MULE DEER DECLINE IN THE WEST
A SYMPOSIUM

APRIL 1976

utah state university
college of natural resources
utah agricultural experiment station
logan, utah 84322
MULE DEER DECLINE IN THE WEST

A SYMPOSIUM

Editors and Symposium Directors:
Gar W. Workman
Jessop B. Low

Sponsored by:
College of Natural Resources, Utah State University
Natural Resources Alumni Association, Utah State University
Extension Services, Utah State University
Utah Chapter of The Wildlife Society
Bonneville Chapter of the American Fisheries Society
Intermountain Section of the Society of American Foresters
Utah Chapter of the Soil Conservation Society of America

April 1976
ACKNOWLEDGMENTS

The session chairmen for this symposium were: Norman V. Hancock, Chief-Game Management, Utah Division of Wildlife Resources; Paul W. Shields, Utah Regional Wildlife Biologist, U. S. Forest Service; Ronald S. Trogstad, Utah Wildlife Management Biologist, Bureau of Land Management.

The following secretaries also assisted in preparation of the program, typing, and providing assistance to speakers and guests: Karen Mitchell, Lonna Beth Bowles, and Marcie Egbert.
FOREWORD

Mule deer numbers in the Western United States experienced a general decline in numbers from the early 1950's until the present mid-1970's. At least a part of this decline was a result of a planned reduction by game managers to adjust deer numbers to the carrying capacity of overused deer winter ranges. In addition to the planned reduction of deer numbers, it became apparent by 1970 that the reduction in number of deer on western ranges was the result of something beyond the planned reduction programs. The cause, or causes, for the reduction was not clearly understood or even defined in many cases. Such influences as predation, competition, weather, disease, habitat changes, and nutrition were suspected causes. Perhaps the main cause of the decline has not been discussed and will need to wait for further research.

This symposium was designed to help natural resource managers become better informed about the reduction and the various reasons for the mule deer decline in the West. The speakers at this conference are considered to be authorities on the various aspects of mule deer populations. Subsequently, the information presented in these proceedings represents some of the important current knowledge pertaining to present-day mule deer populations, research, and management.

Gar W. Workman and Jessop B. Low
Table of Contents

<table>
<thead>
<tr>
<th>Acknowledgments</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foreword</td>
<td>11</td>
</tr>
<tr>
<td>Introduction to Conference</td>
<td>1</td>
</tr>
<tr>
<td>A Historical Account and Present Status of the Mule Deer in the West</td>
<td>3</td>
</tr>
<tr>
<td>Mule Deer Habitat Changes Resulting from Livestock Practices</td>
<td>21</td>
</tr>
<tr>
<td>Alteration of Mule Deer Habitat by Wildfire, Logging, Highways, Agriculture, and Housing Developments</td>
<td>37</td>
</tr>
<tr>
<td>Interspecific Competition Between Mule Deer, Other Game Animals, and Livestock</td>
<td>49</td>
</tr>
<tr>
<td>Deer Range Improvement and Mule Deer Management</td>
<td>55</td>
</tr>
<tr>
<td>An Overview of Big Game Management</td>
<td>67</td>
</tr>
<tr>
<td>Mule Deer Nutrition and Plant Utilization</td>
<td>71</td>
</tr>
<tr>
<td>Mule Deer Productivity--Past and Present</td>
<td>79</td>
</tr>
<tr>
<td>Regulations and the Mule Deer Harvest--Political and Biological Management</td>
<td>87</td>
</tr>
<tr>
<td>Reliability of Mule Deer Population Measurements</td>
<td>93</td>
</tr>
<tr>
<td>Mule Deer Management Myths and the Mule Deer Population Decline</td>
<td>99</td>
</tr>
<tr>
<td>The Possible Influences of the Mountain Lion on Mule Deer Populations</td>
<td>107</td>
</tr>
<tr>
<td>Potential Influence of Coyotes on Mule Deer Populations</td>
<td>111</td>
</tr>
<tr>
<td>Mule Deer Disease Problems</td>
<td>119</td>
</tr>
<tr>
<td>Mule Deer Mortality from Various Causes</td>
<td>125</td>
</tr>
<tr>
<td>Probable Causes of the Recent Decline of Mule Deer in the Western U.S.--A Summary</td>
<td>129</td>
</tr>
</tbody>
</table>
Since pioneer days, the Western mule deer has been of great value and concern to the populace. Earlier settlers were alarmed about scarcity of the animals. At the turn of the century, grandfather and father talked for days about the event if by chance they saw a deer.

Things changed, however, and populations of deer increased. In the late 1940's and early 1950's landowners and livestock people complained bitterly about deer on their land or on federal lands. At that time, game managers recognized the need for reduction of the size of deer herds. A program to reduce deer populations was generally carried on until the middle 1960's. However, hunters generally felt that the game departments were going too far. Unfortunately, we failed to persuade many people this was a calculated management plan, and as a result, many vocal critics emerged.

In my opinion, since the early 1970's there has been a general decline in the population of the Western mule deer.

Big game technicians in the Western Association of State Game and Fish Commissioners held two meetings, one in 1964 and the other in 1968, to discuss the general decline of some of the desert herds in the Southwest.

In 1970, an annual western mule deer workshop was inaugurated because of a decline or fluctuation in most mule deer herds throughout the West. During the first few workshops, emphasis was on productivity and fawn survival. Technicians now recognize that there is probably no single factor to which a decline can be attributed.

Erratic fawn production occurred in the desert herds of the West in the late 1960's. It was the early 1970's when more significant, widespread, and abrupt drops in fawn production occurred throughout most of the Western States. General causes for the decline in Utah were noted. Undoubtedly, most of these factors were operative in other Western States.

Following are some of the causes of the decline in Utah deer herd numbers. They are arranged in order of their importance.

1) The winter loss of 1972-1973. This is the principal factor for a statewide decline in Utah.

2) Does were in poor shape in the spring of 1973 following this bad winter. As a result, fawn production was down. This varied considerably from unit to unit.

3) In the eastern and south-central parts of the state, 1972 fawn crops were down as a result of drought conditions in 1971-1972.


5) The exceptionally long, cold spring of 1975 extended into June and caused significant fawn losses during the peak of the fawn drop in southern and south-central Utah.

6) Another cause is the predator. Principal predators are dogs (domestic and feral), coyotes, and mountain lions.

7) Other general factors are operating also. These are highway mortality, disease, accidents, and poaching. Undoubtedly, there are other things involved which at this time we do not understand.

8) Finally, there is another concern which in importance would be well up on this list, but, for the sake of treatment only, I have reserved for the last. This is habitat loss. This loss is a slow, creeping activity which sometimes is so gradual that we do not recognize it until we begin to see its combined cumulative effects.

Chief habitat losses that we see are caused by urbanization, land speculation, the second-home movement, and adverse plant succession away from browse species. This latter has been intensified by the total elimination of livestock grazing on many deer winter ranges. The philosophical basis for eliminating livestock grazing emerged from a point of view that management of the watershed should be carried out with the ultimate goal of establishing and maintaining a climax vegetation of grasses.

Prior to the Smokey-the-Bear syndrome and modern fire fighting techniques, nature and the Indian provided for a diversification of a climax vegetation by fire. Until very recent times, our colonization further extended several vegetative stages through widespread use of domestic livestock. Unfortunately, now there is developing an antagonistic attitude toward livestock grazing on public lands.

It is necessary to have this grazing as a legitimate range management tool to maintain vegetative types for multiple uses. We should be thinking of it in terms of proper livestock grazing and correct season of use.

In the course of the next day and a half, we are going to have the opportunity of exploring some of these factors and undoubtedly others. By tomorrow afternoon, I hope we are able to see where they fit into the overall status of our past and present mule deer herds throughout the West.

For the peace of mind of the directors of the wildlife agencies of the Western States, an optimistic future is predicated—we are going to look at the future, not just the past and present.
A Historical Account and Present Status

of the Mule Deer in the West

Odell Julander
Professor Emeritus
Brigham Young University, Provo, Utah 84601

Jessop B. Low
Professor
Department of Wildlife Science
Utah State University, Logan, Utah 84322

Abstract

The decline of mule deer (Odocoileus hemionus) has been documented by most western states during the past several years. In the main, the decline has been attributed to a number of causes, principally, however, to overharvesting, range reduction, habitat change from livestock and deer pressure, poor deer reproduction, urbanization, fire control, and management efforts to reduce herds nearer range carrying capacity. The history of the mule deer herds noted scarcity during prepioneer days and the early pioneer settlement period to a large buildup of herds during the second quarter of the twentieth century. The buildup was concurrent with conversion of ranges from grass to browse, control of predators and protection of herds through limited and manipulated harvests. Large herds in the late 1930s through the 1960s were reduced through control permits above the regular harvest. Documented data on a number of individual herds in Utah and Arizona indicate a general decline in numbers as a result of management to bring deer numbers within carrying capacity of the range.

The decline of the mule deer in the West has been of major concern to most state conservation agencies during recent years. Many states have documented this decline in population and harvest trends, as well as hunter success. Following periods of relatively few deer in prepioneer days, then depletion of the populations by the early pioneers and the increasing numbers in the first half of the century, the herds have now decreased and appear to be declining even further.

The declining populations of mule deer was recognized and documented by many workers, as pointed out by Longhurst et al. (1976):

For that matter, the decline of deer has by no means been confined to California, but seems to have been a general phenomenon in a number of western states. By 1964 a number of states recognized that Rocky Mountain mule deer populations had started to decline (Macgregor, 1964) - California; (Mohler, 1964) - Idaho; (McKean and Luman, 1964) - Oregon; (Greenly and Humphreys, 1964) - Nevada; and (Hancock, 1964) - Utah.

3
We acknowledge the fine response from all fish and game organizations in the western states regarding the history of mule deer in their state. We must, of course, in the interest of time, paint with a broad brush the history and present status of mule deer in the West. To do otherwise would entail too much space and time. Since we are most acquainted with Utah, our emphasis will undoubtedly be on the history of the deer in this state. However, the same general picture prevails in most western states.

Relative Numbers Prior to Early Pioneer Days

Relatively little is known concerning the true numbers of mule deer prior to the early pioneers. Trappers and early explorers rarely reported deer, except incident to other observations.

Father Escalante’s party in September and October, 1776, explored the Utah area and other western territories. Although Escalante traveled through and along the borders of some of Utah’s best present-day big game hunting grounds, he made no mention of either deer or elk, both of which he noted in southwestern Colorado. Further, Escalante reported that while traveling south from Utah Lake the party ran out of food and experienced great difficulty in obtaining grain, seeds and nuts from the Indians and found it necessary to kill several of their horses for food. In other areas they reportedly killed buffalo, traded with Indians for bighorn sheep meat, but made no mention of deer.

In the 1820-1834 period of exploration and intensive fur trapping, stalwart mountain men, such as J.S. Smith, 1826-1827; W.A. Ferris, 1830-1834; J.R. Walker, 1833-1834; and others, recorded in diaries and journals only incidental mule deer, although buffalo, antelope, elk, and beaver were regularly recorded.

Osborn Russell recorded mule deer in his diary during the period 1834-1843, while trapping beaver in northern Utah in 1837, he speaks of having a Christmas party with his family and friends in which “The next dish was similar to the first (elk) beefed up with boiled deer meat (or as the whites call it, venison, a term not used in the mountains.).” (Kalnes, 1955, p. 115). Later, in what was probably Utah County, he speaks of the Indians: “If a Sitaw has 8 or 10 good horses, a rifle, and ammunition, he is contented if he fetches a deer at night from the hunt. . .” (Kalnes, 1955, p. 122).

Essentially the same story is told in all western states in pre-pioneer days—that of relatively few deer, apparently in harmony with their environment and habitat. Montana records that:

Mule deer (Odocoileus hemionus) have been an important big game animal in Montana as far back as records exist. The popularity of this native deer among the Indians might be ascribed to the fact the meat, fresh or cured, is very palatable; the hide was used to make buckskin, and even the bones and antlers made useful implements.

The early explorers, fur trappers, and settlers also used and depended on the mule deer as a source of food and clothing. The hides were even used as legal tender (50¢ per hide) in parts of Montana just before the turn of the century.

Lewis and Clark can be credited with writing the first detailed account of mule deer habitat requirements. There is evidence that Lewis coined the name, “Mule Deer,” when he stated, “We have rarely found the mule deer in any except rough country. They prefer the open grounds and are seldom found in woodlands or river bottom.” (Sigma, 1971)

Practically all states with mule deer have records, diaries, and histories pointing out the scarcity of deer in the early pre-pioneer days, but indicating that deer were known to occur in about all the states now having mule deer. Deer was not the choice food of the beaver trappers or explorers, who chose bighorn sheep and elk when possible. Deer was, however, taken when possible as food by explorers and trappers alike. The Lewis and Clark expedition of the early 1800’s detailed the wildlife, including deer, in the northeast. Such trappers and explorers as Peter Skene Ogden, Townsend, and Alexander Ross also recorded in their journals about the relative scarcity of deer in comparison to other wildlife.

Depletion of Mule Deer in Pioneer Days

When the pioneers entered the Great Salt Lake Valley on July 24, 1847, big game animals were scarce, as reported by the trappers and explorers. The hearty pioneers suffered acute food shortages during the first winter. Indians and whites alike vigorously hunted the few deer for their meat and hides.

Captain Stansbury reported that during the winter and spring of 1847-1848, Mormon pioneers in the Great Salt Lake Valley were forced to dig roots and tear hides from their roofs in order to survive. He frequently mentioned that game was scarce this first winter in the valley. Thus, although we have no historical record upon which numerical estimates of deer numbers in Utah can be based at the time of the first settlements, it is apparent that there were relatively few deer.

During the period between the advent of the pioneers and the end of the century, severe depletion of Utah’s grasslands occurred as a result of excessive grazing by domestic livestock gave rise to the spread and abundance of browse species, many of which were choice deer foods, which set the stage for the deer population booms to come not too many years later. The unrestricted hunting and unrestricted grazing by domestic stock over the entire state had, by the turn of the century, depleted much of the native forage and big game numbers to the extent that action was necessary to save both of these resources (Utah Biennial Report, 1946).

One old timer that I interviewed about 1950 recalls that in about 1900, he, as a youth living near the hills directly above Providence in Cache Valley, Utah, found deer tracks scarce. On one occasion, he reportedly followed a deer track for four consecutive
days before getting a fleeting glimpse of the animal.
(Low, personal files).

The significant events and conditions affecting Utah's mule deer populations from early historic times to the present are briefly given in Table 1 and further illustrated in Figure 1.

**Other States**

Populations of mule deer in most, if not all, western states suffered at the hands of the pioneers and early settlers. No game laws or thought of protection made the mule deer, as well as other wildlife, targets of the pioneers for articles of food and clothing. A few excerpts from some of the western states illustrate, although incompletely given, the mule deer situation in pioneer days:

**Arizona**

No records are available, but from some pioneer documents there was an indication that deer populations were very low. Many of the pioneers had to depend on rabbits, etc. for protein. (Rusco, 1976, personal communication).

**California**

There were fewer mule deer in early pioneer days than at present. Herds were depleted primarily during the gold rush by hunting for hides and meat. (Macgregor, 1976, personal communication).

**Idaho**

The Lewis and Clark expedition of the early 1800's reports deer as well as other wild animals:

"On June 3, 1806, two members of their party killed five deer."

Peter Skene Ogden reports:

When the party finally struggled through deep snow over the summit to camp on the Birch Creek side, they wrote of many buffalo, elk, deer, and goats in the country. Ogden said, "wretched country, we had hopes of finding deer, but we all know (now) that there are none to be seen from River Malado (Magic area) to Burnt River."

Townsend's narrative reported:

"Later, as the party moved across the desert to Lost River and over to Big Wood River, they were troubled by lack of game and said they only killed three buffalo in several weeks, but did find deer in good numbers on the Malade (Big Wood) River."

The Alexander Ross Journals:

The Big Wood River area was 'a beaver hunter's paradise.' As the party moved along the lower Boise River in late June, they killed 17 deer and 6 elk. (Edison, 1963).

**Nevada**

Deer were considered abundant in Nevada only since the 1930's. Scattered reports of early explorers and hunters mention few or no deer. (McColm, 1976).

**New Mexico**

In 1880, the first conservation law was passed in New Mexico because of the continued decline in game numbers. Two years later, in 1899, a bag limit of one buck deer was imposed by the Territorial Legislature. Because the public refused to accept the law, decimation of game continued; therefore, the territorial lawmakers placed a five-year closure on the hunting of deer, elk, antelope, and mountain sheep. In 1903, the deer season was again opened for deer. The state's deer herd continued its apparent decline, reaching its lowest ebb about 1924 when the population for all deer on national forests within the state was estimated to be 19,488. By 1926, the statewide deer population was estimated at 41,000. (Stewart, 1967, p. 42.)

**Montana**

Population peaks reportedly occurred in the late 1880's, the early 1900's, and the late 1920's in southeastern Montana. The reported peak of the late 1920's was of small magnitude and was preceded by a period when many residents considered the deer extinct. (Egan, 1971).

**Oregon**

1899 - 1912 Scarce deer populations. Deer generally scarce, but little hunting pressure. Lack of roads and transportation limited harvest and there was little hunting pressure. 1913-1922. Deer continued to be scarce. (Anonymous 1971, p. 1.)

**Washington**

No early records, but mule were uncommon until about 1935. (L. D. Parsons, 1976, personal communication.)

**Wyoming**

Few deer in pioneer days. "In the early 1800's when the white man first entered what is now Wyoming, he found wildlife in abundance, especially bison, antelope, elk, and bighorn sheep. Deer were also abundant, but apparently not in such noticeable numbers as the other animals. Populations of big game animals reached a low about the turn of the century." (Corsi, Wyoming Wildlife, Aug. 1974, p. 3.)

**Build Up of the Herds and Management Measures**

**Utah**

In recognition of the scarcity of mule deer, the Utah legislature ended the "free ride" for hunters in Utah in 1908. The season on deer then was closed and remained closed for five years. In 1913, the legislature declared a season to take buck deer only with antlers 5 inches or longer. The kill of deer during the first buck season (1914) was recorded when "approximately 600 of these magnificent
animals were taken, and these mostly in the eastern parts of the state." (Utah Biennial Report, 1946).

This indeed was the turning point, as deer continued to increase in numbers each year from 1913. Mule deer populations in Utah were given from time to time from the earliest estimate of 8,500 in 1916, to and including the estimated height of the population in the 1945-50 period at about 375,000. These estimated figures by the western state conservation departments were compiled by the U.S. Fish and Wildlife Service (1937 to 1970) in a series of wildlife leaflets issued each year (Table 2). No claim was made by any state or the Service for the accuracy of the figures. Most states stopped publishing estimated populations in the 1940's because of the inaccuracies of past estimations and started using harvest figures and other measurements as more accurate indices to population changes (Tables 3 and 4). The Utah State legislature in 1917 established a series of large game preserves, which by 1923 consisted of nearly a million acres of the state's best deer and elk range, to provide protection for these game animals.

Recognition of the damage caused to farmlands and the competitive nature of elk with livestock resulted in the establishment of the Board of Elk Control in 1927; later, in 1933, this organization was changed to the Board of Big Game Control, with the authority to establish regulations for all big game animals in the state. Its function and responsibilities have been increasingly important since its establishment. This board, composed of members of land managing agencies, has membership representing federal lands, Utah Wildlife and Recreation Federation, Cattlemans' Association, Wool Growers' Association, and the Division of Wildlife Resources. This board was instrumental in taking action on rapidly rising deer herds and to manage them on an available game and range basis.

Severe winter weather, accompanied by deep snows over much of the winter season, has had a devastating effect upon deer populations in Utah, beginning as early as 1936-37, again in 1939-40, 1948-49, and 1951-52, and of late in 1972-73. During some of these winters, more deer have died from malnutrition in localized areas of the state than were killed by hunters (Low, et al., 1949; Hancock, 1976, personal communication).

Undoubtedly many factors had an effect upon the build up of deer herds in Utah, and other western states, during the 1920-40 period. Predator control, which had its beginnings in the 1890's by stockmen, was seriously initiated in 1916, when the federal government entered the control picture. Livestock numbers, which soared to 275,000 range cattle and 2,742,000 range sheep in the 1910's, undoubtedly brought a significant change from grass to browse ranges, which permitted deer populations to increase (Utah Biennial Report, 1946). Habitat losses, early recognised as results of urban sprawl, highway development, farming practices, and others, concentrated or eliminated deer. Buck hunting in the first one-third of the 20th century undoubtedly contributed to population increases.

Pending problems were recognized early in Utah by Fish and Game administrators. In the 1926-28 Utah Biennial Report we read:

"The increase in deer in Utah during the past 10 years has been phenomenal... This increase has been due to several sources: the enforcement of the buck law..., the establishment of game refuges, the reduction in the number of predatory animals, and the more systematic regulation of grazing on the National Forests." (p. 10.)

Further, the next Utah Biennial Report (1928-30) stated:

"Big game problems have, within the past few years, become very acute until now it is imperative that remedial laws be enacted for the correction of some of these unfavorable conditions. For instance, the deer have increased in some localities until they are a menace to foothill farmers and fruit growers and are in severe competition with domestic livestock for range forage, while the Fish and Game Department is without authority to remove these offending animals." (p. 9.)

However, resistance to either-sex hunting was early expressed by the director of the Utah Department of Fish and Game. In the Utah Biennial Report of 1934-36, when populations were beginning to soar, we find the director opposed to the suggestion that either-sex hunting be initiated:

"I recommend to the legislature of this state that they do not enact a law that would permit the killing of deer of either sex. It is our belief that 20,000 deer were killed last year. Under the present set-up, and should legislation be passed, we are sure our deer herds would be annihilated at the end of the third season." (p. 5.)

The first indication in Utah of the need for a balanced herd of deer within the range carrying capacity was given in 1939 (Utah Biennial Report, 1936-38):

"The game animals, as well as the livestock, should be reduced to the carrying capacity of the individual ranges, giving the forage an opportunity to reproduce in kind, something that has been neglected in the past." (p. 6.)

Antlerless permits were first issued in 1934, of the 1600 permits then issued, 623 antlerless deer were killed. In 1935, an additional 2,000 does were killed on special permits.

Antlerless deer permits were suspended in 1936 and 1937 because of severe winter losses; but the following year (1938), 4,000 permits were issued, followed by 10,700 permits in 1939 (Utah Biennial Report, 1938-40).

The numbers of special control permits were continuously increased, until in 1961 there were approximately 40,000 control permits issued (Table 3). The objective of management was to bring the deer herds closer to the carrying capacity of their ranges. The peak of Utah's mule deer numbers occurred during the 1945-50 period (with a second peak from 1964-71).
This special control permit program had started to have its effect on the population and was reflected in the numbers of special control permits issued:

"By 1966 this number had been reduced systematically to less than 4,000 and has exceeded that number only once since then. In 1972, 4,106 were sold, but this number dropped to 1,260 in 1973. In 1974, there were no permits issued which would allow the taking of more than one deer per hunter." (Utah Biennial Report, 1972-74)

Further reaction to the needs of the growing herds was evident as early as 1939 when 4,078 acres of game winter range were purchased by the Department (Utah Biennial Report, 1938-40, p. 15). Since then, the Utah Division has been dedicated to a program of winter range acquisition, with a goal of 577,000 acres of winter range under their management program. To date, about 225,000 acres have been acquired (Hancock, 1976, personal communication).

The bounty system was initiated in Utah in 1938 to further reduce predators. Lions were bountied at $3.10, and bobcats and coyotes at $2.50. At this time, the Department entered into an agreement with the Bureau of Biological Survey for more effective predator control.

Further pressures were exerted for either-sex hunting as early as 1938:

There is yet some agitation for a general open season on deer of either sex. We believe this would prove disastrous and is entirely unnecessary for proper control. (Utah Biennial Report, 1936-38, p. 44)

In 1943, the Interagency Big Game Committee was organized. It consisted of one representative each from the U.S. Forest Service, the Bureau of Land Management, and the Department of Fish and Game, whose duties as land managers was to determine big game conditions in the state and give recommendations to the Board of Big Game Control for the establishment of seasons, limits, and other matters pertaining to big game.

The recognition of the need for either-sex hunting seasons was now expressed by the director in 1946 (Utah Biennial Report, 1944-46):

There is a growing feeling toward a license to kill a deer regardless of sex to substitute the present "buck law", but this might prove disastrous to some of our deer herds, unless a method of control of the number of hunters permitted on a given area were also to be provided. (p. 33).

Supplemental feeding of big game had been sporadically practiced in Utah in the late 1930's, but the severe winter of 1948-49 brought an emergency feeding program for big game not only in Utah, but in many northern Rocky Mountain states (Low, 1950).

A 54 percent hunter success in Utah in the decade of the 50's jumped to 84 percent under the first "Either Sex" law season, 1951, for a total harvest of 101,000 deer.

"Many prophesied after the hunt that the deer herds adjacent to the large cities were 'wiped out' during the first either-sex hunt, but the severe winter of 1951-52 brought many deer down from these same ranges to die, in some cases numbers exceeding the legal harvest." (Utah Biennial Report, 1950-52, p. 8)

Management of Utah continued to cope with the large numbers of deer:

Hunter pressure increased steadily over the years. This steady increase in hunters and liberal hunting regulations had, by the early 1960's brought deer herds into better balance with forage resources.

The Board of Big Game Control, acting on the recommendations of the Division of Wildlife Resources and other resource management agencies, began a systematic cutback in control permits and liberalized seasons at about this time. (Utah Biennial Report, 1972-74)

The reduction in the number of special permits available was a direct result of the deer herds being more closely balanced with proper winter range conditions and hence a lesser need for additional deer removal. (Utah Biennial Report, 1964-66, p. 30)

Further:

Deer management plan in Utah has largely achieved its objective. As judged by the harvest, range trends, and other factors, the population is generally stable and in balance with the habitat. (Utah Biennial Report, 1970-72, p. 13)

And finally:

Deer management continued to follow the course established in the 1960's. The objective of bringing herds into balance with their range had largely been achieved at that time and cutbacks in control permits and liberalized seasons were indicated. (Utah Biennial Report, 1972-74, p. 40)

Recent changes in the regulations further reflects a decline or lower numbers taken formerly in herd populations:

Concurrent with the reduction in control permits, the number of herd units with liberalized seasons also began a general decline. In 1961 and 1962, the number of herd units with seasons more liberal than the 11-day either-sex season was 28. By 1966 this had dropped to 4. In 1974, there were no seasons more liberal than the 11-day either-sex season; in fact, the most liberal seasons in the state in 1974 were those allowing the hunting of antlerless deer for the last seven days and those allowing antlerless...
hunting the first three days of the season. In 1961 there had been no units with regulations more restrictive than the general 11-day either-sex season. These more restrictive hunts increased steadily from 1961 to 1969, then sharply to 1973 when 31 herd units had seasons more restrictive than the 11-day either-sex season. Types of restrictive seasons have included hunts shortened to 5 days, a combination of 3 days either-sex hunting followed by 8 days of buck-only hunting, 6 days of buck-only hunting followed by 7 days of either-sex hunting, and a full season of buck-only hunting. (Utah Big Game Harvest Handbook, 1974, p. 7.)

The decline in the herds, however, may not have been all a result of management to get herds within their carrying capacity, particularly during the past few years. During the past several years, more evidence is at hand that adverse weather--abnormally cold and long winters and prolonged cold and wet springs--has had an effect upon the productivity of some of the herds, especially in central and southern Utah. The hard winter of 1972-73 took a toll of fawns, which reduced from survival in some units to 31 fawns per 100 does. Further drought conditions in 1971-72 and in 1972-73 in southern and eastern Utah adversely effected the growth of vegetation upon which lactating does and weened fawns depended, which resulted in lower fawn survival. Adverse weather conditions, coupled with an increase in antlerless removal in 1971-72-73 in the central part of the state, undoubtedly had an adverse effect upon the present declining population of mule deer in Utah (Hancock, 1976, personal communication).

In summary, the present status of mule deer in Utah appears to be one of declining populations undoubtedly influenced by many factors such as depleted ranges that have not yet recovered from past overuse, drought, cold hard winters, habitat loss from highway construction, summer homes, and plant succession as fewer cattle are grazed. Coupled with these factors may be the influence of predation from feral dogs, coyotes, and other predators, as well as poaching.

Other States

To detail the build-up in numbers of mule deer in most western states would be to duplicate in a large measure the picture in Utah. Most states have shown explosive populations during the first half of the century, accompanied by efforts to reduce herds by greater hunter harvests of one kind or another. Habitat improvement, winter range acquisition, and other management practices have been followed.

Populations in most western states peaked in the 1940's, 50's, and 60's, as in Utah, and populations now appear to be declining even further. In a recent paper by Longhurst et al. (1976), the California mule deer decline is detailed and possible remedial measures given.

A few excerpts from some of the game managers in the western states indicate the population changes, harvests, and measures used to manage the herds:

Arizona

If we can use the Kaibab as an example, what happened there happened statewide. A tremendous herd build-up in the early 1900's and then a sharp die-off about the mid-20's. However, in our more recent history, the date would be 1952-58. (Russo, 1976, personal communication)

Records showing the yearly deer harvests and the number of hunters it took to bring them about are pretty sketchy for the years prior to 1946. Since then, though, accurate records have been kept, and they show a steady increase in the annual harvest to a high point in 1961, followed by a gradual decline to a low in 1968. Buck-only harvest, which also topped out in 1961 at 26,627 animals, hit its modern-day low point of 17,094 in 1965 and has climbed slowly since then.

During the late 50's and early 60's, Arizona was experiencing a boom in its deer population. Range conditions were critical and winter die-offs were common. The seasonal regulations during this period reflected the Departments' concern through large numbers of any-deer permits, and many areas where does were legal with no special permit. By about 1963 the peak in populations had subsided, and while ranges were still in poor condition, the any-deer hunting again became more restricted. This policy has continued to the point where in recent years, only a very small number of any-deer permits has been authorised. (Anonymous, 1970)

California

Longhurst et al.'s (1976) recent summary documents the decline and gives management suggestions to restore deer numbers.

Idaho

Population of deer increased from post-pioneer days to the present time; Estimates given in the literature show the following deer population increases and subsequent decreases to present numbers:

<table>
<thead>
<tr>
<th>Year</th>
<th>Population</th>
</tr>
</thead>
<tbody>
<tr>
<td>1923-24</td>
<td>45,000</td>
</tr>
<tr>
<td>1934</td>
<td>75,000</td>
</tr>
<tr>
<td>1941-42</td>
<td>137,717</td>
</tr>
<tr>
<td>1963</td>
<td>315,000</td>
</tr>
<tr>
<td>1971-74</td>
<td>down 30 ± 2</td>
</tr>
<tr>
<td>1975</td>
<td>215,000</td>
</tr>
</tbody>
</table>

(Thiessen, 1976, personal communication)

Montana

There are many indications that the peak mule deer populations which began in the late 40's and extended into the late 50's and early 60's were greater than has occurred in the past hundred years. However, there apparently has been considerable
change or fluctuation in numbers of deer during the past hundred years in various areas throughout the state.

Thus, during the period 1941-69, mule deer not only increased in number, but also expanded in distribution over the entire state, with peak numbers and distribution being reached around 1950-55. There has been little change since...

The "Buck Law" of the 30's and 40's resulted in few deer harvested and instilled in the minds of many that shooting does and fawns was sinful.

Montana has even employed late winter hunts in an effort to bring deer into balance with their range. Such seasons were often met by much public criticism. The mule deer management program in Montana has reached an "hour of decision". We must in some manner reduce deer to the extent the ranges can recover.

The re-establishment of doe seasons in 1950 and 1951 gave more people an opportunity to hunt and take deer. (J. Egan, 1971)

Since 1970, Montana's mule deer herds have continued to decline. (Allen, 1976, personal communication)

Nevada

Since the early 1960's, all deer herds in eastern Nevada have shown the same population trend; populations declined during the early 1960's, bottomed out in 1965 and 1966, expanded until 1971, and have declined since then. (McColm, 1976)

At the present time, we feel we are experiencing a decided and very drastic crash in populations of eastern Nevada... (Christianson, 1976, personal communication)

Oregon


1945 150,000 estimated populations
1947 350,000 estimated populations
1967 575,000 estimated populations
1975 400,000 estimated populations

Fawn survival was the most important factor in population decline. (Ebert, 1976, personal communication)

Washington

The winter of 1889 seriously depleted or reduced herds. Build-up of large herds occurred between 1935 and 1950 with largest herds believed present in 1947-50, 1955, 1963, and 1968. Mule deer hit bottom in 1969, 1971, and 1972 and have slowly in-

Wyoming

What has happened to our deer herd? This is a question game managers encounter frequently today and certainly it is a proper one. Mule deer populations are not as they were in the late 1950's and 1960's. (Corsi, 1974, p. 3)

Trends in Mule Deer Populations on Specific Units

Well-documented data showing long time trends in deer populations are difficult to find. Except for the first example, we have selected areas where pellet group counts formed the basis for estimating relative intensity of deer use of the range.

Information from the Kaibab (North) National Forest, although based on estimates, is the classical example of what has happened to many of our mule deer herds (Figure 2). The history of the Kaibab is the story of many of the deer herds of the West. The boom was apparently from 1918 (Forest Ranger reports of heavy over-utilization) to 1923-24 followed by the drastic starvation during the next few years. Estimates, by our most experienced men of the time, went from 100,000 in 1924 to less than 30,000 in 1930. Numbers were still high for this depleted range as indicated by the fact that until 1935, Supervisor Walter Mann had a standing offer of $1 for every aspen shoot over 12 inches high that could be found on the Kaibab. In 1936, however, at isolated spots, a few aspen sprouts began to "get away" from deer.

A personal visit in 1942 (Julander personal files) showed rather extensive areas of good aspen reproduction developing over much, but not all, of the forest; agreeing with the estimates that deer numbers were at a low in the late 1930's and early 1940's.

Estimates of deer numbers could not be found between 1947 and 1969, but another visit in 1974 (Julander personal files) showed a sharp deer high-line on the newly established drop of aspen, indicating a higher deer population. During the winter of 1954-55, the Arizona State Game and Fish Department (Swank, 1958, p. 78) estimated a loss of 18,000 deer. In the fall, 1954, a total of 8,058 deer were harvested. This is the largest annual kill on the Kaibab (North) to date, but it was too little and too late.

Clay McCullough's estimates of deer density from 1969 to 1975 inclusive, based on pellet group counts, on the higher portion of the Kaibab summer range (575 miles), gives a reliable picture of trend in numbers for that period (Figure 3). The Kaibab herd again appears to be on a slight upward trend since 1971.

Data from Robinette (personal letters) on the Oak Creek deer range in Utah on estimated deer herd numbers over an 11-year period are well documented. Deer numbers were estimated by pellet group counts over the entire winter range.
Figure 2. Estimated mule deer numbers on the Kaibab (north) National Forest (From D. I. Rasmussen, 1941, and U. S. Forest Service Unpublished Reports.)
Figure 3. Estimated mule deer numbers on the Kaibab (north) National Forest summer range (from pellet group counts); (Data from Arizona Game and Fish Department).
The deer population of this unit reached peak numbers in about 1942 and declined some by 1946 when studies began. Over the 11-year period, 1946-1955 inclusive, estimated numbers did not vary greatly and no definite trend, up or down, is indicated (Figure 4). Efforts were made through liberal doe permits to reduce this herd to proper carrying capacity with no success.

During the period 1958-1975, with less intensive samplings, estimates of deer use at Oak Creek was determined by deer days used and percent utilization of key species (Figure 5), Utah 1952-1975. (Data from Utah Division of Wildlife Resources.) Both estimates indicate a reduction in herd numbers from 1958 to 1966 with a definite lower population in 1966, '67, and '68. This was followed by a rather rapid upward trend from 1969 to 1975 to a population apparently nearing carrying capacity. History of this herd differed from the Kaibab since the decrease from peak numbers were not so drastic and the range, although damaged, was far less severe than the Kaibab. This herd had only a little above average winter losses in 1948-49. However, summer range is somewhat limited and of low quality.

On two neighboring, rather isolated mountain ranges in southeastern Utah, the Henry and the LaSal, deer days use per acre was determined by pellet group counts (Utah, 1952-75). Here, as at Oak Creek, the peak in deer numbers were believed reached and some decline made before data collecting began in 1945-46. The Henry mountain herd shows a sharp decline, reaching a low point in 1956 (Figure 6). From that low point, a slow recovery is indicated. This range was badly depleted by both deer and livestock and was low in forb production on summer range.

Average deer days use per acre on the LaSal mountain reached a low point in 1949 followed by a rather vigorous rise from 1953 to 1955 indicating a fairly productive herd. From 1955 to 1975, a slow downward trend is indicated. However, a high population was still evident during this period (Figure 6). Summer range is of higher quality than on the Henry Mountains. (Patterson and Harper, unpublished data).

Data from the Arizona Game and Fish Department show the trend in relative density of mule deer, as determined by pellet group counts, on the Three Bar Wildlife area in Arizona from 1959 to 1975 (Arizona Game and Fish Department, personal correspondence). (Figure 7). A general decline, from a higher density in 1959-60 to a much lower density in 1969, is indicated. From 1969 to 1975 the density appears to be stabilized at a rather low level.

On all of the above areas, the objective of management has been to bring mule deer numbers within carrying capacity of the range. The different results shown indicate varying degrees of success and possibly different causes and different management.

From general information obtained from most of the western states, there is no doubt that mule deer populations are down as of 1975. However, investigations of individual herd units (with intensity of deer use documented by pellet group counts) indicate that, although deer numbers are much below an extremely high peak, populations since then, and particularly during the last six or seven years, seem to be leveling off, or in some cases, increasing. Based on the overall picture, we ask: "Will the trend continue down? Can management of herds and habitat reverse the downward trend and stabilize or increase the herds? What are the causes of the decline and possible solutions?"

Based on individual herd data, we ask: "Are our mule deer herds, in general, declining below desirable levels which will permit recovery of depleted ranges, or are they adjusting in size to the actual impaired carrying capacity of their habitat?"

We hope the above questions will be answered, or at least enlightened, in the following papers of this symposium.
Figure 4. Mule deer population for the Oak Creek herd unit, Utah, 1946–1956. (Data from W. L. Robinette and O. Julander and Utah Division of Wildlife Resources).
Figure 5. Measure of mule deer use on Oak Creek winter range, Utah, 1957-1975. (Data from Utah Division of Wildlife Resources).
Figure 6. LaSal and Henry Mountains, Utah, deer days use per acre estimated from pellet group counts. Data collected in early spring of each year by Utah Division of Wildlife Resources.
Figure 7. Mule deer population for the Three Bar Wildlife Area, Arizona. Population density based on pellet group counts (November and December data) by Arizona Game and Fish Department.
LITERATURE CITED


MULE DEER HABITAT CHANGES RESULTING FROM LIVESTOCK PRACTICES

Philip J. Urness
Associate Professor and Project Leader
Utah State University
Range Science Department and Utah Division of Wildlife Resources

Abstract
Livestock grazing has had great influence on mule deer habitats since intensive settlement in the latter half of the 19th century. Positive and adverse effects have resulted from vast successional change, land preemption for cultivated crops and habitations, and activities associated with livestock production. Exploitative grazing during the "open range" era and widespread burning of montane forests set in motion sweeping habitat changes. Deer then increased greatly after conservation programs and intensive predator control in the early 1900's reduced mortality below recruitment. Although these habitat changes were largely unplanned, they must be considered in present-day management since adjustments in past practices can be expected to alter deer carrying capacities and populations.

Mule deer (Odocoileus hemionus) are a western North American form that, considering all subspecies, have broad ecological amplitude. They occur, at least seasonally, from hot and cold deserts to montane forests and alpine tundra (Figure 1). The major commonality in this broad geographic variation is mountains, including importantly the foothills or bajadas. Rather few mule deer occupied flatlands and these were quickly supplanted by modern man's agriculture and other developments. Consequently, a consideration of livestock practices, as they impact mule deer, essentially deals with ecology and management of foothill and mountain vegetation.

Complicating elements immediately emerge when attempting to cover a general topic such as this. These elements include (1) migratory populations occupying distinct winter/summer ranges in northern and high elevation southern areas vs. nonmigratory populations occupying desert, chaparral, and coastal zones, (2) very different responses of diverse vegetation types to specific management practices such as class of livestock, season and intensity of use by livestock, and fire use or suppression, (3) varying periods and causes of stress affecting survival and productivity of deer (i.e. winter forage scarcity and deep snow in northern latitudes or high elevations; summer drought and forage quality restrictions in southern latitudes).

Historical Perspectives
Any discussion of how the livestock industry might influence an apparent decline in mule deer populations must be viewed in developmental as well as current perspective. That a general decline has occurred since the mid-1960's is not a point of debate, thus the impetus for our symposium. However, the decline may be of lesser magnitude than some would have us believe, at least in the central portion of mule deer distribution (Figure 2). While we are presently below the peak harvest years in Utah, much of the drop is accounted for in near-elimination of antlerless animals in the harvest. Examination of the buck-only harvest curve suggests much less change, although the downward trend accelerated during the past three years.

Trends in range livestock numbers in Utah show some significant changes that reflect similar patterns over much of the Intermountain West (Figure 3). One of my professors, a prominent zoologist, occasionally would lament the presence of domestic sheep on mountain ranges. It was his belief that elimination of "mountain maggots" from the range would usher in a new deal for mule deer based on a narrow concept of strong dietary overlap. The steady decline in the range sheep industry has not borne out his prophecy.
An extensive literature attests to general abusive rangeland use by livestock over most of western North America from mid-19th century settlement, up to the present in some cases. The period of major abuse was generally from 1880 to 1930, with foothills around valley settlements affected earliest.

Unrestricted selective grazing by livestock, especially in spring, on the palatable grasses and forbs led, in part, to widespread successional change favoring shrubs that were frequently subordinates in presettlement vegetation (Ellison et al. 1951, Hull and Hull 1974, Leopold 1950, McConnel and Dalke 1960). On many areas outright invasion of grasslands by woody plants and succulents occurred (Blackburn and Tueller 1970, Glendening 1952, Humphrey 1953, Reynolds and Martin 1968). Causes for increases in woody plants have been variously ascribed to excessive grazing, fire suppression, promiscuous burning, climatic change, biotic factors besides grazing, and combinations of these factors, depending upon vegetation type.

Successional Relations

Although much foothill habitat was pre-empted by agriculture, additional carrying capacity on remaining habitat was created through progressive and retrogressive successional change resulting from excessive grazing, altered fire patterns, and logging. These changes were sufficiently widespread to permit mule deer increases to unprecedented numbers from about the 1930's to 1950's (Leopold 1950, Leopold et al. 1947, Longhurst et al. 1952).

Influence of early livestock grazing was imposed on all vegetation types affecting mule deer, but impacts differed sufficiently to require separate discussion. In general, fire exclusion in arid or semi-arid types and widespread uncontrolled burning in montane forest types accompanied grazing and positively affected habitat values for mule deer. Major types are desert grassland, sagebrush-bunchgrass, chaparral, juniper-pinyon, and montane forest.

Desert grassland: Extensive grassland areas in the Southwest and Mexico were heavily stocked with cattle after 1800 (Humphrey 1958). Although Spanish settlement had introduced cattle, sheep, and horses in the 1500's, use was generally restricted to areas immediately around widely scattered towns as a result of Indian raids. Woody plants occurred sparsely throughout the grass-dominated uplands and in bosques along stream courses. With heavy use after 1860, the palatable grasses, mostly graminus (Bouteloua spp.), three-awns (Aristida spp.), and hilaries (Hilaria spp.), were quickly reduced under heavy year-long use. Mesquite (Prosopis spp.), other leguminous and non-leguminous desert shrubs, and cacti increased (Figure 4) and assumed dominance on very great areas (Bentley 1958, Branscomb 1950, Brown 1950, Glendening 1952, Humphrey 1953).

Conflicting reports variously ascribe vegetational change to climatic shift toward increasing aridity (Schulman 1956, Branscomb 1958), heavy grazing reducing competition from herbaceous species (Suechner 1946, Whitfield and Anderson 1938, Glendening 1952), and fuel reduction preventing periodic fires (Griffiths 1910, Humphrey 1958, Reynolds and Bohning 1956, Thornber 1910, Wooten 1915). Longterm protection from grazing or light grazing did not materially affect growth of woody plants nor prevent their expansion (Bladyenstein et. al. 1957, Glendening 1952). Once started the process was probably accelerated through propagule dispersal by birds, rodents, and other biotic factors (Arnold 1962, Reynolds 1950, Reynolds and Glendening 1949, Talmans 1942).

A combination of some or all of these factors is probably the most accepted explanation of woody plant invasion in desert grasslands. Regardless of causal factors, the effect in terms of mule deer was a considerable expansion of yearlong habitat which the cacti and shrub fruits, browse, and cover provided.

Sagebrush:bunchgrass: Sagebrush (Artemisia spp.) was apparently dominant in the climax community on the drier areas and on certain soils of this type with bunchgrass—wheatgrasses (Agropyron spp.), bluegrasses (Poa spp.), and needlegrasses (Stipa spp.)—and forbs prominent in the understory. With heavy, selective grazing, especially in spring, the grasses declined and sagebrush and other shrubs increased in density (Robertson 1971, Stoddart 1941, Tueller 1973, Tueller and Blackburn 1974). Where fires occurred, retrogression proceeded to weedy annuals, especially cheatgrass (Bromus tectorum), and sprouting shrubs (rabbitbrush Chrysothamnus spp., and horsebrush Tettadymia spp.). Active fire suppression limited areas burned so big sagebrush dominated very large tracts and, besides, it reestablishes rather quickly on such sites following fire (Blaisdell 1953).

The more mesic foothills apparently exhibited a grass:forb-dominated climax with shrubs more widely spaced (Hull and Bull 1974, Pickford 1931, Stoddart 1941). Intense use in spring reduced the herbaceous understory followed by great increase in sagebrush, rabbitbrush (Chrysothamnus spp.), and some more palatable shrubs such as bitterbrush, Purshia tridentata (Pickford 1931). Soil erosion and site verification appear to have played prominent roles in this process (Ellison 1954, 1960, Leopold 1950). Increase in palatable shrubs were less likely to occur where cattle grazed, less so with sheep (Cotton and Evans 1945). Fall use alone was not nearly so likely to effect composition shifts favoring shrubs (Mueggler 1950).

Generally, the carrying capacity for deer on foothill winter ranges was increased with greater shrub density where fire was excluded (Julander 1962). Later, regulated spring livestock use maintained this condition but late summer and fall use removed a considerable amount of the palatable browse upon which deer depended for winter range.

Chaparral: Grazing and fire have been inextricably intertwined in the development of most, if not at all, chaparral types occupied by mule deer. In Arizona, the presettlement type apparently presented an open, grass-dominated aspect with shrubs present but heavily suppressed by frequent fires carried over large areas with heavy amounts of herbaceous fuels (Leopold 1926, Croxon 1926). The bimodal precipitation pattern favored grass:forb growth when fires kept shrub competition down. Heavy post-settlement grazing, mostly by cattle, quickly
reduced herbaceous fuels and fire frequency. Shrubs and woodlands were increased dramatically. The present-day aspect is one of dense tall shrubs, typically sclerophyllous and evergreen, with little herbaceous understory unless recently burned. Although the type offers great cover value, the quantity of high-quality forages is limited during droughty periods before and after summer monsoons (Swank 1958).

California chaparral had a somewhat different history as well as a distinctly different climate. Long hot, dry summers favored brush species dominance. Purposeful burning was more prevalent after 1850 than during Indian or Spanish domination (Taber and Dammann 1958, Sampson 1944). A major expansion of brushfields up into previously forested areas occurred with early logging and burning, especially in the Sierra Nevada (Longhurst et al. 1952, Sampson and Jesperson 1963). Frequent burning was done primarily to increase livestock forage quality and palatability. Expansion of chaparral into valley grasslands and oak-woodlands was ascribed to overgrazing, reduced competition from grasses, and reduced fire frequency (Leopold 1950, Shantz 1947).

Carrying capacities for mule deer were (and are) greatest on areas in continuous cycles of secondary succession where a mix of grass, forb, and shrub forages was available. Moderate levels of livestock use and frequent small fires of varying age, from newly burned to mature brushfields in close juxtaposition, provided productive yearlong or winter deer habitat (Biswell et al. 1952, Cronenmler and Bartholomew 1950).

Juniper-pinyon: As in the case of other arid or semi-arid types, woody plants in the juniper-pinyon zone have expanded in total area during the past century. Extension of trees into grassland and shrub steppe occurred both upslope and down (West et al. 1975). The causes were no doubt complex but overgrazing and fire suppression appeared prominent as initiating mechanisms (Blackburn and Tueller 1970). Climatic change and biotic influences have also been implicated (Frischknecht 1975, LaMarche 1974, Phillips 1910, Schuman 1956).

Cover values, primarily, and browse forage provision accompanying shrub and tree invasion of grasslands increased mule deer winter range (Terrill and Spillett 1975, Reynolds 1964). In the absence of renewal by fire or mechanical means, however, the trees become dense and practically eliminate the understory, including many shrubs, especially in the Great Basin (Julander 1962, Tausch 1973). Consequently, the increased habitat values wrought by tree invasion have been somewhat ephemeral, with early gains declining in late succession. This has been the basis for widespread tree control projects, namely, to set succession back to a phase more productive for livestock and deer (Dyer 1975, Plummer et al. 1968).

Montane forest and uplands: Higher elevation, forested and non-forested areas provided summer range for large local livestock herds, especially sheep after 1870. These were usually inflated by itinerant herds trailed or shipped in from long distances to graze the "open range." Until the forest reserves were established around 1900 and the Forest Service created in 1905, an increasingly abusive pressure was placed on mountain summer ranges. Grazing on Forest Service lands was placed on a controlled lease system which became increasingly more effective in reducing abuses after 1910. A number of reports emanating from the Bureau of Plant Industry, state agricultural experiment stations and other U.S.D.A. publications appeared about this time documenting the "tragedy of the commons" (Griffiths 1902, 1903, Kennedy 1901, 1903, Wooten 1908).

Some later papers indicate improvement with grazing control but attest to the slow recovery and severity of damage sustained (Darlington 1915, Forsling 1931, Humphrey 1943, Pickford 1931, Sampson and Weyl 1918, and many others). In addition to overgrazing, purposeful burning occurred on many mountain ranges to stimulate forage and make dense brushfields and forested areas more accessible to livestock, especially sheep (Reynolds 1911, Ellison 1954). Soil erosion and denudation of vegetation from grasslands and forests led to invasion or thickening of xerophytic shrubs (Ellison 1960, Ellison et al. 1951).

Slash fires on logged areas and wildfires swept over staggering acreages of forest throughout the West from the late 1800's to about 1940, creating large brushfields that were grazed heavily by livestock and provided excellent habitat for deer, albeit at great cost (Sampson and Jesperson 1963, Leopold 1950). The rapid cycling of accumulated soil nutrients to deer forage was probably responsible, to a considerable extent, for tremendous population increases during this period along with concomitant control of livestock grazing, predator populations, and deer exploitation (Julander 1962, Longhurst et al. 1952).

Secondary succession to closed canopy forest on many of the burned areas is rapidly reducing carrying capacity of deer summer range (Blues 1973, Leopold 1959, Loope and Gruell 1973, Lyon 1966, 1971). Prescribed burning and other forestry and range management practices that integrate forage and timber production will be necessary on many montane forest areas in future if important summer range values affecting deer productivity are to be maintained.

Successional change: Mule deer are adapted to mid-successional communities that contain a good mix of grass, forb, and shrub species, but especially browse communities in winter. Changes leading away from such conditions usually adversely affect deer carrying capacity where they occur over extensive areas. Management of succession, then, is the business we are in if optimization of harvestable game is our goal (Leopold 1950).

Unless site potential has been seriously altered, processes of past change can be reversed and this in no way excludes those wrought by grazing. Indeed, on many areas determined to be best managed without livestock use, municipal and other watersheds come to mind, we can observe secondary succession toward the climax community. A good example is the Wasatch Front in Utah, at least portions of it. Removal of growing season livestock grazing has been followed by surprisingly rapid recovery of bunch-grasses and forbs with a corollary reduction of
Fire in susceptible types such as sagebrush: grass can hasten progression through heavy reduction of shrubs. Where disclimax is the desired objective, as in juniper-pinyon, fire or mechanical control is a necessary element to avoid canopy closure and loss of understory (Plummer et al. 1968). Generally, succession proceeds slowly and there is presently little evidence, outside of some montane forest types, that it is responsible for short-term declines of mule deer. However, extensive change toward a grassland, woodland, or forest climax can be expected to reduce deer carrying capacity over the long term. This should be anticipated in any resource plans and action (or inaction) programs that lead to significant shifts in plant communities. We have been remiss in not monitoring change more closely.

Current Management Status

My assignment unavoidably parallels later symposium papers in several areas; namely, predator control, vegetation manipulation, and competition. As much as possible, an attempt has been made to avoid specific consideration of these and related topics, but they cannot be completely ignored since they are an integral part of livestock production on most rangelands. Livestock practices frequently affect food: space relations (nutrition and behavior) of mule deer and the elements of competition and habitat destruction are potentially strong.

Adjustments of livestock numbers to a carrying capacity that recognizes allocation of resources to diverse uses has come a long way (Smith 1958, 1959), yet there is still need for much improvement on public rangelands (Bureau of Land Management 1974). Our task is to identify the forces of ecological change put into motion by nearly a century of exploitative use, and to utilize those aspects that accidentally produced benefits and to continue to combat negative aspects.

Vegetational management: Manipulative treatments for increasing livestock forage have been condemned in many wildlife circles as made at the expense of deer habitat. In fact, earlier programs did tend to be over-sized and single-purpose with the result that very large acreages were changed from one form of monotony to another. Thus, huge expanses of mature juniper-pinyon were chained and seeded to mule deer from about 1940 to 1970 (Aro 1975). Similarly, large blocks of sagebrush were plowed or sprayed with herbicides in all western states.

Assessments of deer habitat values on projects that were planned with this as an objective are practically nil. The few studies extant are usually examinations of older, single-purpose projects and these studies have often shown conflicting results. For example, deer response to juniper-pinyon chaining has been both positive (Millich 1969, Reynolds 1964) and negative (Terrill and Spillett 1973, McCulloch 1973), depending upon criteria used in evaluation and location.

The story has been much the same in sagebrush: grass (Anderson 1969, Koehler 1970, Lieben 1969, Urense 1966) and chaparral types (Biswell et al. 1952, Pase et al. 1967, Taber and Dasmann 1958, Urense 1975). Creation of vegetational diversity often has provided high-quality forage resources, unavailable on unaltered stands, which can be seasonally important to mule deer (Plummer et al. 1968). Thus green created wheatgrass is sought by deer from fall to early spring when other available forages, mostly browse and indispensible, are much lower in value (Koehler and Leckenby 1970).

Shifts toward management objectives that emphasized created monocles to provide treatment benefits while retaining values innate to the untreated community have been very recent. They came with the growth of environmental concerns after the mid-1960's. Planned diversity of cover types through small projects that blend naturally into the landscape became accepted managerial policy (Forest Service 1973, Toonch 1973). However, by then social, political, and economic pressures were so great that a near abandonment of such programs has ensued. We have, in effect, thrown out the baby with the bath.

While the decline of deer is coincident with a winding down of vegetational control programs on public lands, there is no suggestion of a cause: effect relationship. Conversely, there is little case for argument that a "critical mass" of treated land finally exceeded an upper threshold which was followed by a crash in deer numbers. Most treatments were accomplished well before a decline in deer numbers. To my knowledge, no one has demonstrated a pattern in population levels that parallels differences in amount of treated area.

Grazing systems: Grazing systems that provide some rotation or deferment of livestock use are increasingly adopted on public lands as capital improvements, particularly fencing and better water distribution, permit animal control. The concepts and terminology vary but the basic tenet is periodic heavy use on part of a range unit with rest or deferment on the remainder (Herbel 1974, Stoddart et al. 1975).

Impacts on deer of a change from less heavy and less uniform but continuous livestock use to a deferred system could be profound. 1 Yearly competition between livestock and deer could be eased where portions of the range are rested but available to deer. However, the major impact could be alteration of competitive relations among plant species affecting composition. Indeed, this is the objective of any grazing system over continuous or season-long use, namely, to improve range condition (usually interpreted as an increase in decreaser grasses and forbs, reduction of increaser shrubs).

1Research proposal on "Impacts of specialized grazing systems on multiple-use aspects in the Intermountain Region" on file at Utah State University, Range Science Department, Logan, Utah.
Depending upon vegetation type and season, the opposite effect is possible. Heavy early summer livestock use can effectively increase vigor and production of browse plants valuable as winter forage for mule deer (Jensen et al. 1972, Smith and Doell 1968). Midsummer to fall use in the same area can negate the benefits when livestock shift heavily to browse as forbs and grasses mature. Importance of livestock as tools to control succession on game winter ranges has only recently been investigated. Utah has purchased extensive lands as critical winter range to help offset losses to housing and other developments. Livestock grazing programs to enhance their value for deer are currently active.

Despite some change, grazing systems have not, in my opinion, imposed a controlling influence on near-term deer numbers over entire regions. Reductions in permitted livestock numbers and seasons of use have been slow but continuous on many grazing units in the Intermountain Region. Trucking of livestock from summer to winter range has reduced fall use of deer winter range in some areas. Efforts to secure more uniform and proper use have proceeded during the past several decades. All of these factors tend to suggest an improved range situation for deer relative to livestock grazing or, at the least, only slightly changed status.

Other livestock practices: Development and better distribution of water sources on arid rangelands have permitted yearlong use of ranges to deer that otherwise would be seasonally unusable (Wright 1959). Deer access to livestock water developments should be assured on public lands. Wherever possible, these should be dependable sources, not just available when livestock are present. The tendency to use access to water as a means of controlling livestock use in lieu of fencing can have adverse effects on deer habitat use. It is not a widespread practice on public lands and it should be discouraged. In general, arid lands where water limits seasonal deer use seldom are highly productive habitats. Such areas are not extensive and the water supply situation has not changed materially in recent years or it has improved.

Fencing for livestock control, if improperly constructed, can interfere with deer migrations and access to habitat. Except for major highway fences, these situations are usually local in nature and normally do not constitute a serious threat to deer as they have with antelope.

Greater use of vehicles in livestock management has expanded access roads into more areas in recent years. This, plus the accelerated recreational use of rangelands has probably affected seasonal deer use of habitat somewhat although its importance has not been assessed. Harassment, generally, has increased in intensity on a broad front and should receive greater attention as potential factors affecting herd productivity and mortality.

Probably more than any other aspect associated with livestock management, predator control has changed during the period of immediate concern. I will defer to later papers on the overall question, except to reiterate the ubiquity and effectiveness of control programs over much of the total mule deer range through the mid-1960's. Public as well as private lands were systematically treated over huge areas prior to the toxicant ban in 1972. Withdrawal of toxic compounds, especially 1080, and other restrictions on control methods, have created a storm of controversy within the livestock industry especially from sheep producers (Bowen 1976, Howard 1974, Davenport et al. 1973, Wagner 1972). The benefits derived from the controversy are numerous studies attempting, finally, to quantify predator impacts on livestock and deer populations.

Disease transmission between livestock and mule deer, with a few exceptions, has seldom been more than a local problem. However, such cases are difficult to diagnose on rangelands unless losses are heavy. Die-offs in mule deer are rare aside from late winter losses where concentrations on poor condition ranges occur. The disease indicated in such situations is usually "hollow-belly." A sparse literature related to mule deer either means diseases are much less common than in White-tailed and black-tailed deer, or that less research effort has been expended (Hunter and Yeager 1956, Neiland and Dukeminier 1972). In either case, no apparent increases in disease incidence have been reported over entire regions in recent years. Furthermore, it is unlikely that diseases would seriously affect deer while elk, on the same ranges, have increased.

Conclusions

Factors associated with livestock production on western rangelands that also serve as mule deer habitats have, with the possible exception of predator control and increased human activity, changed comparatively little in the past decade. Indeed, some aspects such as reduced livestock use on many key areas, changes in classes of livestock, and more carefully executed vegetation control projects, should have affected deer positively. Therefore, while it cannot be stated with absolute certainty, I will go on record as believing that livestock grazing practices have had little influence on the general decline in mule deer numbers since the mid-1960's.
Figure 1. Approximate distribution of deer (*Odocoileus hemionus*) in North America after K.D. Taber (1966) and E. Beltrán (1953).

Figure 2. Harvest curves for mule deer in Utah averaged for the preceding five years. Actual harvests are plotted for 1971-75.
Figure 3. Range cattle and sheep numbers in Utah, January 1 inventories (ARS, Reporting Service).
Figure 4. Woody plant increases on desert grassland range at Santa Rita Experimental Range, Arizona (A. taken in 1903, B. retaken in 1948, courtesy of S.C. Martin).
Figure 5. Downslope invasion of grassland by pinyon and juniper provides cover value for mule deer in early and mid-successional phases (Photo supplied by R.J. Tausch).
Figure 6. "We constantly change the world, even by our inaction; therefore, let us change it responsibly." B. Franklin.
Figure 7. Removal of growing season livestock use can result in successional change affecting deer carrying capacity on sagebrush: bunchgrass winter range (Right of fence grazed by cattle in spring, left area ungrazed by livestock for approximately 30 years, photograph supplied by A.D. Smith).
LITERATURE CITED


Humphrey, R. R. 1953. The desert grassland, past and present. J. Range Manage. 6(3):159-164.


ALTERATION OF MULE DEER HABITAT BY WILDFIRE, LOGGING, HIGHWAYS, AGRICULTURE, AND HOUSING DEVELOPMENTS

Olof C. Wallmo
Principal Wildlife Biologist
Rocky Mountain Forest and Range Experiment Station
U.S.D.A. Forest Service
Fort Collins, Colorado 80521

Dale F. Reed
Wildlife Researcher
Colorado Division of Wildlife
Glenwood Springs, Colorado 81601

Len H. Carpenter
Assistant Wildlife Researcher
Colorado Division of Wildlife
Kremmling, Colorado 80459

Abstract

The meager data available fail to support the hypothesis that forest fires, logging, highways, housing developments, or agriculture, singly or in combination, can be held responsible for a decline in the population of mule deer (Odocoileus hemionus hemionus) throughout the western United States. If posed, it would be a vacuous hypothesis in the absence of documentation of such a decline. A uniform resource inventory system clearly is needed. The Forest and Rangeland Renewable Resources Planning Act may provide the opportunity to develop such a system.

The geographic range of the Rocky Mountain mule deer (Odocoileus hemionus hemionus) covers more than 1 million square miles of the United States. Considering the enormous ecological amplitude of the species, it can be presumed that at one time or another in history most of this range was habitable to some extent. That is, it was poor, mediocre, or good mule deer habitat, but probably never static. During the time since the species appeared and differentiated into 11 recognized subspecies, the continent has undergone great changes in climates and floras.

A dynamic system would be necessary to classify mule deer habitat over time. It would detect the influences of epochal changes, lesser climatic fluctuations resulting from irregular behavior of the sun, and, on a still smaller scale, the unpredictable droughts, pluvials, and prolonged winters that are superimposed on larger climatic trends. With that capability, perhaps it would also be able to distinguish from "natural" habitat trends those effects that are imposed by man. Without such a system, we can only say for sure that habitat conditions are in a transition state that we may or may not be modifying significantly. To maintain them in some constant state presumes that we understand that state and the forces changing it.

Commonly, the evidence for habitat change is taken to be the increase or decrease in the populations of the species in question. Observed changes in the environment that correlate with the population change are assumed to be causative, and the casual mechanisms can only be postulated. They might be proven with acceptable levels of confidence after the hypothesis is posed, but not in the process of hypothesizing.

Today we are in the position of posing hypotheses. Managers are concerned over the contentions that mule deer populations are declining over the entire range and that some common cause or combination of causes is behind it. To venture into this position it is necessary first to document the population change in magnitude and location. Unfortunately our knowledge of the history of mule deer populations on a continental scale is based only on guesses derived, commonly second- or third-hand, from subjective impressions. By that means Seton (1917) guessed that there were about 10 million mule deer in North America at the time of the arrival of white men and about one-half million in 1908. Two decades later there were supposed, on equally poor evidence, to be 100,000 mule deer on the Kaibab National Forest alone (Caughley 1970), an area comprising less than 0.1 percent of the range of the species.

The only consistent reports of deer numbers on a nation-wide basis are provided by the U.S. Forest Service. If these estimates are to be believed, there were about 750,000 deer (all species) on the western National Forests in 1930, over 3 million in 1965, and nearly two and one-half million in 1972.
Unfortunately, these figures are not derived from systematic inventories. Nor have the states and provinces of the U.S. and Canada provided a credible body of data from which to infer population trends. Consequently, we are on flimsy ground in tracing events that may have had large effects on mule deer populations.

We do not suggest that the phenomena discussed below are casually related to changes in deer numbers on a region-wide basis. It may be productive to consider them, though, if for no other reason than to emphasize the need for better information. Five types of habitat alteration are discussed: fire, logging, roads and highways, agricultural development, and housing development.

**FIRE**

It is widely accepted that forest fires generally improve the quality of mule deer habitat. Lyon and Stickney (1966) stated that "most of the big-game ranges of western Montana and northern Idaho were created by uncontrolled forest fires" -- principally between 1910 and 1934. The term creating might be too strong, inasmuch as the deer lived there prior to the fires, but the habitat still may have been improved. Post-fire increase in the biomass of vegetation accessible as deer forage is a rational basis for assuming habitat improvement. A chain of reasoning can be constructed to support the hypothesis that larger deer populations would result. But none of the information available to date demonstrates that it has occurred.

While some authors (Pengelly 1963; Lyon and Stickney 1966) contend that forest fires have had a dominant influence on deer populations in the Rocky Mountains, others (Edwards 1956; Picton and Knight 1969; Robinette et al. 1952; Wallmo and Gill 1971) suggest that snow depth and duration on winter range are a major determinant of population levels. At the same time we are led to believe that changes in hunting pressure since white man settled the West may have effected major changes in deer numbers. Whatever correlations we might discover between the histories of forest fires and deer populations, they must be considered in the light of other factors.

The U.S. Forest Service has maintained a thorough fire reporting system since 1909. Data on area burned within the National Forest boundaries in Region 1, the northern Rocky Mountains, and Region 2, central Rocky Mountains, are presented in Table 1. In the 3 decades from 1910 to 1940 over 7 million acres were affected by forest fire. In the 3 decades from 1940 to 1970 less than 1 million acres were burned.

The habitat improvement that may result from fire results from climax ecological succession. Though the literature on post-fire development of vegetation is extensive, the duration of conditions more favorable to deer is not well documented. Lyon (1971) suggests that the benefits would continue for up to 60 years in the Douglas fir (Pseudotsuga spp.) type in southwestern Idaho. In Wyoming, the advantages may be lost in 10-20 years in lodgepole pine (Pinus contorta) stands, 20-50 years in aspen (Populus tremuloides), 50 years in Douglas fir, and 80 years in subalpine fir (Abies lasiocarpa) (U.S. Department of the Interior 1974). Lyon and Avant (1970) estimate that burning aspen stands in New Mexico will improve the habitat for big game for 8 to 10 years.

Whatever the period of effect, it must be considered in estimating the area potentially influencing deer habitat over time. If an average period of 20 years is realistic, in the National Forests of the central Rocky Mountain Region (Region 2) there were some 450,000 acres in "improved" condition in 1929 and 150,000 in 1970 (Fig. 1). If the improved condition lasted an average of 40 years the peak area enhanced would have been about 7.4 million acres in 1950, dwindling to about 1.2 in 1975; a maximum of about 2 percent and a minimum of about 0.4 percent of the total area which the fire reports cover. It seems questionable, at least, that the difference between these fractions of the total area could have influenced regional deer populations to a detectable degree, particularly in view of the fact that we have little evidence to support the belief that forested summer range is deficient in its unburned state.

### Table 1. Acres burned by decades within protective boundaries of National Forests and Grasslands of Regions 1 and 2 of the U.S. Forest Service.

<table>
<thead>
<tr>
<th>Years</th>
<th>Region 1</th>
<th>Region 2</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1910-20</td>
<td>4,749,166</td>
<td>309,039</td>
<td>5,058,205</td>
</tr>
<tr>
<td>1920-30</td>
<td>1,078,000</td>
<td>139,171</td>
<td>1,217,171</td>
</tr>
<tr>
<td>1930-40</td>
<td>710,000</td>
<td>117,354</td>
<td>827,354</td>
</tr>
<tr>
<td>1940-50</td>
<td>128,000</td>
<td>35,644</td>
<td>163,644</td>
</tr>
<tr>
<td>1950-60</td>
<td>62,721</td>
<td>62,721</td>
<td>125,442</td>
</tr>
<tr>
<td>1960-70</td>
<td>220,337</td>
<td>100,190</td>
<td>320,527</td>
</tr>
<tr>
<td>1970-75</td>
<td>66,984</td>
<td>25,761</td>
<td>92,745</td>
</tr>
</tbody>
</table>

1/ Data incomplete.
2/ Data not available.

Alteration of Mule Deer Habitat 38
Fig. 1. Acres presumably in "improved" condition for deer range as a result of fire in National Forests of the central Rocky Mountain Region (relative to a base status in 1910).
LOGGING

In forest environments understory vegetation biomass is inversely related to overstory. This is an acceptable generalization for most forest types in North America (Pfister and Clary 1972). Thus, virtually all timber removal operations could, theoretically, benefit deer habitat, the maximum benefit potentially coming from clearcutting (Wallmo et al. 1972). Pengelly (1963) inferred, ambiguously, that logging in the northern Rocky Mountains was a major factor influencing the increase in deer populations in that region in the first half of this century. Increases in deer populations in the region, specifically as a result of logging have yet to be documented, however.

Research on the subject indicates that use by deer commonly increases after logging (Edgerton 1972; Paxton 1974; Pearson 1968; Wallmo 1969). But Regelin et al. (1974) postulated that other factors kept mule deer populations in the central Rocky Mountains well below the densities that could be supported by unlogged forest. Nevertheless, the circumstantial evidence that logging can be beneficial to mule deer habitat justifies consideration of its potential effect on a regional basis. Wallmo et al. (1972) estimated that clearcutting in subalpine forests of the central Rocky Mountains increased deer forage supplies nearly 50 percent 15 years and 20 years (the latter unpublished) after logging.

Data on timber removals for the entire Rocky Mountain area were not obtained, but complete records from the National Forests of the Central Rocky Mountain Region (Region 2) were examined. Over the period of record, 1911 to date, there has been a progressive increase in the timber harvest, reaching a peak in 1969. A slight decrease since then is attributable to the public opposition to clearcutting and the development of environmentally preferable harvesting systems by Forest Service silviculturists.

In Region 2 the total area logged by all harvesting methods has averaged over 65,000 acres per year over the past decade, compared with an average of about 6,000 acres burned. In Region 1 (northern Rocky Mountains) over 100,000 acres per year are logged (Lyon 1969), compared with an average of about 20,000 acres burned.

As with fire, the beneficial effects of logging to deer habitat can be presumed to last over a period of years (Wallmo et al. 1972). If we assumed an influence lasting 20 years, we could estimate the region-wide cumulative effect of logging (Fig. 2) as we did with fire. The results suggest that the decreasing amount of fire-influenced habitat in the central Rocky Mountains in the past 60 years is more than compensated for by logging-influenced habitat. Together they remain a very small fraction of the total area considered.

Assuming that fire and logging have similar effects on deer habitat, the record does not substantiate that their combined effect could account for decreasing deer populations in the central and northern Rocky Mountains.

ROADS AND HIGHWAYS

It is indisputable that deer are killed in collisions with high-speed motor vehicles. Beyond that, the impacts of roads and highways on western mule deer numbers are not well understood. Indirect impacts would include, first, the physical loss of some natural habitat including forage, water, and cover (Leopold 1951), requiring adjustments by wintering and migrating deer. Secondly, traffic and roadways present auditory and visual barriers which can conceivably adversely affect deer behavior.

Loss of habitat — Reasonable accurate estimates of the number of acres of habitat directly replaced by roads and highway surfaces or lost through removal of native vegetation in right-of-way are not readily available. Thus, we made projections for Colorado to serve as an example of the potential magnitude of mule deer habitat losses from roads and highways (Table 2). Interstate, rural, and county highways increased 4.7, 7.5, and 6.8 percent, respectively, between 1960 and 1974. Consequently, interstate highways represent the type of roadway with the greatest potential impact on mule deer habitat. In mountainous areas of western Colorado most highways are aligned along valleys and water courses, frequently on south-facing slopes for ease of winter maintenance. These specific cases where important acres of deer habitat are modified and migration routes severed or impacted.

In most cases, highway rights-of-way are revegetated with grass or grass-legume mixtures, with crested wheatgrass (Agropyron spp.) being one of the more popular species (Reynolds and Springfield 1953). It is highly palatable in the "early green-up" period (March-April) and is implicated in much of the spring deer mortality on highways. These accidents, plus those occurring during winter and migration periods, account for most of the mule and black-tailed deer (C. hemionus) killed from collisions with vehicles in the western states (Table 3).

Most of the states do not have accurate figures on road kills because it is difficult to routinely monitor all federal, state, and county roads and because animals which escape the rights-of-way before dying usually are not found. In spite of their accuracy, the estimates in Table 3 represent definite losses of deer. We specifically avoid drawing inferences from the sums of 16,896 in 1967 and 18,822 in 1975, an increase of 79.7 percent since 1968. They might represent increased mortality from smaller populations, or decreased mortality from larger populations.

The number of deer killed on any given section of highway in related closely to two parameters, the number of deer coming onto or crossing the traveled portion of highway and the traffic volume. High numbers of deer crossings combined with high traffic volume result in "critical" deer kill areas. For example, Colorado Highway 82, a 4-lane, high traffic volume (Fig. 3) highway, had an annual traffic volume of over 2 million vehicles (5,628 vehicles per day) in 1975, an increase of 79.7 percent since 1968. These "critical" kill areas existed in a 15-mile length of Highway 82 where methods (Reed and Woodard
Fig. 2. Acres presumably in "improved" condition for deer range as a result of logging in National Forests of the central Rocky Mountain Region (relative to a base status in 1910).
Fig. 3. Annual traffic volume on Colorado Highway 82 from 1968 through 1975.
Traffic and road-way barriers -- The behavioral response of ungulates to traffic stimuli may be either a survival advantage or disadvantage. Habituation (Thorpe 1963; Geist 1971) enables most ungulates to use ranges within visual and auditory range of roads and highways. Klein (1971) reported that traffic along highways did not appear to disturb reindeer (Rangifer tarandus) feeding or moving nearby. Grenier (1974) reported on moose (Alces alces) movement and mortality on roads where habituation to traffic stimuli apparently occurred. Altman (1952) indicated that elk (Cervus canadensis nelsoni) became conditioned to the sight and sound of passing cars. She observed a cow elk move her calf off a paved road by walking back and forth, around it, and eventually pushing it sideways. More recently, Ward et al. (1973) reported that elk showed little aversion to traffic within 300 yards of an interstate highway, where noise reached 58 decibels. Carbaugh et al. (1975) found that grazing, lying, walking, or running were exhibited extensively by white-tailed deer (O. virginianus) along Interstate 80 in Pennsylvania. Reed et al. (1975) reported on Rocky Mountain mule deer behavioral responses to a concrete-box underpass under Interstate 70 in western Colorado. When individuals or groups of deer were observed near the underpass entrance, 50 to 100 feet from the westbound highway lanes, the passing of only 7.3 percent of 449 vehicles traveling west caused some flight reaction or escape behavior (as defined by Hediger 1950; Scott 1958). These observations suggest a hypothesis that ungulates, particularly mule deer, habituate to the sight and sound of traffic. Others have reported some reluctance in ungulates to approach or cross highways. In Glacier National Park mountain goats (Oreamnos americanus) often hesitated in cover or on the pavement edge, and walked stiff-legged or ran across the highway (Singer 1975). Ward et al. (1973) indicated that a highway acted as a barrier to elk movement. Behrend and Lubeck (1968) provided evidence that white-tailed deer are more sensitive to disturbance along roads than they are in more removed areas. Villmo (1975) suggested that reindeer, which have habituated to roadways, may still be adversely affected by their proximity. He hypothesized that reindeer forage utilization is decreased along roadways because they interrupt feeding and resting activities each time an automobile passes. In a study by Rost (1975), densities of Rocky Mountain mule deer fecal pellet groups increased with distance from roads in two of three vegetation types. However, the assumption that pellet-group densities are valid measures of habitat use is questionable. The rate of fecal deposition might be affected by many factors (Neff 1968), such as psychological stress caused by traffic-associated stimuli.

The combined result of habitat loss and road kills may be of significance to deer populations but we can cite no quantified examples of the effect. We can only consider it to be one of the ineluctial forces working on mule deer, and one which we are unlikely to reverse but only modify with more intensive management.

AGRICULTURAL DEVELOPMENTS

Linsdale and Tomich (1957:287) stated "Mule deer are more strictly mountain animals than they were in primitive conditions, mainly because of the removal of woody vegetation from the flat lowlands by human cultivation and other use of the soil." This may be a questionable generalization in face of the eastward expansion of mule deer in the prairies, but it is reasonable to believe that agriculture grossly alters the character of mule deer habitat. The net result probably varies with the extent of cultivation, the location, and the crops. Consequently, attempting to correlate changes in mule deer numbers with the history of agricultural development is hazardous at best.

The available historical records of agricultural development offer little information relative to mule deer habitat. Certain national and regional data are reviewed here along with data from Colorado that can be related more specifically to mule deer.

Availability of irrigation water has made crop production possible on many soils of the western U.S. that were previously unsuitable for agricultural development. Irrigated land on farms throughout the U.S. totaled more than 37 million acres in 1964 (National Academy of Sciences 1970). The 17 western states accounted for more than 33 million acres. Nationwide, land under irrigation in 1970 was increasing at the rate of 780,000 acres annually, and during the period 1949 to 1964, western states accounted for 80 percent of the increase (National Academy of Sciences 1970). If this trend continued, by 1976 there would have been over 40 million acres of irrigated land in the western U.S.

Although there has been a steady increase in irrigation, much of the land was already in crop production, particularly in the more humid eastern U.S. However, much of the increase in land irrigated between 1950 and 1965 in the 17 western states also comprised land previously cultivated under dry-land conditions. In the most arid states (New Mexico, Arizona, Utah, and Nevada) the irrigated area increased from 2.7 to 3.0 million acres between 1950 and 1965 and most of this represented "new" cropland (National Academy of Sciences 1970).

It is important to note from the standpoint of mule deer habitat that 51 percent of the irrigated cropland in the West was used for the production of livestock feed (National Academy of Sciences 1970). Much of this land was pasture, hay lands, or other nonharvested crops and may have had a different effect than would the same amount of land irrigated for corn production.

Using Colorado as an example of the western states, it is possible to obtain values that relate more specifically to the magnitude of the encroachment of agricultural development on mule deer habitat. By overlaying maps of mule deer range (Colorado Division of Wildlife) on Colorado's land use maps prepared by the Colorado Land Use Commission, acres of mule deer range encompassed by irrigated and nonirrigated cropland was determined. The land use map was prepared in 1973 but more realistically reflected land use in 1971 or 1972. Since most of the mule deer in Colorado are found from the

43 Alteration of Mule Deer Habitat
Table 2. Miles of Interstate, rural, and county highways and projected areas of right-of-way in Colorado.

<table>
<thead>
<tr>
<th>Year</th>
<th>Interstate</th>
<th>Rural</th>
<th>County</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimated</td>
<td>Projected</td>
<td>Estimated</td>
</tr>
<tr>
<td>Mileage 1/</td>
<td>Acres 2/</td>
<td></td>
<td>Mileage 1/</td>
</tr>
<tr>
<td>1974</td>
<td>890</td>
<td>39,712</td>
<td>8,457</td>
</tr>
<tr>
<td>1970</td>
<td>832</td>
<td>37,103</td>
<td>8,299</td>
</tr>
<tr>
<td>1950</td>
<td>---</td>
<td>---</td>
<td>11,555</td>
</tr>
<tr>
<td>1940</td>
<td>---</td>
<td>---</td>
<td>11,840</td>
</tr>
<tr>
<td>1935</td>
<td>---</td>
<td>---</td>
<td>9,420</td>
</tr>
</tbody>
</table>


2/ Based on 44.6 acres per mile planimetered from aerial photography of Interstate 70 (4-lane divided highway) east of Avon, Colorado.

3/ Based on a calculated 12.1 acres per mile, assuming a right-of-way width of 100 feet.

4/ Based on a calculated 7.3 acres per mile, assuming a right-of-way width of 60 feet.

5/ The decline in mileage was caused by road reclassification and by a declining rural population which led to decreased rural road use and a decline in the number of miles of road maintained.

Table 3. Estimated number of mule and black-tailed deer (Odocoileus hemionus) killed from collisions with vehicles in the western U.S.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizona</td>
<td>135</td>
<td>170 3/</td>
<td>300 3/</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>California</td>
<td>8,387</td>
<td>4,864</td>
<td>4,604 3/</td>
<td>4,932</td>
<td>3,832</td>
<td>4,008</td>
<td>3,499</td>
</tr>
<tr>
<td>Colorado</td>
<td>1,524</td>
<td>2,367</td>
<td>2,539</td>
<td>5,338</td>
<td>5,875</td>
<td>6,406</td>
<td>6,882</td>
</tr>
<tr>
<td>Idaho</td>
<td>700</td>
<td>---</td>
<td>700 3/</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Montana</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Nevada</td>
<td>250</td>
<td>196 4/</td>
<td>184</td>
<td>190</td>
<td>176</td>
<td>144</td>
<td>121</td>
</tr>
<tr>
<td>Oregon</td>
<td>561</td>
<td>3,151</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Utah</td>
<td>1,800</td>
<td>---</td>
<td>1,800 3/</td>
<td>1,683 3/</td>
<td>1,579 3/</td>
<td>1,800 3/</td>
<td>941 3/</td>
</tr>
<tr>
<td>Washington</td>
<td>1,974</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>1,590</td>
</tr>
<tr>
<td>Wyoming</td>
<td>1,210</td>
<td>---</td>
<td>1,546 3/</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Totals</td>
<td>16,896</td>
<td>11,047</td>
<td>12,098</td>
<td>12,647</td>
<td>12,992</td>
<td>14,323</td>
<td>13,350</td>
</tr>
</tbody>
</table>


2/ Arizona Game and Fish Department. 1969. Wildlife Newsletter 3(50):1. (Mule deer only)


4/ Estimates based on fiscal year (1 Jul-30 Jun) tabulations (Per. comm. G. Gates, New Mexico Dept. Fish and Game, Santa Fe).


6/ Per. comm. D. Strickland, Wyoming Game and Fish Dept., Cheyenne.
obtainable. The situation may be improved by the
with their accompanying increases in automobiles,
mule deer. This is mostly due to property ownerships,
the whole of mule deer range, it seems improbable that the
information but summaries of the records are rarely
HOUSING DEVELOPMENTS
Available records of acreage involved in housing
developments are practically nonexistent. County
governments are generally the only source of inform-
but summaries of the records are rarely
obtainable. The situation may be improved by the
increasing activity of county and state land use plan-
ning commissions.
The land use maps prepared by Colorado's Land Use
Commission (1973) indicate that 1,079 square miles
(1.7 percent) of mule deer range in that State were in
housing developments. This represented only those
areas that had been platted and offered for sale and
did not include areas under consideration for devel-

dopment. In the western U.S. in general, and in
Colorado specifically, many of these developments have
occurred on wintering areas that are most critical to
mule deer. This is mostly due to property ownerships,
general topography, and previously located transpor-
tation and utility corridors. These developments,
with their accompanying increases in automobiles,
snowmobiles, other motorized vehicles, dogs, and human
activity, affect large areas beyond the actual boun-
dary of the specific housing development. As a
result, the overall effect of housing developments on
mule deer habitat is greater than indicated by anal-
ysis of only the actual land area impacted.

However, if the values obtained for Colorado on
extent of housing development are realistic for the
whole of mule deer range, it seems improbable that the
small amount of deer habitat involved would result in
a regional decline in numbers of mule deer. Local
developments may essentially eliminate deer from
limited areas. Unfortunately, we are unable to assess
the sum of such influence.

DISCUSSION

Each of the factors discussed — fire, logging,
routes, agricultural and housing development — alters
the habitat for mule deer in some manner. The effect
of these factors, taken either singly or in combina-
tion, on numbers of mule deer remains unknown. It is
difficult to relate cause and effect when neither has
been carefully defined and quantified. If we are
genuinely interested, we must develop uniform data
gathering procedures applicable to the entire range of
mule deer. When we can describe the magnitude of
habitat change over time, we will be in a better
position to assess the impacts on deer populations.

Perhaps the most important message of this
paper is that man keeps poor records of the vie-
itudes of his environment. We have no systems for
inventorying quantitative changes in the habitats on
earth, and only rudimentary concepts of their quali-
tative significance. It is important that this
deficiency be overcome, that we employ reliable in-
formation rather than crude speculation in our
assessment of wildlife habitat on a national scale.

There is a common interest in this matter, and
it will be best served through a common effort. A
potential vehicle for this purpose is the Forest and
Rangeland Renewable Resources Planning Act of 1974
(PL 93-378). It assigns to the U.S. Department of
Agriculture, Forest Service, in cooperation with
other agencies, the responsibility for a continuing
assessment of the renewable natural resources of the
U.S. in the following systems: wildlife and fish
habitat; outdoor recreation and wilderness; range-
land grazing; timber; land and water; human and com-
munity development. A first order of business is
the determination of information needs and the
methodology for fulfilling these. A multidiscipli-
ary group with this assignment has been assembled in
the Rocky Mountain Forest and Range Experiment
Station, headquartered in Fort Collins, Colorado.
The Colorado Division of Wildlife is cooperating in
the development of techniques for monitoring land
and vegetation attributes related to the quantita-
tive and qualitative adequacy of mule deer habitat.
This program will link data from air- and satellite-
borne surveillance systems to on-the-ground evalu-
ations. The results will be built into the national
inventory system for all resources, which, hopefully,
will take us a respectable large step toward more en-
lightened habitat evolution.

LITERATURE CITED

Altmann, M. 1952. Social behavior of elk, Cervus
canadensis nelsoni, in the Jackson Hole Area of

Behrend, D. F. and R. A. Lubeck. 1968. Summer
flight behavior of white-tailed deer in two
Adirondack forests. J. Wildl. Manage. 32(3):
615-618.

Carbaugh, B., J. P. Vaughan, E. D. Bellis, and R. B.
Graves. 1975. Distribution and activity of
white-tailed deer along an interstate highway.

Caughley, G. 1970. Eruption of ungulate popula-
tions, with emphasis on Himalayan thar in New

Edgerton, P. J. 1972. Big game use and habitat
changes in a recently logged mixed conifer
forest in northeastern Oregon. Proc. Annu.
Conf. W. Assn. State Game and Fish Comm. 52:
239-267.

Edwards, R. Y. 1956. Snow depths and ungulate abun-
dance in western Canada. J. Wildl. Manage.
20(2):159-168.

Geist, V. 1971. A behavioral approach to the man-


Picton, H. D. and R. R. Knight. 1969. A numerical index of winter conditions of use in big game management. Montana Fish and Game Dept. Spec-


Reynolds, H. G. and H. W. Springfield. 1953. Re-


vegetation management plan, Grand Teton National Park. 47 p. (Processed)

Wallmo, O. C. 1969. Response of deer to alternate-


INTERSPECIFIC COMPETITION BETWEEN MULE DEER, OTHER GAME ANIMALS AND LIVESTOCK

Richard J. Mackie
Department of Biology
Montana State University
Bozeman, Montana 59715

Abstract

Comparisons of available data on distributions, range use and food habits, and behavior indicate that mule deer may interact in a competitive relationship with each of the other species of wild and domestic ungulates which they associate on western rangelands. Existing studies, however, have not produced substantive evidence for the existence of competition generally or more than very general conclusions about its exact nature and importance; and most current thinking remains rooted in inference and speculation and is controversial at best. This essentially precludes any firm conclusions as to the possible significance of interspecies relations and competition in current trends of mule deer populations in western North America.

Mule deer (Odocoileus hemionus) rarely, if ever, exist in species populations completely isolated from contact with other wild and domestic ungulates. Throughout their distribution, they cohabit rangelands at least seasonally with one or more of the other wild ungulates native to western North America. Most of these rangelands are also grazed by domestic livestock, including cattle, sheep, horses, and occasionally, mules, burros, goats, and hogs. Locally, feral or "wild" populations of domestic animals as well as introduced wild ungulates also occur. Because of this, the possibility of competitive interactions has occupied the minds of wildlife, range, and livestock managers and scientists for many years; and it is not surprising that interspecies relationships of mule deer now loom as a possibly significant factor contributing to recent declines in populations of this species over much of the western United States and Canada. What is surprising, in view of the widespread attention given generally to interspecies relationships of large herbivores and specifically to mule deer during the past half-century or more, is that remarkably few firm conclusions of general application have emerged. Much of our current thinking remains rooted in inference and speculation and is controversial at best. This apparently applies also to almost all of our conclusions about the importance of competition in natural ecosystems generally (Miller 1967).

INTERSPECIES RELATIONS AND COMPETITION

Interspecific relationships of living organisms have been viewed in many ways. Odum (1959) listed eight important interactions which may occur between two or more species populations: (1) neutralism, in which neither population is affected by association with the other; (2) competition, in which each population affects the other; (3) mutualism, in which interaction is obligatory for the growth and survival of both populations; (4) proto-cooperation, in which both populations benefit from a non-obligatory association; (5) commensalism, in which one population is benefited but the other unaffected; (6) amensalism, in which one population is inhibited and the other unaffected; (7) parasitism and (8) predation, wherein one population is dependent upon and adversely affects the other by direct attack.

In the above context, competition is limited to those interactions which adversely affect growth and survival of both species populations involved and ultimately result in the elimination of one as defined by the competitive exclusion principle (Hardin 1960). Others have defined it as active demand by two or more individuals of the same species population (interspecies competition) or members of two or more species at the same trophic level (interspecies competition) for a common resource or requirement that is actually or potentially limiting (Miller 1967). In practical usage, "competition" usually has been applied rather loosely to include almost any interaction with an assumed or real, negative outcome, including those in which the welfare of only one species may be adversely affected (amensalism of Odum 1959).

Competition may involve elements of "interference" as well as "exploitation" (Miller, 1967). Interference refers to any activity which directly or indirectly limits a competitor's access to a necessary resource, usually in a spatial context. Exploitation refers to utilization of a resource once access has been achieved, usually in the sense that two individuals or species with unlimited access to a common source of food or nutrients will have different abilities or opportunity to exploit the available supply.

The role of interference in competition among large herbivores is largely unknown. Interspecies aggression approaching territoriality, as required by Miller's (1967) definition of interference, is not known among ungulates, at least in western North America. However, an element of interference is
Kansas, Oklahoma, and Texas, and parts of Colorado, Washington, from western Manitoba westward to Alberta overlaps that of mule deer generally across the northern United States from the western Dakotas to eastern Montana and northern Idaho, both mule deer and elk may browse extensively throughout the year and prefer similar species.

In general, available data suggest considerable opportunity for interspecific competition between mule deer and elk where species populations occupy the same range. Because elk appear to be more adaptable and flexible in their choice of habitats and forage preferences, most authorities have concluded that, in the event of interaction, elk would be the more efficient competitor and survive at the expense of mule deer. However, there is as yet little quantitative support of competition between the two species being an important factor in the population ecology of either one. Among the few accounts of elk-mule deer interactions in the literature, Cliff (1939) described heavy deer mortality in Idaho during the severe winter of 1931 to 1932 resulting from extensive utilization of important mule deer forage plants by elk.

Bighorn Sheep.—Although the distribution of mule deer almost completely overlaps that of bighorn sheep throughout the western United States and Canada, bighorn ranges comprise only a very small proportion of the total distributional range of mule deer. Studies of local species populations indicate that in many areas at least they may utilize similar habitats and prefer much the same forage; while to others, habits diverged. In general bighorns appear to utilize grasses to a much greater extent and browse to a lesser extent than deer in most areas of comparative study, but sufficient overlap in plant
winter, with some similarities in habitat usage and may not be real because of differences in use of habits of mule deer and cattle have indicated that may occur in association with mule deer as in the

Mule Deer Interactions With Domestic Ungulates

As well as general comparisons of range use and food habits of mule deer and cattle have indicated that some competition may occur wherever the two species occur together. Most comparative studies have indicated broad differences in use of local habitat types and physiographic sites as well as in forage preferences of mule deer as compared with cattle much that competition is likely to be minimal in most cases where ranges are properly stocked and in good to excellent condition. However, cattle often make sufficient use of important deer forage plants and feeding areas to compete seriously where stocking rates are high, when plant growth is reduced by drought or prior heavy usage, or when grazing begins too early, extends too long, or occurs on critical winter or other seasonal range areas. Because of this, both the actual occurrence and the intensity of conflict probably vary widely in time and space.

That cattle may "interfere" with deer usage of all available habitats and exclude deer use in some areas has been suggested by McMahan (1966), Firebaugh (1969), Dusek (1971), and Knowles (1975). However, direct evidences of exclusion and quantification of the effects of competition by cattle on mule deer populations is generally lacking. McMahan and Ramsey (1965) reported a low carrying capacity for white-tailed deer in all pastures continuously grazed by a mixture of livestock including cattle, as compared with deer-only managed areas. Reproduction and survival of fawns in these pastures varied in relation to stocking rates with no fawns ever surviving to yearling age on heavily stocked pastures.

Sheep. -- Range usage and food habits of domestic sheep may overlap those of mule deer even more closely than in the case of cattle. Cumulative data on interactions do little to alter the basic conclusion of Smith and Julander (1953) that "the similarity of sheep and mule deer diets is sure to cause conflict wherever the supply of preferred (forage) species is inadequate to satisfy the requirements of both animals...even though an adequate forage supply obviates any actual conflict, there is competition in the sense that if part of the deer population was removed, sheep numbers could be increased and vice versa." Evidences of "interference" or local exclusion of mule deer from areas grazed by sheep have not been recorded quantitatively in the literature.

Other Livestock and Feral Ungulates. -- Both domestic and "wild" horses and burros may be associated with mule deer, grazing similar local areas and habitat types. While "wild" populations have increased due to protection in recent years, concern for possible competition has also increased; but as yet few quantitative data have appeared. Available information suggests considerable differences in forage preferences, but use of herbage as well as winter browse species of mule deer may constitute serious competition affecting mule deer adversely.

Multi-species Relationships

Frequently, mule deer occur in species populations associated with more than one other ungulate. For example, both elk and cattle occur broadly across the range of mule deer. Where they occur together, interactions may be intensified and/or vary from those of observed when only one is present.
Numerous studies have shown a high degree of similarity in range usage and yearlong forage preferences of elk and cattle. In most respects the habits of elk overlap those of deer on one hand and cattle on the other. Further, elk clearly tend to avoid cattle whenever possible and seek those areas where no cattle occur (Skovlin et al. 1968, Lonner 1975, Komeroc 1976). Thus the presence of cattle tends to intensify opportunities for conflict between elk and mule deer and, perhaps between mule deer and cattle as well. Elk withdraw into areas least grazed by cattle and/or concentrate in areas where no cattle occur, possibly causing or increasing the intensity of interaction where more or less occurred without cattle. Also, reductions in cattle numbers on many ranges, removal from others including many winter deer and elk ranges, and more restrictive management of elk on mutually used areas have all served to favor elk and intensify potential conflict with mule deer.

PROBLEMS IN ASSESSING INTERSPECIFIC COMPETITION

As the preceding discussions indicate, it is not especially difficult to obtain data indicating the possible occurrence of some interaction and/or exploitation-type competition among various species or species populations of larger herbivores. Clearly, mule deer may interact in competitive relationships with each of the other ungulates with which they associate. Opportunity, however, need not prescribe the fact; and, by itself, has little predictive value. Yet, existing studies, even with careful design, continued measurement and observation over several years, and exhaustive analysis, have not produced substantive evidence for the existence of competition or more than very general conclusions about its exact nature and importance. The lack of adequate means of measuring the biological and ecological effects of competition or other interactions and distinguishing these effects from those of other population regulating mechanisms and factors which express themselves in the same way may be a major reason for the fact that few firm conclusions have emerged. In addition, we may lack either adequate means or sufficient perspective to interpret existing data on habitat requirements and relationships. Because of this, both the kinds of data and the criteria which we commonly employ in assessing interactions probably have some important limitations.

The expected effects of interspecific competition among ungulates are those which directly or indirectly depress carrying capacity, create or intensify intra-specific competition, and ultimately result in changes in numbers or distribution, or both. Most wild ungulates, including mule deer, appear to be fairly adaptable in their choice of food and habitat requirements. Thus, under natural conditions they occupy a rather wide range of habitats wherein carrying capacities and species density vary naturally in relation to the kinds, quality, and amounts of food and cover available in local areas. In typical range-land situations, in which population densities of either or both competitors are at or close to their carrying capacities, it is difficult to distinguish the additional effects, if any, of interspecific competition from those of intraspecific competition. It is also difficult to distinguish effects of interspecies interactions and competition from those of various other environmental factors which similarly influence carrying capacity. Normal fluctuations in weather and snow conditions, forage production, predation, hunting, and other factors may elicit changes in carrying capacities or certain species responses and population consequences essentially indistinguishable from intra- or inter-specific competition.

Similarities and/or differences in distribution, range use, and food habits are not evidence a priori for or against a competitive relationship. There may be several reasons for this.

Only rarely, if ever, have we had opportunity to record these kinds of data for mule deer (or any other species) in a situation where no other species occurred. Thus, most existing information has been collected in places or under conditions when interaction was a matter of fact. Because of this, we usually find ourselves using data, which in themselves reflect effects of interaction, to determine whether interaction and competition are occurring.

Secondly, not all interactions need to be competitive. There are numerous reports in range and wildlife literature suggesting increased availability, palatability, or production of forage plants for one animal as a result of grazing or browsing activities of another. Bell (1971) described situations in the Serengeti Plains of Africa in which several species of herbivores grazed the same area and, to a certain extent, the same plants in a mutualistic or commensalistic relationship. On some western rangelands at least, the conversion of perennial grasslands to shrub and/or annual grass-forb types as a result of heavy early livestock grazing is believed to have improved forage conditions for mule deer. Reductions in densities of native perennial grasses paved the way for the subsequent abundance of palatable shrubs and/or introduced grasses and forbs which are more digestible than native perennials (Longhurst et al. 1968, 1976). A similar relationship is implicit in the concept that "round grazing practices play an important role in maintaining adequate browse stands essential for a healthy population of big and upland game (Clawson and Leaperance 1973)."

Furthermore, our preoccupation with more preferred and important forage plants in assessing competition may have ignored vital roles of lesser species in the diets of grazing animals and perhaps more subtle competitive relationships with respect to their use and availability. Biologists have long recognized an apparent requirement for a variety of forage items in the diet of large herbivores; and both Smith (1959) and Longhurst et al. (1966) have indicated that there may be physiological limits as to the amount of certain species, e.g. big sagebrush, that deer can consume. Longhurst et al. (1966) related this to inhibitory effects of essential oils on rumen function. Similarly, Freeland and Janzen (1974) point out that many plants normally fed upon by herbivores contain toxic materials which can have detrimental effects unless consumed with other kinds of plants which either offset or neutralize their toxicity.

Finally, competition for forage may begin long before preferred forage plants used in common are "overused". Livestock grazing trials have shown
repeatedly that rates of weight gain in heavily stocked pastures deviate from those under lighter stocking almost from the time cattle are placed in the pastures (cf. Woolfolk and Knapp 1949, Kipple and Costello 1960, Reed and Peterson 1961). The rate at which an animal can find food depends upon the density of food in its environment, the amount of time and effort spent in looking for food, and its efficiency in feeding all may be influenced by preemption or common usage well before total utilization reaches a "proper" level.

CONCLUSIONS

The fact that we must admit to knowing little about the exact nature and importance of competition essentially precludes any firm conclusions as to its possible significance in the current trends and status of mule deer populations in Western North America. This does not mean that competition is not or has not been of some or even considerable influence. Rather, it serves to point out that much remains to be accomplished in the way of finding ways and means of more effectively assessing interspecies relationships and applying our current knowledge to situations of potential competition on rangelands. Since existing data do not or cannot satisfy the demands of multiple use land managers attempting to accommodate all users, it seems imperative that we redirect our thinking and efforts to establish valid data and conclusions as rapidly as possible. Until we can fully document the biological and ecological significance of interspecies competition we can only continue to say maybe to the questions of whether competition is occurring or important.

LITERATURE CITED


53 Interspecific Competition


Abstract

Range improvements for mule deer in the western United States consist of (1) range seedings, (2) grazing management systems including fencing, (3) tree and brush removal, (4) water development, and (5) miscellaneous land treatments. The benefits, while intuitively positive, have rarely been successfully measured by documenting either changes in mule deer population size or behavior modifications.

Collectively, deer range improvement practices provide a combination of factors that are beneficial to mule deer. Monotypic seedings and most intensive grazing management systems developed within the range of the mule deer are apparently of little benefit. Tree and brush control projects are of greater benefit and water developments are beneficial primarily in the more xeric portions of the mule deer range. Prescribed burning is generally beneficial but only in certain habitats. Large variations in range forage productivity based on seasonal rainfall, "natural" population fluctuations, and intensive interspecific competition may mask the positive benefits of range improvements for mule deer.

It is recommended that the best possible techniques be used to evaluate benefits in terms of population size and behavioral changes that result from the effort to improve ranges.

INTRODUCTION

An estimate of the expenditures for range improvement for mule deer would be revealing. Revealing in the sense that considerable tax dollars have been spent to improve the general quality of the mule deer range while the benefits have rarely been successfully measured. The benefits have been intuitively positive. Ranges with low amounts of "desirable" forage are improved by either reseeding important species, reducing undesirable species, or both. Water developments are sometimes beneficial and fences either help or hinder.

Expected benefits, though seldom measured, have been assumed to be such things as improvement of herd health, increased vigor of individual animals, i.e., healthier does and stronger bucks. This, then, in at least the hypothetical sense, is followed by an increase in fawn/does ratios and herd numbers increase to the improved carrying capacity level.

In this paper I have attempted to review the literature concerned with mule deer range improvement practices. I have, in my search, sought those studies that have shown either an increase in herd number actually attributed to an improvement or, secondly, studies showing how the deer range improvement practice has caused a significant change in deer behavior resulting in management alterations. Negative effects were also sought. Population changes or fluctuations reported here are assumed to be valid. Others in this symposium will tell us how good the estimates are.

DEER RANGE IMPROVEMENTS FOR MULE DEER

It appears to be well established that overpopulations of deer lead to overuse of the habitat, followed by deer mortality (Severinghaus 1951; Russo 1964). Cheatam and Severinghaus (1950) found variations in fertility related to range conditions. Likewise, deer productivity has been shown to vary from habitat to habitat (Taber 1953), depending upon the availability and nutritive quality of the forage (Julander et al. 1961). The latter study showed that two mule deer ranges in Utah and Idaho had striking differences in deer productivity. Fall

weights of the Utah fawn bucks and does were 72 and 65%, respectively, of weights of the Idaho fawns. Forage production, ovulation rates and fetal weights were all higher on the Idaho range. The authors concluded: "A good summer range, capable of carrying deer in good condition through the breeding season is necessary for maximum herd productivity."

Swank (1958) found that summer forage nutrition strongly controlled ovulation rates and the number of fawns developed per doe. A dry summer coupled with excess deer numbers resulted in poor bucks and an extremely low fawn crop (28 fawns per 100 does).

Robinson et al. (1952) studied deer mortality in relation to range condition after the severe 1948-49 winter in Utah and found the following:

<table>
<thead>
<tr>
<th>Herd Mortality</th>
<th>Lbs. green forage/deer-day use</th>
</tr>
</thead>
<tbody>
<tr>
<td>9%</td>
<td>57</td>
</tr>
<tr>
<td>26%</td>
<td>13</td>
</tr>
<tr>
<td>42%</td>
<td>9</td>
</tr>
</tbody>
</table>

Deer winter losses varied inversely with the amount of available forage on the winter range.

Taber (1953) found that black-tailed deer showed differing reproductive rates, depending upon cover type. Open brush types were considerably more productive (147 fawns/100 does) than either burned sites (115.6 fawns/doe) or stands of mature brush (84.3 fawns/100 does) at the beginning of the winter.

Another good example of the strong relationship between deer population changes and habitat differences brought about by management is the study by Biswell et al. (1952) with black-tailed deer in the North Coast Range of California. Three areas were compared: (1) heavy brush cover, (2) wildfire burn, and (3) open brush consisting of an interpersation of grasses with patches of dense brush.

<table>
<thead>
<tr>
<th>Deer/sq. mi.</th>
<th>Ovulation Rates (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heavy brush</td>
<td>10-30</td>
</tr>
<tr>
<td>Wildfire burn</td>
<td>5-160</td>
</tr>
<tr>
<td>Opened brush</td>
<td>40-110</td>
</tr>
<tr>
<td></td>
<td>84</td>
</tr>
<tr>
<td></td>
<td>130</td>
</tr>
<tr>
<td></td>
<td>147</td>
</tr>
</tbody>
</table>

Populations in the heavy brush and opened brush were rather stable; but in the wildfire burn, large numbers of deer moved in when the sprouts were young and tender and moved out during cold winter. These data show how deer vary in their ability to reproduce and grow in different kinds of habitats.

Segelquist (1974) attempted to study the effects of forage clearings on the health and population characteristics of a herd of 23 white-tailed deer from 1968-72 in a 600-acre fenced enclosure in Arkansas. Loss of nearly half the animals as a result of predation, the collecting of animals for necropsy, death from unknown causes, and animals escaping from the enclosure precluded the making of valid conclusions concerning the influence of management changes on population characteristics of deer. This study seems to exemplify the problems that are often encountered.

Several researchers have found a close relationship between the percentage utilization of bitterbrush by deer and fawn survival. For example, Dasman and Biswell et al. (1954) showed a relationship between the intensity of bitterbrush cropping and the success of the succeeding season's fawning as reflected by fall does/fawn ratios. They concluded that bitterbrush can serve as an indicator species in the management of the deer herd. Under conditions of their study, when the cropping of bitterbrush leader growth exceeds 25 percent, a moderate decline in fawn survival can be expected the following year. When utilization exceeds 36 percent, a steep population decline can be expected. Can tag sales and control of hunter success be used to remove animals from these heavily utilized ranges?

It has been known for many years that good deer forage is characteristic of "sub-climax ecologcal conditions" (Leopold 1950). Lyon (1966) described the benefits to deer and elk populations provided by wildfire in the northern Rocky Mountains in the early part of the century. This post-fire disclimax vegetation proved to be very favorable for wildlife. Shrub dominance favorable to deer and elk may continue for another 50 to 80 years but will eventually be displaced by trees. Future managers will be required to make decisions relative to trees versus shrub habitat and the desirable proportions of each.

Over much of the range of mule deer heavy livestock grazing has been instrumental in providing a desirable sub-climax vegetation with grasses reduced and browse and forbs increased. Longhurst et al. (1976) believe that the general shift from sheep to cattle is strongly related to the mule deer decline. Their hypothesis is that cattle tend to overgraze ranges to the detriment of deer forage or that sheep do a better job than cattle in maintaining the successional forbs and grasses which are necessary for deer.

Deer range is enhanced when certain species are prevalent. Numerous studies have described deer food habits (Dasman and Biswell et al. 1954; Anderson et al. 1965; Wood et al. 1970; Tueller and Lesperance 1970; McCulloch 1973; Goodwin 1975; and Tueller 1976) showing the high preference and apparent palatability of a relatively few species. Overbrowsing by deer gives less desirable plants a competitive advantage and the entire flora tends to shift to composition less desirable for mule deer (Leopold et al. 1947). Management programs designed to increase important species are clearly needed. In addition, managers should not lose sight of the fact that certain naturally occurring plant communities are much more desirable than others with respect to deer use. Several authors have shown significant differences among plant communities relative to deer use (Darling 1937; Rasmussen 1941; Biswell et al. 1952; Segelquist and Tueller 1970; Mackie 1970; Tausch 1973; Tueller and Monroe 1975). Plant communities shown to be of special significance should receive the highest priority for improvement and restoration funding. For example, in Montana, Mackie (1970) found the *Pinus-Juniperus* habitat type to be of greatest importance during summer, *Artemisia-Agropyron* in fall and winter, and the *Artemisia-Agropyron* and *Pinus-Agropyron* types received the greatest use in the spring. Tueller and Monroe (1975) reported from Nevada that the *Artemisia*
tridentata/Purshia tridentata/Poa secunda, Cercocarpus ledifolius/Symphoricarpus longiflorus/orb and Artemisia tridentata or Ponderosa/Purshia tridentata/ Festuca idahoensis or Agropyron spicatum plant communities are of considerable importance for mule deer Statewide and therefore should receive the greatest management input.

Other generally uncontrollable factors are known to have strong definite influences on deer range vegetation and subsequently on deer population size. These include, but are not necessarily restricted to, the following: drought, climatic anomalies, flooding with intense erosion, and fire. Wallmo (1959 & 1962) described the influence of drought on mule deer in the Chihuahuan desert of Trans-Pecos, Texas. A severe 6-year drought in the mid-1950's reduced deer density from 4.3 to 6.5 deer per 100 ha. during the drought. Within three years after the drought, the deer populations rose to over 11 deer per 100 ha. Forage, particularly shrubs, significantly increased at the same time. White-tailed deer populations in Texas, Arizona, and throughout the Southwest are regulated to a large degree by precipitation during the preceding year or 18 months (Shaw 1965; Teer et al. 1965). McColl (1976) reported that a Nevada drought between 1959 and 1961 triggered a statewide deer population decline that did not bottom out until 1966. Many years ago, Darling (1937) described significant interactions between climate and vegetation as it related to deer movement. Mackie (1970) described deer movement or land use in relation to steepness of slope and aspect or exposure, as well as climate. Mule deer distribution and migration patterns are strongly influenced by climate in the Great Basin and Intermountain Region and tend to vary considerably from year to year. These data support the intuitive feeling that the welfare of deer is generally enhanced under good range conditions and that the converse is true, namely that poor range conditions diminish the vigor, reproductivity, and general welfare of our deer herds. The logical result of this thinking has been programs to improve range conditions. These programs generally have consisted of the following:

(1) Range seedings - most have been done primarily for livestock, although mule deer may have received some side benefits. Some have been accomplished primarily for mule deer and, in some cases, livestock, as well have benefited.

(2) Grazing management - an obvious example would be fencing to exclude cattle during the summer from important winter deer ranges.

(3) Tree and brush control - removal of mature, overmature, and decadent pinyon-juniper trees, by either cabling or chaining, has been an extensively used technique for improving deer ranges. Also, stands of heavy brush have been opened to increase the relative composition of browse, forbs, and grasses for mule deer use. Prescribed burning has sometimes been used as a technique to accomplish the same results.

(4) Water developments - deer are influenced in their pattern of land use by the lack of water and likewise by the provision of new water sources.

(5) Miscellaneous treatments - fertilization, chemical treatments to remove competing vegetation, and other techniques have been used to improve deer ranges.

Range Seedings

The techniques for seeding to restore mule deer ranges have been carefully described by Plummer et al. 1968. Successful seeding requires a consideration of various techniques, e.g., burning, chemical treatments, interseeding, and other planting procedures. The need is to select species with the following characteristics:

1. High in nutrients for deer.
2. Cured or mature with a high supply of nutrients desirable for mule deer health.
3. Readily available seed source at a reasonable cost.
4. Strong emergence (possible need to protect seed and seedlings from rodents).
5. High establishment percentages (growth through the first field season).
6. High survival percentages (regrowth following the first and second winters).
7. Drought and frost hardiness.
9. High productivity of usable deer forage.
10. Self-renewing (good seed production followed by volunteer establishment).

After seed selection, recommended seeding and management techniques can then be followed to produce a desirable stand of vegetation with the important required characteristic of species diversity (Plummer et al. 1968; Tueller and Monroe 1975).

Plummer's work with actual seedings, along with the observations of Tueller and Monroe (1975), Mackie (1970), and many others, clearly show the importance of providing a mixture of forbs, grasses, and browse for optimum deer use. Plummer et al. (1966) also list the important species that should be considered for use on mule deer ranges and they and others are continuing to screen species for good adaptability.

There is some concern that it is often difficult to objectively evaluate vegetation trends for mule deer. The reason is that animal numbers often are such that the new vegetation is quickly overbrowsed or overgrazed and cannot survive after establishment. This, of course, suggests the need for deer number management, including better distribution.

Revegetation should be accomplished first, where needed, for critical deer ranges. Often, these critical deer ranges are winter ranges and may be critical only one out of 10 years. They are an absolute necessity during that tenth year and may help provide proper use of all adjacent deer ranges during the non-critical years.

Over one million acres in Nevada have been seeded to adapted exotic perennial grasses. Similar acreages have been seeded in adjoining states.
within the range of mule deer. Do mule deer use perennial grass seedings in the Great Basin and Intermountain Region? If so, when and how are they important? Actual studies are limited. Plummer and Stropaly (1959) found Agropyron cristatum (crested wheatgrass) to be one of the grasses grazed by mule deer in the early spring or ranges treated for pinyon-juniper control. Investigations in south-central Nevada revealed 90% utilization of A. cristatum by "deer and rabbits"; however, no apparent effort was made to differentiate the relative degree of utilization by the two species (Stimson 1964). Rumen analysis of two wintering mule deer on rehabilitated pinyon-juniper range in Utah showed the occurrence of mature seedheads of A. cristatum in the sample (Plummer et al. 1966). Urness (1966) concluded that crested wheatgrass "is actively sought by deer on winter range and is, when available, important in fall, spring, and snow-free periods in winter."

Cole (1968), in Nevada, studied created wheatgrass seedings in areas adjacent to known mule deer ranges. Of 25 seedings studied, only three showed a measurable use by mule deer. Those sites found to be used by deer contained residual browse that was thought to account for the measurable deer use based on pellet group counts and browse use. Cole concluded that mule deer range was not extended by created wheatgrass seedings in Nevada on ranges not previously used as winter ranges. The monotypic nature of created wheatgrass seeded range apparently inhibits utilization of all but peripheral areas of such range. If large enough, this monotype may restrict or alter mule deer movements from summer to winter ranges.

Grazing Management Systems

Is it possible to include deer in a grazing system including livestock? There is no reason why not, although it seems that such has been rarely accomplished. The important consideration here would be to assure that deer and livestock are not competing for the same forage. In the Great Basin it has been shown that there is a mule deer-livestock competition period that occurs in late summer and early fall when livestock feed heavily on bitterbrush (Tueller and Monroe 1975). At this time the bitterbrush is still carrying on photosynthesis and restoring carbohydrates to depleted roots and is, therefore, susceptible to browsing damage. Winter deer browsing of the dormant bitterbrush is less damaging if at all.

In Nevada, key winter deer ranges should probably have livestock use removed by fencing. The fences themselves may constitute a hazard, but depending on the terrain, may be placed in places that would not directly interfere with known spring-fall migratory routes. Longhurst et al. (1976) reported black-tailed deer mortality as one deer lost annually for each 8 miles of fence. This was an area with high deer density (100/square mile). They concluded that fences account for the loss of several thousand deer each year in California.

Rest-rotation grazing systems or other systems designed to enhance the vigor, reproduction, and growth of a variety of range plants must also have an influence on populations of wildlife. Grazing management systems designed to enhance monotypic stands may cause a reduction in good mule deer habitat (Cole 1968). Other systems may, because of their design, enhance the accumulation and maintenance of a diversity of species. A diversity of species will then serve to attract deer use (Tueller and Monroe 1975).

No studies of grazing management systems have included definitive analysis of resident deer herd changes. For example, a Wyoming study (Gibbens and Fissel 1970) concluded after a 4-year study of a 65,000 acre rest-rotation grazing system, that, although resident deer were seen in all pastures, "there are no indications of an increase in the resident population."

Fences designed to remove livestock from key deer ranges where competition is known to occur constitute a positive treatment to improve deer range. I found no published studies reporting such benefits but such fences in Nevada have been instrumental in improving heavily used winter ranges that cattle have grazed for browse in late summer and fall.

Tree and Brush Control

Tree and brush control for improvement of mule deer habitat has been practiced rather extensively for the past 25 years. Terrel and Spillet (1975) quote Box et al. (1966) indicating that between 1950 and 1964, 3 million acres of pinyon-juniper woodland in 1200 projects have been converted in the U.S. This, along with the over three million acres of sagebrush control in the West and control of other brush types not so well documented, constitutes a considerable land treatment for the benefit of mule deer.

The basic question that keeps rising is this: Do these treatments actually increase deer numbers via the generalized mechanism discussed in the introduction? First of all, it seems very clear that deer are attracted to the improved areas. Tauch (1973) showed in Nevada that deer use increased on the pinyon-juniper control areas. However, deer use was found to be highest on those areas originally containing the greatest diversity. The level of use was also dependent upon the nearness of untreated escape cover and on the close proximity of the treated area to existing deer use areas.

Cole (1968), also working in Nevada, found increased deer use inside pinyon-juniper control projects. At one site peripheral paired plots showed an 87.3% increased utilization in the treated range. However, analysis over the entire area, i.e., within the chaining, showed only a 3% increase, suggesting the strength of the edge effect.

Terrel (1973) found increasing deer use in the vicinity of pinyon-juniper chaining but in the natural undisturbed pinyon-juniper. In the initial 12 years post-treatment in Terrel's Utah study, no increase in deer numbers was correlated with pinyon-juniper conversion.
In an Arizona study (Urness 1974) deer use was found to be lower by 1/4 to 1/2 on root-plowed areas when compared to adjacent brush fields even though production of high-quality forbs was much greater on the root-plowed area. The author pointed out that the lower deer use figures for the 80-acre root-plowed sites does not necessarily reflect low relative use. Only feeding was taking place on the root-plowed acres, while feeding, resting, ruminating, etc., are taking place on the undisturbed areas. Even though deer spend less time on the brush-controlled areas, the increased feed may compensate for the lack of use, providing treatment size is moderate. This study indicated that brush control areas should not exceed 300-400 yards in width and no more than 50 percent of an area should be treated. Also, some intact brush should be left on all exposures since mule deer in the area of the study change exposure preference, seasonally. Herb population changes were not reported, although management preferences seemed apparent.

An elongated burn area in an “unthinned” treatment on the Wild Bill study site in Arizona was considered to be a “forest opening” known to be preferred by deer (Kruse 1972). Deer use on the burned area showed a consistent yearly rise from 1966-70. Deer use on the clearcut and thinned ponderosa pine areas had been steadily decreasing (after an initial high use value immediately after the treatment) from 1966-67. These data (Table 1) show that the deer moved from the clearcut and thinned area to the fresh burn in the unthinned area, thus concentrating their use on the most favorable sites. The deer readily moved their use to a newly created site, in this case, a wildfire occurring in the control or unthinned site.

Longhurst et al. (1976) have reported data in California to show that a decrease in wildfires due to better fire control, in spite of a trend toward more fire starts, has reduced deer habitat. In some locations they found high correlations between buck kill and acres burned. They suggested the possibility that fires at higher elevations may improve the supply of forbs. However, in much of the Great Basin, most fires occur at lower elevations, thus tending to reduce this benefit over much of the mule deer range although some use may be made of cheatgrass (Bromus tectorum) in winter and early spring. Prescribed burning certainly must be fully developed in future management programs.

An area of lodgepole pine and spruce-fir forest in Colorado was clearcut in narrow strips alternating with uncut strips (Wallace et al. 1970). Production of deer forage 15 years after logging was 47% greater on cut strips. Tame mule deer used in grazing studies obtained 63.2% of their forage from cut strips, 27.4% from uncut strips and 9.3% from logging roads. These sites composed 44.2, 49.4, and 6.4 percent, respectively, of the study area. Mule deer density figures derived from carrying capacity determinations on these sites resulted in numbers far in excess of deer numbers estimated for the area. This is another good example of deer congregating on an area as a result of habitat improvement but without data on benefits to herd size or structure.

Also, a subsequent study (Regelin et al. 1974) showed that the unlogged forest produced enough deer forage, adequate in the nutritional parameters measured, to carry more deer than are presently estimated to occupy the summer range. Deer populations in the study area are apparently limited by the amount of available winter range. In this case further range improvement and revegetation may be futile since the limiting factor is associated with sites removed from those being studied, namely, the winter range.

It seems apparent that new brush or tree control treatments have benefits due to increased use in the years immediately post-dating the treatment. Question! How often and how many treatments of what size in a given habitat are required to provide optimum benefit to mule deer populations?

Water Developments

Water developments have the potential to accomplish at least two things in a deer range improvement project. First of all, increased distribution of water will allow deer to move onto and use ranges not normally used and second, the provision of water in droughty areas can provide a nutritional factor that can be very influential in animal vigor and herd health and subsequent population increases. A negative effect may be the fact that livestock also move in.

In New Mexico (Wood et al. 1970) mule deer densities increased when permanent water sources were developed in areas which had little or no free water. Under conditions of this New Mexico study it was found that the desirable distance between water sources was 2-1/2 to 3 miles. On one poorly watered range, deer densities increased from 1.6 deer per section in the first year to 13.0 the fifth year. Substantial increase in deer densities on some areas within a few months led the authors to conclude that “deer can be attracted into a newly watered area very well and that when the water sources were allowed to deteriorate, it was demonstrated, equally as well, that deer can be forced to leave an area.” They also concluded that these benefits can be maintained and deer held on the areas permanently.

Mackie (1970) in Montana found “that the use of range by mule deer decreased sharply at distances of a mile or more” from water. Observation during summer and fall when “permanent” water sources would be most important, were within 0.75

| TABLE 1. Deer pellet groups/acre on a ponderosa pine site in northern Arizona (from Kruse 1972). |
| Clearcut | Seeded | 16 : 7 : 7 : 2 : 0 : 2 : 4 : |
| Native | 42 : 11 : 11 : 0 : 7 : 0 : - : |
| Thinned | 20) sq. ft./ acre | 4 : 13 : 2 : 9 : - : 1 : 0 : - : |
| 40) | 124 : 31 : 2 : 2 : 0 : 0 : - : |
| 60) baseel | 36 : 33 : 2 : 0 : 2 : 0 : - : |
| 80) area | 36 : 0 : 0 : 2 : 4 : 0 : 1 : - : |
| Unthinned | 18 : 4 : 0 : 0 : 11 : 26 : 67 : Burned |

* Fire
miles of a water source. The number of observations at greater distances decreased as distance increased, with negligible use at 2 miles or more. However, the author concluded that the distribution of water on the study area during the most arid years was not a significant factor in determining mule deer distribution.

Apparently on the more xeric New Mexico site the influence of distribution and density was significant while on the more mesic Montana site the relatively greater availability of water obviated the influence of water distribution on mule deer movements and densities although, in the latter study, density differences were not recorded.

Observations by this author in Nevada indicate that there are several potential summer deer ranges in Nevada that are not used due to a lack of water. One then wonders if, because of their strong habitual nature (Gruell and Papez 1965), deer can be "interested" in these good ranges even if water is provided. Apparently this happened in New Mexico. I am not certain it would be successful in Nevada, but a study has not been conducted.

Miscellaneous Improvement Techniques

It is important that new and innovative deer range improvement practices be developed. The literature reveals a few good examples. Perhaps increased and wiser use of the time-honored techniques will, in the long run, provide the best means of producing deer forage and increased deer populations up to optimum carrying capacity.

Fertilization constitutes one miscellaneous deer range improvement technique, although it is most often used along with revegetation and other procedures. For example, Anderson et al. (1974) studied the influence of fertilizing wavy leaf oak brush in New Mexico for mule deer. Urea or ammonium sulfate was applied to this range and the result was a significant increase in leader growth by mountain mahogany (Cercocarpus ledifolius). No increase in leader growth was found for either fourwing saltbush or wavy leaf oak. Crude protein increased significantly in the oak leaves after urea fertilization. Deer use increased during summer, fall, and winter seasons on areas fertilized with urea. No significant response in deer use resulted from application of ammonium sulfate. The authors also reported that a possible shift in spring food habits from oak because to forbs may have precluded selective mule deer use of the area fertilized areas. No deer density or population changes were presented.

Fertilization tends to increase protein content of native bromes (Anderson et al. 1974). Protein content is strongly correlated with deer weights according to an early study by Elmersen (1946). On burned-over ranges with interspersions of timber in northwest Oregon, mature black-tailed bucks averaged over 200 pounds hog-dressed weight. A second area was characterized by a much more closed canopy with "scattered glades" and more mature browse plants with a much lower protein content. On this latter site mature bucks averaged less than 153 pounds.

A separate example of a miscellaneous or innovative treatment is found in carbon black treatments in Colorado (Regelin and Wallmo 1975). High elevation (2310-2350 m.) deer ranges in Grand County, Colorado are often limited due to deep snow. Carbon black was broadcast on plots at a rate of 336 kg/ha (34.4 t/m²). Melting of snow was accelerated on all treatment plots, but particularly on south aspects. On these slopes average snow depth was reduced by 91.8 percent when compared with control plots (7.4 percent). The reduction was 90.3 percent on east slopes. The influence on the vegetation was not investigated but additional forage could be made available at difficult times.

Winter feeding of deer may possibly be considered as an indirect method of range improvement. How? By "releasing" pressure on heavily grazed winter range. However, this technique is of questionable benefit and desirability. In a 1944 study in Utah, Domian and Rasmussen concluded "winter feeding of mule deer . . . is, at best, only partly successful, and expansion of such a program is of doubtful value. It appears desirable to regulate the deer population so that supplemental winter feeding as a regular program can be discontinued."

INTERPRETATION AND CONCLUSIONS

Deer range improvement practices consist of (1) range seedings, (2) grazing management systems, including fencing to enhance certain native and introduced species, and natural plant communities, (3) tree and brush removal with and without artificial revegetation, (4) water developments, and (5) miscellaneous treatments. The relative amounts of these various practices throughout the range of the mule deer is not well known.

Some general observations can be made. Approximately 1,000,000 acres of perennial grasses have been seeded in Nevada. Only a small fraction of this, probably less than 2 to 3 percent, has been of positive benefit to mule deer. The negative effects have not been studied extensively, only implied, but they might be sizable. Of course, these revegetation projects were accomplished for livestock only. Probably a similar amount of seeding has been accomplished in other states with perhaps a higher percentage felt to be useful in enhancing mule deer range.

Box et al. (1966) reported that between 1950 and 1964, 3 million acres of pinyon-juniper in 1200 projects were converted or controlled in the U.S.A. A large percentage of this land treatment was done to benefit livestock. Numerous other sites have received brush control treatment. Possibly 25 percent is useful for mule deer range enhancement.

The acreage under intensive grazing management that directly benefits wildlife is difficult to determine. On Bureau of Land Management administered lands in Nevada, 6 million acres are under intensive grazing management. The BLM in Nevada estimates that only about 1% of this acreage directly benefits deer ranges. In fact, many of the grazing management designs may be detrimental to mule deer habitat.

Personal communication, Jim Yoakum, Bureau of Land Management, State Office, Nevada.
for two reasons. First, a three-year rotation, the design of many, does not allow for the increased production and reproduction of browse species, and, second, the systems are often based on an important perennial grass as the key species and do not consider the importance of forbs.

I have found no definitive figures for the number of water developments designed to improve mule deer ranges. They are probably numerous and their absolute influence is relatively unknown.

Over much of the range of mule deer there has been little prescribed burning. Wildfires vary considerably from year to year, e.g., in Nevada, 38,803 acres burned in 1972 and 190,025 acres in 1973 (Tuellor and Lorain 1974). I know of only a very few instances where revegetation for mule deer was accomplished on wildfire sites. Burning should be prescribed only on those sites where it has been shown or can be shown to provide benefits to mule deer. It can be expensive. A cost of $563 annually for each additional buck bagged was reported in one California study (Longhurst et al. 1976). Other benefits would have to be included to make such a practice economically feasible.

The relation between forage composition and availability and changes in the structure of a mule deer population change is not well understood. Interactions among habitat factors, biotic factors, and population changes are complex. As one reviews the Kaibab story (Rasmussen 1941; Swank 1958; Russo 1964; Hungerford 1965; Caughley 1970), along with the other studies reviewed here, one is left with the feeling that a definitive study showing how these relationships work has never been accomplished.

Deer population changes reported in the Kaibab references appear to be closely correlated with predation, range deterioration, and range improvement. But, as Caughley (1970) seems to be asking, is there a confounding relationship between these correlations and natural changes in populations of ungulates? Do natural self-regulating population changes, irruptive or otherwise, mask the influence of improvement practices? These questions must be asked and answered before the benefits of range improvement practices can be quantitatively described.

It seems though, that collectively, deer range improvement practices provide a combination of desirable factors and that these factors are beneficial to mule deer. Artificial revegetation and good range or grazing management can lead to good deer range condition with the requisite species diversity (Fig. 1). Good deer range condition may be defined as a prescribed level of productivity and species composition providing optimum forage and cover requirements for mule deer. The many negative factors interact with the beneficial management activities in a complex way (Fig. 1).

Hubbard (1962) described successful seeding of bitterbrush as one that will provide between 500 and 2200 plants per acre, depending on the site. He also reported that it takes between 297 and 587 native bitterbrush plants to feed a 100-pound deer for one month. This indicates, based on bitterbrush alone, that the best stand would produce enough forage on each acre to maintain a deer for 3.7 to 10.6 months.

Providing greater diversity would probably improve this carrying capacity.

Other examples are available but it is still difficult to determine the influence of the improvement on the population. One other important factor is the fact that the literature provides little clear-cut data on forage consumption. And, if total consumption were known, palatability and preference differences constitute additional confounding factors.

Once deer ranges are improved or before they are improved, how do we determine that the practice will do more than just entice deer from surrounding range to a smaller but more desirable area? Sometimes we have difficulty in doing that since it may be, in some cases, difficult to attract deer onto ranges that they do not now use. How can a combination of improvement and management functions provide positive herd changes (Fig. 1) over large areas of suitable habitat? We do this by maintaining optimum numbers with good habitat, ameliorating the negative influences, and influencing deer behavior to obtain greater animal dispersion and proper use.

Possibly there is one single factor operating in the range of mule deer in the western United States that supersedes, or in part, regulates all deer range improvements and population changes. This factor is climate. There is a significant correlation between range forage productivity and seasonal rainfall. This can, on some sites, be as much as a 1200% difference in forage productivity from one year to the next (Tueller and Monroe 1975). In addition to this, adverse winter weather may reduce mule deer survival and thus reduce populations even with reasonable habitat conditions. Longhurst et al. (1976) reported that mean monthly temperature in October, November, and December are positively correlated with buck harvest 1 to 3 years later, and that increased precipitation in December and January is correlated with decreased buck take 1 to 3 years later. Such variations may well supersede or mask the influence of the deer range improvement practice, although the influence of tremendous fluctuations in forage productivity on populations has not been described.

On some sites intense interspecific competition for forage may require that numbers of mule deer be controlled by both sex hunts. In such cases, control of deer numbers is an absolutely necessary prerequisite for the productivity and maintenance of forage on deer range improvement projects and without which the project should not be attempted.

Mule deer numbers in the Great Basin have gone through an upswing and downswing (Fig. 2; Barngrover et al 1975) since the turn of the century. Has this been an irruptive population phenomenon or are the trends related to overgrazing, secondary succession, alterations in predation, or a combination of factors? Surely more than one factor is involved. Since most of the heaviest overgrazing of Nevada ranges occurred prior to or during the period of highest deer numbers, and since judicious grazing, adjudication, and associated livestock cuts have occurred since the peak of mule deer numbers, I suggest that the decline in recent years must be due to factors other than poor habitat. However, I am
FIGURE 1. A preliminary diagrammetric representation of deer range improvement processes as they converge into those vectors leading to positive herd changes (to optimum numbers by age class consistent with carrying capacity). Monitoring of the herd or population change is of paramount importance. The arrow size represents the author’s estimation of the relative importance of various factors. Dashed arrows represent negative inputs in relation to herd health, good deer range condition, and/or a tendency away from an optimum herd size. A wavy line represents a significant inverse relationship. A single solid line represents a known relationship but for which no relative importance is attached.

* A positive short-term benefit but not lasting. May even have a negative influence over time.
(Data courtesy of Nevada Department of Fish and Game.)
sure that deteriorated habitat can be indicted in some instances. The greatest decline in deer harvest, and presumably numbers, occurred in the early 1960's. Most of the ranges had been overgrazed by, say, 1950. Has there been a 10-15 year lag before the mortality if caused by overgrazing? At the least, the heavy livestock grazing has created and maintained the desirable sub-climax vegetation.

In the Great Basin many actual and potential deer winter ranges have been heavily overgrazed. However, the acreage involved is considerable. Winter ranges are probably not limiting if the entire Great Basin is considered as a unit. On the other hand, it is probable that summer ranges are limiting in the center of the Great Basin because of their limited acreage coupled with overgrazing, which has reduced desirable species.

Have changes in migration routes due to freeways, urbanization, and livestock improvement practices (including fences) restricted herd movement and separated herds? If so, has the isolation increased inbreeding in recent years, and has such resulted in a poorer vigor of individual animals, increased mortality, and reduced numbers? If so, this may also result in reducing the benefit of a range improvement project.

I am afraid that this paper has asked more questions than it has answered. Probably one of the greatest needs is the development and use of techniques for monitoring population fluctuations and coupling such data to the habitat, either improved or natural. It is possible to summarize mule deer management techniques as related to range improvement in the following manner:

1. There is additional need to provide additional forage on specific sites throughout the range of mule deer in the western United States.
2. Tree and brush removal to change secondary succession to a condition favorable for mule deer should be continued with greater emphasis on site specificity and aesthetics. Controlled burning will be an important tool.
3. Revegetation projects designed for specific sites generally must provide species diversity. This will require the seeding of grasses, forbs, and shrubs preferred by deer during certain periods of the year. Grasses may provide more forage for deer than has been commonly been thought. Mule deer, while generally considered to be browsers, can have a strong dependency (particularly on winter ranges) on grasses. When Leopold (1950) writes of the lack of deer in the mountains of California and the Great Basin early in the last century with larger numbers reported on the fringes of the Sacramento Valley (historically, a bunchgrass range), this thought is enforced.
4. New water development, especially in the droughty parts of the mule deer range will allow the utilization of forage on both summer and winter ranges that is not now available.

5. Range management grazing systems on public lands must be designed to exclude livestock from "key" sites during certain high competition periods. A reduction in livestock utilization of forbs and grasses on certain sites will benefit mule deer. They must also be designed to enhance species and plant communities valuable for mule deer. Balanced use of the deer range vegetation by both deer and livestock should be sought and then enhanced as a technique for controlling succession and maintaining good condition range.
6. Range improvement techniques, along with livestock management, should be concentrated on specific plant communities with species and other characteristics that will respond. Less valuable plant communities can be improved, but on a much lower priority.
7. New and innovative techniques for range improvements to benefit mule deer must be developed and evaluated. For example, has anyone been successful in their attempts to provide artificial cover with plant communities with good forage but a lack of suitable cover? Perhaps larger shrubs and trees could be planted along natural drainages ways to utilize the moisture there as well as enhancing the natural appearance of such a treatment.

Long term studies to evaluate benefits in absolute terms should, on selected locations, accompany the effort to improve ranges. This will provide evidence of the benefits that will come from deer range improvement practices that are now largely intuitive. A. Starker Leopold (1950) said it over 26 years ago: "We cannot continue slashing and burning the forests and overgrazing the ranges - processes which vicariously have produced some of our best deer ranges in the past. Creation of deer range in the future will have to be deliberately planned as part of wildland management, with due regard for other values and uses."

LITERATURE CITED


AN OVERVIEW OF BIG GAME MANAGEMENT

Daniel A. Poole
President
Wildlife Management Institute
709 Wire Building
Washington, D.C. 20005

Abstract

Mule deer are the most adaptable and widespread western ungulate. Present population depressions, while not uniform, are evident in all kinds of western ecosystems. The states' propensity to duplicate research needlessly may be using limited funds. The unsupported presumption of causes of the mule deer decline may hinder the design and conduct of research to determine root causes. A follow-up workshop of selected participants is proposed to develop new understanding about mule deer in order to improve their management throughout the West.

I commend Utah State University's College of Natural Resources, the Natural Resources Alumni Association, and the program committee for scheduling this badly needed symposium on the major problem of mule deer decline. It is especially fitting that this symposium is being held in Utah, a state long known for the vast amount of recreation provided by mule deer to hunters and nonhunters alike.

Mule deer are so much a part of the natural scene here that it is proper that Utah should be one of the first to formally address the problem of declining deer numbers and to begin to coordinate efforts to determine its reasons and the opportunities for its correction. I also commend all those who helped organize this worthwhile endeavor as well as the participants, speakers and nonspeakers alike. A problem of this geographical magnitude needs all the helping hands that can be mustered into service.

I am gratified by this opportunity to be with you. The Wildlife Management Institute is interested in all wildlife and land management in North America. We have especially strong ties with the West and the vast acreage of public lands that provide manageable habitat for some of the finest wildlife in the nation. The Institute was among the first, if not the first, private organization, to take an interest in and express public concerns for what were then only localized declines of mule deer herds in a few states. It was because of this long-term interest that I quickly accepted the invitation to speak here tonight. I am grateful for the opportunity to share with you our concerns for the present and our hopes for the future of the mule deer.

The Rocky Mountain mule deer is the most adaptable and widespread western ungulate. Mule deer are a part of the western scene. They provide bread and butter recreation for most of the more than three million hunters in the eleven western states, as well as incalculable pleasure to many more millions of wildlife viewers. A major decline in numbers of any species of this importance affects the casual viewer, the hunter, and diverse economic elements, as well. The effects go beyond deer because they invariably result in declining income for the state wildlife department and curtailment of management programs for other species.

I will make one disclaimer. Please bear with me if there is some repetition of what you heard this afternoon or what you believe you may hear tomorrow. Preparing a dinner talk is difficult without an opportunity to read the technical papers of the symposium. Therefore, I am limiting my remarks primarily to the problem in its larger perspective as seen by our staff.

I don't need to tell you that the management of mule deer is, has been, and always will be a complex undertaking. Although present declines are not universal in time or place, they do cut across the entire range of the species in the West. Literature reviews bear this out, and some recent papers detail it extensively.

These declines include all kinds of ecosystems, from desert sagebrush to high mountains. There is no simple answer to any ecosystem problem. Deer, like grass, shrubs, trees, the other plants and the hundreds of vertebrates, are part of an interrelated system. There is no one answer or reason for changes in the numbers of any species. These species are a product of their habitat and they must be related to changes in the total habitat wherever located and however caused. The fact that these changes in mule deer numbers have been and are occurring in a wide range of different habitats is indicative of us of total and general changes in the many western ecosystems.

As the major cosponsor of the recent Bicentennial meeting of the North American Wildlife and
The Institute has several major concerns about the management of mule deer. We are not too solicitous about the detailed management techniques used by the states. But we are concerned with the general effort and thrust with which that management is accomplished and in some of the problems we see in that management direction. We do not rank our concerns in any particular order because all are interrelated. And all are primarily based on the knowledge available and how that knowledge is used in management.

If we accept the assumptions that funds for wildlife management are finite, usually inadequate, and always hard to come by, one of our concerns will be placed in perspective. That concern is parochialism in management and research on mule deer. We have repeatedly witnessed the dampening influence that state boundaries have on the use that is made of research data by some administrators. Simply because something is learned beyond the boundaries of a state should not make it suspect. Nor does it mean that such knowledge should be rejected out of hand because of the attitude that "what affects neighboring states does not apply here." Such an attitude wastes funding and delays development of sound management programs. Some steps have been taken to reduce this parochialism, such as the workshop program of the Western Association. But that program has not done the job that needs to be done, and must be done, to bring successful deer management into the third century of this nation’s history.

Tunnel vision is another major concern. This shows up in the way some states attempt to determine the causes of mule deer declines. Let me illustrate. A major deer area has undergone a serious population decline. A research program is initiated to find out why. State people say, in effect, "the decline may be due to changed livestock use, or to succession changes in the vegetation, or to overhunting, or to predators. But it is probably due to predators, therefore we will research predation and ignore the others." Locking in on a predetermined cause to the virtual exclusion of others is a disservice both to scientific wildlife management and to the future of a magnificent wildlife species.

Another of our concerns is the nonapplication of existing knowledge. The public land manager is changing the public lands daily. The chainsaws are buzzing, range drills are seeding, and tractors are uprooting juniper and pinyon. The land manager asks for help in limiting wildlife damage. The wildlife manager answers, "I do not have the data; I do not have the research." Yet there is a wealth of data available, some of it in summary form, and some of it in professional judgments that can be used to establish land management guidelines that will make a more compatible arrangement between commodity production and wildlife.

Dr. Robert H. Giles saw this in 1962, (Giles 1962) when he wrote:

"A great hindrance to the advancement of a coordinated use program is failure to imaginatively use existing knowledge of forest wildlife needs and to develop these needs into management directives. . . . Certainly, research is needed, but while waiting, we need to work with what we have. Work to be done is not for the research staff, but for the management team who sees the needs, recognizes limitations, and can make modifications to fit existing conditions. The applied ecologist needs to start applying, not waiting for handouts from research personnel who have enough problems of their own. Managers must then share information on the results of their efforts with their colleagues."

Another concern is lack of knowledge. I am certain you all know of specific pieces of information you believe are needed to adequately manage mule deer. Very large pieces of information are needed to help protect and enhance wildlife habitat. Without question, there are gaps in our knowledge of mule deer and their specific habitat requirements and of the animal’s reactions to changes in the ecosystem. At best, this knowledge, when acquired, may enable us to increase deer numbers; at worst, it will enable us to make better trade-offs when habitat is manipulated for commodity production.

Coincidental with this lack of knowledge is a sometimes overabundance of other knowledge. Too many states have conducted nearly identical research on nearly identical problems for many years, when one or two projects would have yielded the knowledge needed for all to manage the animals. Such duplication is a direct result of parochialism. It uses funds that could be better spent for filling knowledge gaps. A hard look should be taken at this duplication by all concerned.

Analysis of wildlife problems requires some knowledge of how each participant views the problems. How do wildlife managers in the Intermountain area, particularly Utah, view the problem of deer decline? I could go through the many cubic feet of agency reports, memoranda, research findings, and harvest regulations. But in this symposium, the work has already been done for me by the program committee. The committee has indicated the importance of the many factors affecting mule deer by the amount of program time allocated to each.

There are seven hours of subject matter on mule deer decline, excluding the introduction, the symposium summary, and my time tonight. Broken down in broad categories, I find two hours are devoted to various problems in habitat. This is 29 percent of the total. I find that predation and other mortalities cover another 21 percent with 1-1/2 hours. Populations, including census and harvest regulations, are important, with 2 hours or 29 percent of the time devoted to them. Disease factors, nutri-
Wildlife management in both the universities and the ranges beyond the point that a prudent livestock operator would graze them. Not to graze to the detriment of the soil and water, but rather as a manipulative tool to maintain or reach certain desirable successional vegetative levels for big game.

We note that mule deer numbers and sheep numbers follow a similar curve: as sheep decline, mule deer also decline. Mule deer are down, sheep are down. Is there a vegetative cause and effect?

Predation research, much of it excellent, is still research devoted to but a small portion of the total ecosystem. If predation is the factor that some obviously believe, then research should be expanded to include the full array of predator-prey relationships and their ties with successional changes. Why, in much of the West, do we not have the great irruptions of jack rabbits that we had ten to thirty years ago? Could it be because, like deer, the jack rabbits need certain successional stages to have a peak population? What are the relations between white-tailed and black-tailed jack rabbits as vegetation moves to higher successional stages?

To the trained eyes of range and wildlife managers, there are changes underway. Western forests and ranges show general and sometimes dramatic vegetative changes toward climax vegetation. What are the implications of this to deer populations? I hear some occasional discussion, but there is little general consideration of the fact that the agencies now are doing a significantly better job of range management over much of the West. This is bound to affect the vegetation deer require. Under such conditions, a mule deer herd, reduced by the catastrophe of a mule deer herd, reduced by the catastrophe of several bad winters, may not have the same habitat that provided its needs when its population was at a peak. Thus, it may not be able to rebound with another irruption.

New, complex, and important relationships of ungulates and cover are being developed and published. Some of you may have attended the elk-logging symposium last winter at the University of Idaho. If you did not, I certainly recommend you study the transactions of that symposium when available; particularly the papers relating to escape and thermal cover. The Forest Service, in cooperation with other agencies, is doing good work on these subjects in the Pacific Northwest. Region 6 is preparing interagency guidelines for wildlife cover in the Douglas fir region. The Pacific Northwest Forest and Range Experiment Station soon will publish, in book form, interagency guidelines for maintaining and enhancing wildlife habitat in the Blue Mountains of Oregon and Washington. These "cook book" approaches will tell the land manager what he must do for each class of wildlife, and what the effects will be if he neglects wildlife. Such data, both scientific and judgmental, can be readily transposed to meet conditions in other parts of the West, particularly for large ungulate habitats.

I am especially impressed with the new concepts that have been developed concerning energy and energy requirements and their relations with cover and land management. These subjects and relations are of such importance that, if they are not fully covered at this symposium, then the wildlife scientists at Utah State University should prepare abstracts and bibliographies for the wildlife managers in all agencies in this region. Some of this material must be transferred from livestock use. Outstanding work has been done by Dr. Cook at this university. Other work, such as that on white-tailed deer by Moen, can be transposed to formulate new concepts for solving questions in mule deer habitat needs (Moen 1973).

A hypothetical example will be of interest. In work on Utah domestic livestock, Cook found that gestating females required 830 kilo-calories per pound of forage in digestible energy. Yet some desert ranges furnish only 803 kilo-calories (Cook). The question posed by a range manager was this: could such a shortage of 26 kilo-calories be offset by better protection and thermal cover on deer winter ranges? Would such protection reduce the energy output and enable not only successful survival but successful parturition?

These complex relationships should be placed in a proper wildlife management conceptual framework and data accumulated to reconcile the entire range management energy and cover interrelations. Such habitat changes as encroachment of timber on mountain meadows may reduce the stored energy the animals take to the winter range. Changes in fall ranges from tall green grasses to fall dormant grasses may reduce the energy intake just enough to be a significant factor in the mule deer declines, when coupled with minor losses of thermal cover. I pose these as questions that will require intensive interdisciplinary research to resolve.

There is another activity underway of vital importance to all wildlife on public lands. I refer...
to the requirements of the environmental acts and federal court decisions. Mule deer are so much a product of public lands that the environmental statements now required on Forest Service unit plans and environmental statements just starting on Bureau of Land Management grazing systems are the best chance the wildlife manager and state wildlife agencies ever have had for significant input into the federal land planning process and the effect of those plans on wildlife. The Institute views them in this light, and we urge you to comment, and comment strongly, on every one of these documents. The plans will not lock resource management into cement forever, but you know how hard it is to turn something around once the footing has been poured. Get into these now. It's your opportunity to do something positive in developing better land management programs.

As a small, private conservation organization, the Institute seeks to help improve wildlife conditions in many ways. Often, one of the best actions we can take to help resolve a problem is to serve as a starter or a catalyst for a beginning. That I now propose.

We believe that a follow-up workshop to survey the state of the art in mule deer management and the strengths and weaknesses of mule deer habitat research is an essential next step. The Institute would be willing to organize or to assist in the organization of such a meeting. The workshop would be patterned after the successful Wild Sheep Workshop, sponsored in 1974 by the Boone and Crockett Club, National Audubon Society and the Institute. It would be structured to assemble the best minds on the subject in a setting conducive to deliberation and discussion for the purpose of producing a summary publication on the mule deer. It would be a working document, useful to administrators, managers and researchers alike in identifying those paths that should be followed to obtain needed new understanding about mule deer and to improve their management throughout the West. The Institute is committed to this goal inasmuch as a new book on mule deer is being readied for publication in our wildlife monograph series.

As we conceive it, the meeting would not be solely for agency directors and the chiefs of research and management. It would be invitational, with participants drawn from universities and colleges and state and federal agencies. Young people would be included, because we want to obtain the most current wildlife thinking. We propose to invite people from the mid-range research hierarchy, at beginning and middle management and administrative levels, as well as some field researchers. Wildlife managers would not predominate. We would want and need strong participation from range and forest management research interests.

The participants will be assigned five major tasks. The first will be to divide the West into comparable habitat units where there is no question that research findings will be applicable within the unit. Two -- they will determine what knowledge is available for each of the habitat units. Three -- they will determine what additional knowledge is needed to properly manage mule deer in each habitat unit. Four -- they will determine what duplications in research are now going on and prepare recommendations for consolidation or elimination. Five -- they will prepare a shopping list of research needs and make recommendations for multi-state and multi-agency projects. The goal would be to attain research efficiency and knowledge needed for improved management.

The published results of such a brainstorming session would be useful in putting mule deer under an ecosystem management concept, hopefully pointing out and starting to solve some of the decline problems. At the least, we will be able to recognize the effects of land management activities and arrange rational trade-offs more beneficial to wildlife than we presently are able to accomplish.

I cannot overemphasize the acute need for improving our capability in this regard. In Washington, we deal regularly with issues involving the management direction of two large holdings that are the domain of the mule deer in much of the West -- the national forests administered by the U.S. Forest Service and the national resource lands administered by the Bureau of Land Management. Two separate legislative proposals dealing with the lands administered by these major agencies are pending in Congress at this moment. How mule deer or any public lands wildlife will fare under the legislation finally approved by Congress will depend in large degree on how well our profession can demonstrate the direct link between permitted management activities and the needs of such wildlife. The more concise and persuasive information that can be pulled together for any species of wildlife, the more effective are conservationists' representations to Congress. The same holds for situations that are encountered within state.

I thank you for the privilege of addressing this distinguished group. Let's not forget our most honored guest -- the Rocky Mountain mule deer. Our purpose these two days is to help him, and to do that we must develop the new concepts and new programs he needs.
MULE DEER NUTRITION AND PLANT UTILIZATION

Donald R. Dietz
Fish and Wildlife Biologist
Office of Biological Service, Region 6
U.S. Fish and Wildlife Service
Grand Junction, Colorado 81501

Julius G. Nagy
Associate Professor
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, Colorado 80521

Abstract

Deer nutrition and range plant utilization are probably both directly and indirectly associated with the possible mule deer decline. The direct effect of malnutrition is starvation; the indirect effects are many and varied, such as susceptibility to disease and parasites, low fawn production and inability to withstand environmental stress. Deer ranges are dynamic; the vigor and productivity of important mule deer food species are partially contingent upon the stage of plant succession. Many important browse plant communities are (1) the result of past site disturbances, (2) near the end of their lifespan and (3) may not be replaced because present land management factors tend to prevent recurrence of important disturbance factors such as fire, intensive browsing and grazing, and severe timber harvesting. Deer nutrition is a function of plant nutritional production, deer feeding habits, and the relation of nutrient intake and digestibility to deer physiological requirements. Digestion in the rumen is a function of the microbial population which can be greatly inhibited by the levels of volatile oils contained by various plant species.

The seasonal deer diet varies from a growth promoting (high protein and phosphorous) diet in spring to a fattening (high carbohydrate, fat, and energy) diet in fall to a maintenance (low protein and energy) diet in winter. Seasonal use of plant types varies from high grass use in spring, high forb use in summer and fall to high shrub use in winter. Variability among seasons, deer ranges and years is exceedingly high. The presence of volatile oils in evergreen and semi-evergreen shrubs such as sagebrush, juniper and pine can greatly affect species use by deer. Land management practices, vegetation type conversion and revegetation programs should consider the selection of low volatile oil bearing plants for protection, enhancement and reestablishment.

Deer nutrition discussions often review and report on the chemical composition and digestibility of their staple food plants without relating these parameters to either the nutritional requirements or to the changing diet of deer. We propose to alter that scheme by following the diet of a mule deer herd through their yearly cycle of activities. Thus we will discuss plant species and groups important in the life of the mule deer for meeting nutritive requirements for various physiological states such as growth, lactation, reproduction and winter maintenance. A brief rationale illuminating the role nutrition may play in the possible mule deer decline in the west is presented in the following section.
Deer Nutrition – An Overview

The fate of mule deer throughout the west is intrinsically entwined with the year-long nutritive regime of their food species. The suspected decline of mule deer populations may be due in part to both direct and indirect nutritional factors. The direct effect of malnutrition is starvation, however, the indirect effects work through such vectors as parasites, disease, weakness and susceptibility to predation, failure to conceive, reabsorption of fetuses, inability to nourish offspring and impaired or decreased ability to digest high roughage feeds such as hay and/or new spring plant growth.

Starvation may result from not only lack of food but also because of inadequate levels of protein and phosphorous and/or coupled with the ingestion of toxic materials such as essential or volatile oils contained in sagebrush, juniper and other evergreens or semi-evergreens.

If, as several biologists propose including Julander (1962), the decline of mule deer is a result of a gradual change in habitat, then malnutrition may be the result of too many deer being forced to eat too much material for too long a time, which is detrimental to their vital physiological processes. We are referring, principally, to undue dependence upon sagebrush, juniper, pine and other species which contain high levels of volatile oils.

While the rationale for the change in mule deer habitat is not within the province of this paper, it could be as simple as a gradual change in plant community structure due to plant succession. There are only a limited number of plants which meet the dietary requirements of deer in winter. Most are deciduous shrubs such as bitterbrush, mountainmahogany and chokecherry. Others mostly evergreens or semi-evergreens contain more than adequate amounts of important nutrients, but also contain volatile oils which can impair rumen function.

Deer ranges are dynamic. Important deciduous shrubs are rather short lived, 60-70 years according to Koughton, (1972), reproduce by seed such as bitterbrush and mountainmahogany or by root sprouting such as serviceberry and chokecherry, and cannot withstand heavy browsing indefinitely (Shepherd, 1971). Many shrub ranges probably resulted from a severe disturbance. In the case of bitterbrush and mountainmahogany this was possible because heavy livestock grazing reduced the competition for space and forb species and created a site with growing space for new seedlings. Several other conditions had to occur concurrently: these were low livestock, deer and rodent numbers; a good seed crop on the remnant shrubs; and several good precipitation years in succession. These conditions are not likely to occur again under present land management practices. As the old shrubs die it is not likely they will be replaced.

The root sprouting shrubs offer more promise. They undoubtly became abundant originally following fire, overgrazing, or logging. The natural succession is likely toward a grassland or toward a mature forest. Neither is a good habitat for mule deer. The match, axe or domestic herbivore are management tools for these situations, but they have to be selectively used and coupled with correct land, human, and animal management practices.

While deer population fluctuations are undoubtedly partially dependent upon nutritional parameters, deer behavior mechanisms may play an even more important part. It has been proposed by Peterle (1975) that white-tailed deer populations may be self-regulatory in that population eruptions do not occur on areas where they are in balance with their food supply, such as on some islands, national parks, etc. Eruptions occur only after some disturbance creates a large surplus of food. Unfortunately the herd is usually still increasing long after the balance between deer and food has passed. A yo-yo effect is then often seen until a new temporal balance is achieved. Possibly mule deer have a similar sociobiology.

Deer are not super-ruminants but rather precise in their dietary needs. Their relatively small rumen is not well adapted to coarse, low quality roughages (Short, 1966, 1969). Given free choice they will select the more nutritious twig tips and young leaves.

Deer nutrition is really rumen nutrition since digestion is carried on in that part of the ruminant stomach by bacteria and protozoa. To remain healthy and carry on all their physiological demands required for body maintenance, growth, and reproduction, deer must supply the rumen with adequate nutritive levels. Rumen microorganisms need nitrogen and certain other minerals and vitamins to breakdown and metabolize carbohydrates. Most of the energy available to deer results from the breakdown of carbohydrates mainly sugars, cellulose, and hemi-cellulose by rumen microorganisms. The most important end products of these fermentations are the volatile fatty acids (VFA) such as acetic, propionic, butyric, valeric, and isovaleric (Annison and Lewis, 1959; Church, 1969). These VFA’s are absorbed mainly through the rumen wall and supply approximately 50-70 percent of the energy requirements of the host animal (Annison and Lewis, 1959). These acids must be produced in both adequate amounts and in the proper proportion for digestive and other body processes to function properly.

Most of the concentrates such as proteins, minerals, fats, vitamins and soluble carbohydrates are contained within the plant cell. The cell wall is composed of cellulose, hemicellulose, and structural carbohydrates. During the spring and early summer the rumen microorganisms can easily breakdown the plant cell wall and most of this material is metabolized. After the autumn period the cell wall becomes increasingly lignified. This lignin complex is not digestible and thus increasingly less of the cell wall and contents can be digested. Not only do plants contain less of the important nutrients during the plant dormant season but they are also less readily available for assimilation.

Spring – Early Summer Period

The spring – early summer period is the time of best feeding conditions for mule deer in much of their range. Not only are summer ranges more

Mule Deer Nutrition and Plant Utilization
heavy producers of dry matter, they also provide a larger variety of plants having higher nutrient content, and plants which are more digestible. Even on non-migratory mule deer range shrubs, forbs and grasses are at their peak levels of the most important nutrients during the early growth phenological stage (Dietz, et al 1962).

Nutrition Requirements: Spring - Summer

The nutritional requirements of mule deer during the spring period vary according to age, sex, and physiological requirement. A dry diet would require lower protein, phosphorous, and energy levels than either pregnant or lactating animals. While 14-16 percent crude protein would be desirable for young animals and lactating females, barren does could get by on 12 percent or less. The need is for nitrogen rather than protein since these ruminants can synthesize all of the amino acids required by the host.

Possibly as important as protein is phosphorous, usually in short supply on western mule deer range. Again as with protein, young growing animals, pregnant and lactating does, and mature bucks all have heavy demands for phosphorous to satisfy physiological requirements. Optimum requirements for these classes of mule deer are probably in excess of that found on most spring ranges. Over 0.50 percent phosphorous would be desirable in the spring diet of mule deer, while any value less than 0.17 percent would probably result in some adverse effect on body function. Vitamins are usually in ample supply during the vigorous plant growth period of spring, especially carotene, the precursor of vitamin A.

A serious problem which may occur on spring mule deer ranges is the high water content of new growth especially of young grass and forb leaves but also in new growth twigs and leaves of shrubs and trees. The relative small rumen-reticulum of mule deer, especially immature animals, can hold only limited amounts of plant material. If 90 percent of this is water, as frequently happens in new grass growth, the deer simply cannot ingest enough material to meet total dry matter and especially carbohydrate and energy demands (Dietz, 1970). Thus, mule deer coming off a hard winter where a prolonged sagebrush-juniper diet has resulted in large body weight losses plus probably some changes in the rumen flora will tend to gorge on the lush spring growth of immature grasses. The sudden switch from hard browse to lush greens results in immediate stress through scours, rumen function impairment, and frequently secondary infection in the digestive tract. The combined impact may often be fatal.

Spring - Early Summer Diet

Kufeld et al (1973) summarized the results of 99 food habit studies conducted on mule deer ranges in the western United States and Canada. They reported the spring diet of mule deer is highly varied with location and in some cases even years. The bluegrasses (Poa spp.) are highly preferred on many meadows used by mule deer as soon as new growth becomes available. Important grass species in the spring diet of mule deer are wheatgrasses especially crested (Agropyrum cristatum) and bluebunch (A. spicatum) according to Kufeld et al (1973). These authors also reported heavy use on brome (Bromus spp.), mutton bluegrass (Poa fendleriiana), Sandberg bluegrass (P. secunda), and needle and thread (Stipa comata). Moderate use was made of many genera including Dactylis, Danthonia, Festuca, Koeleria, Oryzopsis and Phleum.

Forbs reported to be receiving heavy spring use by mule deer according to Kufeld et al (1973) are sulfur wildbuckwheat (Eriogonum umbellatum), cream peanute (Lathyrus ochroleucus), Lomatium (Lomatium spp.,), cinquefoil (Potentilla nevsherry), and mountain deathcamus (Zigadenus elegans). There are a great many species of forbs which are rated moderate as to spring food items.

One of the shrubs and trees reported to be subject to heavy spring use is big sagebrush (Artemisia tridentata). This would presumably be very early spring use. Heavy use has been reported on all the montanaledomahas (Cercocarpus spp.), Mexican cliffrose (Covania mexicana), Utah juniper (Juniperus utahensis), and creeping juniper (J. verticalis), western snowberry (Symphoricarpos occidentalis), and small soapweed (Yucca glauca). A great many species of shrubs are ranked as moderate in use.

Nutritive Levels of Plants in Spring - Early Summer

The new growth in spring of leaves and stems of grasses, forbs, shrubs and trees often equal or exceed good grade alfalfa hay in such important nutrients as protein and phosphorous. Levels of 20 or more percent protein and 0.30 percent phosphorous are not uncommon (Brness, 1973). Forbs are an especially good source of these two mineral components. Annual grasses such as cheatgrass (Bromus tectorum) also rate very high in protein and phosphorous during early spring growth.

Carbohydrates and true fats are low in all plant types during this period, hence gross energy intake may be limited due to low volume capacity of deer rumens and high water content of ingesta.

Summer - Early Fall Period

As the summer progresses and plant growth reaches maturity as characterized by full leaf and complete stem elongation in shrubs and trees and the appearance of the hard dough stage in grasses or forbs, the mule deer diet switches from a growing ration to a fattening ration.

Nutritive Requirements: Summer - Early Fall

Protein and phosphorous requirements decline for adult deer during summer and early fall but remain high for growing fawns. While adult deer would probably do well on a level of 10-12 percent protein at this period, young growing animals would perform better on a level above this amount. Phosphorous levels of feeds for mule deer should probably exceed 0.18 percent at this period but many plants do not sustain this high of a level into the late summer - early fall period. Energy demands are usually easily met at this season.
Summit - Early Fall Diet

As plant species mature and animals prepare for the winter season, diet preferences change. Mule deer begin their trek to transitional ranges during this period which also accelerates the change in dietary items.

Grasses comprise a small proportion of the summer diet - generally anywhere from 0 to 22 percent of the diet (Kufeld et al. 1973). No grass or sedge species were rated as heavy use feeds during summer, however, several were rated moderate in use class. These were smooth brome (Bromus inermis), sedges (Carex spp.), orchardgrass (Bouteloua gracilis), redosier dogbane (Apocynum spp.), Pacific aster (Aster chilensis), Wyoming indiangrass (Sporobolus cryptandrus), hairy goldaster (Chrysopsis villosa), Fremont geranium (Geranium fremontii), American licorice (Glycyrrhiza lepidota), cream peamine (Lathyrus ochroleucus), alfalfa medic (Medicago sativa), yellow sweetclover (Melilotus officinalis), dandelion (Taraxacum ceratophorum) and many others.

Several forbs were rated as heavy deer use in the fall. These were longleaf sagewort (Artemisia longifolia), hairy goldaster, barley larkspur (Delphinium barbey), white buckwheat (Eriogonum wrightii), silverline lupine (Lupinus argenteus), alfalfa medic, yellow sweetclover, toadflax penstemon (Penstemon linarioides), and wildspikenard false Solomon's seal (Smilax canadensis) and many others.

Heavily used shrub and tree species in the fall are white fir, Siberian peabrush, curleaf and true mountain mahogany, redosier dogwood, cotoneaster, Russian olive, Wright silktaessel, honeymuckle, desert peachbrush, desert and antelope bitterbrush, Gambel and wavyleaf oak, smooth and skunkbrush sumac, willows, silver buffaloberry and blueberries. In the fall those most heavily used are: inland ceanothus, curleaf mountain mahogany, Lewis mock orange, avena, desert and antelope bitterbrush, Gambel and wavyleaf oak, skunkbrush sumac, willows, and blueberries.

Nutritive Levels of Plants in Summer and Early Fall

Protein, phosphorous, and carotene levels decline as plants mature in summer, but remain fairly high until leaf color change and subsequently leaffall. The leaves of shrubs range from about 10-15 percent crude protein, while stems are much lower -- 4-5 percent. Phosphorous levels range from around 0.20-0.40 percent in leaves to 0.12-0.20 percent for stems. Gross energy averages about 4.8 kcal/g. in leaves to 4.7 kcal/g. in stems.

Grasses may decrease to 6-8 percent crude protein and 0.10-0.15 percent phosphorous but still contain 4.0-4.2 kcal/g. gross energy. Forbs decrease also in nutrient levels to around 8-10 percent protein, 0.15-0.30 percent phosphorous and 4.4-4.8 kcal/g. gross energy.

Carbohydrate content including cellulose and lignin increase along with the fats and oils found in ether extract or crude fat. True fat content is usually at its peak during late summer - early fall and gross energy intake reaches a seasonal maximum. Digestibility is retarded somewhat by increased lignification.

Late Fall - Winter Period

Mule deer food values change considerably from a fattening diet in early fall to a maintenance diet from late fall through early spring. With onset of leaf-fall, shrubs and trees provide at best only marginal levels of important nutrients. Grasses and forbs dry and wither or shatter providing even poorer nutrient levels. Evergreen and semi-evergreen species hold up better in nutritive composition but many contain tannins and essential oils which may inhibit digestibility. Not only are nutrient levels low at this season, but also lignification of the cell wall depresses digestibility by deer rumin microorganisms.

Nutritive Requirements: Late Fall - Winter

Deer need access to a total dry matter intake of 2.35 lbs. per hundredweight of body mass for maintenance according to Carhart (1954) and Nichol (1938). French et al. (1955) recommended 3 to 4 lbs./100 lb. deer. Deer probably need at least 4,800 kcal of dry matter per hundredweight, however, French et al. (1955) recommended 6,300 kcal per hundredweight of deer. Protein probably should not go much below 8 percent of the diet. Cook (1971) recommended about 4.5 percent digestible protein for herbivores for gestation. French et al. (1955) reported deer need a minimum of 0.25 percent phosphorous for maintenance. However, based on nutritive requirements for cattle and sheep, mule deer should be able to survive on around 0.16 percent which is the level given by Cook (1971) as the gestation requirement for herbivores. Cook also suggested herbivores require about 1.6 to 1.7 mg/lb. of carotene for gestation.

Late Fall - Winter Diet

The onset of winter results in a decreased dependence upon grass and forb species. Kufeld et al. (1973) reported heavy use on only one species of grass during winter - crested wheatgrass. These authors reported moderate use on some species of other wheatgrasses as well as on broom, fescue, timothy, and bluegrass. Heavy forb use was reported on only Newberry cinquefoil and Wyeth wild buckwheat.

Heavy mule deer use was found in winter on Rocky mountain maple (Acer glabrum), silver sagebrush (Artemisia cana), and big sagebrush, most species of mountain mahogany, Mexican cliffrose (Cowania mexicana), green ephedra (Ephedra viridis), creeping juniper, myrtle pachistima (Pachistima myrsinites), both desert and antelope bitterbrush and yucca. Many others were rated moderate in use by Kufeld et al. (1973).
In the Black Hills, heavy winter use was found on old man’s beard (Arctostaphylos uva-ursi), chokecherry (Prunus virginiana), ponderosa pine (Pinus ponderosa), common juniper (Juniperus communis), bearberry (Arctostaphylos uva-ursi), and low Oregon grape (Eriobes repens) (Scheuweiler et al, 1972).

Nutrient Levels of Plants in Winter

Crude protein content of deciduous shrub annual growth decline from the 10 to 12 percent range to 5 to 9 percent range with leaf-fall. In a study in the Black Hills, only the winter twigs of chokecherry of shrubs tested contained over 9 percent protein (Dietz, 1971). Studies in Colorado showed only big sagebrush (a semi-evergreen) of the common important shrub species contained over 10 percent crude protein during the winter period (Dietz et al, 1962). Such important winter browse species as bitterbrush, true mountain-mahogany, and rabbitbrush supply adequate levels (7-9 percent) of crude protein. Shrubs which generally contain less than 7 percent crude protein (possibly the critical level) are Gambel oak, wavyleaf oak (Quercus undulata), snowberry (Symphoricarpos spp.), rose (Rosa spp.), aspen, and many others.

Grasses and forbs are normally deficient in crude protein in winter often dropping down to 3 or 4 percent. Evergreen and semi-evergreen shrubs such as juniper, sagebrush, or rabbitbrush retain higher levels of phosphorous during the winter season than do shrubs such as bitterbrush, mountain-mahogany, serviceberry, and Gambel oak. All of the latter are deciduous shrubs and contain less than the recommended 0.16 percent phosphorous thought to be minimal.

Grasses and forbs are definitely deficient in phosphorous during winter. Only those that produce a green basal rosette that persists late into the fall and early winter supply more than token amounts of phosphorous. Species such as tufted hairgrass (Deschampsia caespitosa) may contain only about 0.05 percent phosphorous even in late summer or early fall.

Grasses are reported by Cook (1971) to be good sources of carbohydrates and energy for herbivores during winter, however, much of this is in the form of fiber and lignin. They are also usually inferior to shrubs in gross energy as determined by a bomb calorimeter. Some shrubs, however, may give erroneously high caloric values because of high volatile oil content.

Relation of Volatile Oils to Male Deer Management

A wide variety of evergreen plant species are found in the western part of the North American continent. Many of these plants contain a class of chemical substances commonly referred to as volatile oils. In chemistry the term "volatile oil" means a volatile compound which can be extracted from plants and plant parts by steam distillation. These "oils", although not soluble in water, but soluble in ether, alcohol, and other organic solvents, are not true oils, but various terpene derivatives. Plant physiologists consider them as metabolic waste products, while ecologists recognize the importance of these compounds as defense mechanisms of plants against overutilization, for example, fir, spruce, pine, etc. Others, such as the wide variety of sagebrush and juniper species, deserve our attention in male deer management, because these plants are considered important, especially during winter, as deer forage and cover.

In general, volatile oils possess antibacterial properties; and, therefore, knowledge of these properties is important in the nutrition of ruminant animals such as sheep, cattle, deer, and elk. It is a well-known fact that for proper digestion, ruminants must rely on their rumen microbial populations. Any substance, such as the volatile oils, which might interfere with proper functioning of the rumen microorganism might ultimately reduce the energy supply for the rumen host.

The antimicrobial activities of volatile oils have been demonstrated on rumen microorganisms in vitro (Nagy, et al, 1964; Nagy, et al, 1967; Oh, et al, 1968; Longhurst, et al, 1968; Nagy, et al, 1968). These works showed that the volatile oils of different plant species may exert different degrees of antimicrobial action. As an example, Figure 1 shows that volatile oils obtained from Artemisia tridentata are more inhibitory than those obtained from Artemisia nova. It should be mentioned also that Artemisia nova contains considerably less volatile oils (1.4 percent on dry matter basis) than Artemisia tridentata (2.5 percent). For this reason, on gram per gram basis A. nova is less inhibitory than A. tridentata. Indeed, observations generally agree that A. nova is preferred over A. tridentata by deer and domestic sheep. One should be aware of the fact, however, that the volatile oil content of the species will depend also on site characteristics and are subject to seasonal variations. Figure 2 shows that small concentrations of volatile oils have no or very little impact on rumen microorganisms. At higher concentrations, however, their inhibitory action accelerates. This activity has been demonstrated in vitro with a rumen fistulated goat. When increasing amounts of sagebrush volatile oils were administered daily through the rumen fistula, the goat, receiving a standard pelleted ration, went off feed when the concentration of volatile oils in the rumen reached a level of approximately 15 microlitres per 10 ml of rumen fluid. This concentration corresponds to the concentration of increased antimicrobial activity observed in in vitro studies (Figure 2).

Further investigations on volatile oils were conducted at Colorado State University (Nagy, 1973) using three species of juniper; J. deppeana (alligator juniper), J. osteosperma (Utah juniper), and J. scopulorum (Rocky Mountain juniper). The volatile oil content of these species varied somewhat according to site, but on the average, J. scopulorum contained the highest concentration, followed by J. osteosperma and J. deppeana.

To examine deer preferences cafeteria type of feeding trials, using fresh branches of the three juniper species every two days, were conducted for two weeks on 6 mule deer. Four animals were placed in individual pens and two (control) were placed
Figure 1. Antibacterial action of the essential oils of A. tridentata and A. nova against E. coli.

Figure 2. Antibacterial action of the essential oils of A. tridentata against the rumen microorganisms of wild and captive deer.
in a pen together. During the trial, the animals received 45 percent of their previous average daily food intake of a concentrate ration. Alligator juniper was much preferred over the other two species. The average total consumption per sample (two days) per deer was 896 grams for Alligator, 113 grams for Rocky Mountain, and 84 grams for Utah juniper. The average volatile oil content of Alligator juniper was 0.6 percent (dry weight basis), that of Rocky Mountain and Utah juniper was 3.5 percent and 0.9 percent respectively. It seemed, therefore, that deer selected against the high volatile oil containing foliage of Rocky Mountain juniper but did not explain why Alligator juniper was preferred over Utah juniper.

For this reason, we wanted to examine the possibility that deer are able to differentiate between different volatile oil levels in a pelleted ration. Volatile oils of Rocky Mountain juniper were mixed in standard pelleted ration in different concentrations (0, 1, 3, and 5 percent volatile oil levels). Deer were fed this ration in three cafeteria type trials. Results showed a strong preference by deer for rations that contained the lowest concentration of volatile oils in each trial.

Gas chro-mograms revealed the presence of approximately 20 to 25 different volatile oils in each of the three investigated juniper species. The amount of each individual compound seems to be a characteristic of the juniper species. These volatile oils can be divided into three main groups: monoterpene hydrocarbons, oxygenated monoterpenes, and sesquiterpenes. Longhurst et al. (1968) suggested that palatability of new growth of Douglas fir may depend on the concentration of oxygenated monoterpenes in the foliage. Our earlier individual trials with rumen microorganisms suggested that oxygenated monoterpenes usually exercised the strongest antimicrobial action. To test the hypothesis that deer, besides total levels of volatile oils in the foliage, would also select according to these groups (or group constituents) pelleted rations containing 1 percent monoterpene hydrocarbons, oxygenated monoterpenes and sesquiterpenes were fed to deer. Results indicated that deer select away from high oxygenated monoterpenes concentrations preferring foliage which contains more monoterpenes hydrocarbons or sesquiterpenes. We feel that this selective ability by deer was the reason why Utah juniper with relatively low volatile oil content was low on preference during the feeding trials with juniper branches. Utah juniper showed a much higher oxygenated monoterpenes content than either Rocky Mountain or Alligator juniper.

The foregoing discussion illustrated that in general volatile oils exercise antimicrobial action on rumen microorganisms. These microorganisms, however, are able to withstand certain low concentrations of the oils without adverse effects. Moreover, it seems that deer during their evolutionary time period learned to recognize these harmful effects and are able to select only for the lowest volatile oil containing forage, but also for the forage that contains fractions of oils with the least antimicrobial action.

Conclusions

There is an indication that in many deer ranges of the west, deciduous shrubs species are decreasing in numbers with the simultaneous increasing of some volatile oil containing species such as sagebrush and juniper. Land management agencies are at the same time faced in many areas with large-scale alteration of traditional deer winter ranges, due to proposed energy development and other activities. The task to determine which species and subspecies of plants should be used during revegetation of depleted deer winter ranges will fall on the land use manager. His knowledge in practical and theoretical deer nutrition will be of prime importance during the accomplishment of these tasks.

The solution to reestablishing nutritious shrubs containing low levels of volatile oils may be the recreation of those environmental conditions which originally permitted their establishment and subsequent proliferation. Thus, the judicious use of site disturbance mechanisms coupled with favorable climatic conditions and animal and human management may be the best hope for saving our prime mule deer ranges.

Literature Cited


MULE DEER PRODUCTIVITY--PAST AND PRESENT

Phillip J. Zwank
Ph.D. Candidate
Utah Cooperative Wildlife Research Unit
Utah State University
Logan, Utah 84322

Abstract

Productivity data demonstrate that the potential for rapid increase exists in mule deer populations. Fawns are capable of breeding; yearlings generally have single fawns; adult and old does usually produce twins, with recorded instances of triplets and quadruplets. Net productivity is significantly less than potential productivity. Ovulation rates are strongly affected by the quality of nutrition prior to the rut. It appears there are always sufficient bucks for breeding purposes. Approximately 10 percent losses occur between fertilization and parturition. The greatest loss in net productivity appears to occur during the post-natal period. During the first 45 days after birth, 50 percent of the fawn crop may die. Nutritional deficiencies, predation, diseases, parasitism, weather, and accidents may cause post-natal mortality. Nutritional deficiencies appear to be the primary factor responsible for post-natal mortality and winter fawn losses. In certain areas, predation, especially by coyotes, accounts for a large percentage of fawn losses. The incidence and effects of diseases on productivity are little known.

A population is a dynamic entity, the numbers of which fluctuate as a result of changes in productivity, mortality, immigration and emigration. While migration must be considered (Quick 1962), productivity is the primary factor responsible for population gains.

Murie (1951) noted that the rate of increase in a population is of vital interest to the game manager, but is the most difficult factor to determine. This is especially true for mule deer (Odocoileus hemionus), whose productivity varies with both age and geographical area and whose secretive nature hinders accurate determination of reproductive success. For these reasons, extreme care must be taken when comparing productivity of mule deer populations or when generalizing about mule deer productivity.

Both potential and net productivity should be recognized. Robinette (1956) stated that potential productivity is the theoretical rate at which a species can increase if no mortality occurs, and net productivity or net increase is the actual yearly rate of increase after mortality from all causes have been deducted. Only rarely does the net productivity of a herd in the wild ever closely approach the potential productivity (Robinette 1956).

Reproductive Potential

The maximum rate of increase in a population depends upon the genetically controlled reproductive potential (Andrewartha and Birch 1954), which for a mule deer population is determined by the number of does in the population capable of reproducing, and the fecundity of each.

Mule deer inherently possess a high reproductive potential. While mule deer usually breed first as yearlings (Robinette et al. 1955; Asdell 1964), they occasionally breed as fawns. After examining 274 reproductive tracts, Robinette et al. (1955) found evidence that 7 does (2.6 percent) had conceived as fawns. Brown (1960), however, found that 4 of 19 females (21 percent) in the Guadalupe Mountains of New Mexico became pregnant when less than 1 year of age. Papez (1976) determined that 3 of 12 does (25 percent) had ovulated first as fawns in the Ruby Butte Mountains in Nevada, and 1 had given birth. While these examples show that female fawns are capable of being bred, their reproductive capacity is believed to be insignificant in the breeding potential of most herds (Hickman 1971).

Yearlings generally bear single fawns, although twins may be produced (Youkum 1966). Prime adult does (between 3 and 7 years of age) usually produce twins, occasionally triplets (Robinette et al. 1955), and instances of quadruplets have been recorded (Sears and Browman 1955; Trodd 1962).

The reproductive potential appears to drop only slightly for old (7+ year-old) does (Hickman 1971). I recaptured and laparotomized one doe this past winter which had been tagged as a fawn in 1964. She was pregnant with twin fetuses. A second doe, determined to be more than 12 years old by cementum annulation aging, also was carrying twins.

Table 1 illustrates the theoretical reproductive potential for mule deer. Note that the original doe may have 104 direct descendants within a 6-year
period. In addition, penned deer studies indicate that highly productive does produce more female than male fawns (Verwe 1969; Robinette et al. 1973). Thus, fawn crops from highly productive populations may be weighted toward females.

Two captive herds of white-tailed deer (Odocoileus virginianus) have approached their theoretical reproductive potential. The George Reserve herd in Michigan (Table 2), which was started with 4 adult does and 7 bucks in March 1938, increased to 180 deer by December 1943. Investigators also found two dead deer on the Reserve during this 6-year period (Chase and Jenkins 1962). As fawns were not thought to breed, the reproductive potential of this herd was 188, which is very close to the 162 deer observed. On the Seneca Army Depot in New York, a herd of 30 white-tailed deer in 1948 grew to 1,121 in 1953 (Hesselson et al. 1962).

The explosive character of mule deer populations is demonstrated on the Kaibab Plateau in Arizona and in Cache National Forest in northern Utah. On the Kaibab Plateau the deer population was estimated to be 4,000 in 1906 (Russo 1964). By 1924, the population was estimated to be between 30,000 and 100,000 (Caughley 1970). Doman and Rasmussen (1944) estimated the Cache population at 250 in 1917 and 6,000 in 1939. While these examples of exponential rates of increase were under unusual conditions, given favorable habitat, deer usually produce a net annual population increase of between 20 and 30 percent (Hesselton et al. 1965). Two captive herds of white-tailed deer (Odocoileus virginianus) have approached their theoretical reproductive potential. The George Reserve herd in Michigan (Table 2), which was started with 4 adult does and 7 bucks in March 1938, increased to 180 deer by December 1943. Investigators also found two dead deer on the Reserve during this 6-year period (Chase and Jenkins 1962). As fawns were not thought to breed, the reproductive potential of this herd was 188, which is very close to the 162 deer observed. On the Seneca Army Depot in New York, a herd of 30 white-tailed deer in 1948 grew to 1,121 in 1953 (Hesselson et al. 1962).

Ovulation Rates

Ovulation rates may be estimated through microscopic ovarian analyses. Accurate sampling is difficult, because non-fertilized corpora degenerate rapidly and accessory corpora lutea and other luteinizing structures, which may be found in the ovary, must be differentiated (Gill 1972).

Ovulation rates appear to be affected strongly by the quality of nutrition just prior to and during the rut (Longhurst et al. 1952; Robinette 1956; Chase and Jenkins 1962; Nellis 1968; Nickman 1971).

Net Productivity

The number of fawns recruited into the breeding population determines net productivity (Salwasser 1975). Male deer productivity generally is estimated by game managers from observed pre-hunting and post-hunting season doe:fawn ratios, which may be biased. If the previous year's net productivity was high, a large proportion of less productive yearlings are included in the population and the doe:fawn ratio. This would tend to depress the apparent size of the present year's fawn crop (Nellis 1968). Post-season ratios may add an additional bias, if differential mortality favored a certain age-class, either during the harvest or in the "winter kill" (Nickman 1971). While the validity of either method may be questioned, doe:fawn ratios are used extensively to monitor population trends.

Productivity trends show that recruitment is declining throughout the West (Table 3). Significant losses appear to be occurring either during pregnancy, the immediate post-natal period, or during the first few months after birth.

Intra-uterine Mortality

Reproductive losses that occur between fertilization and parturition appear to be minimal in male deer. Robinette et al. (1955) observed an ova loss of 7.5 percent (789 embryos or fetuses from 853 corpora lutea) during the first month following conception and a 10.5 percent loss at midpoint of pregnancy. Recent studies by both Nellis (1968) in Montana and Papez (1975) in Nevada found a similar 10 percent decrease between corpora lutea and fetal rates (25 fetuses from 26 corpora lutea in Montana; 69 fetuses from 71 corpora lutea in Nevada).

Salwasser (1975) found only 1 resorbing fetus and no other signs of abnormality in a necropsy sample consisting of 142 all age-class does. Nellis (1968) observed an intra-uterine mortality rate of 2 percent or 4 atrophic fetuses from 226 recovered fetuses. Again, this is very similar to the 1.7 percent mortality (21 of 1,263), based upon visible remains of dead fetuses, observed by Robinette et al. (1955).
Early Post-Natal Mortality

The greatest loss in net productivity appears to occur during the post-natal period. Of 224 births recorded under penned conditions, 17 fawns (7.6 percent) died during the first 48 hours (Robinette et al. 1973). Trainer (1975), in Oregon, found only 6 of 189 fawns (3 percent) examined in the field immediately post-partum to be dead or emaciated and not likely to survive. While Trainer's (1975) data showed few fawns to die immediately post-partum, both Salwasser (1974) and Trainer (1975) observed losses approximating 50 percent of the fawn crop during the first 45 days after birth. Habitat deficiencies, predation, diseases, parasitism, weather, and accidents may cause post-natal fawn mortality.

Nutrition

The recurring theme through past and present literature is that nutrition is the prime factor affecting productivity (Leopold et al. 1951; Longhurst et al. 1952; Robinette et al. 1955; Robinette 1956c; Julander 1961; Pederson 1970; Salwasser 1974). Does on inadequate winter diets show large weight losses, which impair development of the fetus, resulting in fawn mortality at birth or shortly thereafter (Verme 1969). Fawns born to does in poor condition, stillborn, small, weak, unable to nurse or the mother does not produce enough milk to rear multiple fawns (Yoakum 1966). While insufficient protein usually is considered as the first deficient nutrient, diets lacking in phosphorus also have been shown to reduce productivity (Swank 1956).

Cover

Fawning cover has been implicated as an important factor in summer fawn survival. Salwasser (1975) found when comparing fawn survival on two areas, while one supported a higher density of coyotes than the other, it also yielded nearly twice the percentage of summer fawn survival. He related the better fawn survival to superior fawning cover.

Water

In drier areas, lack of available free water and low nutritional intake exist during periods of drought. Plants become dormant and protein levels drop below the optimum for deer growth (Swank 1958). Deer concentrate in the vicinity of permanent water and compete for the low quality forage. Longhurst et al. (1952), Swank (1956), and Yoakum (1966) thought that a lack of free water and low nutritional intake may reduce recruitment. Urness et al. (1971), however, determined that reduced recruitment in Arizona was due to high fawn mortality, and nutritional deficiencies probably were not responsible.

Predation

Early authors reported that predation was influential in mule deer population dynamics and that coyotes were responsible for many fawn losses (Murie 1935; Horn 1941; Cabalane 1947). Robinette and Olsen (1944), in Utah, reported 49 percent (22 of 45) of a fawn crop was taken by a coyote in a 500-acre enclosure. Richens (1961), however, recorded Utah mule deer predators (in descending order of importance) to be: mountain lions (Felis concolor), coyotes (Canis latrans), and bobcats (Lynx rufus).

Trainer (1975) determined that coyotes accounted for 55 percent of the summer radio-monitored fawn losses. Salwasser (1975), on the other hand, felt that it was unlikely that coyotes were totally responsible for summer fawn losses. He further stated that the occurrence of fawn remains in coyote scats probably represented scavenging to a large degree.

Diseases and Parasites

Little information is available concerning the quantitative effects of parasites and diseases on young deer. The incidence of parasitism and diseases generally are linked closely to the nutritional level of the host. Cowan (1956) and Yoakum (1966) claimed that, given a satisfactory food supply, deer appear to resist the various diseases and parasites to which they are susceptible.

In penned studies, Robinette et al. (1973), observed cases of necrotic stomatitis or necrobacillosis caused by Sperophores necrophores. I also observed necrotic stomatitis in Utah mule deer fawns reared in pens.

Parasitic blood worms (Glaesophora schneideri) may be responsible for neonatal fawn losses in New Mexico (Snyder 1968). In Arizona, a bacteria (Pseudomonas aeruginose), which would be fatal to newborn fawns, was found in the udder of a doe (LaCount 1972). Oregon, Arizona, Utah, and New Mexico currently are investigating the incidence of diseases and parasites in mule deer and their influence on productivity.

Weather

Weather affects net productivity by its direct effect upon forage production (Tee 1965). Also, inclement weather during the fawning period may cause considerable losses. In 1975, 12 dead fawns were found in the Uinta Mountains of northern Utah after a 10-inch snowfall during the fawning period (personal conversation dated 18 April, 1976, with D. Winn, Dept. of Wildlife Science, Utah State University, Logan, Utah 84322).

Accidents

A few fawns may die from accidents, such as falls and drownings (Robinette 1956). During the neonatal period, some fawns are killed on farms by moving machines, because they attempt to hide rather than flee (Baugen and Specko 1958). Also, fawns have difficulty crossing fences and often become entangled in them and die (Franzen 1968).

Nutrition

Winter die-offs from malnutrition usually involve differential mortality between age-classes, because certain age groups are less able to compete. Fawns, because of their smaller size, cannot move well in deep snow, nor reach as high as adults to browse on shrubs for forage (Huddleston 1964). In 1936, Doman and Rasmussed (1944) observed that of 114 "winter-killed" deer in northern Utah, 80
percent were fawns. Robinette et al. (1957) determined that fawn losses are usually from two to three times that of older deer. Huddleston (1964), however, observed 58 percent (21 of 34) of the winter mortality in the Cache Valley of northern Utah was comprised of fawns.

Predation

Predation, primarily by coyotes, accounted for 79 percent (15 of 19 deaths) of radio-tracked winter fawn losses in Oregon (Trainer 1975). In Utah, 28 of 31 dead deer found during the winter of 1975 were determined to be coyote kills and, of the 28 all but 3 were fawns (Nielson 1975). In Montana, a doe:fawn ratio of 100:40 at the end of the 1975 hunting season dropped to 100:10 in February. This occurred during a relatively mild winter, therefore, coyote predation was thought to be a major cause of mortality (letter dated 10 March, 1976 from R. G. Janson, Montana Dept. Fish and Game, Missoula, Montana 59801).

Summary

Productivity data demonstrate that the potential for rapid increases in mule deer populations still exists. Net productivity estimates, derived from doe:fawn ratios, show that significant losses may be occurring during pregnancy, the immediate post-natal period, or during the first few months of the fawn's life. Nutrition appears to be the primary limiting factor responsible for reduced ovulation rates, post-natal mortality and winter fawn losses. In certain areas, predation, especially by coyotes, accounts for a large percentage of fawn losses. The incidence and effects of diseases on productivity are as yet, little known, but ongoing studies may help to determine how these limiting factors influence mule deer populations.

Table 1. Reproductive potential of mule deer over a 6-year period.

<table>
<thead>
<tr>
<th>Year</th>
<th>Adult</th>
<th>Yearling</th>
<th>Fawns</th>
<th>Total population</th>
<th>Annual population percent increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>1(2)</td>
<td>0</td>
<td>2(1M, 1F)</td>
<td>3</td>
<td>33</td>
</tr>
<tr>
<td>Year 1</td>
<td>1(2)</td>
<td>1(1)</td>
<td>3(1M, 2F)</td>
<td>5</td>
<td>60</td>
</tr>
<tr>
<td>Year 2</td>
<td>2(2)</td>
<td>2(1)</td>
<td>6(3M, 3F)</td>
<td>10</td>
<td>50</td>
</tr>
<tr>
<td>Year 3</td>
<td>4(2)</td>
<td>3(1)</td>
<td>11(5M, 6F)</td>
<td>18</td>
<td>55</td>
</tr>
<tr>
<td>Year 4</td>
<td>7(2)</td>
<td>6(1)</td>
<td>20(10M, 10F)</td>
<td>33</td>
<td>55</td>
</tr>
<tr>
<td>Year 5</td>
<td>13(2)</td>
<td>10(1)</td>
<td>36(18M, 18F)</td>
<td>59</td>
<td>56</td>
</tr>
<tr>
<td>Winter count</td>
<td>23</td>
<td>18</td>
<td>64</td>
<td>105</td>
<td></td>
</tr>
</tbody>
</table>

( ) Fawns produced

Table 2. Reproductive potential of George Reserve white-tailed deer.

<table>
<thead>
<tr>
<th>Year</th>
<th>Adult</th>
<th>Yearling</th>
<th>Fawns</th>
<th>Total population</th>
<th>Annual population percent increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>1939</td>
<td>4(2)</td>
<td>0</td>
<td>8(4M, 4F)</td>
<td>12</td>
<td>50</td>
</tr>
<tr>
<td>1939</td>
<td>4(2)</td>
<td>4(0)</td>
<td>8(4M, 4F)</td>
<td>16</td>
<td>75</td>
</tr>
<tr>
<td>1940</td>
<td>8(2)</td>
<td>4(0)</td>
<td>16(8M, 8F)</td>
<td>28</td>
<td>64</td>
</tr>
<tr>
<td>1941</td>
<td>12(2)</td>
<td>8(0)</td>
<td>24(12M, 12F)</td>
<td>44</td>
<td>61</td>
</tr>
<tr>
<td>1942</td>
<td>20(2)</td>
<td>12(0)</td>
<td>40(20M, 20F)</td>
<td>72</td>
<td>62</td>
</tr>
<tr>
<td>1943</td>
<td>32(2)</td>
<td>20(0)</td>
<td>64(32M, 32F)</td>
<td>136</td>
<td>62</td>
</tr>
<tr>
<td>Winter count</td>
<td>52</td>
<td>32</td>
<td>104</td>
<td>188</td>
<td></td>
</tr>
</tbody>
</table>

( ) Fawns produced
Table 3. Mule deer productivity trends as reported by state representatives at the Fifth Western States Mule Deer Workshop, 1974.

<table>
<thead>
<tr>
<th>State</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arizona</td>
<td>&quot;Production came up a year ago, but has probably dropped back down... The statewide low has been 25 fawns/100 does and the high has been 65 fawns/100 does.&quot;</td>
</tr>
<tr>
<td>California</td>
<td>&quot;Twenty years ago production was about 65 fawns/100 does, but now has declined to 35 fawns/100 does.&quot;</td>
</tr>
<tr>
<td>Colorado</td>
<td>&quot;There are no fawn production figures on a statewide basis, but on one area there were 31 fawns per 100 does in 1974 compared to 1965 when there were 60-70 fawns per 100 does.&quot;</td>
</tr>
<tr>
<td>Idaho</td>
<td>&quot;Fawn production is up over the last year by about 5 fawns per 100 does for a state average of 75 fawns per 100 does.&quot;</td>
</tr>
<tr>
<td>Montana</td>
<td>&quot;Production in the western part of the state is relatively low and still declining... In 1973 they had 40 fawns per 100 does; in 1974 so far there has been 37 fawns per 100 does.&quot;</td>
</tr>
<tr>
<td>Nevada</td>
<td>&quot;Population trends are down prior to this year, but there are no fawn production figures.&quot;</td>
</tr>
<tr>
<td>New Mexico</td>
<td>&quot;Population trends are down slightly. Fawn production varied from a low of 12 fawns per 100 does to a statewide trend of 35-45 fawns per 100 does.&quot;</td>
</tr>
<tr>
<td>Oregon</td>
<td>&quot;Mule deer are still declining and have been doing so since 1968-1969 winter. A statewide average of 34 fawns per 100 does remained in December 1974.&quot;</td>
</tr>
<tr>
<td>Texas</td>
<td>&quot;Fawn ratios are 19 fawns per 100 does.&quot;</td>
</tr>
<tr>
<td>Utah*</td>
<td>&quot;The severe winter of 1972-1973 resulted in fawn losses and a decrease in the following summer's fawn crop due to the poor physical condition of does.&quot;</td>
</tr>
<tr>
<td>Washington</td>
<td>&quot;The pre-season classification shows 65 fawns per 100 does. This is down from about 80 fawns per 100 does of a year ago.&quot;</td>
</tr>
<tr>
<td>Wyoming</td>
<td>&quot;Reproduction looks good and is increasing.&quot;</td>
</tr>
</tbody>
</table>

*(Personal conversation dated 5 March, 1975, with Rodney John, Division of Wildlife Resources, Salt Lake City, Utah 84101).*
Table 4. Past and present comparison of productivity from does 1½ years and older on good and poor ranges.

<table>
<thead>
<tr>
<th>Area</th>
<th>Years</th>
<th>Corpora lutes/doe</th>
<th>Percent pregnant</th>
<th>Fetuses per doe</th>
<th>Fawn:doe ratio</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrubland, CA</td>
<td>1951-1953</td>
<td>1.60(18)</td>
<td>94(18)</td>
<td>1.45(18)</td>
<td>81/100 post-season</td>
<td>Taber and Basmann (1958)</td>
</tr>
<tr>
<td>Hoparrai, CA</td>
<td>1949-1950</td>
<td>0.82(11)</td>
<td>97(11)</td>
<td>0.71(11)</td>
<td>72/100 post-season</td>
<td></td>
</tr>
<tr>
<td>Devil's Garden, CA</td>
<td>1975</td>
<td>1.87(67)</td>
<td>99(67)</td>
<td>1.73(67)</td>
<td>20-50/100 pre-season</td>
<td>Salwasser (1974)</td>
</tr>
<tr>
<td>Crooked Creek, CA</td>
<td>1975</td>
<td>1.62(48)</td>
<td>90(48)</td>
<td>1.56(48)</td>
<td>45-75/100 pre-season</td>
<td></td>
</tr>
<tr>
<td>Sublette, ID</td>
<td>1954-1956</td>
<td>1.95(41)</td>
<td>100(9)*</td>
<td>1.85(33)</td>
<td>122/100 post-season</td>
<td>Julander et al. (1961)</td>
</tr>
<tr>
<td>Antimony, UT</td>
<td>1954-1956</td>
<td>1.31(114)</td>
<td>63(8)*</td>
<td>1.19(27)</td>
<td>51/100 pre-season</td>
<td></td>
</tr>
<tr>
<td>LaSal Mountains, UT</td>
<td>1967-1969</td>
<td>-----</td>
<td>-----</td>
<td>1.01(305)</td>
<td>93/100 pre-season</td>
<td>Pederson (1970)</td>
</tr>
<tr>
<td>Henry Mountains, UT</td>
<td>1967-1969</td>
<td>-----</td>
<td>-----</td>
<td>.59(299)</td>
<td>59/100 pre-season</td>
<td></td>
</tr>
</tbody>
</table>

( ) Sample size
* Yearlings only

Table 5. Comparison of productivity from does 1½ years and older for mild (1969) and severe (1970, 1971) winters in Colorado.

<table>
<thead>
<tr>
<th>Years</th>
<th>Corpora lutes/doe</th>
<th>Percent pregnant</th>
<th>Fetuses per doe</th>
<th>Fawn:doe ratio</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle Fork 1969</td>
<td>2.02(41)</td>
<td>100</td>
<td>1.93</td>
<td>93/100 pre-season</td>
<td>Gill (1972)</td>
</tr>
<tr>
<td>1970</td>
<td>1.76(42)</td>
<td>88</td>
<td>1.64</td>
<td>72/100 pre-season</td>
<td></td>
</tr>
<tr>
<td>1971</td>
<td>1.73(52)</td>
<td>98</td>
<td>1.61</td>
<td>73/100 pre-season</td>
<td></td>
</tr>
</tbody>
</table>

( ) Sample size
LITERATURE CITED


85 Male Deer Productivity—Past and Present


Abstract

The mule deer population in Colorado, and in the west generally, began increasing during the 1920's from a low at the beginning of the century to an accelerated high in the late forties to the early sixties, then began a rapid decline to the present. Harvests followed this same pattern. The applicable season regulations resulting in these harvests stem from biological considerations (various population and forage parameters) and political influences (true politics, as well as sociologic and economic factors). The application of computerized systems analysis in the form of herd simulation models is advanced as a means of measuring the impact of variable man-controlled management practices. This can not only identify areas of concern, but also point out types, amounts and qualities of data needed, without impacting the actual resource with trial and error methods.

INTRODUCTION

During the mid-1850's the pioneers arriving in the territory of what is now Colorado found vast numbers of deer, elk, bighorn sheep and bear in the mountains west of Denver. Though most of these pioneers were initially in search of gold, many communities were established, and, because trade and store goods were limited and difficult to obtain, wild game was the primary source of meat for these people. As the communities became more permanent their meat needs were supplied increasingly by professional exploiters of the abundant wildlife. Market hunters began to make such inroads on various big game populations that the citizens became alarmed. Hunter (1959) estimated that 100,000 big game animals per year must have been killed to supply Colorado's population at that time. In 1867 the first game laws were enacted, which prohibited the taking of wildlife during the breeding season. Still, no specific seasons or licenses were in effect, but game laws became increasingly restrictive. By 1903 the first deer license was authorized at $1.00, but elk, antelope and bighorn sheep seasons were still closed, and bison had disappeared by the turn of the century. The early 1900's represented the low point in Colorado's big game populations, but through sound wildlife management the game herds were built up to the point that by 1960 they were some of the most important in the nation.

This is similar to the history of big game in most of the western states. During the 1950's, however, the management of mule deer in the various western states was affected through many different types of regulations and administrative philosophies. Regardless of the management approach, whether it was ultra-conservative or super-exploitive, the mule deer trend has followed essentially the same pattern throughout the west: a gradual build-up 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.

There is an increasing number of advocates of the concept that wildlife constitutes an early warning system of ecosystem deterioration. In the face of current knowledge this can hardly be refuted. There are many people, particularly the general public, who are quick to lay the mule deer decline on overshooting allowed by liberal regulations. The fallacy of the antlered only management concept is illustrated by the fact that states (Arizona, California and Oregon) with primarily buck only hunts have critically low buck to doe ratios, while states harvesting both sexes (Colorado, Idaho, Nevada and Utah) have experienced only half the harvest decline of the former (Salwasser 1975). Inasmuch as the mule deer decline is general throughout the west, it is obvious that the cause must be a composite of many factors, some of which we probably have not identified to date. In view of the return to population fluctuations of the
past, is it possible that certain cyclic phenomena are being exhibited in a species that we never previously considered to be cyclic? I doubt this, but in the light of the habitat decrease and degradation experienced in the west in the past 20 years, we will never again see the incredible harvests of a century ago, or the documented kills of the recent past.

This paper will attempt to evaluate the various regulations pertaining to mule deer harvest in Colorado (probably applicable to the entire west), how they were effected by biological and political considerations and how such considerations may affect regulations in future mule deer management.

COLORADO MULE DEER HARVEST

During the period 1940 through 1975, Colorado has yielded a mule deer harvest of 2.7 million animals to over 4.7 million hunters for an average success ratio of 57 per cent. This 36-year period covers an era of relatively gradual mule deer population increase until a peak was reached in the late fifties and early sixties, at which time an accelerated decline to the present was experienced. The antlered and total harvests, hunter pressure and success ratios are indicated in Figure 1.

Figure 1. License sales and deer harvest, 1940-present, Colorado.

During this 36-year period a total of 1,533,121 bucks, representing an annual average of 42,587, was harvested. Broken down into the three most recent five-year periods, the annual antlered harvest averaged 60,951 during 1961-65, 43,853 during 1966-70, and 44,788 during 1971-75. During the 36-year period, 1971 was the only year in which the harvest was limited to bucks only.

Hunter success during this period has ranged from a low of 26 per cent in 1973 to a high of 88.6 percent in 1957, but does not represent a function of the deer population alone. The harvest regulations affecting these harvests were two deer of either sex in 1957, and antlered only with some limited either sex permits in 1975. What were the considerations involved in these types of divergent seasons?

Biologically-Based Regulations

Colorado has attempted to manage its big game populations on the basis of herd units. The on-the-ground biological data obtained by Division personnel included:

1. Population trend counts obtained on winter concentration areas by aerial and ground observations.
2. Pre- and post-season sex and age ratios obtained by aerial and ground observations on selected seasonal ranges.
3. Wounding loss assessment based on field observations.
4. Winter mortality based on field work in winter concentration areas.
5. Browse production and utilization data derived from measured intensive transects and estimated extensive transects on winter ranges.
6. Deer-days use per acre derived from pellet group counts in association with game range analysis transects.
7. Research data from specific projects on deer range and population dynamics.

Additional biological data which have been considered in formulating season regulations, but derived after-the-fact, are the buck, doe and fawn statistics of the annual harvests, and the percentage of yearlings as determined from dentition determinations at check stations, cementum annuli from incisors obtained at check stations or mailed in by hunters, and antler configuration inspected at check stations or obtained from surveys.

A brief comment on each of the biological factors and their effect in setting season regulations follows:

1. Population Trend Counts. Aerial and ground counts of deer are made on established areas or routes, usually on winter ranges, and under as nearly comparable conditions of time of year, snow-cover and systematics as possible. Inconsistencies in weather, affecting snow depth and coverage, ambient temperatures and winds, detract from the reliability of such counts by introducing variables in flight or count conditions, visibility and deer behavior. Population determinations are not possible from such counts, and, at best, they can only serve as an index to the general population trend over a relatively long period of time.

Another type of trend count has been employed on the Piceance deer herd since 1947, and that is a count during one or two days in April of comparable phenological condition each year of the deer concentrating on the native hay meadows of Piceance Creek and its tributaries. A track count was made of a portion of this migrating herd, usually during the month of May, for a number of years until about 1957 when road conditions on
Flag Creek forced its termination. However, during its life, the track counts were up to two or three times higher than the meadow counts on comparable years. All that can be said of such counts is that they may represent a minimum number present, but what per cent of the total herd population in that area is unknown.

Trend counts on mule deer have had little direct input in the formulation of season regulations.

2. Sex and Age Ratios. While we talk about pre- and post-season sex and age ratios, the emphasis has been on post-season classifications, and these are primarily aerial, although some ground counts are conducted in selected areas. These data have a greater potential in influencing the establishment of regulations than has been realized in practice. The best of our knowledge, one buck to three ratios have never been low enough to influence fawn production. The number of fawns yields an index to hunting season survival, and, barring unusual winter mortality, an indication of herd recruitment in the yearling age class the following spring.

Similarly, we have long used the percentage of yearlings in the harvest as an indicator of herd health. The utilization of sex and age data in herd management regulations will be discussed in more detail in another section of this paper.

3. Wounding Loss. Other than superficial surveys, we have no documentation of the impact of wounding loss. We have used a rule-of-thumb figure of 5-and-10, that is, a wounding loss of five per cent of the harvest in buck only areas, and ten per cent of the harvest in either sex areas. I feel that this is too conservative. Wounding loss receives little consideration in establishing regulations, but may receive attention when more refined management is implemented.

4. Winter Mortality. Evaluations of winter mortality are based on field checks after the critical winter period, and usually in areas of winter concentrations. The percentage of such loss in a specific herd area is estimated on the basis of dead deer counts, and relative to past data. These losses are primarily considered to be a function of malnutrition and associated overcrowding and over-utilization of limited winter ranges, though the amount and character of snow, minimum sustained temperatures, protective cover and wind are known factors. Such data impact on regulations pertaining to entered only or either sex seasons, and formerly on bag limits when we held two and three-deer seasons.

5. Range Analysis. Production and utilization estimates on key browse species on important winter range areas at one time formed the primary basis for Colorado mule deer management. Unfortunately, this is no longer true, and will be discussed under political considerations. During most of the fifties and sixties, however, range transect data provided significant input in regulation determinations, and could still do so.

Two deer seasons were initiated in 1950 primarily on the basis of range conditions in an effort to bring the herds into what was felt to be the carrying capacity of the winter range, and two, and even three-deer, seasons were held in large areas of the state until 1969. These seasons were established in the beginning because hunter pressure was limited and we had to utilize the sportman resource we had available. As hunter receptiveness and pressure increased, certain political considerations were brought to bear, as discussed later.

6. Pellet Group Counts. Pellet group counts were conducted in conjunction with range transects, and converted to deer days per acre on the basis of 13 pellet groups per deer per day as determined by research investigations at the Little Hills Experiment Station on Piceance Creek. Because of the many variables and controversy we did not convert these data to populations, but rather used them as a deer winter range pressure index relative to past years and other areas, and correlated with browse utilization. The other comments under Range Analysis also apply here.

7. Research. Deer investigations in important areas have yielded data which have influenced season regulations to some extent in those areas specifically. It was an early Federal Aid project that stimulated the two-deer season concept in the Uncompahgre Plateau, which eventually was applied almost western-slope wide. Certain types of seasons and mandatory check stations were part of and resulted from the Middle Park deer study. The results of current deer studies and task forces will undoubtedly be applied to future regulations.

Political Considerations

Political, in the sense used here, is a real Pandora's box. It not only includes politics in the commonly accepted definition, but also in the context of economics and sociology.

The constraints imposed by state statutes or political bodies can directly affect the latitude that a conservation agency can exercise in wildlife management. Colorado is fortunate in that its statutes authorize the Wildlife Commission to establish policies and set regulations for wildlife management. Even with this type of authority, state wildlife agencies can be subjected to considerable pressure through implied threats of alternative laws, or even manipulations of budget requests. For example, a western state's commission established a regulation intended for a three-year longevity, but after two years it was found to be ineffective, and, in fact, detrimental to that agency's objectives and supportive data justified the repeal or revision of the regulation. However, word was received from the state legislature that they would set the seasons if the agency's regulations were not consistent. In the political world, it seems that consistency is of higher merit than being flexible enough to admit a mistake and correct it! In another case a legislative committee handling a conservation agency's budget request subtly suggested a regulation pertaining to the identification of sex on a big game carcass be less restrictive, and it was changed.

A major political impact on state wildlife...
agencies could be in the offing, pending the findings of courts and the results of appeals in New Mexico and Montana on nonresident license fees. If nonresidents become entitled to hunt on the same license structure that residents do, season regulations will have to be tailored to meet an increased hunter demand through restrictions on sex and numbers of harvest and shortened seasons, to lessen the biological impacts on the big game.

Many political impacts on regulations are so intertwined that they involve economics, sociology and biology. An example is intra-agency politics where for public relations and economic reasons it was decided to set the general season regulations in March to facilitate getting the information on opening dates and areas out to the public. This early setting of seasons was to meet printing deadlines and allow the sportsmen to arrange necessary vacation time for hunting. The impact of this reached to the field level, because winter mortality counts and range transects could not be completed before May due to continuing winter range use and lack of access, although the numbers of limited either sex permits would be set in May. This time schedule has probably been one of the greatest contributing factors to the decline in obtaining the indicated biological data. Furthermore, in regard to legal politics, the attorney general has decreed that the agency must have its recommendations for season regulations available for public inspection 20 days prior to commission action. This means, in reality, that the regulations must be written for big game season opening dates and areas in February.

Public safety and welfare are a form of political consideration in setting seasons. For example, in Colorado, to spread the first day of season pressure and reduce the possibilities of hunter fatalities and accidents, the deer season and elk season were separated in 1971 from their previously concurrent timing. Though a high percentage of elk hunters were also deer hunters, they then had to hunt these respective species at different times, thus reducing the total number of hunters in the field during one season. True, there was some economic impact in reduced total license sales, because many hunters, particularly nonresidents, who previously hunted through species could not afford two separate hunting trips, and therefore only hunted one species.

When archery deer hunting was started in Colorado in 1968, the bow hunters could hunt on a regular deer license which was validated for that purpose, and if unsuccessful in bowhunting, they could use that license in the regular deer season. In 1961 an archery deer license was established by the legislature, and if an archer was unsuccessful during bowhunting season, he could then purchase a regular deer license and hunt with a rifle. Again, in desiring to divert hunter pressure from the regular season, a one-and-only hunt concept was established in 1974 through regulation, wherein no one could purchase more than one license for a given species during the year. The effect that this had was to weed the marginal bowhunters out of the archery ranks and put them right back into the more sure-fire rifle season. The biologically-based regulations providing for two-deer seasons in the early fifties were quite effective, and license sales increased as a result. A new philosophy, economically-oriented, arose. Why give that second deer away, when with increased hunter pressure we could sell a second license at a reduced fee and generate some more income? The multiple license was born in 1957, and was utilized until 1970.

The increases in Colorado license fees effective in 1976 will result in socio-economic influences on season regulations. Resident deer license fees have gone from $10.00 to $13.00, while nonresident fees have gone from $50.00 to $90.00. We will have to experience at least one season under this new structure to evaluate the effect of probable decreased hunter pressure on herd management objectives, then consider what regulation options will best attain the desired harvest.

HERD SIMULATION MODEL

For almost 20 years Colorado's deer management efforts were directed toward reducing overpopulations to the carrying capacity of the most critical factor - the winter range. It was always stated and generally accepted that the deer could come back faster than the browse. The regulations instituted to affect this reduction began with either sex seasons, then two deer seasons, and finally multiple license seasons (varying from unlimited additional licenses to one additional license, with one deer per license to two deer allowed on the second license, and, in some cases, two deer on both the original and the multiple license). In addition to multiple bag limits, the times and lengths of seasons were varied to obtain increased harvests. Post seasons were utilized in relatively small areas when deer were on late fall transitional or winter ranges. Since 1963 management objectives generally have been either to stabilize the deer herds, or to increase them numerically.

Current harvest data alone do not allow an accurate determination of mule deer populations, particularly on a statewide basis, due to more variable and restrictive seasons applied under present management practices. Therefore, management units have been combined to form data analysis units, which are considered to be more realistic total herd year-round habitat. Herd data can now be analyzed by a computer simulation of herd structure, as well as the effect of various impacts, both real and simulated, on that herd, other factors remaining equal. This type of systems analysis is guided by Dr. Jack Gross, U. S.
Fish and Wildlife Service, and conducted by Tom Pojar, Colorado Division of Wildlife. Systems analysis has the potential for indicating the impacts of regulations on a given herd, whether they be biologically or politically generated. By plugging in known data for the past several years, certain causative factors may be indicated as responsible for given herd reactions.

The Uncompahgre Plateau in southwestern Colorado represents a deer herd on which our most complete data are available. This herd unit is composed of two game management units, 61 and 62, comprising deer data analysis unit D-19. The systems model begins in 1963 and is projected through 1980. Actual harvest data are displayed in Figure 2 relative to total and buck (antlered) harvest, hunter pressure and success ratios from 1950 to 1975. Inasmuch as the complete simulation printout is extensive, only certain details of the analysis will be highlighted here.

A mortality rate of 22 per cent was used from 1963 through 1971, 40 per cent for 1972, 50 per cent in 1973, then 22 per cent from 1974 onward. Using the yearling harvest as an index to fawn survival from the previous winter, the yearling harvests in 1973 and 1974 support the indicated increased winter loss of fawns reported for 1972 and 1973. This additional fawn mortality resulted in a downward population trend in the simulation, which is actually what happened in the field. The alignment of these data with the simulation is probably one of the strongest points of this analysis.

Table 1 lists a comparison of simulated and reported values for pre- and post-season bucks and fawns per 100 females. The pre-season buck to doe ratios are simulated above the reported values, as the regional biologist, Hal Burdick, feels that many bucks are missed during these counts.

The alignment of these data lend support to the closeness of the simulation model to the actual herd structure, and even though specific values are not always in agreement numerically, the general trends follow the same curves.

The model indicates a population of this herd right now of approximately 35,000 deer, with a post-season population projection by 1980 of just over 50,000 animals, IF the 1975 harvest of 2,500 is maintained, and IF the system remains stable.

CONCLUSIONS

As important and necessary as biological management of mule deer is, the various facets of political management may present significant obstacles to sound wildlife management, and the constraints imposed by politically-oriented regulations may have on mule deer herds can now be indicated experimentally through systems analysis with simulation models, thus sparing the resource from the consequences of ill-advised or poorly timed impacts within human control.

The application of systems analysis to simulation modeling of wildlife populations is
relatively new. Several states are beginning to explore the possibilities of this system, including the Interstate Deer Herd Study of California and Oregon (Salwasser 1975a, Salwasser and Rutherford 1975), and the Nevada Fish and Game Department (Glenn Christensen, pers. comm.).

Computer analysis is not a panacea, and is only as reliable as the data programmed. Simulation modeling will not of itself solve the enigma of the mule deer decline in the west, but it can help identify areas of concern where additional or more reliable data are needed.

LITERATURE CITED


RELIABILITY OF MULE DEER POPULATION MEASUREMENTS

Michael L. Wolfe
Department of Wildlife Science
Utah State University

Abstract

Various methods of enumerating mule deer population trends are reviewed. Naïve acceptance of the results of certain "traditional" methods without recognition of their limitations may account in part for recent declines in deer numbers. This probably has occurred in some states where harvest regulations have been formulated primarily from vegetation-based indices. The problems of failure to meet the requisite assumption of population stability in the estimation of demographic parameters from age-structure data are also discussed. Since individual estimates of animal abundance are each based on assumptions of questionable validity, management agencies are cautioned to avoid reliance on a single method or informational input to formulate harvest regulations.

The objective of most deer management programs is to maintain the largest huntable population possible which the habitat can sustain in a healthy condition and is compatible with other recognized land uses. Achievement of this goal requires two informational inputs. One is a knowledge of the vegetation, particularly in terms of the number of animals it can currently support and the effects of plant succession on future species composition and production. At the same time, the manager requires knowledge of deer demography (i.e. population trends, reproductive and mortality rates and the effects of various exploitation levels on the population). With this basic premise, the objective of this paper is to examine critically the current state of the arts with reference to the assessment of mule deer population trends.

Table 1 summarizes the different approaches and information sources employed to measure deer population trends as a basis for the formulation of harvest levels. Virtually all the western states that I surveyed employ these methods or some subset thereof. The categorization of methods is not mutually exclusive but depends to some degree upon the level of resolution, with which they are employed. The application, requisite assumptions and limitations of most of the methods in the second group have been discussed extensively in the wildlife literature and are reviewed by Davis (1961), Overton and Davis (1969), Seber (1973) and others. I will direct my comments here primarily to the first and third approaches.

Measures of occupancy and utilization

In the past, management agencies in several western states have relied heavily on observed trends in deer occupancy (animal days use) of critical winter range areas and their utilization of "key browse species" (Aldous 1945, Cole 1959) as indirect indices of deer population trends. This system was initiated during an era (the early 1950's), when deer populations were excessive and damaging range vegetation as a result of long-standing restrictive harvest regulations. At that time the reduction of deer numbers and protection of their habitat was a necessary and justifiable consideration. The system was useful in effecting liberal harvests to reduce deer numbers, but today — a quarter of a century later — the basic premise is for the most part no longer applicable.

Harvest regulations, formulated solely on indices of occupancy and utilization, are subject to several serious shortcomings. Differential winter severity may greatly influence animal occupancy of a pre-determined key area and the intensity of utilization of browse species on that area. Thus, measurements of occupancy and vegetation-use patterns for a given winter may imply spurious population trends. It may be true that the mean level of browse utilization and pellet group counts may be higher over an extended period of high deer densities than during a similar period with low densities. However, annual variations in such indices probably reflect variations in winter weather rather than actual changes in big game numbers. Hence, they constitute a questionable basis for annual decisions on harvest levels. Furthermore, these measurements are (by definition) not predictive, but rather terminal or ex post facto symptoms of a big game animal's impact on its habitat. This contention has been corroborated empirically by Mackie's (1976) findings in Montana. He concluded that browse surveys appear mainly to provide hindsight and reflect cumulatively events and conditions of the past more adequately than those at the time the surveys are conducted.

It is my opinion that this frequently overlooked limitation may account in part for the decline in mule deer numbers in some states. A possible explanation of how this could happen is illustrated in Fig. 1 (modified from Aney 1972). The straight line I is the scalar relationship between actual
Table 1. Overview of Approaches to Assessment of Mule Deer Population Trends

<table>
<thead>
<tr>
<th>Utilization and Occupancy Data</th>
<th>Indicators of Population Trend</th>
<th>Dynamics Data</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. BROWSE UTILIZATION TRENDS</td>
<td>1. TREND COUNTS</td>
<td>1. HERD COMPOSITION SURVEYS</td>
</tr>
<tr>
<td>2. PELLET GROUP COUNTS</td>
<td>A. AERIAL</td>
<td>A. FAWN-DOE RATIOS</td>
</tr>
<tr>
<td>(DEER DAYS USE)</td>
<td>B. GROUND</td>
<td>B. SEX RATIOS</td>
</tr>
<tr>
<td>3. OTHER TREND INDICES</td>
<td>2. INDIRECT POPULATION ESTIMATES</td>
<td>2. AGE STRUCTURE OF THE HARVEST</td>
</tr>
<tr>
<td></td>
<td>A. CHANGE-IN-RATIO</td>
<td>3. DEAD DEER SURVEYS</td>
</tr>
<tr>
<td></td>
<td>B. PELLET GROUP COUNTS</td>
<td></td>
</tr>
</tbody>
</table>

Assumption: The degree of utilization on "key areas" or of important browse plants reflects the level of the population.

Hypothetical relationships between population size and vegetation-based indices of population trend (modified from Aney, 1972). Relationship I represents the linear relationship between actual population size and vegetation-based indices of population trend, if measurements of animal use (i.e., browse utilization and animal days use) were accurate indicators of animal numbers. Relationship II might exist when indices are based solely on measurements in non-preferred habitat. Figure 1 indicates the index value is inversely related to population size. Relationship II might exist when indices are based solely on measurements in non-preferred habitat.
More importantly, naive acceptance at face value of the results obtained by these measurements without recognition of their inherent weaknesses may have contributed indirectly to or aggravated population declines in some cases. The dual approach of measuring animal population trends annually in conjunction with periodic and more sophisticated vegetational measurements, to evaluate long-term trends in range condition, productivity and species composition represents a more realistic approach.

Indices of population trend:

As game biologists began to question the adequacy of occupancy and utilization measurements, some states have moved in other directions. One of these was toward refining local pellet-group counts to obtain "estimates" or at least indices of actual deer population levels. The pellet group technique has received considerable attention in the wildlife literature and has been comprehensively reviewed by Neff (1968).

Detailed treatment of the method is not within the scope of this paper, but a few brief comments seem apropos.

The fundamental weakness of the pellet group technique as a source of information for management purposes, is human error. This comes as no surprise to any manager, who has "picked pellets" at some time in his career, or all the means of collecting data on big game animals, this is the problem. Even if the manager is fortunate enough to have well-intentioned and responsible field personnel and he can convince them of the necessity for accurate pellet tallies, some unavoidable errors will occur. Unfortunately, these cannot be rectified and we will probably have to live with them in the future.

Beyond this, the use of pellet group counts as a population estimator requires certain refinements in addition to those necessary for the application of the method as a mere index of animal use. Perhaps the most important of these is that of stratifying sampling allocation. Big game animals are rarely distributed randomly or uniformly on winter range areas. This is particularly true in the West, where marked topographic variation and associated vegetational differences produce more or less distinct strata of differential deer distribution and density, which vary annually in response to winter severity (Edwards 1956, Loveless 1967, Gilbert et al. 1970). Sampling variance in magill and associated distributions increases with density. If differential density strata are considered in the statistical design of pellet group counts, sampling intensity can be allocated proportionally or optimally to the various strata, thereby increasing the precision of the population estimate obtained (Siniff and Skoog 1964, Bergerud 1968). It might be noted that this generalization is applicable, not only to pellet group counts, but also to some of the other methods of assessing population trends and related parameters (e.g. dead deer surveys), listed in Table 1.

In theory, sampling effort in pellet counts should be allocated on the basis of observed deer distribution patterns in the winter immediately prior to the surveys. This implies the use of temporary plots. However, western conditions necessitate some departures from the ideal design. Sparse, xerophytic vegetation on many big game winter ranges precludes reliance upon autumnal leaf-fall to conceal pellets of older origin than the current winter. This and the fact that older pellets may persist for several seasons dictates the use of permanent "swept" plots. Some of the benefits of stratification could be realized by a compromise solution, whereby sampling effort is allocated on the basis of past patterns of winter deer distribution. Clusters of plots, as used by Eberhardt and Van Etten (1956), Smith (1964), and Stormieght et al. (1970), might be employed to vary sampling intensity on transects of standardized length. Several authors (Eberhardt 1960, Bowden et al. 1969, McConnell and Smith 1969) have analyzed the nature of frequency distributions in pellet-group tallies. The results of these or similar investigations should provide additional information with reference to optimal allocation within density strata.

Dynamics data:

The concept of employing demographic parameters in the analysis of deer population dynamics is not novel, as attested by the classical papers of Taber and Bagam (1937) and Eberhardt (1960). However, this approach has received renewed attention within the past decade, largely as the result of two important developments in wildlife science. One is the increasingly widespread application of the cementum annihilation technique for age determination. This technique has given game managers the means to obtain reasonably accurate data on the age distribution of large harvest samples from different herd units and relate them by conventional methods of population analysis to varying harvest strategies. The other important development is the advent of computer technology, which has greatly facilitated the iterative processes involved in demographic analysis and opened up the field of population simulation.

Despite the apparent sophistication in this approach, its limitations should not be overlooked. Referring to Table 1, let us examine the basic assumption involved in this approach. We assume that it is possible to measure accurately reproductive increments to the herd and the mortality or survival rates operating on the population — especially within the female segment — under varying harvest regimes. If this is possible, we can determine the level of harvest, which just crops the annual increment, while allowing for natural decrements. We will further stipulate that it is within the manager's wherewithal to assess reliably the recruitment to the population and concentrate on the problem of measuring mortality rates.

Given a sample of the relative age frequencies in a population at a point in time, the age-specific and total mortality rates operative within the population from which the sample derives can be estimated subject to certain important assumptions:

1. That mortality and natality have been constant and the population has remained numerically constant for some time previous to the point at which the sample was taken;
2. That the sample accurately reflects the relative strengths of the various age classes in the population;
3. That the method of age determination is accurate.
While the iterative procedures involved may differ, the assumptions upon which they are predicated are basically the same. We should be able to satisfy the third condition, given the methods of age determination that are currently available. We also know that some age classes, notably fawns and yearlings, are differentially vulnerable to the gun and will probably not be accurately represented in a hunter-killed sample (Smith et al. 1969, Hayne and Eberhardt 1952, Maguire and Severinghaus 1954), but there exist methods for dealing with these biases (vide Robson and Chapman 1961).

The greatest single bugaboo remains the rigorous and seldom met condition of population stability. The effects of failure to meet this assumption can be illustrated by a simple demographic convention (Table 2). The strictly hypothetical population shown below is generated over time from an initial cohort of 1000 animals (50:50 sex ratio) of one year of age, in which each yearling or adult female produces two young (i.e. natality = 50 percent); the mortality rate for all age and sex classes is 55 percent. Admittedly, this is not a very realistic representation of actual mule deer population parameters, since it fails to account for age-specific fecundity and mortality rates and assumes that all females breed as fawns. These simplistic parameters have been purposely chosen, however, to preserve the clarity of the point that I am trying to make. Examining the total number of animals in the population over time, it is obvious that the population is decreasing by 10 percent per annum. This is to be expected in terms of discrepancy between natality and mortality rates (50 vs 55 percent).

Table 2. Cohort shrinkage in a declining population; annual mortality rate = 55 percent; natality = 50 percent. See text for further explanation.

<table>
<thead>
<tr>
<th>Age</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1000</td>
<td>900</td>
<td>811</td>
<td>729</td>
<td>656</td>
<td>590</td>
<td>531</td>
<td>479</td>
<td>436</td>
<td>396</td>
<td>3510</td>
</tr>
<tr>
<td>1</td>
<td>1000</td>
<td>450</td>
<td>405</td>
<td>365</td>
<td>328</td>
<td>295</td>
<td>266</td>
<td>239</td>
<td>216</td>
<td>195</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>450</td>
<td>235</td>
<td>202</td>
<td>164</td>
<td>135</td>
<td>113</td>
<td>97</td>
<td>85</td>
<td>74</td>
<td>67</td>
<td>97</td>
</tr>
<tr>
<td>3</td>
<td>235</td>
<td>91</td>
<td>61</td>
<td>41</td>
<td>37</td>
<td>33</td>
<td>30</td>
<td>27</td>
<td>24</td>
<td>19</td>
<td>49</td>
</tr>
<tr>
<td>4</td>
<td>91</td>
<td>58</td>
<td>38</td>
<td>30</td>
<td>27</td>
<td>24</td>
<td>21</td>
<td>18</td>
<td>15</td>
<td>12</td>
<td>43</td>
</tr>
<tr>
<td>5</td>
<td>58</td>
<td>38</td>
<td>30</td>
<td>27</td>
<td>24</td>
<td>21</td>
<td>18</td>
<td>15</td>
<td>12</td>
<td>10</td>
<td>34</td>
</tr>
<tr>
<td>6</td>
<td>38</td>
<td>30</td>
<td>27</td>
<td>24</td>
<td>21</td>
<td>18</td>
<td>15</td>
<td>12</td>
<td>10</td>
<td>8</td>
<td>26</td>
</tr>
<tr>
<td>7</td>
<td>30</td>
<td>27</td>
<td>24</td>
<td>21</td>
<td>18</td>
<td>15</td>
<td>12</td>
<td>10</td>
<td>8</td>
<td>6</td>
<td>22</td>
</tr>
<tr>
<td>8</td>
<td>27</td>
<td>24</td>
<td>21</td>
<td>18</td>
<td>15</td>
<td>12</td>
<td>10</td>
<td>8</td>
<td>6</td>
<td>4</td>
<td>21</td>
</tr>
<tr>
<td>9</td>
<td>24</td>
<td>21</td>
<td>18</td>
<td>15</td>
<td>12</td>
<td>10</td>
<td>8</td>
<td>6</td>
<td>4</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>21</td>
<td>18</td>
<td>15</td>
<td>12</td>
<td>10</td>
<td>8</td>
<td>6</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1820</td>
<td>1522</td>
<td>1458</td>
<td>1372</td>
<td>1280</td>
<td>1192</td>
<td>1025</td>
<td>898</td>
<td>760</td>
<td></td>
<td>8580</td>
</tr>
</tbody>
</table>

The actual mortality rate operative within a cohort, born in any given calendar year. However, if one attempts to ascertain the mortality rate from the age-class frequency tables in a vertical segment of the population in a given calendar year, (say year 9) the implied mortality rate thus obtained underestimates the true mortality by a factor equivalent to the rate of population change (in this case 10 percent). Ironically, if the level of harvest were formulated on the implied mortality rate alone, the population decline would be aggravated. Given an independent estimate of the rate of population change, the true mortality rate could be derived from the implied rate. Paradoxically, accurate and independently derived estimates of the rate of population change are more often than not lacking, and if they were available they would obviate this somewhat circuitous approach to assessing deer population trends. Without them, however, the inference of population trends based on survival rates derived from the vertical age structure of a population is tautological.

The implications of this problem are well known to population ecologists (Caughley 1966, Eberhardt 1969), but may be overlooked by the manager, especially when he may be lulled into a false sense of security with the aforementioned advances in age-determination techniques and computer technology. Computerized iteration of dynamics data and population simulation techniques can and will not rectify biases inherent in the basic data.

This is merely one of numerous problems involved in the estimation of population parameters from life tables and related methods. Rarely, if ever, are the histories of the several cohorts represented in a time-specific sample of the population indenical as represented in Table 2. Hence substantial annual variations in productivity and winter survival may produce seeming anomalies in the age structure of a population, which complicate or preclude derivation of mortality rates. Separation of these effects from the vagaries of sampling effect may be difficult.

Referring again to Table 2, it was noted that the mortality rates operative within a given cohort could be determined by examining the relative strengths of that cohort in samples taken at consecutive points in time. Such a horizontal approach is of relatively limited utility for deer management for several reasons. Foremost is the requisite assumption of equal sampling intensity over time. Obviously, this assumption does not obtain, when the degree of removal varies annually due to differential harvest regulations and/or differences in weather conditions during the hunting season. Certainly, differences in the relative vulnerability of various age classes must be taken into account here also.

Moreover, stochastic variations in natural sources of mortality (e.g. winter losses) will affect the apparent strength of a given age class (especially that of yearlings) and thereby preclude estimation of mortality rates by this method.

CONCLUSIONS

In summary, we find that despite the staggering resources and effort expended annually, real accuracy and precision in the enumeration of mule deer population trends remain elusive. Looking to the future, I do not see any pat solutions to the problem on the immediate horizon. A few years ago, some biologists hailed remote sensing (Croon et al. 1968, Graves et al. 1972, Parker and Driscoll 1972) as the paragon of the future. To date at least, this technique has not lived up to original expectations. Continued...
development of remote sensing, especially the implementation of more sophisticated hardware and innovative approaches, may ultimately provide more reliable results. However, this will undoubtedly require several years of additional research and development.

1. Management agencies should not rely on a single method or source of information to assess deer population trends and formulate harvest regulations. Individual estimators of animal abundance and related demographic parameters are each based on assumptions of questionable validity. Moreover, problems of sampling error reduce precision and further confound the reliability of population estimates. Given these circumstances, the only feasible alternative is to weigh carefully the results obtained by several independent indices and the effects of inherent biases on these indices to derive a qualified "best guess" of population levels on an annual basis.

2. Lacking any single, totally reliable census method, a concerted estimate should be directed toward quantifying the fraction of a deer population that is removed annually by hunting. The need for information of this nature seems singularly appropriate in an era of increasing demands — both on the part of the hunting public as well as non-consumptive interest groups — to know the magnitude and impact of various harvest strategies and natural decrements on deer populations. One possible approach to this problem would be estimation of "harvest rates". Ideally, this would involve the admittedly difficult task of large-scale tagging programs on summer ranges and the use of a reward system to insure reporting most or all of the tagged animals that were harvested. The recovery rates thus obtained would provide an index of the fraction of the population which is harvested. These rates could be correlated to differential harvest regulations, levels of hunting pressure, deer vulnerability as related to topography and access on different herd units. Comparison of the hunting removal rate under a spectrum of harvest strategies and natural decrements on deer populations. One possible approach to this problem would be estimation of "harvest rates". Ideally, this would involve the admittedly difficult task of large-scale tagging programs on summer ranges and the use of a reward system to insure reporting most or all of the tagged animals that were harvested. The recovery rates thus obtained would provide an index of the fraction of the population which is harvested. These rates could be correlated to differential harvest regulations, levels of hunting pressure, deer vulnerability as related to topography and access on different herd units. Comparison of the hunting removal rate under a spectrum of harvest strategies and natural decrements.

LITERATURE CITED


MULE DEER MANAGEMENT MYTHS AND
THE MULE DEER POPULATION DECLINE

R. B. Gill
Section Chief, Big Game Research
Colorado Division of Wildlife
Wildlife Research Center
P. O. Box 2287
Fort Collins, Colorado 80522

Abstract

This paper entertains the thesis that a
general decline in mule deer numbers in the West
is a myth. Conclusive evidence of such a decline
is lacking because there are no real estimates of
numbers of mule deer in western United States.
Inadequate census methodology, insufficient knowl-
edge of mule deer ecology, and impossible staffing
assignments combine with a tradition of uncritical
acceptance of new ideas and techniques to produce
and perpetuate the myth of the mule deer decline.

INTRODUCTION

The prevailing opinion among wildlife managers
in the western United States is that mule deer popu-
lations in the West have been declining since the
early 1960's (Sandfort 1968; Greenley 1968).
Evidence cited in support of this hypothesis includes
decreasing harvests, erratic but generally declining
deer counts on trend areas, reduced grazing pressure
on "key browse plants" within "key areas", and in-
tuition. It is my contention that the great mule
deer decline is a myth, as are many of the corner-
stones of evidence cited in proof of the decline.

This does not mean there hasn't been a western-
wide mule deer decline. It simply means the evidence
for this thesis is inadequate or lacking, and there-
fore the conclusion of a general decline in mule
deer numbers is speculative or "mythical". The
definition of a myth as used in this paper is: "a
belief given uncritical acceptance by the members of
a group, especially in support of existing or
traditional practices and institutions" (Gove 1961).
In this context, not only is the phenomenon of a
mule deer decline a myth, but so also are some of
the most cherished "principles" of mule deer manage-
ment. The purpose of this paper is to examine some
of the more pervasive and invidious mule deer manage-
ment myths and relate them to the myth of the great
mule deer decline.

MULE DEER MANAGEMENT MYTHS

Myths of Mensuration

The Numbers Game

Some time ago Cronemiller and Fischer (1946:349)
wrote ... "As far back as the time when aboriginal
man learned to count by tallying things on the
fingers of one hand, he has probably been counting
big game animals. As a science, the determination
of wild animal populations has gotten little beyond
the point where we can count up to multiples of the
fingers on both hands." This statement, true in
1946, remains a reasonable summary of the state of
the art in 1976. With respect to the great mule
deer decline we should ask ourselves, where are the
numbers? If they exist, what is the nature of their
quality?

After reviewing the pertinent literature, I am
convinced there are no valid estimates of numbers of
free-ranging mule deer on any large portion of
western deer range. There are published figures of
deer numbers in various western states such as
200,000 in Washington (Lauckhart 1968); 300,000 in
Colorado (Colo. Div. Wildl. 1974; Meyers 1975), etc.
However, these figures are not estimates but, rather,
are guesses devoid of reliable, quantified substan-
tiation. The bulk of the evidence for a general mule
deer decline comes from indirect information gener-
ated from sources such as: trend counts, harvest
estimates, and range use estimates. In addition,
there is also the evidence of opinion, intuition, or
"the fieldman's savvy". Let's look at these sources
individually and see what sense (or nonsense) can be
made from them.

Trend Indexes to Deer Abundance

Tracking populations of wild animals through
space and time has always been an elusive wildlife
management goal. In the 1930's when the myth of
professional wildlife management was born, census
was accorded primacy in the hierarchy of things to
do in order to properly manage wildlife (Leopold
There followed an initial flurry of activity to develop census techniques to estimate total numbers of deer (e.g., Bennett et al. 1940; Erickson 1940; Hahn 1949; Rasmussen and Donan 1943). But total estimates proved to be laborious and costly, so new approaches were sought. Most western states ultimately settled on indexes called "trend counts." The idea was to select a "key area" for counting. This area was presumed to be representative of a larger area of interest. Annual counts of deer were made on the key areas and compared to previous counts. Fluctuations in "key area" counts were assumed to proportionally reflect fluctuations in deer populations inhabiting larger areas.

The problem with trend counts lies in their implicit assumptions. First, no one area is ever representative of another (Eberhardt 1963). If there is one attribute common to all aspects of biology it is infinite variation. Hence, the first assumption is both absurd and impossible. Secondly, sample data (i.e. trend counts) tell us only about the sample, not about the real population, unless a relationship has been established. This has never been done with trend counts. Consequently, faith in the extrapolation is unjustified. Yet no myth of mensuration occupies a more hallowed position in mule deer management folklore.

It is my opinion that trend counts were widely adopted because of two predisposing conditions. First, trend counts — especially when conducted from aircraft — are relatively easy and inexpensive. Second, historically in the wildlife profession, there has been no truly effective forum for critical reviews of new ideas or techniques in wildlife ecology, so trend counts gained respectability only because so many people unquestioningly adopted them.

Harvests as Indexes to Population Trends

Kills statistics have long been used as an index to deer abundance. The degree of apparent sophistication has varied from mathematical projections of total populations based upon sex and age structure of the pre- and post-harvest population, sex and age structure of the harvest, and total harvest (Dasmann 1952; Boyd 1970; Aney 1972; Lipscomb 1974; Seber 1973) to simple comparisons of annual harvest fluctuations and direct extrapolations to deer population changes (Greenley 1968; Hancock 1968).

In the case of mathematical projections from change-in-ratio and harvest data the result is only as good as the data used in the calculations. In most applications of this technique the data (pre-and post-season sex and age structure of the harvest; and total harvest) are all treated as absolutes (Hanson 1963). Seldom are they considered as variables, but when they are and when this variation is included in mathematical projections, the estimates can be ridiculously imprecise (Wallmo 1964). Also, because the parameters are frequently considered to be absolutes, little serious attention is given to measuring the extent of their variability. In other words, pre-designed, statistically logical sampling strategies are seldom employed. In addition, few wildlife managers have considered the appropriateness of the probability models describing frequency distributions of these parameters; a binomial distribution is usually assumed. Recent tests suggest the simple binomial distribution is not the most appropriate model (Johnson 1976).

Consider also some of the potential biases encountered in trying to measure these variables (Paulik and Robson 1969). First, there is good reason to suspect a detectability bias while sampling sex and age ratios of deer populations. My own experience and that of others (Wallmo 1964; Dasmann and Taber 1956; Poux 1972) suggests that fawns and does are likely to be more easily detected than bucks except possibly during the rut when the reverse may be true. If this is the case then population classification counts may produce false estimates of population composition. But the extent of such bias remains unquantified, as does the variability of the bias over time.

A second consideration is the possibility of bias in the reported sex and age structure of the harvest (Eberhardt 1971; Coe 1974). Most western states use data from either hunter survey or check stations to estimate the harvest structure. Both sources are susceptible to bias. First, there could be a tendency for hunters to errantly report killing a buck when they actually killed a doe or a fawn (Menzel 1968). Second, not all hunters stop at check stations, even if they are required by law to do so. It is possible that hunters with mature bucks submit to checking more readily than those with fawns or does. Neither source of bias has been adequately evaluated (Neilson and Williams 1968).

Finally, the estimates of total mule deer harvests are also subject to reporting bias by hunters. In Idaho this source of bias was checked by comparing the known kill of individual hunters to their respective reported kills. Results indicated the estimated statewide harvest was inflated by 16 percent because a portion of the unsuccessful hunters reported killing a deer when they had not (Neilson and Williams 1968). All of these questions taken together cast considerable doubt on the reliability of population estimates generated from population structure and harvest data.

What can be said then of using harvest data by themselves as indications of population trend. When one considers all of the variables other than changes in population density that can cause fluctuations in harvests it is perplexing that this myth has persisted so long (Longhurst et al. 1976). Harvests can be expected to vary in response to a bewildering array of factors unrelated to deer density. Among the more obvious are weather; changes in season length, type (antlered only, hunter-choice, etc.), and bag limits; hunter distribution; hunter experience; land access; other concurrent competing sources of recreation; etc. Each factor can directly influence harvest totals, and they also can interact with each other in multiple combinations to produce complex and unpredictable effects. Consequently, it is unreasonable.
to assume that harvest trends consistently mirror population trends. But even if they did, one would have to know a priori what the real population was doing before the relationship was obvious.

**Intuitive Index or the Fieldman's Savvy**

Somewhere through the years a persistent myth developed in which the intuitive judgment of the "man in the field" was attributed a degree of high reliability which it did not deserve. Bump (1943:324) summarized this development as follows: "Beset by an ever mounting pressure to initiate management activities and produce results, in many cases they [game managers] were forced to fall back on so-called practical measures based on individual experiences and keen observations, rather than on results gained through careful scientific tests."

But the fieldman's savvy has been woefully inadequate when it has been put to a test. The following pertinent examples clearly illustrate this point. On July 12, 1924 an outbreak of foot and mouth disease was discovered among deer in the Stanislaus National Forest in California. A decision was made to exterminate the Stanislaus herd to eradicate the disease. An initial poisoning program proved ineffectual, so shooting was decided upon as the next alternative. In order to properly staff and prepare for such an enormous task, some preliminary information was needed about the estimated size of the population. The best experts available were contacted and asked to estimate the herd population level. These estimates ranged from 6,000 to 10,000 deer. Shooting commenced on December 1, 1924 and continued for almost a year, though most of the killing was accomplished in the winter months while deer were concentrated. The final tally of deer that were found in the herd was 213 - 3 times the original estimate (Andersen 1953).

In summary it may be said that current estimates of mule deer population levels in the West and extrapolations to historic trends are not reality, but myth. This is said because the methods from which the information was generated do not stand the test of critical evaluation, but rather have been accepted simply because they were institutionalized in print.

**MUTCH OF THE BROWSER**

Several of the western states employ an indirect method for estimating changes in relative mule deer abundance. These procedures have been variously called "range analysis methods", "range condition and trend transects", "browse production and utilization transects", etc. (Sandfort 1968; Hancock 1968). But all methods have certain common characteristics. Key areas are selected which supposedly represent areas critical to the survival of deer populations. Within the key areas, key browse species are selected which are supposed to define the capability of the key area to support deer. Finally, transects are established within the key browse types within the key areas. These transects purportedly provide indexes to fluctuations in mule deer food production and utilization from year to year (Demney 1962). There are several deficiencies in this approach to carrying capacity and deer abundance. First, is almost total disregard of the principles of statistical sampling methodology. In most cases transect locations are selectively placed rather than allocated by some technique which minimizes personal bias (Eberhardt 1971). Because of this neglect the resultant data are really pertinent only to particular plants and transects upon which they are measured. No legitimate extrapolations can be made to general populations of browse plants growing on key areas nor can extrapolations be made from key areas to general winter range complexes.

**Mule Deer Management Myths**

In summary it may be said that current estimates of mule deer population levels in the West and extrapolations to historic trends are not reality, but myth. This is said because the methods from which the information was generated do not stand the test of critical evaluation, but rather have been accepted simply because they were institutionalized in print.

But even more insidious is the primary assumption basic to the entire procedure. This assumption is that mule deer are primarily dependent upon browse for winter survival (e.g., Julander 1937; Carhart 1941a; Hill 1956; Elmsen 1956). The "myth of the browser" is one of the most ancient, persistent, and pervasive of all mule deer myths and continues even today to dominate most mule deer management philosophy and activity.

The "myth of the browser" developed in much the same way as most mule deer myths. Methods to determine what deer eat were chosen uncritically, and the results obtained were accepted uncritically. Early information on mule deer foods was based primarily on four methods: observations of free-
ranging wild deer (Dixon 1928), stomach content analyses (Dixon 1934), snow-trailing (Carhart 1941b), and observations of feeding sites for evidence of grazed plants (Lovasa 1958). Little critical thought was devoted to potential biases in methodology that might seriously distort the results.

Wallmo et al. (1973:562) tested the deer observation method and the feeding site method under semi-controlled conditions. They remarked that at best, most of the major forage species used by deer might be identified by the grazing-minutes or the feeding site method. Quantification, however, can be considerably in error. The grazing observation method particularly favors detection of browse use over other forage species (Wallmo et al. 1973).

Biases in stomach content analyses have been reported by several authors (Norris 1943; Bergerud and Russell 1964; Scooter 1966; Murie 1933; Eastern 1974). Norris (1943:249) compared the results of domestic sheep feeding trials and rumen content analyses where known diets were offered. Among his several conclusions, he reported that "stomachs may show large percentages of coarse browse which has been eaten over a period of days leading the analyst to conclude that browse is the chief article of the diet, while, in reality, rapidly digested, succulent forage may have been consumed in much larger amounts."

Bergerud and Russell (1964:813) reached similar conclusions in similar studies with caribou. They stated that "There appear to be two serious biases in abundance comparisons of plant groups and plant species between groups in a result of differential digestion: (1) plant groups are not proportionally represented in the larger (identified) fragments and the smaller (unidentified) particles, and (2) the identifiable fragments of some plants disappear more quickly than others."

Snow trailing results are susceptible to the same kind of shrub bias as the other 3 methods but for different reasons. Snow cover profoundly influences the forage choices of deer. Smith et al. (1975) reported that grass and forb consumption increased in the diets of tame deer and shrub consumption decreased as snow melt increased grass-forb availability. Bergerud and Nolan (1970) observed the same general phenomenon while studying food habits of tame caribou. In Middle Park, Colorado, diets of tame deer shifted abruptly over a 24 hr period following a 6-8 inch snowfall. Shrub use was accentuated and grass-forb use diminished following the snowfall (Carpenter et al. 1976, unpublished data). These studies suggest that snow trailing can be expected to over-emphasize the winter-long importance of browse, while de-emphasizing the role of grasses and forbs.

All of the foregoing suggests that the over-simplified classification of deer as browsers is erroneous and misleading. But even if data derived from these different techniques were taken at face value, they still don't justify the over-simplification. Several studies which were based upon these various methods belied the generalization that deer are predominantly browsers (e.g., Dixon 1934; Leach 1956; Nichol 1974; Dunkerson 1955; Bellis and Ross 1969). The conclusion of Bergerud and Nolan (1970:350) that "caribou are not specialized feeders but are generalists. They appear opportunists and when necessary eat most kinds of vegetation", in equally germane to mule deer.

Some might argue that although deer may eat a variety of foods, there is still a relationship between trends in the production and utilization of browse and trends in deer numbers. If this contention is true it still remains to be demonstrated. One of the few attempts at such a demonstration (Anderson et al. 1972) was inconclusive. The considerable evidence that browse twigs may not be preferred, but contingency food, complicates the interpretation of measurements with respect to deer population levels (Short 1969). Improved forage conditions conducive to population increases may be accompanied by decreased browse use. Poor forage conditions conducive to population decreases may result in increased use of browse. Meanwhile, growing conditions for browse species can either accentuate or mask the evidence of use irrespective of the direction of change in the deer population. Consequently the deficiencies of sampling methodology and inadequate knowledge of the ecology of mule deer on shrub ranges render statewide or regionwide deer population trend evaluation with this method both meaningless and mythical.

MYTH OF THE MULTI-PURPOSE MAN

In the foregoing sections, technique deficiencies were related to the evolution of mule deer biological myths. In this section attention will be directed toward an organizational and philosophical deficiency which serves to perpetuate the biological myths. Most western states did not really get into comprehensive wildlife management programs until after the passage of the Wildlife Restoration Act or the Pittman-Robertson Bill of 1937. This act provided necessary funding to expand state programs, which historically had been "protectionist" or law enforcement oriented, to include detailed investigations of the biology and ecology of game species. Initially, new personnel were hired specifically as game biologists. Their responsibilities were to acquire the knowledge requisite to effective management strategies for realizing the harvest potential of these species.

In the 1940's and early 1950's the endeavor and amount of knowledge generated was truly impressive. With respect to deer, serious attempts were made to sample population dynamics parameters and habitat attributes (Cronemiller and Fisher 1946; Carhart 1941b; Edwards 1942; Longhurst et al. 1952; McColl 1946). Then early in the 1950's, a trend began to combine the duties of trapper, game warden, and game damage officer into a single position. In Colorado this position was called the Wildlife Conservation Officer (Feltner 1961), and the standards for recruitment and salaries were raised to reflect increased professionalism. Activities funded by Federal cost-sharing programs (Pittman-Robertson) were still left to the game biologists.
A long-simmering conflict between the game biologists and the wildlife conservation officers flared into open hostility over who should be responsible for game management functions. Eventually in Colorado this conflict was decided in favor of the Wildlife Conservation Officers and their duties were expanded to include game and fish management. These developments marked the birth of the multi-purpose man concept.

Today these responsibilities have been expanded still further to include information and education, environmental impact assessment, assistance in county land use planning, interagency liaison, and non-game and endangered species management, to name only a few. In short it become impossible to do all things well. Responsibilities simply expanded beyond capabilities and staffing. The result was that something had to suffer. That "something" in Colorado has been wildlife management.

The organizational structure required that wildlife population and habitat data and management recommendations originate with the Wildlife Conservation Officer level. Since there was little time available to devote to wildlife population and habitat measurements, only those techniques which were expeditious and simple were retained. The result was the development and institutionalization of the myths of mensuration and the myth of the multitasker. In the process, a new myth became part of our wildlife heritage - the myth of the multi-purpose man. When one considers the infinite complexity of ecosystems it is incredible that a reasonable person could still believe that any single individual could do an adequate job of wildlife management alone, disregarding the remainder of his multitudinous functions.

Still, the myth persists and meaningful wildlife management progress is stymied. In the minds of administrators, politicians, and the general public, the image and the myth of the multi-purpose man, who does all things competently, is firmly entrenched. With a heritage of inappropriate methodology in his tool bag, and too little time to apply it, he understandably has resorted to this reputation to carry him through the trials of decision-making. It takes only the concurrence of several such persons to turn an unsubstantiated opinion into an accepted truth. The "fact" of a western-wide decline in mule deer populations rests on such a foundation.

**MYTH MANAGEMENT**

If, by now, you accept the original thesis of this paper - that the assumption of a decline in mule deer numbers in the West and much of mule deer management methodology is mythical rather than factual - then what can be done to extricate management philosophy and practice from counter-productive traditions? I suggest the following prescriptions as steps in the right direction:

1. Establish a tradition of critical evaluation of wildlife ecological principles, theories, and techniques. A necessary corollary is to use the education process as a forum to encourage novice wildlife ecologists to think analytically, critically, and objectively. This process is not so used now.

2. The individual states with mule deer populations must establish goals and priorities for obtaining minimum information requisite to realistic management decisions. The first priority within these programs is to develop basic population inventory systems (Eberhardt 1971). These systems will have to consolidate the best knowledge of statistics and biology to insure a high probability of obtaining real and generally pertinent data. Initially this information will be crude because that is the current status of the art (Overton 1971). Much research is needed concerning mule deer behavior, remote sensing technology, and biometrics to significantly advance this status.

3. It is clear to me that the multi-purpose man concept, as it is employed in Colorado, at least, can not possibly produce mule deer management data of sufficient quality and quantity to support fundamentally sound management programs. These programs are a full-time job in themselves. At least 3 alternatives are available: (a) Remove wildlife management from the several responsibilities of the Wildlife Conservation Officer and reduce the WCO staffing levels. Replace these WCO staff reductions with local wildlife management biologists who design and direct mule deer management surveys. These mule deer management survey teams could be staffed by temporary employees or with WCO's on temporary, seasonal assignments; (b) Increase statewide staffing of wildlife biologists without reducing WCO staffing. The wildlife biologists could work in teams over large areas or regions to secure management data; (c) Plan all activities within a WCO district on a priority basis with wildlife management (and specifically mule deer management) receiving a very high priority. Then allocate money and manpower necessary to adequately execute these plans.

These suggestions are over-simplified and tentative. Reorganizing the bureaucracy is futile if we continue to do the wrong things under the new organization. At the heart of the present issue is the fact that we have not employed inventory systems capable of detecting whether or not deer populations are changing statewide or region-wide. To have done so would not assure that we would then make the best management decisions; the problem of human sociology compounds the infinitely complex ecological problems that confront us in wildlife management. However, it would increase the possibility for realistic, objective problem analysis.

Meanwhile, we should be forewarned by Overton (1971:404): "Complexity is the price of realism and the present degree of realism is none too great." There is no pat method for estimating deer numbers over large areas. If, as this symposium suggests, it is important to have such information, we must face our responsibilities more rationally and objectively.

It is important, first, that we recognize that we are a large part of the problem (Anderson 1962). We have been too eager to believe, too quick to...
apply, and too busy to think!

LITERATURE CITED


Hanson, W. R. 1963. Calculation of productivity, survival, and abundance of selected vertebrates from sex and age ratios. Wildl. Monogr. 9. 60 p.


Any discussion of the influence of mountain lion predation on prey populations becomes, of necessity, a discussion of predator-prey relationships. The reason is obvious - there are practically no data available on lion-prey interactions. Lions are known to kill deer wherever the two species occur together but this merely establishes the fact. The effect of this killing on deer numbers - the really meaningful and important aspect to consider - has scarcely been looked at in an objective way.

Therefore, today we are a bit limited. We can't critically review the literature because there isn't any. We will discuss what is known of lions and their effect on prey from research thus far reported. We will talk about the possible influence and effect, or lack of either, of lions on mule deer populations and the factors that are important in these relationships. We'll also consider some negative evidence concerning the effect of lion predation, the role control might play, and needed research.

I don't intend to launch into a generalized discussion of predation - I don't believe that's necessary here. It will, however, be helpful to outline a few of the things basic to predator-prey relationships. Some of these are my original thoughts - they are those of numerous authors set down over a long period of time.

First, what are the possible effects of lion predation (or any predation for that matter) on prey populations?

1. The predator can be strongly limiting to the point of reducing the prey to extinction or near extinction.

2. The predator can be regulatory in that it helps keep prey populations within the carrying capacity of their resources, or another way, it contributes to a steady state in the density of the prey.

3. The predator may be neither limiting nor regulating; in other words, the predator is insignificant in the population dynamics of the prey.

Which situation exists between the predator and its prey depends on different factors. Leopold (1933) classified these into 5 groups:

1. density of the prey population
2. density of the predator population
3. characteristics of the prey
4. density and quality of alternate foods available for the predator
5. characteristics of the predator

Further, it is important to know the history of interacting populations. Did the species evolve together? Is the relationship an old one or is it of recent origin? Is the ecosystem stable or changing? Knowing this, we can make some general statements:

1. The limiting effects of predation tend to be reduced and the regulatory (or steady state) effects increased where the interacting populations have a common evolutionary history and they occur in a relatively stable ecosystem.

2. Violent predator-prey interactions happen frequently when the interaction is of recent origin or when there has been recent large scale disturbance of the ecosystem by climatic change, natural holocaust, or by man.

So much for the possible effects of predation. What are its influences?

1. Predation can dampen and protract violent fluctuations in numbers of prey animals. Damping can act to reduce range damage and serious overstocking may be averted until such time as other limiting forces, such as disease, may come into operation.

2. Predation is also a strong selective force acting to remove prey individuals possessing less desirable adaptive characters.

3. Predators may also act to disperse prey animals and thus cause them to be more evenly distributed on critical range.
These are the theoretical possible effects and influences of mountain lions on mule deer populations. What is the real-world evidence for any of these relationships? This is, or could be, quite important at a time when we are experiencing a region-wide decline in mule deer populations.

Unfortunately we don't have much information. Published information largely, again, deals with the fact, not the effect. There are several research projects currently under way, but most of them are in their early stages. The work by my colleagues and I is the only recent published data on the interaction of lions and mule deer and the effects of that lion predation. In 10 years of study we found that lions were not limiting populations of mule deer in a wilderness environment in central Idaho. Their predation had little effect on ultimate numbers of a wilderness environment in central Idaho. Their predation had little effect on ultimate numbers of mule deer during this period. The deer population increased steadily during the first five years, stabilized and remained stable for the remainder of the project. At the same time the mountain lion population remained stable because of a fairly rigid system of territoriality. In this situation under these ecological conditions, lion predation was considered beneficial.

Harley Shaw (pers. comm.) of the Arizona Game and Fish Department has worked with a lion population for several years in Arizona. He has assessed the lion kill of domestic stock and has recorded kills of deer. Shaw concludes that lion predation is an important factor in determining mule deer numbers on his study area. He believes that deer numbers could be increased on his area by removing lions.

These differing results point up the fact that differing ecological units have their own properties and each must be looked at individually if valid interpretations are to be made. This is particularly important with the mountain lion, a reasonably adaptable predator.

We are, of course, specifically concerned about the mule deer decline. It is vital to question what role lions play in this decline. Lacking objective data, it may prove useful to examine past histories of interacting populations.

It is generally accepted that mule deer populations peaked in western North America during the period 1940-1970. During this time, mountain lions were regarded as vermin in all western states, and unregulated killing was encouraged. We could point to the control of lions as the factor responsible for high deer numbers, but there is negative evidence to refute this. First, the decline began before unregulated lion killing ceased. Deer numbers rose similarly during this period in areas where there was no lion control at all - in several of our large national parks and some of the larger relatively inaccessible wilderness areas. Similar negative evidence is available today - the decline of mule deer appears uniform throughout the West in areas where few or no lions occur as well as areas where they are believed to be numerous. Further, white-tailed deer populations are not declining. On the contrary, they appear to be flourishing, at least in the Northwest, where lions occur and where they do not.

So we really don't know a great deal about the effect and influence of mountain lions on mule deer throughout their range. We do know that once prey population size is lowered then any depressing factor may have a proportionately greater effect on that prey population, acting to depress it even further. It appears self-evident to many people that removal of any depressing influence will result in greater numbers of a prey species. Predators are the most obvious of the depressing factors and naturally attract the most attention. It is here that public and political pressure comes for control.

We know that predator control in some cases will obtain the desired results. We also know that these results often are short-lived and do not solve the long-range problem. Further, the costs are high, both in an economic and ecological sense as pointed out by authors from Errington's time on. To these we can add cultural costs - public relations problems. At the same time, some control programs will always be initiated on a basis of political or emotional expediency only, with no biological or ecological considerations at all.

To rectify this situation we need the right kind of research. This research needs to address itself, simultaneously and concurrently, to the predator population, the prey population, and an assessment of the prey habitat. Further, the effects, and not merely the fact, of the predation on the prey population should be the foremost objective. Too often in the past, this kind of research has gotten side-tracked on predator biology only, on the revealing facts of predation (gee whiz, these critters are sure knocking off the deer!), on irrelevant facts of all kinds. These things are important, but the real issue, the effects of predation, are never really learned. At the same time we need to study populations not subjected to predation - what happens to deer population levels in the absence of predation? This often is long-term research and so far federal and state agencies haven't been eager to provide funding. But short-term efforts won't help.

If I may, I'd like to quote from some things I said about predators and predator control in 1972. I believe these comments still are valid, and are appropriate for a discussion of our understanding of mountain lion-mule deer interactions:

"We need to know more of the biology and ecology of predatory species. We need to know more about self-regulating mechanisms and how they can be used to advantage. We need to study and compare, simultaneously, exploited and unexploited populations. We need to recognize the genetic differences between populations of predators and prey that have evolved together and those that have not. We need objective assessments of the socio-economics of predator management. We need research on alternatives to direct killing, or reduction control. . . . I believe the application of species biology, as suggested by Knowlton (1972), is the key to future predator management. But first, we must know species biology."
1. We don't have much objective data concerning lion-mule deer relationships.

2. Lion predation, like any other predation, may under certain conditions act to limit prey populations. When a prey population is lowered drastically by whatever factor then any depressing factor gains more importance. In this situation, predator control may help, but usually doesn't solve the problem.

3. Lion predation, like any other predation, normally is ineffective in drastically reducing numbers of prey species when that prey species has suitable habitat.

4. Predator control is a valid wildlife management tool, but if suitable habitat is not available for a prey species, then no amount of predator control will bring about flourishing populations of that prey species.

Mountain lions and mule deer evolved together in the West. Both have survived, often flourished. Their relationship is a simplified straightline one: habitat → mule deer → lions. Mule deer depend on habitat, lions depend on mule deer. If we improve habitat, we can increase the numbers of deer in the long run; if we decrease lions only, with no habitat change, the results won't be the same.

LITERATURE CITED


POTENTIAL INFLUENCE OF COYOTES
ON MULE DEER POPULATIONS

Frederick F. Knowlton
U. S. Fish and Wildlife Service
Logan, Utah

Abstract

There have been no comprehensive studies of the influence of coyotes upon populations of mule deer. Such a study of a white-tailed deer herd in Texas indicated that coyote predation was a major mortality factor among new-born fawns, accounting for 53 to 75 percent of the fawns born. Coincidental observations, however, showed that other environmental factors were important mediators of the percent of fawns killed by coyotes. Precipitation, as it influenced the quality and quantity of forage available to does, affected the number, size and vigor of fawns born. This was secondarily reflected in the survival rates of fawns and ultimately in the sex ratio of the adult portion of the herd. Exclusion of coyotes from a portion of the herd resulted in increased survival rates of fawns during the first three months after birth, but in subsequent years these gains were offset by increased mortality in later months. Observations from several mule deer and black-tailed deer herds seem consistent with these interpretations. In addition to their impact during the neonatal period, coyotes may kill significant numbers of deer, primarily those under one year old, in mountainous areas where winters are harsh. Malnutrition appears to be a common "facilitator" in many of these cases of predation. In summary, it is apparent that coyotes kill and eat substantial numbers of deer, but the evidence suggests nutritional health of the deer is an important arbitor of many environmental effects, including predation. There are some indications that increased fawn survival can be achieved for brief periods and that deer populations can react more quickly to favorable environmental circumstances in the absence of coyotes. Whether these effects can be translated into a greater abundance, or harvest, of deer remains to be demonstrated.

In assembling and synthesizing the fragments of data that might convey some information about the potential impact of coyotes upon mule deer populations, I feel like a novice paleontologist at the edge of some prehistoric bone pile. Collecting and examining each "specimen," I am haunted by questions of propriety. Is each really part of the same entity or phenomenon? Are we indeed looking at a common process, and do we have the "pieces" arranged appropriately? If not, we may be placing the foot of a Brontosaurus upon a Pterodactyl fitted with the head of a Tyrannosaurus.

To maintain some semblance of order in this presentation, I chose to synthesize from a sequence of studies of coyotes and white-tailed deer and then seek analogs among the data available for coyotes and mule deer.

Throughout, I have relied heavily on researches and data provided by others. I am grateful to the individuals who were so willing to share.
THE WELDER DEER STORY

The 7,800-acre Welder Wildlife Refuge on the Texas Gulf Coast harbors a herd of 1,100 to 1,600 deer (1 deer per 5-7 acres). The herd is essentially nonmigratory and the only "hunting" results from collections made to assess biological parameters. The deer are grazers, feeding primarily on grasses and herbs year around, (Chamrad and Box 1968). Forage conditions may become restrictive during the cool winter months as well as the hot, dry summers.

General Biologic Parameters

We determined from the number of ova and fetuses produced (Table 1) that gross productivity was high (F = 169 and 163 per 100 does respectively) with relatively little mortality through gestation. By January 1, however, the number of fawns was reduced appreciably, with mean calculated survival rates approximately 34 percent (Table 2). Considerable year to year variation in the ovulation rates, numbers of fetuses produced, and survival of fawns through the first six months was apparent.

Two sources of information were used to define the period when most fawns were lost. On the basis of the remains of 174 fawns found dead in the field, most died within the first 3 weeks after birth (Fig. 1). Minimum survival of fawns tagged and marked shortly after birth, also suggested the majority were lost within the first 21 days of life (Fig. 2). Both data sets suggest the first three weeks post-partum is critical to fawn survival.

Concurrent studies of the feeding patterns of coyotes on the Welder Refuge suggest that deer comprised nearly 40 percent of the annual diet of coyotes (Knowlton 1964). There were two periods when deer were particularly important in the diet. During the summer, coinciding with the fawning period, deer comprised up to 80 percent of the coyote diet (Fig. 3). Another period of heavy use of deer was noted in winter.

To determine the nature of the relationship between the large loss of neo-natal fawns and heavy feeding upon fawns by coyotes, Cook et al. (1967) initiated a program of placing radio transmitters on young fawns to facilitate surveillance over an extended period. As reported by White (1966), 81 fawns were tagged with radio transmitters. Fifty eight (72 percent) of these fawns died within the next few months. Fifty-three percent apparently died as a direct result of predation and an additional 22 percent had been fed upon by coyotes, but direct evidence that coyotes had killed the fawns was obscure. Thus coyotes appear to have been responsible for the death of between 55 and 75 percent of the instrumented fawns.

If our analyses had terminated at this point, we would have been professionally negligent not to conclude that the high postnatal loss of fawns was a significant factor influencing herd dynamics and that coyote predation was a primary factor in the low survival rates observed. Furthermore, to enhance herd productivity, there seemed little else to suggest but to eliminate the "nasty little varmints."

While analyzing the data from these studies, we noted several intriguing relationships. The adult sex ratio of this unbunted deer population approximated 40 males per 100 females. Furthermore, extrapolations of age ratio regressions (Fig. 4) combined with the adult sex composition of the herd suggested 10.7 male and 17.0 female fawns per 100 adults needed to survive until January 1 to maintain the herd size and structure. This implies that the sex ratio among fawns surviving to six months of age should be 63 males:100 females. Small samples of fall-trapped fawns revealed a ratio of 55.6 to 100, very close to the calculated figure. Since the fetal sex ratio was 117 males per 100 females, twice as great a mortality rate is suggested for male fawns as compared to female fawns.

Variations in gross productivity (the number of ova and/or fetuses produced) appear related to precipitation in the year prior to conception (Fig. 5). This was primarily a function of the frequency of twinning rather than changes in the percent of does that became pregnant. Precipitation patterns also appear to effect changes in the temporal aspects of the fawn drop, possibly as much as 10 to 14 days. An advance in parturition dates could be expected following years of above normal precipitation and a delay in parturitions frequently followed more arid conditions.

Net productivity, which is largely a function of fawn survival rates, appeared to be related to the amount of precipitation during gestation (Fig. 6). When precipitation was plentiful, fawn survival was higher than when relatively little precipitation fell.

As a result, we were faced with the dilemma of trying to explain excessive fawn losses, apparently resulting from coyote predation but whose effect is mediated by precipitation. Furthermore, we had to account for an apparent "preference" of coyotes for male fawns.

Current Interpretations

Fruit is an important constituent of the coyote diet (Fig. 7). Following years of below average precipitation, when conception is delayed, parturition of the fawn drop occurring while the coyotes are "still in the berry patch;" and (b) over-saturation with fawns for a short period with coyotes being unable to take full advantage of those available. Both phenomena enhance fawn survival.

In addition, fetal growth rates are greater during wet years than dry (Knowlton and White, in press) resulting in a 20 percent difference in the mean birth weight of fawns (Fig. 9). Presumably the larger fawns are healthier and more viable. We also have data indicating that the postnatal growth rate of male fawns is appreciably greater than their female cohorts (0.45 vs. 0.33 lb./day respectively).

Potential Influences of Coyotes

Some Related Observations
At this point it does not seem inappropriate to speculate that on this area:

1. The nutritional content of forage, both in quality and quantity, is related to precipitation;
2. secondarily, these effects are reflected in the number, size and presumably vigor of the fawns at birth;
3. such nutritional considerations could be expected to intensify during lactation when the energy and protein demands on the does are maximal;
4. the effects would probably be most pronounced among the animals with the greatest nutritional demands (male fawns) for growth and with the greatest activity schedules (Jackson et al. 1972); and that
5. the foregoing may be compounded by seeming slight changes in the timing of the parturant process and possibly even the ability of a doe to meet the nutritional demands of the fawn.

Consequently, precipitation operating through nutrition, becomes a primary determiner of fawn survival and ultimately the sex ratio among the adult portion of the herd (Fig. 10). At this point it is important to remember that coyote predation is a major instrument of this dynamic process, but apparently precipitation is the programmer.

Effects of Excluding Coyotes

The obvious question concerns the possible effects of eliminating the impact of coyotes from the herd. In 1972 a 965-acre predator enclosure was completed. As reported by John Kie (pers. comm.), fawn survival through 3-months postpartum was significantly greater inside the enclosure than outside during 1973; an effect which carried through March of the next year. In 1974, the gains apparent in early postnatal survival within the predator enclosure (compared to outside) were negated by increased mortality in later months (Table 3).

Fall density of deer inside the enclosure was nearly double that outside at the start of the study. Concurrent with the high fawn survival in 1973 and 1974, density inside nearly doubled. Subsequently, the population leveled off and/or declined (Fig. 11). In the meantime, deer densities outside the enclosure increased but at a substantially lower rate and were slightly lower than inside the enclosure by the spring of 1976.

HOW DOES THIS APPLY TO MULE DEER?

There is little doubt that coyotes eat mule deer. Horn (1941) reported about forty percent of the coyote diet on the Los Padres National Forest was comprised of mule deer (Fig. 12). In Washington, Brigham (1938) noted an abrupt increase (to over 50 percent) of deer fawn in the coyote diet coincident with the fawning period. On the basis of tooth punctures and subcutaneous hemorrhages, Nielsen (1976) reported that 28 of 31 deer found dead near Hardware Ranch in Utah had been killed by coyotes. There are problems, however, in trying to reconstruct the circumstances surrounding these observations and in assessing the population consequences.

The Interstate Deer Herd

On the bases of data provided by Salwasser (1976), it seems apparent that the Interstate Deer Herd has been declining since the 1960's, precipitously in the past 5-7 years (Fig. 13). Gross productivity has remained high, in the vicinity of 150 fawns per 100 mature does. Fawn survival, especially through summer and fall, has been declining since the mid-1950's (Fig. 14). As depicted in Figure 15, the number of bucks per 100 does has also declined (since the sex ratio data was collected after the hunting season, the impact of the harvest upon the sex ratio should be kept in mind). From an earlier paper (Salwasser 1976) it is apparent that coyotes in comparable situations feed extensively on deer during the early postnatal period (Fig. 16). On the other hand, Eastman (pers. comm.) offers evidence suggesting there has been no substantial change in coyote abundance on the summer range of the Interstate Deer Herd (Fig. 17) which might account for the declines noted in survival and recruitment within the deer herd.

The Steens Mountain Deer Herd

The state of Oregon has been concerned about declining deer productivity in the Steens Mountain area. As reported by Trainer (1975), 106 new-born fawns were captured and equipped with radio transmitters. Fifty-five percent of the fawn mortality within the first 45 days of life apparently was related to predation. Coyotes were responsible for 69 percent of it (Table 4). However, since the loss of fawns to coyotes did not exceed 10 percent, it hardly seems to be a pivotal event among the herd dynamics.

There is reason for concern, because as Trainer points out, the number of fawns per hundred does declined from 131 in June to 86 by September and 29 by March (Table 5). This implies a 78 percent loss of fawns before one year of age. To address this problem, fawns were radio-collared in early winter. Subsequently, 50 percent died between January and April, with coyotes the immediate cause of death in 74 percent of the cases. It may be significant, however, that two thirds of the carcasses examined revealed advanced states of malnutrition.

With this in mind, it may be pertinent to recall that Nielsen (1975) reported that 28 of 31 deer found dead during winter were killed by coyotes and that 25 of the 28 were fawns. Since the 'state of health' in these instances were not assessed, we can only ponder whether this represents some general pattern.

Enclosures and Exclosures

To my knowledge, there have been two "fencing experiments" which provided some information with regard to the impact of predators on mule deer populations. The first involved the inadvertent
Table 1. Gross productivity per 100 does among white-tailed deer on the Welder Wildlife Refuge (from White, 1966).

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>Number of corpora lutea</th>
<th>Number of fetuses</th>
</tr>
</thead>
<tbody>
<tr>
<td>1961</td>
<td>--</td>
<td>--</td>
<td>165</td>
</tr>
<tr>
<td>1962</td>
<td>33</td>
<td>167</td>
<td>164</td>
</tr>
<tr>
<td>1963</td>
<td>46</td>
<td>150</td>
<td>143</td>
</tr>
<tr>
<td>1964</td>
<td>20</td>
<td>160</td>
<td>150</td>
</tr>
<tr>
<td>1965</td>
<td>30</td>
<td>197</td>
<td>187</td>
</tr>
<tr>
<td>1966</td>
<td>15</td>
<td>187</td>
<td>173</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>169</td>
<td>163</td>
</tr>
</tbody>
</table>

Table 2. Net productivity per 100 does among white-tailed deer on the Welder Wildlife Refuge (from White, 1966).

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of fawns (January 1)</th>
<th>% fawn survival (through 7 months)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1961</td>
<td>51</td>
<td>41</td>
</tr>
<tr>
<td>1962</td>
<td>26</td>
<td>21</td>
</tr>
<tr>
<td>1963</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>1964</td>
<td>48</td>
<td>40</td>
</tr>
<tr>
<td>1965</td>
<td>72</td>
<td>54</td>
</tr>
<tr>
<td>1966</td>
<td>50</td>
<td>38</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>42</td>
</tr>
</tbody>
</table>

Table 3. Fawns per 100 does inside and outside predator exclosure on Welder Wildlife Refuge (from Kie, pers. comm.).

<table>
<thead>
<tr>
<th>Year</th>
<th>Predator Enclosure</th>
<th>Outside Enclosure</th>
</tr>
</thead>
<tbody>
<tr>
<td>1972 (Sept.)</td>
<td>45</td>
<td>45</td>
</tr>
<tr>
<td>1973 (Sept.)</td>
<td>66</td>
<td>28</td>
</tr>
<tr>
<td>1974 (Mar.)</td>
<td>47</td>
<td>31</td>
</tr>
<tr>
<td>(Sept.)</td>
<td>63</td>
<td>47</td>
</tr>
<tr>
<td>(Dec.)</td>
<td>51</td>
<td>46</td>
</tr>
<tr>
<td>1975 (Mar.)</td>
<td>45</td>
<td>43</td>
</tr>
</tbody>
</table>

Table 4. Mortalities of mule deer fawns on Steens Mountain, Oregon (from Trainer, 1975).

<table>
<thead>
<tr>
<th></th>
<th>Number</th>
<th>% of total</th>
<th>% of preceding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radio-instrumented</td>
<td>106</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>June-July mortality</td>
<td>29</td>
<td>27</td>
<td>27</td>
</tr>
<tr>
<td>Predation caused</td>
<td>16</td>
<td>15</td>
<td>55</td>
</tr>
<tr>
<td>Coyote induced</td>
<td>11</td>
<td>10</td>
<td>69</td>
</tr>
</tbody>
</table>

Table 5. Mule deer fawn mortality based on age ratios from Steens Mountain, Oregon (after Trainer 1975).

<table>
<thead>
<tr>
<th>Month</th>
<th>Fawns per 100 does</th>
<th>% mortality from birth</th>
<th>% mortality in interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>131</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>September</td>
<td>86</td>
<td>34</td>
<td>34</td>
</tr>
<tr>
<td>December</td>
<td>54</td>
<td>59</td>
<td>37</td>
</tr>
<tr>
<td>March</td>
<td>29</td>
<td>78</td>
<td>46</td>
</tr>
</tbody>
</table>

Table 6. Mule deer fawns per 100 does (January) inside and outside predator exclosure on Three Bar Ranch, Arizona (after LeCount 1974, 1975).

<table>
<thead>
<tr>
<th>Year</th>
<th>Inside Enclosure</th>
<th>Rest of three bar</th>
</tr>
</thead>
<tbody>
<tr>
<td>1971</td>
<td>22</td>
<td>26</td>
</tr>
<tr>
<td>1972</td>
<td>118</td>
<td>42</td>
</tr>
<tr>
<td>1973</td>
<td>82</td>
<td>70</td>
</tr>
<tr>
<td>1974</td>
<td>111</td>
<td>59</td>
</tr>
</tbody>
</table>
Figure 1. Age at death of 174 fawns found dead on the Welder Wildlife Refuge (from White, 1966).

Figure 2. Minimum longevity of 128 tagged deer fawns on Welder Wildlife Refuge (from Knowlton, 1964).

Figure 3. Percent of the coyote diet comprised of deer (after Knowlton, 1964).

Figure 4. Age ratio regressions for adult male and female white-tailed deer on Welder Wildlife Refuge (after Knowlton, 1964).

Figure 5. Comparison of gross productivity of white-tailed deer on Welder Wildlife Refuge and precipitation in the year preceding conception (after White, 1966).

Figure 6. Comparison of fawn survival to 6 months of age with precipitation during gestation (after White, 1966).
Figure 7. Percent of coyote diet on Welder Wildlife Refuge comprised of fruit (after Knowlton, 1964).

Figure 8. Chronology of fruit and deer in the coyote diet during a "dry" year on the Welder Wildlife Refuge (after Knowlton, 1964).

Figure 9. Fetal growth rates of white-tailed deer during periods of high and low precipitation (from Knowlton and White in press).

Figure 10. Comparison of annual precipitation, fawn survival, and sex composition within the adult portion of the Welder white-tail herd (after White, 1966).

Figure 11. Deer densities within and outside the predator exclosure on the Welder Refuge (from Kie pers. comm.).

Figure 12. Percent frequency of mule deer in the coyote diet on Los Padres National Forest (from Horn, 1941).
Figure 13. Relative abundance of mule deer in the Interstate area, 1949-1973 (from Salwasser, 1976).

Figure 14. Estimated fawn survival rates for the Interstate mule deer herd between 1954 and 1974 (from Salwasser, 1976).

Figure 15. Post-harvest sex ratio in the Interstate deer herd 1950 through 1974 (from Salwasser, 1976).

Figure 16. Percent occurrence of mule deer fawn in the coyote diet in the North Kings deer herd (from Salwasser, 1974).

Figure 17. Index of coyote abundance on the summer range of the Interstate deer herd (from Eastman pers. comm.)
enclosure of one coyote with a group of mule deer in Central Utah. As reported by Robinette and Olson (1964), productivity was 49 percent lower in the pasture with the coyote as compared to an adjacent pasture with no coyotes.

A predator exclosure was built on the 3-Bar Ranch in Arizona in 1971. According to LeCount (1974, 1975), net productivity within the enclosures (measured in January) averaged nearly twice that observed on the rest of the 3-Bar Ranch (Table 6). The number of deer within the enclosure was relatively small and substantial fluctuations in productivity were evident. It is also interesting that the lowest productivity outside the enclosure was identified with a drought, and the highest productivity with a year of abundant precipitation.

SUMMARY

At the outset, it is essential to recognize that coyotes eat and kill deer. It is equally important to recognize that other environmental factors may be important mediators of the impact predators may have on deer populations. In some instances, predation may be symptomatic of other environmental deficiencies. Certain similarities between studies on mule deer and the Welder whitetail herd are inescapable.

Evidence at this point suggests the nutritional status of the deer may be a key to a host of environmental effects; effects which frequently synergize in natural environments. Within the Welder herd, the number, size, health and survival of fawns appears closely linked to the quality of food available to the doe. Some parallels seem appropriate among mule deer. Additionally, nutritional health of mule deer in winter may contribute to the impact of coyotes at that season. While it may be relatively easy to assess the "nutritional state" of the winter range, we may not yet be prepared to define, much less evaluate, the late gestation and fawning ranges which appear so vital to the vigor of white-tailed deer fawns in South Texas. Ecology 52(2):262-270.


Potential Influence of Coyotes

Literature Cited


Potential Influence of Coyotes
Viral, bacterial, and parasitic diseases are considered important potential causes of mortality among mule deer populations. Various aspects on the pathologic manifestations and epizootiology are presented for the hemorrhagic disease complex (bluetongue and epizootic hemorrhagic disease), necrobacillosis, gastrointestinal trichostrongylosis and lungworm disease.

The importance of diseases affecting human and livestock health long has been recognized and is evidenced in the United States today by enormous expenditures by the Departments of Health, Education, and Welfare and Agriculture as well as by states and private philanthropic agencies. In contrast, diseases of free-living wild animals largely have been ignored, and only recently have diseases of wildlife received attention. As a result, a relative dearth of knowledge exists on diseases affecting wild populations. This fact was all too evident when searching the literature for accounts of diseases affecting mule deer (Odocoileus hemionus). As a result, this presentation is largely speculative based on information derived from the literature and extrapolated from our experiences with diseases of white-tailed deer (O. virginianus).

In 1969 we presented a list of 12 fundamental causes of morbidity and mortality among wildlife populations (Table 1) and described a process of elimination whereby potential causes of death could be narrowed from 12 to 3 or 4 (Hayes and Prestwood 1969). When considering diseases potentially capable of causing a widespread decline of mule deer populations, we applied this method of elimination. As a result, a list of diseases of potential importance to mule deer populations was compiled (Table 2).

Viral Diseases - Three viral agents producing two clinical syndromes, hemorrhagic disease (HD) and malignant catarrhal fever (MCF) respectively, are considered threats to mule deer populations.

<table>
<thead>
<tr>
<th>Table 1. Fundamental Causes of Morbidity and Mortality Among Wild Animal Populations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anomalies</td>
</tr>
<tr>
<td>Stress</td>
</tr>
<tr>
<td>Trauma</td>
</tr>
<tr>
<td>Suffocation</td>
</tr>
<tr>
<td>Neoplasia</td>
</tr>
<tr>
<td>Toxins</td>
</tr>
<tr>
<td>Nutritional Deficiencies</td>
</tr>
<tr>
<td>Viruses and Rickettsia</td>
</tr>
<tr>
<td>Bacteria</td>
</tr>
<tr>
<td>Fungi</td>
</tr>
<tr>
<td>Parasites</td>
</tr>
<tr>
<td>Senility</td>
</tr>
</tbody>
</table>

The so-called "hemorrhagic complex" consists of two viral diseases, bluetongue (BT) and epizootic hemorrhagic disease (EHD), which cannot be distinguished clinically or by gross or microscopic lesions. Hemorrhagic disease is characterized by hemorrhage and vascular thrombosis with resultant necrosis of affected tissues.

Bluetongue is enzootic throughout much of the United States. In 1974 BT virus was recovered from
Hemorrhagic disease is seasonal and usually occurs with the first frost. However, these animals may harbor the virus occasionally. Bluetongue disease is manifest clinically in cattle, occurring in the late summer and early fall when flies are abundant. Epizootics characteristically cease inapparently for extended periods. This finding led to the hypothesis that cattle are reservoirs for BT virus (Bowen 1975).

The role of cattle in the epizootiology of EHD presently is unknown, however, antibodies to EHD have been detected among sentinel cattle placed in contact with white-tailed deer during an outbreak of HD and also in feral cattle in contact with whitetails where HD was not recognized (Thomas and Prestwood 1976).

Although we were unable to locate published reports of clinical BT in mule deer, one of the authors (CPH) has recovered BT virus from captive mule deer which were dying of an acute hemorrhagic disease syndrome. Mule deer reportedly are relatively resistant to infection with EHD virus, and in outbreaks of EHD, carcasses of white-tailed deer outnumber those of mule deer 23 to 1. Sero-positive reactors to EHD virus were prevalent among mule deer following an outbreak of EHD in deer of North Dakota during 1970 and 1971, suggesting that they were similarly exposed to this viral agent (Hoff et al. 1973). The effects of BT and EHD viruses, particularly latent infections, in mule deer require further study before these diseases can be properly assessed for mule deer populations.

Acute and chronic hemorrhagic disease in white-tailed deer have been delineated (Prestwood et al. 1974). The primary pathogenic mechanism appears to be disseminated intravascular coagulation (Tsai and Karstad 1973). The acute disease is characterized by extensive hemorrhagic and thrombotic manifestations. Pathologic lesions are generally variable but reflect sequelae of vascular damage. These changes are more pronounced in the digestive tract and often involve the coronary band of the hooves. Necrotic stomatitis, rumenitis, and omasitis often occur, and ulceration of the ruminal pillars may be pronounced. Laminitis may be sufficiently severe to cause sloughing of the hooves. Fawns infected while nursing frequently exhibit severe destruction of the ruminal lining. These animals may survive initial infection only to succumb after weaning when the diet shifts to roughage. Starvation or predation are the usual fate for these animals. In adult survivors, secondary infections of the digestive tract and feet are usual sequelae. These lesions may be manifest as necrotic stomatitis, ulcerative rumenitis, or pyogenic infections of the feet. Involvement of the feet often is observed in hunter-killed deer. Infection of does during the early stages of gestation may result in stillbirths or malformations of does during the early stages of gestation may result in stillbirths or malformations of fetuses as observed with domestic livestock. The long term effect of BT on productivity of white-tailed or mule deer populations has yet to be explored.

Presumptive diagnosis of HD can be made on the basis of gross and microscopic lesions, however isolation and characterization constitute the only means for distinguishing the viruses of BT and EHD.

Malignant catarrhal fever (MCF) is a viral disease of domestic and wild ruminants characterized by catarhal, mucopurulent, or necrotizing inflammation of the respiratory and digestive tracts and eyes. The disease is worldwide in distribution, and most outbreaks in North America are sporadic in occurrence. In the United States, MCF has been diagnosed in axis (Axis axis) and white-tailed deer in southern Texas (Clark et al. 1970; Clark and McConnell 1972), in white-tailed deer of New Jersey and Connecticut (Wyand et al. 1971), and in greater kudu (Tragelaphus strepsiceros) in Missouri (Bolver and Kurka 1974). Additionally, MCF has been recognized in American bison (Bison bison) and...
Mule deer have been experimentally transmitted MCF to mule deer. Among cattle the disease appears sporadically in sheep-raising areas of the midwest and west.

The mode of transmission of MCF is unknown, however the recent discovery of MCF virus in nasal secretions of blue wildebeest (Connochaetes taurinus) led to the hypothesis that nasal shedding of MCF virus may be a mechanism for transmission of virus among wildebeest and from wildebeest to cattle (Rweyemamu et al. 1974). In Africa, wildebeest are natural reservoirs of MCF virus. Sheep are considered natural reservoirs elsewhere.

In cattle, peracute, alimentary, head and eye, and mild forms of MCF have been described. Among deer, the disease was best described for axis deer (Clark et al. 1970). Axis deer with MCF were lethargic, emaciated, weak, ataxic, and apparently blind. Neurologic disturbance was present in some animals. Gross lesions consisted of corneal opacity, areas of alopecia encrusted with thick, dried exudate, greatly enlarged lymph nodes and enlarged arteries. Gross lesions in white-tailed deer ranged from none to hemorrhagic sepsis and sudden death. Diagnosis of MCF is based on histologic lesions consisting of fibrinoid necrotizing vasculitis which are considered pathognomonic for this disease (Jubb and Kennedy 1970). Eye lesions and neurologic signs, when present, serve to distinguish MCF from BT and EHD.

Bacterial Diseases - Only one bacterial disease, necrobacillosis, is considered a serious threat to mule deer populations. The disease is caused by Pseudobacterium (=Spherophorus) necrophorum. Considerable controversy exists on whether F. necrophorum acts as a primary or secondary invader. Jubb and Kennedy (1970) state, "In no instance has it yet been credited with the role of primarily penetrating pathogen." Rosen (1970) considered F. necrophorum a probable opportunist awaiting an abrasion or injury to serve as an avenue for invasion.

Necrobacillosis has been diagnosed in a variety of wild cervidae, primarily in the western United States. It has been considered a major cause of mortality among mule deer in California (Rosen et al. 1951; Rosen 1970) and among wapiti (Cervus canadensis) of Wyoming (Murie et al. 1944 cited in Rosen 1951). Periodic outbreaks of necrobacillosis occur in many species of domestic livestock. Among sheep and cattle, frequently necrobacillosis is encountered when the environment is dark, dirty, damp, and overcrowded. Epizootics in California deer have occurred when animals have been overly concentrated near muddy water holes due to drought (Rosen et al. 1951). When the environment is sufficiently seeded with F. necrophorum organisms the disease apparently becomes contagious (Jubb and Kennedy 1970).

Lesions produced by F. necrophorum in mule deer are variable depending on the site of infection. A foot rot syndrome often is present, which is characterized by necrosis of the interdigital tissue, inflammation of the coronary band and sensitive laminae, and extension into the proximal joint above the hoof (Rosen et al. 1951). Necrotic stomatitis, ulcerative rumenitis and abscesses in other organs may occur. Diagnosis of necrobacillosis is based on isolation of F. necrophorum from affected tissues. It should be mentioned that the lesions of chronic hemorrhagic disease with secondary bacterial infection in white-tailed deer are markedly similar to those described for necrobacillosis in mule deer. The role of BT virus in producing a portal of entry for F. necrophorum should be a fruitful area for future study.

Parasitic Diseases - Two major groups of nematodes, trichostrongyles and lungworms, are of potential significance in portions of the mule deer's range.

The gastrointestinal trichostrongyles infecting mule deer comprise several genera (Walker and Becklund 1970), and in areas where climatic conditions are conducive to parasitism, Haemonchus contortus s.l.; the large stomach worm, is of particular importance. This helminth may cause considerable blood loss among fawns. The occurrence of H. contortus is worldwide, however it is locally more common in some areas than others even in humid environments. In the southeastern United States, for example, H. contortus is more prevalent and has a higher intensity of infection in deer of the lower coastal plain than in more upland terrain (Prestwood et al. 1972). The host range for H. contortus includes cattle, sheep, goats, and numerous wild ruminants. Although species of Haemonchus infecting cattle and sheep have been separated, the genus appears to be in a state of evolutionary flux. Das and Whitlock (1960) considered H. contortus to be actively evolving and that the species contains a number of well defined demes, each adapted to a particular host-microclimate interaction.

The principal effects of Haemonchus are due to anemia, which in heavily infected animals is accompanied by edema, emaciation, and generalized digestive disturbances. Both 4th stage larvae and adult H. contortus cause blood loss. At necropsy submandibular edema ("bottle jaw"), enlarged lymph nodes, and thin, watery blood may be obvious. The lining of the stomach may be swollen, and have petechial hemorrhages with shallow ulcerations. Young deer usually are more heavily infected than the adults (Prestwood and Kellogg 1971).

Conditions that predispose animals to H. contortus also are conducive to heavy infections with other abomasal or intestinal trichostrongyles, and pure infections with a single species of nematode are uncommon. Similarly, nutritional status of the animal is of paramount importance since poor nutrition and parasitism often occur concomitantly. Although one helminth, e.g. H. contortus, may be the actual cause of death in deer, overcrowding, food shortage, and competition by other ruminants or swine are important contributing factors leading to death from gastrointestinal parasitism.

Two types of lungworms infect mule deer, viz. 1. those whose adult stage is found in the lung (Dictyocaulus viviparus) and 2. those whose adult stage occurs in sites remote from the lungs but whose eggs and larvae pass through the lungs to the external environment (Parelaphostrongylus spp.).

The large lungworm, Dictyocaulus viviparus, is located in the bronchi and bronchioles of mule deer.
where it produces a parasitic bronchitis. Dictyocaulus
is worldwide in distribution, with increased prevalence
in cool, moist areas. Like other trichostrongyles, D.
viviparus has a direct life cycle. Cattle and various
wild ruminants serve as definitive hosts for large
lungworms, however, recent work has shown that
Dictyocaulus of wild ruminant origin has low infectiv-
ity in cattle suggesting that there may be host
specific strains of this helminth (Presidente et al.

In the southeastern United States, about 30
percent of white-tailed deer harbor D. viviparus.
Infection is most prevalent and intense in young
animals, particularly buck fawns. Dictyocauliasis is
seasonal in occurrence; the prevalence and intensity
of infection are higher in late summer and early fall.
The parasite is least common during the winter
(Prestwood et al. 1971). Outbreaks of D. viviparus
pneumonia have been recorded in captive black-tailed
deer in Oregon (Presidente et al. 1972).

At necropsy, lesions caused by D. viviparus may
be mild to severe. Extensive pneumonia may be present,
and there may be numerous lungworms and exudate in
the bronchi. Pleuritis and interlobular thickening may be
obvious. Occasionally edema and enlarged lymph nodes
and lymph vessels are detected. Lung damage may be
particularly severe when first-stage larvae of
Parelaphostrongylus sp. also are present (Prestwood
et al. 1971).

Mule deer may be infected by at least two species
of Parelaphostrongylus, viz. P. odocoi lei and P. tenuis.
Parelaphostrongylus odocoi lei is located adjacent to
or within small vessels in the musculature of the hind-
body of black-tailed and mule deer. It also has been
found within small vessels in the lungs. This helminth
has been reported only from deer of California
(Hobmaier and Hobmaier 1934; Brunetti 1969). Recently,
however, similar protostrongylid larvae were found in
the feces of mule deer from Western Canada (Samuel and
Holmes 1974). One of the authors (CPH) has seen
protostrongylid larvae in feces of southwestern mule
deer.

The life cycle of P. odocoi lei is indirect. Eggs
are deposited in the circulation and arrive as emboli
in the lungs where hatching occurs. First-stage
larvae ascend the bronchial passageways and trachea,
are swallowed and eliminated with the feces. Various
terrestrial snails and slugs (Helix aspersa,
Agriolimax agrestis, A. compestris, Planorbis sp.)
serve as intermediate hosts. Deer become infected
after ingesting snails containing infective P.
odocoi lei larvae. The pre-patent period is approxi-
mately 2 1/2 months.

Adult P. odocoi lei produce small hemorrhages in
the musculature. Extensive tissue damage caused by
eggs and larvae of P. odocoi lei has been seen histo-
logically in the lungs and lymph nodes and has been
considered a cause of death among California deer
(Brunetti 1969).

Mule deer have been experimentally infected with
the meningeal worm, Parelaphostrongylus tenuis
(Anderson et al. 1966). This helminth is widely
distributed throughout the range of its usual host,
the white-tailed deer, and has been recorded as far
west as Oklahoma and Minnesota. Adult helminths are
located in the subdural space and venous sinuses of
the cranial meninges of white-tailed deer. The life
cycle is indirect, and similar to that of P. odocoi lei.
Detailed studies by Anderson (1963; 1965) and
Anderson and Strelive (1967) have shown that after ingestion,
infected larvae penetrate the abomasal wall and
travel to the spinal cord of white-tailed deer.
Development occurs in the dorsal horns of gray matter
for 30-40 days, after which worms move to the subdural
space. First-stage larvae appear in the feces 90 days
or more post-infection.

Neurologic signs are rare in white-tailed deer,
however, neurologic disturbances leading to paralysis
and death have been observed in unusual hosts, e.g.
domestic sheep, moose (Alces alces), wapiti, caribou
(Rangifer tarandus terranovae) and reindeer (R. t.
tarandus) (Anderson 1970). A mule deer fawn was
experimentally infected with P. tenuis, and a fatal
paralysis ensued (Anderson et al. 1966). Black-
tailed deer translocated into Tennessee from Oregon
also were afflicted with fatal neurologic disease
caused by P. tenuis, which apparently has been a
primary limiting factor for establishing black-tailed
deer in Tennessee. Experimental infection of a
hybrid deer (O. h. columbianus x O. virginianus)
resulted in fatal paralysis 52 days post-infection
(SCWDS, unpublished).

It appears that the encroachment of white-tailed
deer onto the range of mule deer is a definite threat
because of the likelihood of exposing mule deer popu-
lations to P. tenuis.

Although each of the aforementioned diseases has
been considered a specific potential mortality factor
for mule deer populations, we should emphasize that
seldom does one entity alone cause significant
mortality of a wild population. Rather, multiple
factors usually are involved, and the specific
disease is a product of complex interactions between
the animal and its environment. Judging from the
apparent lack of information on diseases of mule deer,
we respectfully suggest that concerned game and fish
agencies place more emphasis on investigating dis-
ases of mule deer. These investigations should
include specific information on causes of "die-offs"
and probably more importantly, should consider what
potential mortality factors are present within
apparently healthy populations. Only until we have
a basic understanding of the interactions between
the disease agent, the animal, and the environment
can the causes of the mule deer decline in the west
be ascertained.

Acknowledgments: This study was supported in part by
Funds administered and coordinated under the Federal
Aid in Wildlife Restoration Act (50 Stat. 917) and
through Contract No. 14-16-0008-2028, Fish and

LITERATURE CITED

Anderson, R. C. 1963. The incidence, development, and
experimental transmission of Pneumostrongylus
tenuis Dougherty (Metastrongylidae:
Protostrongylidae) of the meninges of the white-
tailed deer (Odocoileus virginianus borealis) in


MULE DEER MORTALITY FROM VARIOUS CAUSES

W. Leslie Robinette
Retired Wildlife Research Biologist
U.S. Fish & Wildlife Service
Present Address: 488 So. Alkire St.
Lakewood, Colo. 80228

Abstract

Evidence is presented that several Great Basin deer herds produced fall fawn crops of 100 or more fawns per 100 does before widespread use of the range. Subsequently, fall fawn crops dropped to only 60 or 70 percent. It is the writer's contention that poorer nutrition caused by range depletion was responsible for the reduction in fawn crops and that this has been a major factor in the general decline in mule deer populations. The solution would seem to lie in even further herd reductions through hunting to a level that will permit range recovery through natural plant succession or artificial revegetation.

I suspect that those responsible for this symposium intended that this paper should cover all classes of deer mortality not covered by previous papers and that they dropped the general mule deer decline. There is little doubt that vehicles, starvation and poaching, for example, have been or are currently important mortality factors among some herds and in some years. Many deer are killed by vehicles, particularly where interstate highways cross migration routes or winter ranges. Starvation losses are less common now than 2-4 decades ago but still may occur during severe winters, prolonged droughts, or among inadequately hunted herds. While these classes of mortality may be locally important, it is doubtful that they have been the major causes for the general decline.

I should like to take this opportunity to discuss what I feel has been one of the major causes for the decline among Great Basin herds and one which can be corrected by management. This involves the generally lower fawn crops which have resulted, I believe, from deteriorating ranges, caused primarily from excessive deer use. Deer highlining or hedging of preferred browse has long been recognized as a sign of excessive use, but less recognized has been the more subtle disappearance of preferred forbs on the summer ranges. For many of the Great Basin herds the summer range is even more critical for optimum productivity than winter ranges. Several herds for which I have fall composition counts had 100 fawns per 100 does even when the herds were approaching or at peak numbers. However, after widespread range damage, the fawn crops generally fell into the 60 to 70 range. In many of these herds the decrease in fawn production equals the present legal kill.

Fall fawn crops of 100 or more were recorded for the Duck Creek herd in eastern Nevada for 1942, 1943, and 1944, but they dropped to around 90 in 1945 and 1946 and even further to an average of 73 for the 6 subsequent years (Aldous 1948; Robinette, unpublished data). The decline continued despite the introduction of "1080" in 1947 which drastically reduced coyote numbers. The decline was almost certainly associated with an overstocked summer range. The most striking evidence is the highlining of curlleaf mountain mahogany (Cercocarpus ledifolius) and aspen (Populus tremuloides) and the absence of regeneration. Observations have indicated that when this occurs, most of the palatable forbs have likewise been depleted.

A decline in fawn crops also occurred on the Dixie National Forest in southwestern Utah, but it took place a few years earlier than in Duck Creek. Classifications gave a fawn crop of 101 percent in 1936; 94 for 1937; but an average of only 65 for the 6 years, 1940-45 (Noel 1948). Overstocking was recognized by the U. S. Forest Service and Utah Fish and Game Department in the late 1930's, so depleted ranges are again believed responsible for the decline in fawn crops. A decline of fawn crops also occurred on the Fish Lake National Forest in central Utah, but they started at a period intermediate to that of Duck Creek and the Dixie. Fawn crops of 92 to 100 were recorded for 1930, 1937, and 1939, but they dropped to 87 in 1940; 75 in 1941; and 71 in 1942 (Olson and Turpin, 1931; Costley, 1938; Robinette, 1950). On the Pahvant Range, which is a part of the Fish Lake Forest, the values were 90 for 1939 (well after overstocking was first recognized); 82 in 1940; and an average of only 68 for 12 years (1941-42, 1946, 1949-57) when classifications were made (Robinette, unpublished data).

An area on which I made a rather intensive deer herd study, the Oak Creek drainage in west central Utah, showed a similar decline in fawn production and one almost certainly resulting from summer range depletion. Limited classifications by myself and Costley (1940) indicated a fawn crop of 100 percent for 1939. The herd was heavily damaging its range at that time; and despite substantial doe removals beginning in 1940, which perhaps reduced herd numbers to one-half in 1946, the relief was
Insufficient for summer range recovery. From the fall of 1946 through 1957 when my study was made, fall alfalfa crops averaged but 68 percent or nearly one-third less than in 1939. The lower alfalfa crops prevailed despite a substantial reduction in deer numbers, cattle use, and even coyote numbers during part of the study. Failure of the preferred deer forbs to recover was evident from observations within a set of exclosures established by the Utah Fish and Game Department in 1952. A check which I made in July, 1971, revealed that 9 forbs palatable to deer had a canopy ground coverage of 29 percent in the deer exclosure compared to only 2 percent in an adjacent exclosure which permitted deer to feed but excluded livestock. The exclosures were not constructed until several years after peak deer use so that it is entirely possible that some of the most palatable forbs had already been eliminated from the site.

The Oak Creek winter range was generally considered to be in reasonably good condition, but even here there was evidence that the most palatable shrub, bitterbrush (Purshia tridentata), was not regenerating itself satisfactorily. A growth ring count made in 1958 of all bitterbrush plants from a plot 15 x 30 feet on a productive bitterbrush site revealed that the youngest plant of 22 years dated back to 1936. This was about the time when the herd was probably nearing or at carrying capacity. Observations at Oak Creek make it quite evident that merely reducing herd numbers will not necessarily recover a herd that is in poor condition and held there until the range can recover. Deers numbers must be reduced below carrying capacity and held there until the range can recover.

Many deer workers have noted the adverse influence of severe winters upon herd productivity. Not only may deer be lost outright through starvation, but because the surviving does are in poor condition, the subsequent postnatal fawn loss may likewise be severe. The most practical means of minimizing such losses is to maintain a stock of deer that will insure maintenance of the preferred forage species. This insures a forage surplus for times of stress on which the herd can rely. This view was emphasized by results of winter mortality studies of some Utah herds following the winter of 1948-49 (Robinette et al., 1952). This winter was considered to have been the most severe by the U.S. Weather Bureau since the inception of weather records in Utah. The herd loss on the South Oak Creek range where there was an abundant supply of cliffrose (Cowania stansburiana), a preferred forage browse, was in contrast to losses of 20 to 50 percent on other ranges within 100 miles where there was little preferred browse. The more forage available to a deer over winter, the greater its chances for survival. The deer not only expends less energy in filling itself but its opportunity for selecting palatable plant parts is enhanced, thereby insuring a better diet.

Longhurst et al. (1968) concluded that penned deer did best on forage species that they preferred. Similarly, a captive herd at the Denver Federal Center responded dramatically to increased rations of preferred foods (Robinette et al., 1973). When the deer were fed increased quantities of hydroponically-grown barley and a commercial concentrate, both of which they preferred over alfalfa hay, several important things happened. Food consumption rose, weights increased, fawn production jumped from 1.4 to 1.9 per doe of breeding age, while fawn mortality of the first week postpartum declined from 10 to 4 percent.

A comparative study of two wild herds in the Great Basin provided corroborative evidence for the importance of preferred forage during summer to optimum herd productivity (Julander et al., 1961). Summer range on the Sublett unit of southern Idaho was found to have substantially more preferred deer forage than the Antimony unit of south-central Utah. There was 50 times more good deer forage per acre in the aspen type on the Sublett unit than on the Antimony area and 11 times more in the mountain shrub type. In addition, deer stocking on the Sublett unit was only half that of the Antimony unit. Sublett deer weights were substantially higher as was the fetal rate of 1.85 per doe compared to 1.19 for Antimony. Fall composition counts indicated around 50 fawns per 100 does for Antimony and double this for the Sublett.

I have a feeling that had not the Oak Creek summer range been so depleted by overuse in the late 1930's and early 1940's, it could have adequately supported the post-hunt density of 1 deer per 15 acres that prevailed during the 1947-56 study. If this assumption is accepted and two other reasonable assumptions are made (that the does reproduced at the 1.85 rate achieved by the Sublet herd rather than the actual 1.32 and that the fawn loss from birth to the hunt was a reasonable 15 percent instead of the actual 33 percent), the herd's fall fawn production would have been an estimated 1,753 instead of 932. The average legal kill was 447 per year during the study, a value which seemingly could have more than doubled had the herd realized its full potential.

It is doubtful that any Great Basin herd has been stabilized through hunting before damaging its range. Even the Sublett herd with its excellent summer range had depleted its winter range along the south side of the Raft River Mountains in Utah. Even though hunting, starvation losses, and lowered fawn production have combined to reduce many Great Basin herds, it is doubtful if the reductions were great enough and made soon enough to have permitted full range recovery.

Several long-term range studies with livestock have shown that moderate stocking provides greater economic returns than excessive stocking. Moderate stocking insures adequate supply of preferred forage and this in turn provides for higher yields of meat and production of young (Hutchings, 1954; Johnson, 1953; Klipple and Costello, 1960). By the same token, it is possible for a well-managed deer herd to produce as many or more animals for hunter take than a herd twice the size on overstocked range.

In years past, many game managers have been guided in their recommendations for deer removals by utilization data on preferred winter browse. This is perhaps good if there is some built-in assurance that the key browse species are regenerating themselves, but too often this has not been the case. On ranges such as Oak Creek where the summer range is even more critical to the herd's welfare than the winter range, there have been few, if any, vegetative transects for the purpose of determining condition and trend among the preferred forbs.
Deer management has come a long way in the past three or four decades, but it is unfortunately true that sportsmen still pack such a political wallop that they can effectively negate needed herd reductions. If winter starvation losses or lowered fawn production result in poorer hunting, the sportsmen usually clamor for buck hunting only, or even complete closure until the herd can recover. In actuality, starvation losses and lowered fawn production are firm evidence for the need of even further herd reductions. Rehabilitation of depleted deer ranges will take time, whether accomplished artificially or through natural recovery, and will probably necessitate even further herd reductions. The long-term potential for increased hunter take, however, would seem to make the program worthwhile.

Bibliography


The solutions to mule deer management seem simple to many people. However, in reality this is not the case. Deer management is still in its infancy and is understood only in part by even the best biologists. Perhaps the most cheerful way to look at low mule deer numbers is to look back at populations in 1900. This makes present-day mule deer numbers look great. Winter "die-offs" as a result of poor ranges and overpopulations initiated increases in harvests to reduce mule deer numbers. These increased harvests have resulted in a kill of over six million deer in recent years. Except for the effect of hunting, indications are that when deer are on a high quality diet, other environmental factors are not as important.

I approach this assignment of summarizing the fact and the fiction associated with the alleged decline of mule deer with the same enthusiasm that Marie Antoinette approached the scaffold. If it weren't for the honor of it, I think I'd decline the trip. Other titles for such a summary could be equally appropriate—"A Pooling of Ignorance" or "What Do We Know For Sure?"—because we seem to be discussing more of what we don't know than what we do. If I were to paraphrase this situation, I would say that learning anything about the mule deer decline at this conference is like learning about love in a brothel. The lessons are clear but oversimplified.

Anyone attempting to summarize this conference in 30 minutes has to be foolhardy, and it just occurred to me why I was asked to do this. As one wag says, "If he seems lost in thought, it's because it's such unfamiliar territory." I tried to anticipate what would be said at this conference by not writing to any of the speakers. They anticipated it by not sending me any advance copies. Everything I've had to do here is what any one of you could have done, and that is ask your neighbors, read the Transactions and various journals, and go through the popular literature. I even thought about going into the airport newsstand on the way down to see if the latest Outdoor Life had the problem solved. That's probably where it will first come out. My suggestion for anybody working on such a topic in the future, is to write your report on a magic slate. Then you can rip it off if you see anybody approaching.

As you can see, I'm in a great mood for this assignment. I'm not even sure at the end of these two days whether the mule deer are declining or not. After listening to Bruce Gill, one may wonder if this meeting was even necessary. We could say, without too much fear of contradiction, that there probably were fewer deer in 1975 than there were in the 1960's, and then we can say that there are a lot more deer now than there were in 1900. Instead of telling the public about the high deer numbers in 1960, we ought to compare today's populations with the 1900 estimates and then conditions wouldn't appear so gloomy.

If the deer are actually declining, I think the answer is quite simple. It's only because mortality is exceeding natality, so now we can all go home. What we're really trying to do, though, is determine if this is the case so we can proceed with the audit and find out who tapped the buckskin till. How about that for mixing metaphors? Our profession has been described by some of its detractors as a form of slipshod animal husbandry. This is something I think we should consider. In a recent Audubon article describing the grizzly bear controversy, Bill Gilbert wrote down all the conflicting arguments in embarrassing detail. At one point he paused and
said, "So much for the art of wildlife management." What a put down.

The pattern of the alleged decline, whatever it is, seems to have been repeated in all the states simultaneously. Since all the workers in all the deer states involved seem to write to each other, and then average out the results, this is not surprising. But let's assume that mule deer numbers are down from the peak populations of twenty years ago, and then seek the probable answers. Bud Phelps gave us one when he said, "In Utah we intended to knock deer numbers down--we had too many." We tell them that in Montana, too. It's analogous to the bear at Yellowstone Park. When the tourists complain about not seeing any bears they are told that they're up in the hills picking huckleberries. We need an equivalent of that when the public asks us where the deer are.

The 1940's was the turning point in mule deer numbers, with notable increases recorded in most of the western states. We can show that the deer have declined since then in direct proportion to the increase in professional wildlife managers. This is called a nonsense correlation. When it is shown that 90 percent of all the train wrecks involve the caboose, the solution is to take off the caboose. We're doing similar things, I think, in the field of wildlife management.

We did hire a lot of professionally trained wildlife biologists with the newly available PR funds. Simultaneously, we had some tremendous deer die-offs in the winters of 1948 and 1950, which made a lot of headlines all over the West. Hay and pellets were airlifted in to livestock, as well as deer, and the new game managers dove right into the fray. They put on pressure to increase the harvest in order to offset the twin calamities of starvation and land depredation. About the same time, the ranching interests were attempting to force the sale of public grazing land. The significance of that will come a little bit later. The available harvest records indicate a rapid increase in deer numbers in the past 25 years. We've also increased the hunter numbers, liberalized the seasons, and increased access by putting many more roads into formerly inaccessible areas. In other words, the history of deer management has been characterized by an ultraliberal approach--"a 20-year blood-letting" according to some--and how we're having withdrawal symptoms.

Many of the speakers at this conference have pointed out the multiple game bags and the various combinations of seasons that have evolved during this period, mostly trial and error, with new research findings being applied as fast as the public would accept them. Each state has its own peculiar history with non-residents, license fees, and landowner-sportsman problems. Now we are all facing a public reaction to reduce this liberal management program, and many state agencies tacitly admit that deer numbers may be lower than we care to admit. Wolfe and others have commented upon how the various states arrive at their population data. The increases and decreases can be due to a host of things that have nothing to do with the total number of animals. The first thing any student learns in wildlife management is that a total census is probably something that he won't be able to do. I remember writing that down as a student in 1946. Last week I told a class the same thing, and they wrote it down. I think we have institutionalized it and it's probably true.

The reason most often quoted for the alleged decline is overhunting, but it's by no means uniformly true. A unique, and probably odd, characteristic of this two-day conference has been that there hasn't been one speaker discussing the removal of mule deer by the gun. Approximately 6 million deer have been harvested in the 11 western states in the last 10 years. If 6 million deer have been removed by hunting, including many females, it is probable that we have had some effect on the slope of the population curve. Game departments then say, "We intended to reduce the populations"; but simultaneously they seem to reject the notion that hunting is a significant mortality factor. This latter notion seems to be changing recently.

On the other side of the question, we use that same theme of hunter removal by talking about the effects of early market hunting. They overharvested deer in many cases, to the point of extinction in some areas. The history of deer management always includes reference that predator reduction, creation of game refuges, and reduced legal and illegal harvests, coupled with "bucks only" seasons, helped bring back the deer. It is also possible that we can find the true cause in almost everybody's summary. So, we've got some strong cases for a wide variety of possibilities for the decline, excluding sunspots, aerosol sprays, or something that somebody is putting in the water in the nature of an anti-fertility substance. I don't think we ought to be surprised that some factors are compensatory. Our job is to unravel these complexities. Low and Julander pointed out that the decline began in Utah approximately 10 years ago, but it varies in states--some earlier, some later, and some unsure.

If we have removed about 6 million deer by legal hunting, I'd like to know why it hasn't been mentioned here. The 1972 proceedings of the Western Association, which deals with the harvest in 1972, listed approximately a half a million deer taken in 1972-73. The years 1974-76 are not listed, but if so, an additional estimated 2 million harvested deer have not been accounted for. We've had plenty of time to double those totals, and game management has been characterized by an ultraliberal approach--"a 20-year blood-letting" according to some--and how we're having withdrawal symptoms.

The reason most often quoted for the alleged decline is overhunting, but it's by no means uniformly true. A unique, and probably odd, characteristic of this two-day conference has been that there hasn't been one speaker discussing the removal of mule deer by the gun. Approximately 6 million deer have been harvested in the 11 western states in the last 10 years. If 6 million deer have been removed by hunting, including many females, it is probable that we have had some effect on the slope of the population curve. Game departments then say, "We intended to reduce the populations"; but simultaneously they seem to reject the notion that hunting is a significant mortality factor. This latter notion seems to be changing recently.

On the other side of the question, we use that same theme of hunter removal by talking about the effects of early market hunting. They overharvested deer in many cases, to the point of extinction in some areas. The history of deer management always includes reference that predator reduction, creation of game refuges, and reduced legal and illegal harvests, coupled with "bucks only" seasons, helped bring back the deer. It is also possible that we can find the true cause in almost everybody's summary. So, we've got some strong cases for a wide variety of possibilities for the decline, excluding sunspots, aerosol sprays, or something that somebody is putting in the water in the nature of an anti-fertility substance. I don't think we ought to be surprised that some factors are compensatory. Our job is to unravel these complexities. Low and Julander pointed out that the decline began in Utah approximately 10 years ago, but it varies in states--some earlier, some later, and some unsure.

If we have removed about 6 million deer by legal hunting, I'd like to know why it hasn't been mentioned here. The 1972 proceedings of the Western Association, which deals with the harvest in 1972, listed approximately a half a million deer taken in 1972-73. The years 1974-76 are not listed, but if so, an additional estimated 2 million harvested deer have not been accounted for. We've had plenty of time to double those totals, and game management has been characterized by an ultraliberal approach--"a 20-year blood-letting" according to some--and how we're having withdrawal symptoms.

Many of the speakers at this conference have pointed out the multiple game bags and the various combinations of seasons that have evolved during this period, mostly trial and error, with new research findings being applied as fast as the public would accept them. Each state has its own peculiar history with non-residents, license fees, and landowner-sportsman problems. Now we are all facing a public reaction to reduce this liberal management program, and many state agencies tacitly admit that deer numbers may be lower than we care to admit. Wolfe and others have commented upon how the various states arrive at their population data. The increases and decreases can be due to a host of things that have nothing to do with the total number of animals. The first thing any student learns in wildlife management is that a total census is probably something that he won't be able to do. I remember writing that down as a student in 1946. Last week I told a class the same
The hunter harvest data are almost always a year late, they arrive after the seasons are set, and may reflect political pressure as much as herd condition. Colorado and Utah have good mule deer habitat, and both of these states recorded increases in 1972. Utah is 11th in area, with about 85,000 square miles; Colorado is 8th largest, with 104,000 square miles, and yet they are among the leading producers of mule deer year after year. An inspection of a vegetation map of Colorado reveals that only half the state would qualify as habitat for mule deer. From that half, you start eliminating poor deer habitat, and you end up with scattered remnants of mule deer range. Many of these areas have a continually evolving system of sex, age, time, and area restrictions, changing license fee structure, and changing non-resident quotas. There are so many variables that it makes you wonder if you'd blow every fuse in town if you put this through the computer.

The other considerations include the political, legal, social, cultural, economic, and whatever. Let me read you two sentences out of a politically oriented statement from a Nevada Game Commission member shortly after the Director of the Bureau of Land Management said, "We're going to improve the ranges in Nevada." It's two pages long, but I'll only read these two paragraphs. It says:

"Today you could remove all livestock from Nevada ranges and never hunt deer again. Without doing anything more, in a short period of time the ranges would be in a worse condition, and the deer herds would continue to dwindle."

"In closing, I'd like to say that not only is it proven that livestock and wildlife are compatible, but that they are desirable. We, therefore, defend the livestock industry in the state of Nevada and feel that is the wildlife and the sportsman ever had a friend, it would be a rancher."

Dick Mackie missed that point yesterday in his literature survey. He said he didn't know it had been proven that cattle and deer were good for each other, but here we have it. It's a political proof, but it's one that we'll probably hear more of. Dean Thad Box talked to you yesterday about more people on the same amount of land with increasing pressures, and he said the answer is allocation. Allocations may be based on stronger political than biological rationale, but I'm sure the proponents will stress the need for cooperation.
about cooperation that says: "There's room enough
for one of us on this piano bench if you'll get off."

At the recent (1976) N.A. Wildlife and Natural
Resources Conference in Washington D.C., a fish and
game biologist, Steve Gallizioli, stated that, "In
Arizona, the single most important range manage-
ment problem which limits the attainment of potential fish
and wildlife benefits is overgrazing by livestock. I
believe the problem is not unique to our state."
Speakers at this conference (Macle, Urmess, Tueller)
seemed reluctant to confirm this observation.

Enough of this short course on public relations
on public lands. When we get to the point where we've
got enough food for either the coyote or the deer, but
not enough for both, I think we'll find out how much
cooperation is going to take place. The statement
from the Nevada Commission shows that when the po-
itical pressures are on, all those great stochastic
perturbations that statisticians alarm me with really
don't count for much in the management decision.

Let's move on to some of the other subjects.
Dick Denney got into the question of population regu-
lations and raised the question, "Is the deer decline
a sign of ecosystem deterioration?" Practically
everything we've heard at this conference indicates
that when deer are on a high quality diet, other en-
vironmental factors are not as important. Speakers
discussing predation and winter survival have also
stressed the overriding importance of good nutrition.
Zwank stressed the importance of nutrition in fawn
survival.

Hornocker and Knowlton reviewed much of the same
material that I did on predation. Hornocker pointed
out that no correlation exists between deer numbers
and lions in most areas. There has to be some other
correlation. He talked about the importance of the
effect, not the fact, of predation, and I think the
same idea was stressed by Knowlton. Hornocker missed
the best quote from Durward Allen, whose grandmother
watched his dog run the cat up the tree. She said,
"Oh, Lord, why can't they be nice." Predators have
a poor press, and I think that when we get into
public relations, that's probably how we ought to
approach it. Knowlton was quite candid when he said
"maybe" in regard to whether predation was a signifi-
cant limiting factor. The nutritional aspect is
obvious in his work—healthy deer can withstand more
predation by compensatory reproduction than can deer
on low quality ranges. Neither Hornocker nor Knowlton
said that the removal of the coyote or the lion could be
proven to help deer. The average wildlife biolo-
gist is poorly equipped to evaluate nutritional fac-
tors. He ships plants to somebody else for proximate
analysis. Then we find out that that's only the be-
ginning. Volatile oils that are bactericidal and
fungicidal upset all the calculations based on pro-
tein levels. Synergistic effects cause foodstuffs to
act differently in combinations. Just switching the
combinations on two species in eight different combi-
nations would blow your mind, and some of the animals
eat as many as 20 different kinds of plants. You can
appreciate what Nagy and his colleague talked about
today—the need for more basic research of high qual-
ity. Several speakers quoted the Kaibab case in the
face of articles in BioScience, Ecology, and various
National Park releases pointing out that the Kaibab
deer irruption really never occurred, that it was a
figment of someone's imagination, or a clerical error.

No one in this audience challenged it, although
Tueller from Nevada did comment on it. This debate
needs to be continued.

Wolfe was telling us, in effect, to challenge
assumptions. The computer can't overcome poor in-
puts. I've got a hunch that maybe we'll have to
admit that there are some things we just can't do,
like nailing jello on the wall, or putting the tooth-
paste back in the tube. Namsi, Reid, and Carpenter
analyzed existing data in Colorado to provide clues
for the decline, and they concluded that their meager
data failed to support the hypothesis that all these
things, singly or in combination, could be held
responsible. That's the approach the Chamber of
Commerce uses when you tell them that air pollution
is causing a problem. I would like to have heard
them say that the meager data failed to support the
hypothesis that all these things are not responsible.
There are some pragmatic aspects to consider. If
deer are not in evidence, something must have hap-
pened to them. Longhurst said that the shift to
cattle from sheep in California was detrimental to
mule deer, and on annual grass ranges that may well
be. Sheep can be far more easily manipulated on
ranges instead of ranges than livestock. That may be what he had in
mind when he said that the increase in cattle and
decine of sheep was detrimental to deer ranges.

Tueller made the observation that deer numbers
decine in proportion to lack of vegetative diver-
sity. That's in every basic text on ecology I've
ever seen. We talk about the stability of diversity,
and yet biologists have been guilty of aiding and
abetting ecological insults. We spray ranges, we
poison ponds with toxaphene, we've suggested mass
burning of forests to produce monocultures, and
we're probably guilty of other ecological insults
on a large scale without really knowing what the
consequences are.

Another point that Tueller made that's worth
repeating is that not all forage produced can be
shown to directly influence productivity. We feel
that food is important, but it may not be the only
limiting factor. There are many cases where we've
increased forage supplies without increasing the an-
imal numbers. The fact that deer are seen in an
area doesn't mean that they are produced there. We
may be shifting them or drawing them from one area
to another.

I want to comment on the use of jargon in our
profession. We smirk when a sociologist defines
murder as accelerated, interpersonal altercation,
but wildlife aren't above doing their bit to in-
crease the fog index either. Here's an example from
the Master Plan for Grand Teton National Park. "New
insights gleaned from recent problem-oriented re-
search within the parks suggest that environmentally
regulated ecosystems can ultimately be reestablished.
For example, research has suggested that the popu-
lation may tend to be self-regulating without the
presence of significant predator populations. In the
context of increasing knowledge of these factors,
park management will continue to work toward the
elimination of hunting in the park." The state of
Wyoming responded more succinctly saying, "To hell
you will."

I'd like to make a brief comment on the wildlife
disease paper. It was of interest to me because in
our zeal to rid the ranges of the predators, we feel we're helping the herbivores. Now we're finding out in some cases that carnivores and herbivores are vectors for other diseases. If we do have these reservoirs of infection with livestock and wildlife interchanging, we've got some real problems: Brucellosis is found in the bison in Yellowstone and every time a Park bison crosses the Montana line, by law we have to kill it due to stockmen's fears. I think you can see the consequences. We've taken an animal that evolved from ancient times and juxtaposed it with a domestic animal. Since sick animals are predisposed to losses by predation and accidents, it is difficult to assess the nature and extent of the losses.

THE FUTURE

Robinette told us that it would have been great if we could have cut the deer numbers down before the range was damaged so severely, and many authors have pointed out previously that when deer exist on second-class forage, periodic die-offs can be expected in severe winters. We need far more experimental evidence of that fact. Looking into the future, I think that we can agree that simple minds seek simple solutions. Some of you are going to go home disappointed because I didn't tell you the solution to the mystery of the deer decline. The conference speakers didn't tell me the answer either. The answer may be that we should challenge the basic assumptions under which we have been managing deer these past 30 years. The demand for more hunting opportunity can go no way but up. It seems to be increasing despite all the hard caps we've imposed upon the hunters, and the rate of increase is still as rapid as the increases in the 60's. The hunter himself appears to be becoming less skillful, more reliant on equipment, more reliant on somebody else to write him a book on how to hunt, how to build a fire, and how to dress out a deer. I think he's going to be subject to the whims and vagaries of political pressure, which may not be a part of, and they may not understand the reasons. There is going to be increasing pressure on land managers to produce quality access, all these things. Hunters are also going to be subject to the whims and vagaries of political pressure, which they may not be a part of, and they may not understand the reasons. There is going to be more pressure on land managers to produce quality habitat, to experience a better number distribution. There will be more anti-nonresident sentiment. The provincialism in our own state is pretty obvious. Simultaneously, we're being challenged by court cases, which may cause us to repay all the nonresident license differentials back to 1970. This would mean that we'll probably sell the place and go into another line of work.

The anti-hunter pressure is expected to increase everywhere, which may shift the deer harvest from the hunter to the coyote. California's recent report by Longhurst and his colleagues said rather gloomily, "We don't think we can stem the tide of habitat destruction and anti-hunter pressures." California is kind of a bellwether here. They've had the problems longer than other states.

The game departments are faced with increasing costs, and increasing demands for more complex information, and simultaneously they are facing a reduction in income. Even I can figure out what that means. We are probably going to have to put more money into non-game activities, and I don't think it will come fast enough to fill in the gap between now and when the legislature does it. So we're having to put our funds into other areas because of the public relations aspects. We have a need for more internal cost accounting and planning to see where the money has gone. We may be startled by the amount of money that goes into some research projects when it is finally summarized. Game departments are now faced with a rash of legislative interventions after many years of relatively free sailing. It seems to be our turn. Eisenhower once said, "I don't think we need easier problems, I think we need better men." How selective have we been in our hiring practices in wildlife agencies? We've hired a lot of people in the past 30 years. Perhaps what I'm suggesting is that we've been getting along in a rather slip-shod fashion which won't work now that we're getting into the big leagues. The research has got to be better and deeper, and I don't think the universities, at present, are preparing the personnel to do it. They are reflecting the market. You can't get a job in some of the federal agencies if they're in a declining budget year because they have to do what they call "GS averaging." If you've got the home office full of 15's and 16's, you've got to hire 3's and 4's so you'll average out at 12. Some of the agencies have really not made much of an effort to improve the quality of their people.

Thad Box pointed out that 12 credits is the minimum Civil Service requirement to be a range examiner. I submit that 12 credits in range hardly qualifies one to go out and make decisions influencing the future of the public lands as well as the financial welfare of many citizens. Game damage complaints are increasing in the western states, and it has become a very serious issue. Fish and game commissioners and the other politically appointed administrative types deal with axe handle measurements, the game manager follows along with a yardstick, and the researcher is measuring stuff to four decimal places. This is particularly ironic when we can't even make one simple breakdown, such as are we gaining, losing, or holding our own on mule deer? Those are false intervals of 33 1/3 percent. I'm not really impressed with decimal points. I'd like to know if we have such a thing as a "lack of confidence" interval?

The land itself is obviously under continually increasing pressure. Land is finite and recreational pressures are in addition to all the traditional uses. We can't buy all the needed game ranges and are going to have to learn to get along with what we have. This is going to involve a degree of cooperation, which has heretofore been unknown between the agencies. Arizona charges an extra fee to hunt on lands that they have improved. I think it's a good idea. A $5 fee to hunt on the Kaibab might be the right way to finance the studies, because we may soon run out of dollars. The demand for the deer is obviously going to exceed the supply. More buck hunting and less trophy hunting will be the rule. Colorado is already going for less trophy hunting and more meat. This is just the opposite of what they're finding on African game ranges where they shoot bucks and fawns. They don't shoot their productive herd segments. Why the difference? I think the tradeoffs between the deer or elk and livestock are going to be hard fought. Remember that some game departments, under political pressure, don't provide much of a fight when the livestock interests remind them of their loyalties.

133 Probable Causes of the Recent Decline
Crippling losses will probably increase. Long-range shooting, fear of fines (abandonment of does and yearling bucks), more illegal hunting because more restrictions make it more possible to hunt illegally, and a probable increase in poaching can be expected. Wildlife diseases will probably increase, as Dr. Hayes mentioned, with the increase in stocking on public lands and with resultant poor nutrition. The sad thing is that there are probably very few wildlifers and probably no hunters that know anything about wildlife diseases. We generally note in our reports that disease did not seem to be a problem, perhaps because we don't recognize it. An old Ozark hillbilly said, "We're generally down on what we ain't up on." Predation will probably increase as the habitat shrinks, or degenerates, and it may decrease if the public demands more predator control. That's a toss-up. Starvation can be controlled by reducing deer numbers if other forms of range competition do not exist, or it may be brought about by changes in the weather, which we can't do anything about. We can improve the ranges at great cost, and discover that it helps cattle at the expense of deer. The public may end up insisting on an artificial feeding program like that at Jackson Hole where the state plus the federal government put out $700,000 annually for supplemental feed for elk. Just consider what $700,000 could be used for in other projects. If you don't have a winter range, you go to the substitute.

Deer losses to accidents are very likely going to increase with more roads, more fences, more reservoirs, and more ditches. I don't see how we can predict the future of deer habitat except that we'll continue to lose more of it. What habitat we do have can be manipulated with the use of fire, and the control of fire. But I think the qualitative losses, such as from overuse, are bound to increase. The quantitative aspects of habitat loss pose an endless, one-way attrition. Twenty thousand acres a year are converted from one kind of agricultural use to another, and a million acres a year is lost under the freeways. It takes 60 acres to build an interchange. The new national plant will probably be a cloverleaf. We'll be lucky to level off the mule deer losses and then fight to hold our own in the face of these endless problems.

In closing, I'd like to quote from Santayana, who said, "All problems are divided into two classes. Soluble questions, which are trivial; and important questions, which are insoluble." Thank you.