S.; District Wildlife Manager, Colorado Division of Wildlife, Sterling, Colorado.

GILBERT, DOUGLAS L., Ph.D.; deceased, formerly Head, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado.

MIERAU, GARY W., Ph.D.; Electron Microscopist, Department of Pathology, The Children's Hospital, Denver, Colorado.

SCHMIDT, JOHN L., Ph.D.; Associate Professor, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado.

STEINHOFF, HAROLD W., Ph.D.; District Director, Cooperative Extension Service, Colorado State University, Durango, Colorado.

WHITAKER, ALLEN F., M.S.; Wildlife Program Specialist, Colorado Division of Wildlife, Denver, Colorado.

Mesa Verde Museum Association, Inc.
Mesa Verde National Park, Colorado

Deer figure adapted from Anasazi pictograph.

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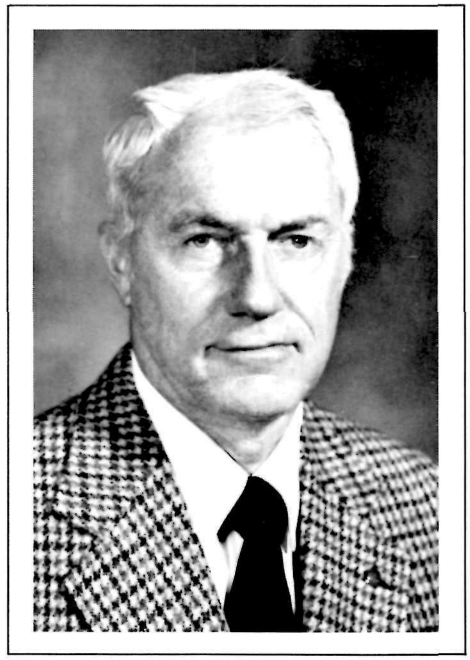
William Cooper



Douglas Gilbert

To William Cooper
and to Douglas Gilbert,
this work is dedicated
as a slight testimony of
our friendship, deep respect
and sincere admiration.

Acknowledgements

A large portion of the credit for the project's success must go to the Mesa Verde National Park administration and staff, who without exception lent us their full support and cooperation. Particularly helpful was biologist J. Hammond Eve, III, who became actively involved in virtually all aspects of the study. Well remembered and especially appreciated are the many acts of personal kindness extended to us by "Scotte" Highland.

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October 1980

Gary W. Mierau
John L. Schmidt

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Summary

The objective of this study was to provide basic ecological data on the mule deer of Mesa Verde National Park. Included were studies on population dynamics, movement patterns, physical condition, and condition of the habitat.

At the onset of the study in 1967, the population density was high. Approximately 30 deer per square kilometer inhabited the mountain brush vegetative stand, 20 per square kilometer were found in the sagebrush-grass stand, and 5 per square kilometer in the pinyon-juniper stand. Census techniques revealed the summer population to total approximately 4,500 deer, with the number temporarily increasing to about 5,200 animals during the late autumn and early winter months. The autumn increase in population density is believed to result from nonresident deer using the Mesa Verde as a transitional range along their route to wintering grounds at lower elevations. Over the period of study the deer herd experienced a dramatic decline in numbers. In 1968 the summer population fell to 3,500 and in 1969, to 2,400. A final census taken in 1975 and 1976 indicated that only about one-fourth as many deer remained as were present at the beginning of the study.

Examination of 151 deer carcasses failed to reveal a cause for the population decline. In fact, the deer proved to be exceptionally large and, in general, in excellent health. Mature males averaged 94 kilograms in (live) weight, with the largest 130 kilograms. Mature females averaged 63 kilograms, with the largest 77 kilograms. No evidence of malnutrition was found. The observed incidence of infectious disease was relatively low and none of the diseases thought capable of causing a significant population decline was detected in the Mesa Verde herd.

Using a variety of techniques 198 deer were captured and marked for movement and home range studies. An additional 150 to 200 deer were estimated to have been marked with automatic tagging devices. Most of the deer returned to the Park in late March or early April from their wintering ranges at lower elevations. Typically, they reestablished the same home ranges occupied in previous summers. The average maximum diameter of the home range of adult deer was approximately 1.0 kilometers in the mountain brush stand and about 1.8 kilometers in the pinyon-juniper stand. The fawning season was relatively short, with most of the young being born between 20 June and 1 July. Most of the breeding activity occurred between 29 November and 10 December. The deer deserted their summer ranges as the depth of accumulated snow approached 25 centimeters. This usually occurred in late December or January. A small number of deer normally wintered at lower elevations within the Park but even these left during periods of unusually high snowfall. The distance between summer and winter ranges varied between 10 and 21 kilometers. Migratory movements took deer in every direction from the Park. It was not possible to predict the location of a deer's winter range from the location of its summer range. These behavioral studies provided no insight into the nature or causes of the population decline.

The Mesa Verde habitat was judged to be in good condition at the time our studies were conducted, but did exhibit signs of severe overutilization in the recent past. Soil conditions were rated as good throughout the Park. Ground cover was rated as medium in all three primary vegetative stands. Desirable browse species were present in wide variety and abundance, except in the pinyon-juniper forest. The vigor of many key browse species in the mountain brush stand was low, however; the plants had not fully recovered from an earlier period of overbrowsing. Browse vigor was rated as medium in the sagebrush-grass stand and, probably due to competition with the overstory, low in the pinyon-juniper stand. The level of browse utilization was moderate, with from 9 to 43% of the annual growth of key browse species being harvested. Analysis of rumen contents from 142 deer revealed their annual diet to consist of 61% browse, 20% forb, and 16% grass species. Utah serviceberry, antelope bitterbrush, Gambel oak, and big sagebrush were the most heavily utilized browse species. The population decline appears to have been well underway by the time our studies were initiated. Habitat degradation resulting from range overutilization was likely the initial cause. Our studies

revealed, however, that the range was already in a recovery phase while the deer population was still declining, suggesting that other factors were acting upon the population to prolong its decline.

Failure to maintain a stable herd size could not be attributed to low reproductive rates, for these were generally high among Mesa Verde deer. Ovulation rates were 1.55 for yearling and 1.96 for adult does. The fetal rate of adult does was 1.79. All adult does examined during the gestational period were pregnant. An unusual prenatal sex composition of 32% males and 68% females was discovered, but sex ratios in older age classes were more typical of mule deer populations elsewhere.

Life table/age structure analysis and computer simulation modeling indicated that the Mesa Verde mule deer population was in a downward trend because of high mortality among fawns. The mortality rate for fawns was 32% during their first few months of life, resulting in a late summer fawn: adult doe ratio of 1.17:1. Only 25% of the fawn crop ultimately survived to become yearlings. The "predator lag" phenomenon is presumed to have been responsible for the high fawn mortality, and thus, for the prolongation of the population decline. Reversal of the population trend is anticipated as the predator population restores its former balance with the deer population.

1. Introduction

By the mid-1960's, deer inhabiting Mesa Verde National Park had increased in numbers to the point where park rangers were becoming concerned. The number of animals any parcel of land can support is limited; and when that number is exceeded, overutilization may result in habitat destruction with disastrous consequences to the entire ecologic community.

Ranger Thomas Hobbs, in June 1964, initiated a study to determine if the deer population was indeed exceeding the carrying capacity of its range. His conslusion (MVNP File Ref. N 1427), following a year and a half investigation, was that "... the deer range is in very poor condition. If the present severe overbrowsing is allowed to continue, within a few years the range will be in a very critical condition." Hobbs' recommendations were (1) that the summer resident deer herd be substantially reduced in size and (2) that an intensive "... research program be established to determine the ecological relationship between the deer herd and the habitat in Mesa Verde National Park."

A program to reduce the resident deer herd by 25% (about 200 animals) was planned for the summer of 1966. A controversy which became something of a political issue soon developed. This was associated with the mechanism by which the proposed reduction was to take place. The National Park Service maintained that only park rangers could be allowed to shoot animals within park boundaries. The Colorado Game, Fish and Parks Department contended that the surplus deer should be harvested by sportsmen in a special public hunting season. When it became evident that this dispute would not be quickly resolved, it was decided that an immediate attempt would be made to remove the excess deer using the relatively inefficient technique of live trapping. Another interim measure was to implement the second of ranger Hobbs' recommendations. To this end, a contract (#14-10-9-990-19) was awarded by the National Park Service to Colorado State University for an in-depth study of the Mesa Verde deer herd.

Under the direction of professors Douglas L. Gilbert and Harold W. Steinhoff, four graduate students of the Department of Fishery and Wildlife Biology began field work in June 1967. Members of the project team actively participated in all aspects of the study but each held responsibility for a specific portion: John L. Schmidt for studies of population dynamics, Gary W. Mierau for determination of deer distribution and movement patterns, William D. Cooper for evaluation of the physical condition of the deer, and Kenneth C. Dillinger for assessment of habitat condition. In December 1968, Allen F. Whitaker replaced Gary Mierau who had been drafted into military service.

As the study progressed, it became apparent that a number of important basic research problems could be concurrently investigated without additional expense to the National Park Service. Several studies under the direction of Dr. Julius G. Nagy were subsequently initiated to investigate the energy and nutrient requirements of mule deer. The nutrient content of the digestive tract, nutrient composition of muscle, and mineral content of bone were studied by John C. Olson, Lawrence Wookey, and Bruce D. Murphy, respectively. Complementing Murphy's studies of cyclic changes in the male reproductive system, an investigation into cyclic changes in the female reproductive tract was undertaken as a second responsibility by John Schmidt.

Each month, throughout the year, the entire project team assembled in the Park for several days of concentrated work. At these times deer were collected and autopsied, helicopter or fixed-wing aircraft census flights were made, deer were live-captured and marked, and previously tagged animals were relocated. The most intensive periods of field investigation were necessarily the summer months, during which most project members lived in the Park. At least one member usually remained in residence through the other seasons as well.

The initial phase of the Mesa Verde deer study was completed in June 1970. It was discovered that the size of the herd had spontaneously begun to decline and that a reduction program was no longer necessary. We came then to realize that what we had observed in the Mesa Verde herd was part of a generalized phenomenon affecting much of the western United States. At this point a decision was reached to extend some aspects of our research for several additional years in order to capitalize on this unique opportunity to study further, within the microcosm of Mesa Verde National Park, a population decline that was widespread and natural. The downward trend continued for nearly a decade but seemed to be leveling off when a final census of the Mesa Verde herd was undertaken in June 1976. A year later, ten years after we began, field studies were discontinued.

2. The Study Area

History

About the time of Christ, ancestors of the present Pueblo Indians entered the "Four Corners" region — where the boundries of Colorado, New Mexico, Arizona, and Utah now meet. These early inhabitants found shelter in the numerous shallow caves which dot the Mesa Verde landscape. Over the next 700 years they gradually became more sedentary, and developed greater dependence on agriculture. A period of spectacular cultural advancement followed; during which the bow and arrow replaced the atlatl and spear, farming implements began to be manufactured, cotton weaving appeared, beautiful pottery was crafted, and a complex system of religious beliefs and practices was developed. Most striking, though, were their architectural achievements which culminated in the magnificent cliff dwellings for which these people are remembered. In the late 1200's, at the height of their cultural evolution, the Anasazi people suddenly and inexplicably abandoned the cliff dwellings to forsake the Mesa Verde forever.

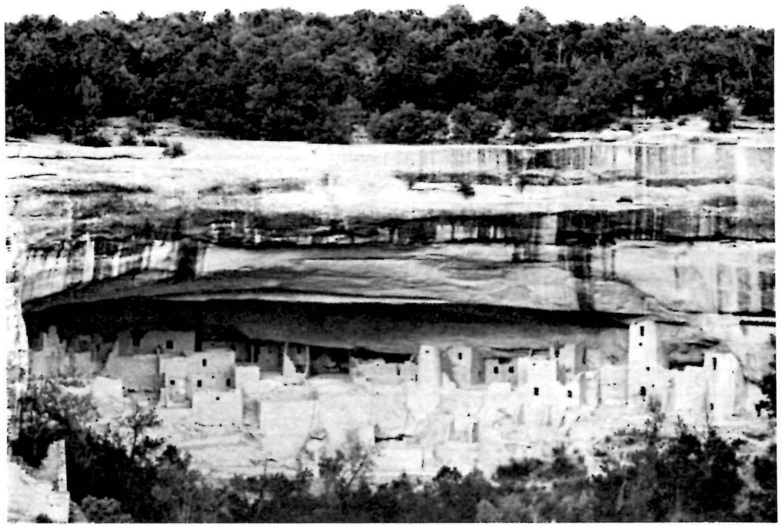

Figure 1. Cliff Palace, first of the major Anasazi ruins to be discovered, characterizes the cliff dwellings for which Mesa Verde National Park is known. Photo by J. Brenman.

William H. Jackson, the famed photographer, was possibly the first white man to discover the ancient ruins. In 1874 he photographed a cliff dwelling in the Mancos Canyon which he named Two Story Cliff House. The significance of Jackson's discovery went largely unappreciated until 1888, when cowboys Richard Wetherill and Charles Mason happened across the majestic Cliff Palace (Fig. 1) while chasing strays. With the subsequent discovery of Spruce Tree House, Square Tower House and other major dwellings, the dimension and magnificence of this ancient civilization soon became evident. In 1906, Mesa Verde National Park was established by act of Congress.

Physiography

The name Mesa Verde is believed to have been given to this "green table" by early Spanish traders. This awesome tree covered landmass juts impressively above the surrounding southwestern Colorado Landscape. The 200 square kilometer area set aside as a national park (Fig. 2) comprises slightly less than half of the total Mesa Verde formation; the remainder is part of the Ute Mountain Indian Ute Reservation.

The Mesa Verde landmass is composed of marine sediments deposited during the Upper Cretaceous age. Technically it is a cuesta (a ridge with a steep escarpment on one side and a long gentle slope on the other) rather than a mesa. Its north-facing escarpment rises nearly 600 meters from the floor of the San Juan Basin (Fig. 3). Then from an

Figure 2. Map of the "Four Corners" region indicating the location of Mesa Verde National Park.

elevation of approximately 2591 meters at the north rim, the landmass slopes gently to about 2073 meters at the southern end of the Park (Fig. 4). Canyons have formed where erosion has broken through the once continuous sandstone cap rock to the soft shale and coal-bearing deposits beneath. Originating near the north rim, the canyons increase dramatically in size over their 25 kilometer southward course to the Mancos River, some becoming

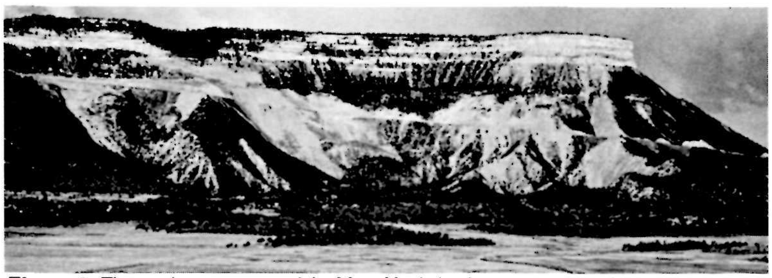

Figure 3. The north escarpment of the Mesa Verde landmass, as well as the east escarpment shown here, rises precipitously from the surrounding Montezuma Valley. Photo by J. Brenman.

Figure 4. View south from the north rim reveals the gently sloping "green table" to be fragmented by deep canyons. Photo by G. Mierau.

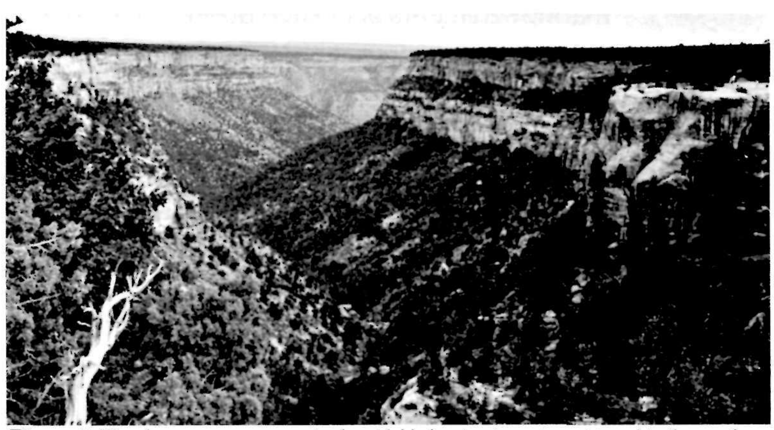

Figure 5. The deep canyons present a formidable barrier to east-west travel in the southern portion of the Park. Photo by G. Mierau.

300 meters deep and nearly a kilometer wide (Fig. 5). The deep canyons dissect the Mesa Verde into relatively isolated fragments which are locally also referred to as "mesas" (Fig. 6).

Soils of the area are quite variable in both composition and depth (Erdman et al. 1969). Along the north rim, where soils are in part derived from weathered sandstone, they are generally shallow (50 to 100 centimeters to bedrock), slightly acidic and contain large amounts of gravel and coarse rock. Mesa-top soils are primarily wind-deposited loess. Near the southern end of the Park they are fairly deep (1 to 5 meters to bedrock), highly calcareous, and of uniform texture. Alluvial deposits up to 5 meters in depth are found in the canyon bottoms.

Climate

An excellent detailed description of the Mesa Verde climate has been provided by Erdman et. al. (1969). In general, the climate is semiarid and mild. Climatic conditions, it should be noted however, are appreciably different at the northern and southern ends of the Park. The north rim receives more precipitation and experiences winters of greater severity than the lower elevations, factors directly and indirectly exerting a profound influence on the deer population.

A distinct climatic feature of the region is its uniformity of weather from day to day. Severe cold waves are uncommon. Winter daytime temperatures are usually fairly high but nights are cold, especially when snow covers the ground. Summer temperatures are surprisingly mild for a semiarid region, rarely exceeding 38°C. Weather records have been kept in Mesa Verde National Park since 1923, when a United States Weather Bureau station was established on Chapin Mesa near Park headquarters. Average monthly

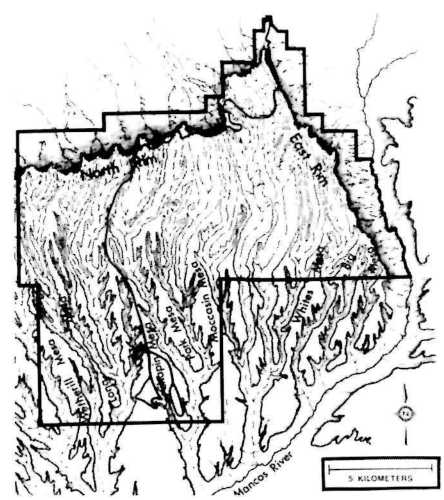

Figure 6. Map identifying the major "mesas" of Mesa Verde National Park.

temperatures for the 54-year record period (1923-1976) are presented in Fig. 7.

It is precipitation rather than temperature, however, that is the more important climatic factor influencing plant and animal life in Mesa Verde. Annual precipitation since 1923 has averaged 45.7 centimeters. Precipitation received during the study period (1967-1976) was near normal (45.5 centimeters per year) as was that of the preceding decade (47.2 centimeters per year). The seasonal distribution of annual precipitation can be as important as the total received. Ground water supplies are recharged far more effectively by the slow snow melt of spring than by the brief and highly localized intense thunderstorms of late summer. Adequate winter moisture is therefore critical to the plant community and also, although less directly, to the animals depending upon the plants for food. Deer, especially when lactating, are equally dependent upon summer rainfall to replenish the temporary potholes which are often their only source of drinking water. As was the case with total precipitation, seasonal distribution patterns during the study period did not significantly differ from normal (Fig. 7).

Flora

The environmental factors discussed previously (climate, soils, topography) are largely responsible for determining the abundance and distribution of plant species within an ecologic community.

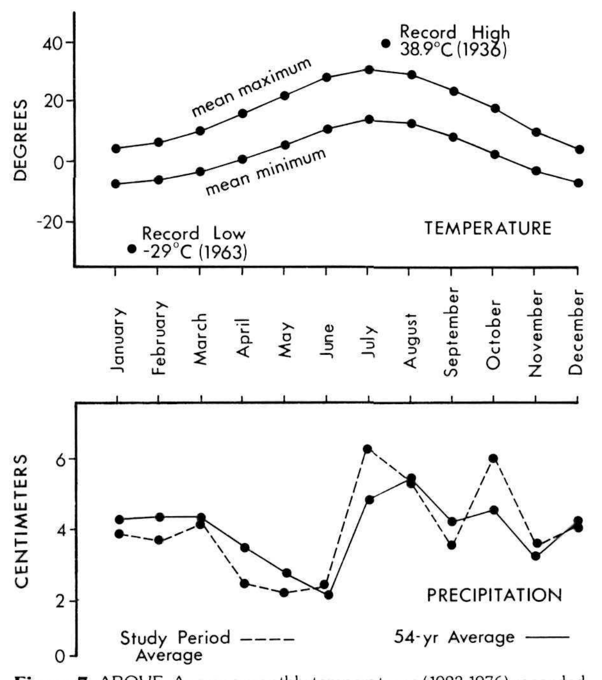

Figure 7. ABOVE: Average monthly temperatures (1923-1976) recorded for Mesa Verde National Park. BELOW: Comparison between overall average monthly precipitation (1923-1976) and that received during the study period (1967-1976).

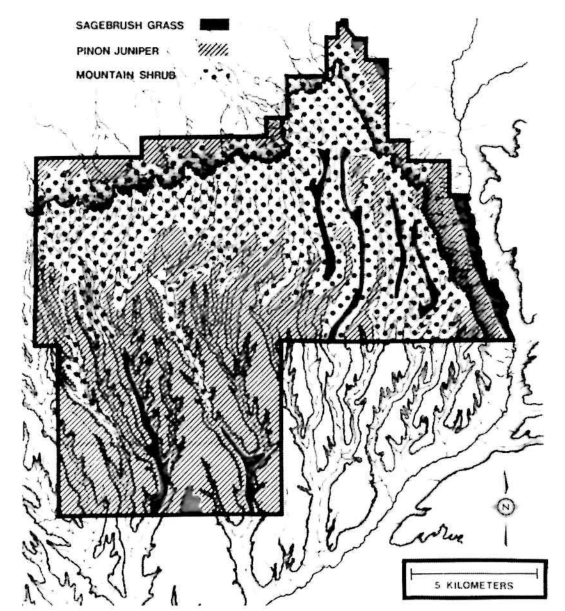

Figure 8. Map indicating the approximate distribution of the Park's three major vegetative stands.

It is the vegetation in turn, more than any other factor, that determines the abundance and distribution of the animal species present. An extensive listing of the plant species present in Mesa Verde National Park has been provided by Welsh and Erdman (1964) and will not be duplicated here. Common and scientific names used are listed in Appendix I. Relevant to the deer population, three distinct major vegetative stands are recognized within the Park.

A pinyon-juniper forest covers approximately 50% of the Park, mainly the southern portion (Fig. 8). Pinyon pine and Utah juniper are the dominant species. Compared to most pinyon-juniper forests, the trees are tall (up to 9 meters) and closely spaced. The understory is sparse because of the dense tree canopy. Mutton grass is the dominant understory species, but yucca and various shrubs are conspicuous in some locations (Fig. 9). Antelope bitterbrush, the most common shrub, is a preferred food of mule deer.

Given sufficient time, biotic communities progress through a series of orderly steps (seral stages) until a terminal stabilized "climax" stage is achieved. Although Mesa Verde lies within the extensive pinyon-juniper climax region of the American Southwest, a dense stand of mountain brush vegetation is found to cover approximately 40% of the Park (Fig.8). Erdman (1970) has provided convincing support for the theory that recurrent natural fires have served to maintain the transitional (between oak and pinyon-juniper) portion of the Park in this mid-successional stage. Following a major fire, about 25 years are required to establish the mountain brush stage but an additional 100 years must elapse before trees begin to reappear and another 200 years before the pinyon-juniper climax is reestablished in the transitional areas (Erdman 1970). Oak is now considered at least a temporary (i.e. 500+ years) climax on moister sites such as those in the northern portions of Mesa Verde (Steinhoff 1978). The long lasting effects of fire are not entirely negative, however, for a mountain brush habitat is more favorable to deer than is pinyon-juniper forest. The mountain brush stand is a patchwork of

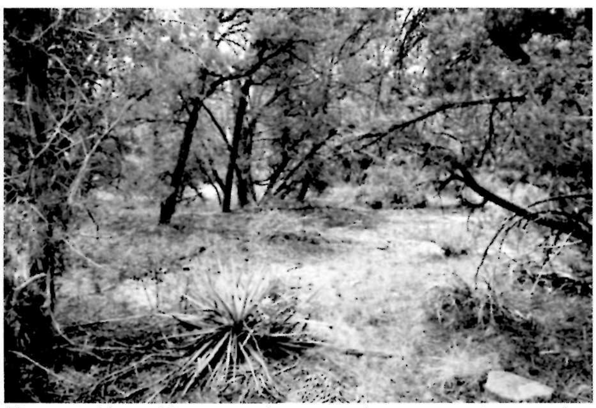

Figure 9. Mutton bluegrass and yucca are the most conspicuous understory plants of the dense pinyon-juniper forest. Photo by G. Mierau.

Figure 10. The mountain brush vegetative stand provides the best deer habitat in Mesa Verde National Park. Photo by G. Mierau.

Gambel oak, Utah serviceberry, black sagebrush, and other browse species (Fig. 10). Grasses and forbs are abundant in the openings between the dense shrub thickets. Scattered trees are becoming reestablished in some areas.

A sagebrush-grass stand is found in some canyon bottoms, and occupies approximately 10% of the Park (Fig. 8). The alluvial terraces of the deeper canyons support almost pure stands of big sagebrush (Fig. 11) but at the canyon's upper reaches these frequently give way to open grassy areas (Fig. 12). The more common grasses include

Figure 11. Nearly pure stands of big sagebrush are found in the deep canyons of the southern portion of the Park. Photo by G. Mierau.

western wheatgrass, mutton bluegrass, needle-and-thread, and smooth brome. The canyon habitat is of greater importance to the deer herd than its limited area might suggest, for it is here that many deer find food and shelter during the harsh winter months.

Fauna

Mesa Verde National Park was the first to be established primarily to preserve a work of man rather than nature. To protect the delicate Indian ruins, policy has been very restrictive. Visitors are allowed access to only a few small segments of the Park, and then under close ranger supervision. The wildlife community subsequently has experienced minimal disturbance by man. Surrounding and further insulating this wildlife sanctuary from outside influence is a substantial buffer zone of rugged, sparsely populated land.

The Rocky Mountain mule deer is the only large herbivore found in abundance. This species occupies a dominant position in the biotic community and is unquestionably capable of exerting a profound influence on its environment.

Potentially in direct competition with deer for available habitat are several species present

Figure 12. Grasses dominate the canyon bottoms at higher elevations near the Park's north and east rims. Photo by G. Mierau.

in lesser numbers. Mountain sheep, common in prehistoric times, were reintroduced in 1946. Although the herd apparently prospered for a time, only a few stragglers remain. Elk likewise probably are not sufficiently abundant to be of consequence. We observed but a single individual during the course of our studies. Stray and semi-wild domestic stock are certainly the most visible source of competition. Much of the boundary between the Park and adjacent Indian reservation is unfenced. Horses, cattle, and occasionally goats find free access into the Park where they often remain for extended periods of time. Small numbers of cattle can usually be found in the deep canyon bottoms. A herd of from 6 to 14 horses (Fig. 13) occupied the northwestern portion of the Park throughout the study period. While the impact of cattle on the environment has undoubtedly been slight, that of the horses continues to be significant and warrants formal study and management.

Figure 13. A herd of six feral horses on Wetherill Mesa. The stallion leader is seen nearest the helicopter's shadow. Photo by G. Mierau.

The number of carnivores present in a given ecologic community is largely determined by the relative abundance of the species upon which they prey. Where deer are abundant, it follows that predators capable of preying upon deer should be plentiful. This is indeed the case at Mesa Verde. Coyotes and bobcats are very common in all parts of the Park. Although they are capable of killing adult deer only under special circumstances, they undoubtedly take large numbers of fawns during the spring and summer months. Black bears are fairly common but probably are not effective enough predators to be of consequence to the deer herd. Wolves at one time inhabited the Park but are no longer present. The only predator remaining which is capable of killing adult deer in significant numbers is the mountain lion. Although rarely observed, mountain lions are not uncommon and range throughout the Park.

3. The Deer Population

Numbers and Distribution

The Historic Population

That deer were present when the Anasazi arrived is well documented in the earliest traces of this ancient culture. Little else regarding the deer population of prehistoric times can be determined with certainty. One might speculate, however, that since the climate and the vegetation of the Mesa Verde region are known to have remained remarkably stable over the past 2000 years, the size of the deer population may well have been similar then to what it is today. These earliest residents, armed only with the atlatl (a device for throwing spears), were poorly equipped for hunting and depended primarily upon agriculture for their existence. If predation by the ancient Indians did exert an appreciable impact on the deer population during their time, the intervening 700 years certainly should have been ample for the population to recuperate fully. Except for occasional bands of nomadic Indians, the area was not reinhabited by man until the 1870's when conflict with white settlers forced some Ute Indians to take refuge in the rugged canyons. A few abortive attempts at ranching followed, but since 1906 the area and its wildlife have enjoyed full protection under national park status.

The first recorded observations regarding deer do not appear in the Mesa Verde National Park files until 1937. For a number of years thereafter only casual observations on deer abundance are available. As one might expect, the majority of these reports appear to have been filed only when the observation seemed sufficiently unusual to warrant documentation. A sampling of such reporting is as follows (MVNP File Ref. N 1427): "People report seeing as many as 20 [deer] from entrance to headquarters" (October 1937); "76 [deer] seen between entrance and headquarters" (November 1940); "Unusually plentiful - 118 [deer] seen from entrance to headquarters" (November 1942); "Deer plentiful, 45-50 seen commonly from entrance to headquarters" (October 1943); "20 [deer] between entrance and headquarters" (September 1944); "57 [deer] seen on entrance highway" (April 1950).

The first systematic attempt to survey the deer population was begun in 1954. This "Deer Trend Study" (MVNP File Ref. N 1427) consisted of a mail carrier's roadside count conducted during the autumn, winter and spring months of three successive years. Roadside counts have long been a standard procedure for obtaining trend indices. Unfortunately, they are subject to a number of potentially important variable factors. In an attempt to minimize the effects of these variables, the counts were conducted by a single individual traveling a specific route at standardized times during comparable seasons and weather conditions. If one allows the perhaps unwarranted assumption that the roadsides are representative of the Park in general, a crude population estimate can be derived from the raw counts by relating the number of deer observed to the observable area along the route traveled. In the absence of better data such an extrapolation was attempted, with the results presented in Fig. 14.

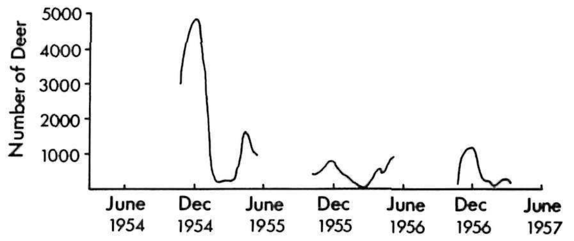

Figure 14. Population size estimates based upon "Deer Trend Study" data, 1954-1957.

The accuracy of these estimates must be regarded as highly questionable, especially in view of the fact that no plausible explanation can be offered to account for the remarkable apparent annual variation in population size observed during the study period. It is interesting and perhaps important to note that the most impressive individual counts recorded during the course of this study were similar in size to the anecdotal accounts of previous years alluded to in the preceding paragraph.

The "Deer Transect Study" (MVNP File Ref. N 1427) conducted by Ranger Hobbs from June 1964 through September 1965 used the pellet count technique to estimate deer abundance. This technique will be described in greater detail at a later point but in essence involves counting the number of deer fecal pellet groups in a given sample area then relating this data to the expected defecation rate, the length of time deer were present, and the total area of the study site. Unfortunately, except for the first three months of the study, detailed records have been lost from the files. The data for this brief period yield an estimate for the entire Park of 14,800 deer. This figure undoubtedly overestimates the size of the summer herd by a substantial margin because all of the sampling sites deliberately were located in areas believed to be receiving heaviest deer utilization.

The official Park Service estimate of the size of the resident deer population at the time our study study began was 800 deer. It is not clear from what data base this surprisingly low figure was derived.

The Population, 1967-1970

Perhaps no task is as frustrating as attempting to census accurately a population of animals as elusive as deer inhabiting an area as rugged and densely vegetated as Mesa Verde National Park. Wildlife biologists over the past half century have directed their best efforts toward developing the necessary methodology for dealing with census problems, yet unfortunately have so far met with only limited success. We began the study utilizing several techniques simultaneously in an attempt to determine which would be best suited to the Mesa Verde situation.

Direct counts of the deer were conducted from fixed-wing aircraft at approximately monthly

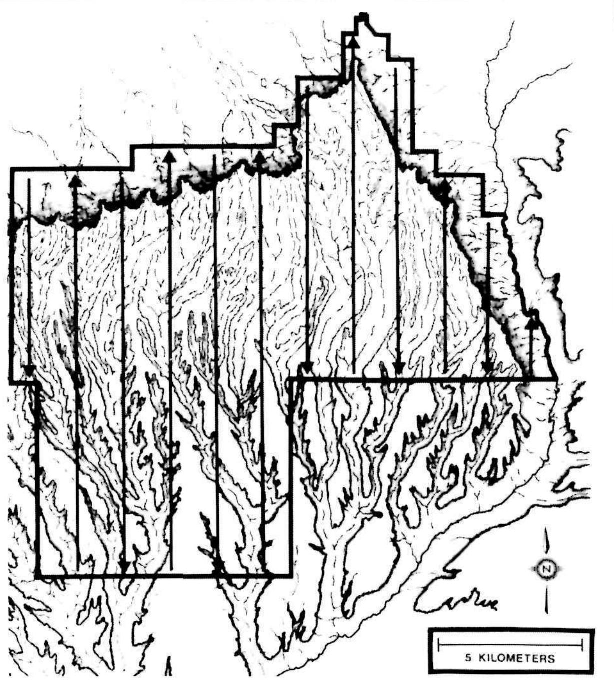

Figure 15. Map indicating the location of aerial census transects.

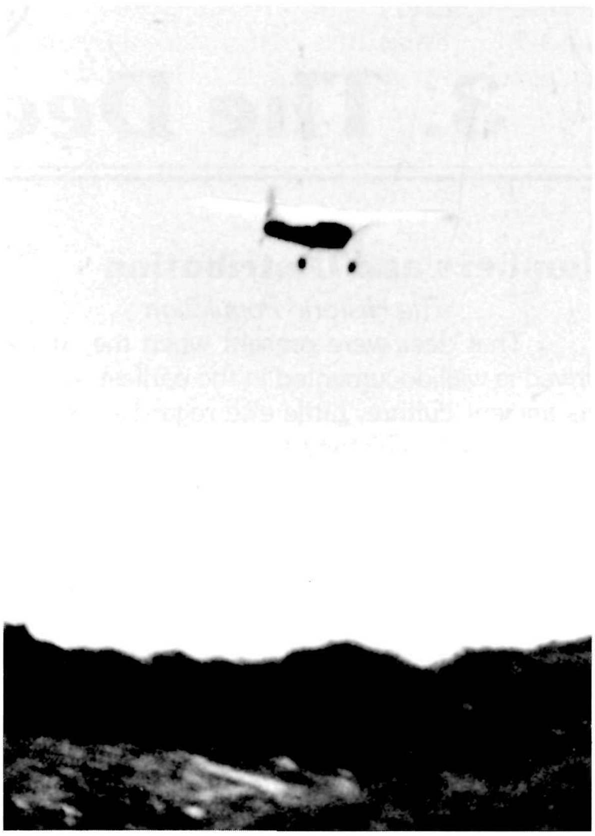

Figure 16. Aerial census being conducted at sunrise over Mesa Verde National Park. Photo by H. Steinhoff.

intervals. Characteristically turbulent air currents and the rugged canyon and mesa terrain made counting difficult and relatively dangerous. A Cesna 185 equipped with a 300 horsepower engine, expertly piloted by Gordon Saville, was generously furnished by the Colorado Division of Wildlife for our use. The minumum safe flying speed of this necessarily powerful craft varied from 145 to 160 kilometers per hour, considerably faster than optimal for counting deer. Transects approximately 1.5 kilometers apart (Fig. 15) were flown at an altitude of 15 to 30 meters (Fig. 16). Flights were restricted to the early morning hours when flying conditions were most suitable; nevertheless, on eight occasions flights had to be abandoned because of air turbulence. Gilbert and Grieb (1957) observed that even under ideal conditions less than half the deer in a given area can be counted from fixed-wing aircraft. Conditions at Mesa Verde were far from ideal with flights made over rough, densely vegetated terrain usually without the benefit of snow cover, under suboptimal flying conditions, and using relatively inexperienced observers. It was therefore not surprising to find that only about 10% of the deer which had previously been marked with brightly colored neck bands could be seen from the air during any one flight.

Population size estimates ranging from 4,500 for the summer herd to nearly zero in winter could be derived by relating this ten percent figure to the actual numbers of deer counted. The aerial counts, as a census technique, were discontinued after the first year of the study. The data generated seemed of too low quality to justify the associated risks and expense.

We attempted also to estimate population size using a variation of the "King strip census" technique (Overton 1971). Beginning an hour after sunset, two observers in the back of a pickup truck would carefully search for deer with the aid of spotlights while the driver slowly and systematically traveled the Park's network of roads. As the attention of the deer was attracted to the moving vehicle, light reflecting back from their eyes made the animals quite conspicuous. Measuring the distance from the vehicle to each deer observed enabled the effective width of the sample strip to be determined. When the deer density in each vegetative stand was weighted for its area, a density of 19 deer per square kilometer was computed for the Park as a whole. The size of the resident herd as estimated by this technique was 4,000 deer, a figure in reasonably close agreement to that obtained with the aerial census technique. After a year's trial, spotlight counts ceased to be used for census purposes. The inherent variability associated with this technique, like that of the aerial census technique, led us to conclude that it would not serve our purpose in a cost effective manner.

An indirect technique, similar to that employed previously by Park Service personnel, was utilized as a third method of estimating population size. In conjunction with studies of vegetative utilization, 13 pellet count transects were established in the mountain brush stand and 3 in the pinyon-juniper stand. The transects consisted of 10 circular plots, each 0.004 hectare in size, spaced in a straight line at 20 meter intervals. The number of deer per hectare in each vegetative stand was calculated by counting the number of pellet groups deposited on the plots, dividing this number by the defecation rate of 14 per day (Rogers et al. 1958, Smith 1964), and finally dividing this figure by the number of days since the plots were last cleared of pellets (McCain 1948). The mean for each vegetative stand was weighted for its area to compute the overall mean. The pellet count technique yielded an estimate of 5,500 for the summer population and indicated a migratory influx of about 700 additional deer in the fall.

From these three sources we estimated the size of the 1967 summer population to be 4,500 deer, with an increase to about 5,200 in the fall. Previous estimates made by Park Service personnel appear quite conservative in comparison; the size of the summer herd had been placed at 800 deer, with an increase to 2,800 during the autumn months.

We lacked confidence in our first year's pellet group data because the distribution of the transects was not random or representative and the area sampled was small. It had become obvious, however, that this census technique was best suited to the Mesa Verde situation. The pellet group technique has been found to yield reliable estimates under most conditions (Eberhardt and Van Etten 1956, Neff 1968) and therefore was used almost exclusively through the remainder of the study. In June 1968, 55 new permanent pellet group transects were systematically established and then read twice annually until June 1970. Twenty-four of the transects were located in the mountain brush

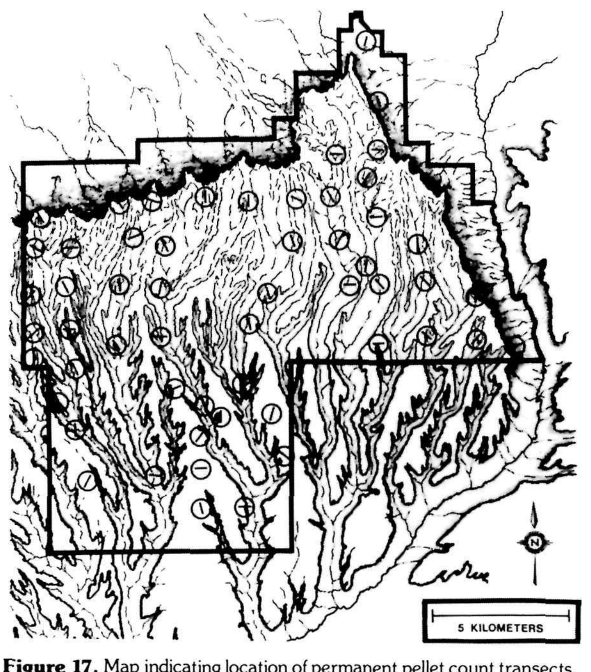

Figure 17. Map indicating location of permanent pellet count transects. The lines show the direction of the transects and have been drawn to scale.

stand, 22 in the pinyon-juniper stand, and 9 in the sagebrush-grass stand (Fig. 17). These transects were distributed on the mesa tops, sides of the canyons, and in the canyon bottoms. The technique as described previously was modified slightly to account for varying migratory movement patterns. From the total number of days over which pellet groups were allowed to accumulate on the sample plots were subtracted the number of days the deer were estimated to have spent outside of the Park on their winter range. Population estimates

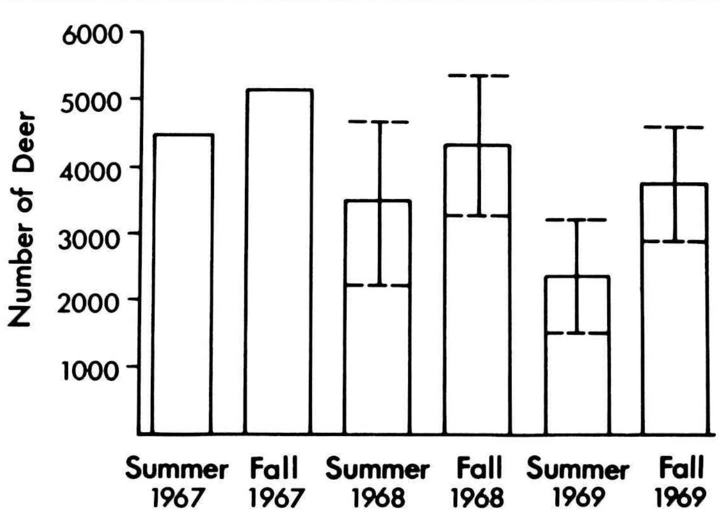

Figure 18. Seasonal and annual variation in total numbers of Mesa Verde mule deer, 1967-1969 (brackets represent 95% confidence limits).

for the first three years of the study are shown in Fig. 18. The wide confidence intervals, even on what we consider to be our most reliable data, vividly illustrate the difficulties encountered in attempting to census this deer population.

The deer herd, as one might expect, is not uniformly distributed through the Park. Data from the permanent pellet group transects (Table 1) confirmed our initial impression that deer density was considerably higher in the mountain brush vegetative stand than in the pinyon-juniper forest. Although the mountain brush stand covers only about 40% of the Park, 86% of the summer herd was found to reside there. Most of the remainder occupied, at a low level of population density, the more extensive pinyon-juniper habitat. Intermediate population density levels were found in the sagebrush-grass habitat of the canyon bottoms, but the area occupied by this vegetative stand was too limited to account for more than a small portion of the total deer population.

During the autumn months a temporary influx of migratory deer initially boosted population densities in all parts of the Park (Table 1), but as the winters progressed deer began vacating the mountain brush zone in favor of lower elevations. Abandonment of the mountain brush habitat was virtually complete by late December of each of the years studied. Observations recorded in the Mesa Verde National Park files support the supposition that this occurs in all but possibly the mildest of winters. Depending upon the severity of the winter, deer may however continue to occupy the canyon bottoms or even the pinyon-juniper forest. The entire Park is deserted, at least temporarily, during periods of unusually severe weather. The following excerpt is from an anonymous Park ranger's report dated 10 February 1949 (MVNP File Ref. N 1427):

> "Due to over 30 inches of snow on the level nearly all deer have left the mesa tops. Airplane survey shows deer concentrated in deep canyons south of Park headquarters and most deer are outside of Park boundaries."

During the course of our study, a record 132.6 centimeters of snow fell during the month of December 1967. Intensive aerial and ground searches conducted the following month located only two deer, both in the extreme southern portion of the Park.

Population Trends

Mule deer populations, which are not subject to the cyclic fluctuations characteristic of many species, might be expected to remain relatively

Table 1. Seasonal variations in mule deer density, 1968-1969.

Period of Occupancy		Number of deer per square kilometer[a] Entire Park	Mountain brush stand	Sagebrush-grass stand	Pinyon-juniper stand
1968	Jun 22 - Sep 5	17	30	20	5
	Sep 5 - Dec 21[b]	20	29	58	7
1969	Apr 26 - Sep 1	10	20	18	4
	Sep 1 - Dec 15[c]	18	29	22	9

[a] Based on 55 permanent pellet group transects.

[b] It was estimated that 95% of the fall population was out of the Park during the period between December 21, 1968 and April 26, 1969.

[c] It was estimated that the pinyon-juniper vegetative stand was occupied until January 15, 1970.

stable over extended periods of time. The record, however, speaks instead of a long history of shifting population trends.

The journals of Lewis and Clark and other explorers of the late 1700's and early 1800's, and those of the fur trappers of the 1820's and 1830's, indicate that mule deer then occupied nearly all of their present range but at surprisingly low population densities (Julander and Low 1976). The vigorous uncontrolled hunting that accompanied the settling of the West apparently was responsible for a further reduction in deer numbers, to a point of near extinction by the turn of the century. With, although not clearly because of, the implementation of stronger conservation measures during the early 1900's, deer herds began to recover their former numbers. This era also coincided with the extirpation of the wolf in the West. Denney (1976) has made the interesting point that, regardless of whether the management approach of the individual states was conservative or exploitive, the mule deer trend followed essentially the same pattern throughout the West. This was "... a gradual buildup of herds beginning in the 1920's, with a peaking somewhere in the late forties or early fifties to the early sixties, and then a general decline during the sixties, and continuing to the present."

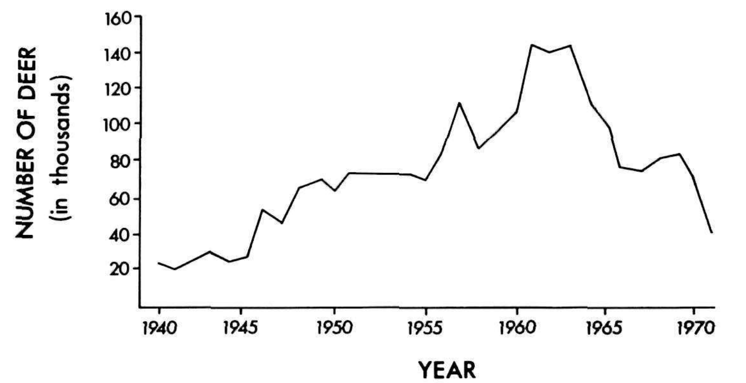

Figure 19. Hunter harvest data for the state of Colorado demonstrate the timing and magnitude of the most recent generalized mule deer population fluctuation.

Although the prevailing opinion among wildlife professionals is that a recent general population decline as described above has indeed occurred, it is important to note that factual support for this contention is virtually nonexistent. Reliable data for all (or any) of the western states affected are not available. This is not too surprising, considering the problems we encountered in attempting to census the relatively small Mesa Verde herd alone. An example of the kind of information available is shown in Fig. 19. These deer harvest data for the state of Colorado, despite their obvious limitations, seem to depict reasonably well the general population trends over the past thirty years.

The magnitude and the timing of the population decline witnessed in the Mesa Verde herd do fit comfortably with the graphic data presented in Fig. 19 and, to that extent, lend support to the notion of a general population decline. Unfortunately, however, our initial studies were of too short duration to yield conclusive evidence that even the apparent decline in the Mesa Verde population was indeed factual. By the time we realized that the observed population decline was of more than parochial interest, continued operation of the pellet group transects was no longer feasible. A series of helicopter and fixed-wing aircraft counts were, instead, conducted during the autumn of 1975 and summer of 1976. Only about one fourth as many deer were counted as had been observed during comparable seasons nine years earlier; providing convincing evidence, although technically still not proving, that a population decline had truly occurred.

Our most intensive period of field investigation happened to coincide with the crucial early stages of the population decline. Because we did not yet have convincing evidence of the decline, however, we were unable at the time to direct our efforts specifically toward an analysis of its causative factors. Despite the limitations of our data, in the remaining chapters an attempt will be made, along with a general characterization of the Mesa Verde deer herd, to assess the role that a number of possible causative factors may have played in the population decline.

4. Physical Characteristics

General Characteristics

A race of black-tailed deer known as the Rocky Mountain mule deer (*Odocoileus hemionus hemionus Rafinesque*) inhabits Mesa Verde National Park. Rocky Mountain mule deer are the largest of the black-tailed deer and have the widest geographic distribution of any subspecies in North America. They inhabit most of the western United States and Canada. It is for their characteristic large mule-like ears and a slender black tipped tail that they are named.

When born in late spring, the fawns are covered with a coat of reddish brown hair containing nuumerous white spots (Fig. 20). Molting of this juvenile coat normally begins in mid-summer and is complete by late summer. Late born fawns may, however, retain their spotted pelage well into autumn. Molting thereafter occurs twice annually, in the spring and again in late summer. The summer adult pelage has a distinctly reddish hue while that of the winter coat is grayish and much darker. Although true albinos are apparently quite rare, deer exhibiting a partly white mottled coat are observed not uncommonly in some populations. Only one such individual was discovered during the course of our studies but, over the years, a number of partly white deer have been observed at Mesa Verde National Park. In 1946, Park naturalist Don Watson reported an "albino" deer (MVNP File Ref. N 1427) but, because its eye color could not be determined, that this was a true albino cannot be established.

Figure 20. A fawn approximately one week of age (early July). Photo by J. Schmidt.

Growth in mule deer is rapid during the first two years of life, much slower thereafter, and essentially complete by the age of four years (Anderson et al. 1974). Growth, however, as one might expect, does not proceed at an even rate. During the harsh winter months the growth rate not only slows, but deer actually lose weight. Mesa Verde deer fell about 16 percent from their autumn weight peak during the winter months. Experimental studies of growth in black-tailed deer have shown that winter weight losses occur even when food is abundant, and are the result of voluntary reductions in food intake (Brown 1961, Wood et al. 1962, Bandy et al. 1970). During cold weather deer exhibit a remarkably depressed metabolic rate, and this apparently accounts for their diminished appetite. Bandy et al. (1970) and Anderson et al. (1974) have pointed out that possibly this is an adaptation of survival value, reducing energy requirements during the lean winter months when energy demands would often be otherwise difficult to satisfy because of a critically short food supply.

Sexual dimorphism is not apparent in fawns. Even among yearlings (Fig. 21) the sexes cannot reliably be distinguished under field conditions until the first sets of antlers appear. After about 18 months of age, however, it is no longer difficult to distinguish the sexes, even in late winter after antlers have been shed. Mature females (Fig. 22) have a less muscular physique, a more slender head and neck, and more uniform coloration than males. Females also are considerably smaller than males; mature does of the Mesa Verde herd averaged 63.1 in weight, about a third less than the bucks which averaged 94.4 kilograms. In addition to differences in size and conformation, mature males display a distinctive dark patch of hair on their brow and, at most times of the year, antlers (Fig. 23). Antler development in deer is clearly related to the reproductive cycle. Growth, which begins in early spring, is completed by late summer just before the breeding season gets underway. The velvet, or antler skin (Fig. 24), is then shed, leaving exposed the hard, dead bone of the mature antler. During the breeding season, in addition to fully developed antlers, males display a striking enlargement of the neck (Fig. 25). These features apparently play an important role in establishing social dominance, with the most physically impressive individuals assumed to do most of the breeding. Following the breeding season, the neck returns to normal size and the antlers drop off. Occasionally, female mule deer are found also to possess antlers. Usually these are small malformed antlers that are continually in velvet and never shed. Their owners typically lead normal reproductive lives. The very rare doe that exhibits well developed "male" type antlers is usually a hermaphrodite, a pseudohermaphrodite, or has a masculinizing tumor. In the Mesa Verde population was discovered a unique example of an antlered female deer, a detailed account of which has been presented elsewhere (Mierau 1972). This individual possessed "male" type antlers but gave birth to a number of fawns, at least one was a female that subsequently also developed antlers (Fig. 26).

Figure 21. A yearling approximately 13 months of age (mid-July). Photo by G. Mierau.

Figure 22. Mature does, except for their larger size, are similar in appearance to yearlings (mid-July). Photo by G. Mierau.

Figure 23. Mature buck just before the onset of the breeding season (mid-September). Photo by G. Mierau.

Physical Condition

In the health and vigor of a deer population are reflected the aggregate extrinsic and intrinsic stresses under which it struggles to exist. When the majority of individuals are found to be in good physical condition, it can be assumed that their physiological and psychological requirements are adequately satisfied. A deer population in a poor state of health may exhibit an increased mortality rate and/or a decreased birth rate, either or both of which can result in a population decline such as that seen in the Mesa Verde herd. A reasonable place to begin the search for causative factors would seem therefore to be with an examination of the deer themselves.

One hundred fifty-one deer carcasses were examined during the course of our study. Some use was made of deer killed by automobiles but most were obtained through a systematic collection program. At approximately monthly intervals from 1 July 1967 to 15 January 1969, variable numbers of deer (ranging from 1 to 16) were killed for the purpose of obtaining detailed morphologic and physiologic data. An effort was made to gain a representative sampling of each sex and age class during each of the collection periods. Most deer were shot through the cervical spine, causing instantaneous death. Following measurement of body tempera-

Figure 24. Mature males with "velvet" covered developing antlers (mid-July). Photo by G. Mierau.

Figure 25. Mature male during the breeding season (late November) displaying fully developed antlers and marked enlargement of the neck. Photo by J. Schmidt.

Figure 26. A family group in which the mature female (marked with a neck band) and yearling female offspring (far right) both possess antlers. The smaller of the two fawns, both of whom have lost their spotted pelage (late August), was "adopted" into the family group after the twin of the larger fawn had been killed. Photo by G. Mierau.

ture, eye examination and aspiration of blood from the heart for subsequent analyses, the intact carcasses were transported to a central location where detailed autopsies were performed. Using a calculated birth date of June 25 for this population, the age of each deer was estimated to the nearest month based on the tooth replacement chronology for deer with temporary dentition (Robinette et al. 1957a) and by counting the annular rings in the dental cementum of the first incisor for deer with permanent dentition (Erickson and Seliger 1969).

Fortuitously, a recent study of another Colorado mule deer herd has provided a benchmark against which data relating to the physical condition of the Mesa Verde herd may be compared (Anderson et al. 1970, 1972, 1974). This exquisitely detailed study of the Cache la Poudre herd was conducted, using similar techniques, just prior to the time the generalized population decline was first detected. Because the Cache la Poudre herd is subjected to nearly the same enviromental influences as the Mesa Verde herd, and was found to be in a state of good health, it should serve well as a basis for "normal" values.

Other factors being equal, animals in good health can be expected to grow faster and larger than their counterparts in poor health. If the population decline resulted from a general diminishment of the deer herd's health and vigor, one might anticipate finding Mesa Verde deer to have been smaller than those of the normal control population. In Table 2 are compared various body measurements between the Mesa Verde and Cache la Poudre deer herds. Rather than smaller, the deer of Mesa Verde are clearly shown to be the larger of the two populations. Males weighing more than 115 kilograms proved to be fairly common; the largest buck collected weighed 130 kilograms, and the two largest does 77 kilograms. Even by Rocky Mountain mule deer standards, these are large deer indeed. Certainly there is no evidence here to suggest that these were animals in a poor state of health.

Taber et al. (1959) have defined "physical condition," when applied to wild ruminants, as the energy reserves (i.e. fat deposition) of the animals with respect to internal and external demands. Fat deposition must occur during the summer and autumn months to allow survival through the lean months of winter and spring. Although at times these fat stores may become substantial, obesity is not recognized as a significant medical problem in free-ranging deer. Three measures of carcass fat have traditionally been the most popular means of assessing physical condition in deer; the kidney fat index (Riney 1955), depth of back fat (Riney 1955), and color of bone marrow (Bischoff 1954). These were the measures of fat deposition employed in our study. More recently, Anderson et al. (1972)

Table 2. Comparison by sex and age class of body measurements between Cache la Poudre[a] and Mesa Verde mule deer.

Parameter	Age	Sex	Cache la Poudre	Mesa Verde
Body Weight[b]	<1 - 5 months	M	30.08 ± 6.58(6)[f]	27.15 ± 4.31(6)
		F	29.11 ± 11.11(7)	23.70 ± 6.58(6)
	6 - 11 months	M	35.39 ± 4.71(12)	38.41 ± 3.41(5)
		F	32.69 ± 3.21(7)	29.92 ± 5.13(7)
	12 - 17 months	M	52.44 ± 6.50(16)	59.10 ± 8.81(14)*
		F	46.64 ± 11.56(9)	51.89 ± 6.13(14)
	18+ months	M	74.04 ± 17.19(51)	94.53 ± 19.66(36)**
		F	58.99 ± 7.44(91)	63.02 ± 7.08(63)**
Body Length[c]	<1 - 5 months	M	110.17 ± 9.60(6)	121.92 ± 6.35(6)
		F	108.57 ± 20.06(7)	116.33 ± 12.70(6)
	6 - 11 months	M	120.12 ± 6.96(12)	144.53 ± 4.06(5)*
		F	118.07 ± 7.02(7)	135.85 ± 5.59(7)
	12 - 17 months	M	135.12 ± 5.61(16)	163.83 ± 13.72(14)**
		F	132.00 ± 10.36(9)	155.45 ± 6.86(14)
	18+ months	M	152.29 ± 11.00(51)	179.07 ± 10.41(36)**
		F	142.37 ± 6.83(90)	163.58 ± 6.35(63)**
Shoulder Height[d]	<1 - 5 months	M	75.50 ± 4.59(6)	79.25 ± 5.33(6)
		F	71.29 ± 10.14(7)	73.66 ± 8.64(6)
	6 - 11 months	M	80.42 ± 4.89(12)	89.92 ± 2.03(5)**
		F	77.71 ± 2.43(7)	86.61 ± 5.84(7)**
	12 - 17 months	M	89.06 ± 2.86(16)	101.09 ± 6.10(14)**
		F	85.67 ± 5.77(9)	95.25 ± 4.83(14)**
	18+ months	M	96.58 ± 5.46(52)	111.00 ± 5.33(36)**
		F	90.80 ± 3.76(91)	100.33 ± 3.56(63)**
Chest Girth[e]	<1 - 5 months	M	68.33 ± 5.54(6)	71.12 ± 9.14(6)
		F	66.29 ± 12.75(7)	66.55 ± 9.91(6)
	6 - 11 months	M	74.00 ± 3.29(11)	80.52 ± 4.32(5)**
		F	71.86 ± 3.08(7)	73.91 ± 6.35(7)
	12 - 17 months	M	83.48 ± 5.04(15)	89.41 ± 6.35(14)*
		F	79.56 ± 7.92(9)	85.34 ± 5.59(14)*
	18+ months	M	96.62 ± 8.93(52)	106.68 ± 9.40(36)**
		F	88.72 ± 4.55(89)	92.71 ± 5.59(63)**

[a] Anderson et al. 1974.

[b] Body weight is the intact carcass less the blood and tissue loss from gunshot, expressed in kilograms.

[c] Body length is the distance from the anterior edge of the nose (with the head extended) to the posterior edge of the last coccygeal vertebra, expressed in centimeters.

[d] Shoulder height is the distance from the superior angle of the scapula (with the leg fully extended) to the posterior edge of the hoof, expressed in centimeters.

[e] Chest girth is the circumference of the chest immediately posterior to the posterior edge of the scapulae, expressed in centimeters.

[f] Mean ± standard deviation (sample size).

* Statistically different from comparable values ($P < 0.05$).

**Statistically different from comparable values ($P < 0.01$).

have shown that, even when performed under exacting conditions, these measures exhibit such extreme variability as to render them of very limited usefulness. This problem is compounded by additional observer and technical variability introduced when data from different studies are compared. Recognizing these limitations, carcass fat measurements obtained from the Mesa Verde herd are presented for comparison with similar data from the Cache la Poudre herd (Table 3). While these data may not be strictly comparable and must be interpreted with caution, it should be noted that no striking differences between the two populations are apparent. As fat stores in bone marrow become depleted in response to malnutrition, the marrow changes in color from creamy white or yellow to red. This occurs, however, only in the late stages of the starvation process and is a sign of very limited usefulness because by this point in time the deer usually appear emaciated even to an inexperienced observer. No such individuals were observed in the Mesa Verde population.

Blood serum protein levels can also be an indicator of physical condition. Although elevated values are occasionally associated with disease states, generally it is subnormal values that give greatest cause for concern. Depressed serum protein levels can result from inadequate diet or a variety of diseases. In Table 4 is presented a comparison of total serum protein levels between Mesa Verde and Cache la Poudre deer. The values may not be strictly comparable because Anderson et al. (1972) used a colorimetric procedure while we used a refractometer to measure serum protein levels. Rather than lower, total serum protein levels as measured were consistently higher in Mesa Verde deer than in the control population. The values established for the Mesa Verde population also exceed those published for another wild population of Rocky Mountain mule deer (Taber et al. 1959). The higher serum protein values for Mesa Verde deer might simply reflect variation in measurement

Table 3. Comparison by season and sex class of carcass fat indices between Cache la Poudre[a] and Mesa Verde mule deer 18 months of age or older.

Parameter	Season	Sex	Cache la Poudre	Mesa Verde
Kidney Fat Index[b]	Autumn	M	64.6 ± 38.8(10)[d]	72.1 ± 40.9(17)
		F	55.9 ± 48.5(14)	42.4 ± 39.0(14)
	Winter	M	10.6 ± 4.7(17)	6.5 ± 5.7(4)
		F	29.4 ± 15.2(25)	17.1 ± 16.2(9)
	Spring	M	7.2 ± 4.1(19)	2.0 ± 2.8(5)
		F	13.0 ± 8.7(26)	9.0 ± 4.6(17)
	Summer	M	45.9 ± 24.6(5)	35.6 ± 14.6(9)
		F	14.8 ± 16.5(24)	18.8 ± 7.9(15)
Depth Back Fat[c]	Autumn	M	15.6 ± 15.1(9)	29.1 ± 12.7(17)
		F	12.5 ± 12.7(11)	12.1 ± 10.2(13)
	Winter	M	0.0 ± 0.0(14)	0.0 ± 0.0(4)
		F	3.9 ± 3.6(17)	7.1 ± 7.6(9)
	Spring	M	0.8 ± 1.9(15)	0.0 ± 0.0(5)
		F	0.6 ± 1.0(18)	0.8 ± 2.0(18)
	Summer	M	29.0 ± 17.8(4)	21.3 ± 10.7(8)
		F	3.2 ± 7.1(18)	7.9 ± 8.6(11)

[a]Anderson et al. 1974.

[b]Kidney fat index is the ratio of the weight of kidney associated fat to the weight of the kidneys without associated fat, expressed as percentage.

[c]Depth of back fat is a measurement of the thickness of subcutaneous fat in the midline immediately superior to the sacral vertebrae, expressed in millimeters.

[d]Mean ± standard deviation (sample size); minor differences in techniques employed preclude direct statistical comparison between study sites.

Table 4. Comparison of total serum protein measurements between Cache la Poudre[a] and Mesa Verde mule deer.

Age	Sex	Cache la Poudre	Mesa Verde
<1 - 5 months	M	5.07 ± 0.31(3)[b]	8.13 ± 0.47(6)
	F	5.63 ± 0.91(3)	8.61 ± 0.70(6)
6 - 11 months	M	6.19 ± 0.77(7)	9.53 ± 0.82(4)
	F	5.50 ± 0.57(5)	8.23 ± 0.94(5)
12 - 17 months	M	6.50 ± 0.52(8)	8.83 ± 0.72(15)
	F	6.46 ± 0.50(5)	8.89 ± 0.42(14)
18+ months	M	6.02 ± 0.82(25)	9.00 ± 0.50(35)
	F	6.02 ± 0.86(45)	8.68 ± 0.87(61)

[a]Anderson et al. 1972.

[b]Mean ± standard deviation (sample size), expressed as grams per 100 millimeters; minor differences in techniques employed preclude direct statistical comparison between study sites.

techniques. Because free water is scarce at Mesa Verde, the deer may exist in a state of relative dehydration which could also account for their apparent hyperproteinemia.

The physical condition of mule deer may under certain circumstances be reflected in measurements of blood cell parameters (Rosen and Bischoff 1952). Unfortunately, it is difficult to compare hematologic data gathered by different investigators because even seemingly minor differences in technique often significantly affect results. For this reason, direct statistical comparison of blood cell measurements between Mesa Verde and Cache la Poudre deer (Table 5) is not attempted even though similar methods were used. Higher values for erythrocyte packed cell volumes and hemoglobin levels are generally associated with good physical condition. The Mesa Verde deer exhibited values for these parameters that were at least as high as those from the control population. High neutrophil: lymphocyte ratios may be an indicator of increased stress in deer populations (An-

Table 5. Comparison of blood cell measurements between Cache la Poudre[a] and Mesa Verde mule deer.

Parameter	Cache la Poudre	Mesa Verde
Erythrocytic Series		
Packed cell vol. (%)	46.7 ± 8.9(177)[b]	46.8 ± 6.9(152)
Hemoglobin (g/100 ml)	16.4 ± 4.0(174)	17.8 ± 2.9(144)
Mean corpuscular hemoglobin concentration (%)	35.1 ± 2.6(173)	38.1 ± 4.4(142)
Leukocytic Series		
Neutrophil (%)	41.7 ± 16.1(176)	31.6 ± 15.1(100)
Lymphocyte (%)	43.4 ± 14.6(1,76)	46.5 ± 18.4(100)
Monocyte (%)	6.2 ± 6.0(176)	4.1 ± 2.3(100)
Eosinophil (%)	8.3 ± 8.1(176)	16.9 ± 13.8(100)
Basophil (%)	0.4 ± 0.1(176)	1.0 ± 0.9(100)
Neutrophil: Lymphocyte ratio	1.2 ± 0.1(176)	1.2 ± 2.7(100)

[a]Anderson et al. 1970.

[b]Mean ± standard deviation (sample size); minor differences in techniques employed preclude direct statistical comparison between study sites.

derson et al. 1970). Despite some rather striking differences in the percentages of leukocytes reported in the two series (perhaps reflecting errors of inexperience in the Mesa Verde data), the neutrophil: lymphocyte ratios proved to be remarkably similar.

Additional morphologic, hematologic, and physiologic data are presented in Appendix II. These measurements do serve to further characterize the deer of Mesa Verde National Park but are not included in this discussion because either they do not relate directly to physical condition or because comparative data from other populations are not available.

Essentially all of the pathologic conditions observed in Mesa Verde deer involved infectious disease processes. A few deer exhibited one or two small fibromas (benign wart-like growths on the skin, caused by a virus). What was probably an infected epidermal inclusion cyst was found in one individual. Another exhibited bilateral testicular degeneration (Murphy and Clugston 1971), probably the result of a chronic infection of the testes. One deer was found to be in danger of losing its incisor teeth due to an infection of the surrounding tissue. A potentially life threatening condition, that of a large lung abcess, was observed in one deer. Another exhibited extensive dense adhesions between the surface of one lung and the adjacent chest wall, probably the result of an earlier bout of pneumonia. In none of these instances was an attempt made to isolate the infectious organism, therefore exact diagnoses cannot be established. Most are presumed to have been caused by viral or bacterial organisms, although parasites may have played a role in the production of the lung lesions. Free-ranging deer commonly harbor large numbers of parasites, usually without detectable adverse effects. In Table 6 are listed the parasites found in deer at Mesa Verde National Park. Although many of the deer examined did harbor some parasites, no deleterious effects were associated with their presence.

In part because of their importance to the livestock industry, several diseases were looked for in a systematic fashion. Deer are known to be susceptible to brucellosis, leptospirosis, and anaplasmosis and can serve as natural reservoirs for these diseases. Ninety-eight blood serum samples were tested for brucellosis and 25 for leptospirosis (*Leptospira pomona* and *L. icterohemorrhagiae*).

Table 6. Parasites collected from mule deer at Mesa Verde National Park.

Parasite	Location of infection
Winter tick *(Dermacentor albipictus)*	Most commonly around the ears and anus.
Spinose ear tick *(Otobius megnini)*	External ear canal.
Bot fly larvae *(Cephenemyia sp.)* 1st instar	Retropharyngeal pouch, trachea and bronchi.
(Cephenemyia sp.) 2nd and 3rd instars	Retropharyngeal pouch, nose and mouth.
Footworm *(Wehrdikmansia cervipedis)*	Subcutaneous regions of legs, shoulders and brisket.
Arterial worm *(Elaeophora schneideri)*	Carotid arteries.
Lung worm *(Dictyocaulus* sp.*)*	Bronchi and bronchioles.
Bladder worm *(Cysticercus tenuicollis)*	Abdominal cavity, usually attached to viscera.
Sheep measles *(Cysticercus tarandi)*	Embedded in loin and femoral muscles.
Fringed tapeworm *(Thysanosoma actinioides)*	Abomasum and small intestine.
Tapeworms *(Monesia expansa and M. benedini)*	Small intestine.

All were negative. Of the 98 deer tested for anaplasmosis, 59 were negative, 12 were suspects, and 19 were reactors. These data suggest that Mesa Verde deer may serve as a natural reservoir for anaplasmosis, although they themselves showed no clinical signs of the disease.

Prestwood et al. (1976), largely on theoretical grounds, have compiled a list of diseases potentially capable of causing a widespread decline in mule deer populations. Epizootic hemorrhagic disease, bluetongue, and malignant catarrhal fever were the viral diseases listed. None of the Mesa Verde deer manifested the clinical signs or autopsy findings characteristic of these diseases. Only one bacterial disease, necrobacillosis, was considered a serious threat to mule deer populations. The characteristic lesions produced by this disease were not observed among Mesa Verde deer. Two major groups of nematodes, trichostrongyles and lungworms, were considered to be the parasitic diseases of greatest potential importance. Gastrointestinal roundworms were not observed in Mesa Verde deer and even fecal flotation analyses revealed only a single strongyle egg. Eleven of 102 deer examined harbored small to moderate numbers of lungworms (*Dictyocaulus* sp.). No identifiable lesions were associated with these parasites, therefore it is concluded that they were of little pathologic significance.

Malnutrition is probably the most frequently encountered serious disease in free-ranging deer. It can exert a direct effect on the birth rate and/or the death rate, or act indirectly by lowering resistance to infectious diseases. No evidence of malnutrition was detected in Mesa Verde deer. Neither is the incidence of infectious diseases observed in the Mesa Verde population considered to be abnormally high. It is perhaps worth pointing out in this regard that populations of wild animals are never found to exist in a state of perfect health. Throughout the data collection phase of the study it was our impression that the deer of Mesa Verde were in excellent physical condition. Analysis of the data has clearly demonstrated our subjective opinion to have been correct. Having discovered no clues to the population decline along these lines, we must turn our attention elsewhere.

5. Behavioral Characteristics

General Characteristics

The year at Mesa Verde for most of the deer begins in late March or early April when they return from their wintering grounds at lower elevations. The deer, usually traveling in small groups, drift leisurely back into the Park over a period of several weeks. Upon arrival they normally take up residence in the same locations occupied in previous summers.

Life is easy during the months of late spring. With food now plentiful, the deer begin to regain the weight they lost during the preceding winter months. The importance of quickly replenishing their exhausted energy reserves is reflected in the daily activity patterns of the deer. They spend most of each day (and night) alternating between periods of eating and resting, with cud chewing occupying nearly all of the time spent resting; deer apparently have little or no need for sleep. The length of these alternating intervals is quite variable, but only rarely is more than two continuous hours spent engaged in either activity. Deer frequently travel along well worn trails as they move about in their daily activities. Networks of these interconnecting trails crisscross the range, providing easy access to food, water and cover. When suddenly startled, however, deer do not restrict themselves to the trails but bound off with their characteristic stiff-legged gait along any escape route convenient.

With the Memorial Day weekend the number of people visiting Mesa Verde National Park increases dramatically. This influx of tourists, however, has little impact on the deer population. In contrast to their natural fear of a man on foot, they show little concern for humans remaining in their automobiles. The increase in vehicular traffic, therefore, has little effect on the deer. Human activity is otherwise so concentrated into a few small areas of the Park (which exhibit low deer densities naturally) that its significance is nearly inconsequential.

As the fawning date approaches, pregnant does become less tolerant of other deer in their immediate vicinity. It is at this time that the separation process between the doe and her previous year's offspring begins. The fawning season at Mesa Verde extended from June 14 to July 19, with maximum activity occurring between June 20 and July 1. During the first few days of life fawns remain in hiding when not nursing. At this time they are completely dependent on camouflage and immobility for protection. By the end of the first week, however, they can run well enough to usually avoid capture by a man on foot. They are then able to accompany the doe in foraging, although they still spend much of the time resting. Fawns begin eating plants at two or three weeks or age but do not become fully weaned until early October.

The doe and her fawns, sometimes referred to as the milk group (Lindsdale and Tomich 1953), are at first the primary unit of social organization. By mid-summer the does become more tolerant of other deer and often will allow their fawns of the previous year to rejoin the maternal group. Combinations of milk groups, maternal groups, and other deer frequently assemble into temporary feeding groups, but it is the maternal group that remains the fundamental unit of social organization. Bucks may assemble into small bands but these fraternal groups are not as stable or tightly knit as are the maternal groups.

Beginning in early October and continuing into November, just prior to the breeding season, deer migrating into the Park from higher ranges swell the population to its maximum size. Based upon measurements made on 53 embryos and fetuses from 31 pregnant does (Appendix III), breeding dates were estimated using the method of Hudson and Browman (1959). The earliest breeding date was November 23 and the latest December 28, with maximum activity (65 percent) occurring from November 29 to December 10 (Fig. 27). The fawning dates alluded to earlier were calculated from these dates, using the 203 day mean gestational period established by Anderson and Medin (1967) for Colorado mule deer. Fawning dates were corroborated by dates of observation of new-born fawns. Bischoff (1958) found that yearling females bred three to four weeks after the first adults bred. The yearlings examined at Mesa Verde, however, conceived at the same time as did older deer. Male

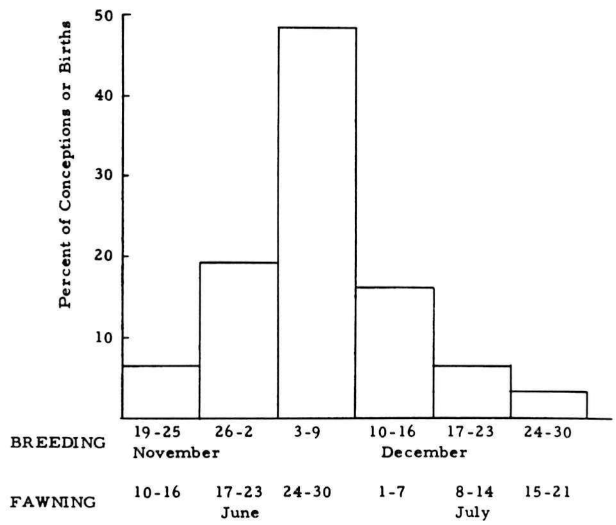

Figure 27. Distribution of breeding and fawning dates of mule deer in Mesa Verde National Park.

energy demands in the face of decreased energy supplies can, however, combine to make life very difficult indeed for a deer in winter. When winter conditions were at their very worst, we could not help but marvel at the tenacity with which they cling to life.

Movement Patterns

A major effort was expended in attempting to determine the movement patterns of the deer. This required capturing and marking as many deer as possible, then relocating them at a later date. The dense vegetation and rugged topography of the Park made this a very difficult task.

Using a variety of techniques, a total of 198 deer were captured and marked. Immobilizing drugs administered with projectile syringes proved to be the most successful method (Fig. 28). Drug

Figure 28. Hunting with dart guns in densely vegetated terrain was facilitated by the use of an elevated platform on a pickup truck. Photo by V. Mierau.

Figure 29. Fawns, located at night with the aid of a spotlight, could occasionally be pursued on foot and captured. Photo by W. Cooper.

deer are more visible during the breeding season than at any other time of the year. They are in fact so active in their pursuit of sexually receptive does that they seldom stop even to eat, and as a result may lose a good deal of weight. Does, on the other hand, do not exhibit notably altered activity patterns, except when being actively pursued by a buck. Actual mating is rarely observed. It is presumed to take place usually during the hours of darkness.

How long the deer remain in the Park after the breeding season depends in large part upon the weather. Sometime in late December or January, usually prodded by a heavy snowfall, most of the deer leave for winter ranges at lower elevations. Somewhat surprisingly, large numbers of fallen antlers could be found even in the northernmost portions of the Park, the areas first to be deserted for the winter season. This is significant in that it establishes that antler shedding, at least in many instances, occurred relatively early in the winter. Deer in good physical condition are known to shed their antlers earlier in the winter than do those in poor condition (Einarsen 1956); therefore, we are provided with yet another bit of evidence that the deer of Mesa Verde were in good physical condition during the period of the population decline.

We were able to learn very little about life on winter ranges outside of the Park. The few nonmigratory deer that remained in the Park did, however, afford us an opportunity to make some observations on deer behavior during this critical period. For the most part it seemed to be "business as usual," although foraging activities did appear to occupy a greater portion of their time. Increased

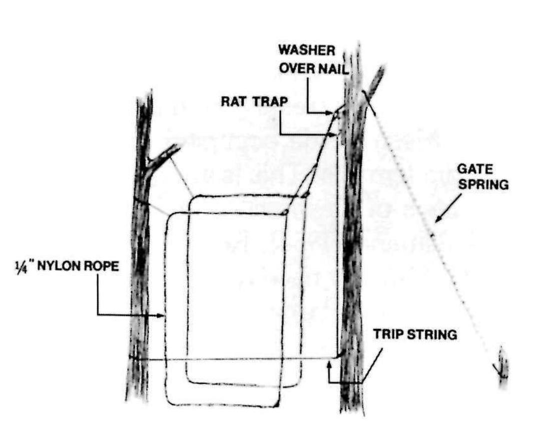

Figure 30. Design of a body snare used with limited success.

Figure 33. Automatic tagging device being set in a deer trail. Photo by V. Mierau.

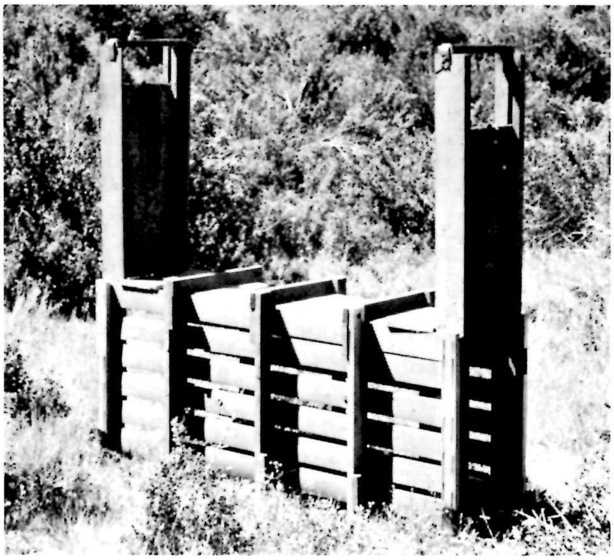

Figure 31. Deer could be lured into Stephenson live traps only during the winter months when natural forage was scarce. Photo by G. Mierau.

Figure 32. Drug-captured deer being marked with a collar and ear tags with brightly colored plastic streamers. Photo by V. Mierau.

capture data are presented in Appendix IV. Three very young fawns were captured by hand at night with the aid of a spotlight (Fig. 29). Another small fawn was rescued from an attack by a bobcat. One older fawn was captured with a body snare (Fig. 30). Nine adult deer were captured and tagged by Park rangers using Stephenson live traps (Fig. 31). Colorful plastic coated canvas collars were used in combination with colored ear streamers to enable positive identification of individual deer at a distance (Fig. 32). Fawns were marked with ear tags and streamers only. These marking devices did not appear to affect the animals' behavior.

An additional 150 to 200 deer are estimated to have been marked with automatic tagging devices (Verme 1962, Siglin 1966). These consisted of a snare-like apparatus set along deer trails (Fig. 33) which left a nylon rope collar with a numbered tag and bell around the neck of a passing deer. We found no evidence to suggest that the bells attached to these marking devices had any detrimental effect on the deer. Belled deer interacted normally with other deer and were accompanied by a normal number of fawns, supporting similar observations made by Jordan (1958) and Gruell and Papez (1963).

Aerial as well as ground reconnaissance was employed to obtain resighting records of the marked deer. Project and Park personnel were depended upon to provide the bulk of the data but an intensive publicity campaign was conducted to enlist also the cooperation of the public. This included the use of posters, local radio announcements, newspaper and magazine articles, and postal mailings to area residents.

Home Range

An animal's home range is the area it occupies in its daily travels. Considering the distance deer are capable of traveling, their home ranges are often suprisingly small. Within this limited area, however, all of the animal's food, water, shelter, escape cover, and other needs can be met. Home ranges of individual deer often overlap. Except perhaps for does with very young fawns, deer do not establish territories which they defend from others of their species.

Deer that are seasonally migratory are known to establish home ranges on both their summering and wintering grounds. We were, however, only able to gather data on the summer home ranges of Mesa Verde deer. Home range size is usually described in terms of length and width or total area occupied. By simply plotting resighting records of marked deer on a map we were able to determine the size of their home ranges in these terms (Table 7). Using similar techniques, Leopold et al. (1951) and Dasmann and Taber (1956a) reported the average maximum diameter of California black-tailed deer home ranges to be about 1.2 kilometers. Zalunardo (1962) reported the home range of Oregon mule deer to be about 1.8 kilometers in greatest dimension. The average home range length for Mesa Verde deer was intermediate in comparison. The data presented in Table 7 are interesting in that they suggest that males at Mesa Verde occupied smaller home ranges than did females. This is in conflict with the reported findings of Dasmann and Taber (1956a), Taber and Dasmann (1958), Robinette (1966) and others who consistently have reported home ranges of male mule deer to be larger than those of females.

A more sophisticated approach to home range measurement, developed by small-mammal workers Dice and Clark (1953) and Calhoun and Casby (1958), has been adapted for use with mule deer by Robinette (1966). This technique recognizes that an animal's activities are concentrated near the center of its home range with use decreasing as the distance from the center of activity increases. When the home range size of Mesa Verde deer is expressed in these terms (i.e. proportion of activity occurring within a given distance from a center of activity), the values (Table 8) remain similar to those reported in previous studies and also suggest that males occupy larger home ranges than females. Robinette (1966) reported an activity radius of 446.6 meters (SD 454.6) for bucks and 356.1 meters (SD 348.0) for does and fawns on the Oak Creek drainage in Utah. The activity radius of four does on the Hastings Reservation in California (calculated from the data of Linsdale and Tomich 1953 by Robinette 1966) was 195.1 meters (SD 162.9).

Table 7. Summer home range dimensions for Mesa Verde mule deer.

Habitat type	Sex	Age class	Number of deer	Number of observations	Home Range		
					Length	Width	Area
Mountain brush	M	Adult	11	327	1007[a] (330-1918)	746[a] (336-1220)	27.3[b] (7-65)
Mountain brush	M	Yearling	5	267	672 (264-1403)	439 (183-640)	25.0 (3-61)
Mountain brush	F	Adult	25	1475	1009 (336-1983)	536 (183-1250)	36.8 (7-128)
Mountain brush	F	Yearling	4	170	1142 (703-1564)	442 (330-743)	42.0 (22-61)
Pinyon-juniper	F	Adult	8	268	1772 (764-2438)	737 (366-1220)	26.3 (7-56)

[a]Mean (range), expressed in meters.
[b]Mean (range), expressed in hectares.

Table 8. Average summer activity radii (home range) of Mesa Verde deer.

Habitat type	Sex	Age class	Number of deer	Number of obser-vations	Activity Radius
Mountain brush	M	Adult	3	25	352.0 ± 325.9 [a]
Mountain brush	F	Adult	13	142	239.4 ± 215.2
Pinyon-juniper	F	Adult	5	29	967.6 ± 1080.3

[a] Mean ± standard deviation, expressed in meters.

Twenty-four deer were observed to return with the spring migration to the same home ranges they occupied in previous summers. We have no record of a deer relocating its home range once it was established.

Dispersal and Wandering

Juvenile deer forced out of the family group may travel a considerable distance before establishing a permanent home range. Two examples of dispersal movements were noted among Mesa Verde deer. Within a month of being tagged, one young male was observed at Pole Spring on Hay Camp Mesa, 35.4 airline kilometers northeast of the Park, and another at Thompson Park, 24.2 airline kilometers east northeast of the Park.

Dasmann (1953) commented upon several adult deer which wandered distances of up to 5.6 kilometers from their home ranges. Only one example of wandering was noted at Mesa Verde. This was an adult male who was observed on 20 July 1968 3.9 kilometers west of the center of its home range and on 29 August 1968 4.3 kilometers west northwest of this point. By mid-September, however, it had returned to the home range it occupied earlier that summer and in the year previous.

Migratory Movements

Migratory behavior shows great diversity from herd to herd and even from deer to deer within a herd. Some deer herds are entirely migratory and others nonmigratory, depending in large part on the environmental conditions of the region. Commonly, even when most deer migrate to winter ranges at lower elevations a small number remain behind.

The nature of the stimulus (or stimuli) releasing migratory behavior is not well understood. It seems likely, however, that it is a two stage process. An initial factor, perhaps photoperiod length, apparently places the deer into a state of readiness for migration. Some deer may respond to this stimulus alone. A few marked deer were observed to have left the Park for their winter ranges as early as the 10th of October. The vast majority, however, remain until a second stimulus, usually a severe storm or deepening snow, triggers their emigration. The data available suggest that an accumulation of 25 centimeters of snow is sufficient to initiate the event. This is illustrated nicely by the data from a deer trend count conducted during the winter of 1967-68 (Fig. 34) by a car pool of commuting Park

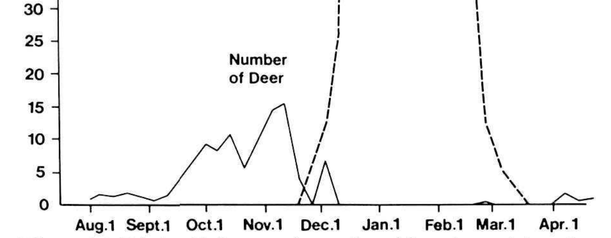

Figure 34. Relationship between the number of deer observed along the Mesa Verde National Park entrance road and the depth of accumulated snow, 1967-1968.

employees. Similar patterns were observed during the winters of 1954-55, 1955-56 and 1956-57 (Mail Carrier's Trend Study, MVNP File Ref. N 1427). The nonmigratory subpopulation responded similarly to increasing snow depth (Fig. 35). These deer, however, only moved down temporarily into the sheltered canyons, and returned to the mesa tops as soon as conditions permitted.

It was not possible to predict the location of a deer's winter range from the location of its summer

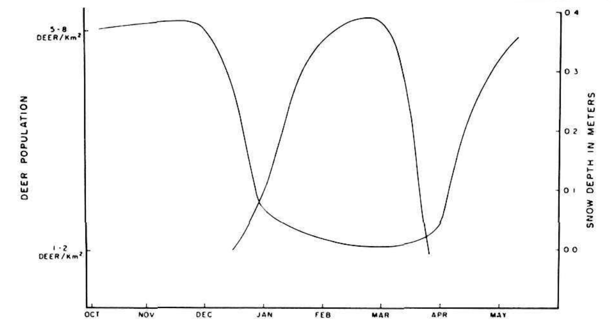

Figure 35. Relationship between deer abundance and snow depth in the pinyon-juniper forest of Mesa Verde National Park, 1968-1969.

range. Deer sharing overlapping home ranges often migrated in opposite directions, sometimes passing through suitable wintering habitat on the way to their ultimate destination. In Figure 36 is shown the approximate locations of marked deer resightings

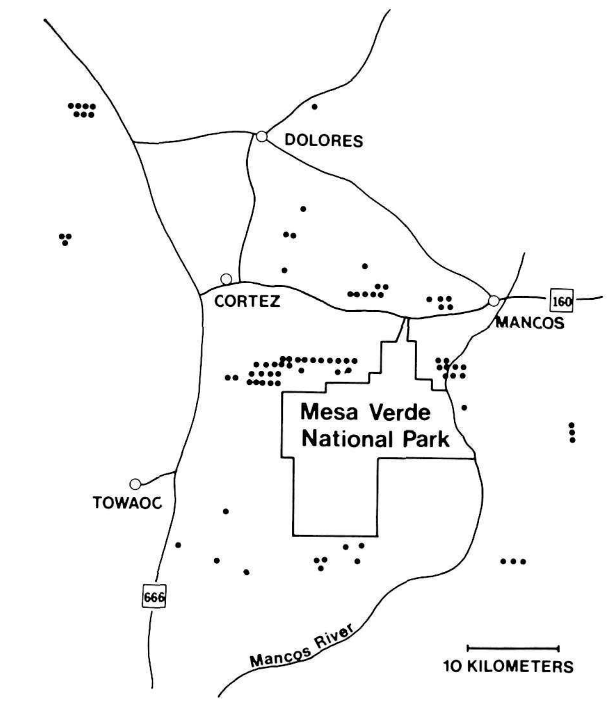

Figure 36. Location of marked deer observed on winter ranges outside of Mesa Verde National Park.

during the winters of 1968-69 and 1969-70. The average airline distance between summer and winter ranges was calculated to be 20.9 kilometers for the winter of 1968-69, but only 9.7 kilometers for the winter of 1969-70, a difference probably reflecting the limitations of our data rather than real variation in migratory patterns between the two years. Other Colorado mule deer herds have been shown to migrate similar distances. Gilbert and Harris (1959) reported that deer in Colorado's Middle Park region migrated an average of 12.6 kilometers between summer and winter ranges and Siglin (1965) that deer of the Cache la Poudre herd traveled an average distance of 20.6 kilometers between ranges.

The trend study data (Fig. 14 and 34) indicate that the reappearance in spring of the Park's migratory deer is somewhat variable, but usually occurs in late March or early April. Conditions in the spring of 1968 were particularly favorable for use of the track counting technique to study migratory movements (Fig. 37). The first group of returning migratory deer was observed near the

Figure 37. Counting sets of tracks made in the soft soil of an undisturbed road bed allowed the relative numbers of deer entering the Park over a given time period to be determined. Photo by G. Mierau.

Visitor Center on Northern Chapin Mesa on April 5. Tracks revealed that these deer had returned from an area south of the Park. A track count on April 21 along the Park's north rim and east rim showed that large numbers of deer had entered the Park using well defined trails over the steep escarpment. Another track count conducted a week later showed the spring migration to be nearly at its end.

An aerial census on March 3 resulted in only 2 deer observations within Park boundaries. Another flight on May 2 resulted in 456 observations, about twice the summer average. The number dropped to 393 on May 16, afterward returning to normal summer values. Similar springtime population fluctuations are suggested by the mail carrier's trend count data (Fig. 14). This transient increase in population density probably results from nonresident deer traveling back through the Park on the way to their summer ranges at higher elevations. Because they do not linger on this transitional range as long as they do in autumn, the increase is not as readily apparent.

6. Habitat Relationships

Range Condition

An indicator of a deer herd's well-being is the general condition of its range, especially soil and vegetative conditions. Eroding soil, a preponderance of undesirable plants, and the presence of numerous severely hedged browse plants would indicate poor range conditions, a possible causative factor in a declining deer population. Conversely, stable soil, a majority of desirable forage species, and desirable browse plants in good condition would indicate good range.

Soil conditions, browse composition, browse cover, and browse vigor were estimated by the interagency big game range analysis technique (Forest Service 1968). The starting point for the 55 permanent transects utilized for this purpose were the same as those described previously (Chapter 3, Fig. 17) for conducting pellet group counts. However, these transects consisted of 100 sampling points three paces apart. The direction of travel was randomly selected.

Soil Conditions

Soil is the basic resource. Over a long period, satisfactory range conditions can be maintained only on stable soils. Therefore soil conditions were evaluated for evidence of past and present erosion, for the amount of plant cover which is present to protect the soil, and for presence or absence of litter. Litter has several important benefits; these are mainly through reduction of evaporation, retardation of surface runoff, and prevention of raindrop splash erosion. It is also important to soil structure and fertility.

Evaluation of soil conditions is relatively subjective. Evidence of past and present erosion is estimated by observing the number and depth of gullies or ravines, alluvial deposits, and pedestaling of plants. At each sampling point on the transects soil conditions were classified within a ¾ inch loop; criteria used were those on the rating sheet shown in Appendix V (Forest Service 1968).

Soil conditions (Table 9) were judged to be good throughout the Park. Pedestaling of vegetation (the eroding away of soil around the root collar) was present in some open areas, however it was not widespread. The plant and litter cover were effective in protecting the soil. There was no indication of any serious erosion problem.

Ground Cover

Ground cover estimates were determined using the same paced transects described under "Soil Conditions." At each stop ground cover observations were made within the ¾ inch loop and classified according to the categories in Table 9.

Browse cover expresses the percentage of total ground area covered by the live crown of browse plants. It reflects, to some extent, the amount of deer forage being produced. Browse cover data are shown as a component of Table 9. Browse cover was judged as medium in the mountain shrub and sagebrush-grass vegetative stands. Enough forage was present to make these areas useful as deer range and also to protect the soil adequately. Browse cover was generally low throughout the pinyon-juniper stand. On the edges of the forest the browse cover was relatively high; however, it quickly declined as the tree canopy increased in density and, in the heart of the forest, dropped only to 2 or 3%. This area was incapable of supporting many deer because of the limited forage production.

Browse Composition

The composition of browse species is an important indicator of range condition as it expresses the quality of the forage available to browsing animals, such as mule deer. Good ranges can be expected to provide a variety of desirable forage species. Desirable species will maintain their number in an ecologic community as long as proper foraging levels exist. With excessive herbivore numbers, however, desirable species usually decrease while the least desirable species increase in abundance. Species in the intermediate group may decrease, increase, or remain static under conditions of range overutilization. In general, they are the first to replace undesirable species when poor range conditions are improving and also the first to replace desirable species when good range con-

Table 9. Ground cover in Mesa Verde National Park, 1969.

Cover	Mountain brush stand (%)	Sagebrush-grass stand (%)	Pinyon-juniper stand (%)
Bare ground	36.5	38.7	38.6
Litter	26.6	32.5	30.0
Browse Cover	22.2	17.0	7.5
Overstory Cover	2.6	1.6	15.6
Grass and Forbs	5.8	9.7	3.6
Rock	6.3	0.5	4.5
Moss	0.0	0.0	0.2
Total	100.0%	100.0%	100.0%
Ground Cover Index [a]	63.5	61.3	61.4
Rating	Medium	Medium	Medium

[a]Ground cover index = the total percentage of surface area with some kind of cover = 100 - % of bare ground.

ditions are deteriorating.

Browse composition data were obtained using the paced transects described previously. At each stop where a browse species appeared, its name, age class, and hedging class were recorded. The desirability rating for the habitat type was determined using the scorecard illustrated in Appendix VI.

The browse composition data for each major vegetative stand are presented in Tables 10, 11, and 12 and, for the entire Park, are summarized in Table 13. The wide variety of browse species present and the good combination of desirable and intermediate browse species make Mesa Verde National Park an excellent deer range.

Browse Vigor

Vigor is a reflection of the intensity of past grazing use and competition from other plants. It is appraised by classifying plants by age and by past use or "hedging."

The amount of consumption can significantly affect browse vigor. Deer may browse a plant so heavily that the seed stalks are consumed prior to dropping the seeds. The deer may so disturb the physiology of the plant as to prohibit seed formation. Excessive use can also kill a plant. Death results when the plant is no longer able to produce and store enough food to initiate regrowth in the spring and maintain its normal metabolic functions (Stoddard et al. 1975). It is generally acknowledged that a normal or healthy population of living organisms is one in which the birth rate equals the death rate resulting in a self-maintaining population. The age structure curve for such a population exhibits a characteristic "die-away" form with a greater number of individuals in the younger age classes and progressively diminishing numbers in older age classes (Roughton 1966). A decadent population, in which the death rate exceeds the birth rate, has more individuals in the older age classes and fewer in the younger age classes, resulting in an age structure curve which is the reverse of the "healthy" curve (Roughton 1966).

In the mountain brush stand (Table 14) many of the key browse species were heavily hedged (Figs. 38 and 39) and possessed a decadent age structure. These species may have difficulty reproducing and maintaining themselves. This was especially true for true mountainmahogany, antelope bitterbrush, Utah serviceberry and big sagebrush. Of the important browse species, only Gambel oak had high vigor. Most of the least desirable species had high vigor and seemed to be maintaining their populations.

Vigor of browse species was also low in the pinyon-juniper stand (Table 15). This did not seem to be due to excessive use, but perhaps competition with overstory. Regardless of the reason, the principal browse species (Utah serviceberry, true mountainmahogany, antelope bitterbrush, cliff fendlerbush, and big sagebrush) all had large percentages of decadent plants in their stands.

Browse vigor was somewhat better in the sagebrush-grass stand (Table 16). Vigor was classifed as medium for the key browse species, except for rabbitbrush which was rated low because of the large number of decadent plants present.

Table 10. Browse composition in mountain brush stand.

Species	Forage Class[a]	Percent Composition	
Utah Serviceberry	Desirable	15.9	
Antelope Bitterbrush	Desirable	6.6	
True Mountainmahogany	Desirable	5.8	
Fourwing Saltbush	Desirable	2.4	
Common Chokecherry	Desirable	0.7	
Creeping Barberry	Desirable	0.1	
			31.5
Big Sagebrush	Intermediate	22.9	
Gambel Oak	Intermediate	13.8	
Cliff Fendlerbush	Intermediate	4.5	
Squawapple	Intermediate	0.6	
			41.8
Rubber Rabbitbrush	Least Desirable	11.1	
Mountain Snowberry	Least Desirable	8.8	
Dwarf Rabbitbrush	Least Desirable	2.8	
Gray Horsebrush	Least Desirable	1.8	
Fragrant Sumac	Least Desirable	0.6	
Woods Rose	Least Desirable	0.6	
Black Greasewood	Least Desirable	0.5	
Golden Currant	Least Desirable	0.4	
Common Winterfat	Least Desirable	0.1	
			26.7
Total			**100.0**

[a]As defined by Forest Service (1968)

Table 11. Browse composition in pinyon-juniper stand.

Species	Forage Class[a]	Percent Composition	
Antelope Bitterbrush	Desirable	40.8	
True Mountainmahogany	Desirable	13.3	
Utah Serviceberry	Desirable	7.4	
Creeping Barberry	Desirable	0.8	
			62.3
Big Sagebrush	Intermediate	11.8	
Gambel Oak	Intermediate	9.8	
Cliff Fendlerbush	Intermediate	6.3	
Myrtle Pachistima	Intermediate	0.8	
			28.7
Mountain Snowberry	Least Desirable	3.7	
Rubber Rabbitbrush	Least Desirable	1.9	
Dwarf Rabbitbrush	Least Desirable	1.4	
Others	Least Desirable	2.0	
			9.0
Total			**100.0**

[a]As defined by Forest Service (1968)

Table 12. Browse composition in sagebrush-grass stand.

Species	Forage Class[a]	Percent Composition	
Fourwing Saltbush	Desirable	12.0	
Utah Serviceberry	Desirable	1.2	
Creeping Barberry	Desirable	0.5	
Common Chokecherry	Desirable	0.3	
True Mountainmahogany	Desirable	0.2	
			14.2
Big Sagebrush	Intermediate	32.0	
Gambel Oak	Intermediate	2.3	
Squawapple	Intermediate	0.3	
			34.6
Rubber Rabbitbrush	Least Desirable	38.7	
Mountain Snowberry	Least Desirable	4.2	
Black Greasewood	Least Desirable	2.5	
Dwarf Rabbitbrush	Least Desirable	1.9	
Golden Currant	Least Desirable	1.2	
Common Winterfat	Least Desirable	1.0	
Woods Rose	Least Desirable	0.7	
Gray Horsebrush	Least Desirable	0.5	
Fragrant Sumac	Least Desirable	0.5	
			51.2
Total			**100.0**

[a]As defined by Forest Service (1968)

Table 13. Browse desirability classes.

	Percent Composition		
Vegetative Stand	Desirable	Intermediate	Least Desirable
Pinyon-juniper	61.3	30.1	8.6
Mountain brush	29.5	41.8	28.7
Sagebrush-grass	14.2	36.5	49.3

Range Utilization And Trend

Another frequently used indicator of the quantity of forage available to browsing ungulates is the percentage of browse utilization. The amount of use each species can stand has not been accurately determined. Garrison (1953) reported that bitterbrush in Oregon could sustain 65% utilization of the current annual growth without injuring the plant. Studies by Shepherd (1956) in Colorado revealed that the annual removal of from 20 to 80% of the current annual growth of true mountain-mahogany and Gambel oak did not significantly affect forage production.

Browse production and utilization were estimated by a combination of two methods: measured transects and extensive utilization transects, as defined by the Forest Service (1968). Measured transects were established only for the key browse species (i.e. antelope bitterbrush, Utah serviceberry, true mountainmahogany, and cliff fendlerbush) on Wetherill, Long, Chapin, White, and Big Mesas. After their annual growth was complete (mid-July), selected stems of the browse plants were measured (Fig. 40). In early September these stems were remeasured to determine the extent of their utilization by deer over the summer

Figure 38. Antelope bitterbrush plant showing severe hedging. Photo by E. Orsini.

Figure 39. Large Utah serviceberry plant showing moderate hedging to the height deer could reach. Photo by G. Mierau.

Figure 40. Selected stems of browse plants were remeasured periodically to determine browse production and utilization. Photo by D. Sanders.

Table 14. Indices of plant vigor in mountain brush stand.

	Age Class			Hedging Class			
Species	**Y**	**M**	**D**	**1**	**2**	**3**	**Rating**
Desirable							
Creeping Barberry	20	80	0	100	0	0	High
Common Chokecherry	38	62	0	90	10	0	High
Squawapple	0	94	6	44	56	0	High
True Mountainmahogany	3	56	41	15	58	27	Low
Antelope Bitterbrush	3	85	12	10	39	51	Low
Utah Serviceberry	5	56	39	10	32	58	Low
Intermediate							
Gambel Oak	15	73	12	90	10	0	High
Big Sagebrush	2	67	31	44	41	15	Medium
Cliff Fendlerbush	0	74	26	8	54	38	Medium
Least Desirable							
Golden Currant	0	83	17	100	0	0	High
Common Winterfat	0	100	0	100	0	0	High
Fragrant Sumac	0	82	18	100	0	0	High
Woods Rose	35	59	6	100	0	0	High
Black Greasewood	0	53	47	100	0	0	High
Mountain Snowberry	3	82	15	99	1	0	High
Rubber Rabbitbrush	1	53	46	95	3	2	Low
Gray Horsebrush	4	37	59	85	15	0	Low
Dwarf Rabbitbrush	0	90	10	84	15	1	High

Y-Young, M-Mature, D-Decadent
1-Light, 2-Moderate, 3-Heavy (see Appendix VII)

Table 15. Indices of plant vigor in pinyon-juniper stand.

Species	Age Class Y	M	D	Hedging Class 1	2	3	Rating
Desirable							
Creeping Barberry	20	80	0	100	0	0	High
True Mountainmahogany	2	31	67	51	39	10	Low
Antelope Bitterbrush	1	67	32	39	53	8	Medium
Utah Serviceberry	10	33	57	34	33	33	Low
Intermediate							
Gambel Oak	14	79	9	91	9	0	High
Squawapple	0	42	58	79	21	0	Low
Big Sagebrush	1	51	48	52	42	6	Low
Cliff Fendlerbush	2	45	53	43	43	14	Low
Least Desirable							
Mountain Snowberry	0	90	10	100	0	0	High
Golden Currant	0	100	0	100	0	0	High
Fragrant Sumac	0	91	9	100	0	0	High
Rubber Rabbitbrush	0	60	40	93	7	0	Low
Dwarf Rabbitbrush	0	76	24	91	9	0	Medium
Woods Rose	10	90	0	90	10	0	High

Y-Young, M-Mature, D-Decadent
1-Light, 2-Moderate, 3-Heavy (see Appendix VII)

Table 16. Indices of plant vigor in sagebrush-grass stand.

Species	Age Class Y	M	D	Hedging Class 1	2	3	Rating
Desirable							
Fourwing Saltbush	0	82	18	86	11	3	Medium
Utah Serviceberry	0	100	0	14	57	29	Medium
Intermediate							
Gambel Oak	14	79	7	96	4	0	High
Big Sagebrush	4	64	32	51	42	7	Medium
Squawapple	0	100	0	50	50	0	High
Least Desirable							
Dwarf Rabbitbrush	0	73	27	100	0	0	Medium
Mountain Snowberry	0	72	28	100	0	0	Medium
Black Greasewood	0	53	47	100	0	0	Low
Golden Currant	0	75	25	100	0	0	Medium
Woods Rose	50	50	0	100	0	0	High
Rubber Rabbitbrush	1	53	46	97	0	3	Low
Others	0	63	37	87	13	0	Low

Y-Young, M-Mature, D-Decadent
1-Light, 2-Moderate, 3-Heavy (see Appendix VII)

period and again in late April to determine winter utilization. Extensive utilization transects supplemented measured ones by providing a larger sample that included other plant species. These were placed in the same locations as the range condition and trend and pellet count transects (Fig. 17), insuring that utilization was adequately sampled in all areas of the Park. The percentage of twigs eaten method (Stickney 1966) was employed with this technique to estimate browse utilization.

Total utilization as estimated from measured transects is shown in Table 17. Extensive utilization data are shown in Tables 18, 19, and 20. It was not feasible to remeasure the extensive utilization transects in the spring of 1968 before deer reentered the park. The level of browse utilization observed during the course of our study was judged to have been within acceptable limits.

One must look elsewhere to explain the hedged condition and low vigor of browse plants found in the Park. In 1967 the deer were essentially gone from the park by December 15 and were not seen in large numbers again until early April 1968. The same weather and migratory pattern was repeated during the winter of 1968-1969. The winter of 1969-1970, however, was mild. Deer were known to be on Big Mesa until late in February. Utilization averaged 80% on true mountainmahogany, 95% on antelope bitterbrush and 50% on big sagebrush. Some two year old growth was used on both true mountainmahogany and antelope bitterbrush. Thus some damage to the browse undoubtedly does occur during unusually mild winters when an increased number of deer winter in the Park. Also, it is worth noting that the various browse species often attain a considerable age. Antelope bitterbrush plants, for example, may live 160 years or more (Nord 1959). Knowing that the effects of severe hedging can be observed for many years after the primary insult, it seems reasonable to conclude that much of the severe hedging observable at this time actually occurred in previous decades when deer populations in the Park were much larger than at present.

In any case, during the period of the deer population decline the habitat was found in general to be in excellent condition and without signs of active deterioration. A series of small fires, together with the accelerated action of root fungus on pinyon pine, has served recently to open the overstory of pinyon-juniper forest in many sites, thus favoring the production of additional forage for deer in future years. Selective chaining of pinyon-juniper stands on winter ranges outside of the Park appears also to favor the trend toward improving range conditions for Mesa Verde deer.

Food Habits

The diet of Mesa Verde deer was studied by analyzing the botanical contents of the rumen chamber of the stomach. Rumen contents of 142 deer, collected in conjunction with studies of physical condition (Chapter 4), were analyzed using the point frame technique as described by Chamrod and Box (1964). Briefly stated, rumen material was randomly collected from several locations within the rumen and preserved in 10% formalin. For analysis, the material was washed then spread evenly over the bottom of a laboratory tray. A frame containing five pins, placed at a 45 degree angle through the frame, was fitted to slide along the top of the tray (Fig. 41). Each pin was lowered into the tray until it first hit on a plant fragment, whose identity was then recorded. One hundred hits constituted a sample. Percentage volume estimates were taken directly from the number of hits. The frequency

Table 17. Browse utilization data (measured transects), 1967-1968.

	1967		1968	
Species	**Summer**	**Total**	**Summer**	**Total**
Antelope Bitterbrush	10.0[a]	30.0	2.2	42.6
True Mountainmahogany	3.7	19.2	1.6	27.4
Utah Serviceberry	1.9	7.6	3.7	11.1
Cliff Fendlerbush	1.4	9.0	6.3	11.2

[a] Expressed as percent of current annual growth used.

Table 18. Browse utilization data (extensive), summer 1967.

Species	Mountain brush stand	Pinyon-juniper stand	Sagebrush-grass stand	Weighted Mean
True Mountainmahogany	9.8[a]	9.0	9.5	9.6
Antelope Bitterbrush	6.7	5.8	0.0	6.0
Utah Serviceberry	4.8	6.3	0.0	5.0
Gambel Oak	4.8	5.7	0.0	4.9
Cliff Fendlerbush	2.9	0.5	0.0	2.4
Rubber Rabbitbrush	1.2	1.7	2.2	1.3
Big Sagebrush	1.1	0.4	0.6	0.8
Mountain Snowberry	0.6	0.0	0.0	0.6
Squawapple	0.5	0.0	0.0	0.5
Dwarf Rabbitbrush	0.0	0.0	0.0	0.0
Gray Horsebrush	0.0	0.0	0.0	0.0

[a] Expressed as percent of twigs eaten.

Table 19. Browse utilization data (extensive), summer 1968.

Species	Mountain brush stand	Pinyon-juniper stand	Sagebrush-grass stand	Weighted Mean
True Mountainmahogany	10.6[a]	4.3	0.0	7.5
Antelope Bitterbrush	13.8	3.9	0.0	7.3
Common Chokecherry	12.9	0.0	0.0	6.9
Utah Serviceberry	6.4	2.1	0.0	5.4
Fourwing Saltbush	0.0	0.0	10.0	3.6
Cliff Fendlerbush	4.8	1.4	0.0	3.5
Gambel Oak	3.9	1.3	0.0	2.9
Squawapple	2.8	2.5	0.0	1.6
Mountain Snowberry	1.8	0.3	0.0	1.4
Rubber Rabbitbrush	0.7	0.0	1.6	1.2
Dwarf Rabbitbrush	0.9	0.0	0.0	0.9
Gray Horsebrush	0.8	0.0	0.0	0.8
Big Sagebrush	0.9	0.2	0.1	0.6
Fragrant Sumac	0.6	0.0	0.0	0.6
Black Greasewood	0.0	0.0	0.0	0.0

[a] Expressed as percent of twigs eaten.

Table 20. Browse utilization date (extensive), winter 1968-1969.

Species	Mountain brush stand	Pinyon-juniper stand	Sagebrush-grass stand	Weighted Mean
Fourwing Saltbush	0.0[a]	0.0	43.3	43.3
Rubber Rabbitbrush	22.0	0.0	18.6	19.1
Antelope Bitterbrush	34.1	11.2	22.5	14.4
True Mountainmahogany	21.3	5.2	2.7	13.0
Big Sagebrush	13.7	6.2	15.1	13.0
Dwarf Rabbitbrush	14.4	0.0	0.0	8.7
Squawapple	7.1	8.0	0.0	6.7
Gray Horsebrush	6.3	0.0	0.0	6.3
Cliff Fendlerbush	5.9	5.8	2.0	5.8
Utah Serviceberry	5.4	4.6	6.3	5.3
Gambel Oak	4.6	5.6	4.5	4.9
Mountain Snowberry	0.9	0.9	1.1	0.9
Black Greasewood	0.0	0.0	0.0	0.0

[a] Expressed as percent of twigs eaten.

Table 21. Seasonal food habits of Mesa Verde mule deer.

	January-March (23)[a]		April-June (33)		July-September (44)		October-December (42)		Total (142)	
Food Item	Mean Volume	Frequency Index	Mean Volume	Frequency Index	Mean Volume	Frequency Index	Mean Volume	Frequency Index	Mean Volume	Frequency Index
Browse										
Utah Serviceberry	6.0[b]	0.47	25.5	0.85	28.0	0.96	5.8	0.58	17.3	0.74
Big Sagebrush	39.1	1.00	7.3	0.30	0.0	0.0	0.5	0.24	8.4	0.30
Gambel Oak	0.2	0.09	1.7	0.24	21.8	0.84	4.2	0.55	8.4	0.49
Antelope Bitterbrush	1.5	0.22	2.8	0.18	3.1	0.25	17.4	0.74	7.0	0.37
Rubber Rabbitbrush	6.6	0.26	0.0	0.0	0.0	0.0	9.4	0.34	3.8	0.14
Common Chokecherry	0.0	0.0	1.9	0.12	7.3	0.53	3.0	0.17	3.6	0.24
True Mountainmahogany	2.1	0.09	2.1	0.21	4.9	0.64	5.4	0.48	3.5	0.40
Pinyon Pine	15.1	0.70	0.3	0.09	Tr.[c]		0.9	0.04	2.8	0.29
Mountain Snowberry	0.0	0.0	0.5	0.18	6.0	0.27	0.6	0.20	2.2	0.18
Utah Juniper	10.1	0.70	0.0	0.0	0.0	0.0	0.6	0.10	1.9	0.14
Dwarf Rabbitbrush	4.5	0.26	0.1	0.03	0.0	0.0	0.8	0.19	0.9	0.11
Squawapple	0.0	0.0	1.9	0.18	0.5	0.45	0.0	0.0	0.6	0.18
Green Ephedra	1.5	0.22	0.5	0.03	0.0	0.0	0.2	0.05	0.4	0.06
Myrtle Packistima	0.3	0.04	0.1	0.06	0.0	0.0	0.4	0.05	0.2	0.04
Tarragon Sagewort	0.0	0.0	0.0	0.0	0.1	0.02	0.0	0.0	Tr.	0.0
Cliff Fendlerbush	0.0	0.0	0.1	0.06	0.4	0.16	0.6	0.05	Tr.	0.0
Creeping Barberry	0.0	0.0	0.2	0.06	0.0	0.0	2.0	0.17	Tr.	0.0
Total Browse Volume	**87.0**		**45.0**		**71.9**		**51.8**		**61.1**	
Forbs										
Vetch	0.6	0.09	5.4	0.55	9.5	0.73	0.7	0.02	4.5	0.37
Sulfur Eriogonum	Tr.	0.03	3.4	0.52	0.5	0.23	4.6	0.55	2.3	0.35
Tailcup Lupine	0.0	0.0	0.0	0.0	2.3	0.18	4.3	0.31	2.0	0.10
Toadflax Penstemon	0.0	0.0	2.1	0.33	0.7	0.14	1.9	0.21	1.3	0.18
Oregon Fleabane	0.0	0.0	1.9	0.48	0.6	0.30	1.8	0.24	1.2	0.27
Arrowleaf Balsamroot	0.0	0.0	3.9	0.33	1.0	0.21	0.0	0.0	1.2	0.14
Aspen Peavine	0.0	0.0	1.2	0.21	2.3	0.34	0.1	0.45	1.0	0.29
Golden Corydalis	0.0	0.0	4.4	0.39	0.0	0.0	0.0	0.0	1.0	0.09
White Prairie Aster	0.0	0.0	0.0	0.0	1.4	0.20	0.7	0.12	0.7	0.10
Evening Primrose	0.0	0.0	0.0	0.0	1.4	0.07	0.6	0.14	0.7	0.06
Louisiana Sedgewort	0.0	0.0	0.0	0.0	0.2	0.12	0.9	0.13	0.3	0.08
Spindleroot Bluebells	0.0	0.0	0.1	0.03	1.0	0.16	Tr.	0.02	0.3	0.06
Rocky Mountain Penstemon	0.0	0.0	0.5	0.05	0.6	0.11	0.0	0.0	0.3	0.04
Tapertip Hawksbeard	0.0	0.0	0.7	0.15	0.0	0.0	0.3	0.05	0.3	0.05
Arizona Wyethia	0.0	0.0	0.0	0.0	0.2	0.45	0.3	0.07	0.2	0.16
Fireweed Willow-herb	0.0	0.0	0.0	0.0	0.4	0.45	0.0	0.0	0.1	0.14
Wayside Gromwell	0.0	0.0	0.0	0.0	0.3	0.07	Tr.	0.15	0.1	0.07
Yellow Sweetclover	0.0	0.0	0.4	0.15	Tr.	0.05	0.0	0.0	0.1	0.05
Hairy Goldenaster	0.0	0.0	0.5	0.15	0.0	0.0	0.0	0.0	0.1	0.04
Total Forb Volume	**0.6**		**31.6**		**23.8**		**16.7**		**19.6**	
Grass	10.5	0.52	21.2	0.97	3.2	0.50	29.6	0.96	16.4	0.75
Unidentified	1.9	0.76	2.2	0.70	1.9	0.77	1.9	0.76	1.7	0.67

[a] Sample size.
[b] Expressed as percent.
[c] Trace.

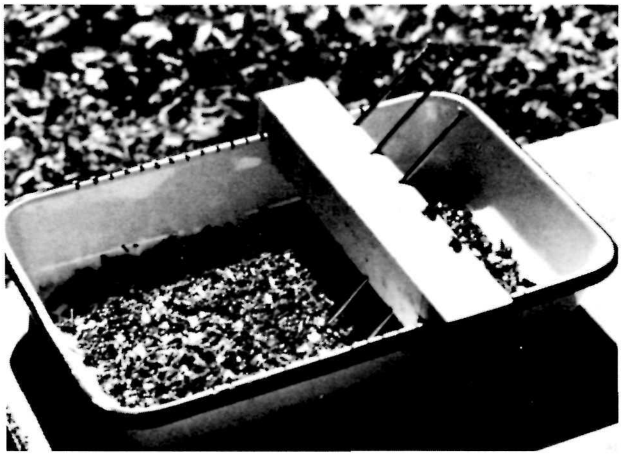

Figure 41. Point frame used in analyzing rumen contents. Photo by K. Dillinger.

index was determined by dividing the number of rumen samples in which the food item occurred by the total number of samples obtained during a particular period (Dice 1952). The food items were categorized as browse, forbs, or grass and summarized by mean percentage volume and frequency by season.

The results of these analyses are shown in Table 21. The yearly diet consisted of 61% browse, 20% forb, and 16% grass species. Unidentified material comprised 2% of the diet. Utah serviceberry, antelope bitterbrush, Gambel oak and big sagebrush were the most utilized shrub species. Utah serviceberry was used heavily from April through September, while antelope bitterbrush became more important in the fall. Gambel oak comprised a large portion of the diet only in the summer, although it was eaten throughout the year. Big sagebrush was most important in the winter months. Two other shrub species of significance were true mountainmahogany and rubber rabbitbrush. True mountainmahogany was used consistently through the year, but never at high levels. Rubber rabbitbrush was an important dietary component during the fall and winter months. Conifers were important only during the winter months, with pinyon pine and Utah juniper the only species used. Forbs comprised significant amounts of their diet in all seasons except winter, when they were less than 1%. Vetch and sulfur eriogonum were the most heavily utilized forb species. Grass as deer forage was noted in all months of the year but was highest in spring and fall. Grasses in the rumen contents were not identified to species. Several samples of rumen contained balls of deer hair. Ticks, ants, flies, and other insects were found in a small percentage of the samples. These were undoubtedly ingested incidentally with vegetation or during grooming.

These results are not indicative of a depleted range for deer. A large majority of the diet was composed of desirable forage species and little use was made of undesirable species.

7. Population Characteristics

Productivity

The productivity of a wildlife population is a major concern of wildlife biologists. If productivity is too low, mortality may exceed it and the population will decline. Conversely, if productivity in a population of large ungulates is exceedingly high and the high productiveness is not offset by high mortality, the population may become overly abundant and perhaps damage its range.

Of the indicators commonly used by wildlife biologists to describe productivity in ungulate populations, the ovulation rate and the percent pregnant are two of the most important. These reflect the quantity and quality of the diet before and during pregnancy. Fawn:doe ratios are perhaps the most frequently used indicator of productivity. These are primarily a measure of fawn survival; deaths of adult females also influence the ratios, but are normally insignificant by comparison.

Most of the data for this aspect of the study were obtained during the monthly collections described in Chapter 4. Ovaries were removed, labeled, and preserved in 10% formalin. They were later sectioned and analyzed using Cheatum's (1949) method. If the doe was at least two years old and collected between November and March, both corpora lutea (endocrine bodies formed in the sites of ruptured ovarian follicles) and corpora albicantia (pigmented scars of previous corpora lutea) were counted, thus supplying ovulation rates for two breeding seasons. The diameter of each corpus luteum, corpus albicans, and each follicle over 2mm was measured. Reproductive tracts of deer collected in November and December were flushed and dissected for blastocysts or embryos. Fawn:doe ratios were counted using Dasmann and Taber's (1956b) method (Fig. 42) and helicopter flights (Fig. 43). The percent of yearlings was calculated from age structure data and Dasmann and Taber's (1956b) method of classification.

To reduce confusion, several terms will be defined at this point:

Ovulation rate = Mean number of ova shed per female per esterus, the standard measurement of which =

$$\frac{\text{Number of corpora lutea or corpora albicantia}}{\text{Number of females}}$$

Fertilization rate =

$$\frac{\text{Number of prenatal young}}{\text{Number of current corpora lutea of pregnancy}}$$

Percent ova loss = 100 - 100x (fertilization rate)

Percent pregnant =

$$100\text{x} \frac{\text{Number of pregnant females}}{\text{Number of females}}$$

$$\text{Fetal rate} = \frac{\text{Number of prenatal young}}{\text{Number of females}}$$

Adult = fully grown, and the majority of their cohort have completed one or more breeding seasons; mule deer one and a half years old are considered adults (Hanson 1963).

Fertility = qualitative term denoting the ability to produce viable young.

Figure 42. Ground level fawn:doe and tertiary sex composition counts were conducted with the aid of a spotting scope and binoculars. Photo by G. Mierau.

Figure 43. A Bell 47G3B1 helicopter was used in conducting aerial counts. Photo by G. Mierau.

Ovulation

Corpora lutea and corpora albicantia counts were made on 102 pairs of ovaries. The ovulation rate for all does older than yearlings was 1.96, and 2.00 for those over two years old.

The ovulation rate for Mesa Verde yearling deer, 1.55, was higher than any found in the literature. The highest, 1.44, was reported by Nellis (1968) on the National Bison Range, Montana. The ovulation rate for older does was also high, but higher rates were reported by Jensen and Robinette et al. (1955) from an area in northwestern Utah. Although the ovulation rate tends to rise with increasing age, the percent ova loss rises correspondingly so there is little consistent change of the fetal rate with age after two years. The age at which female mule deer can no longer reproduce is unknown. Robinette et al. (1955) believed there is no impairment in fertility until the age of at least 11 or 12 years; free-ranging deer seldom attain this age. The oldest deer observed at Mesa Verde was 13 years of age. This doe, which had been tagged as a yearling 12 years earlier, was observed in the summer of 1980, and had consistently borne twin fawns over this period.

Gestation

Fetuses were collected from 31 pregnant does. The fetal rate, fertilization rate, and percent ova loss for each class is shown in Table 22. The fetal rate for does older than yearlings was 1.79. All adult does collected after mid-January were carrying visible fetuses, and all those collected after mid-December had fully developed corpora lutea. The percent pregnant, therefore, has been estimated as 100. Ovaries from a 13-month old doe collected 18 August 1967 contained two pigmented corpora albicantia indicating that she had become pregnant as a fawn. This was the only incidence of pregnancy or ovulation found in the fawn age class.

Of the 31 pregnant does, nine (29%) were carrying single fetuses, and 22 (71%) were carrying twins; no triplets or quadruplets were found. All three pregnant yearlings were carrying single fetuses. No atrophic deer embryos or fetuses were found. The percent pregnant and fetal rates were relatively high. Only Jensen and Robinette (1955) reported a higher fetal rate. The complete lack of atrophic fetuses is somewhat unusual. Robinette et al. (1955)

Table 22. Productivity of mule deer in Mesa Verde National Park.

Age (yrs.)	Sample Size	Fetal Rate	Fertilization Rate	% Ova Loss
0	10	0.00	—[a]	—
1	3	1.00	1.00	0
2	7	1.57	0.92	8
3	6	2.00	1.00	0
4	5	1.80	0.82	18
5	4	1.75	0.88	12
6	2	2.00	0.67	33
7	0	—	—	—
8	1	2.00	0.67	33
9	2	2.00	0.80	20
10	1	1.00	0.50	50
Total (excluding fawns)	**31**	**1.71**	**0.85**	**15**

[a]No data.

Table 23. Fawn:doe ratios, late summer and fall.

Date		Method	Sample Size		Ratio	
			Fawns	Does	Fawns:doe	Fawns: adult doe
1968	Aug	Spotting Scope	46	88	0.58	1.10
	Oct	Helicopter	94	187	0.50	—[a]
	Dec	Helicopter	150	203	0.74	—
1969	Sep	Spotting Scope	58	71	0.82	1.23
	Nov	Helicopter	206	243	0.85	—
Total			**554**	**792**	**0.07**	**1.17**

[a]No data. It was not possible to distinguish yearlings from adults using a helicopter.

reported 1.7% atrophied fetuses in a sampling of 1,263 deer in Utah and Bischoff (1958) reported a 2.9% and 3.3% for the Lassen-Washoe and Truckee-Verdi herds, respectively, in California.

The high level of productivity observed at Mesa Verde is probably attributable to a high level of nutrition. Verme (1969) experimented with reproduction and nutrition using white-tailed deer as subjects. The 129 does on a high nutrition diet had 1.73 fawns per doe, whereas the 61 does on a low nutrition diet had 1.15 fawns per doe. Good nutrition seems to be most important during the summer and fall. Jones et al. (1956) and Julander et al. (1961) studied reproduction on a severely depleted summer range in Utah and on good summer range in Idaho. They found that the average ovulation rate on the depleted range, 1.31, was only 67% of that on the good range, 1.95. Furthermore, the fetal rate for the depleted range was 1.19, compared to 1.85 for the good range. Robinette et al. (1955), Swank (1958), and Julander (1962) have also indicated that summer range is important in determining productivity.

Postpartum

Fawn:doe counts were made in the late summer and fall of 1968 and 1969. Results are shown in Table 23. The 1968 fawn:doe ratio was 290:470 or 0.62 fawns per doe (including yearlings). In 1969 the counts totaled 264 fawns and 314 does (including yearlings) or 0.84 fawns per doe. The average fawn:adult doe ratio in the fall, 1.17, is 0.54 lower than the fetal rate for this same age group. Based on these values, 32% mortality occurred within the first two to three months of life. Cook et al. (1967) in their radiotelemetry study of white-tailed deer fawns reported that 58 of 81 (67%) died within one month of birth or shortly thereafter. They further stated that predators were involved in 71% of the deaths as revealed by conditions prior to death and necropsy. Julander and Robinette (1950) reported that fawn mortality in mule deer amounted to 39% during the first three months on the Oak Creek Range in Utah, with most of the mortality occurring during the first month.

The percentage of yearlings was calculated from spotting scope, autopsy, and drug capture data. The average for the first year of the study was 21% yearlings, 40% for the second year, and 32% for the third year. A greater percentage of yearlings was estimated with the spotting scope than from the autopsy and drug capture sample. It was easier, and undoubtedly more accurate, to distinguish yearlings by tooth eruption patterns than by Dasmann and Taber's (1956b) spotting scope method. Their method is "facilitated when deer are in family groups." When deer, especially adult females, are not in family groups their method may yield an overestimation of the percent yearlings. The percent yearlings estimated at Mesa Verde (34%), is high in comparison with other herds. Swank (1958) found the Bill Williams area of Arizona to have the highest percentage of yearlings, 30%, of all areas he studied. Robinette and Olson (1944) found 22% yearlings in a central Utah herd.

Sex Composition

In a normal deer population, the sex ratio at birth is approximately equal. After birth, however, males tend to have an accelerated natural mortality rate resulting in the sex ratio gradually

Table 24. Sex composition of adult mule deer.

Date		Method	Sample Size	Percent Males
1968	Aug	Spotting scope	124	35
	Oct	Helicopter	287	35
	Dec	Helicopter	318	36
1969	Sep	Spotting scope	101	30
	Nov	Helicopter	408	40
Total			**1238**	**37**

becoming unbalanced in favor of females.

During the study, 53 fetuses were collected. Six of these were too small to determine sex. The remaining 47 included 15 males and 32 females for a secondary sex composition of 32% males and 68% females. Chi-square analysis indicated that these were significantly different ($P<0.05$) from equality. This prenatal sex composition is quite unusual and nothing similar was found in the literature. Combined results of other studies (Taber 1953, Robinette et al. 1955, and Hudson 1959) yielded an average of 53% males bases on 1,755 mule deer fetuses. Robinette et al. (1957b) found a greater percentage of males in does carrying their first young. They also found that as the litter size increased, the percentage of males decreased. Verme (1969) found that does on restricted rations when bred had more males, 72%, than well-fed does, 43%. The high quality of forage consumed by Mesa Verde does, in addition to their high fetal rate, may be responsible for their skewed prenatal sex composition.

The percent of males in the fawn class was also lower than that of females. Of the 43 fawns examined, 42% were males. The results of the adult herd composition counts are summarized in Table 24. The adult composition from all sources for 1968 was 36% males and for 1969, 38% males. While males comprised 42% of the fawn population, only 37% of the adult population consisted of males. These figures are typical of populations assumed to have had an equal secondary sex composition. Robinette et al. (1957b) and Klein and Olson (1960) found that males tend to suffer a higher mortality rate. Taber and Dasmann (1957) attributed the higher mortality rate of male fawns to their higher metabolic rate and nutrient requirements. In their

Table 25. Life table for mule deer in Mesa Verde National Park.

x	l_x	d_x	q_x	e_x	m_x	$l_x\ m_x$
0-M[a]	251	32	.13	1.48	0.00	0.0
M-1	219	165	.75	0.84	0.00	0.0
1-2	54	14	.26	1.52	0.63	34.0
2-3	40	9	.23	1.61	1.13	45.2
3-4	31	7	.23	1.56	1.13	35.0
4-5	24	8	.33	1.35	1.13	27.1
5-6	16	7	.44	1.34	1.13	18.1
6-7	9	0	.00	2.00	1.13	10.2
7-8	9	0	.00	1.72	1.13	10.2
8-9	9	5	.56	1.11	1.13	10.2
9-10	4	1	.25	1.50	1.13	4.5
10-11	3	1	.33	1.50	1.13	3.4
11-12	2	0	.00	1.50	1.13	2.3
12-13	2	2	1.00	0.50	1.13	2.3
Total	**673**					**202.5**

[a] Mid-pregnancy

x = age class; l_x = number alive at beginning of interval, d_x = number dying during interval; q_x = mortality rate; e_x = mean expectation of life; m_x = fetal rate (63% females times a fetal rate of 1.00 for age class 1-2 and 1.79 for older age classes).

study of black-tailed deer in California, Taber and Dasmann (1957) found an average mortality rate for male fawns of 63% as compared to 45% for female fawns.

Age Structure And Life Tables

Age structure and life table analysis is a useful technique for studying ungulate populations. Healthy deer herds whose numbers are increasing normally contain a high proportion of animals in the younger age classes. Conversely, declining populations have a preponderance of animals in the older age classes. Mortality and survival in a population can be expressed in the form of a life table (Table 25). Life tables are classified as either "cohort" (dynamic) or "time specific." Data for a cohort life table is gathered by monitoring mortality of all of the individuals born or hatched at the same time until all have died. Data for a time specific life table is collected by recording mortality of all age classes in a population over a year's time. At Mesa Verde a modification of the time specific life table was used.

Age data for 203 deer, excluding fawns, were collected in conjunction with studies of physical condition (Chapter 4) and from live captured animals. For construction of the life table (Table 25) it was assumed that this sampling was random. The number of fawns was an estimate based on the assumption that 63% of the 203 deer were females and that each female produced 1.71 fawns. The number of ova was calculated using an ovulation rate of 1.96. The weighted average mortality rate for deer 1 to 11 years of age was 27%.

If the population were stable and the m_x data accurate, the summation of the $1_x m_x$ column of the life table should equal the number of deer, 219, in the M-1 age class. The 202 $1_x m_x$ total, however, indicates an 8% annual decrease. A simple extrapolation, assuming this level of annual decrease to be continuously sustained, would lead to the prediction that the Mesa Verde deer population would be reduced to somewhat less than half its initial size by the end of the study period. The census data obtained at the conclusion of the study appear to bear this out.

8. The Population Decline

Without much factual knowledge to stand in the way of speculation, the causative factors of the population decline have been much debated. In an effort to consolidate and evaluate that which was known, in 1976 a symposium was held in Logan, Utah entitled "Mule Deer Decline in the West." Many of the leading authorities attending the symposium expressed the view that poor nutrition was probably the basic underlying factor responsible for the population decline. Robinette (1976) suggested that poor nutrition caused the decline of several Great Basin deer herds. Dietz and Nagy (1976) commented that on many deer ranges in the West nutritious deciduous shrubs are decreasing in number and that the decrease probably was both directly and indirectly associated with the mule deer decline. The direct effect is starvation; the indirect effects are, among others, increased susceptibility to disease, low fawn production, and inability to withstand environmental stress. A similar conclusion was reached by Zwank (1976) who reported nutrition as being the primary limiting factor responsible for reduced ovulation rates, post-natal mortality, and winter fawn losses in mule deer populations. In a paper entitled "Potential Influence of Coyotes," Knowlton (1976) concluded that the nutritional health of deer is an important factor in many environmental effects, including predation.

At the time our studies were conducted the Mesa Verde habitat was found to be in generally good condition and without signs of active deterioration. Forage for deer was plentiful, with desirable plant species comprising the bulk of their diet. That the nutritional requirements of the deer were currently being well satisfied was attested to by their large size and excellent state of health. Obviously, however, times had not always been as good. Evidence remained of a recent history of severe range overutilization (i.e. "hedging" and low vigor of key browse species in some areas of the Park). We postulate that the deer of Mesa Verde, as elsewhere, increased their numbers steadily over a half century with the herd reaching record proportions during the 1950's. The effects of range overutilization began to be seen at this time. By the mid-1960's the deer range was judged to be in very poor condition (MVNP File Ref. N 1427). It seems likely that, with poor nutrition as the underlying cause, the deer population had already begun its decline. When we arrived in 1967 the habitat was in a recovery phase but the deer population was still declining. The reasons for this were not immediately obvious.

It is worth emphasizing that the deer population declined in much the same fashion at Mesa Verde as it did elsewhere, despite the fact that many of the factors variously implicated in the generalized decline were not operating in this evironment. The Mesa Verde deer population has not felt the impact of habitat reduction resulting from highway, housing or recreational projects or from increased agricultural or ranching activities. The herd was not hunted. Direct competition for forage between mule deer and other species is virtually nonexistent, at least on summer ranges within the Park. Weather conditions were not unusually severe during, or preceding, the population decline. Disease was apparently not a factor in the decline at Mesa Verde National Park.

The reproductive rate of Mesa Verde deer is known to have been high, therefore an accelerated mortality rate must have accounted for the population decline. Although deer carcasses were commonly found when the decline first began (probably resulting from the combined effects of poor nutrition and severe weather), examples of natural mortality among adult deer (Fig. 44) were only rarely encountered during the course of our study. A computer simulation study (Sheriff, unpublished) suggested that the Mesa Verde mule deer population was in a downward trend because of a high mortality rate in the fawn age class. Our data indicated the mortality rate among fawns to be exceptionally high. While the causes of this mortality were not determined, studies on other mule deer populations have attributed high fawn losses to predation (Trainer 1975, Ebert 1976, Austin et al. 1977). Evidence of predation on fawns was occasionally observed (Fig. 45), but no formal assessment was made of predator related mortality. The role of predators in the decline of the Mesa Verde herd must therefore remain somewhat speculative.

It is generally acknowledged that under nor-

Figure 44. Cause of death could not be determined in the few examples of natural mortality observed during the course of our study. Photo by G. Mierau.

Figure 45. Fawn injured in an encounter with a bobcat. Photo by W. Cooper.

mal circumstances predators do not limit the size of their prey population; rather, it is the size of the prey population that usually limits the size of their predator population. Several investigators who have specifically examined the effects of predation on mule deer have reported that predators did not control or limit the size of the deer herds studied. These authors, the states in which they conducted their research, and the species of predator studied are as follows: Longhurst et al. (1952), California, coyote; Smith and Le Count (1976), Arizona, coyote; Robinette et al. (1977), Nevada, coyote; Leopold et al. (1951), California, coyote and black bear; Richens (1967), Utah, mountain lion and coyote; and Shaw (1977), Arizona, mountain lion. Hornocker (1970), in his classic study of mountain lions in the Idaho Primitive Area, found that mule deer increased during the four years of his study despite a stable mountain lion population. There are, however, special circumstances under which predators may exert a profound infuence on their prey populations, at least on a temporary basis. This appears to have happened at Mesa Verde. We postulate that as the size of the deer population slowly increased to unprecedented levels so did the size of their predator population (predator control has never been practiced at Mesa Verde National Park). Predators did not exert an appreciable impact on the deer herd until, relatively suddenly, the deer population began to decline as a result of range overutilization. At least several years are required before a predator population can fully adjust to such a change and reestablish its former balance with its prey population. During this period, often referred to as the "predator lag period," the predator population exists in a state of relative overabundance and can further depress the already declining prey population by taking a greater than usual proportion of the fawn crop. We believe that our research was conducted during this period when "predator lag" was exerting a strong secondary effect in accentuating and prolonging the population decline.

If this hypothesis is correct, the outlook for the mule deer of Mesa Verde National Park is very optimistic. The population trend should reverse itself in the near future, if it has not already begun to do so. The deer are now in good physical condition and their range is well along the way toward recovery from previous damage. A population decline was needed and appears to have served its purpose.

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Appendices

Appendix I. Common and Scientific Names

PLANTS

Common Names	Scientific Names
Antelope Bitterbrush	*Purshia tridentata*
Arizona Wyethia	*Wyethia arizonica*
Arrowleaf Balsamroot	*Balsamorrhiza sagittata*
Aspen Peavine	*Lathyrus leucanthus*
Big Sagebrush	*Artemisia tridentata*
Black Greasewood	*Sarcobatus vermiculatus*
Black Sagebrush	*Artemisia nova*
Cliff Fendlerbush	*Fendlera rupicola*
Common Chokecherry	*Prunus virginiana*
Common Winterfat	*Eurotia lanata*
Creeping Barberry	*Mahonia repens*
Dwarf Rabbitbrush	*Chrysothamnus depressus*
Evening Primrose	*Oenothera* sp.
Fireweed Willow-herb	*Epilobium angustifolium*
Fourwing Saltbush	*Atriplex canescens*
Fragrant Sumac	*Rhus trilobata*
Gambel Oak	*Quercus gambelii*
Golden Corydalis	*Corydalis aurea*
Golden Currant	*Ribes aurem*
Gray Horsebrush	*Tetradymia canescens*
Green Ephedra	*Ephedra virides*
Hairy Goldenaster	*Chrysopsis villosa*
Louisiana Sagewort	*Artemisia ludoviciana*
Mountain Snowberry	*Symphoricarpos orcophilus*
Mutton Bluegrass	*Poa fendleriana*
Myrtle Pachistima	*Pachistima myrsinites*
Needle-and-Thread	*Stipa comata*
Oregon Fleabane	*Erigeron speciosus*
Pinyon Pine	*Pinus edulis*
Rocky Mountain Penstemon	*Penstemon strictus*
Rubber Rabbitbrush	*Chrysothamnus nauseosus*
Smooth Brome	*Bromus inermis*
Spindleroot Bluebells	*Mertensia fusiformis*
Squawapple	*Peraphyllum ramosissimum*
Sulfur Eriogonum	*Eriogonum umbellatum*
Tailcup Lupine	*Lupinus caudatus*
Tapertip Hawksbeard	*Crepis acuminata*
Tarragon Sagewort	*Artemisia drucunculus*
Toadflax Penstemon	*Penstemon linarioides*
True Mountainmahogany	*Cercocarpus montanus*
Utah Juniper	*Juniperus osteosperma*
Utah Serviceberry	*Amelanchier utahensis*
Vetch	*Astragalus scopulorum*
Western Wheatgrass	*Agropyron smithii*
Wayside Gromwell	*Lithospermum ruderdale*
White Prairie Aster	*Corydalis aurea*
Woods Rose	*Rosa woodsii*
Yellow Sweetclover	*Melilotus officionalis*
Yucca	*Yucca baccata*

ANIMALS

Common Names	Scientific Names
Black Bear	*Ursus americanus*
Bobcat	*Lynx rufus*
Coyote	*Canis latrans*
Elk	*Cervus elaphus*
Mountain Lion	*Felis concolor*
Mountain Sheep	*Ovis canadensis*
Mule Deer	*Odocoileus hemionus*

Appendix II-A: Average values of morphological measurements of mule deer at Mesa Verde National Park, Colorado.

		Age groups			
		1 to 6 months	7 months to 2 years	3 years and older	All ages
Sample size		**3**	**20**	**18**	**41**
Measurements (Males)					
Total body weight	(1)	30.9 ± 2.7*	60.6 ± 3.4	96.3 ± 4.5	74.1 ± 4.2
Total body length	(2)	134.9 ± 7.9	158.8 ± 2.5	186.4 ± 2.0	166.9 ± 2.8
Interorbital width	(2)	8.6 ± 0.3	10.2 ± 0.3	12.2 ± 2.0	10.9 ± 0.5
Neck circumference	(2)	34.8 ± 4.3	39.6 ± 1.8	62.7 ± 3.0	49.5 ± 2.5
Shoulder height	(2)	85.3 ± 1.5	99.6 ± 1.5	111.8 ± 1.0	103.9 ± 1.5
Heart girth	(2)	75.4 ± 4.8	88.4 ± 1.8	107.7 ± 1.8	96.0 ± 2.0
Hind foot length	(2)	43.9 ± 1.0	48.0 ± 0.5	50.6 ± 0.5	48.8 ± 0.5
Sample size		**5**	**28**	**30**	**63**
Measurements (Females)					
Total body weight		26.3 ± 3.4	49.9 ± 2.4	65.1 ± 1.2	55.2 ± 1.9
Total body length		121.7 ± 6.9	153.2 ± 2.0	164.6 ± 1.0	162.8 ± 1.8
Interorbital width		7.9 ± 0.5	9.1 ± 0.3	10.4 ± 0.07	9.4 ± 0.3
Neck circumference		28.5 ± 3.3	36.8 ± 1.0	40.4 ± 1.0	37.1 ± 1.0
Shoulder height		77.5 ± 4.0	95.5 ± 1.3	100.6 ± 0.8	96.5 ± 1.0
Heart girth		69.6 ± 5.0	84.8 ± 1.5	93.2 ± 1.3	87.6 ± 1.3
Hind foot length		38.9 ± 1.5	46.2 ± 0.5	48.0 ± 0.3	46.5 ± 0.5

(1) Weight expressed in kg.

(2) Length expressed in cm.

* Standard error of the mean.

Appendix II-B. Relationships between age; morphological and other measurements expressed by correlation coefficients from mule deer at Mesa Verde National Park, Colorado.

	Correlation Coefficients*	
	Males	Females
Sample size	**43**	**61**
Measurements		
Age vs. Weight	0.83	0.73
Age vs. Total body length	0.80	0.71
Age vs. Interorbital width	0.82	0.57
Age vs. Neck circumference	0.71	0.24
Age vs. Shoulder height	0.78	0.64
Age vs. Heart girth	0.86	0.66
Age vs. Hind foot length	0.58	0.65
Age vs. Adrenal weight	0.69	0.51
Age vs. Kidney fat percentage	0.24	0.01
Age vs. Depth of rump fat	0.40	0.27
Weight vs. Total body length	0.84	0.87
Weight vs. Shoulder height	0.88	0.81
Weight vs. Heart girth	0.93	0.87
Weight vs. Hind foot length	0.68	0.84
Weight vs. Adrenal weight	0.52	0.45
Weight vs. Kidney fat percentage	0.56	0.22
Weight vs. Depth of rump fat	0.73	0.40
Weight vs. Antler beam diameter	0.83	—
Length vs. Heart girth	0.87	0.82
Length vs. Shoulder height	0.87	0.88
Length vs. Hind foot length	0.83	0.92
Length vs. Kidney fat percentage	0.34	0.05
Heart girth vs. Hind foot length	0.73	0.81
Heart girth vs. Kidney fat percentage	0.51	0.38
Heart girth vs. Depth of rump fat	0.66	0.50
Heart girth vs. Adrenal weight	0.64	0.38
Neck circumference vs. Testes weight	0.71	—
Neck circumference vs. Antler beam diameter	0.71	—
Antler length vs. Testes weight	0.86	—
Antler beam diameter vs. Testes weight	0.88	—

**An index measuring the closeness of fit of the n observed points to the estimated line of regression. The larger value; the closer the points will fit the line, and the closer relationship between the two variables.*

Appendix II-C. Hematological values, from male mule deer at Mesa Verde National Park, expressed as averages for age classes.

		Age Classes			
		1 to 6 Months	**7 months to 2 years**	**3 years and older**	**All male deer**
Sample size		**3**	**20**	**18**	**41**
Blood component					
Glucose	(1)	120.0 ± 7.5*	118.0 ± 11.2	146.0 ± 17.4	131.0 ± 9.5
Cholesterol	(2)	62.0 ± 1.3	60.0 ± 3.0	53.0 ± 4.2	57.0 ± 2.4
Serum total protein	(3)	8.6 ± 0.5	8.8 ± 0.1	9.1 ± 0.1	8.9 ± 0.1
Hemoglobin	(4)	17.3 ± 2.7	18.3 ± 0.8	19.1 ± 0.5	18.6 ± 0.5
Hematocrit	(5)	42.5 ± 4.7	49.1 ± 2.0	47.1 ± 1.6	47.2 ± 1.2
MCHC	(5)	40.0 ± 1.8	37.5 ± 0.9	40.9 ± 0.9	39.2 ± 0.6
Sedimentation rate	(6)	3.0 ± 0.0	5.0 ± 1.2	6.5 ± 1.4	5.7 ± 0.9
Neutrophils		20.0 ± 7.3	28.0 ± 2.7	42.0 ± 4.7	34.0 ± 2.7
Lymphocytes		69.0 ± 9.5	53.0 ± 3.1	35.0 ± 4.2	47.0 ± 3.0
Monocytes		6.0 ± 1.5	4.0 ± 0.6	4.0 ± 0.7	5.0 ± 0.4
Eosinphils		4.0 ± 2.0	12.0 ± 1.5	17.0 ± 3.0	14.0 ± 1.6
Basophils		1.0 ± 1.0	1.0 ± 0.2	1.0 ± 0.2	1.0 ± 0.1

* Standard error of the mean.
(1) Values expressed in mg/100ml of blood (Folin-Wu method).
(2) Values expressed in mg/100ml of serum (Bloor's method).
(3) Values expressed in g/100ml of serum (Refractometer method).
(4) Values expressed in g/100ml of blood (Cyanmethemoglobin method).
(5) Values expressed as a percent (Calculation).
(6) Values expressed in mm/hour (Westergren method).
(7) Values expressed as percent of total leukocytes (Wright's stain, 100 cell count differential).

Appendix II-D. Hematological values, from female mule deer at Mesa Verde National Park, expressed as averages for age classes.

		Age Classes			
		1 to 6 Months	7 months to 2 years	3 years and older	All female deer
Sample size		**5**	**28**	**30**	**63**
Blood component					
Glucose	(1)	169.0 ± 37.5*	143.0 ± 7.9	138.0 ± 6.4	143.0 ± 5.4
Cholesterol	(2)	71.0 ± 8.6	60.0 ± 3.0	58.0 ± 2.7	60.0 ± 2.0
Serum total protein	(3)	8.6 ± 0.3	8.7 ± 0.1	8.9 ± 0.1	8.8 ± 0.1
Hemoglobin	(4)	18.5 ± 1.0	18.9 ± 0.7	19.3 ± 0.4	19.0 ± 0.4
Hematocrit	(5)	46.9 ± 2.8	45.9 ± 1.4	47.9 ± 0.8	47.0 ± 0.8
MCHC	(5)	39.6 ± 1.7	40.5 ± 1.3	40.0 ± 0.6	40.3 ± 0.6
Sedimentation rate	(6)	1.0 ± 0.0	3.6 ± 0.7	3.2 ± 0.6	3.3 ± 0.4
Neutrophils	(5)	30.0 ± 4.1	23.0 ± 2.0	37.0 ± 2.6	30.0 ± 1.8
Lymphocytes	(5)	59.0 ± 3.0	55.0 ± 3.5	36.0 ± 2.6	47.0 ± 2.3
Monocytes	(5)	5.0 ± 1.0	4.0 ± 0.6	4.0 ± 0.4	4.0 ± 0.3
Eosinophils	(5)	5.0 ± 1.7	18.0 ± 2.7	23.0 ± 3.1	19.0 ± 2.0
Basophils	(5)	1.0 ± 0.5	1.0 ± 0.1	1.0 ± 0.2	1.0 ± 0.1

* Standard error of the mean.

(1) Values expressed in mg/100ml of blood.

(2) Values expressed in mg/100ml of serum.

(3) Values expressed in g/100ml of serum.

(4) Values expressed in g/100ml of blood.

(5) Values expressed as a percent.

(6) Values expressed in mm/hour.

Appendix II-E. Seasonal differences of levels of blood glucose, serum cholersterol, and serum total protein from mule deer at Mesa Verde National Park, Colorado.

		Seasons			
		Winter (1)	Spring (2)	Summer (3)	Fall (4)
Sample size		**4**	**9**	**15**	**13**
Component (Males)					
Glucose	(5)	126.3 ± 28.4*	102.6 ± 9.3	146.0 ± 14.6	133.8 ± 22.1
Cholesterol	(6)	64.5 ± 7.9	50.7 ± 2.1	60.0 ± 3.8	55.2 ± 5.2
Serum protein	(7)	9.1 ± 0.2	9.0 ± 0.1	8.6 ± 0.1	9.2 ± 0.2
Sample size		**18**	**15**	**19**	**11**
Component (Females)					
Glucose		149.1 ± 10.8	141.8 ± 10.7	135.3 ± 7.6	149.7 ± 17.5
Cholesterol		62.6 ± 4.0	56.5 ± 3.1	54.7 ± 3.6	67.5 ± 4.8
Serum protein		8.4 ± 0.2	9.1 ± 0.1	8.7 ± 0.1	9.2 ± 0.1

(1) Winter—December 21 to March 20.
(2) Spring—March 21 to June 20.
(3) Summer—June 21 to September 20.
(4) Fall—September 21 to December 20.
* Standard error of the mean.
(5) Values expressed in mg/100ml of blood.
(6) Values expressed in mg/100ml of serum.
(7) Values expressed in g/100ml of serum.

Appendix II-F. Fetal blood values from four mule deer at Mesa Verde National Park, Colorado.

Component	Value
Glucose	237.9 mg/100 ml of blood
Cholesterol	63.5 mg/100 ml of serum
Serum Total Protein	6.4 g/100 ml of blood
Hemoglobin	10.9 g/100 ml of blood
Hematocrit	33 %
MCHC	34.5 %
Neutrophils	77 %
Lymphocytes	11 %
Monocytes	5 %
Eosinophils	7 %
Basophils	1 %

Appendix II-G. Body temperatures of mule deer at Mesa Verde National Park (Degrees F).

Sex	Fawns	One year olds	One and two year olds	Three year olds and older
Females	101.9 ± 0.3*	101.3 ± 0.2		100.9 ± 0.2
Males	101.6 ± 0.2		101.2 ± 0.2	100.6 ± 0.2

*Standard error of the mean.

Appendix III-A. Ovarian measurements and fetal counts.

Date of Collection	Age of doe (yrs)	Size of corpora albicantia (mm)	Size of corpora lutea (mm)	Number of fetuses
7/1/67	8	3		
7/12/67	2	5		
7/13/67	6	4,4		
"	10	5,5		
7/20/67	1			
8/16/67	1			
"	8			
"	1	3,3		
"	2	3,2,2		
8/17/67	4	2,3		
"	3	2,3,2		
9/8/67	5	3		
"	2	3,2		
"	1			
"	3	2,2		
10/20/67	3	2,2,2		
"	3	2,2		
"	1			
11/23/67	4	2,2		
"	7	2		
"	2	2,2		
11/23/67	4	2,1,2		
"	fawn			
12/20/67	9	3,2	9,9	
1/13/68	4	2,1	8,7,8	2
3/21/68	4	quit reading	7,8	2
"	4		11	1
"	fawn			
"	2		9,9	2
"	1		9	1
"	5		8,9	2
3/22/68	9		9,4,9	2
"	fawn			
"	fawn			
"	fawn			
"	2		10,9,8	2
"	3		10,10	2
"	9		9,5,9	2
"	fawn			
4/20/68	2		10,10	2
"	6		9,9,10	2
5/17/68	2		12	1
"	3		11,11	2
"	4		9,9	2
"	2		10	1
"	5		9,9,9	2
5/18/68	fawn			
"	3		10,10	2
"	2		10,11	2
"	1		11	1
"	1		11	1
"	2		11	1
"	4		10,10,8	2
"	3		10,11	2
6/26/68	fawn			
"	"			
"	1	5		
"	2		9,10	2
6/27/68	4		11,10	2
7/16/68	4	4,3		
"	2	3		

Appendix III-A (continued).

Date Collection	Age of doe (yrs)	Size of corpora albicantia (mm)	Size of corpora lutea (mm)	Number of fetuses
7/16/68	1			
"	3	4		
7/17/68	1			
8/9/68	5	2,3		
"	1			
"	fawn			
8/10/68	1			
"	3	3,3		
"	7	3,3		
9/9/68	1			
"	4	2,2		
"	3	2,2		
10/12/68	1			
"	4	2,3		
"	1			
11/19/68	7	2,2,2		
11/23/68	9	1,2	5,5,6	
"	9	2,1,1,2,1		
"	fawn			
12/4/68	4	1	5,4,3,5	
12/17/68	3		9,8	
"	3	1,1	9,7	
"	1		3,9	
1/15/69	1		9,10	
"	6	2,2	9,9,10	2
"	3	quit reading	10,10	2
"	1			
5/10/69	10		9,9	1
"	9		9,9	2
"	5		10	1

Appendix III-B. Fetal measurements.

Collection date of mother	Weight (gm) L. horn	Weight (gm) R. horn	Forehead-rump length (mm) L. horn	Forehead-rump length (mm) R. horn	Hindfoot length (mm) L. horn	Hindfoot length (mm) R. horn	Ear length (mm) L. horn	Ear length (mm) R. horn	Sex L. horn	Sex R. horn
1/13/68			26	27						
3/21/68	300	310	229	231	79	81			F	F
″		88		145		46				F
″	258	244	211	208	71	76			M	F
″	323		224		74				F	
″	326	337	231	231	79	84			F	F
3/22/68	375	405	234	236	84	84			F	M
″	303	305	206	198	74	74			F	M
″	450	459	244	246	94	94			F	F
″	524	467	251	249	97	94			M	F
4/20/68	875	870	305	304	131	126	43	41	F	F
″	1283	1096	341	333	153	141	49	48	M	M
5/17/68	1730		387		181		74		F	
″	1616	1701	370	366	168	169	68	68	M	M
″	2509	2948	406	419	209	224	88	90	M	F
″		2183		394		194		76		F
″	1871	2154	387	408	193	200	83	81	F	F
5/18/68	1842	1673	398	392	182	182	78	75	F	F
″	1332	1219	340	343	157	153	60	61	F	F
″		2353		415		198		&&		F
″		2126		396		194		67		M
″		2831		407		198		77		M
″	1616	1786	368	370	176	185	76	78	F	F
5/18/68	2239	2154	414	413	210	198	84	82	F	M
6/26/68	3964	4134	499	494	264	265	111	111	F	M
6/27/68	4389	3681	496	490	260	262	118	101	M	F
1/15/69	1	1	22	22						
″	1	1	20	20						
5/10/69				364		167		61		M
″			372	378	176	181	75	77	F	F
″			343		149		62		F	

Appendix IV. Succinylcholine chloride dosages for Mesa Verde deer (mg./lb. body weight).[a]

Sex	Age	Number effective	Ineffective	Effective				Fatal
			1	2	3	4	5	6
F	fawn	6	—	—	0.130 (0.114-0.133)	—	—	0.100
F	1	14	0.108 (0.094-0.133)	—	0.121 (0.096-0.167)	0.123 (0.115-0.130)	0.138 (0.120-0.150)	0.129 (0.125-0.136)
F	adult	54	0.100 (0.090-0.122)	0.100 (0.086-0.115)	0.097 (0.064-0.125)	0.103 (0.075-0.115)	0.112 (0.103-0.125)	0.110 (0.103-0.133)
M	fawn	6	—	—	0.140 (0.114-0.160)	—	—	0.125
M	1	15	—	—	0.101 (0.067-0.125)	0.096 (0.067-0.125)	0.125	0.214
M	fawn	27	0.074 (0.058-0.100)	0.076 (0.065-0.077)	0.076 (0.054-0.093)	0.081 (0.052-0.107)	0.080	0.082 (0.041-0.119)

[a]Stages of immobilization and their characteristics:

1 Loss of coordination; slight stumbling.

2 Incomplete immobilization of limbs; manual restraint necessary.

3 Complete immobilization of limbs but jaw and neck muscles unaffected; no excess salivation or respiratory difficulty.

4 Complete immobilization of limbs, jaw and neck; modest respiratory difficulty not requiring artificial respiration.

5 Severe respiratory difficulty; artificial respiration required.

6 Cardiac arrest; fatal.

Appendix V. Soil stability condition class (Forest Service 1968).

	Rating
Soil movement slight or none. Soil movement may be difficult to recognize. There may be evidence of past accelerated erosion, but is now stabilized; plant and litter cover appear effective in protecting the soil; plant pedestals are few or sloping sided. Rills, alluvial deposits, and gullies are absent or completely healed. On sloping lands some litter may be dammed against vegetation, forming miniature alluvial fans; trampling displacement is slight; rodent activity is normal or below. Usually 65 or more hits on ground cover and rocks .... (Deming "two-phase" soil condition score over 70)	H(high)
Soil movement moderate. Plant and litter cover only partially protecting the soil. Some bunchgrass in openings pedestaled; some pedestals have steep sides; erosion pavement if forming in openings. On sloping land, occasional rills and alluvial deposits are present. Gullies, if present, are not steep sided and raw; trampling displacement and compaction are noticeable, but not excessive; runoff is murky. Usually 35-65 hits on ground cover and rocks .... (Deming "two-phase" soil condition score 31-70)	M(medium)
Soil movement advanced. Herbaceous plant cover and litter are ineffective in preventing soil movement. Openings between plants are almost completely bare with well-formed erosion pavement; pedestals beneath sagebrush, and plant pedestals in openings are 4+ inches higher than the surrounding bare soil. Rills are common sloping land; gullies, if present, have steep, raw sides; trampling displacement and compaction are common; rodent activity may be excessive; runoff is muddy. Usually less than 35 hits on ground cover .... (Deming "two-phase" soil condition score 0-30)	L(low)

Appendix VI. Browse condition class scorecard (Forest Service 1968).

To use scorecard: Apply basic data (on composition, density and vigor) from condition transect record to scorecard. Start at highest class in each category and work down until data fits a condition class description.

Example (for composition only): A shrub stand has 31% bitterbrush (D), 48% sage (I), 13% skunkbrush (LD), 8% snowberry (LD). It fails to fit "High", (too few D's.). It fits "Medium" (well over 50% D's. and I's, well over 15% D's.).

COMPOSITION

Desirable and intermediate species (must be two or more) making up 75% or more of the composition, with desirables at least 45% of the composition.	H(high)
Desirable and intermediate species making up 50% or more of the composition with desirables at least 15% of the composition.	M(medium)
Desirable and intermediate species making up less than 50% of the composition, or desirables less than 15%.	L(low)

DENSITY

66% plus	V(very dense)
36% to 65%	
16% to 35%	M(medium)
15% minus	L(low)

VIGOR

Hedging on key species mostly light or moderate with less than 16% of plants heavily hedged, <u>and</u> decadent minus young *less than 16% of total number of plants.			H(high)
Hedging on key species mostly moderate, not more than 35% heavily hedged;	and	Decadent minus young not more than 35%	M(medium)
More than 35% of plants of key species heavily hedged,	or	Decadent minus young more than 35%	L(low)

*Subtract the number of "young" plants from the number of "decadents". The principle is that if young plants are replacing decadents plants, the condition is satisfactory. If there is an excess of decadents, condition is unsatisfactory. Compute separately for each key species.

Appendix VII. Age and hedging classes.

Age Classes

Young—Established seedlings and young plants. Elongate growth form, simple branching: usually less than six years old, and basal stem diameter not over ¼ inch.

Mature—Distinguished by heavier, often gnarled stems, complex branching, rounded growth form. Crown made up of more than three-fourths living wood.

Decadent—Crown made up of more than one-fourth dead wood.

Hedging Classes

Light—Little or no hedging, indicating light use in the past three or four years. Growth tends to be linear.

Moderate—Use past three or four years causing much development of lateral branching and more complex growth form.

Heavily Hedged—Heavy use in past three or four years causing a very much "broomed" or "clubbed" appearance.