Declining Mule Deer Populations in Colorado: Reasons and Responses

A Report to the Colorado Legislature
November 1, 1999

Declining Mule Deer Populations in Colorado: Reasons and Responses

Prepared by

R. Bruce Gill

Contributors
(in alphabetical order)

T. D. I. Beck
C. J. Bishop
D. J. Freddy
N. T. Hobbs
R. H. Kahn
M. W. Miller
T. M. Pojar
G. C. White

A Report to the Colorado Legislature

Colorado Division of Wildlife

November 1999

Table of Contents

List of Figures and Tables

Executive Summary

- Widely fluctuating numbers of deer apparently characterize mule deer populations. Numbers have varied considerably in historic times, primarily in response to climatic fluctuations, habitat change, and market hunting. Apparently mule deer were common but not abundant prior to European American settlement of the West. They were abundant in the late 1800s and scarce during the first 3 decades of the 20th century. Somewhere between 1935 and 1955 there were more mule deer in the West than at any time since. Subsequently, mule deer numbers have fluctuated primarily in response to climatic conditions and effects of hunting. However, in general, deer numbers have been declining at least since the late 1950s and 1960s. Today, mule deer populations in Colorado may number less than ½ of peak populations in the 1940s.

- Some evidence suggests that deer may have been too numerous when populations peaked. Heavy browsing pressure, combined with conversion of deer habitats to other land uses, may have lowered the carrying capacity of current mule deer habitats to the extent that they now are not capable of supporting historic deer numbers.

- Both the quality and quantity of Colorado mule deer habitats have changed over time. Rapid expansion of housing and other cultural developments in formerly rural areas have perforated and reduced the extent of critical deer habitats. Aggressive suppression of wildfires has resulted in maturation of key food plants in some mule deer habitats, reducing food availability and quality. Exotic plant species have replaced native species throughout many mule deer habitats. Often the exotic species are less palatable to deer and less nourishing. Grazing by both livestock and deer and elk have favored less palatable and less nutritious species. Although wildlife managers are aware of these habitat changes, currently there is no information which quantifies the extent of mule deer habitat change. Neither are there reliable analyses which evaluate the effects of these changes on trends in mule deer numbers.

- Elk populations in Colorado have increased dramatically over approximately the same time span that mule deer numbers have declined. Elk can and do consume many of the same food species that mule deer eat, but can exist on foods that can not support deer. In theory, elk could gain a competitive advantage over mule deer on rangelands commonly used by both species. Analyses of available data, however, fail to show consistent relationships where increasing elk numbers have been associated with declining deer herds.

- Although a variety of disease organisms are known to infect mule deer, rarely are disease outbreaks sufficiently virulent or widespread to account for statewide or region-wide declines in mule deer abundance. Chronic wasting disease has the potential to cause widespread declines in mule deer numbers. At the present time, however, chronic wasting disease appears to be limited to northeastern Colorado and can not, by itself, account for statewide declines in mule deer.

- Predation, particularly by coyotes, has been proposed as a primary factor in the decline of mule deer throughout the West. The only certainty is that predators kill and eat mule deer. However, studies that investigated responses of entire mule deer herds to intensive coyote control have failed to demonstrate that mule deer numbers increased as a result of coyote control. The contribution of predation to the mule deer decline remains uncertain.

- Excessive deer harvests have been proposed as another primary cause of declining mule deer herds. If deer populations were being hunted so intensively that populations were kept well below carrying capacity of deer habitats, reproductive rates of does should be high and mortality rates of fawns should be low. Studies show exactly the opposite patterns. On the other hand, hunting has been a major factor contributing to reductions in numbers of bucks throughout Colorado deer herds over the past 3 decades. Some believe that current buck numbers are so low that many does are not being bred each year and poor breeding success causes fawn production to decline. Yet, available evidence fails to substantiate that declining deer populations can be attributed to low buck numbers. Reproductive rates measured in a recent study of does on the Uncompahgre Plateau of southwestern Colorado are as high as reproductive rates from earlier studies despite much lower numbers of bucks today.

- Factors causing the current decline in mule deer numbers in Colorado and elsewhere are richly speculated but not well understood. Available evidence suggests that important deer habitats have deteriorated through time and that the current capacity of those habitats to support deer is now lower. Habitat effects are amplified perhaps by increasing elk numbers, disease, predation, and hunting, but very few experiments have been conducted to test for effects at scales of entire deer herds. As a result, the answer to the question, "*What caused mule deer numbers to decline?*" remains both speculative and controversial.

- Over the last 2 years the Colorado Division of Wildlife implemented intensive population monitoring studies in the Uncompahgre, Middle Park, and Red Feather areas; increased numbers of deer counts in western Colorado; and notified hunters that 1999 buck deer licenses would be restricted and issued by drawing only. For fiscal year 1999-2000, we reallocated $1 million internally and received an additional $225,000 from the General Assembly for expanded research, inventory, and habitat improvement work; all buck deer licenses for 1999 were limited and issued by drawing.

- Several complex factors acting in combination probably contribute to declining mule deer numbers. Various management actions and research studies have been initiated or are being planned to evaluate relative contributions of these factors and to develop effective management remedies:

    ✓ Deer inventory procedures are being upgraded wherein deer population data are being collected frequently and intensively from a few areas that represent extensive mule deer habitat complexes;

- ✓ Enhanced analyses of mule deer population and hunting data will be routinely analyzed with rigorous statistical tests to evaluate benefits from changes in hunting seasons and regulations;

- ✓ Research experiments are proposed to evaluate the effects of high doe numbers and high buck numbers on fawn production as reflected in winter ratios of fawns per 100 does;

- ✓ Management studies are underway to evaluate the effects of hunting seasons on buck mortality due to poaching and inadvertent wounding loss of bucks;

- ✓ Research studies will assess the contribution of long-term habitat changes to the mule deer decline;

- ✓ Ongoing research studies evaluate the contribution of diseases, particularly chronic wasting disease, to declining mule deer numbers;

- ✓ Research experiments are proposed to assess the effects of high elk numbers on mule deer habitat use and fawn production;

- ✓ Research experiments are proposed that will evaluate the contributions of predation vs. habitat quantity and quality to high fawn mortality rates.

Introduction

Across the West, mule deer researchers and managers, hunters, guides and outfitters, rural community residents, and land managers have expressed concern that mule deer numbers have been declining. Much of that concern is based upon experience and belief rather than science because there are no reliable estimates of total mule deer numbers across the West nor for any of the individual western states. Nonetheless, these concerns have prompted wildlife management agencies and political representatives to intensify efforts to identify causes of declining mule deer numbers and develop action plans to reverse downward trends. This report summarizes responses of the Colorado Division of Wildlife to those concerns.

How Much Have Deer Numbers Changed?

Mule Deer Numbers: 1700-1900

It is difficult to assess long term trends in deer numbers because prior to 1970 few attempts were made to count entire deer herds. Prior to the turn of the century, information concerning deer abundance came from diaries, letters, and reports of mountain men, settlers, and explorers. These records are irregular in both time and space and are usually descriptive rather than quantitative. For the most part it is difficult to infer mule deer abundance from these historical records, but it is possible to infer distribution. Collectively, the records indicate mule deer distribution from 1750 to 1850 was not much different than today except where historic habitats have been dramatically altered by roads, reservoirs, cities, agriculture, etc.

The diary of one market hunter, Frank Mayer, is the exception to the rule that historic records lack quantification of deer abundance. Mayer hunted the Middle Park Basin near Kremmling, Colorado between August and November, 1878. He recorded his exploits and included numbers and weights of animals he shot and transported to markets in Leadville, Colorado. At the conclusion of his 1878 hunting expedition, Mayer had killed and shipped nearly 250 big game animals, including 89 mule deer during a span of 78 days (Fig. 1). Mayer could have killed many more, but he spent much of his time dressing and preparing his kills for shipment to Leadville meat markets. He quit hunting before the onset of winter migration because he simply tired of killing. Mayer's diary clearly indicates that big game species, including mule deer, abounded in Middle Park in the late 1870s. The diary entry for October 1, 1878 includes the following comment: "*As the migration is now well begun, I encounter elk and deer at all hours of the day. They are crossing the river junction* (the confluence of the Blue River and the Colorado River just south of Kremmling, Colorado) *in such numbers that shooting them requires no skill*."

Mule Deer Numbers: 1900-1935

Actual mule deer numbers are unnecessary to assess population trends from 1900 through 1940. Market hunting, unrestricted sport hunting, and subsistence hunting drove many big game populations to local extinction. For example, here in Colorado the last bison were killed in 1897

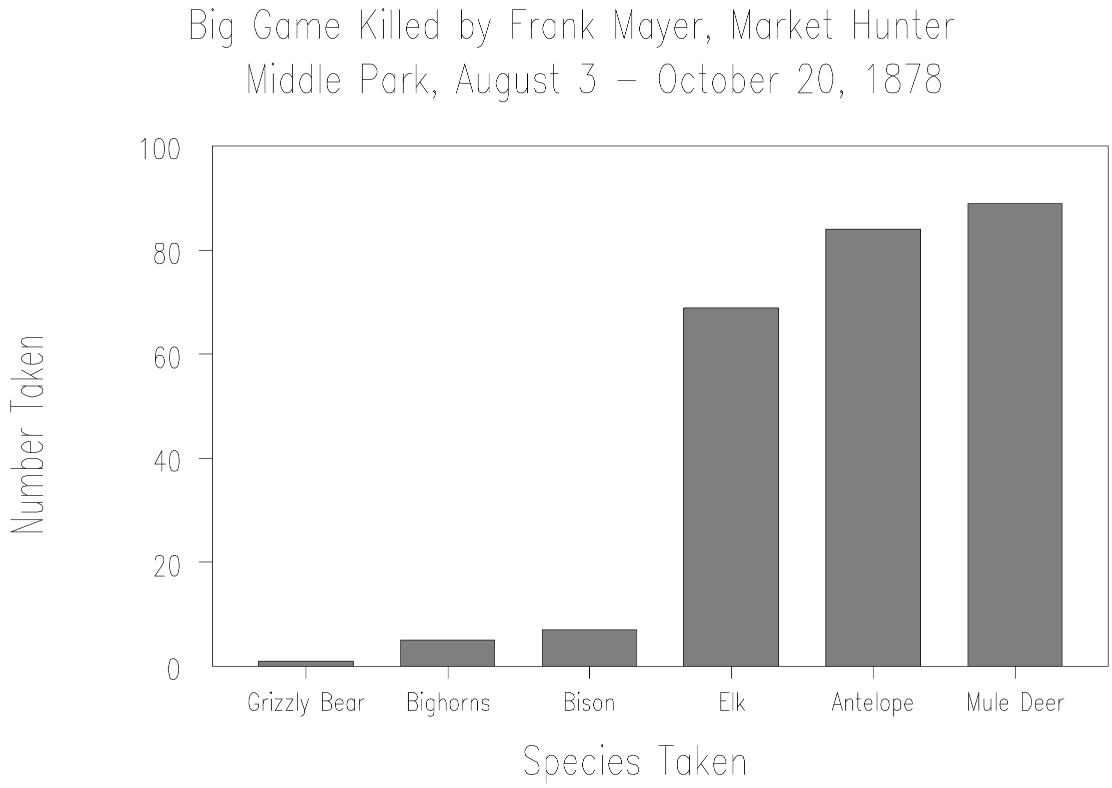

Figure 1. From August 3 to October 20, 1878, market hunter Frank Mayer killed and shipped 80 mule deer from Middle Park, Colorado to Leadville meat markets.

and elk were nearly extinct by 1900. Mule deer numbers were so depleted that by 1912, state wildlife commissioner James A. Shinn reported to the state legislature: "*The time was in Colorado when deer were so plentiful that it seemed almost impossible for them to be killed off; but with the increase* (human) *population, and the more general settling-up of our state, the deer have been killed until now they must be carefully protected, or they will meet the fate of the buffalo and become entirely extinct.*"

Mule deer populations did not begin to recover until the mid-1930s following the dust bowl era. Although there are no numbers to verify this recovery, it is clear that deer numbers rebounded dramatically particularly from 1930 through 1935.

Mule Deer Numbers: 1935-1970

By the late 1930s and early 1940s attitudes of wildlife managers shifted from anxiety over too few deer to alarm over too many. Mule deer were so numerous, they conflicted with agriculture and damaged crops. Apparently they also were damaging important winter ranges because visual evidence of intensive browsing was widespread. Deer numbers probably reached all time highs, at least in recorded history, between the 1940s and 1950s. For example, deer numbers on the intensively studied Oak Creek herd unit in Utah peaked in 1946, followed by a slow decrease until 1950 when they began to increase again (Fig. 2). Much of the fluctuation in deer numbers was caused by unusually harsh winter conditions in the late 1940s and early 1950s. Unfortunately, there is no way other than conjecture to compare total deer numbers in Colorado during the peak years of the 1940s and today. But wildlife professionals of the time who are still alive today speculate that deer were 2-3 times more numerous in the mid-1940s as they are today.

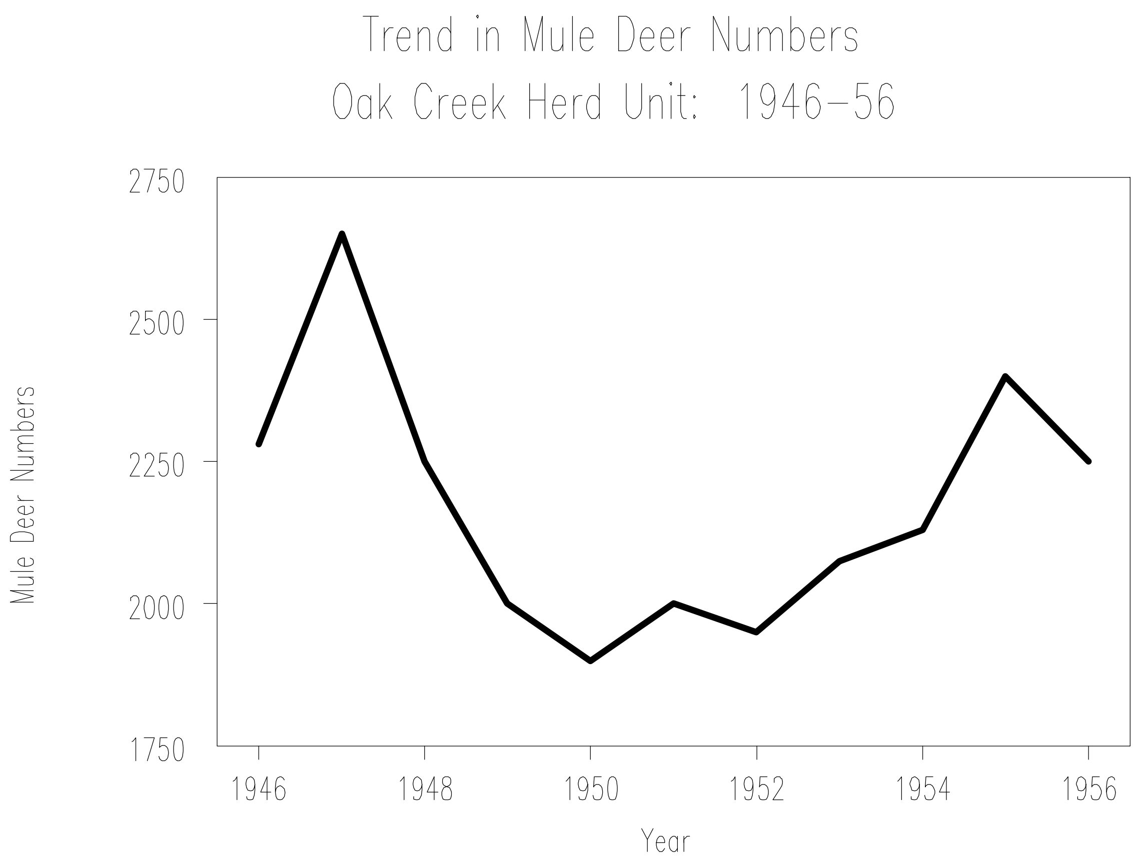

Figure 2. Deer numbers on the intensively studied Oak Creek area in Utah apparently reached their highest levels in the late 1940s.

In 1940, surveys of both mule deer numbers and deer habitat were conducted in the Gunnison Basin of southwestern Colorado. Deer numbers were estimated by attempting to count every deer on each of several winter concentration areas. Habitat carrying capacity was assessed by estimating total production of important forage plants, the concentration of digestible nutrients in forage, and dividing nutrient density by deer forage requirements. The mule deer population was estimated at approximately 22,000 deer while carrying capacity was estimated at approximately 12,000 deer. Wildlife managers recommended reducing deer numbers by about

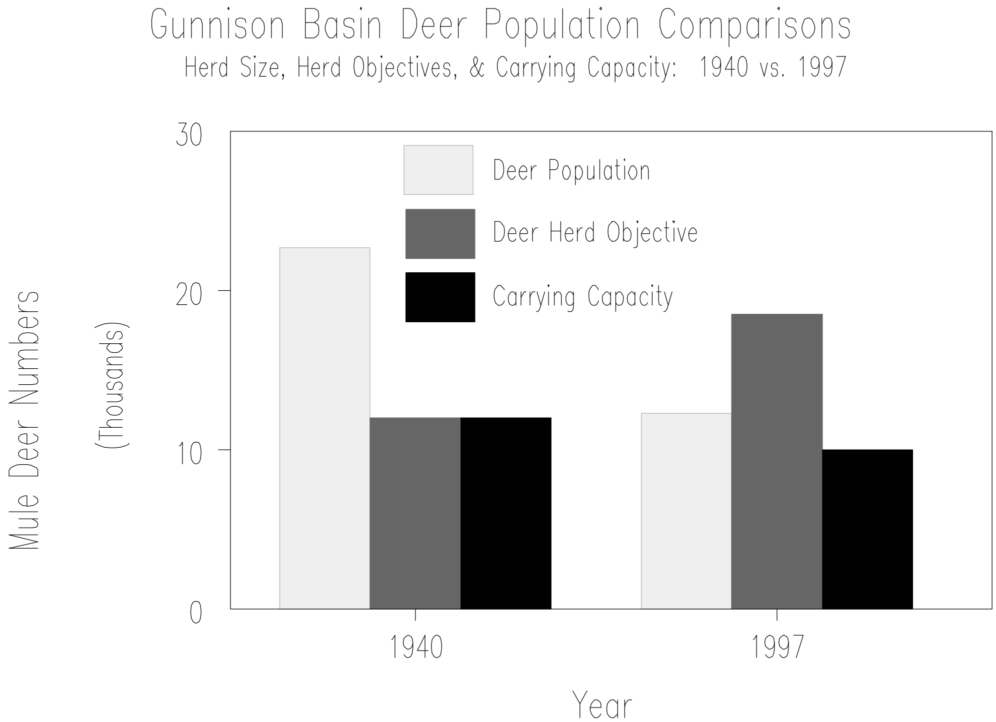

Figure 3. Deer numbers in the Gunnison Basin apparently reached peak levels in the mid-1940s when numbers were estimated at approximately 20,000 deer. This was nearly double the capacity of their habitats. Today deer number about 10,000, carrying capacity has declined from the 1940s, yet the herd objectives approach 1940 population levels.

10,000 deer to prevent habitat destruction (Fig. 3). Nearly ½ century later similar estimates were repeated for Gunnison deer permitting then vs. now comparisons. These comparisons prompt at least 4 observations. First, as early as 1940 biologists were concerned that mule deer exceeded carrying capacity of their winter ranges. Second, current deer numbers in 1997 approximate range carrying capacity estimates of 1940. Third, carrying capacity seems to have decreased since 1940. Fourth, current population objectives may not be sustainable given current habitat constraints. These observations suggest that, in the Gunnison Basin at least, attempting to recover mule deer populations to population levels of the 1940s will be extremely difficult and costly (in both economic and social capital) and is probably unwise. They also suggest that current population objectives are probably unrealistic without considerable improvements in habitat quality that may be ecologically unattainable.

Mule Deer Numbers: 1970-Present

It was not until 1967 that the Colorado Division of Wildlife developed aerial count techniques to estimate mule deer numbers across entire deer herds. The first of these population estimates was developed and tested near Kremmling in the Middle Park Basin of northcentral Colorado in 1967. Total deer numbers were projected from averages of deer counted on random square miles. These so-called "quadrat counts" have been expanded so that today estimates of several of Colorado's important mule deer herds are derived from quadrat counts. Deer numbers estimated from quadrat counts vary considerably from year to year. Part of this variation results from random error normally associated with sample-based counts. Weather conditions also contribute to the variation by altering both the distribution and concentration of deer from year to year. Additional annual variation in deer counts results from hunter harvests and fluctuations in birth and death rates of deer populations. As a result, valid inferences of deer population trends can be made only after data are available for several years. Population trends from 3 deer herd units exhibit contrasting trends. Deer numbers in the Middle Park Basin (Fig. 4a) and on the Uncompahgre Plateau west of Delta (Fig. 4b) are stable or perhaps increasing slowly, but fawn recruitment has declined. Conversely, deer numbers have declined in the Red Feather unit northwest of Fort Collins, but fawn recruitment seems to be rising (Fig. 4c).

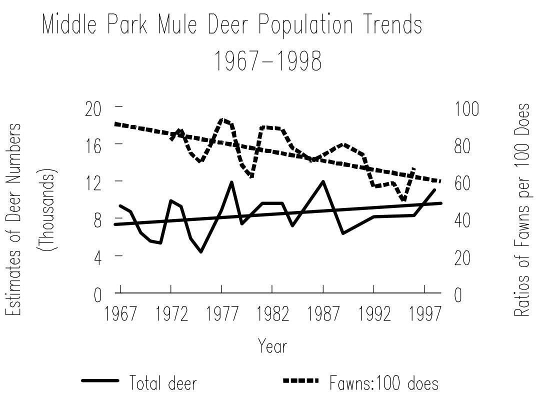

Fig. 4a.

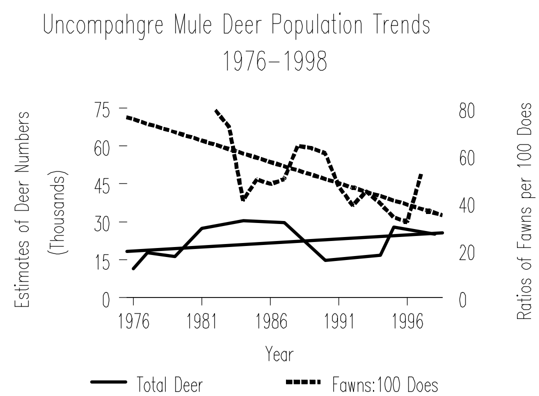

Fig. 4b.

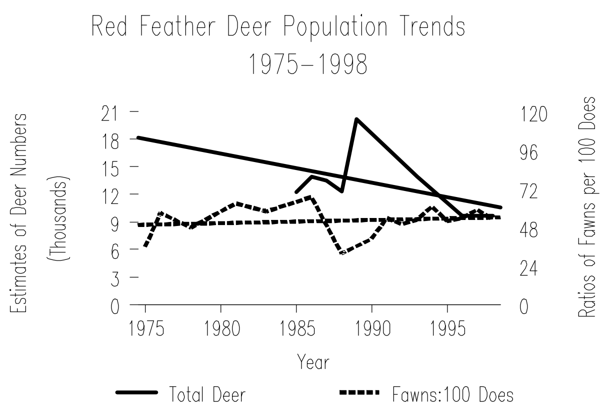

Fig. 4c.

Figure 4. Long-term trends in deer numbers vary from herd unit to herd unit in Colorado. Deer numbers in Middle Park (Fig. 4a) and on the Uncompahgre Plateau (Fig. 4b) appear to be stable or perhaps increasing despite declining fawn recruitment. Deer numbers in the Red Feather herd unit (Fig. 4c) appear to be declining, but fawn recruitment seems to be slightly increasing. Nonetheless, recruitment is still below levels required to maintain overall deer numbers.

Each year, ratios of fawns per 100 does are derived from deer counts of several deer herds in Colorado. The ratio of fawns per 100 does is an index to annual fawn production and survival. Population models indicate that when fawn:doe ratios drop below 50-60 fawns per 100 does, mule deer populations can not sustain themselves and decline. The analysis indicates that Colorado mule deer herds crossed the threshold of sustainability in the early 1990s (Fig. 5). Recent data suggest that ratios of fawns per 100 does in some herds, at least, may once again be increasing and allowing herds to rebound.

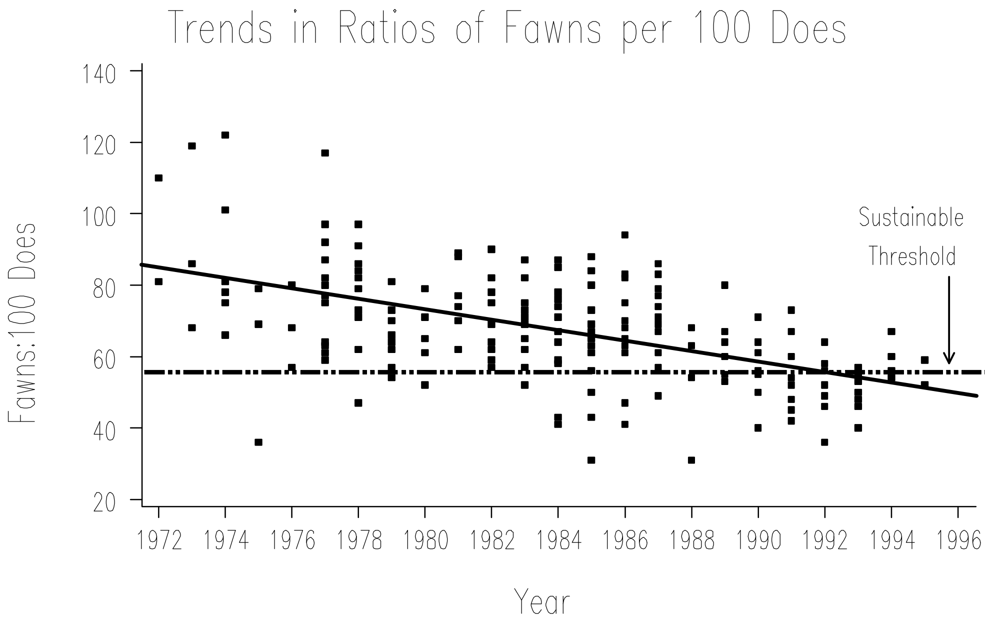

Figure 5. Ratios of fawns per 100 does are an index to annual fawn production and survival. Ratios of fawns:100 does in Colorado's deer herds have been declining since at least 1972. When ratios decline below 50-60 fawns per 100 does, deer herds can not sustain themselves.

Summary

- Widely fluctuating numbers of deer apparently characterize mule deer populations. Numbers have varied considerably in historic times, primarily in response to climatic fluctuations, habitat change, and market hunting. Apparently mule deer were common but not abundant prior to European American settlement of the West. They were abundant in the late 1800s and scarce during the first 3 decades of the 20^{th} century. Somewhere between 1935 and 1955 there were more mule deer in the West than at any time since. Subsequently, mule deer numbers have fluctuated primarily in response to climatic conditions and effects of hunting. However, in general, deer numbers have been declining at least since the late 1950s and 1960s. Today, mule deer populations in Colorado may number less than ½ of peak populations in the 1940s.

- Some evidence suggests that deer may have been too numerous when populations peaked. Heavy browsing pressure, combined with conversion of deer habitats to other land uses, may have lowered the carrying capacity of current mule deer habitats to the extent that they now are not capable of supporting historic deer numbers.

What Caused Deer Numbers to Decline?

In 1976, following an earlier western-wide decline in mule deer numbers, a symposium was held in Logan, Utah to discuss both the extent and causes of the decline. Mule deer researchers and biologists implicated at least 5 major factors believed to be responsible for the decline: 1) decreases in amounts and quality of critical deer habitats, 2) competition with elk and other grazing livestock, 3) diseases, 4) predators, and 5) hunting. Again, in 1999 the same factors have been suggested as causes of the current mule deer decline. A discussion of the evidence supporting each of these potential factors follows.

Habitat Deterioration and Loss

The performance of Colorado mule deer populations is inextricably linked to the amount and quality of habitat required to meet their needs to reproduce successfully and to survive. It is clear that habitats used by deer are changing. These changes, in turn, may explain the widely observed decline in the abundance, distribution, and performance of deer populations. If habitat change is responsible for poor population performance, then the decline of deer may be symptomatic of a broad suite of environmental problems in Colorado's ecosystems; problems that affect manifold species of plants and animals. It follows that management directed at manipulating deer habitats may offer benefits to many ecosystem components, particularly those associated with early- to mid-seral stages of shrub-steppe rangelands.

The idea that deer are indicative of broader problems stems from understanding sources of stress on deer habitat, stressors that likely affect other species in addition to deer. There are four principle agents of change operating on deer habitats in Colorado. These include the following:

Perforation of traditional ranges by residential development: Human population growth in Colorado is causing rapid expansion of housing into traditional deer range. In particular, development at exurban densities (approximately 1 house per 10-40 acres) exerts broad impact on Colorado rangelands used by deer. Much of this development has occurred at mid-elevation in mountain valleys, along ecotones that have traditionally provided critically important deer habitat. Projections of demographic and land-use models predict these impacts are likely to continue.

Degradation of seral shrub communities as a result of fire suppression: Many shrub communities evolved with episodic disturbance, particularly disturbance from fire. Burning reverts mature plants to rapidly growing stages, releases nutrients immobilized in mature woody tissue, and in so doing, enhances accessibility, palatability, and nutritional value of food for deer. Plant communities that emerge following fire provide important nutritional alternatives for grazing and browsing ungulates. The absence of burning leads steadily to widespread canopy closure, which can degrade forage production in the understory.

***Invasion of exotic plants*:** Invasion of non-native plants has emerged as a pervasive and potent stressor on ecosystems throughout the western United States. Although some exotic plants offer nutritional benefits to deer, deer will generally avoid areas of the landscape that are infested with noxious weeds. Moreover, the effects of exotic invasion can be accelerated by canopy closure. For example, in pinyon-juniper communities, non-native plants can occupy the entire understory in closed canopy stands. It follows that invasion of exotic plants can compress the area of habitat available to mule deer.

Feedback to plant communities from excessive densities of native ungulates and livestock: It is clear that browsing and grazing by large herbivores can dramatically alter the structure and function of plant communities (Fig. 6). Excessive levels of herbivory can reduce forage supplies and cause reductions in daily forage intake. Feeding by herbivores can shift the composition of plant communities, often in favor of unpalatable plants. Repeated browsing on shrubs diminishes accessibility of leaves and stems and can promote production of plant toxins and digestion inhibitors.

Figure 6. Grazing exclosure at the mouth of Beaver Creek near Hot Sulphur Springs, Colorado. Browsing by mule deer has dramatically reduced the amount and vigor of palatable shrubs outside the exclosure compared to inside. In this example, 40 years of browsing has altered the quality and quantity of deer habitat.

These four stressors may interact to harm the reproduction and survival of deer. For example, reduction in the area of deer habitat exacerbates the effects of overabundant populations. This is because deer population density increases as growing populations become concentrated on smaller areas of landscape. Such concentrations are likely to amplify density-dependent feedbacks to survival, particularly survival of fawns.

Effects of habitat change on deer may also operate independently of their density. Reductions in nutritional quality of plant species and shifts in the nutrient distributions of plant communities can degrade reproductive performance despite constant or declining population density. During most of the annual nutritional cycle of deer, it is not physiologically possible for foraging animals to compensate for reduced concentrations of plant nutrients by increasing food intake. Moreover, it is clear that the biomass of forage available per deer does not necessarily promote higher forage intake rates. These observations mean that large amounts of forage (or low population density) may not substitute for nutritious forage in deer habitats. It follows that deer habitat can be substantially degraded even when forage supplies appear to be plentiful with no obvious signs of "overbrowsing."

Competition with Elk

While deer populations across the West have declined, elk populations have boomed. The coincidence of booming elk populations and dwindling mule deer populations raises the question, have elk increases caused mule deer populations to decline? Several pieces of circumstantial evidence suggest that elk could be responsible for deer declines. First, elk have increased substantially throughout the West at nearly the same time mule deer were declining. Not only have elk numbers increased, but they have expanded their distribution as well. Here in Colorado, elk are now found in areas and habitats where formerly elk were absent and deer were abundant.

Second, elk are much larger than deer, and size confers several competitive advantages. The larger elk can traverse deep snows more efficiently than mule deer, considerably reducing energetic costs. Elk are able to exploit a larger variety of foods than deer. Because their digestive organs are absolutely and proportionately larger than those of a deer, elk can eat lower quality foods and still derive enough nutrients to reproduce successfully and survive winter rigors without suffering high rates of mortality. Faced with the same circumstances, mule deer reproductive rates decline and mortality rates of young animals often exceed 50%. Because elk are taller than deer, they also expand the 3-dimensional space within which they can exploit foods.

Third, elk are less vulnerable to predation than mule deer. Although individuals of both species isolate themselves to give birth to young, elk soon rejoin groups of other cows and calves and group membership affords them greater protection from predation. Mule deer does, in contrast, tend to remain apart from other does and fawns until much later, increasing vulnerability of young to predatory attacks. In addition, cow elk tend to be more aggressive in defending their young than mule deer.

Fourth, observational evidence suggest that elk can displace mule deer from choice feeding areas. During the winter of 1983-84, the Colorado Division of Wildlife fed populations of deer and elk to prevent large-scale winter starvation. At feed grounds where both deer and elk were present, elk aggressively drove mule deer from the grounds until elk had finished feeding.

Fifth, mule deer can not subsist on dry, senescent grasses in winter. They require easily digested plants and plant parts such as the leaves of evergreen shrubs (sagebrush, for example), and the terminal twigs of deciduous shrubs where plant nutrients concentrate. When large numbers of mule deer and elk occupy the same habitats, both species consume browse plant tissues. Most browse plants can not tolerate removal of more than 50% of their annual twig growth year in and year out. If browsing removes more than 50% of the annual twig growth for several years in succession, browse species begin to die, encouraging species that are less palatable and nutritious to expand and invade. These developments favor growth in elk numbers at the expense of deer.

Rocky Mountain National Park offers an illustrative example. Prior to 1913, elk were exterminated from Rocky Mountain National Park. They were reintroduced by transplanting elk from Yellowstone National Park beginning in 1913. Elk populations were well-established by 1939, but nowhere near as numerous as they are now. Park naturalists Merlin Potts and Howard Gregg, for example, censused deer and elk in the winter of 1939. They tallied 648 deer and 263 elk. A similar count in the winter of 1997 yielded over 1,000 elk and no more than 150 mule deer (Fig. 7).

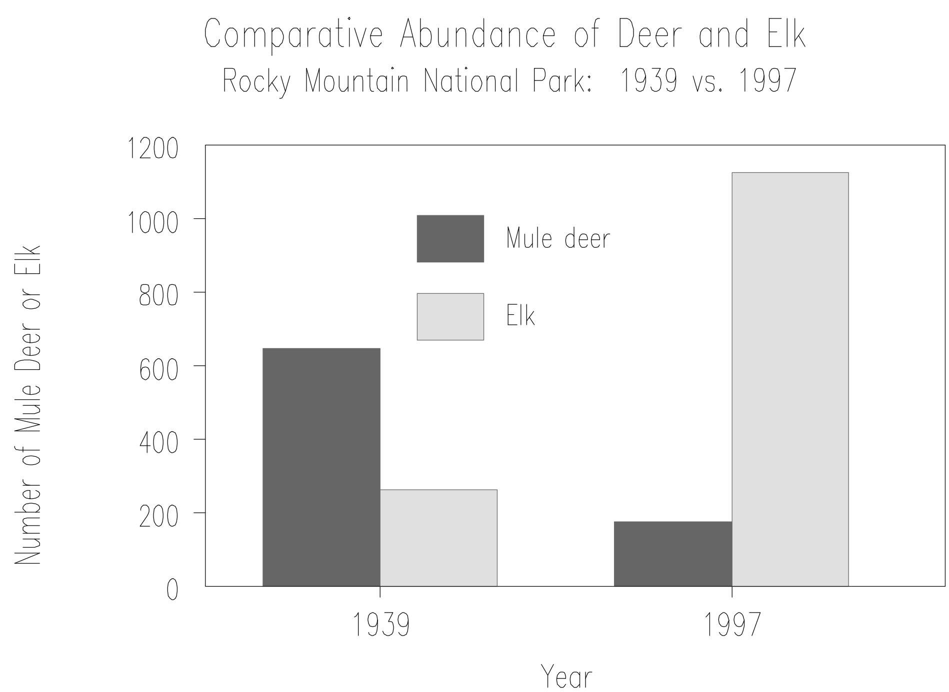

Figure 7. Trends in mule deer and elk numbers in Rocky Mountain National Park, Colorado suggests that as elk numbers have increased, they have increased at the expense of mule deer. This has led some experts to conclude that mule deer numbers have declined because they were unable to successfully compete with elk.

Rocky Mountain National Park is not the only example where mule deer numbers declined coincident with increasing elk numbers. Similar trends of mule deer and elk numbers were observed in the Blue Mountains of Oregon in the 1930s. By 1929, evidence was mounting that browse plants were being used excessively by a large deer population (about 20,000 deer) and a growing elk population (nearly 3,000 elk). Following severe winters in 1931 and 1932, deer numbers declined roughly by half, mostly from starvation. In contrast, elk losses during those same winters were normal. U.S. Forest Service biologist Edward Cliff wrote, "*There is evidence that the unfavorable range conditions and competition with elk are reducing the size of the deer on the problem area on the Whitman Forest. The elk are spreading out and increasing on adjacent forests in the Blue Mountains and the mule deer herds and ranges are threatened...*"

These and other anecdotes suggest that elk populations may expand at the expense of deer. Nonetheless, few western states have analyzed statewide data to assess apparent effects of elk numbers on mule deer populations. Here in Colorado, when winter ratios of fawns:100 does (an index of fawn recruitment) are correlated with bull elk harvests (an index of elk abundance) results are mixed. If the increase in elk populations statewide caused low fawn recruitment, one would expect to see a close association between high bull elk harvests and low fawn:doe ratios. Instead, high elk harvests were just as likely to be associated with high fawn:doe ratios as they were with low fawn:doe ratios (Fig. 8). However, bull harvest data and fawn:doe ratios are only crude approximations to elk abundance and fawn recruitment.

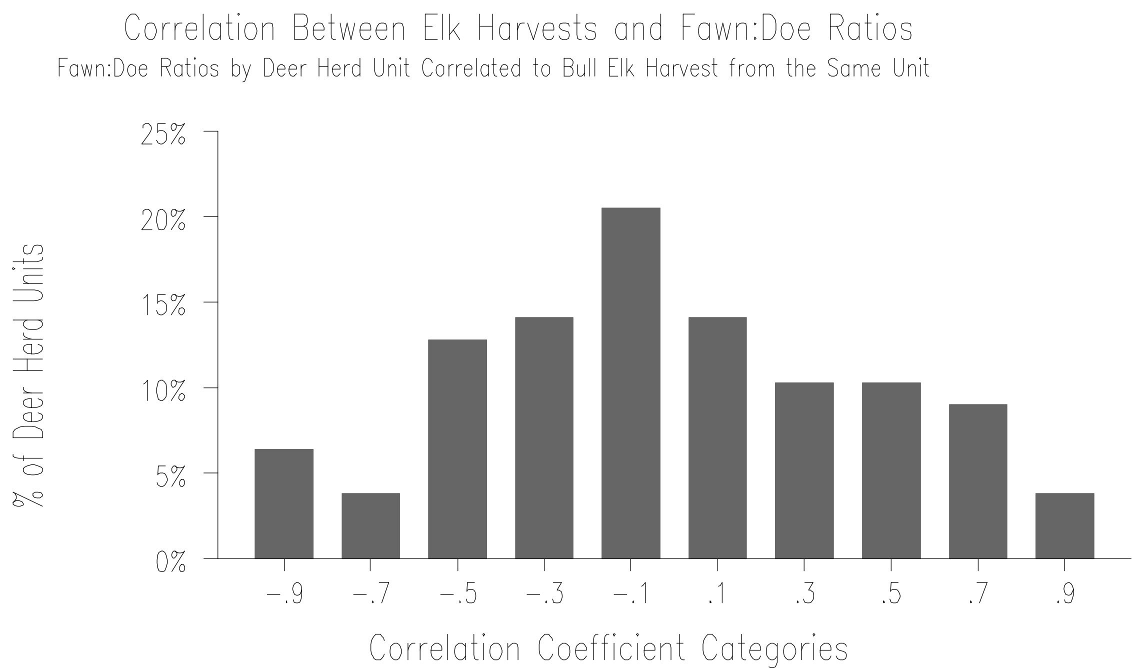

Figure 8. The ratio of fawns per 100 does (an index to fawn recruitment) from several deer herd units was correlated with bull elk harvest (an index to elk abundance) from the same units to assess whether low fawn:doe ratios were consistently associated with high bull elk harvests. High elk harvests were just as likely to be associated with high fawn:doe ratios (positive correlation coefficients) as they were with low fawn:doe ratios (negative correlation coefficients).

Disease

Mule deer are susceptible to a variety of infectious, noninfectious, and parasitic diseases that can affect survival and/or reproduction (Table 1). Most of these diseases affect individual deer, and have not been detected at rates sufficient to affect deer population performance on regional, state, or range-wide levels. Death from diseases may mask ultimate causes of mortality. For instance, malnutrition can increase susceptibility of deer to both diseases and predation.

Deer Diseases in General

Several diseases (e.g., plant intoxications, intestinal parasitism, miscellaneous viral and bacterial infections) could be symptomatic of more fundamental problems with deer habitats or populations: such underlying problems could include large-scale habitat loss or degradation, livestock encroachment on native ranges, and/or overabundance of deer relative to range capacity. In addition to habitat and population factors, annual and seasonal variations in temperature and precipitation patterns could influence the occurrence, frequency, and/or severity of disease problems in deer. Based on ongoing survival studies, diseases appear responsible for a relatively small proportion of the annual deaths in adult mule deer (although actual cause of death often cannot be determined reliably under current monitoring regimes). Whether disease-related mortality simply replaces other forms of mortality or is additive to these other causes remains undetermined; consequently, the overall influence of disease on mule deer population performance is uncertain.

A few of the diseases documented in adult mule deer do appear capable of density-independent depression of population performance. Epidemics of "hemorrhagic disease" are caused by multiple strains of either bluetongue virus (BTV) or epizootic hemorrhagic disease virus (EHDV). Both viruses are transmitted by biting midges. Cattle appear to be reservoirs for BTV while both cattle and white-tailed deer can serve as reservoirs for EHDV (Fig. 9). Bluetongue viruses were introduced into North America via imported cattle, and it is likely that imported cattle also brought EHDV to Colorado from the southeastern US. Epidemics occur sporadically in Colorado, affect all age classes of deer, and typically arise in late summer and early fall after midge populations build to levels sufficient to transmit infections among large numbers of animals. Spring precipitation, summer and fall temperatures, and the availability of reservoir hosts all contribute to the likelihood of an epidemic. Mortality attributable to hemorrhagic disease can reach catastrophic levels on western ranges where losses of $\geq$50% of affected populations over a period of several weeks have been estimated. Such losses appear to be largely density-independent and probably should be considered additive to other sources of mortality. Smaller-scale epidemics could easily go unnoticed in many parts of Colorado, but have been suspected in several West Slope deer populations.

Chronic Wasting Disease

Chronic wasting disease (CWD), a transmissible spongiform encephalopathy (i.e., prion disease) of mule deer, white-tailed deer, and elk, is endemic throughout northeastern Colorado and southeastern Wyoming. Mule deer appear to be most commonly affected, although white-tailed deer are probably quite susceptible. In Colorado, CWD prevalence is highest in game

Table 1. Infectious and noninfectious diseases that could affect survival or reproduction in Colorado mule deer.

Assessment of select diseases as a potential factor in deer declines

Agent	Processes affected[a]	Age classes susceptible[b]	Geographic magnitude[c]	Documented in Colorado?[d]	Comments
Noninfectious					
Trace minerals	R, S	all	L-R	S	Cu and Se most notable potential problems in CO.
Plant toxins	R?, S	all	L-R?	N	Probably rare; locoism touted as potential problem in northcentral CO, but never documented in deer.
Agricultural toxins	R?, S	all?	L-R?	S	Individual cases suspected; subclinical effects could be difficult to detect.
Infectious					
“Parasites”	S	F, OA	L	I	Individual cases, primarily in fawns; large-scale problems unlikely.
Enteric bacteria & viruses	S	F>>A	L-R?	I	Fawns susceptible; potential impacts on neonatal survival; local impacts more likely than regional impacts.
Respiratory bacteria & viruses	S	F>A	L-R	I (E)	Rarely reported in CO; epidemic pasteurellosis reported historically in UT and CA.
Hemorrhagic disease (BTV, EHDV)	S	all	L-R	E	Large-scale epidemics (~50% mortality) documented; probably underreported; cattle are reservoir for BTV.
Adenovirus	S	all	L-R	N (E)	Only documented in BTD in CA; relatively new agent; high morbidity & mortality.
CWD	S	all	L-R	E	Could be impacting deer populations in endemic areas; spreading slowly.

[a] R = reproduction; S = survival.
[b] F = fawn; A = adult; OA = older age-class adult.
[c] L = local; R = regional.
[d] I = individual cases documented in CO; E = epidemics documented in CO; S = suspected but not in CO, diagnosed elsewhere; N = not documented to occur.

Figure 9. Disease outbreaks, such as epizootic hemorrahgic disease virus (EHDV) have caused high deer losses in local areas of Colorado. Diseases, such as EHDV, may not be directly responsible for large-scale deer losses, but may predispose deer to death from other causes such as starvation and predation.

management units (GMUs) in northeastern Larimer County (Fig. 10), but CWD-infected deer have also been documented throughout the South Platte River bottom corridor from Gilcrest to Julesburg. Prevalence is currently high enough in some Larimer County GMUs to be depressing deer population performance, but inventory data available from these areas are insufficient to demonstrate such trends. Although ongoing surveys indicate Western Slope deer herds are free from CWD, there is potential for CWD to spread to deer populations in western Colorado via either natural deer and elk movements or accidental introduction by infected game farmed elk or deer. Such introductions could have severe long-term consequences and should be prevented if possible. Transmission routes and management strategies for CWD are under investigation. Fortunately, current research indicates CWD is not naturally transmissible to domestic livestock or to humans.

Although not documented to date in Colorado, other diseases have potential to cause significant all-age mortality in mule deer. Epidemic pasteurellosis reportedly caused significant deer die-offs in Utah and California during the 1940s and 1950s, but epidemics have not been seen in Colorado deer herds. A new deer adenovirus recently described in California also could cause widespread mortality if inadvertently introduced into Colorado. Precautions designed to prevent this adenovirus from being introduced into Colorado are clearly warranted. Similarly,

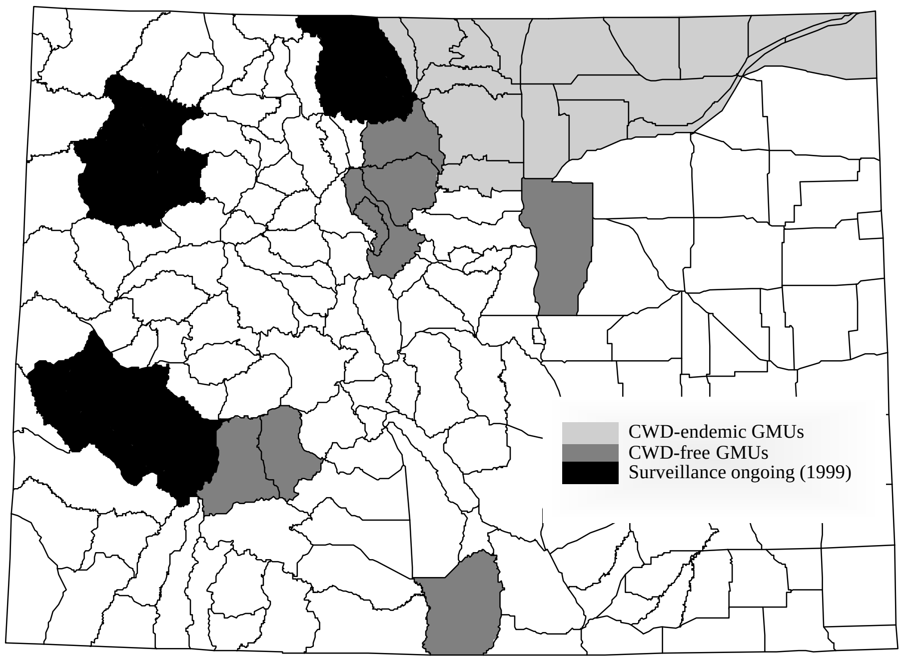

Figure 10. Chronic wasting disease (CWD) potentially can cause deer populations to decline. However, the distribution of CWD infections in deer do not indicate that CWD alone is responsible for the statewide decline in deer numbers.

intentional or inadvertent introduction of foreign animal diseases like rinderpest or foot-and-mouth disease could have catastrophic effects on Colorado's deer resources, as well as its livestock industries.

In contrast to diseases of adult deer, there are a variety of parasitic and infectious diseases that could be contributing to summer fawn mortality in deer herds throughout Colorado. Whether these diseases are truly acting as primary causes of death or are merely symptomatic of underlying malnutrition (in fawns or their dams), habitat degradation, or some other factor(s) remains undetermined. In a recent western Colorado study, malnutrition and/or some disease agent apparently caused at least half of the fawn mortalities examined. Because sick fawns are probably quite vulnerable to predators and scavengers, it is likely that illness also contributed to some proportion of fawn mortality proximately attributed to predation in the areas studied. The most likely sources of enteric viruses (bovine viral diarrhea virus, rotavirus, coronavirus), coliform bacteria, respiratory viruses and bacteria, and intestinal parasites that infect deer fawns are adult deer, cattle, and perhaps other domestic or wild hoofstock. Some of these pathogens probably could kill otherwise healthy deer fawns, but all likely would be exacerbated by malnutrition or some other environmental stressor. The fact that no single pathogen has emerged as a common thread among summer fawn mortalities studied to date suggests one or more underlying factors may be increasing fawns' vulnerability to whatever pathogens they encounter in early life. It follows that identification of the underlying factor(s) could be critical to improving overall recruitment in Colorado's mule deer populations.

Predation Effects

Relationships between deer populations and predator populations are complex yet poorly understood. Each time mule deer populations have declined in Colorado and other western states, predation has been implicated as a potential cause for the decline. Yet, given the current state of knowledge about mule deer populations and predation, the only certainty is that predators kill and eat mule deer (Fig. 11). The evidence concerning the effects of these predatory activities on the performance of mule deer populations is much less clear, partly because there are few well designed experiments to examine responses of mule deer populations to predator control.

Figure 11. Although several studies demonstrate that coyotes kill considerable numbers of mule deer and that predation can affect deer numbers locally, no studies have demonstrated that coyote predation has caused entire deer herds to decline or have prevented herds from increasing.

The relationship of a mule deer population to its food supply is a critical factor governing the impacts of predation. When mule deer numbers are at or near the food production capacity of their habitats, deer numbers are unlikely to increase when predators are removed. In contrast, when severe winters or other natural calamities temporarily drop mule deer numbers well below the food producing potential of their habitats, it is theoretically possible for predators to keep deer numbers depressed for long periods of time. Under these circumstances, reduction in predator numbers can result in a substantial increase in the size of the deer population. Evidence from past studies, nonetheless, fail to demonstrate that deer herds increase when predators are removed. At least part of the problem with earlier studies was that they often lacked control areas or were conducted on small study areas where applicability of results to entire deer herds was questionable.

***Predator Control Study in the Piceance Basin of Northwestern Colorado: 1981-1988*:**

Here in Colorado, we studied the mortality rates of mule deer fawns and adult does in the Piceance Basin area west of Meeker, Colorado beginning in 1981. We found fewer than 40% of fawns born each year survived the entire year while annual survival rates of does ($\geq$1 year of age) continually exceeded 85%. Fawns and does differed markedly in their abilities to survive each year, particularly during winter. The ability of fawns to survive from year to year had much greater impacts upon the growth rate of the deer population than the survival rates of does. Although both circumstantial and experimental evidence implicated food shortages as the major cause of low fawn survival, coyotes were responsible for the deaths of many fawns which perished during the winter months.

Subsequently, we studied the effects of coyote control on fawn survival during winter. Mortality rates of fawns were documented for 4 years before coyote control was started and compared to mortality rates for the following 3 years during which 218 coyotes were killed (1.3 coyotes/mi^2/yr). If coyote predation was a major factor limiting deer, fawn survival was expected to increase during the periods when coyotes were killed. If food shortage was a major factor, fawn mortality rates were not expected to change during periods when coyotes were controlled. It was anticipated that the mortality rates would not change but deaths from coyote predation would decline and be replaced with deaths from other causes. Prior to coyote control (1981-82 through 1984-85), an average of 83% of the fawns died during winter. Coyote predation on deer fawns varied from year to year, accounting for 49-77% of the total winter fawn mortality. Winter fawn mortality during years when coyotes were controlled averaged 76% and was not significantly different from mortality rates during years when coyotes were not controlled (Fig. 12). Decreases in fawn deaths due to coyote predation were largely offset by increases in starvation rates.

***Recent Studies of the Effects of Coyote Control on Mule Deer Populations*:**

<u>Montana</u> - Montana Fish, Wildlife, and Parks initiated studies in 1997 to assess the benefits of coyote control to pronghorn and mule deer populations in central Montana. Coyote control was conducted on one herd unit, and not on 2 adjacent units. Mule deer and pronghorn population

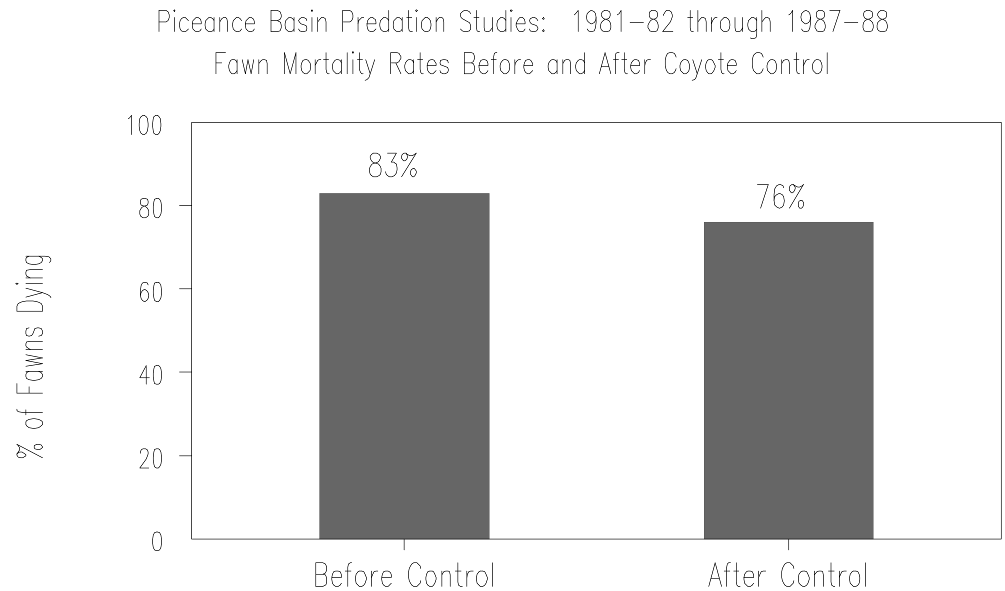

Figure 12. Fawn mortality was studied in the Piceance Basin of northwestern Colorado before and after coyote control. Mortality rates before coyote control were slightly higher than after coyotes were controlled, but the difference was not statistically significant.

responses from the unit where coyotes were controlled were compared to those where coyotes were not controlled. Coyotes were killed via aerial gunning from helicopters and fixed-wing aircraft and snaring. During the first 2 years of study (1997 and 1998), nearly 200 coyotes were killed, 68% from helicopter gunning, 21% from fixed-wing aircraft gunning, and 11% from snaring. Aerial gunning required slightly more than 1 hour of aircraft time per coyote killed at a cost of approximately $225 per hour. Although pronghorn populations increased on the unit subjected to coyote control, they also increased in one area where coyotes were not controlled and decreased in the other. Ratios of fawns per 100 mule deer does on areas where coyotes were controlled did not differ from areas where coyotes were not controlled and deer populations declined across all 3 areas. Researchers summarized the early results of the project by commenting, "*It would appear, that to this point, the killing of coyotes in HD 530 has had little positive affect (sic) on mule deer fawn:doe ratios or populations*."

Utah - Beginning in 1997, the Utah Division of Wildlife Resources began implementing coyote management plans to increase deer numbers in herd units where: 1) mule deer herds were 50% or more below herd objectives, 2) where winter ratios of fawns per 100 does were 50:100 or lower, and 3) where populations were not increasing. Fawn production and survival, as indexed by winter ratios of fawns:100 does, seemed to increase in these units during 1997 and 1998 when coyotes were being controlled compared to 1995 and 1996 when coyotes were not controlled. However, when the Utah data were subjected to statistical analyses, ratios of fawns:100 does increased over time regardless of whether or not coyotes were controlled (Fig. 13). An alternative explanation for the observed increase in ratios of fawns per 100 does is favorable weather. The past 4 winters have been unusually mild in both Utah and Colorado and one would expect deer populations to increase following mild winters.

Any inferences to the effectiveness of coyote control based on this study will be controversial because the experimental design was incomplete. Ordinarily, areas where coyotes were controlled would be paired with similar units without coyote control to adequately separate the effects of controlling coyotes from possible effects of weather. In this study, if we were to assume the data are perfect predictors of mule deer responses to coyote control, increasing ratios of fawns per 100 does from 43 (1995 levels) to 69 (1998 levels) would have required the removal of over 500 coyotes per year.

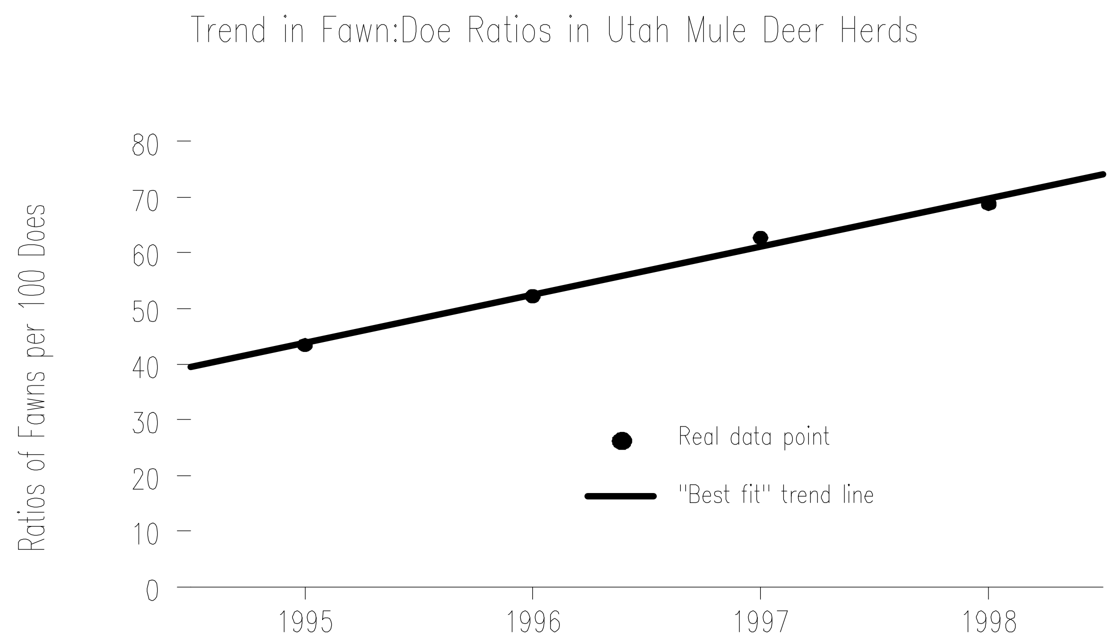

Figure 13. In Utah, 15 mule deer herds were selected for coyote control to increase fawn survival. Coyotes were controlled in 1997 and 1998, but not in 1995 and 1996. Although the ratio of fawns per 100 does increased over time, this increase could not be attributed to coyote control.

Idaho - Idaho Department of Fish and Game initiated a study in 1997 to assess the effects of coyote control on mule deer populations. In their experiment, predators (primarily coyotes and mountain lions) were controlled in several deer herd units. Deer responses in coyote control units were compared to herd responses in similar units where no predator control occurred. Adult does and fawns on all herd units were equipped with radio transmitters and used to compare mortality rates of deer on coyote control units with those units where coyotes were not controlled.

After 2 years of study, mortality rates of adult does and fawns in areas where predators were controlled were not different from areas where predators were not controlled. Coyote numbers in spring were reduced significantly by coyote control, but by fall coyote numbers had rebounded to levels comparable to herd units where coyotes were not controlled. Although coyotes were responsible for fewer fawn deaths in herd units where they were controlled, overall, fawn mortality did not decrease because more fawns died from starvation even in mild winters. The studies are ongoing, but preliminary results indicate that deer populations have not benefitted from predator control.

New Mexico - Deer biologists from the Jicarilla Apache Reservation in northern New Mexico reported that mule deer numbers increased from 1991 through 1999 (Fig. 14a) and attributed much of that increase to aggressive predator control programs. However, most of the increase in deer counted each year can be accounted for by the number of hours flown while counting them. For example, in winter 1990-91, 2024 mule deer were counted during 50 hours of aerial counting effort. In contrast, 6719 mule deer were counted during winter 1996-97 with 117 hours of aerial counting effort. When number of deer counted is related to the number of hours flown per count, nearly 70 additional deer are counted for every 1 hour that count time is increased, and counting time is the only variable that is consistently correlated with temporal increases in deer numbers (Fig. 14b). When the number of coyotes killed each year is related to the ratio of fawns per 100 does the following year, killing 800 coyotes per year is predicted to increase the fawn:doe ratio by only a single fawn per 100 does (Fig. 14c). The results from the Jicarilla Apache Reservation are further confounded because, in addition to coyote control, biologists improved deer habitats in several areas and greatly increased law enforcement effort to reduce mule deer poaching losses. Coyote control, habitat improvement, counting effort, increased law enforcement, climate effects, etc. collectively influenced mule deer numbers and ratios of fawns per 100 does. There is no way to unravel their combined effects to reliably assess the effects of any one of these factors acting alone. Despite all of these efforts to improve deer populations, fawn:doe ratios on the Jicarilla Apache Reservation (Fig. 14d) are similar to or less than current fawn:doe ratios throughout most of Colorado's deer herds (Fig. 5).

***Recent Fawn Survival Studies of Several Colorado Deer Herds: 1997-present*:**

Recently, Colorado researchers have started other studies to further investigate effects of coyote predation on mule deer fawns. One study documented fawn mortality rates from birth to 6 months of age. Another documented fawn mortality rates from 6 months to 1 year.

Fawn Mortality from Birth to 6 months of Age - Until recently, nearly all studies of the extent and causes of mortality among mule deer fawns in the central Rocky Mountain region have focused on the winter period roughly from November through May. In summer 1999, the Colorado Division of Wildlife initiated a study on the Uncompahgre Plateau to investigate fawn mortality from shortly after birth through 6 months of age. These data combined with the ongoing studies of over-winter fawn mortality should provide a more complete picture of mule deer mortality from birth through the first year of life. Results of this first year of study reveal that nearly ½ of fawns born alive died before the end of summer (Fig. 15). Starvation or illness could have been the ultimate cause of death for fawns dying from predation. Sick or starving fawns presumably were weaker than healthy fawns, impeding their abilities to escape predators once they were detected, and many fawns that were suffering from illness or starvation also suffered from diarrhea which presumably enhanced their detection by predators.

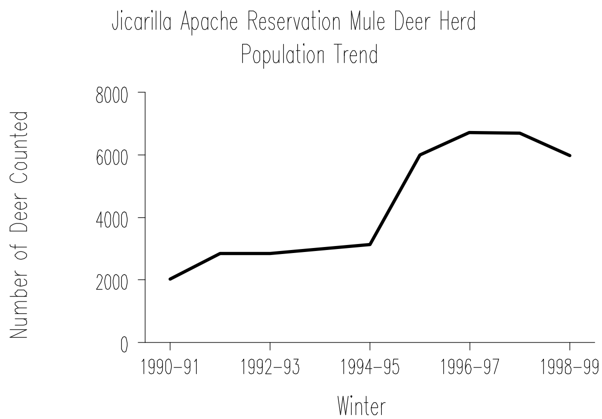

Fig. 14a.

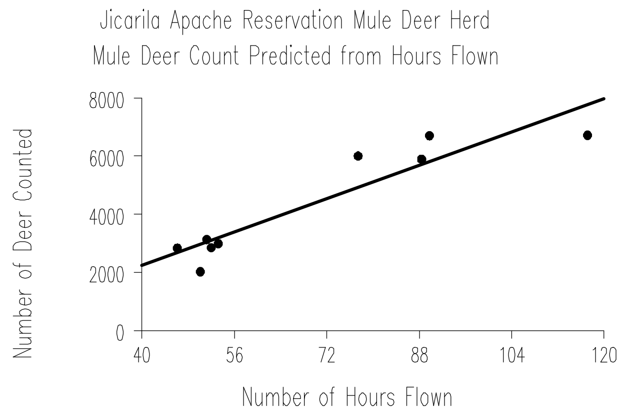

Fig. 14b.

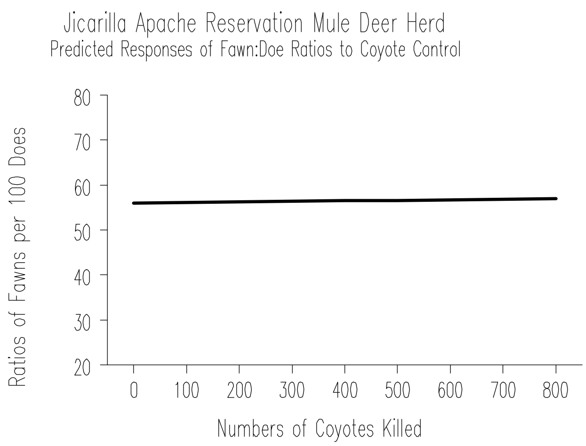

Fig. 14c.

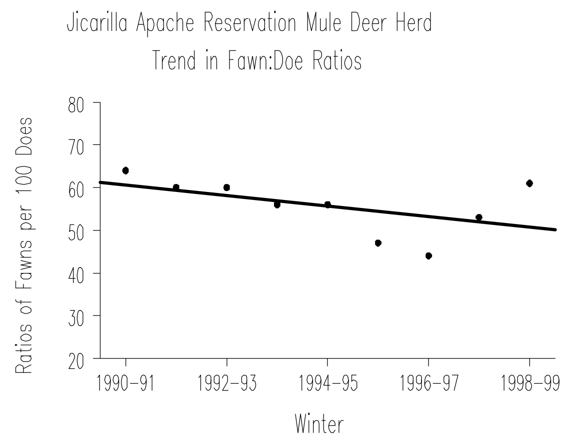

Fig. 14d.

Figure 14. Mule deer numbers have increased from 1990 to 1999 on the Jicarilla Apache Reservation of northern New Mexico (Fig. 14a). Most of the apparent increase in deer numbers can be attributed to increased counting effort. Deer counts increased in direct proportion to the number of helicopter hours expended to count them (Fig. 14b). Biologists attributed much of this increase to aggressive coyote control. However, when coyote removals were correlated with changes in ratios of fawns per 100 does, fawn:doe ratios did not increase even when up to 800 coyotes were killed (Fig. 14c). Despite coyote control, habitat improvements, and increased law enforcement, fawn:doe ratios remain at or below current fawn:doe ratios for most of Colorado's mule deer herds (Fig. 14d).

Fawn Mortality from 6 months of Age to 1 Year - Samples of does and fawns from each of 3 deer herds were captured in November of each year and equipped with radio transmitters. The studies are planned to continue for several years, but preliminary data are available for the past 2 winters (1997-98 and 1998-99). Transmitters were constructed so that the radio signal tone changed if a deer remained inactive for several hours, an indication it was probably dead. Each radio-equipped deer was monitored regularly from November through May of each year and mortality rates were calculated for adult does and fawns. When a radio signal indicated a deer was dead, biologists attempted to locate the carcass and determine the cause of death.

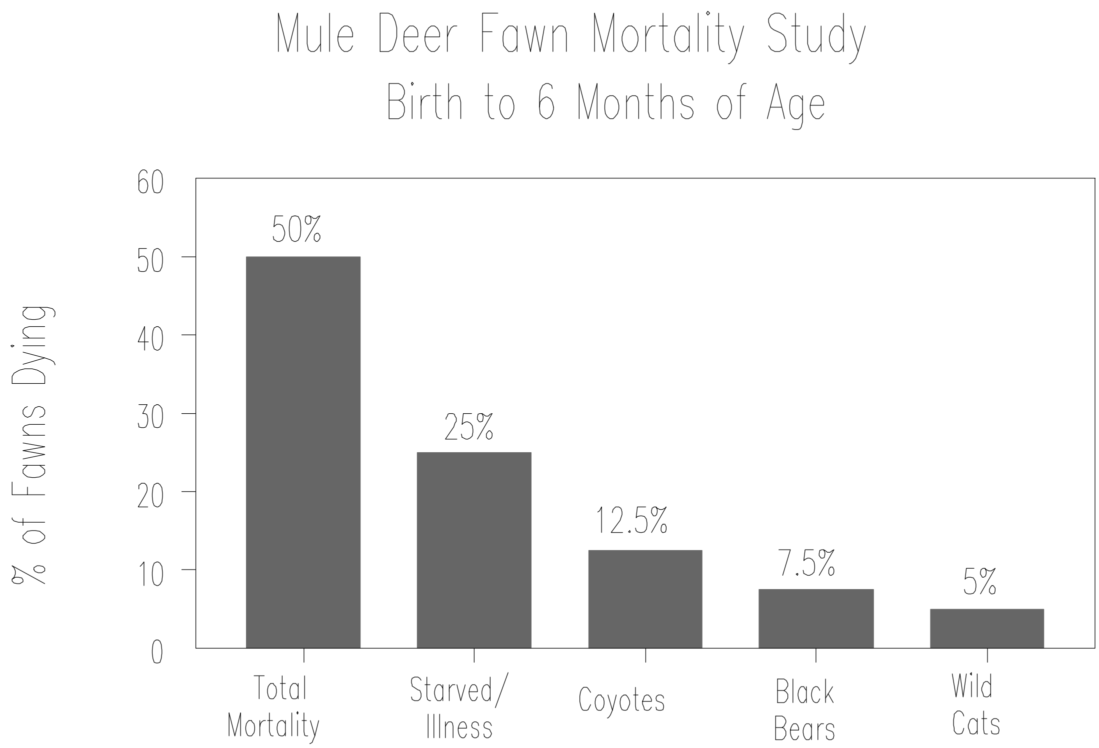

Figure 15. Fawn mortality from birth to 6 months of age was studied on the Uncompahgre Plateau of southwestern Colorado. One-half of fawns captured alive died before 6 months of age. Most fawn deaths (1/2 of total deaths) were attributed to starvation and/or sickness. Coyotes were responsible for the deaths of 1 of every 8 fawns.

Mortality rates of adult does during winter were less than 15% and were similar to those in the Piceance Basin study conducted from 1981 to 1995. The few does that perished died mostly from hunter kills or as a result of vehicular collisions. Fawn mortality rates varied between areas and between winters. In the Red Feather area, death rates were rather low in both winters. In contrast, fawns from the Uncompahgre herd unit experienced high mortality the first winter but mortality declined by nearly ½ the second winter. In Middle Park, data are available only from winter 1998-99 and fawn mortality was the lowest of the 3 herd units (Fig. 16).

Predation accounted for 47% of the fawn deaths across all 3 areas during the winter of 1997-98 and 57% of the fawn deaths in the winter of 1998-99. Coyotes were responsible for over ½ of the predator-related deaths both winters (Fig. 17). These data should be interpreted with caution for at least 3 important reasons. First, identifying the immediate cause of death does not necessarily eliminate another predisposing cause. Fawns that are weakened from malnutrition may be more vulnerable to predation and may have been doomed to death whether predators killed them or not. Second, identifying the cause of death of any wild animal is more art than science. It is especially difficult to differentiate between an animal that has been fed upon by a predator from

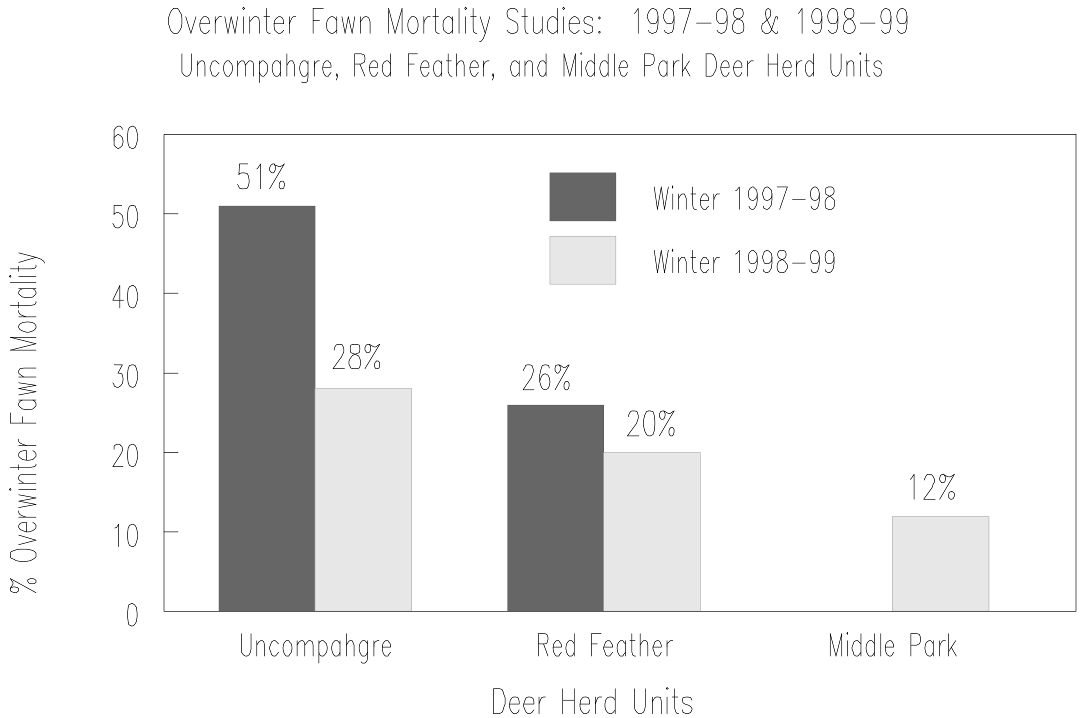

Figure 16. Mule deer fawn mortality during the winters of 1997-98 and 1998-99 varied by area and winter. Overall mortality was higher in 1997-98 than 1998-99. Fawns from the Uncompahgre herd unit experienced higher mortality rates than those from the Red Feather and Middle Park herd units.

one that has actually been killed by a predator. Third, even if predators kill significant numbers of mule deer fawns, losses to predation may not be limiting deer numbers. Deer populations can saturate available habitat and still experience high predation rates.

By comparison, winter fawn mortality during the 14-year Piceance Basin deer study ranged from 20 to 90% and averaged about 40%. Even though coyote predation accounted for a majority of the fawn deaths in the Piceance Basin study, limited deer winter food was implicated as the ultimate cause of high winter fawn mortality. Many fawns killed by coyotes would likely have died from starvation or some other cause, absent coyote predation. Likewise, studies of winter fawn mortality in Montana and Idaho provided similar results where combined winter fawn mortality from Montana, Idaho, and Colorado averaged 56% over several years. Fawn mortality seemed to fluctuate erratically, depending upon winter severity. Evidence from all 3 states indicated that chronically high fawn mortality during winter kept mule deer herds from increasing, and limited food during winter was the ultimate factor that kept fawn mortality high.

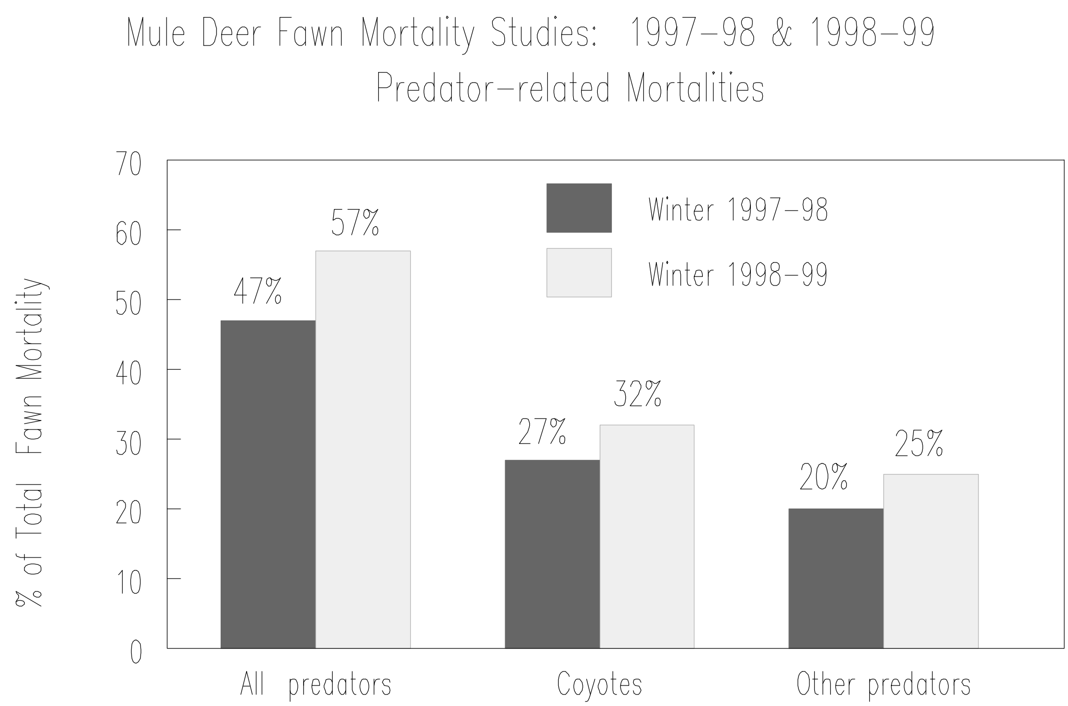

Figure 17. Predators were responsible for nearly ½ of all fawns dying during the winters of 1997-98 and 1998-99. Coyotes killed over ½ of the fawns whose deaths were attributed to predators.

Hunting Effects

Three paramount concerns have been raised about the effects of hunting on Colorado deer populations: 1) excessive deer harvests have caused deer numbers to decline; 2) excessive buck harvests have reduced buck numbers to the point that a portion of the adult doe population remains unbred each year; and 3) excessive buck hunting has reduced the age of breeding bucks which, in turn, has reduced the thriftiness of offspring.

Effects of Harvests on the Mule Deer Decline

Records of annual mule deer harvests are the only long-term data sets which can be used to assess hunting impacts on Colorado mule deer. Analysis of nearly 60 years of harvest data reveals two predominant trends. From 1940 to 1965, deer harvests increased steadily; much of the harvest in the 1960s was directed towards antlerless deer with the intent of reducing deer numbers. Harvests dropped dramatically following the severe winter of 1964-65 and cessation of liberal antlerless seasons, and stabilized or perhaps declined slowly thereafter (Fig. 18). These 2 contrasting trends have been interpreted by some as evidence that hunting removals during the

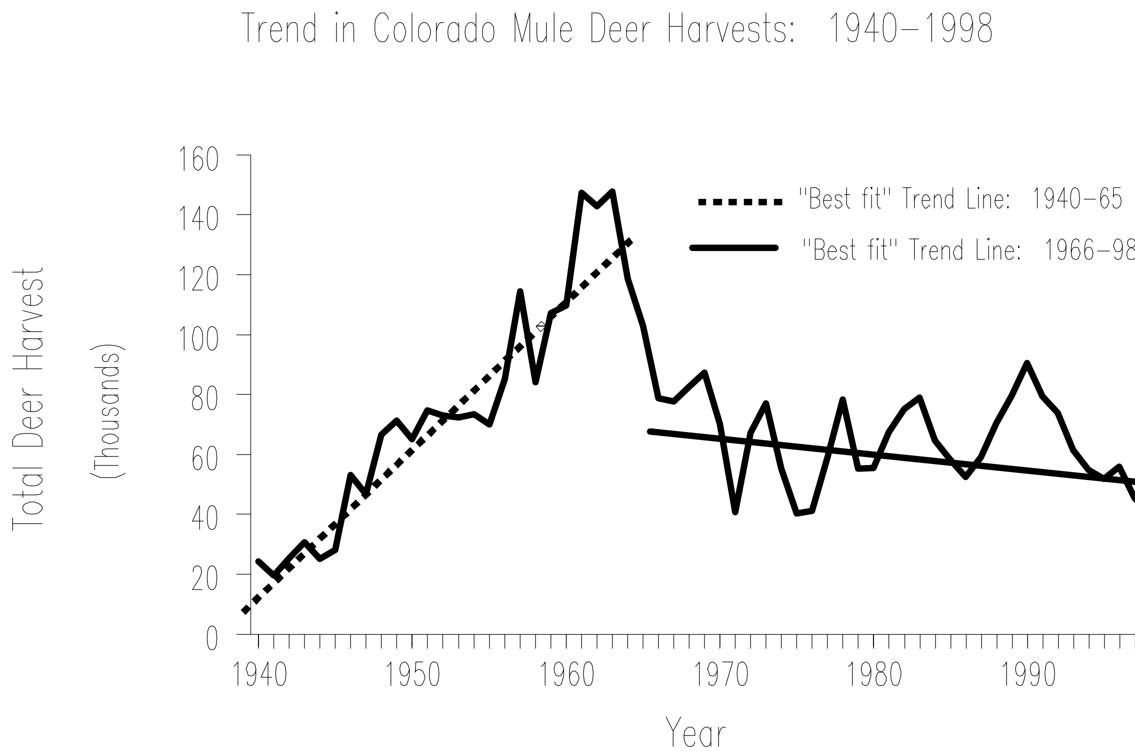

Figure 18. Analysis of Colorado deer harvests from 1940 through 1998 reveal 2 distinct patterns: (1) harvests increased steadily from 1940 to 1965; and (2) harvests dropped sharply in the late 1960s and have remained static or declined slowly thereafter.

early 1960s exceeded the renewal capacity of Colorado deer herds causing populations to collapse. Once populations collapsed, hunter kills combined with predator kills to prevent populations from recovering.

However, the relationship of deer harvests to the mule deer populations and declining mule deer numbers is unclear. Annual deer harvests are only crude reflections of overall deer numbers. Deer abundance, annual variation in deer distribution and weather at the time of the hunt, changes in hunting regulations, timing and duration of seasons, hunter numbers, varying skill levels, and myriad other factors all interact to affect the size of the annual deer harvest. The 2 predominate trends observed in the harvest data may reflect nothing more than the learning curve of deer managers as they sought a stable, sustainable harvest objective.

Two bodies of evidence suggest that excessive hunter harvest has not been responsible for the decline in mule deer numbers. When deer populations are reduced below the food capacity of their habitats, characteristically they respond with increased reproductive rates and decreased mortality rates. Ratios of fawns per 100 does began declining just after deer harvests peaked (Fig. 5). If excessive hunter kill was the primary cause of declining mule deer numbers, ratios of fawns per 100 does should have been increasing rather than decreasing.

Likewise, over-winter mortality rates of mule deer fawns exhibit patterns opposite those expected when deer populations are being exploited heavily by hunting. Under conditions of excessive hunting, average annual mortality rates of fawns should be relatively low (< 40%). Instead, the observed pattern is one of high over-winter fawn mortality rates (Fig. 19).

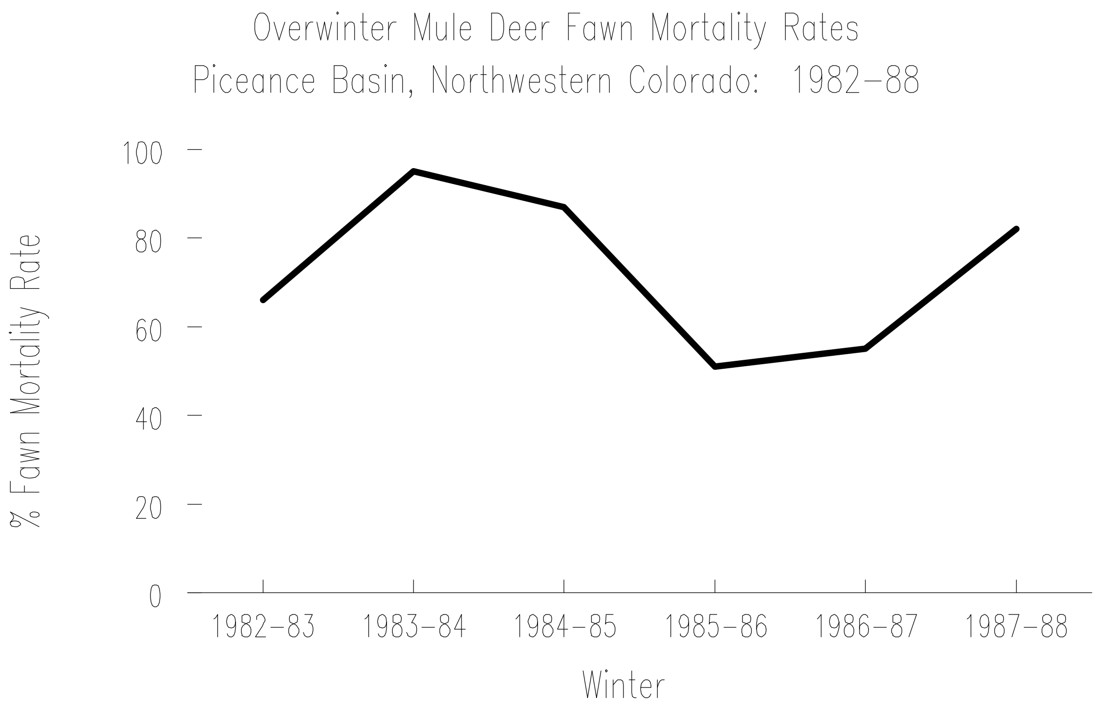

Figure 19. Winter mortality rates of mule deer fawns in the Piceance Basin consistently exceeded 50% from 1982 to 1988. If hunter kills were excessive, a pattern of low fawn mortality in winter would be expected.

Effects of Buck Harvests on Fawn Production

Excessive hunter kills could have contributed to the mule deer decline by way of another mechanism. Even though mule deer are polygamous, intensive hunting removals of bucks could reduce buck numbers to the point that there are insufficient bucks to breed all receptive does. This could result in the kind of declines in ratios of fawns per 100 does Colorado deer herds experienced from 1970 through 1995 (Fig. 5).

There is little doubt that Colorado bucks have declined over the past 2-3 decades and that hunting played a major role in that decline. Prior to 1966, bucks comprised slightly over ½ of the annual deer kill. Between 1966 and 1998 the buck kill had risen to the point that bucks comprised 75% of the annual deer kill statewide. The percentage of bucks in the annual harvest increased because there were no limits on availability of buck licenses while availability of doe licenses was increasingly restricted.

At the same time, hunter numbers were growing. During the period 1949-1965, numbers of deer hunters average about 150,000 per year. For the period 1966-1998, average number of people hunting deer annually increased by nearly 20% (Fig. 20). This combination of escalating

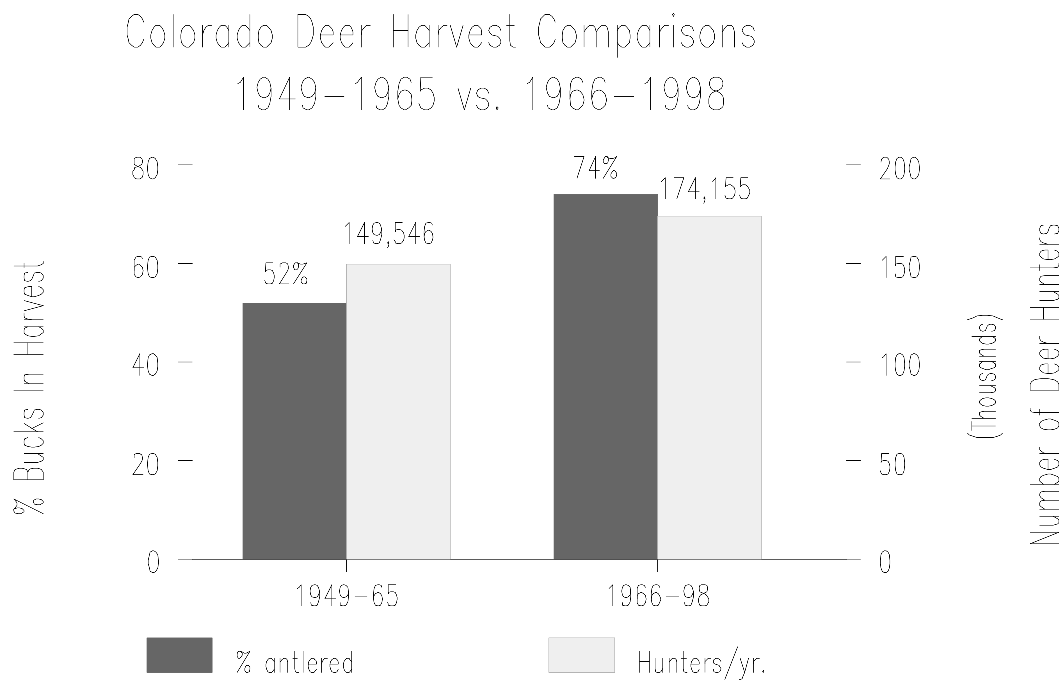

Figure 20. Prior to 1966, percent bucks in the total deer kill averaged 52%. Antlerless license numbers were reduced from 1966 onward and the average percentage of bucks in the deer kill increased to 74%. Fewer antlerless deer licenses combined with increasing hunter numbers intensified hunting pressure, resulting in declining buck numbers.

hunter numbers and reductions in numbers of antlerless deer licenses intensified hunting pressure on bucks. Intensified hunting pressure was one factor contributing to a steep decline in numbers of bucks following each hunting season.

Data from annual winter deer counts clearly reflect dwindling numbers of bucks. Relative abundance of bucks can be indexed by computing the ratio of the buck tally for every 100 does counted. This ratio is called the buck:doe ratio. In the early 1970s, ratios of 40-60 bucks per 100 does following the hunting season were not uncommon. Over the past decade 10-20 bucks per 100 does is normal (Fig. 21).

Nonetheless, available evidence does not support the conclusion that low buck numbers have been responsible for the drop in ratios of fawns per 100 does over the past 25 years. Buck:doe ratios from the Uncompahgre Plateau herd are among the lowest in the state. During this decade they have varied from 8-20 bucks per 100 does after the hunting season. Yet, a 1999 study indicated that 93% of does examined from the Uncompahgre Plateau were pregnant. The average number of fetuses carried per doe (1.72) did not differ from does studied elsewhere in the state before ratios of fawns per 100 does had begun to decline (Fig. 22). If low buck numbers were responsible for the observed decline in fawn:doe ratios, both pregnancy rates and the average number of fetuses per doe observed in the 1999 study of does on the Uncompahgre Plateau should have been much lower.

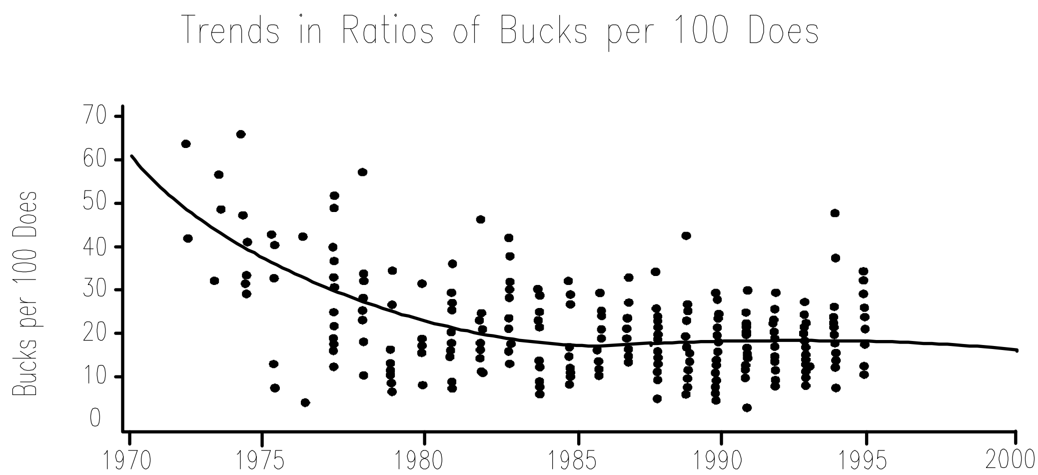

Figure 21. The ratio of bucks:100 does is an index to relative buck numbers and is derived from annual mule deer counts conducted after each hunting season. The buck:doe ratio dropped sharply throughout Colorado from 40-60 bucks:100 does in the early 1970s to 10-20 bucks:100 does by the mid-1980s. Heavy hunting pressure on bucks is one reason for the decline.

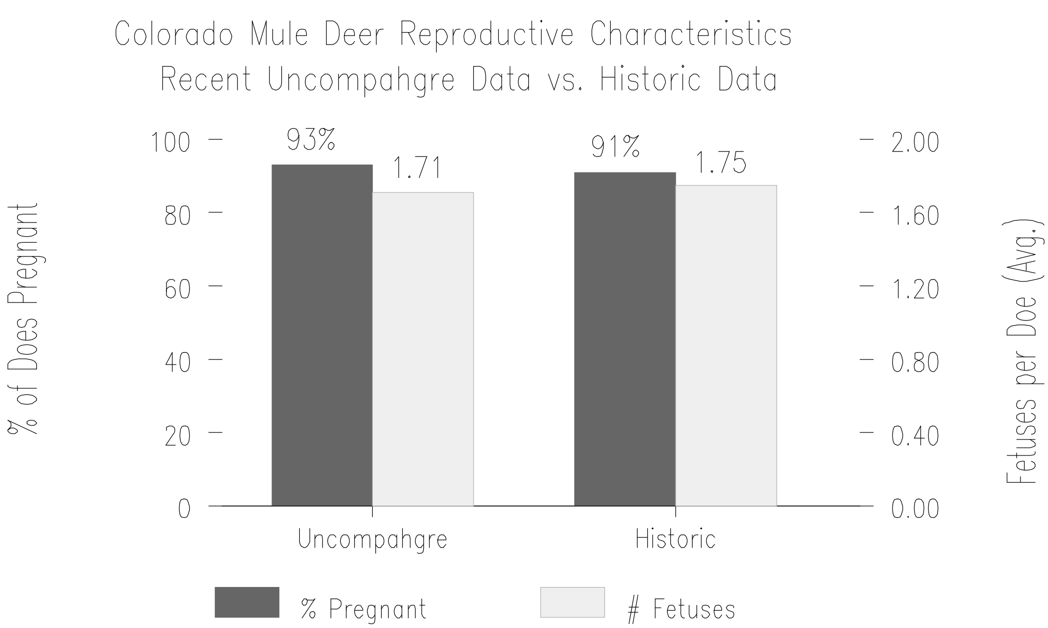

Figure 22. Reproductive characteristics of mule deer does were studied on the Uncomphagre Plateau in 1999 and results were compared with similar studies prior to the mule deer decline. There were no differences between pregnancy rates and average number of fetuses per doe from the recent Uncompahgre study and historic studies. These data indicate sufficient bucks were available in the Uncompahgre deer herd to successfully breed available does.

Summary

- Both the quality and quantity of Colorado mule deer habitats have changed over time. Rapid expansion of housing and other cultural developments in formerly rural areas have perforated and reduced the extent of critical deer habitats. Aggressive suppression of wildfires has resulted in maturation of key food plants in some mule deer habitats, reducing food availability and quality. Invasion of mule deer habitats by exotic plant species has replaced native species. Often the exotic species are less palatable to deer and less nourishing. Grazing by both livestock and deer and elk have favored less palatable and less nutritious species. Although wildlife managers are aware of these habitat changes, currently there is no information which quantifies the extent of mule deer habitat change. Neither are there reliable analyses which evaluate the effects of these changes on trends in mule deer numbers.

- Elk populations in Colorado have increased dramatically over approximately the same time span that mule deer numbers have declined. Elk can and do consume many of the same food species that mule deer eat, but can exist on foods that can not support deer. In theory, at least, elk could gain a competitive advantage over mule deer on rangelands commonly used by both species. Analyses of available data, however, fail to show consistent relationships where increases in elk numbers have been associated with declining deer herds.

- Although a variety of disease organisms are known to infect mule deer, rarely are these disease outbreaks sufficiently virulent or widespread to account for statewide or region-wide declines in mule deer abundance. Chronic wasting disease has the potential to cause widespread declines in mule deer numbers, but to date chronic wasting disease seems to be limited to northeastern Colorado and can not, by itself, account for declines in mule deer statewide.

- Predation, particularly by coyotes, has been proposed as a primary factor in the decline of mule deer throughout the West. The only certainty is that predators kill and eat mule deer. However, studies that investigated responses of entire mule deer herds to intensive coyote control have failed to demonstrate that mule deer numbers increased as a result of coyote control. The contribution of predation to the mule deer decline remains uncertain.

- Excessive deer harvests have been proposed as another primary cause of declining mule deer herds. If deer populations were being hunted so intensively that populations were kept well below carrying capacity of deer habitats, reproductive rates of does should be high and mortality rates of fawns should be low. Studies show exactly the opposite patterns. Over the past 3 decades, hunting has been a major factor contributing to reductions in numbers of bucks throughout Colorado deer herds. Some believe that current buck numbers are so low that some does are not being bred each year and poor breeding success is the cause of declining fawn production. Yet, available evidence fails to substantiate that declining deer populations can be attributed to low buck numbers. Reproductive rates measured in a recent study of does on the Uncompahgre Plateau of southwestern Colorado are as high as reproductive rates from earlier studies, despite some of the lowest ratios of bucks per 100 does in the entire state.

- Factors causing the current decline in mule deer numbers in Colorado and elsewhere are richly speculated but not well understood. Available evidence suggests that important deer habitats have deteriorated through time and that the current capacity of those habitats to support deer is now lower. Habitat effects are amplified perhaps by increasing elk numbers, disease, predation, and hunting, but very few experiments have been conducted to test for effects at scales of entire deer herds. As a result, the answer to the question, "*What caused mule deer numbers to decline?*" remains both speculative and controversial.

What is the Colorado Division of Wildlife Doing to Reverse the Declining Mule Deer Numbers?

Over the last 2 years the Colorado Division of Wildlife implemented intensive population monitoring studies in the Uncompahgre, Middle Park, and Red Feather areas; increased numbers of deer counts in western Colorado; and notified hunters that 1999 buck deer licenses would be restricted and issued by drawing only. For fiscal year 1999-2000, we reallocated $1 million internally and received an additional $225,000 from the General Assembly for expanded research, inventory, and habitat improvement work; all buck deer licenses for 1999 were limited and issued by drawing. For fiscal year 2000-01, the Division of Wildlife is requesting $100,000 additional spending authority for predator management planning and to commence the habitat enrichment study described below.

Much of the previous research on mule deer has focused on relatively small groups of deer on comparatively small study areas. Few studies have been designed as true management-level experiments where entire deer herd units were subjected to various management treatments and compared with herd units that were not treated. Consequently, there is considerable knowledge about the behavior and ecology of groups of deer in specific habitats, but inadequate knowledge about the behavior of entire deer herds living in complex landscapes.

The Division of Wildlife designed and is in the process of implementing action plans wherein deer management efforts will be designed as herd-unit experiments. Biologists and researchers from several resource management agencies and states are cooperating in the design, staffing, funding, implementation, and interpretation of these "experiments in management" to increase efficiency, effectiveness, and applicability of findings.

Management Actions

The Colorado Division of Wildlife has been asked why it took so long to detect and react to declining mule deer numbers. In part the delay was due to the necessity to collect several years of data before a statistically reliable trend could be established. The trend lines in Figs. 5 and 21 are the best mathematical fits of the linear trajectories to the data points. But those data vary considerably among herd units within years as well as varying among years. In general, it takes at least 5 years before a trend in these kinds of data can be detected with any degree of statistical reliability.

Nonetheless, some of the blame for failing to detect the mule deer decline sooner lies with the processes used to gather and analyze mule deer population data. Hunters and other publics interested in deer expect the Division of Wildlife to know the size and trends of mule deer herds throughout the state. To meet these demands, the Division attempted to inventory vital statistics of Colorado's important deer herds every year. However, estimating numbers, birth rates and mortality rates of a deer herd is expensive. It is not unusual to spend $50,000 per herd per year to gather the minimum amount of data needed to reliably track deer trends. With nearly 100 important deer herd units in the state, estimating vital statistics of each deer herd every year could require annual expenditures in excess of $5 million in inventory costs alone. Two strategies were adopted to control costs and still conduct the necessary inventories: 1) grouping ecologically similar herd units into larger inventory units called Data Analysis Units and 2) conducting inventories in Data Analysis Units in alternate years. The result was fewer estimates of mule deer population statistics and longer time spans required before reliable trends could be established.

Currently, counts of key deer herds are scheduled to be made annually; and efforts are underway to upgrade deer inventory procedures, data analysis methodologies, and evaluations of hunting season and regulatory strategies through the use of management experiments.

Upgrade Deer Inventories

Beginning in 1997, the Colorado Division of Wildlife began to incorporate previously tested deer inventory procedures designed to estimate deer numbers, ratios of bucks:100 does, ratios of fawns:100 does, overwinter survival rates of does and fawns, and hunter kill statistics over broad habitat types or ecosystems rather than over individual herd units. These population statistics will be incorporated into revised mule deer population models, which should provide more powerful diagnostic tools for monitoring and understanding trends in deer numbers and responses of deer populations to changes in hunting seasons and regulations. This year (1999) these upgraded inventory procedures will estimate vital population statistics for deer residing in mixed forest-shrub habitats of the Uncompahgre Plateau west of Delta, Colorado, sagebrush grassland habitats of the Middle Park Basin near Kremmling in northcentral Colorado, forest-shrubland habitats of the Red Feather area of northeastern Colorado, and pinon-juniper parklands west of Cañon City in southeastern Colorado.

Enhance Data Analysis

Contracts are ongoing with Colorado State University to upgrade the statistical basis for deer population inventories, deer population models, and statistical analyses of population and harvest data. This year, for example, CSU contractors will analyze responses of bucks in various herd units to reductions in hunter numbers resulting from limitations on licenses. Previously, responses of post-season buck:doe ratios to antler point regulations were analyzed. Antler point restrictions allowed hunters to kill a buck only if its antlers met or exceeded a minimum number of antler tines. These regulations were designed to protect younger bucks with smaller antlers from being killed by hunters, theoretically allowing them to survive to older age and grow larger antlers. Statistical analyses of buck responses to antler point restrictions revealed that they were ineffective, largely because some hunters tended to sort deer after they were shot rather than before. In other words, several younger bucks with smaller antlers were shot but left afield because their antlers failed to meet the minimum antler tine threshold. For next year the Division will recommend to the Commission that antler point regulations be discontinued in the few remaining areas where they remain in effect, and rely on limitations on total numbers of buck licenses as a strategy to increase buck numbers.

Management Studies

In the past, evaluation of responses of deer and hunters to changes in hunting season formats and regulations have been difficult or impossible to evaluate. For example, recent hunting seasons and regulations have featured changes in timing and length of seasons, license availability, antler point regulations, etc. These changes varied among years and areas to the extent that it was not possible to evaluate the effects of any one change independently of other changes. For instance, the cause of the statewide decline in buck harvest from 1990 through 1998 (Fig. 23) could have reflected true declines in numbers of deer and bucks, or the decline may have just as easily been

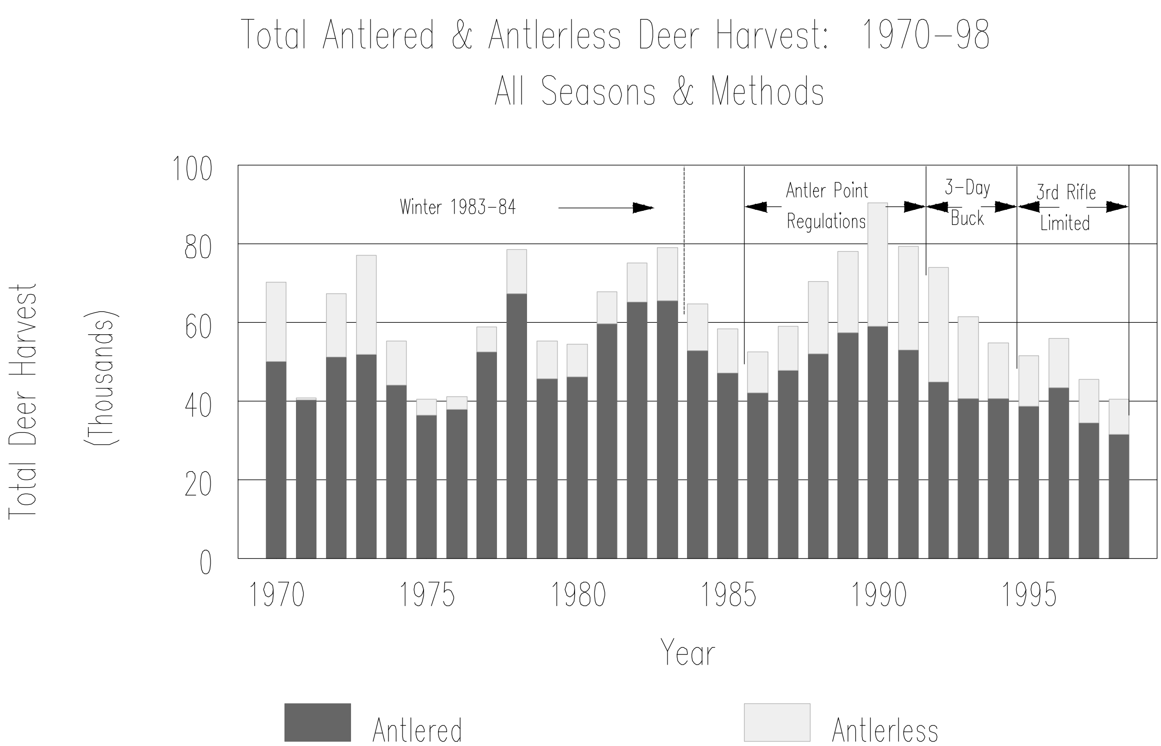

Figure 23. Numbers of antlered and antlerless deer harvested in Colorado varied considerably from 1970 to 1998. Prior to 1986, it was legal to shoot any buck and licenses were not limited in number. Prominent declines in buck harvest occurred after the severe winter of 1983-84 and during the last years of antler-point restrictions, 3-day buck seasons, and years when buck licenses were limited in the third rifle season.

caused by the most restrictive buck hunting regulations since 1970 that depressed both numbers of buck hunters and numbers of bucks killed. Changes in hunting seasons should be predicated on establishing specific goals and experimental areas such that experiments can be conducted to truly evaluate the impacts of new regulations. A caveat to such management experiments will be that some local communities and economies could be either positively or negatively affected by management experiments.

For example, two competing explanations have been proposed to account for declining ratios of fawns per 100 does in Colorado deer herds. One explanation proposes that high fawn losses observed in several deer herds are a consequence of too many females. If hunting seasons since 1965 have served to spare does at the expense of bucks, one consequence could be that does are too numerous. When does are too numerous, they compete with each other and with fawns for forage during critical periods of the year. High fawn mortality can be one consequence of this competition and would be reflected in declining ratios of fawns per 100 does. These circumstances could also contribute to low buck numbers because if few fawns survive to adulthood, then few bucks are being recruited to replace those killed by hunters.

A second explanation to account for declining fawn:doe ratios contends that hunter kills are primarily responsible for declines in numbers of bucks, particularly mature breeding bucks. Consequently, fewer does are being bred or does are being bred by immature bucks which produce unthrifty fawns. As the proportion of unthrifty fawns increase, fawn mortality rates increase as reflected in the declining ratios of fawns per 100 does.

Two experimental hunting manipulations have been proposed. In the first, deer numbers in at least 2 deer herd units would be lowered through antlerless harvest. Deer numbers would not be lowered on 2 or more similar herd units. December ratios of fawns per 100 does would be measured in all herd units and herd units where deer numbers have been reduced would be compared to those units where numbers have not been lowered. The study should be continued for at least 4 years to assure that changes in density are primarily responsible for any observed changes in ratios of fawns per 100 does (Fig. 24).

In a second experiment, buck:doe ratios would be doubled to measure the impact on December fawn:doe ratios, without changing deer density. The most effective method of increasing buck:doe ratios would be to discontinue all buck hunting. As with the previous experiment, at least 2 sets of paired deer herd units would be required. Collectively this pair of experiments should determine whether deer density or sex ratio is a predominant variable affecting declining ratios of fawns per 100 does.

Other management studies will evaluate the effects of limited buck licenses on illegal buck kills. Here the issue is whether restricting numbers of buck hunters, when previously there were no restrictions, increases the incidents of poaching losses. Another study has evaluated the effects of antler point regulations on buck:doe ratios.

Research Studies

Research plans include several studies designed to evaluate the contributions of various competing hypotheses to explain the mule deer decline. Once critical factors have been identified, researchers and biologists will cooperate to devise potential mitigations.

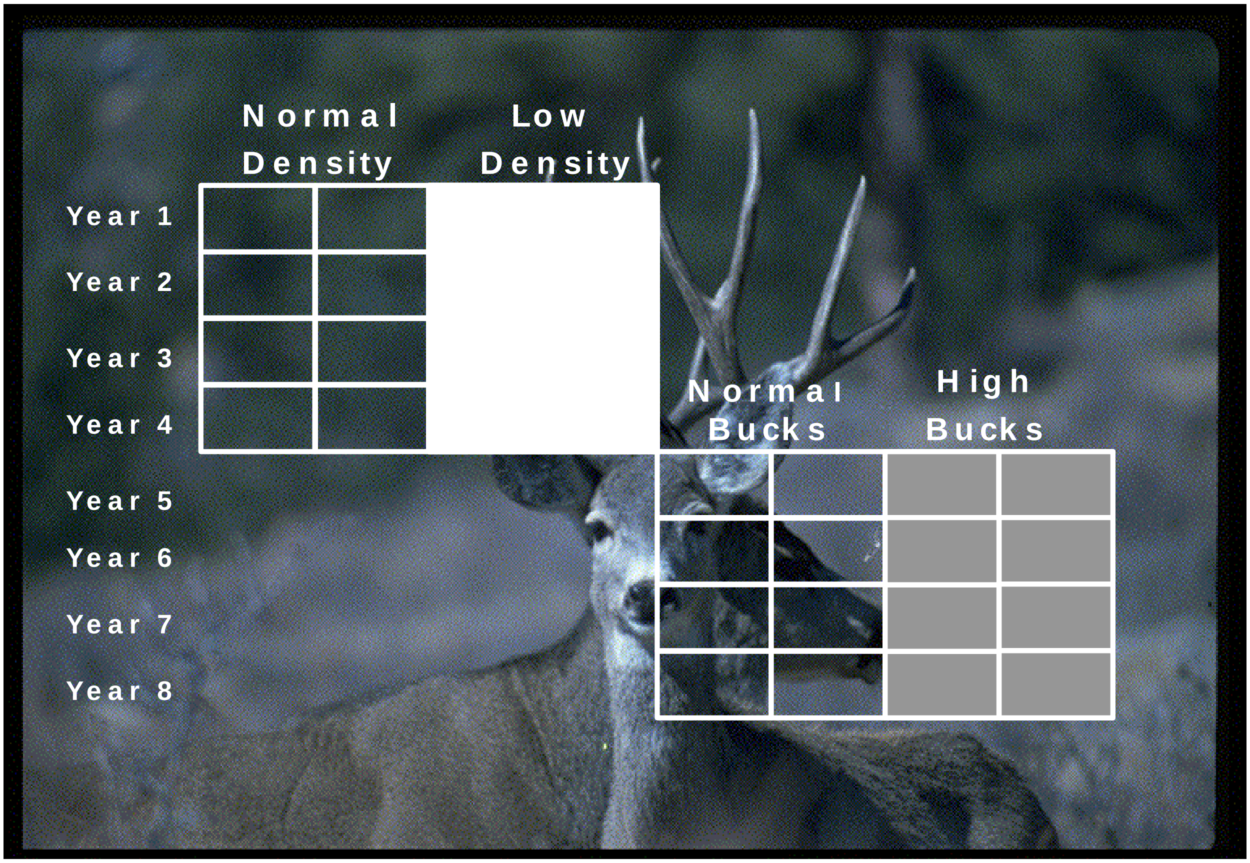

Figure 24. Two experiments are being considered to evaluate the responses of mule deer populations to hunting. The first would examine the effects of doe numbers on ratios of fawns per 100 does by comparing herd units where doe numbers are reduced to units where they are not. The second experiment would examine the effects of buck numbers on ratios of fawns per 100 does by comparing herd units where buck numbers are increased to units where they are not.

Habitat Studies

A three-pronged approach is underway to document changes in mule deer habitat.

➤ First, historic (ca 1940) and contemporary maps will be developed to compare changes in woody canopy cover on deer winter and summer ranges. Historic and current aerial photographs will be combined with current satellite imagery to develop then vs. now maps for comparisons. It is important to understand changes in canopy coverage because it controls the amount of deer forage available in the understory.

➤ Long-term trends in vegetation patterns on deer winter ranges will be examined by revisiting big game grazing exclosures established during the 1950s and repeating measurements taken inside and outside the exclosures when they were established.

Analysis of these measurements will reveal how vegetation composition and quantity has changed during the last half century. The data from these 2 studies will be integrated using an ecosystem simulation model to examine potential consequences of changes in habitat for nutritional condition of deer and the implications of changes in deer condition for deer population performance.

- The ecosystem simulation model will also be used to evaluate alternatives for improving deer habitats. Preferred alternatives will be designed as management experiments and real habitat responses will be compared to the simulation evaluations to improve the quality of the simulation model and habitat improvement practices.

Elk Competition Studies

Proposed studies to investigate the effects of elk and mule deer competition on mule deer population responses would focus on 2 research hypotheses:

- Forage competition between elk and mule deer will occur primarily in the spring during spring green-up and then only at high elk densities.

- At high densities of elk, elk will prevent mule deer does from obtaining high quality forage necessary to sustain health of fetuses during the last trimester of pregnancy, resulting in undernourished and underweight newborn fawns, which will cause high rates of mortality shortly after birth. High mortality rates among newborn fawns in competition with high densities of elk is an important mechanism resulting in low fawn:doe ratios in winter.

These hypotheses would be tested by varying elk densities in experimental pastures and recording habitat use by both deer and elk and measuring fawning success of mule deer does exposed to different densities of elk. The U. S. Forest Service's Starkey Experimental Forest and Range in northeastern Oregon offers the best physical locale to conduct this research because game-proof fenced pastures create the essential ability to establish and control elk and deer densities and measure associated responses of deer. Furthermore, the automated telemetry system at Starkey allows spatial locations of elk and deer to be monitored continuously and efficiently without disturbing either species. Elk and deer habitats at Starkey are primarily conifer-bunchgrass ranges modified in part by logging and fire to create a mosaic of habitats and forages available to deer and elk and is considered to be traditional transition and summer range habitat. Although habitats dominated by shrubs are not present on Starkey, we believe existing habitats adequately represent the spring green-up process common to a variety of habitats used by deer and elk throughout the western states. Mule deer are likely to be even more heavily dependent on spring green-up at Starkey than in areas where shrubs are abundant.

Disease Studies

The Colorado Division of Wildlife will continue to assess the importance of diseases in mule deer population dynamics, and will also continue to develop experimental strategies for mitigating or managing important disease problems affecting Colorado's mule deer resources. In conjunction with ongoing and planned survival studies, greater efforts will be made to determine both proximate and ultimate causes of morbidity and mortality in mule deer throughout Colorado. Whenever feasible, carcasses or appropriate parts thereof will be submitted to one of several regional veterinary diagnostic laboratories for evaluation. Greater efforts will be made to specifically screen for evidence of hemorrhagic disease, chronic wasting disease, and other diseases that could potentially affect population performance. In addition, the Division will continue to monitor deer herd health via an ongoing statewide wildlife health monitoring program designed to detect and investigate unusual wildlife mortality events. When disease epidemics are detected, greater efforts will be made to estimate the magnitude of mortality associated with those epidemics.

The Division is committed to limiting distribution and occurrence of chronic wasting disease in Colorado. An ongoing surveillance program to determine distribution and prevalence of chronic wasting disease will continue for at least 2 years. Within endemic portions of northeastern Colorado, annual surveys will continue through 2000 to assess short-term epidemic trends. Thereafter, annual surveys will be suspended pending adoption of policies and plans for experimental management of chronic wasting disease. If intensive management is not attempted, natural prevalence trends will be assessed about every 5 years. Statewide surveys to detect other significant endemic foci of chronic wasting disease will be completed by 2001, and once completed, less intensive but more sensitive surveillance strategies will be used to continue monitoring chronic wasting disease distribution.

Research on various aspects of chronic wasting disease transmission, diagnosis, and management will also continue in collaboration with other agencies and institutions. Specific planned research projects include the following:

- Continued study of cattle susceptibility to chronic wasting disease.
- Continued development and evaluation of tests for detecting infection in live-animals.
- Experimental study of natural routes for chronic wasting disease transmission.
- Development of tests for detecting strain variation in chronic wasting disease.
- Studies of potential environmental reservoirs of chronic wasting disease.

Information obtained from surveillance and research, as well as from studies and surveys already completed, will be used to further refine strategies for managing chronic wasting disease in deer and elk.

Predation Studies

Predation is perhaps the most controversial issue surrounding the mule deer decline. If one asks representatives of sport hunting groups what is the single most important factor contributing to declining deer numbers, predation will be high on the list of responses. If you ask the same question of wildlife managers, habitat change will be high on the list. It is critically important that sportsmen and wildlife managers know which of these 2 factors is more important before broadly implementing deer management strategies because costs of manipulating predator numbers or habitat conditions are large. Not only are economic costs likely to be high, but social costs could be high as well. For example, aggressively controlling coyotes may not be popular with the general public. Habitat modification has social costs also. Deer may not benefit from habitat alterations without changes in livestock management strategies, and ranchers may not regard changes in livestock grazing strategies favorably.

Deer researchers propose several interrelated studies designed to assess the relative contributions of predator control and habitat management before either strategy is implemented broadly.

Fawn Mortality from Birth to 6 Months of Age - In spring 1999, a study was initiated to monitor fawn survival from birth to 6 months of age. Newborn fawns were captured and equipped with small radio-transmitters which changed radio signals if fawns died. Dead fawns were located soon after death and carcasses were examined to assess cause of death. This study is scheduled to continue for at least 3 more years to evaluate annual changes in overall fawn mortality as well as annual changes in deaths attributed to predators and other causes of death. Two important pieces of information are expected from this study. First, it will reveal when fawns are dying and provide wildlife managers with both a temporal and spatial context to plan management strategies. Second, it will provide clues to cause of death which should allow wildlife managers to develop the most appropriate management strategies.

Fawn Mortality from 6 Months to 1 Year of Age - Mule deer does and fawns are being captured and equipped with radio-transmitters in 3 areas with contrasting deer habitat characteristics. Plans in 2000 will expand this number to 4 areas. Does and fawns in each area are being monitored at least once each week to monitor mortality rates from December to June. Again, cause of death will be assessed soon after mortalities occur. Trends in mortalities among years and areas should provide valuable clues to the importance of mortality factors, including predation, as they change over time and vary between areas.

Predation or Habitat as a Mule Deer Limiting Factor - Three years ago, Colorado Division of Wildlife Director Mumma challenged the research staff to attack the mule deer problem boldly, broadly, and brilliantly. Boldly, in the sense that researchers not limit conceptual thinking with concerns about dollars and personnel. Broadly, in the sense that researchers approach the mule deer problem as a regionwide problem, not just a problem in Colorado. Director Mumma encouraged his staff to develop cooperative approaches to the mule deer problem with other agencies and other western states. Brilliantly, in the sense that researchers were challenged to "think outside the box" of traditional research approaches.

Idaho Predator Control Experiments - In response to Director Mumma's challenge, researchers have developed an innovative and cooperative approach to resolve the question of whether predation or habitat change is fundamentally responsible for low deer numbers. Division researchers cooperated with researchers of the Idaho Department of Fish and Game in the design of an experiment to reduce predator numbers and evaluate deer population responses. Several deer herd units were selected for coyote control. Equal numbers of ecologically similar units where coyotes were not controlled were paired with the coyote control units to evaluate deer responses on units with and without control.

Conducting the coyote control study in Idaho offered several advantages unavailable in Colorado:

- ➤ Deer herds in Idaho tend to be spatially separate from one another so that immigration of deer from adjacent areas are less likely to confound responses of deer to reduced coyote numbers.
- ➤ Enactment of Amendment 14 in Colorado limited coyote control tools to aerial gunning and sport-hunting. Idaho, on the other hand, can use aerial gunning and sport hunting in combination with trapping, snaring, coyote getters, and other coyote control tools, enabling effective reductions in coyote numbers.
- ➤ Adverse public reactions to coyote control are less likely to result in additional ballot initiatives in Idaho than in Colorado.

<u>*Colorado Habitat Enrichment Studies*</u> - In Colorado, researchers developed a proposal to complement the Idaho coyote control study. If habitat, rather than predation, is the primary factor limiting deer numbers, deer populations should increase when habitats are enriched despite ongoing predator effects. The proposal aims to enrich habitats in 2 ways. First, selected deer groups within several herd units will be fed highly nutritious deer supplements which mimic optimum nutritional benefits of habitat improvement practices. Second, habitats in other deer herd units will be renovated with the best habitat improvement practices currently available (Fig. 25). Several possible outcomes to this complex experiment are possible. First, deer populations might fail to respond to habitat improvements, indicating that habitats are not the primary cause of low deer numbers. Second, deer populations could respond positively to herd units with nutritional supplementation, but not in those with habitat renovation treatments, indicating that current habitat renovations are not really improving deer habitats. Third, deer populations could respond positively to both nutritional supplement treatments and to habitat renovation treatments, indicating that habitats, not predation, are limiting deer populations and that current habitat renovation practices indeed improve habitats for deer. This study could be implemented as early as 2000-2001 if feasibility analyses currently underway are resolved favorably. Funding of $500,000 for the habitat improvement work has been allocated as part of the $1 million redirected within the Division’s 1999-2000 budget.

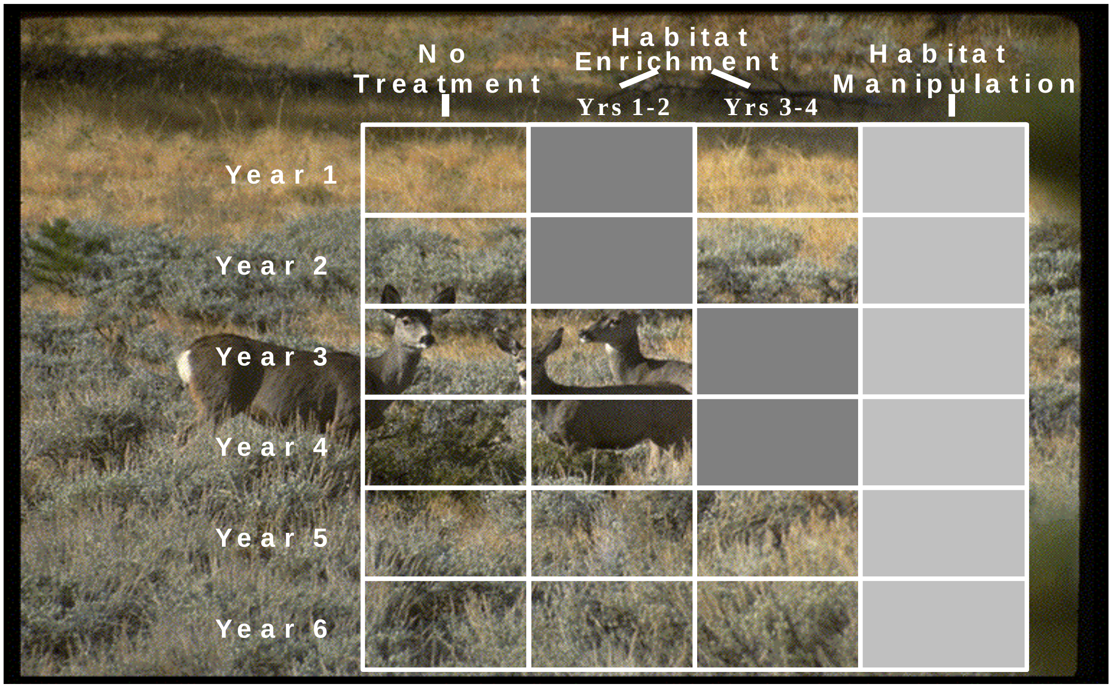

Figure 25. Two primary causes have been implicated in the decline of mule deer throughout the West, habitat change and predation. An experiment was designed to distinguish between the two causes. Habitats would be nutritionally enriched on some units and compared to units without enrichment. If habitat is primarily responsible for low fawn production, fawn numbers should increase with habitat enrichment despite predation effects. Habitat enrichment coupled with habitat improvement practices should allow for evaluation of the benefits that habitat improvement practices provide to deer.

Summary

Several complex factors acting in combination probably contribute to declining mule deer numbers. Various management actions and research studies have been initiated or are being planned to evaluate relative contributions of these factors and to develop effective management remedies:

- Deer inventory procedures are being upgraded wherein deer population data are being collected frequently and intensively from a few areas that represent extensive mule deer habitat complexes;

- Enhanced analyses of mule deer population and hunting data will be routinely analyzed with rigorous statistical tests to evaluate benefits from changes in hunting seasons and regulations;

- Research experiments are proposed to evaluate the effects of high doe numbers and high buck numbers on fawn production as reflected in winter ratios of fawns per 100 does;

- Management studies are underway to evaluate the effects of hunting seasons on buck mortality due to poaching and inadvertent wounding loss of bucks;

- Research studies will assess the contribution of long-term habitat changes to the mule deer decline;

- Ongoing research studies evaluate the contribution of diseases, particularly chronic wasting disease, to declining mule deer numbers;

- Research experiments are proposed to assess the effects of high elk numbers on mule deer habitat use and fawn production;

- Research experiments are proposed that will evaluate the contributions of predation vs. habitat quantity and quality to high fawn mortality rates.

Reference Materials

Austin, D. D., P. J. Urness, and M. L. Wolfe. 1977. The influence of predator control on two adjacent wintering deer herds. *Great Basin Naturalist* 37:101-102.

Baker, D. L., and D. R. Hansen. 1985. Comparative digestion of grass in mule deer and elk. *Journal of Wildlife Management* 49:77-79.

Baker, D. L., and N. T. Hobbs. 1985. Emergency feeding of mule deer during winter: tests or a supplemental ration. *Journal of Wildlife Management* 49(4):934-942.

Baker, D. L., and N. T. Hobbs. 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. *Canadian Journal of Zoology* 65:1978-1984.

Baker, R. H. 1984. Origin, classification and distribution. Pages 1-18 *in* L. K. Halls, editor. *White-tailed deer ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.

Ballard, W. B., and V. Van Ballenberghe. 1997. Predator/prey relationships. Pages 247-273 *in* A. W. Franzmann, and C. C. Schwartz, editors. *Ecology and management of North American moose.* Smithsonian Institution Press. Washington, D.C.

Barrows, P., and J. Holmes. 1990. *Colorado's wildlife story*. Colorado Division of Wildlife. Denver, CO.

Bartmann, R. M. 1983. Composition and quality of mule deer diets on pinyon-juniper winter range, Colorado. *Journal of Range Management* 36:534-541.

Bartmann, R. M., and T. M. Pojar. 1998*a*. *Deer conservation: deer reproductive assessment*. Colorado Division of Wildlife Game Research Report, July: in press.

Bartmann, R. M., and T. M. Pojar. 1998*b*. *Deer conservation: experimental deer inventory*. Colorado Division of Wildlife Game Research Report, July: in press.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs* 121:5-39.

Bergstrom, R. 1992. Browse characteristics and impact of browsing on trees and shrubs in African savannas. *Journal of Vegetation Science* 3:315-324.

Blank, R., R. F. Allen, and J. A. Young. 1994. Growth and elemental content of several sagebrush-steppe species in unburned and post-wildfire soil and plant effects on soil attributes. *Plant and Soil* 164:35-41.

Bork, E. W., R. J. Hudson, and A. W. Bailey. 1997. Populus forest characterization in Elk Island National Park relative to herbivory, prescribed fire, and topography. *Canadian Journal of Botany* 75:1518-1526.

Bowyer, R. T. 1994. Sexual segregation in southern mule deer. *Journal of Mammalogy* 65:410-417.

Brown, B. W., C. Brauner, A. Chan, D. Gutierrez, J. Herson, J. Lovato, and J. Polsley. 1993. *STPlan, Version 4.0*. University of Texas, M. D. Anderson Cancer Center. Houston, Texas.

Bryant, L. D., and C. Maser. 1982. Classification and distribution. Pages 1-59 *in* J. W. Thomas and D. E. Toweill, editors. *Elk of North America, ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.

Bryson, C. T. 1991. Tree size and understory phytomass production in a western juniper woodland. *Great Basin Naturalist* 51:236-243.

Buchholtz, C. W. 1983. *Rocky Mountain National Park: a history*. Colorado Associate University Press. Boulder, CO.

Campa, H., III, J. B. Haufler, and D. E. Beyer, Jr. 1992. Effects of simulated ungulate browsing on aspen characteristics and nutritional qualities. *Journal of Wildlife Management* 56:158-164.

Carpenter, L. H. 1979. Forage diversity and dietary selection by wintering mule deer. *Journal of Range Management* 32:226-229.

Carpenter, L. H., R. B. Gill, D. L. Baker, and N. T. Hobbs. 1984. *Colorado's big game supplemental winter feeding program, 1983-84*. Colorado Division of Wildlife, Denver, Colorado, USA.

Caughley, G., and A. R. E. Sinclair. 1994. *Wildlife ecology and management*. Blackwell Scientific Publications, Boston, Massachusetts, USA.

Clark, W. R., and J. R. Medcraft. 1986. Wildlife use of shrubs on reclaimed surface-mined land in Northeastern Wyoming. *Journal of Wildlife Management* 50:714-718.

Clements, C. D., and J. A. Young. 1997. A viewpoint: Rangeland health and mule deer habitat. *Journal of Range Management* 50:129-138.

Cliff, E. P. 1939. Relationship between elk and mule deer in the Blue Mountains of Oregon. *Transactions North American Wildlife Conference* 4:560-569.

Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. *Journal of Wildlife Management* 47:646-663.

Connolly, G. E. 1981. Trends in populations and harvests. Pages 225-243 *in* O. C. Wallmo, editor. *Mule and black-tailed deer of North America*. University of Nebraska Press. Lincoln, Nebraska, USA.

Cooper, S. M., and N. Owen-Smith. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68:446-455.

Coughenhour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. *Journal of Applied Ecology* 28:71-82.

Coughenour, M. B. 1992. Spatial modeling and landscape characterization of an African pastoral ecosystem: a prototype model and its potential use for monitoring drought. Pages 787-810 *in Ecological Indicators, Vol. I*. Elsevier Applied Science. London and New York.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecological Applications* 6:573-593.

Eberhardt, L. L., and J. M. Thomas. 1991. Designing environmental field studies. *Ecological Monographs* 61:53-73.

Elton, C. 1927. *Animal ecology*. Methuen, London, England.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* :2043-2058.

Frank, D. A., and S. J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oeocologia* 96:157-161.

Freddy, D. J., D. L. Baker, R. M. Bartmann, and R. C. Kufeld. 1993. *Deer and elk management analysis guide, 1992-94.* Colorado Division of Wildlife Report No. 17. Fort Collins, Colorado, USA.

Fremont, J. C. 1988. *The exploring expedition to the Rocky Mountains*. Smithsonian Institution Press. Washington, D.C.

Frost, P. H. G., and F. Robertson. 1987. The ecological effects of fire in savannas. Pages 93-141 *in* B. H. Walker, editor. *Determinants of Tropical Savannas*. International Union of Biological Sciences. Paris.

Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwestern Colorado. *Journal of Wildlife Management* 51:634-643.

Geist, V. 1981. *Behavior: adaptive strategies in mule deer*. Pages 157-223 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University Nebraska Press, Lincoln, Nebraska, USA.

Geist, V. 1982. Adaptive behavioral strategies. Pages 219-277 *in* J. W. Thomas and D. E. Toweill, editors. *Elk of North America, ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.

Gill, R. B., L. H. Carpenter, R. M. Bartmann, D. L. Baker, and G. G. Schoonveld. 1983. Fecal analysis to estimate mule deer diets. *Journal of Wildlife Management* 47:902-915.

Gross, J. E., and M. W. Miller. 2000. Chronic wasting disease in mule deer: A model of disease dynamics, control options, and population consequences. *Canadian Journal of Zoology*. In review.

Gross, J. E., N. T. Hobbs, and B. A. Wunder. 1993*a*. Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size? *Oikos* 68:75-81.

Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993*b*. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology* 74:778-791.

Gruell, G. E. 1983. *Fire and vegetative trends in the northern Rockies: interpretations from 1871-1982 photographs*. USDA For. Serv. Gen. Tech. Rep. INT-158.

Hamlin, K. L., S. J. Riley, D. Pyrah, A. R. Dood, and R. J. Mackie. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *Journal of Wildlife Management* 48:489-499.

Hanley, T. A. 1996. Potential role of deer (Cervidae) as ecological indicators for forest management. *Forest Ecology & Management* 88:199-204.

Hay, K. G., G. N. Hunter, and L. Robbins. 1961. *Big game management in Colorado: 1948-1958*. Colorado Department of Game and Fish. Denver, Colorado, USA.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695-713.

Hobbs, N. T., and D. S. Schimel. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *Journal Range Management* 37:402-205.

Hobbs, N. T., and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. *Journal of Wildlife Management* 48:551-560.

Hobbs, N. T., and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *Journal of Wildlife Management* 49:814-822.

Hobbs, R. J., and C. H. Gimingham. 1987. Vegetation, fire, and herbivore interactions in heathland. *Advances in Ecological Research* 16:87-173.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate grazing in sagebrush grassland: Effects of resource competition on secondary production. *Ecological Applications* 6:218-227.

Hobbs, N. T., D. L. Baker, J. E. Ellis, and D. M. Swift. 1981. Composition and quality of elk winter diets in Colorado. *Journal of Wildlife Management* 45:156-171.

Holechek, J. L., and M. Vavra. 1981. The effect of slide and frequency observation numbers on the precision of microhistological analysis. *Journal of Range Management* 34:337-338.

Holechek, J. L., and B. D. Gross. 1982. Evaluation of different diet calculation procedures for microhistological analysis. *Journal of Range Management* 35:721-723.

Humphrey, L. D. 1985. Use of biomass predicted by regression from cover estimates to compare vegetational similarity of sagebrush-grass sites. *Great Basin Naturalist* 45:94-98.

Hunter, G. H. 1954. *Deer-elk-bear seasons in Colorado: 1948-53.* Colorado Department of Game and Fish. Denver, Colorado, USA.

Isaaks, E. H., and R. M. Srivastava. 1989. *An introduction to applied geostatistics*. Oxford University Press. Oxford, U.K.

Jarman, P. J., and A. R. E. Sinclair. 1979. Feeding strategy and the pattern of resource partitioning in ungulates. Pages 130-163 *in* A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti, dynamics of an ecosystem*. University Chicago Press, Chicago, Illinois, USA.

Jassby, A. D., and T. M. Powell. 1990. Detecting changes in ecological time series. *Ecology* 71:2044-2052.

Jensen, J. 1996. *Introductory digital image processing: A remote sensing perspective*. Prentice-Hall.

Julander, O., and J. B. Low. 1976. A historical account and present status of the mule deer in the West. Pages 3-19 *in* G. W. Workman, and J. B. Low, editors. *Mule deer decline in the West: a symposium.* Utah State Univ. Logan, UT.

Keay, J. A., and J. M. Peek. 1980. Relationships between fires and winter habitat of deer in Idaho. *Journal of Wildlife Management* 44:372-380.

Kie, J. G., C. J. Evans, E. R. Loft, and J. W. Menke. 1991. Foraging behavior by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 55:665-674.

Kiker, G. 1998. *Analyses of large herbivore distributions, abundances, and carrying capacity using ecosystem modeling*. Cornell University, Ithica, New York, USA.

Lee, K. N. 1993. *Compass and Gyroscope: Integrating Science and Politics for the Environment*. Island Press. Washington D.C..

Leistritz, F. L., F. Thompson, and J. A. Leitch. 1994. Alien taxa in the north American shrub-steppe four decades after cessation of livestock grazing and cultivation agriculture. *Biological Conservation* 68:95-105.

Leslie, D. M., Jr., E. E. Starkey, and M. Vavra. 1984. Elk and deer diets in old-growth forests in western Washington. *Journal of Wildlife Management* 48:762-775.

Lindzey, F. G., W. G. Hepworth, T. A. Mattson, and A. F. Reese. 1997. *Potential for competitive interactions between mule deer and elk in the western United States and Canada: A review*. Wyoming Cooperative Fisheries and Wildlife Research Unit, Laramie, Wyoming, USA.

Loft, E. R., J. G. Kie, and J. W. Menke. 1993. Grazing in the Sierra Nevada: home range and space use patterns of mule deer as influenced by cattle. *California Fish and Game* 79:145-166.

Loft, E. R., J. W. Menke, and J. G. Kie. 1991. Habitat shifts by mule deer - the influence of cattle grazing. *Journal of Wildlife Management* 55:16-26.

Lundberg, P., and M. Astrom. 1990. Low nutritive quality as a defense against optimally foraging herbivores. *American Naturalist* 135:547-562.

Luo, J., v. Monamy, and B. J. Fox. 1998. Competition between two Australian rodent species: a regression analysis. *Journal of Mammalogy* 79:962-971.

Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with a few large, hooved mammals. *American Naturalist* 119:757-773.

Mackie, R. J. 1976. Interspecific competition between mule deer, other game animals and livestock. Pages 49-54 *in* G. W. Workman and J. B. Low, editors. *Mule deer decline in the west: a symposium*. Utah State University College of Natural Resources and Utah Agricultural Experiment Station, Logan, Utah, USA.

Mackie, R. J., K. L. Hamlin, and D. F. Pac. 1982. Mule deer, *Odocoileus hemionus*. Pages 862-877 *in* J. A. Chapman and G. A. Feldhamer, editors. *Wild mammals of North America: biology, management, and economics*. Johns Hopkins University Press, Baltimore, Maryland, USA.

Main, M. B., and B. E. Coblentz. 1996. Sexual segregation in Rocky Mountain mule deer. *Journal of Wildlife Management* 60:497-507.

McCullough, D. R. 1979. *The George Reserve Deer Herd: population ecology of a K-selected species*. University of Michigan Press, Ann Arbor, Michigan, USA.

Means, H. 1940. *Range survey: Gunnison winter range, August 12th - September 1st, 1940*. Colorado Game and Fish Commission Pittmann-Robertson Report. Project Colorado 4-R. 14pp.

Meffe, G. K., and C. R. Carroll. 1994. *Principles of conservation biology*. Sinauer and Associates, Sunderland, Massachusetts, USA.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63:327-366.

Milewski, V. A, T. P. Young, and D. Madden. 1991. Thorns as induced defenses - experimental evidence. *Oecologia* 86:70-75.

Miller, M. W., and R. H. Kahn. 1999. *Chronic wasting disease in deer and elk: Colorado statewide monitoring and experimental management plan.* 30 September 1999 Draft. Colorado Division of Wildlife, Fort Collins, unpublished.

Miller, M. W., E. S. Williams, C. W. McCarty, T. R. Spraker, T. J. Kreeger, C. T. Larsen, and E. T. Thorne. 2000. Epidemiology of chronic wasting disease in free-ranging cervids. *Journal of Wildlife Diseases*. In review.

Mitchell, J. E., and P. N. S. Bartling. 1991. Comparison of linear and nonlinear overstory-understory models for ponderosa pine. *Forest Ecology & Management* 42:195-204.

Nelson, J. R. 1982. Relationships of elk and other large herbivores. Pages 415-441 *in* J. W. Thomas and D. E. Toweill, editors. *Elk of North America, ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.

Odum, E. P. 1971. *Fundamentals of ecology*. Third edition. W. B. Saunders, Philadelphia, Pennsylvania, USA.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48:474-488.

Pastor, J. B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74:467-480.

Pastor, J. R., and J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139:691-705.

Patterson, D. T. 1996. Impact of alien plants on Grant Basin rangelands. *Weed Technology* 10:384-391.

Pearson, J. T., A. D. Sparrow, and R. T. Lange. 1990. Prolonged exposure to sheep grazing reduces the palatability of Australian saltbush populations. *Australian Journal of Ecology* 15:337-344.

Pearson, S. M., M. G. Turner, L. I. Wallace, and W. H. Romme. 1995. Winter habitat use by large ungulates following fire in northern Yellowstone National Park. *Ecological Applications* 5:744-755.

Peek, J. M. 1982. Elk, *Cervus elaphus*. Pages 851-861 *in* J. A. Chapman and G. A. Feldhamer, editors. *Wild mammals of North America: biology, management, and economics*. Johns Hopkins University Press, Baltimore, Maryland, USA.

Peek, J. M., and A. L. Lovass. 1968. Differential distribution of elk by sex and age on the Gallatin winter range, Montana. *Journal of Wildlife Management* 32:553-5570.

Phillips, G. E., and A. W. Alldredge. 1999. Effects of human-induced disturbance during calving on reproductive success of elk. *Journal of Wildlife Management*. Submitted.

Pike, Z. M. 1966. *Sources of the Mississippi and western Louisiana Territory*. University Microfilms, Inc. Ann Arbor, Michigan, USA.

Roath, R., L. Carpenter, B. Riebsame, and D. Swift. 1999. *Gunnison Basin habitat assessment project. Report to the Habitat Partnership Program Committee grazing animal-habitat balance*. Unpublished Report. 23pp. + Appendices.

Robinette, W. L., C. H. Baer, R. E. Pillmore, and C. E. Knittle. 1973. Effects of nutritional change on captive mule deer. *Journal of Wildlife Management* 37:312-326.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. *Ecology* 76:2097-2106.

Roth, C. 1963. Diary of a market hunter. *Colorado Outdoors* 12(6):30-39.

Rowland M. M., L. D. Bryant, B. K. Johnson, J. H. Noyes, M. J. Wisdom, and J. W. Thomas. 1997. *The Starkey Project: history, facilities, and data collection methods for ungulate research*. U. S. Department of Agriculture Forest Service General Technical Report PNW-GTR-396.

Sinclair, A. R. E. 1979. The eruption of the ruminants. Pages 82-103 *in* A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti, dynamics of an ecosystem*. University of Chicago Press, Chicago, Illinois, USA.

Smith, R. L. 1980. *Ecology and field biology*. Third edition. Harper and Row, New York, New York, USA.

Sparks, D. R., and J. C. Malecheck. 1968. Estimating percentage dry weight in diets using a microscopic technique. *Journal of Range Management* 21:264-265.

Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* 140:325-348.

Stewart, O. A., W. W. Murdoch, and K. R. Parker. 1986. Environmental Impact assessment: "Pseudoreplication" in time? *Ecology* 67:929-940.

Stohlgren, T, J, L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications.* In press.

Stohlgren, T. J., G. W. Chong, M. A. Kalkhan, and L.. D. Schell. 1997. Multi-scale sampling of plant diversity: effects of the minimum mapping unit. *Ecological Applications* 7:1064-1074.

Theobald, D. M., J. M. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. *Landscape and Urban Planning* 39:25-36.

Thorne, E. T., N. Kingston, W. R. Jolley, and R. C. Bergstrom (editors). 1982. *Diseases of Wildlife in Wyoming*. Second edition. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.

Tracy, B. F., and S. J. McNaughton. 1997. Elk grazing and vegetation responses following a late season fire in Yellowstone National Park. *Plant Ecology* 130:111-119.

Trammell, M. A., and J. L. Butler. 1995. Effects of exotic plants on native ungulate use of habitat. *Journal of Wildlife Management* 59:808-816.

Turner, M. G., Y. Wu, L. L. Wallace, W. H. Romme, and A. Brenkert. 1994. Simulating winter interactions among ungulates, vegetation and fire in Northern Yellowstone Park. *Ecological Applications* 4:472-496.

Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. *Journal of Wildlife Management* 63:315-326.

Veblen, T. T., and D. C. Lorenz. 1991. *The Colorado Front Range: A Century of Ecological Change*. University of Utah Press. Salt Lake City, Utah, USA.

Verme, L. J. 1965. Reproduction studies on penned white-tailed deer. *Journal of Wildlife Management* 29:74-79.

Verme, L. J. 1967. Influence of experimental diets on white-tailed deer reproduction. *Transactions North American Wildlife and Natural Resources Conference* 32:405-420.

Verme, L. J. 1977. Assessment of natal mortality in upper Michigan deer. *Journal of Wildlife Management* 41:700-708.

Verme, L. J. 1979. Influence of nutrition on fetal organ development in deer. *Journal of Wildlife Management* 43:791-796.

Wallmo, O. C. 1981. Mule deer and black-tailed deer distribution and habitats. Pages 1-25 *in* O. C. Wallmo, editor. *Mule and black-tailed deer of North America*. University of Nebraska Press, Lincoln, Nebraska, USA.

Walters, C. J., S. Collie, and T. Webb. 1988. Experimental designs for estimating transient responses to management disturbances. *Canadian Journal of Fishery and Aquatic Science* 45:530-538.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060-2068.

Walters, C. J. 1986. *Adaptive Management of Renewable Resources*. Macmillian, New York. 300pp.

Warner, T. J. (editor). 1995. *The Dominguez-Escalante journal: their expedition through Colorado, Utah, Arizona, and New Mexico in 1776.* University of Utah Press. Salt Lake City, Utah, USA.

White, G. C. 1996. NOREMARK: Population estimation from mark-resighting surveys. *Wildlife Society Bulletin* 24:50-52.

White, G. C., and R. M. Bartmann. 1996. *Mule deer status report*, unpublished. Colorado Division of Wildlife, Fort Collins, Colorado, USA

White, G. C., and R. M. Bartmann. 1997. *Mule deer status report, revised*, unpublished. Colorado Division of Wildlife, Fort Collins, Colorado, USA.

White, G. C., and R. M. Bartmann. 1998. Effect of density reduction of overwinter survival of free-ranging mule deer fawns. *Journal of Wildlife Management* 62:214-225.

Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285-1301.

Williams, E. S., and I. K. Barker (editors). 2000. *Infectious diseases of wild mammals*. Third edition. Iowa State University Press, Ames, Iowa. (in press)

Wisdom, M. J., J. G. Cook, M. M. Rowland, and J. H. Noyes. 1993. *Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range*. U. S. Department of Agriculture Forest Service General Technical Report PNW-GTR-311.

Wood, A. K., R. E. Short, A. E. Darling, G. L. Dusek, R. G. Sasser, and C. A. Ruder. 1986. Serum assays for detecting pregnancy in mule and white-tailed deer. *Journal of Wildlife Management* 50:684-687.

Wydeven, A. P., and R. B. Dahlgren. 1985. Ungulate habitat relationships in Wind Cave National Park. *Journal of Wildlife Management* 49:805-813

Young, T. P. 1987. Increased thorn length in Acacia drepanolobium- an induced response to browsing. *Oecologia* 71:436-438.

Young, J. A., and W. S. Longland. 1996. The role of United States Department of Agriculture, Agricultural Research Service in the control of introduced weeds. *Castanea* 61:261-270.