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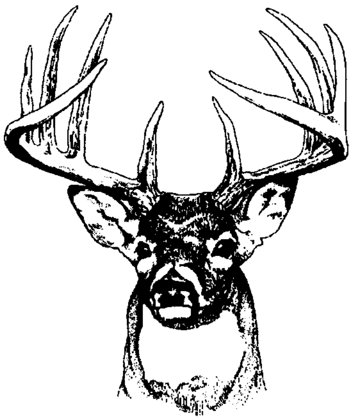

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SENIOR AUTHORS

DONALD J. ARMENTROUT
Eagle Lake Resource Area
Bureau of Land Management
Susanville CA 96130

JEFFREY L. BECK
Department of Fish and Wildlife
Resources
University of Idaho
Moscow ID 83844-1136

KIRBY D. BRISTOW
Arizona Game & Fish
Department
2221 W Greenway Rd
Phoenix AZ 85023

LEN H. CARPENTER
Wildlife Management Institute
4015 Cheney Dr
Fort Collins, CO 80526

BOB K. CARROLL
Texas Parks and Wildlife
3852 Pine Ridge Road
La Grange, TX 78945

ART FULLER
Arizona Game & Fish
Department
5325 N Stockton Hill Rd
Kingman AZ 86401-5499

SONIA GALLINA
Depto. Ecología y
Comportamiento Animal
Instituto de Ecología A.C.
Apdo. Postal 63
Xalapa 91000, Veracruz
Mexico

JIM HEFFELFINGER
Arizona Game & Fish
Department
555 N Greasewood Rd
Tucson AZ 85745-3612

MIKE HESS
Nevada Division of Wildlife
PO Box 10678
Reno NV 89520

V. W. HOWARD, JR.
Department of Fishery and
Wildlife Sciences
New Mexico State University
Las Cruces NM 88003

RAYMOND M. LEE
Arizona Game & Fish
Department
2221 W Greenway Rd
Phoenix AZ 85023

SALVADOR MANDUJANO
Departamento Ecología Y
Comportamiento Animal
Instituto De Ecología A.C.
Apdo Postal 63 Xalapa 91000
Veracruz, Mexico

PATRICK E. MATTHEWS
Oregon Department of Fish &
Wildlife
65495 Alder Slope Rd
Enterprise OR 97828

DALE R. MCCULLOUGH
Ecosystem Science Division
Department of Environmental
Science
151 Hilgard Hall
University of California
Berkeley CA 94720-3110

ERIK E. NORELIUS
Department of Zoology and
Physiology
University of Wyoming
Laramie WY 82071

RICHARD A. OCKENFELS
Arizona Game & Fish
Department
2221 W Greenway Rd
Phoenix AZ 85023

ROCKY MOUNTAIN ELK FOUNDATION
PO Box 8249
Missoula MT 59807

GARY J. ROLOFF
Timberland Resources
Boise Cascade Corporation
PO Box 50
Boise ID 83728-0001

HALL SAWYER
Wyoming Coop. Fish and
Wildlife Research Unit
Box 3166 University Station
Laramie WY 82071

HARLEY SHAW
PO Box 370
Chino Valley AZ 86323

WENDELL G. SWANK
2326 Quail Run Rd
Cottonwood AZ 86326

JOHN C. TULL
Wildlife & Fish Science
School of Renewable
Resources
325 Bio Sciences East
University of Arizona
Tucson AZ 85721

MARK C. WALLACE
Department of Range,
Wildlife, and Fisheries
Management
Texas Tech University
Lubbock TX 79409-2125

GARY C. WHITE
Fisheries & Wildlife Biology
Colorado State University
Ft Collins CO 80523

Deer in the West

LEN H. CARPENTER
Wildlife Management Institute, 4015 Cheney Drive, Fort Collins, CO 80526

Abstract: A historical review of mule deer and white-tailed deer population estimates is presented for both species. Problems involved in obtaining white-tailed deer population estimates for the western states and provinces are discussed with a recommendation for all agencies to separate the 2 species in their management programs. It is pointed out that when mule deer and white-tailed deer populations coexist; white-tailed deer generally are favored. The complex question of what is rangeland health relative to mule deer is explored through a review and synopsis of a recent paper on mule deer habitat in the Great Basin (Clements and Young 1997). It appears that a common factor in today's decline of mule deer as compared to historic populations in the Southwest is lowered fawn:doe ratios. The big question, yet unanswered is why are these fawn ratios lower? Blame is commonly placed on factors such as increased competition from elk, impacts of predators, loss of habitat, over harvest, or some combination of all. The role of "good food" and importance to deer nutritional well being is discussed. It is suggested that absence of standardized inventory and management methodologies complicate this problem. It is recommended that efforts be focused on measuring fawn survival rates and incorporating these data into improved population models. The opportunity to explore use of Adaptive Harvest Management on a regional (multi-state) basis is suggested as a way to stabilize the volatile and political arena of hunting season establishment. A call for greater unity and broader partnerships in deer management is highlighted.

INTRODUCTION

I have been asked to provide a general overview of population trends for the deer species in the West and discuss habitat and political challenges that affect deer management. I have been asked to assess what the future holds for managers of these populations and to provide anything else I feel important. I have a suspicion that the "anything else" category may dominate my presentation. But what the heck, I am giving a keynote address and I figure that should license me to free lance a bit! On the serious side, I will try to follow form of a keynote address and hit on topics or issues that I feel all of you are gathered at this meeting to discuss. I will not attempt to pursue any of them in too much depth as I am confident that others on the agenda will do an adequate job of that.

Key Issues

Let us begin with a quick overview of the key issues that are before us at this workshop. I will focus on issues labeled as "causes" of the apparent mule deer decline. At the top of the list I would put habitat quality and quantity. As I travel over the West, the impacts of man's activities are obvious everywhere. More often than not, these changes are occurring on deer ranges. This is especially true in the intermountain West. Today, questions of interspecies competition seem to be high on most everyone's list. This would include impacts of increasing elk populations on mule deer, and impacts of expanding white-tailed deer populations on mule deer.

We would be abrogating our responsibility if we did not add impacts of hunting to the list. The growing demand for hunting of mature bucks is a common problem in almost every state. This demand has to be balanced with expectations of hunters to hunt every year, and with consequences to agency and local economies if hunter numbers are limited too severely. The low buck:doe ratios occurring in most states as a result of unlimited or very liberal hunter numbers are becoming an untenable problem in many states. We must find ways to better balance this equation.

From the beginning of time, any discussion on deer management would include a discussion on predation. That is true today. It appears that when populations are at their lowest, questions on impacts of predators become more intense. Whether this is cause and effect is not clearly understood. It does seem that effect of predators is greatest when populations are struggling or at lower levels. Effect of predators is also greater when habitat is in poor condition. One thing for sure, the changing social climate in today's world precludes any widespread predator control programs. The practice of single species management is over.

Another topic frequently mentioned in the decline of mule deer is disease. This is a difficult one. Our ability to assess presence or impact of diseases on free-ranging wildlife is very limited. Diseases do affect deer populations. In general, it seems that these impacts are limited to localized areas and under specialized environmental conditions. However, 1 emerging disease found in mule deer and elk in northern Colorado and southern Wyoming that is generating growing concern is chronic wasting disease (Spraker et al. 1997). This disease has similarities to scrapies and appears to be present in a larger segment of the deer and elk population than initially thought. This situation must be watched carefully.

The final issue on my radar screen is apathy. I believe part of the problem is that overall management of deer has been neglected over the past decade. In many states, managers, hunters, and agencies have become enamored with elk. Deer have been taken for granted. It is time that deer management and deer habitat conservation receives more attention.

Population Trends for Mule and White-tailed Deer

Details on population trends for the deer species in each of the western states and provinces will be presented elsewhere at this conference, consequently I will not attempt to detail population status for each state and province at this time. I will present historic range-wide population estimates for mule deer and white-tailed deer with comparisons to more recent estimates. I will not address black-tailed deer numbers separately.

I consulted several sources for my historic population estimates for the 2 species (Seton 1937, Rue 1978, Schmidt and Gilbert 1978, Wallmo 1981, Halls 1984). In addition, past reports from the western states deer workshops were reviewed and in some cases further interpretations of the estimates presented were made. Timely, range-wide estimates for deer species are not readily available.

Almost any biologist is familiar with estimates of populations of North American game animals in 1600 made by the famous naturalist Ernest Thompson Seton (Seton 1937). Seton made his projections by estimating the total land base that would have been habitat for a given species and combined this with an estimate of density per land unit and projected the totals. As one can imagine, considering the huge land bases available for deer to occupy in the 1600s, the estimates are large.

Seton's estimate for white-tailed deer populations in 1600 was 40 million. Almost all experts have considered this estimate too high (Rue 1978, McCabe and McCabe 1984). A total of 30 million is frequently used. In 1800, Seton estimated 14 million white-tailed deer. For a more detailed presentation on historic white-tailed deer distribution and density, the reader is referred to the discussion on historical aspects of white-tailed deer presented by McCabe and McCabe (1984).

For mule deer, Seton estimated 10 million in North America at the arrival of Europeans (Rue 1978). The next key date when range-wide population estimates were generated was shortly after the turn of the century in 1908. This was a time of great natural resource concern following several decades of rapid deplenishing numbers of most all wild animals in North America. Interestingly, the estimate were similar and thought to be less than 500,000 white-tailed deer (McCabe and McCabe 1984) and 500,000 mule deer (Wallmo 1981).

The next range-wide estimates I could find for the 2 species were made for mule deer in 1950 at 2.3 million (Wallmo 1981), and for white-tailed deer in 1980, 14 million (McCabe and McCabe 1984). More recent estimates (early 1990s) total 35 million white-tailed deer (my extractions of several data sets) and approximately 3 million mule deer (Western States Summaries). Interestingly, total estimates for mule deer over their entire range have varied little for the past 25 years (Western States Summaries).

I totaled numbers for white-tailed deer for the 11 western states and provinces reporting white-tailed deer in the 1995 Western States Deer and Elk Workshop Report. In certain states or provinces, I had to interpret or calculate the number of white-tailed deer as these states or provinces did not separate white-tailed deer from mule deer in their data. The resulting total was approximately 5 million white-tailed deer in the West. Of this total, Texas reported nearly 4 million.

Obviously, any of these estimates must be taken with a bit of caution, but they do illustrate the magnitudes of change and the large impacts (both good and bad) that man and man's activities have had on these populations and their habitats.

I urge representatives from the various states and provinces who still combine data for the 2 species to seriously consider separating the data bases. The need will only grow for more definitive estimates of these important species. For various reasons, there is a growing trend for states and provinces to not present population data in their biennial reports to the western deer workshop. This is regrettable as there is no other source for this information. I urge organizers of each workshop to request this information.

Mule Deer-White-Tailed Deer Interactions

For my discussion on deer in the West, I will highlight what we know about interactions of mule deer and white-tailed deer populations when they occupy the same habitats. Frequently where the 2 species occur together, managers express concern that white-tailed deer are increasing at the expense of mule deer. Why is this? The reason most often advanced is that agricultural changes to the habitat favor white-tailed deer over mule deer. White-tailed deer seem to adapt well to agricultural crops. Geist (1991) theorized that mule deer need a more complex habitat, either broken by topography or downed logs etc. to favor their "stotting" strategy for predator avoidance. It has also been theorized by Geist (1991) that white-tailed deer are more competitive breeders when the 2 species are together, with white-tailed bucks breeding mule deer does. Geist further suggests that resulting hybrids, unable to "stot," are inefficient at predator avoidance making them more susceptible to predation.

Geist also suggests that hunting practices in most states today that place heavy pressure on bucks results in a greater reduction of mule deer bucks than for the more nocturnal and secretive white-tailed bucks (Geist 1991). Geist further proposes that use of heavier cover for escape by white-tailed bucks is an advantage over the tendency for mule deer bucks to flee in more open terrain. Like so many other topics concerning deer, however, the generality that white-tailed deer fare better than mule deer when they are together apparently does not hold true everywhere. deVos (pers. commun. 1997) reported that in Arizona mule deer seem to be holding their own in these situations.

From my perspective, over the broad range of deer in the West it seems that distribution of white-tailed deer is increasing substantially. I attribute this change largely to alteration of native habitats to agriculture and agriculture-related activities. It may become necessary for managers to consider more intensive habitat and/or hunting management if this trend is undesirable.

Rangeland Health and Mule Deer

The apparent decline in mule deer numbers raises the question of the health of the habitat. What is rangeland health relative to mule deer? Is it shrub density, yield, and vigor? Is it status of the under story forbs and grasses? Is it age structure of the shrubs or extent of tree canopy? Is it a diverse mixture of various habitat types? These questions and others have been debated for decades.

One thing for certain, the relationship between "health" of the land and mule deer population performance is complex. Numerous studies and a myriad of exclosures across the range of mule deer demonstrate that grazing herbivores have definite impacts on the vegetation complex. It is tempting to compare deer habitats today to those present at the time of the mountain man making the assumption that the "undisturbed" vegetation complexes of that time were optimum for deer. This may not be true.

In a recent viewpoint paper, (Clements and Young 1997) point out that in the Great Basin area of western Nevada and eastern California, journals of the mountain man during the period 1820-1840 indicate few mule deer. These areas during the 1950s supported thousands of mule deer. What happened in 100 years? It is likely that many unrelated, but contributing events shaped this response. While I may not agree with all of the points in the paper by Clements and Young, I do think it provides a good framework for discussion on the topic of mule deer habitat.

Clements and Young (1997) restructure key events in the Great Basin from the 1880s to recent times and paint a picture of the types of habitat changes that may have occurred to produce the mule deer responses recorded over time. The story begins when livestock were introduced into the western Great Basin in 1860s. Livestock numbers increased rapidly in the 1870s. Dominant perennial bunch grasses could not tolerate the intense grazing and were greatly reduced (Clements and Young 1997). As grasses decreased they were replaced by sagebrush seedlings. In addition, the winter of 1889-90 was severe and resulted in large losses to both livestock and wildlife. Furthermore, the years 1889-1896 were extremely wet in the Great Basin (Upchurch and Brown 1951). Finally, records demonstrate that apparently this combination of events led to the large stands of bitterbrush characteristic of the Great Basin to establish in the period 1890-1910 (Hormay 1943).

The increase in shrub cover caused

shepherds to set fires to reduce the shrubs (Clements and Young 1997). Small mammals cache bitterbrush seeds resulting in the existence of seed banks for bitterbrush. This is not the case for sagebrush and sagebrush plants were reduced. Lack of competition for soil moisture would have further favored establishment of large stands of bitterbrush. Reduced numbers of deer and livestock following the hard winter also contributed to this vegetation response. Clements and Young (1997) speculated that these large stands of bitterbrush came into their productive best during the 1950s, resulting in the large deer populations recorded at that time.

The point of this discussion is that a series of events occurred approximately 60 years before the response was noted in the deer population. This long time lag makes cause and effect predictions almost impossible. Long-term and small vegetative changes may be occurring annually, but our ability to detect or measure the change is limited. As discussed in Clements and Young (1997), Sneva (1972) working in the sagebrush steppe of Oregon reported that for every 1% cover in sagebrush canopy between 10 and 20% canopy, there was a 10% decrease in herbaceous yield.

Sneva further pointed out that if at 10% canopy cover of sagebrush the herbaceous yield was 100 units per m^2, an increase in sagebrush cover to 15% would decrease herbaceous yield to 50 units, and if canopy cover increased to 20%, herbaceous yield would approach zero. These changes would be dramatic for a grazing mule deer. Furthermore, a 5 or 10% change in sagebrush canopy would not be detectible by casual observation.

Because of the long time lag and the difficulty in measuring rangeland health relative to mule deer, it is not worthy of investing huge amounts of fiscal or human resources into the problem. These resources could best be spent monitoring responses of the mule deer population(s) in question.

Mule Deer Recruitment--A Change Over Time?

As identified earlier, there are a number of factors commonly referenced as causes of the apparent mule deer decline. These include habitat quality, habitat quantity, inter-species competition, hunting, predation, diseases, and apathy. Of these, what appears to be the more important? To answer this question, it is first important to try to better understand what population response is resulting in the lower numbers of mule deer. Is it adult or fawn survival? Is it a lower conception rate? Is it early fawn survival? Based on discussions with earlier mule deer workers, and on the literature, I propose that a key difference in mule deer parameters today, as compared to times when populations were expanding, is a lower measured fawn:doe ratio in early winter.

Robinette (1976), summarizing several study areas and many years of observation in Utah and Nevada during the 1930s, 40s and 50s, presented fawn:100 doe ratios that approached or exceeded 100. Average fawn doe ratios of >75 fawns per 100 does were common. Interestingly, Robinette (1976) reported that several herds he studied had fall composition counts with 100 fawns per 100 does, even when herds were approaching or at peak numbers. These peak numbers were the large mule deer populations in the Great Basin that are so commonly referred to today as "the good old days." These populations were huge.

Robinette conducted his Oak Creek, Utah, study from the late 1940s into the 1950s. His measured fawn:doe ratios averaged about 68 fawns:100 does which was about 1/3 less than ratios measured in the late 1930s and early 1940s. Robinette

(1976) observed that "the lower fawn crops prevailed despite a substantial reduction in deer numbers, cattle use, and even coyote numbers." Robinette further stated *"the decline continued despite the introduction of "1080" in 1947 which drastically reduced coyote numbers. The decline was almost certainly associated with an overstocked summer range."*

Robinette's analyses continued with comparisons of vegetation enclosures that were established in the early 1950s. He remarked, *"failure of the preferred deer forbs to recover was evident from observations within a set of enclosures established in 1952."* He concluded with the remark that *"observations at Oak Creek make it quite evident that merely reducing a herd is no assurance that damaged range will recover."*

I conclude several things from these studies and observations. First, they demonstrate that in times of expanding deer populations, observed fawn:doe ratios are high, sometimes exceeding 100 fawns:per 100 does. Secondly, at times of decreasing populations, fawn:doe ratios are considerably less. Thirdly, Robinette associates this continued decline with condition of the summer range. I interpret this to be a nutritional-reproductive link. These observations do not tell us if the decrease in fawn ratios is a result of poor fawn production or poor fawn survival. Based on reproductive performance for mule deer reported in many studies across the West (Connolly 1981), it is probable that conception or fawn production *in utero* remained high. If this were the case, then loss of fawns primarily occurs from birth to the fall measurement time.

Evidence that this reduced fawn recruitment ratio is operating today is manifested in many western deer herds. As an example, in Wyoming over the time frame of the early 1970s to 1995, 2 mule deer herds have shown decreases from more than 90 fawns:100 does to ratios of less than 60 fawns:100 does (Bohne 1997) Conversations with, and reports from, many state mule deer biologists further document this trend. Cause of this loss is not clear.

I suggest, however, that efforts to monitor mule deer populations recognize this characteristic and focus on measurements that would elucidate fawn survival rates from birth through the first 6 months of life. It would be important to learn if the reduction in fawns is coming before birth, at birth, or shortly after birth.

Speculated Causes of the Decline

The most common listed causes of the apparent mule deer decline seems to be the following: competition from elk, predation, loss of habitat, over harvest, or some combination of the above. It is probable that no 1 cause is responsible across the range of mule deer. As discussed in the previous section, information as to the timing of fawn losses would shed more light on the ultimate cause for the problem. It is my professional judgement that the overall combination of listed causes are involved and all exacerbated by a continuing loss of habitat quality and quantity. A good portion of the loss of habitat (both quality and quantity) is resulting from vegetation succession. This is especially true with increases in pinyon-juniper (*Pinus edulis-Juniperus* spp.) forests across the Southwest. Natural plant succession is not generally conducive to deer habitat.

If we are to accept the idea that lowered fawn recruitment is the main problem, it follows that habitat quality (either summer or winter or both) is a major factor. Habitat quality could manifest its impact in several ways. If summer ranges are inadequate, mule deer would be unable to obtain sufficient nutrition to withstand upcoming winter. Fawn nutrition as provided by the does' milk could be an issue. Poor fawn nutrition would lead to poor growth and result in fawns being small heading into winter. If habitat quality is poor in summer, this could also lead to lower reproductive rates of the doe. It is known that all mammalian females must reach some level of body fat before they are able to ovulate and conceive. Obtaining this level of body fat is especially a problem for yearling female deer that are also still growing.

Inadequate winter ranges could contribute to poor fawn recruitment as fawns would find inadequate forage to get them through the winter (Bartmann et al. 1992). Competition for "good food" (Hobbs and Swift 1989) between fawns and does may be a problem with inadequate winter ranges. Deer with a smaller rumen require higher quality food than do elk. Elk can feed on much lower quality forage and prosper. Obviously, poor winter ranges with small amounts of "good food" could result in lower nutrition of does. Growth and development of fawns suffer and this could result in lower fawn survival. Even though this relationship is unclear, observations by Robinette (1976), speculation on rangeland health by Clements and Young (1997), and hypotheses by many other workers over many different study areas and time periods suggest that the nutritional link between mule deer habitat and mule deer population performance is real.

Habitat quality as reflected by vegetative cover and structure, is an issue for predator avoidance (Geist 1991). Poor nutrition could render deer more susceptible to predators as well. More work needs to be done on interaction of habitat quality and predator avoidance for deer. The listed factor of elk competition would contribute to a decrease in overall habitat quality for mule deer.

What Should We Measure?

Given this background, what measurements should deer managers focus on to improve knowledge bases? The complexity of measuring vegetation and the long-term interactions of habitat with population performance suggest that measurements of population performance are the most promising.

Rising costs of inventory mandates that only the most efficient and most applicable measures be taken. Modeling processes have identified the "most sensitive parameters." These are measures that contribute most significantly to outcomes of the model. A characteristic of these parameters is that they tend to vary most over time. In other words they have a wide range of values from year-to-year. With mule deer, it appears that yearly fawn survival is 1 parameter that fits this description best (White and Bartmann 1998). Consequently, fawn survival should be the focus of monitoring efforts.

Radio telemetry has greatly facilitated this inventory, albeit it is expensive. It is necessary to mark adequate numbers of animals before data obtained are statistically reliable. In addition to cost of collars and applying them, there is the additional cost of monitoring animals on a frequent basis. However, data obtained are most useful to constructing useable population models. It is suggested that 1 approach may be the selection of "key" population units representing varying vegetative and climactic conditions. These "key" areas can then be used as indices to other unmeasured populations for modeling purposes.

It will also be necessary to have basic population structure information. It is probable that a combination of the fawn survival data and population composition measures would be most efficient (White and Bartmann 1997). Sampling studies to elucidate the best combination of inventory efforts should be done. The goal of this work should be development of the most dependable and defensible population models to guide management. These data, gathered over a series of years with varying weather components, would significantly improve management models.

The increasing political arena affecting establishment of deer hunting seasons results in an unstable harvest future. These political decisions continue to erode application of the best biology and science into the process. Another result is a wide "hodge podge" of deer hunting seasons among the various states that are constantly varying with little opportunity to measure effects of the established seasons. This uncertainty across states necessitates that we take a more innovative approach to the process of setting hunting and harvest methodologies. This same problem was faced in waterfowl management in recent years (Williams and Johnson 1995) . The approach taken was to apply concepts of adaptive management (Walters 1986). In waterfowl circles the term is adaptive harvest management.

I propose that adaptive harvest management concepts would work for deer management as well. First there would need to be a plan initiated that organized a regional (multiple state approach) that established agreed upon inventory approaches for census, herd composition, fawn survival, and harvests. Standardized data analyses procedures would also be implemented. To fund this effort I suggest administrative funding from Federal Aid. I also suggest that this program be headquartered and supervised from 1 location in the West. A cooperative fish and wildlife research unit might be the most logical place for coordination of this initiative. This centralized unit would be most important to the rigorous treatment of the data, especially with relation to development of alternate models that best use the data. It would be important to recognize that many political, cultural, and environmental differences exist in the individual states and that these differences must be considered as this process was implemented.

Adaptive harvest management calls for development of goals for harvest management activities. Goals could be defined as desired buck:doe ratios, fawn:doe ratios, or as population density levels. The process also calls for selection of a limited number of regulation alternatives. The process would also necessitate identification and selection of alternative models that best explained deer population dynamics. For instance, model options of additive or compensatory mortality responses to hunting (Bartmann et al. 1992) could be selected. Using these goals and models, a set of regulation options would be chosen and evaluated.

Each year, or group of years, an optimal regulation package would be implemented that seemed to best fit the environmental and habitat conditions. After the regulatory decision was made, each alternative population model would be used to predict population size and attributes for the following year(s). Once monitoring data become available, models that more accurately predict observed population size or attributes gain credibility, while models that are poor predictors lose credibility. These new assessments of model credibility are used to start another iteration of the process.

Other Management Recommendations

Some states continue to combine data on white-tailed deer and mule deer. Efforts should be made to separate these databases. Issues and management of the 2 species are sufficiently different to warrant this effort. This is especially important for population and harvest inventories.

Deer biologists should strive to standardize inventory procedures. This is especially important in model development. Similarly designed studies across several states would be valuable in increasing applicability of results.

It is also important that deer biologists and managers recognize that days of single species management are over. This will necessitate different approaches to plans for harvest and habitat management. Management frameworks encompassing ideas of landscape ecology and ecosystem management are in place and must be considered when single species outputs are desired.

Finally, apathy towards deer and deer management should be overcome with fresh and enthusiastic approaches to these species. They have been taken for granted for too long. It is the era of partnerships. Many of the problems cannot be solved by 1 agency or state alone. It will take everyone working together to make a difference in deer management as we near the new millennium.

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Status of Elk in the West

Rocky Mountain Elk Foundation, PO Box 8249, Missoula MT 59807

INTRODUCTION

Prior to the arrival of European settlers, an estimated 10 million elk roamed North America. Unregulated hunting by both subsistence and market hunters, along with loss of habitat, decimated elk numbers to less than 100,000 animals by the late 1800s. Today, North American elk populations have reached their highest levels in recent history. At the end of 1995, Canadian and U.S. elk populations totaled more than 960,000 animals.

State and provincial wildlife agencies manage elk herds primarily through annual hunting seasons. Each year, elk harvests can vary based on a state's overall population management objectives and hunter success. In 1995, hunters killed the most elk in Colorado - which is also the state with the highest elk population. The same trend occurred in Canada, where British Columbia has the most elk and also the most elk harvested.

Elk populations have experienced dramatic growth over the last 2 decades. Over the next 3 to 5 years, states and provinces will individually manage for specific population objectives and, overall, continental elk populations should remain stable. Elk hunter numbers are expected to stabilize or grow slightly in the near future. Small changes to existing elk numbers will occur as midwestern and eastern states, where elk historically roamed, explore the possibilities of elk reintroduction.

HISTORY OF ELK POPULATIONS

Ernest Thompson Seton (1927) estimated 10 million elk lived in North America prior to European settlement. By 1907, due to uncontrolled hunting and habitat loss, less than 100,000 elk survived and populations continued to decline. In 1922, around 90,000 elk remained, with nearly 40,000 of those in the Yellowstone-Teton area and Canada. Reintroductions of elk back into their historic ranges began in the early 1900s, with most of the transplant stock taken from Yellowstone National Park and the National Elk Refuge in Jackson Hole, Wyoming. By 1970, North American elk populations had risen to around 500,000.

RECENT HISTORY

Together in 1975, Canada and the United States were home to more than 552,000 elk in 19 states and 5 provinces. At that time, the U.S. elk population had reached about 512,000, and Canada's 5 elk provinces held just over 40,000 elk.

Ten years later, elk populations had grown to more than 708,000 in the United States, with more than 60,000 in Canada - almost a 40% increase overall. Three additional states - Arkansas, Kansas, and North Dakota - had elk populations to add to the list. Most of the elk population growth from 1976 to 1985 occurred in 6 states: Colorado added 70,000 elk, Idaho's population was up by 35,000, Wyoming's increased by 27,000, Utah had an additional 22,000, Arizona's herds jumped by 20,000, and Montana herds grew by 10,000 elk. In Canada, British Columbia added 15,000 elk. This growth in elk numbers came mostly from Rocky Mountain elk herds. But, tule elk also more than doubled their numbers from 600 in 1975 to 1,400 in 1985.

By 1995, more than 878,000 elk roamed the United States and more than 89,000 lived in Canada. The total number of elk states grew again in 1995, with the reintroduction of 25 wild elk to Wisconsin. Today, most elk herds live in the western states and provinces. Colorado's 203,000 elk make up nearly 21% of the 1995 total continental population. Rounding out the remaining top 5 elk states are: Oregon (120,000 elk), Idaho (116,000 elk), Wyoming (102,439 elk) and Montana (93,401 elk). Together, the top 5 elk states harbor 65% of North America's elk. Canada's elk are most abundant in British Columbia, with 48,300 animals, followed by Alberta's 21,000 elk and Saskatchewan's 11,000.

Throughout the last 20 years, the 9 largest elk states (Arizona, Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Washington, and Wyoming) have maintained well over 95% of the total U.S. elk population. One state, Colorado, has consistently maintained more than 20% of the total U.S. elk population. In just 20 years, Canada's elk population rose by 122% going from 40,000 in 1975 to 89,000 in 1995.

As the numbers show, North America's elk populations have nearly doubled in just 20 years. But today, even with nearly a million elk roaming North America, these majestic creatures only exist at about 10% of their estimated pre-settlement numbers.

ELK HUNTERS AND DAYS AFIELD

The number of elk hunters has steadily increased over the last 2 decades. During 1975, more than 530,000 people hunted elk in the United States and more than 21,000 in Canada. By 1985, U.S. elk hunters numbered about 647,000 with 55,000 elk hunters in Canada.

From 1976 to 1985, Arizona's elk hunters nearly doubled to more than 10,000, Utah's 10,000 new hunters brought their total to 30,000 hunters, and 23,000 new elk hunters went afield in Oregon, bringing their total to 130,000. Colorado had the largest number of elk as well as elk hunters in 1985, with more than 140,000 hunters. By 1985, more folks began hunting Roosevelt elk, with an increase of nearly 15,000 Roosevelt elk hunters in Oregon and 13,000 in Washington.

A decade later, nearly 800,000 people hunted elk in the United States, an increase of nearly 150,000 hunters in just 10 years. In Canada during that same period, elk hunters decreased by 18,000 to around 37,000. Colorado hunters killed the most elk in 1995 (36,171), followed by Idaho (22,437) and Oregon hunters (22,395). British Columbia's 1995 elk harvest totaled 2,893, with 2,241 elk killed in Alberta, and 850 in Manitoba.

In 1975, U.S. elk hunters spent almost 2.5 million days afield hunting elk. By 1985 U.S. hunters were out chasing elk for 3.5 million days, and 10 years later, they spent a total of 5 million days afield. Elk hunting days peaked in Canada in the mid-1980s at about 333,000 days then dropped to 260,000 in 1995.

Over the last 20 years, the number of U.S. elk hunters has always remained near a 1-to-1 ratio with the number of elk: In 1975 there were 530,000 elk hunters and 512,000 elk; in 1985 elk numbers had reached 708,000, with 648,000 hunters; and in 1995, nearly 800,000 elk hunters pursued 878,000 elk. (An interesting note regarding the Roosevelt elk subspecies: the number of hunters pursuing Roosevelt elk in 1995 [103,000] exceeded the number of elk [93,000] - not necessarily a surprising fact considering Roosevelt elk can absorb more hunting pressure in their densely wooded habitat.) Canada did have a near 1-to-1 ratio of elk to hunters in 1985, with 60,000 elk and 55,000 hunters. But by 1995, that ratio had shifted to 1 hunter per 2.4 elk, with 89,000 elk and 37,000 hunters.

HUNTING OPPORTUNITIES

The sale of elk licenses provides significant income for state and provincial wildlife agencies. In 1975, states and provinces sold just over 500,000 licenses, permits, and tags to hunt elk. Between 1976 and 1985, elk license sales increased to near 700,000, then again increased to more than 900,000 by 1995.

ELK HARVEST

The number of elk harvested has increased significantly over the last 20 years, but has not slowed the growth in elk numbers. In the United States in 1975, hunters killed close to 20% of the post-season elk population. By 1985, the harvest had dropped to 16% of the post-season population. In 1995, with an increased number of antlerless elk killed, total harvest equaled 18% of the winter population.

During 1975, hunters took just over 100,000 elk in the United States and about 2,900 in Canada. In 1985, the U.S. harvest increased slightly to 112,000 elk, while Canada's harvest jumped to 8,000 elk. Between 1985 and 1995, the U.S. elk harvest increased significantly, with 43% more elk taken. Canada's harvest decreased to 5,900 elk. As wildlife managers in several states have sought to slow the growth of some herds (or in some cases reduce the herd size overall), they've increased the numbers of antlerless tags dramatically.

ELK POPULATIONS AND MANAGEMENT: THE NEXT 5 YEARS

The dramatic 20th century continental elk population increases have been a cause for celebration in the wildlife conservation community. However, times and landscapes are changing and with them the ability for elk populations to continue aggressive growth into historic habitats. Overall, states that are aiming to reduce or stabilize populations will offset the minor expansion of elk herds into remaining western habitats and elk herd restoration efforts by midwestern and eastern states. Wildlife management agencies will continue to maintain or slightly increase elk hunting opportunities overall. Coupled with more hunting opportunity is the likelihood of increased elk harvest as states attempt to reach population objectives within biological and social carrying capacities. All this factored in, elk populations should remain fairly stable into the new millennium.

LITERATURE CITED

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History of the Kaibab Deer Herd, Beginning to 1968

WENDELL G. SWANK
2326 Quail Run Road, Cottonwood AZ 86326

SIGNIFICANCES OF THE KAIBAB DEER HERD

The Kaibab deer (*Odocoileus hemionus*) herd has been prominent in wildlife management circles for years. A wildlife biologist in the past could not have received a degree from any recognized university without knowing the history of the Kaibab deer herd. And it has had a long history. Details of studies made by some of our most distinguished leaders in the wildlife profession go back to the early 1920s, and notes of reconnaissances made through the area go back even farther.

Another attraction of the Kaibab is the beautiful country occupied by the deer. The hunts have traditionally been held in 2 sections. The first hunt has usually occurred in mid-October when the weather is pleasant, the fall colors are gorgeous, and the deer are on the plateau in the open ponderosa pine (*Pinus ponderosa*) forest. This hunt is a family outing. The second hunt has been held toward the last of November, and is considered the "trophy hunt" because the bucks are in the rut and the deer are in the more open winter range, hence are more vulnerable to the hunters. Snow can, and usually does, fly sometime during this hunt. But trophy deer hunters are a dedicated lot, and this is the most popular of the hunts.

The Kaibab has long been noted for large trophy heads, and the area has been featured in hunting magazines as a place to go for big bucks. The possibility of getting a Boone and Crockett record head has attracted many outdoor writers, thus publicizing the area. Deer from the area tend to have a high number of points, and there are more non-typical heads from the Kaibab in the record book than typical heads.

I examined the mule deer listings in the last 4 editions of Records of North American Big Game; the 7th, published in 1977, the 8th, published in 1981, the 9th, published in 1988, and the 10th, published in 1993. I looked only at the first 100 listings in both typical and non-typical heads. In those first 100, there were only 3 heads from the Kaibab in the typical category. Those heads were entered in 1938, 1939, and 1957. In the 7th Edition the head taken in 1938 was ranked 18th, the 1 in 1939 was ranked 51st, and the 1 taken in 1957 was ranked 57th. In the 10th edition these 3 heads had slipped in ranking to 23rd, 75th, and 85th respectively.

In the non-typical category the Kaibab is much more prominent. In the 7th edition 10 heads were listed in the first 100; all but 1 had been taken prior to 1954. The 10th Edition lists the number 3 head as taken on the Kaibab in 1943 and the number 6 head as taken there in 1941. Only 1 head, ranked number 32, was taken after the 1954-55 die-off, and that was taken in 1969. In spite of that, the Kaibab, at least in Arizona, is the place to go for a record-book head.

WHY LOOK AT THE KAIBAB?

The Kaibab mule deer herd is an ideal herd to study. It is, to a great extent, an isolated herd, bounded on all 4 sides by inhospitable deer habitat. To the south it is bounded by the Grand Canyon, which falls away precipitously and at its greatest depth to desert type vegetation. Similar conditions prevail to the west, where the land falls away to Kanab Creek. On the east the transition is less abrupt, but the vegetation changes from ponderosa pine to juniper (*Juniperus* spp.) and pinyon pine (*P. edulis*), then to the open grassland of House Rock Valley. At the north end the deer-occupied range is made up primarily of sagebrush (*Artemisia tridentata*), and there may be some intermixing of deer from the Vermillion Cliffs to the north-east and from Utah to the north.

The habitat of the Kaibab Plateau is typical of mule deer range in the inter-mountain West. The area used by the deer in the summer consists of a mixed ponderosa pine, northern coniferous forest vegetative type. The intermediate range, which the deer pass through on their spring and fall migration, consists of sparse stands of ponderosa pine with an understory of Gambel's oak (*Quercus Gambelii*) and black locust (*Robinia neomexicana*) at the upper periphery, and gradually changes to pinyon pine and juniper. This gives away to juniper that is less dense, and mixed cliff-rose (*Cowania mexicana*) and sagebrush, the dominate vegetation of the winter range.

The Kaibab deer herd has been under scrutiny for at least the last 75 years, and pages reporting on the results and conclusions would probably fill a room. That is the reason I think an examination of the North Kaibab deer herd is appropriate for this workshop.

EARLY HISTORY

Mule deer evidently have always been a major part of the fauna on the North Kaibab. In fact the early name for the area was Buckskin Mountain, because that is where early settlers and those that came before them went to get deer to make clothing. In 1893 the area was established as the Grand Canyon Forest Preserve by Executive Order of President Benjamin Harrison, although there was no U. S. Forest Service to protect and administer the area until 1905 (Trefethen 1975). The Kaibab received additional protection in 1906 under an act of Congress that made the area a National Game Preserve which gave protection to all game animals. Grand Canyon National Park was dedicated in 1919, withdrawing a portion of the north rim of the canyon from the Game Preserve, making the administrative division of land about as we know it today.

As written by Jim Trefethen, "*When President Theodore Roosevelt created the Grand Canyon National Game Preserve on November 28, 1906, he set aside the finest deer herd in America. But in doing so, he unintentionally wrote the first chapter of a harsh lesson whose impact is felt to this day in every deer management plan on the continent*" (Trefethen 1967). The prohibition on hunting of deer and systematic removal of deer predators was a great success in building a deer population; in fact it was soon obvious that it was too successful. There are no recordings of deer numbers, but Rasmussen (1941) said that the population in 1906 was estimated at 3,000 to 4,000, and that by 1924 the herd had increased to 100,000. By that time the combined deer and livestock had decimated the range. Almost every type of vegetation within reach was hedged, both on the summer range and the winter range. A high proportion of the annual fawn crop died every winter, and was so common that it was considered normal. In January of 1924, Henry C. Wallace, the Secretary of Agriculture appointed a committee to assess the North Kaibab situation and come up with recommendations. The Committee confirmed that range conditions on the area were critical, and that immediate action was essential if the deer herd was to avert disaster. Recommendations of the Committee included live trapping of deer and transplanting them to other areas, and shooting of deer. Trapping turned out to be less productive than anticipated, and the Forest Service prevailed upon the State of Arizona to authorize hunting. Accordingly, in October of that year the first hunting season to take deer on the North Kaibab was instituted. For a fee of $5.00 hunters could take 3 deer of either sex, but getting to the Kaibab was a long and difficult journey and the 270 hunters who showed up took only 675 deer. Another scheme to reduce the deer has been attributed to Zane Grey, but that is undocumented. What is documented is that George McCormick of Flagstaff organized a drive to gather deer on the Kaibab Plateau and with the help of cowboys and Indians, herd them into the Grand Canyon and across the Colorado River to the south side. The "Great Drive" took place on the morning of December 16, 1924, when 50 cowboys and 70 Navajo men began the drive toward Saddle Canyon and the Rim beyond where "counters" were stationed to tally the deer. In the thick brush it became impossible to see either deer or the adjacent driver, and when the drivers arrived at the edge of the rim not a deer was recorded to have dropped into the canyon (Russo 1967).

Hunting continued under Arizona regulations of 1 deer per hunter from 1924 through 1928 and the annual kill remained at less than 1,000 deer. Since all other programs to reduce the deer had failed, the Forest Service proposed to shoot deer to reduce the number. Accordingly, shooting by federal employees started on December 15, 1928, and 1,124 deer were killed before the then Governor Hunt of Arizona threatened to call out the National Guard to prevent such action. During the court battle that followed, the Forest Service abstained from killing deer and a limit of 1 deer per hunter was instituted to comply with Arizona regulations. The Supreme Court Decision, Hunt vs. The United States (1928) affirmed the right of the Secretary of Agriculture to have deer killed to protect the forage resources on the Kaibab.

In 1929, the Arizona Game and Fish Commission was established by the Legislature, and an agreement for management of the Kaibab deer was concluded between the Commission and the Forest Service. The killing of deer by government employees was permanently discontinued. The record is not clear, but evidently the probation against taking mature does was lifted and hunters could take more than 1 deer. Hunters jumped to 2,372 and the deer kill increased to 3,688. In 1930, 2,704 hunters killed 5,033 deer.

For some unexplained reason, the number of hunters in 1931 dropped to 980 (Russo 1967). It probably can be attributed to a reduction to 1 deer per hunter, as the hunt record shows that the 980 hunters killed 879 deer. There is also evidence that there was a continuation of the winter die-offs, and Trefethen (1967) stated that starvation, disease, malnutrition, and shooting had reduced the deer herd to less than 20,000. Russo (1967) reports that during the summer of 1930 there was above normal rainfall, which was followed by an open winter and above normal rainfall during the summer of 1932. This increase in moisture on the range seemed to have reversed the downward trend of forage plants, although he records that the deer herd in 1932 was estimated at 14,000 head. In any event hunters did not seem to be attracted by conditions on the Kaibab, and during the remainder of the 1930s hunter numbers hovered around 1,500 with a hunter success of around 80%.

During the first half of the 1940s hunters numbered around 800; the reduction was probably caused by World War II activities. The hunter success of that period was around 70%. In 1945, the hunt was restricted to 1,000 permits, and the 704 hunters that showed up took only 398 deer for a hunter success of 56.6%. This alarmed the hunters and the Commission, resulting in 1946 of a return to buck only hunts and a reduction to 500 permits. Obviously, this was a mistake, because it was almost immediately apparent that the deer herd was again getting too numerous for the food supply; hence permits were doubled over the previous year in 1947, 1948, and in 1949. In 1949, only about 2,700 of the authorized 4,000 permits were sold. Deer numbers were estimated at 57,000 animals; range conditions had continued to deteriorate, and it became clear that changes had to be made to induce hunters to the area.

This inducement was provided by Commission regulations in 1950 for 2 hunts, with 2,500 permits in each section and the taking of antlerless animals in the later hunt on the winter concentration area on the west side. Permits sold numbered 4,860 and 2,858 deer were killed, of which 604 were does and fawns (Kimball and Watkins 1951). This was the highest hunter take on the Kaibab except for 1929 and 1930 when hunters could take 2 deer, but the removal was inadequate to stem the tide.

During this period biologists from the Forest Service and the Arizona Game and Fish Department jointly conducted pre-hunt and post-hunt surveys and monitored forage conditions. Deer continued to increase and forage conditions declined. Field personnel recommended more liberal hunts. The Commission did increase permits to 7,000 in 1952 and 10,000 in 1953, and any deer was a legal deer. Forty-three hundred deer were taken in 1952 and 6,000 in 1953, and hunter success in 1953 reached 84.5%.

PRELUDE TO A DIE-OFF

On Monday, April 5, 1954, personnel of the Forest Service, Park Service, and the Arizona Game and Fish Department gathered on the North Kaibab at Big Springs Ranger Station to formulate the recommendations to the Arizona Game and Fish Commission for the 1954 hunting season. I was there, and the following is a summary from my field notes:

Tuesday, April 6. The inspection party visited Sowatts and Jumpup points on the west side. On Sowatts, the deer had eaten all of the current year's growth on most browsed plants, and were using last year's growth. On Jumpup the browse was in slightly better condition, probably due to more moisture during the growing season.

Wednesday, April 7. We went over to the east side. Conditions of the browse there were only slightly better. We went back over to the west side to check the Horse Springs and Little Springs points. On both areas the browse was not in good shape. On the return to Big Springs I personally counted 76 deer.

Thursday, April 8. We had the Study Group meeting at Big Springs this morning. Phil Cosper was appointed Chairman, and it was decided that all comments would be confidential so members of the group could express their feelings without constraints. Each person was invited to speak. Sam Sowell, Assistant Supervisor of the Kaibab National Forest, said he believed that quite a few more deer needed to be removed, and that Russ Rey, the Kaibab Supervisor was also of this opinion. He thought the removal should be 12,000 deer.

Fred Faver, member of the Arizona Game and Fish Commission, stated that he declined to give his opinion because he would have to be 1 of those making the final decision on the regulations.

Phil Cosper, Assistant Federal Aid Coordinator, Arizona Game and Fish Department, said that in his opinion the range is in poorer shape than it was 2 years ago and that more deer should be removed. For once, he would like to see enough deer removed to get on top of the herd.

Ted Knipe, Biologist, Arizona Game and Fish Department, said that the range is in worse shape than last spring. The deer appear to be in good shape, probably because of the open winter and the deer were able to spend more time in the intermediate range where there had been less use of the food plants. The deer herd will not be hurt if more are removed, and there are a lot of deer here.

Flick Hodgen, Regional Office of the Forest Service, Albuquerque, said he wasn't here last year, however, he is concerned about the downward trend in range condition. The cause is difficult to determine, that is, it can be related to cattle and/or deer use, or drought, but whatever it takes we must reverse the trend. It is imperative that we decrease the deer herd, and there is no lasting danger of overshooting. We are losing our major browse species, and it seems that as more deer are removed the fawn crop gets higher.

John Hall, Biologist, Arizona Game and Fish Department, said that it has been the same story for the last 7 years. The range continues to deteriorate, and the deer continue to increase. Something should be done to increase the productivity of the range. We need more deer removed, but we couldn't sell a removal of 12,000 deer to 20 people in the state.

Kenny Diem, Biologist, Game and Fish Department, assigned to the Kaibab, noted that there has been an increase of 163% in hunter harvest since 1941, and deer per mile counted on the annual surveys has increased 137%. Range analysis has shown 77% more use on the available browse and annually there has been a 20% die-off of browse plants. Last winter there was a 5% increase on the use of browse on the winter range and a 54% increase on the intermediate range. On the west winter range the deer are using last year's growth of browse. There should be a removal of around 12,000 deer.

Lee Hover, President of the Arizona Game Protective Association, stated that he represented the unmanageable portion of the puzzle, the sportsmen. Whatever the Commission came up with it was his job to sell the program to the sportsmen. In the eyes of the sportsman the cow gets most of the blame for the poor range conditions on the Kaibab, and there is more concern on the drop in buck weights. In his opinion, the range appears to be in worse shape than last year.

Charley Pase, Wildlife Biologist of the Forest Service assigned to the Kaibab, said lack of moisture on the Kaibab this past year had decreased forage production, and over-utilization had begun to decrease plant vigor. This year the deer took a lot of their food from the intermediate range, and we are just 1 jump ahead of a die-off. A season of poor growth on the browse, coupled with a hard winter, will result in a tragedy.

Jay Craven, District Forest Ranger for the North Kaibab, said that he is the local person responsible for the forage condition, and as far as he is concerned the deer have first priority. He is also concerned about the drop in weight of the bucks.

Bob Bendt, Wildlife Biologist for Grand Canyon National Park, said the Park cannot take direct action unless there is danger of extinction of a species. He believes that the Park should receive more emphasis in studies, such as livestock/deer competition, because on the Park there is no livestock grazing and the area could be used as a check on damage to browse caused by deer. He favored more emphasis on late hunts, because more deer from the Park are harvested on those hunts. There are areas on the Park, such as points leading into the Canyon, where cliffrose is completely gone.

Bid Clark, Game Warden for the Utah Department of Fish and Game, said that the Kaibab is a beautiful deer range, but it has been severely abused. He continued by stating that this is not a problem confined to the Kaibab. Many of the western deer ranges have been or are being abused, but thus far no deer herd has been depleted by over-shooting. One problem in wildlife management is that sportsmen don't believe the Wildlife Department Directors, and the Directors don't believe their people in the field.

After a brief discussion and a last word by anyone wanting to speak, Phil Cosper suggested that the group should recommend a hunt that would remove 10,000 deer. The group then recommended that 12,000 permits be made available in a 3 section hunt of 4,000 for each section.

The Commission regulations authorized 12,000 permits and 11,553 permits were sold. About 1,000 permit holders did not show. This was not unusual, for at that time in Arizona permits were not required to hunt in most management units and hunters frequently bought permits for the Kaibab in case they were not successful in earlier hunts, or they were persuaded to go hunting somewhere else by friends after they had purchased a Kaibab permit. Eight thousand and fifty-eight deer were checked through the checking station, of which about half were bucks and the remainder antlerless (Table 1). Most deer were in poor body condition and mean buck weights dropped to 124 pounds from 145 pounds the previous year and 155 pounds in 1952.

THE AFTERMATH

In 1955, the original regulations for the North Kaibab deer hunting season was for 2 sections; 4,000 permits for each section. However, there was a marked reduction in the number of deer observed on the pre-hunt survey and the permits were reduced to 3,200 in the first section and 1,500 in the second. There were 4,146 hunters checked in for the 1955 hunt, and they removed 2,311 deer. Many hunters reported seeing old deer carcasses on the winter range. Why the die-off during the winter of 1954-55 was not detected earlier, I do not know. The resident Arizona Game and Fish Biologist, Kenny Diem, had departed shortly after the 1954 hunt, and evidently no one was aware of the situation. To determine the extent of the die-off a "body count" was conducted by Game Department and Forest Service personnel November 28 through December 2, 1955 on the winter ranges of both east and west sides. This was done by walking transects randomly selected, calculating the area covered and dead deer found, then expanding the results to the winter deer ranges. The results indicated that about 18,000 deer, or 2 out of every 3 deer present were lost in the die-off. Thus, the die-off of 1954-55 and the hunt of 1955 removed about 20,000 deer from the area.

POST DIE-OFF PERIOD, 1956-1968

Range conditions improved after the 1954-55 die-off. The average adult buck weight went up from 124 pounds taken in the 1954 hunt to 137.7 pounds in 1956 and 163.4 pounds in 1957. From 1958 to 1961, buck weights hovered around 160 pounds (Table 2). Russo (1964) emphasized the importance of moisture to summer plant growth on the Kaibab, which in turn affects the body condition of deer in the hunting season. Average weight was 164 pounds in 1961 and continued to climb to 170 pounds in 1962 and, with the help of an exceedingly wet summer, reached 186 pounds in 1963. Weight of yearlings, however, is a better gauge of forage condition because the younger animals are less able to compete and must use energy for body growth rather than putting on fat as do the older animals. The weight of yearling bucks followed the trend of the older deer.

Measuring range conditions and trends has been fraught with many difficulties as it has on other deer ranges. Methods used were revised several times from 1951 through 1968 to improve the reliability of

Table 1. Hunter harvest data taken on the North Kaibab, Arizona, 1950 to 1968.

Year	Bucks	Does	Fawns	Total	Number Hunters	% Hunters Success
1950	2,254	604	C*	2,858	4,556	62.7
1951	1,905	614	C	2,519	4,754	53.0
1952	1,770	2,188	354	4,312	6,446	66.9
1953	2,884	2,556	613	6,053	7,166	84.5
1954	3,973	3,373	712	8,058	10,648	75.7
1955	1,084	1,022	205	2,311	4,146	55.9
1956	1,189	1,084	414	2,687	4,321	62.2
1957	1,748	1,117	374	3,239	5,377	60.2
1958	2,273	2,672	966	5,911	9,693	59.6
1959	1,411	1,851	499	3,761	4,867	55.3
1960	789	601	144	1,534	3,983	40.1
1961	296	400	114	810	2,585	31.6
1962	666	366	171	1,203	2,586	47.4
1963	787	402	239	1,428	2,610	54.7
1964	1,039	507	296	1,842	3,178	58.0
1965	1,065	867	408	2,340	6,127	38.1
1966	1,410	1,194	465	3,069	6,173	49.7
1967	561	602	225	1,388	6,295	22.0
1968	352	194	54	600	1,594	37.6

*C = Closed

Table 2. Weight of bucks from hunter-harvested deer on the North Kaibab, Arizona, 1950 to 1968.

Year	Average weight, mature bucks, pounds	Percent yearlings more than 80 pounds
1950	149	
1951	168	
1952	159	
1953	148	
1954	124	
1955	146	94.7
1956	137	74.1
1957	163	92.2
1958	148	84.3
1959	155	82.4
1960	153	86.7
1961	164	97.6
1962	170	100.0
1963	186	100.0
1964	173	97.6
1965	171	96.2
1966	155	80.7
1967	167	95.5
1968	157	96.6

the results (Russo 1964), but because of the many variables involved none appeared to be completely satisfactory. The amount of moisture available during the growing season tends to be the dominant influence on range conditions on the Kaibab, as it is over most of Arizona. Also, as in most of Arizona, rainfall fluctuates greatly from year to year. Overall range conditions, however, continued to improve after the 1954-55 die-off.

WHAT WE LEARNED FROM THE KAIBAB EXPERIENCE

1. Integrating the management of deer and people requires a great amount of lead time by the management agency. The attitudes of people are not readily changed, so we must plan ahead if we anticipate making changes in our management programs. As an example, how long did it take us to gain acceptance by hunters of the necessity of taking antlerless deer? I would say a half century, and perhaps we have convinced no more than 50% at that.

2. We must have data that the public can easily comprehend, stated in terms that are normally used in daily discourse. As an example, the Wildlife Management and Research Divisions of the Arizona Game and Fish Department began calculating and using numbers of deer to replace trends as a management tool in 1952. There was a lot of opposition and some ridicule because logic tells anyone that we can't get a precise figure on the population of deer in an area. Nevertheless, the general public thinks in numbers. They balance their check books, adjust their budgets, and get reports on their investments in numbers of dollars. Using trends they may see whether their stocks and bonds have gone up or down, but they cannot determine how much money they lost or gained if they do not know the number of dollars they have invested. Moreover, numbers became important when we first began issuing permits to hunters because we anticipated and projected the number of deer that would be removed by a given number of hunters. On the Kaibab after the 1954-55 die-off we calculated the number of deer on the Kaibab back to 1951 (Swank 1958). Those data said that we had 24,668 deer prior to the 1951 hunting season and 36,627 prior to the 1954 season. The pre-hunt data for 1955 indicated that 11,889 deer were present before the hunt, so we had lost about two-thirds of our deer herd. Also working with actual numbers we showed that from 1951 through 1955 hunters removed a low of 10.2% of the population in 1951 and a high of 19.5% in 1955. As Russo (1964) points out, getting an estimate of the population gives us something concrete to work with, but we should constantly look at our data in an effort to come up with more accurate results.

   Information such as percent hunter success the preceding season and deer seen per mile on surveys may be acceptable when things are not critical, but when we are dealing with possible over populations of deer, over harvesting of deer by hunters, or low recruitment to deer populations we need better data, and finer tuning of our management. People expect it, and we should provide it.

3. We must be more diligent in getting continuity of data and emphasizing the importance of long-term research. I must say that preparing this paper is more of a rehash of previous experiences than of new experiences. Following the trail of data after the 1954-55 die-off was like following smoke. It became obscure, then disappeared completely. John Russo's book gave good information through 1961, but he skimmed through 1962 and 1963 because there was no resident biologist at the Kaibab for those years. There are few places where wildlife information is available over such a long period and as detailed as there is for the North Kaibab, but even there it is sketchy and incomplete. We must do better.

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The North Kaibab Deer Herd 1968-1983: The "Research" Years

HARLEY G. SHAW
P. O. Box 370, Chino Valley, AZ 86323

Abstract: The North Kaibab mule deer herd declined from approximately 15,000 to 5,000 deer between 1966 and 1976. The cause for this decline is unknown. A study of deer mortality, combined with an assessment of mountain lion numbers, began in 1977. The deer herd increased rapidly in size after 1978. This increase was due to concurrent occurrence of buck-only hunting, improved precipitation, declining mountain lion numbers, and reduction of cattle. No 1 factor can be clearly implicated as the cause of either the decline or of the subsequent deer herd recovery. This overview illustrates the insufficiency of reactive, short-term research and supports the need for long-termed monitoring of deer populations, along with major factors that may create fluctuations in those populations.

INTRODUCTION

Swank (1998) has summarized the history of the North Kaibab mule (*Odocoileus hemionus*) deer herd to about 1968. As we can see from his presentation, calling the 1970s the research years is somewhat of a misnomer. Field studies of the Kaibab deer herd began in the late 1940s (Kimball and Watkins 1951, Diem 1954). Ryan Station was built in 1952 as a base for a biologist assigned to work on Kaibab deer, and Ken Diem initiated studies. Following Diem, John Russo took over work on the Kaibab and produced the first major publication on that herd (Russo 1964). After Russo's work, studies evaluating the effects of juniper eradication on Kaibab deer were carried out by McCulloch (1967).

The years surrounding the decade of the 1970s are significant on the North Kaibab, because an unexpected decline in deer numbers occurred in spite of intense management of the herd through the 1950s and early 1960s. Between 1966 and 1976, the estimated herd size dropped from 15,000 to approximately 5,000 (Fig. 1). Arizona Game and Fish Department responded in 1977 by switching to buck-only hunting and initiating an intense research effort to identify the factors suppressing the herd. In 1979, the deer population began to increase, and by 1984, it was approaching numbers similar to the pre-1966 levels.

The mortality study, extending from 1977 to 1984, involved 5 years of intensive radiotracking the deer (Barlow and McCulloch 1984, McCulloch and Brown 1986, McCulloch and Smith 1991), documenting causes of death, and a 3-year study of mountain lion (*Felis concolor*) densities and predation on the Kaibab Plateau (Shaw 1980). I do not intend to review in detail the results of these various studies. Rather, I will summarize events occurring on the Kaibab between 1966 and 1983 and provide an overview of the factors that potentially affected the herd.

A variety of factors affect the Kaibab mule deer herd at all times. These include harvest rates, predation, disease, climate, and competition with other herbivores. These factors can cause direct mortality of deer or they can affect fawn production of the herd. At no time in the history of Kaibab deer herd management have all of these factors been monitored and related to fluctuating deer numbers.

The Initial Decline

The cause of the decline in deer numbers from 1966 to 1976 is unknown. Drought and increased predation, particularly by mountain lions, were implicated (Barlow and McCulloch 1984). Legal harvest was considered to be a small

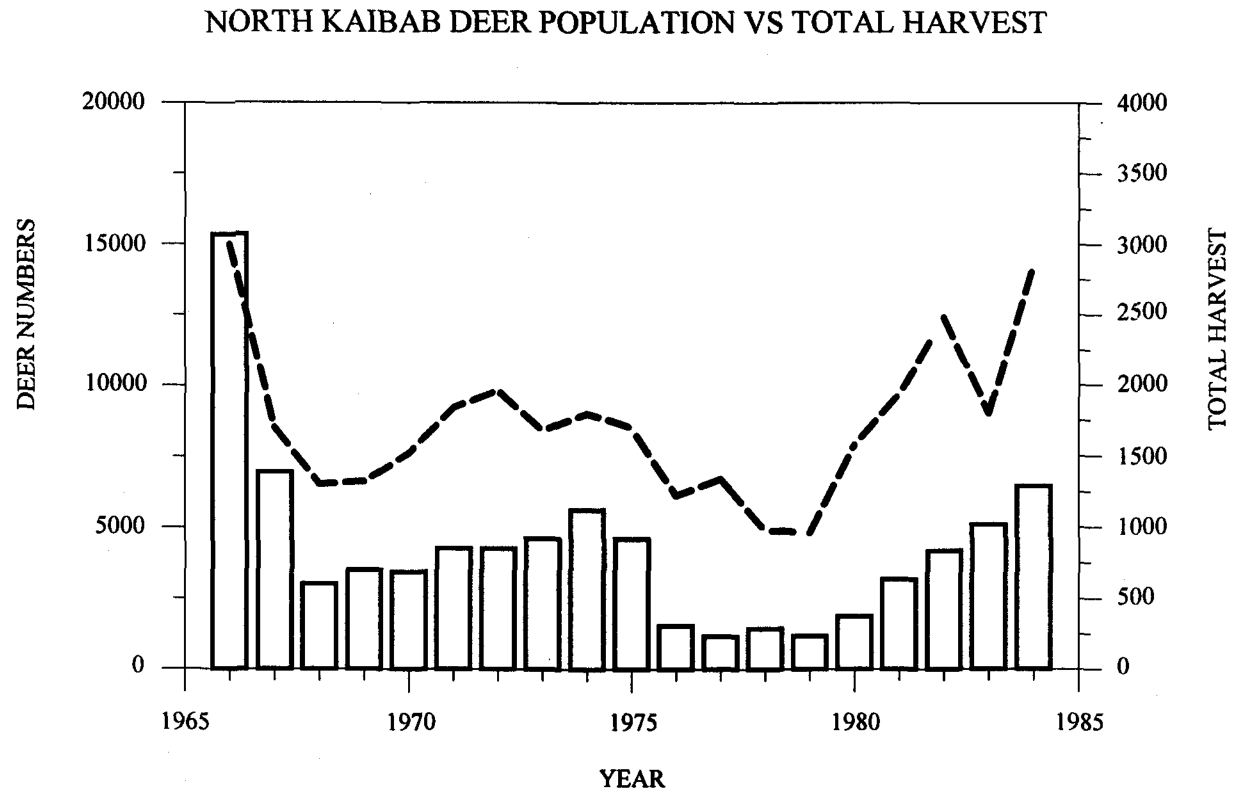

Figure 1. Variations in the North Kaibab mule deer herd 1966-84. Broken line is pellet group data from summer range. Bar graph is harvest data.

portion of the total mortality during this period (McCulloch and Brown 1986), but high any-deer harvest in 1967, combined with then unsuspected increased natural mortality, may have helped to accelerate the decline (T. L. Britt, Arizona Game and Fish Department, pers. commun.).

Harvest Effects

In 1967, 2 10-day any-deer hunts, with 4,000 permits allowed for each hunt, were held on the North Kaibab. This was in response to estimates of an increasing number of deer on the area and was intended to stabilize the herd below carrying capacity. In spite of the relatively large number of permits and long season, the harvest was 1 of the lowest experienced before that time. Extremely heavy snows occurred throughout northern Arizona during December 1967. The winter range of the Kaibab received 1-2 ft of snow within a single week. However, the deer hunts were over before these snowfalls occurred. Thus, a sudden decline in deer numbers had apparently occurred between 1966 and 1967, before the hunting effort was increased and prior to the 1967 snowfall.

The total harvest of deer through the 1970s parallels fairly closely the estimated deer herd based upon pellet group data (Fig. 1). The extremely low harvest from 1976 to 1980 reflects both the low deer numbers and a shift to buck-only hunting in 1977. Buck-only hunting was initiated just before the deer herd began to increase in 1979, and the cessation of doe harvest must be considered as a possible factor in reversing the deer decline. However, deer harvest amounted to less than 15% of the total mortality during the period of 1972 to 1978 (McCulloch and Brown 1986), hence cannot be considered the only factor suppressing the herd during that period (Fig. 2). Mortality due to

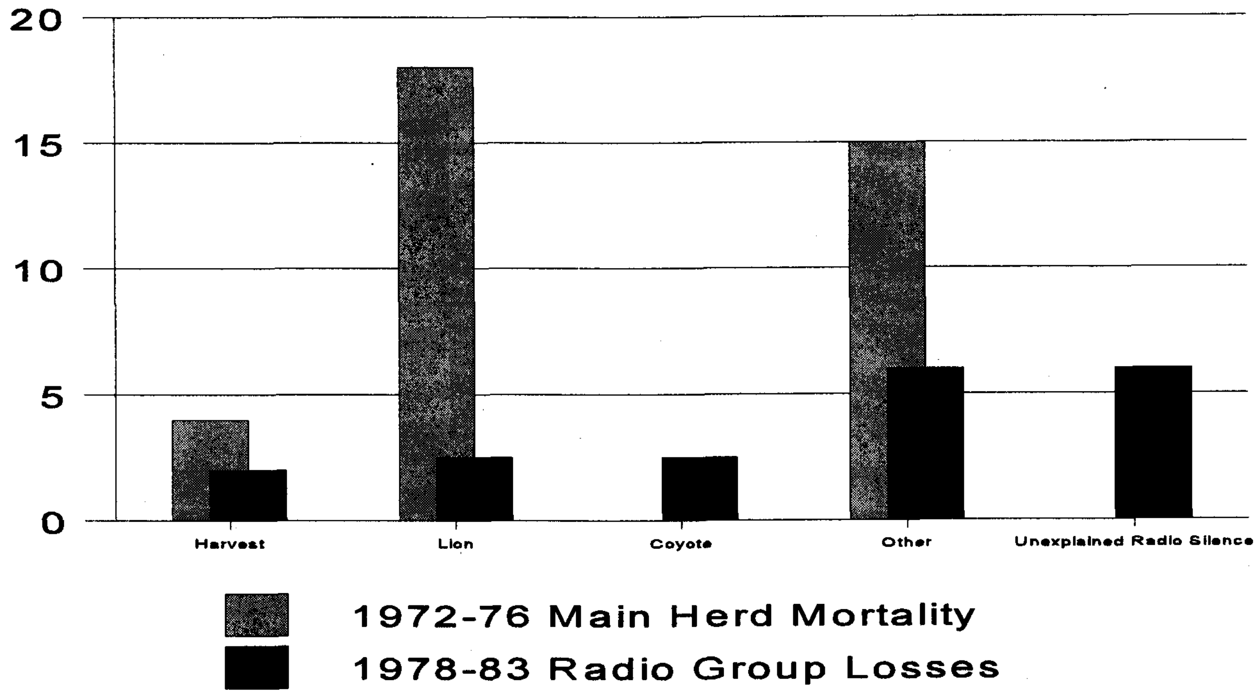

Figure 2. Mortality sources for does older than 12 months in the North Kaibab mule deer herd during the period of deer decline (1972-76) and during period of herd increase (from McCulloch and Brown 1986). Mountain lion mortality data for 1972-78 are based upon an extrapolation from the mountain lion population estimated in 1977 and may be unrealistically high. Lack of mortality due to coyotes during this period is also unrealistic. Mortality figures for 1978-83 are based upon mortality rates of radiomarked deer.

hunting made up an even lower portion of total mortality during the period of herd increase after 1978. Based upon these data, hunting cannot be considered the cause of deer decline or suppression in the 1970s.

Productivity

Post-hunt fawn:doe ratios do not reflect the decline in deer populations, nor do they explain the apparent continued low population during the 1970s decade (Fig. 3). While fawn survival rates, based upon classification counts, tend to be lower throughout Arizona than they are in states further north, a ratio of 50 does per 100 fawns is generally considered to be adequate to sustain a deer population under normal conditions of adult mortality. With the exception of 1978, fawn:doe ratios remained above 50%, with only 3 years dropping below 60 (Fig. 3). Ratios were actually more stable during this period than they were during the 1960s, when the herd increased. It must be noted, however, that deer classification data were gathered from helicopters during the period from 1971-74, and McCulloch and Smith (1991) rejected helicopter surveys for this period. They were mainly critical of the buck:doe ratios gathered by aerial surveys, however. Fawn:doe ratios for the years that helicopter surveys were used are included here.

Precipitation

McCulloch and Smith (1991) have provided an in-depth analysis of the relationship of weather to the North Kaibab deer herd. Fluctuation in deer numbers was found to correlate with cumulative precipitation beginning as early as 3 years prior to a given year. Data for the October

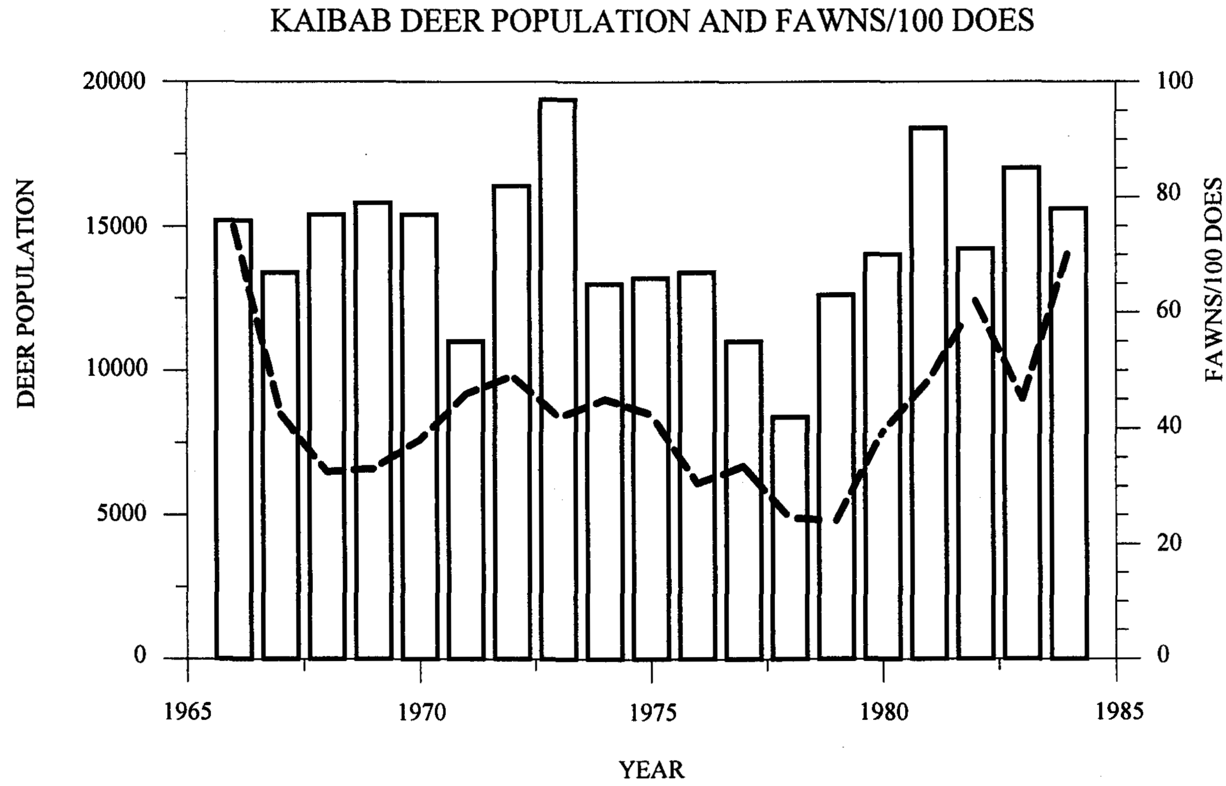

Figure 3. Fawns:100 does (post-hunt surveys — bar graph and population estimates based upon pellet group surveys (broken line) for the North Kaibab deer herd 1966-85.

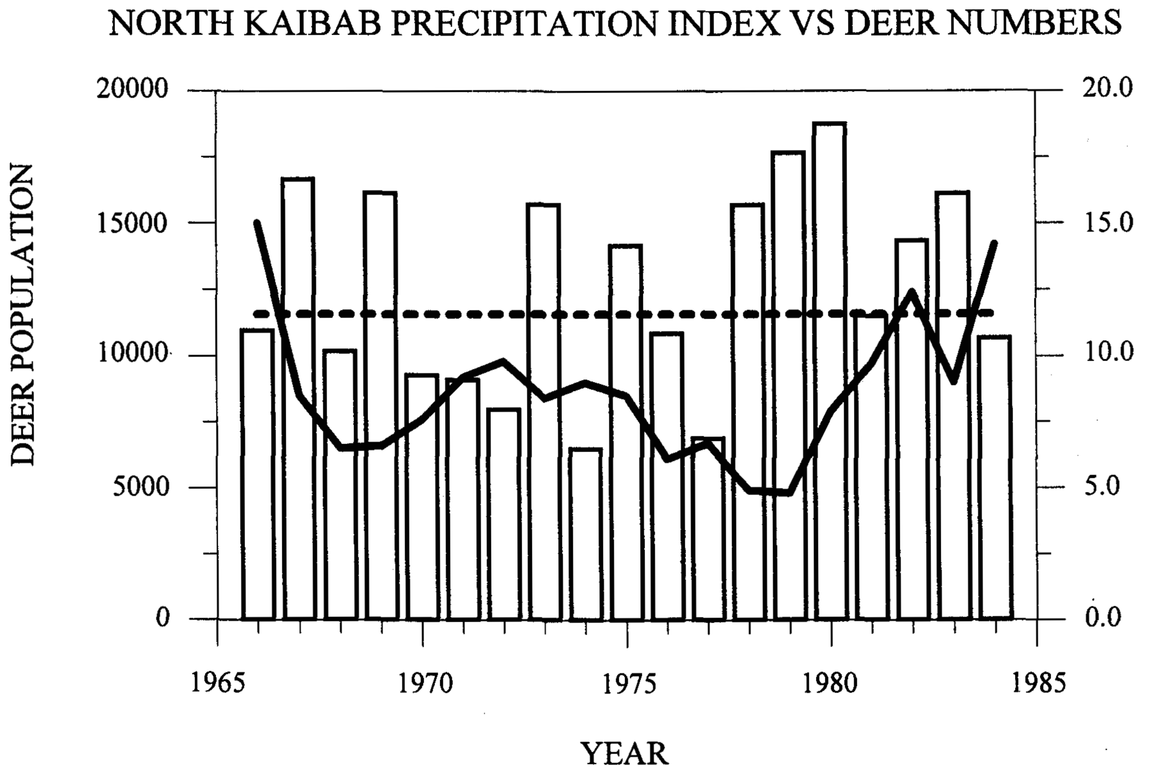

Figure 4. Water year (October-September) precipitation index (bar graph) and mule deer population estimate (solid line) for North Kaibab, 1966-84. The dashed line is the long-term average precipitation on the Kaibab Plateau.

to September water year preceding the deer herd estimate (Fig. 4) suggest that 1966 through 1977 was a period of water deficit, with 8 of 12 years having precipitation below the long-term average. This pattern changed in 1978, and precipitation was at or above the average through 1983. Good rainfall and its effect on forage was undoubtedly a factor in the increase in deer numbers on the Kaibab that began in 1979.

Predation

Mountain Lions. Mountain lions were implicated as a major component of deer mortality during the period of decline and depression of the deer herd (McCulloch and Brown 1986; Fig. 2). Prior to 1977, however, no actual measurement of lion numbers or numbers of deer taken by lions were available for the area, and the estimate of lion mortality shown in Figure 2 is based upon a backward extrapolation of the estimate of lion numbers made in 1977-78. The mortality estimates for 1978-83 are based upon actual losses of radiomarked deer. A mountain lion tagging, radiotracking, and reconnaissance effort began in 1977 and continued throughout the summer of 1980 (Shaw 1980). Forty adult lions were estimated to be on the area in 1977 (Fig. 5). By 1979, this number had decreased to approximately 15 adults. Mortality of adult lions between 1977 and 1980 was attributed to hunter kill (21 animals), capture mortality (1), and natural mortality (3). Eighteen of the hunter-killed lions were taken between 1977 and 1979. One female lion lost 3 of 4 litters birthed during the study, and another female known to have kittens starved during the severe winter of 1978-79. The deer herd began its increase in 1979, after the lion population declined. The 5-year average lion-caused mortality rates of adult does during this period was only 0.028, compared with a speculated rate of approximately 0.15 during the period of decline.

Coyotes. No data are available for coyote (*Canis latrans*) numbers or coyote-related deer mortality during the period of decline. Scent post surveys made between 1977 and 1981 fluctuated widely and suggest a declining coyote population after 1978 (Fig. 6). The highest coyote population index occurred in 1977, at the end of a period of high fur prices and increased trapping effort throughout the state. Fur trapping on the North Kaibab during this period, however, was carried out by locals who traditionally trapped each winter. Effects of trapping probably did not increase significantly in the area due to fur price fluctuations. During the period of increasing deer numbers, coyote-related mortality of adult does was 0.038, actually slightly exceeding lion-caused mortality.

Disease

No data are available on the effects of disease on the deer herd, either through the period of decline or during the mortality study. Disease was included as unidentified mortality factors by McCulloch and Brown (1986).

Livestock

Actual effects of cattle numbers on deer numbers on the Kaibab is not known. Cattle numbers on the winter range dropped in 1978 and continued to decline through 1986, reaching a low for the century (Fig. 7). McCulloch and Smith (1991) noted that total ungulate animal units (including both deer and cattle) correlated negatively with deer physical condition between 1970 and 1986. Thus, a decreasing number of cattle should allow a larger number of deer to maintain healthy condition.

CONCLUSIONS

This paper obviously presents a highly over-simplified history of factors affecting

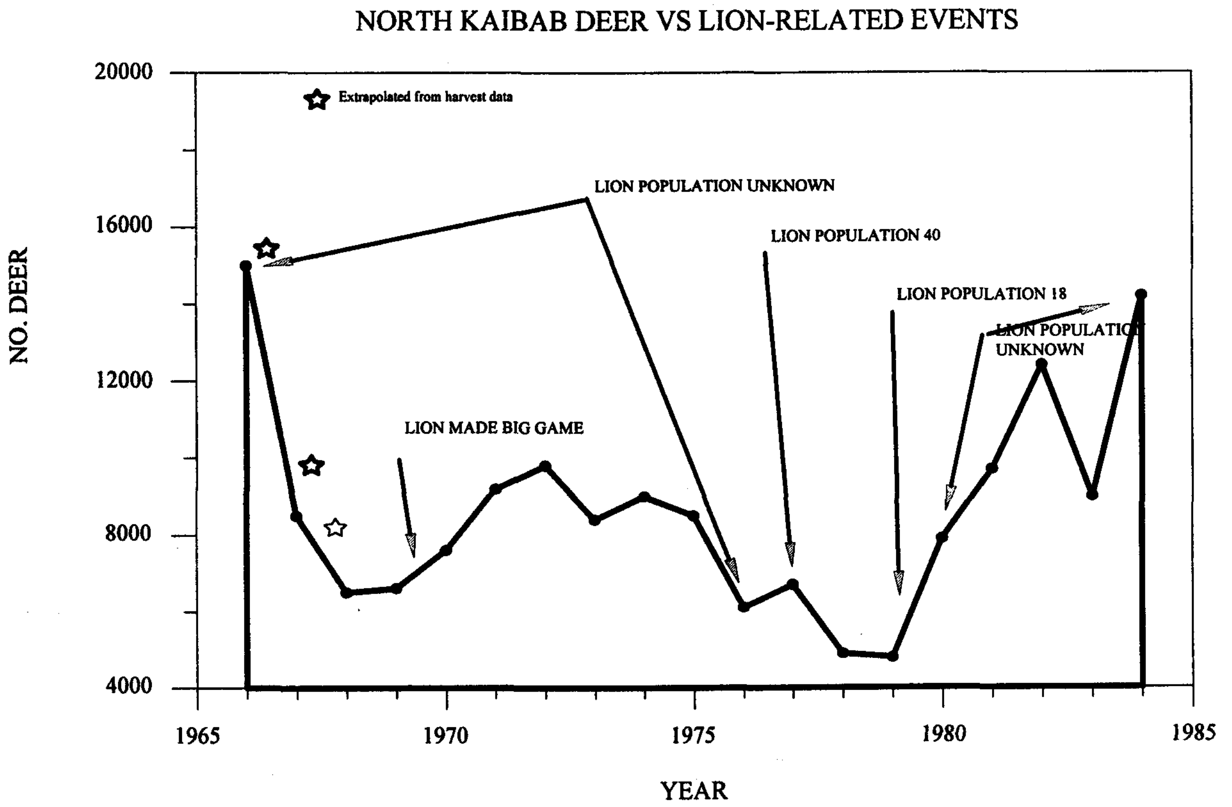

Figure 5. Mountain lion-related events on the North Kaibab as they relate to deer population fluctuations, 1966-84.

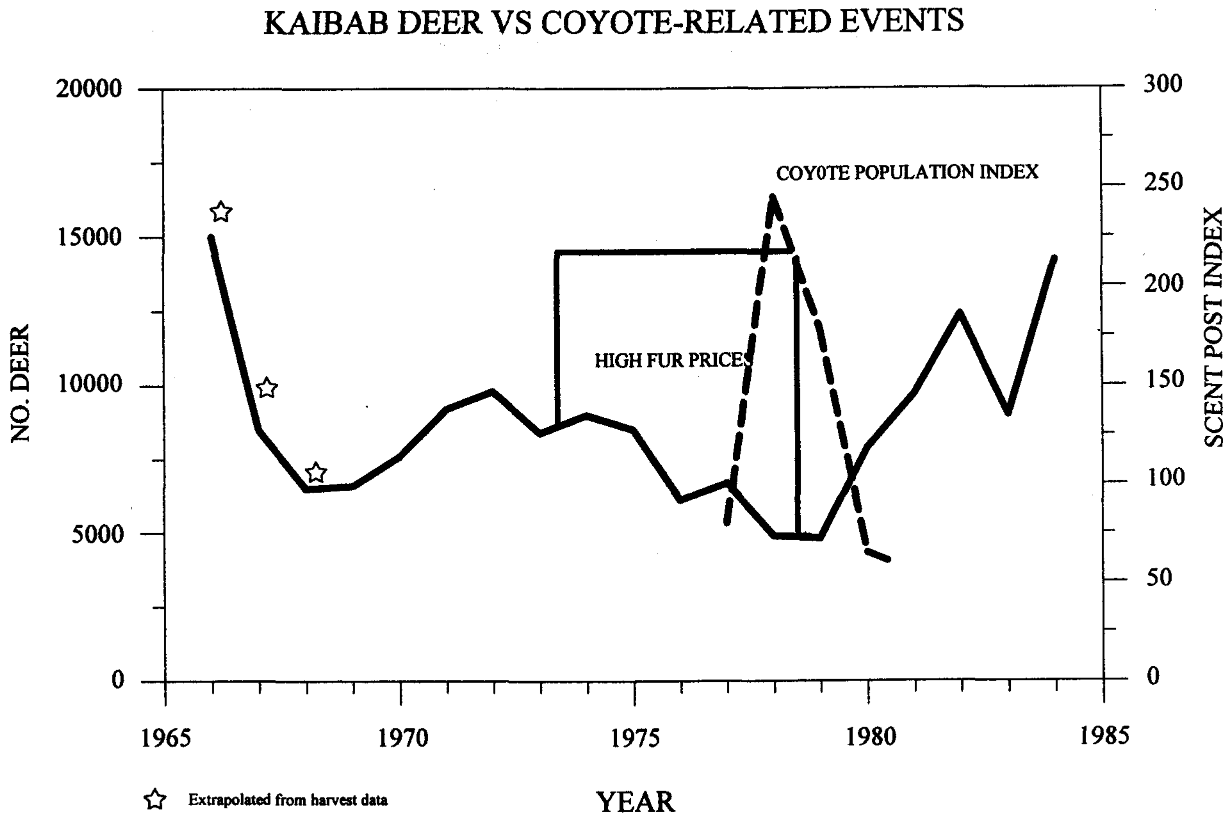

Figure 6. Coyote-related events on the North Kaibab as they relate to deer population fluctuations, 1966-84.

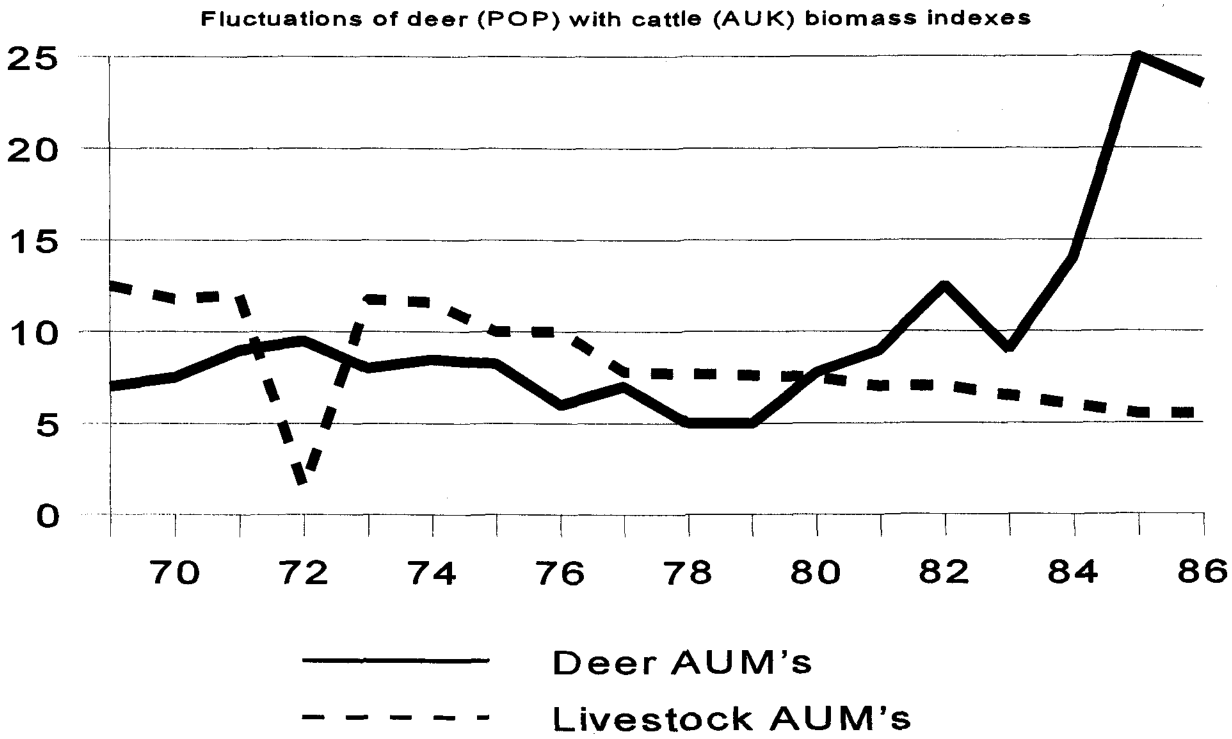

Figure 7. Cattle stocking AUMs versus deer AUMs on the North Kaibab, 1969-86 (from McCulloch and Smith 1991).

the Kaibab deer herd between 1966 and 1984. It is not intended to be exhaustive, and anyone interested in greater detail are referred to Russo (1964), Shaw (1980), McCulloch and Brown (1986), and McCulloch and Smith (1991). From the above discussion, however, a few conclusions are possible.

1. The North Kaibab mule deer population declined between 1966 and 1977, going from an estimated 15,000 deer to approximately 5,000. The cause for this decline is unknown, and it was unexpected when it occurred. The available evidence implicates low precipitation combined, perhaps, with a high mountain lion population.

2. The herd reversed its downward trend in 1979, when several factors combined to create favorable conditions. These include a change in 1977 from any-deer hunting to buck-only hunting, a shift in the precipitation patterns from drought to above-average precipitation, a significant decline in lion numbers on the area, and a long-termed reduction of livestock.

3. While the Kaibab deer herd was monitored closely prior to and during the 1970s decline, intensive efforts to identify mortality sources began after 1977. As a result, estimates of the lion population, a coyote population index, and an estimate of mortality sources were not available until after the deer herd had actually begun to increase. As a result, we do not know what the relative effects of lion predation, coyote predation, and precipitation patterns may have been during the period of decline. Similarly, after the deer herd

began to recover, monitoring of predator populations and deer mortality ceased. Hence, information available covers only a period when conditions were particularly favorable to deer.

4. Short-termed, reactive research, such as the work done on the North Kaibab between 1977 and 1985, is therefore of limited value. The importance of sustaining long-termed studies that intensively monitor not only deer numbers but also potential factors that may influence those numbers, including predator populations, is evident. With all of the literature available on the Kaibab deer herd and for all of the years of study that have occurred there, solid documentation of events surrounding periodic declines in deer numbers has not yet been accomplished.

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The Kaibab: The Modern Years

RAYMOND M. LEE
Arizona Game and Fish Department, Phoenix, AZ 85023

Wendell Swank, Harley Shaw, and I decided to divide the history of deer (*Odocoileus hemionus*) management on the Kaibab along the lines of the years covered during our respective tenures. Wendell already covered from the Pleistocene to the 1960s, Harley then took over and brought us up to around 1982. That was the year when I started with the Department. Now that I've been around long enough for our new Wildlife Managers to feel that I must have started my career managing dinosaurs, and with similar success, I'd like to conclude our history of the Kaibab - and perhaps provide a brief glimpse into the future.

As John Russo, the first "Kaibab biologist" wrote, *"from the beginning, the Kaibab was destined to evolve into a significant feature of this earth."* While Russo was implying geologically, it could just as easily have been applied to the Kaibab's political and biological evolution. From the formation of the Grand Canyon National Game Preserve in 1906 to the present, the Kaibab has epitomized man's interactions with nature in the western United States.

While both Wendell and Harley talked mostly about deer management, I'm going to talk mostly about people management. Surely you each remember 1 of your wildlife professors pontifically intoning that wildlife management was mostly people management. You probably rolled your eyes and tried to imagine how you were going to get away from all of the people and out into the field again. But that is what we do now. Trophy hunters, muzzleloader-only hunters, juniors-only hunters, challenged hunters, archery-only hunters - we've aided in this subsetting of hunters, to their detriment, but also by their choice.

Erwin Bauer revisited *"The Terrible Lesson of the Kaibab"* in the Fall 1996 issue of *Mule Deer*, effectively continuing the education of a new generation of deer hunters on the predator killing, deer driving, politically motivated, so called Kaibab deer "management."

We have started seeing our Department attempt to become more "user friendly," more responsive to the public - unless you've tried 1 of our phone mail information trees so popular nowadays. We are actively seeking public input into our strategic plans and management processes. Nowhere is this more evident than on the Kaibab where we have generated Alternative Mule Deer Management Plans (though amended at the most recent Commission Meeting - after more public input). We even have a Quality Deer Group specifically to provide the Department guidance on how to manage the Kaibab deer.

Deer hunting can certainly generate strong emotions, and the Kaibab perhaps more so than in most other areas. I well remember a gentleman standing in my office yelling *"I'd rather shoot dogs on Main Street than does on the Kaibab."* This was during the return to the "hey days." The period from 1979-1984 seemed to have an ideal combination of weather and ungulate numbers, which allowed optimum forage production. Cumulative annual precipitation was high and there was a succession of mild winters. During this time we saw 4-point yearlings, recruitment levels of 85 fawns:100 does (recruitment averaged 80:100 for 1983-85, while the rest of the state averaged below 50), and average yearling buck weights reached 111 lbs. We went to antlerless and then even any deer hunts. Harvest levels reached 3,749 animals

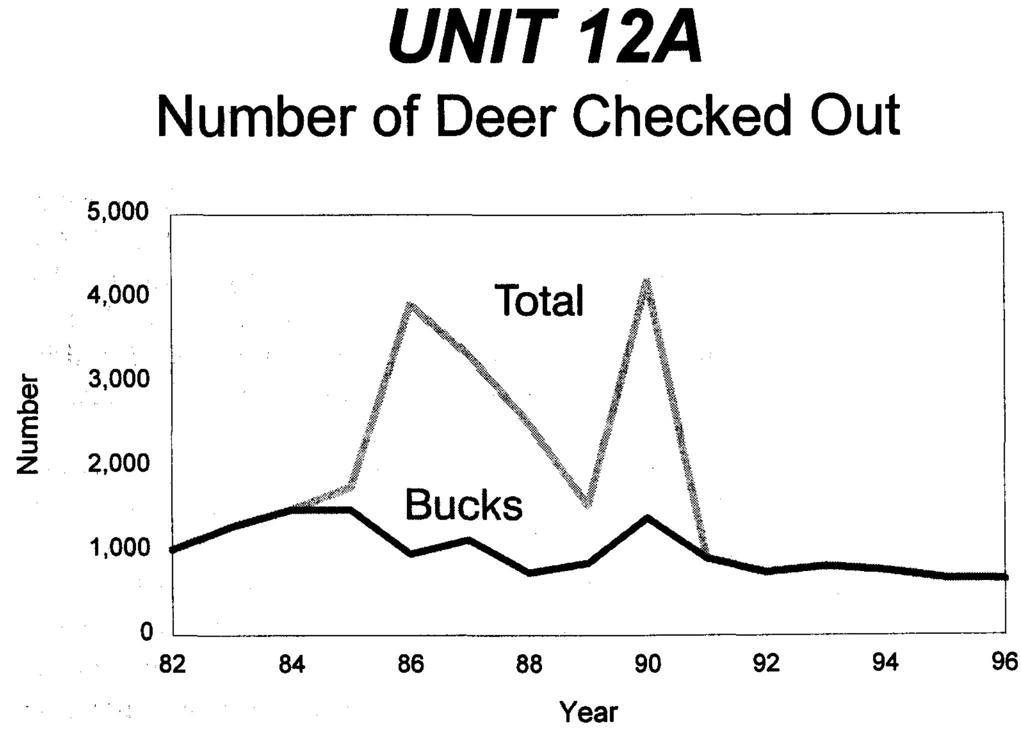

Figure 1. Recent history of deer harvest on the Kaibab.

in 1990, of which 2,191 were females (Fig. 1). These were the highest harvests since the record year of 1958. The Kaibab alone provided 27% of the statewide mule deer harvest.

Eventually, climatic conditions changed and deer numbers declined. This led to the reduction in permits and the eventual partitioning of hunting opportunities on the Kaibab. We've now added juniors-only hunts and muzzleloader-only hunts. In response to complaints of overcrowding, in 1996, the archery season was changed to overlap with the archery elk season dates. This effectively reduced the number of archers who participated on the Kaibab.

A number of comprehensive studies have occurred on the Kaibab. Perhaps the first to produce a definitive report was accomplished by Rasmussen (1941). Then, as Russo observed, *"investigations continued!"* The Kaibab proved to be a veritable game management laboratory. The relatively isolated deer population, the extensive historical data base (mandatory check stations had been maintained since the first hunt), limited entry hunting, a funding base, and national interest set it up as a prime research location. Kaibab deer studies have generally been directed towards management purposes. Despite these years of research, however, biologists still avoid making definite statements about deer numbers for fear of disagreement.

AGFD research efforts continued in Russo's footsteps. Clay McCulloch assumed the mantle of "Kaibab biologist" in the late 1960s. For the next 20-some years, McCulloch collected data from throughout the Kaibab ecosystem in an attempt to determine the various factors affecting the deer herd in an effort to develop predictive factors. The prime management question being asked was whether "changes in yearling production and deer herd size could be forecast from weather and deer data" prior to the hunting season. The relationships between such variables as acorn abundance, numbers of tent caterpillars, and the mushroom abundance index with deer welfare were examined. This work produced a number of interesting conclusions which were compiled by McCulloch and Smith (1991). This work, along with that of Haywood et al. (1987), gave managers the following information - deer pellet counts don't necessarily follow other methods for population estimation and average annual yearling buck weights provide the best relationship with environmental variables (Fig. 2).

One of the most important conclusions was the positive correlation between the health and productivity of the deer herd with precipitation, and the negative correlation between deer and livestock numbers. This information led to the upper population limit of 17,000 deer on summer habitat during unusually wet periods. Experience suggests that mean carcass weight of yearling bucks is likely to fall below 103 lbs if the total ungulate biomass exceeds 22,000 AUMs. The potential productivity of the deer herd is shown in the rapid growth of individual deer. Several yearling bucks have achieved live weights in excess of 200 pounds. During their 17-month life span, some yearling bucks have shown a weight gain of 162 pounds.

Some of the most questionable Kaibab data are the early deer herd population estimates. In the 1920s, simple extrapolations were made from deer counted on prescribed portions of the winter range. In the 1950s and 1960s deer numbers were calculated from changes in pre- and post-hunt ratios of field observed deer and from the known composition of the harvest by hunters. Surveys had been changed to obtain sex and age ratios, rather than to merely obtain a count of the animals observed.

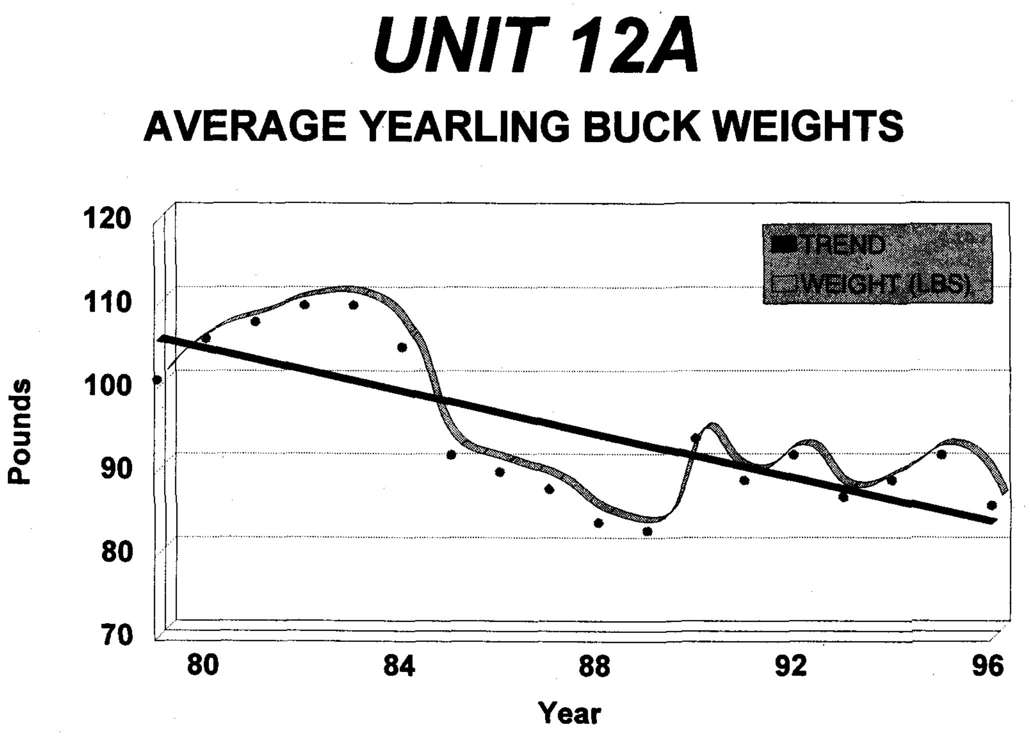

Figure 2. Average yearling buck weights of deer harvested on the Kaibab; with the trend between 1979 and 1996.

Problems in estimating populations arose. Over a period of several years the field classified ratio of bucks per doe at pre-hunt (October) surveys was about half that of the ratio estimated by change in the harvested age ratios. In addition, field surveys to estimate sex and age ratios were especially questionable as bases for forecasting changes in either yearling production or huntable deer numbers.

From 1972-1996, population estimates were derived from fecal pellet groups on 3,736 circular plots of 100 ft^2 each. Despite the magnitude of work necessary to read these plots, assessment of the several biases inherent in the pellet count technique showed that it usually underestimated herd size. Pellet transects were discontinued in 1996 after several years of diverging from the results of other estimation techniques (Fig. 3).

Other changes were made in data collection techniques (i.e., the specific area of harvest). The Kaibab used to be divided into 12 subunits for data collection purposes. After finding how many hunters got lost each year it was felt that the accuracy of these returns were somewhat dubious.

Since John Russo stopped collecting data for his manuscript following the 1963 season, changes have also occurred in the management of mule deer on the North Kaibab. Most of these changes have occurred due to the fluctuations of mule deer population levels in response to varying environmental conditions. In years of poor rainfall, harvests and hunter opportunities were comparatively low. Following several years of good production, however, the responsive population could, in Russo's words, "*provide the kind of hunting they wanted. A forest of Eden with a deer behind every tree, and a deer behind every deer.*"

Favorable precipitation occurred from

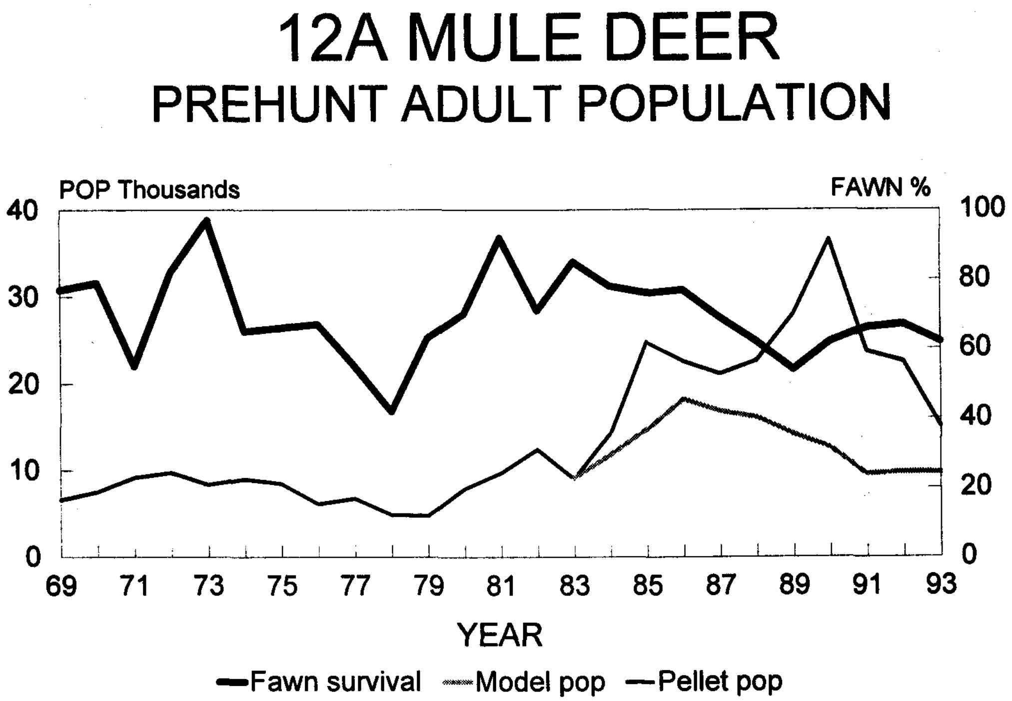

Figure 3. Pre-hunt adult deer population on the Kaibab as estimated between 1969 to 1993. This provides a comparison between the computer model and the pellet group population estimates.

1978-1982. The resulting increase in population led to splitting the Kaibab into an east and west side in 1983. The east side was to be managed as a trophy area with a stratified hunt of 200 permits each. After a buck-only harvest of 1,288 in 1984, the Department authorized a 450 permit antlerless hunt and increased the east side trophy permit levels to 325 for each hunt.

In 1986, 3 season dates, with any-antlered, antlerless, and even any-deer hunting opportunities, were offered. Antlerless deer permits were available on the east side for the first time and trophy permits were reduced to 250. Harvest levels reached 3,393, of which 2,552 were antlerless. These were the highest harvest totals since 1959.

In 1990, 8 different seasons were offered with an October 19th opening date for antlerless permits and the addition of 250 trophy permits to the middle, east side season. Since 1963, 32,063 deer have been harvested from the Kaibab, an average of 1,233 deer per year. The majority of these, 17,514, were bucks.

Through the 1990s, drought conditions were more the rule and the population on the Kaibab has declined, as have the number of hunts. In 1996, 5 hunts were offered with 3 on the east side with 300, 50, and 100 juniors-only permits, and 2 on the west side with 1,000 and 250 permits. The season was moved later so that the east side hunt ended December 1. In 1997, the hunt structure was again 3 hunts on the east side with 350, 50, and 50 muzzleloader-only permits respectively, the 2 hunts on the west side declined to 950 and 150 permits each. Harvest has now fallen to 789 bucks, with a 50% hunter success.

The stature of the North Kaibab deer herd can be seen in a comparison between this area and the rest of Arizona. From 1948 to the present, using the 29 years of comparable data, the statewide harvest success for mule deer hunters averaged 28.6%. For the Kaibab this figure is 47.2%. The Kaibab provides about 20% of the statewide archery deer harvest, with a peak in 1987 of 28% of the total harvest. Even the size of the legendary Kaibab bucks have remained despite a recent downturn in range conditions due to an extended drought. The 5 heaviest bucks harvested last year tipped the scales in excess of 190 pounds.. The largest rack was an 8X7, with a 34-inch spread, still respectable by most standards.

Habitat improvements to enhance wildlife have been utilized for many years. Many of these improvements have been provided by the livestock industry; although obviously intended for livestock, wildlife often benefit from them as well. The $5.00 permit fee for hunting on the Kaibab has provided a regular source of funds for range improvements. These improvements over the past 60 years have served to increase the ungulate carrying capacity of the North Kaibab National Forest.

The special permit system was authorized by the Arizona legislature in the fall of 1983. This program was a joint effort by wildlife conservation groups and the Department to raise additional revenue for wildlife management through the raffle or auction of special permits. The first permit offered under this program was a bighorn sheep tag in 1984. The auction produced a bid of $64,000. The deer tags were offered first on the Kaibab, later to include the entire Arizona Strip, and now cover all open areas in the State. The tags brought $12,500 apiece in 1989. This has now risen to $51,000 apiece in 1996. The revenue from these tags is specifically allocated for mule deer management programs.

John Russo felt that while the North Kaibab Game Reserve was controlled by a multiple resource agency like the United States Forest Service, that wildlife management efforts in this area would be compromised. As usual, he was accurate in his conclusion. The Arizona Game and Fish Department and the Forest Service are frequently at odds over the rate of timber cutting on the forest. These differences of opinions have led to official appeals of timber sales and even the threat of legal action to stop the timber harvest on this forest. Until there is a resolution of these difficulties, the cooperation necessary to successfully manage the North Kaibab deer herd will be missing.

In *A Sand County Almanac*, Aldo Leopold wrote "*I now suspect that just as a deer herd lives in mortal fear of its wolves, so does the mountain live in mortal fear of its deer. And perhaps with better cause, for while a buck pulled down by wolves can be replaced in 2 or 3 years, a range pulled down by too many deer may fail of replacement in as many decades.*"

As Russo stated, "*The history of management of the Kaibab North deer herd is one of removing too few too late.*" Deer herds recover very rapidly in periods of favorable environmental conditions. Habitat is much slower at taking advantage of similar conditions, however, it will respond when given protection from its ungulate predators. The management objective for any population is to keep population numbers within the capacity of the habitat and in harmony with other uses. Past research has shown that "*every precaution must be exercised to hold this deer herd in check. Two or 3 years of conservative hunts may well jeopardize the welfare of the Kaibab North deer herd and range.*"

If the management goal is a high ratio of bucks to does, it is better to narrow that ratio by hunting antlerless deer than to curtail buck hunting during periods when deer numbers are high and precipitation is not. Under some conditions the doe herd can suppress rather than enhance buck production, and more is not necessarily better. Whenever there are periods of favorable precipitation, some antlerless deer hunting will be necessary to control the growth of the deer herd.

The history of the North Kaibab deer herd is 1 of the more dramatic in the annals of wildlife management. I hope you have enjoyed revisiting *"The Terrible Lesson of the Kaibab."*

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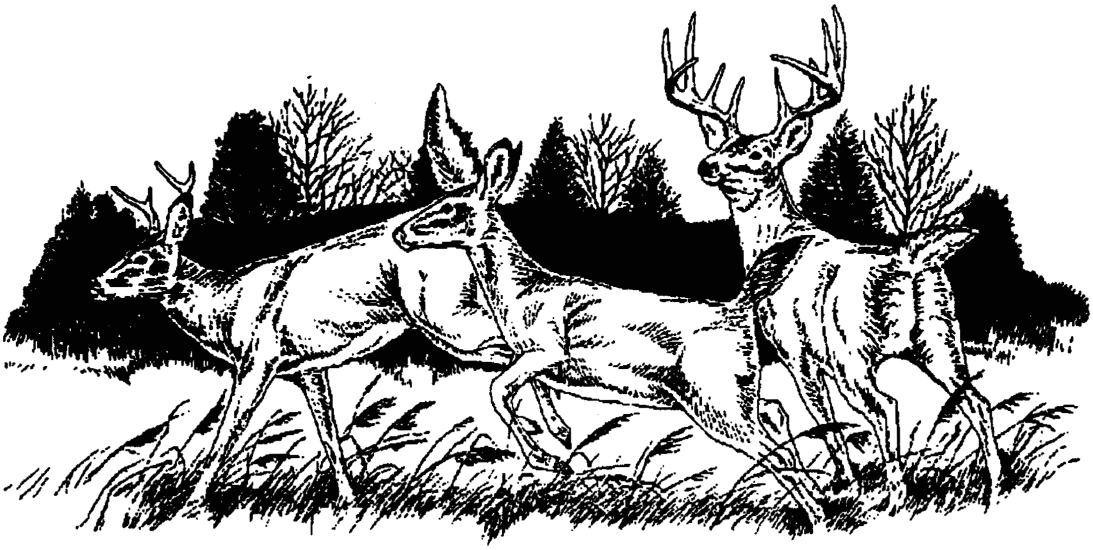

Effect of Disturbance on Reproduction of Coues White-tailed Deer

KIRBY D. BRISTOW[1]

Arizona Cooperative Fish and Wildlife Research Unit
University of Arizona, Tucson, AZ 85721

Abstract: I examined the influence of human disturbance on reproduction of Coues white-tailed deer by subjecting deer to different levels of disturbance during 2 breeding seasons, 1990-92. I found no difference in reproduction in response to increased disturbance of 4 hunter-days/km^2 during the peak of rut (January). Fetal rates and conception dates were not significantly different between treatment and control groups ($P > 0.05$). Firearms hunts, which occur before the peak of rut, are not likely to significantly affect herd productivity.

Key words: Arizona, disturbance, fetus, ovary, reproduction, white-tailed deer.

INTRODUCTION

Many animal species alter their behavior when human activity increases (Freddy et al. 1986, Anderson et al. 1990). Changes in behavior and movement patterns have been documented in elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) (Edge et al. 1985, Ward 1985). White and Thurow (1985) found that raptor nest success decreased when human disturbance increased. However, effect of human disturbance on reproductive rates of ungulates has received little attention. Coues white-tailed deer (*O. virginianus couesi*) are hunted during the rut in southern Arizona, and Wildlife Managers have expressed concern that this disturbance can interfere with breeding behavior and thus reduce productivity.

White-tailed deer increase their daily movement and activity in response to human disturbance (Marshall and Whittington 1968, Pilcher and Wampler 1982). Female white-tailed deer move to areas of their home-range where human disturbance is lower (Kammermeyer and Marchinton 1976, Root et al. 1988). Welch (1960) found that concentrated hunting pressure caused Coues white-tailed deer to shift their feeding periods and bedding areas.

If human disturbance causes female white-tailed deer to shift their movements and activity periods during estrus, then rutting males may not easily locate receptive females. Human disturbance could further hinder the search for receptive females by affecting behavior of rutting males. This situation could delay or prevent reproductive opportunities, which would ultimately reduce herd productivity.

I wanted to assess effects of human disturbance on reproduction in a population of Coues white-tailed deer. My objectives were to determine if increased disturbance through simulated hunting resulted in a measurable influence on conception dates, intrauterine loss, and fetal rate on a sub-population of Coues white-tailed deer.

Special thanks go to N. M. King, C. J. Schleusner, and R. A. Vega, for their assistance with data collection. I also thank O. E. Maughan, R. A. Ockenfels, J. A. Casteel, K. F. Bahti, and J. C. deVos, Jr. for

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[1] Present address: Arizona Game & Fish Department, Research Branch, Phoenix, AZ.

their logistical assistance throughout the study. Dr. N. S. Smith's continued support and guidance throughout all aspects of the study were invaluable.

STUDY AREA

I conducted this study in the foothills of the Santa Rita Mountains north of Patagonia, Arizona. Semi-desert grassland was found on the lower elevations (1,300-1,550 m), encinal at mid-elevations (1,350-1,700 m), and oak-pine (*Quercus* spp., *Pinus* spp.) communities dominated on upper (1,600-2,100 m) elevations (Brown 1984).

I selected 2 study area subunits, each approximately 15 km², based on historic levels of hunting pressure. The treatment subunit (TS) had been hunted heavily during the previous October, November, and December rifle deer hunts, while the control subunit (CS) had historically received less deer hunting pressure due to restricted access (K. F. Bahti, Arizona Game and Fish Department, pers. commun.). Vegetation of the 2 subunits was similar (Bristow 1992). Female white-tailed deer are faithful to their home-ranges, and radiomarked does had not moved between the 2 subunits in the past (Ockenfels et al. 1991, Fig. 1). Thus, I assumed that marked does and most unmarked does would not move between the 2 subunits.

METHODS

Movement

Each subunit contained ≥2 (CS = 2, TS = 6) female white-tailed deer that had been fitted with radiocollars (Telonics Inc., Mesa, Ariz., Ockenfels et al. 1991, Fig. 1). To establish presence and subunit fidelity of marked does, I obtained ≥1 location/week for each marked doe during field seasons (Oct-Jan) 1990-1992. I visually located each marked doe using a variable channel radio receiver (Telonics Inc., Mesa, Ariz.) and a hand-held yagi antenna. I made every effort to avoid disturbing marked does while radiotracking during pre-disturbance periods (Oct-Dec), and throughout the field seasons within the CS.

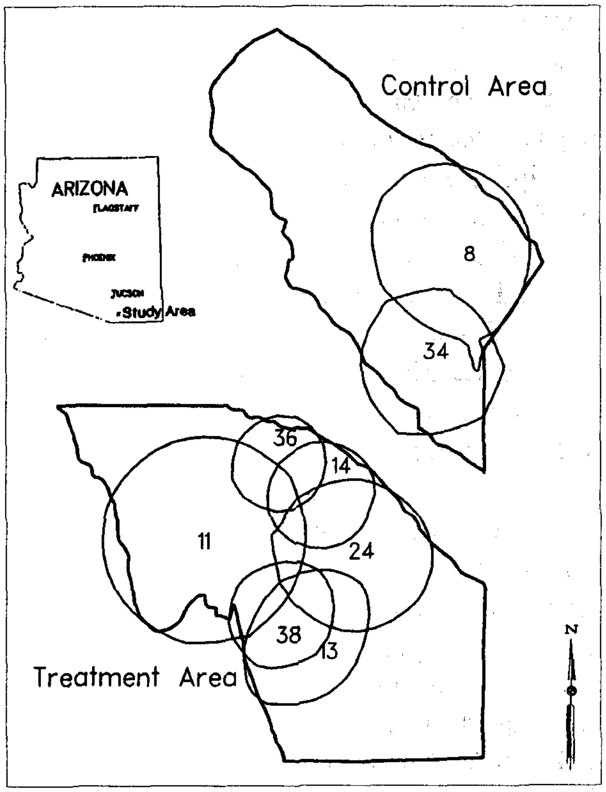

Figure 1. Study area showing home-ranges (70% harmonic mean core-areas, Ockenfels et al. 1991) of marked female white-tailed deer in the control and treatment subunits of the Santa Rita Mountains, Arizona, 1990.

Disturbance

I measured background and experimental disturbance in number of hunter-days/subunit. I measured background disturbance, exerted by the public, in both subunits, throughout the field seasons. There were 3 general firearms white-tailed deer seasons/year within each subunit. I placed hunter survey boxes at main entrances to each subunit during the 3 general deer hunting seasons each year. A majority of the hunters in these areas would pass through these access points (Ockenfels et al. 1991). A sign directed each hunter to take a survey card and record number of days hunted in that particular subunit. I multiplied average number of days hunted within each subunit by number of cards taken to determine hunter-days. I also counted people, vehicles, and camps, and recorded type of activity (e.g., hiking, quail hunting, deer hunting). I compared number of hunter-days/hunting season between subunits using 2-sample *t*-tests.

I exposed deer within the TS to experimental disturbance throughout January 1991 and 1992 (disturbance period). During the second and third weekends of January each year we conducted simulated hunts. Groups of 2-3 people hiked along designated routes and searched for white-tailed deer. When we found deer, we fired blank, large caliber rifles to simulate hunting. We pursued and disturbed all deer that we found until they left the area or could no longer be located. We conducted our disturbance throughout January, however, when fewer people were available we concentrated on marked does. I recorded the number of people present for each day of disturbance to tally hunter-days within the TS during the disturbance period.

Reproduction

From June 10 to July 21, 1992, 10 adult female white-tailed deer were collected from each subunit. This period corresponded to the later stages of gestation for white-tailed deer in this region (Ockenfels et al. 1991). The sample represented ≥10% of the total female deer population estimated within the study area (K. F. Bahti, Arizona Game and Fish Department, unpublished data). We attempted to collect all marked does, with the remaining does being collected as encountered from the population of each subunit. We tried to collect only females ≥2 years old. Given the home range fidelity of female white-tailed deer (Hood and Inglis 1974, Ockenfels et al. 1991), I assumed that does collected from each subunit represented those present under experimental conditions.

I recorded weights for each female, fetus, uterus and conceptus, and collected ovaries, and lower jaws. I estimated female age from tooth eruption and wear (Severinghaus 1949). I calculated a kidney fat index (Riney 1955), and used live weight minus conceptus weight, as measures of condition of each doe collected. I also qualitatively ranked (1-5) each female based upon the estimated amount of subcutaneous fat. I compared age and condition estimates between study groups using Mann-Whitney *U*-tests.

I examined ovaries for presence, number, and size of corpora lutea (CL), accessory CL (ACL), and corpora albicantia (CA) according to Cheatum (1949). I used numbers of CA as an index of the 1991 fetal rate. I used 2-sample *t*-tests to compare numbers of ovarian structures (CL, ACL, and CA), and fetuses between study groups.

I estimated age of fetuses as outlined in Hugget and Widdas (1951) using weight$^{1/3}$ and a birth weight of 2.48 kg (Smith 1984). I estimated birth and conception dates by assuming a gestation period of 200 days and projecting forward and back from fetal age. I compared fetal age at July 1 between study groups using a 1-tailed 2-sample *t*-test. I considered all statistical tests significant when $\alpha \leq 0.05$.

RESULTS

Disturbance

Someone tampered with the hunter survey boxes in December 1990 and I was not able to get an accurate measure of hunter-days for that period. Hunter-days in the CS for October and November 1990 were 64 and 120, respectively; whereas hunter-days in the TS were 125 and 148 for October and November, respectively. There were 60, 64, and 24 hunter-days in October, November, and December, respectively in the CS in 1991. In the TS in 1991, there were 157, 201, and 69 hunter-days in October, November, and December respectively. Surveys of hunters, vehicles, and campsites each year reflected hunter-days within each subunit. Number of hunter-days was greater in the TS during all seasons ($P = 0.02$, Fig. 2).

Average numbers of people participating in the simulated hunts on the second and third weekends in January were 15/day in 1991 and 17/day in 1992. We disturbed an average of 28 deer/day, with an average of 2 being marked does. We fired an average of 18 shots/day, and ≥2 deer were disturbed ≥2 times each day. During the remainder of January there were 2-3 people available for disturbance on weekends. I calculated an average of 60 hunter-days for January each year within the TS (15 km^2), including simulated hunts (Fig. 2). This was the maximum level of potential disturbance (60 hunter-days/15 km^2 = 4 hunter-days/km^2).

Movement

I relocated the marked does a total of 160 times over both field seasons ($\bar{x} = 16$ locations/doe/year). I disturbed marked does 43% of the time while radiotracking during pre-disturbance periods. I relocated marked does 31 times within the TS during the disturbance period, each time I disturbed the doe causing it to flee. Due to mortalities and transmitter failure there were only 4 marked does with operating transmitters throughout the field seasons 1990-92. Marked does were usually ($n = 148$) found within the study area subunit where they were captured, and there was no interchange of marked does between subunits.

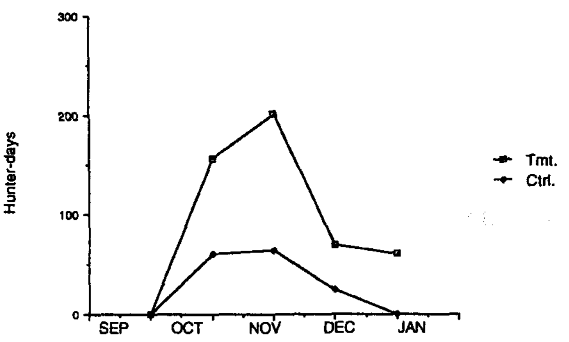

Figure 2. Hunter disturbance levels for the control and treatment subunits in the Santa Rita Mountains, Arizona, 1992.

Reproduction

There were no differences among ages, kidney fat indices, subcutaneous fat estimates, and body weights for the females collected from both subunits (Table 1).

I collected 11 fetuses from each subunit. I collected 2 females, 1 yearling and 1 2-year old, within the TS that were not pregnant. Sex ratios of fetuses in both groups were 4 males:7 females. Numbers of ovarian structures and fetuses were not significantly different between sample groups (Table 2).

Mean and median birth dates for both groups were in the fourth week of July (Fig. 3), and mean and median conception dates were in the first week of January. One 4 year-old doe, collected on June 22 in the CS, had already given birth. When I examined her ovaries I found 2 CL, and several cotyledons were present in both horns of the uterus. She was lactating when I collected her, and I saw 2 fawns in the area. Mean fetal ages at July 1 for control and treatment groups were 178 days and

Table 1. Age, kidney fat indices (KFI), body weight (BW), and subcutaneous fat (SF) estimates of female Coues white-tailed deer collected in the control (n = 10) and treatment (n = 10) subunits in the Santa Rita Mountains, Arizona, 1992.

	Age		KFI		BW(kg)		SF	
Subunit	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	Med.	Range
Control	3.7	2-5	34.5	16-45	32.5	27-36	3	1-3.7
Treatment	4.2	1-8	35.2	11-46	31.5	23-39	4	1-4.7
P^a	0.50		0.91		0.85		0.15	

[a] Mann-Whitney U tests.

Table 2. Corpora lutea (CL), corpora albicantia (CA), accessory corpora lutea (ACL), and fetuses taken from female Coues white-tailed deer collected in the control (n = 10) and treatment (n = 10) subunits in the Santa Rita Mountains, Arizona, 1992.

	CL		CA		ACL		Fetuses	
Subunit	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Control	1.3	1-2	0.9	0-2	0.3	0-2	1.1	0-2
Treatment	1.1	0-2	1.1	0-3	0.2	0-1	1.1	0-2
P^a	0.34		0.73		0.74			

[a] 2-sample t-tests.

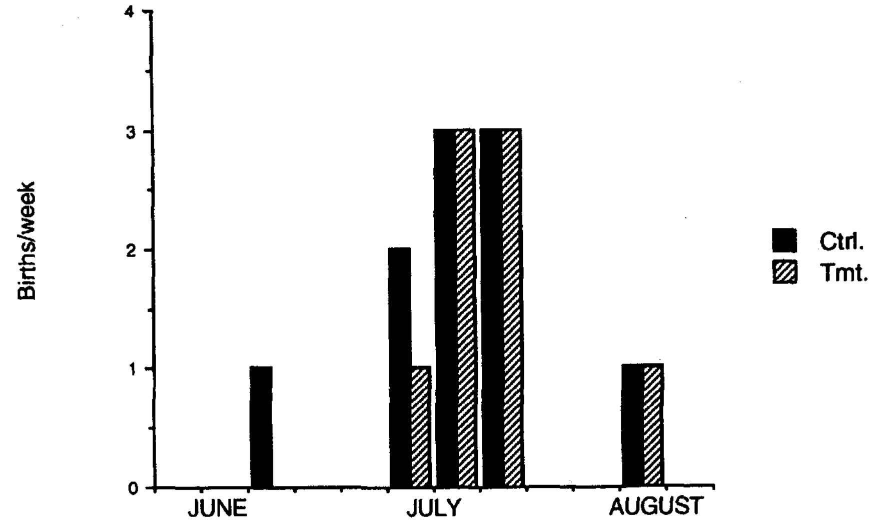

Figure. 3. Projected birth dates of Coues white-tailed deer fetuses *in utero* from the control and treatment subunits in the Santa Rita Mountains, Arizona, 1992.

176 days, respectively. Range of fetal ages was larger in the CS but their distributions were not significantly different ($P = 0.32$).

DISCUSSION

Results of this study indicate that my level and timing of disturbance did not affect reproduction of Coues white-tailed deer. We disturbed deer to a greater extent (4 hunter-days/km^2) than occurs during normal hunting seasons. The concentration of hunters during the simulated hunts was greater than that for the same area during the regular hunting seasons. Within the TS, the highest density of hunters for 1 weekend was 2.3 hunter-days/km^2 in October 1991.

Concern has been expressed that human disturbance affecting movement patterns of white-tailed deer during the rut could reduce conception rates. Ivey and Causey (1984) showed that during rut, female white-tailed deer increased activity, but restricted movement to small areas of their home range. Holzenbein and Schwede (1989) observed similar behavior and hypothesized that females restricted their movements to these "intensive search areas" (ISA) to facilitate their location by rutting males. If human disturbance can cause does to abandon these ISAs then rutting males may not easily locate receptive females. Simulated hunts coincided with peak rut, and should have produced the greatest impact upon productivity. However, conception rates for each year were not significantly different between treatment and control groups.

Reproduction in white-tailed deer can be affected by several factors such as age and physical condition of the doe (Verme 1969). The only does collected in 1992 that were not pregnant ($n = 2$) were from the TS, however, both were younger does with low KFIs and body weights. Condition estimates and age structures of sample groups were not significantly different, therefore, it is unlikely that the influences of nutrition or age-specific fertility affected the results.

Another potential effect of disturbance during rut is a delay in breeding and consequently in fawning periods. Female white-tailed deer have a 24-hour estrus period, and if not bred during that period, a doe may come into estrus approximately 28 days later (Cheatum and Morton 1942). Lost breeding opportunities during a female's first estrus could prevent reproduction, or delay breeding and parturition by 28 days and this shift may ultimately affect herd productivity.

High neonatal predation has been hypothesized as the selective force behind the evolution of synchronous fawning (Sadlier 1969). Opportunistic predators such as coyotes (*Canis latrans*) will attempt to prey upon white-tailed deer fawns whenever they are encountered (Smith 1984). When all fawns are born, and are vulnerable, during a shorter period, individual probability of a chance encounter with a potential predator is reduced. If breeding opportunities are delayed such that the fawning period becomes asynchronous, then more fawns may be lost to predation.

Since fetal age was not significantly different between the treatment and control groups, it can be assumed that birth dates would not differ. If disturbance level caused a delay in breeding opportunities, then calculated birth dates between sample groups should have differed. There were no differences in conception rates and birth dates between study groups, and thus no measurable effect of differential disturbance upon breeding.

MANAGEMENT IMPLICATIONS

Disturbance during peak rut did not affect reproduction of Coues white-tailed deer. Hunting prior to the peak of the rut is likely inconsequential relative to the effect of hunting on reproduction. If hunt structures are designed so that potential disturbance is <4 hunter-days/km^2, managers could be confident that disturbance would not affect herd productivity.

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Home-Range Size of White-tailed Deer in Northeastern Mexico

SONIA GALLINA
SALVADOR MANDUJANO
JOAQUIN BELLO
CHRISTIAN DELFIN

Depto. Ecología y Comportamiento Animal, Instituto de Ecología, A.C. Apdo. Postal 63, CP 91000, Xalapa, Veracruz, Mexico.

Abstract: Radiotelemetry was used in the current study to obtain information on home-range variation of white-tailed deer in northeastern Mexico. A drop net was used to capture 13 deer (6 does and 7 bucks) that were marked with Telonics collars for monitoring from November 1994 through October 1996. Monthly triangulation bearings were achieved hourly during 2 or 3 24-hr cycles. Home-range modeling was achieved for 95% and 50% Minimum Convex Polygon (MCP). Annual cycles were divided in 3 physiological seasons: breeding (November to February), postreproductive (March to June), and fawning (July to October). Estimated mean MCPs during these 3 seasons were 231, 215, and 172 ha for does; and 246, 209, and 160 ha for bucks. There were no significant statistical differences between the home-ranges of sexes ($F = 0.002$, $P = 0.96$). Differences did occur seasonally ($F = 4.005$, $P = 0.028$). Differences between the breeding and fawning seasons (SNK test) were most notable. Mean home-range values were greater during the breeding season and were possibly caused by a search for the opposite sex. The lack of annual differences between the home-range of sexes could be the result of availability of artificial water holes. Permanent artificial water holes totaled 32 in the study area.

Key words: arid land, home-range, Mexico, *Odocoileus virginianus*, white-tailed deer.

INTRODUCTION

In Mexico, white-tailed deer (*Odocoileus virginianus*) are widely distributed. Fourteen subspecies occur in Mexico and they are found throughout the country, with the exception of Baja California. In the Northeast, white-tailed deer are found mainly in arid lands. It is important to understand the ecology and behavior of this animal if biologist are to design effective management programs.

The home-range concept, as being the area in which an animal performs most of its activities, was formally suggested by Burt (1945). Therefore, home-range size is an important prerequisite to understanding a species' behavior, ecology, and management (Sanderson 1966). Home-range characteristics are influenced by the manner in which individual animals react to their habitat and to each other. Such factors may reflect population features such as deer density and social structure. Home-range size is dependent on diet and metabolic need (McNab 1963, Mace and Harvey 1983 cited by Braun 1985).

The objectives of this study were to obtain information on home-range sizes as they relate to seasonal and annual variations, sex variation, what factors influence these, and to understand animal strategies in this arid region. Knowledge relating to home-ranges may provide insight into various facets of the species' social organization and foraging ecology.

Management of the species could benefit from knowledge relating to habitat use, reproduction, activity patterns, predator avoidance strategies, and resource partitioning between sexes.

STUDY AREA

The study was conducted at Rancho San Francisco, located in the northeast section of Mexico, in the states of Nuevo Leon and Coahuila, between 27°19' and 27°22'N and 100°36' and 100°39' W, with an elevation of 430 m. The ranch has been a property of Ducks Unlimited of Mexico (DUMAC) since 1983. DUMAC established a wildlife research center on the property consisting of 1,500 ha, 1,000 ha of which is enclosed by a 2.4-m high deer fence (Herrera 1993).

Climate of the area is warm and dry. Annual precipitation is less than 400 mm, and is distributed primarily between May and September. Heaviest rainfalls occur during September. High temperature is 40 C, with a mean temperature of 29 C during July. December and January are the coolest months, with a mean temperature of -1 C.

Dominant vegetation is xerophytic scrub with cenizo (*Leucophyllum frutescens*), chaparro prieto (*Acacia rigidula*), hojasen (*Flourencia cernua*), and gobernadora (*Larrea tridentata*) being the dominant species. Briones (1984) identified 6 different plant associations. Inside the fence enclosure, there are 3 waterholes (bordos) with water in the wet season and 32 permanent artificial waterholes (1,500 L capacity) that are filled periodically to be used by wildlife.

METHODOLOGY

Deer were captured using drop nets (15 x 15 m) with corn as bait. Between November 1994 and October 1995, 13 deer (7 bucks and 6 does), were captured and equipped with radiocollars (Mod 400, Telonics, Inc. Mesa, Arizona). Two TR-4 receivers and 2 "H" antennas (150-154 MHz), were used simultaneously to receive signals for locating collared deer. Radiolocations were made from 2 towers (10 m high) each hour on 24-hr cycles. Each month during 1995 and 1996, 2 or 3 24-hr cycles were completed.

The TRIPOLY Program (Laundré 1990) was used to transform original data to UTM coordinates with a magnetic deviation of 9.15 degrees. With the CALHOME Program (Kie et al. 1994), home-range sizes were calculated for individual deer using the Minimum Convex Polygon (MCP) at 95% and 50%. Three biological seasons were studied: breeding (November-February), postreproductive (March-June), and fawning (July-October). To compare home-range sizes for the different seasons and for sexes we used ANOVA tests. The SNK method was used to separate treatments where there were statistical differences (Zar 1996).

RESULTS AND DISCUSSION

We analyzed 4,818 locations obtained from October 1994 to October 1996 (2,590 for does and 2,228 for bucks) The minimum number of data points used to calculate home-range size was 90.

The mean value of the home-range size for does was 206 ± 13 (SE) ha, and for bucks was 205 ± 14 ha. Hence, there were no significant differences ($F = 0.002$, $P = 0.96$) between sexes. We attribute these results to the fact that in the Ranch there is water management and there are many waterholes distributed in all the area, so the water is not a limiting factor in this arid ecosystem. The other factor that could have influenced the results was the deer fence that could have restricted male movement.

Beier and McCullough (1990) reported the mean size of home-ranges for white-tailed does, using MCP as 45 ha, and those of males averaged 142 ha at the George Reserve (464 ha with deer proof fencing), Michigan. Home-range of deer on the George Reserve were considerably smaller than those noted in previous studies of white-tailed deer. This was probably due to the high interspersion of habitat types when compared to other study areas. In addition to habitat interspersion, 2 other factors may have contributed. First, the Reserve's relatively high deer density may have been a factor, but it is not clear if this increased or decreased home-range sizes. As density increases, deer could either increase home-range size in response to forage depletion (McNab 1963, Harestad and Bunnell 1979 cited by Beier and McCullough 1990) or reduce to minimize intraspecific encounters. Secondly, the existence of a deer-proof fence possibly limited male movement and ultimately home-range size, especially during the fall rut. It is possible that in the study site, the deer fence was a factor which affected long-range movements of bucks, thereby resulting in similar home-range sizes for both sexes. Also, home-ranges were larger in the study area compared to Michigan, because of varying vegetation types and food availability.

Significant home-range differences between biological seasons ($F = 4.005$, $P = 0.028$) were noted. Home-ranges were smallest during the fawning season ($\bar{x} = 166 \pm 21$ ha). In contrast, in the reproductive season the home-range size value was 238 ± 14 ha, and postreproductive mean size estimated was 212 ± 15 ha. These variations may indicate deer occupied larger areas when they were searching for a mate and when food supplies were low. The fawning season coincided with an increased availability of food resources (rainy season), and with reduced doe mobility because does were lactating and protecting their fawns. Thus we supposed that the animals could find the needed requirements (food, water, and cover) in smaller areas. In others studies, the size of the home-ranges decreased during summer. It is assumed home-range sizes are proportional to deer metabolic needs. Hence, a decrease in the size of the area utilized reflected an increase in the availability of resources that exceed the increment in the metabolic demand (Beier and McCullough 1990).

The core area (50% MCP) where deer concentrated their activity was calculated to be 28% of the total home-range. The mean core area for does was 57 ± 6 ha and for bucks was 59 ± 7 ha. There were no significant differences ($F = 1.97$, $P = 0.16$) between seasonal core areas. Mean core area for the 3 seasons were: breeding season 66 ± 7 ha, postreproductive 64 ± 7 ha, and fawning 43 ± 10 ha.

MANAGEMENT IMPLICATIONS

On the ranch, water management is intense as there are waterholes throughout the area, and so in this arid ecosystem, water is not a limiting factor for deer. The home-range size reflects resource availability, with significant differences between biological seasons that we attribute to the fawning season (smallest home-range) when the wet season occurred resulting in high food and water availability. We think that the fence could have influenced the results (no differences in home-range size between the sexes) due to movement restrictions.

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The Increasing Complexity of Deer Management: Is More Better?

JAMES R. HEFFELFINGER
RONALD J. OLDING

Arizona Game and Fish Department, Tucson, AZ 85745

Abstract: Increasingly complex deer hunt structures may reduce participation, recruitment, and retention of hunters. A permit system was initiated for Arizona deer hunts in 1971 in response to concerns for declining deer populations statewide. This was better justified for the desert mule deer inhabiting open habitat, however, Coues white-tailed deer are more resistant to over-exploitation because of the rugged terrain and brushy habitat they occupy, as well as a higher reproductive rate. Whitetail hunt structure in Arizona has grown from 8 General deer hunts on 2 season dates in 1969 to 117 General deer hunts occurring in 8 different season dates in 1997. Increases in complexity of hunt regulations usually give deer managers more control over hunter distribution and harvest. However, such changes in management strategy may create unnecessary confusion to the hunting public with little benefit to the wildlife resource. Throughout a proliferation of season dates, Arizona Coues deer populations have fluctuated in response to factors other than buck-only hunting.

Key words: Arizona, deer management, harvest, mule deer, *Odocoileus virginianus couesi*, *O. hemionus*, white-tailed deer.

INTRODUCTION

Hunt structures and management guidelines are continually changing in an attempt to improve management and meet hunter expectation. Harvest strategy modifications are most often a continuation of the past trend toward increased complexity. These changes must be accurately and easily conveyed to the hunting public to promote compliance and effectively communicate management goals.

Increased management complexity, while usually allowing more control, frequently causes confusion among the hunting public and may not actually result in improved management (McCaffery and Ishmael 1995). A recent simplification of deer hunting regulations in Indiana was well-received by hunters and improved perceptions of responsiveness to the public (B. Frawley, Indiana Dep. Nat. Res., pers. commun.). The confusion of complex and ever-changing regulations can reduce recruitment and retention of hunters (Enck and Decker 1990, Bissell and Duda 1993:54-56), and also increase the incidence of inadvertent wildlife law violations (J. Romero, Ariz. Game & Fish Dep., pers. commun.). This can create discontent among the very constituents who provide the greatest support for the agency and have historically provided the greatest support for the wildlife resource.

HISTORY OF ARIZONA'S DEER PERMIT SYSTEM

In 1971, the Arizona Game and Fish Department (AGFD) initiated a statewide permit system for deer hunting. The permit system was better justified for mule deer (*Odocoileus hemionus*) than white-tailed deer (*O. virginianus*) because of their lower reproductive rate (McCullough 1987) and greater vulnerability in the open desert grassland/desert scrub habitat they occupy. Mule deer are more likely to allow a closer approach by hunters, however, whitetails avoid danger by either taking flight quickly, or hiding in thick cover (Geist 1981) in a habitat which is characterized by rough, rocky, and brushy terrain which is difficult to access. This allows whitetails greater protection against over-harvest than mule deer.

There were 8 different General (firearms) deer hunts in Arizona in 1969 occurring over only 2 season dates. The 1997 Fall Hunt Regulations contain 117 different General deer hunts covering 8 season dates. In addition, there are 13 Juniors-Only, 10 Muzzleloader, Juniors-Only Muzzleloader, and 8 archery hunts. The number of non-reservation Game Management Units (GMU) has grown from 55 to 78 in that same time period.

Within each GMU (or hunt area comprising several GMUs) permits are allocated to limit the number of hunters and harvest in that area. These permits can be adjusted annually based on harvest and survey data for that hunt unit. The Species Management Guidelines, which are used to adjust permits, are primarily based on post-hunt bucks:100 does ratio, fawns:100 does ratio, and hunt success. A permit increase is indicated when these indices are above the guidelines and a decrease is warranted when the data fall below the guidelines. Hunt success guidelines for both species is 20-25%. The survey guidelines for mule deer are 15-25 bucks:100 does and 40-50 fawns:100 does; while whitetail guidelines are 20-30 bucks:100 does and 35-45 fawns:100 does. In addition, trends in all indices available (e.g., days/kill, deer observed per hour of helicopter flight, etc.), as well as hunter density, requests for special seasons (ie. Juniors-only hunts), and limitations to access are considered in the recommendation of permits.

EVOLUTION OF WHITETAIL MANAGEMENT IN SOUTHEASTERN ARIZONA

Changes made in an attempt to refine and improve management, meet public demands, and placate land owners often increase the complexity of the hunt structure and corresponding regulations. The history of the whitetail hunt structure in southeastern Arizona (Region V) illustrates this point. Region V had 83% of Arizona's whitetail tags in 1996 allocated to more than 13 GMUs. In this Region alone, the number of General whitetail-only hunts that hunters had to choose from has changed from 1 November hunt in 1977 to the current 39 whitetail-only hunts (Fig. 1), 3 muzzleloader, and 2 Juniors-Only hunts in 1997. In addition, Region V units are included in 5 different archery hunt structures.

The single November whitetail hunt was divided into a November and November/December hunt (the latter is referred to as a December hunt) in 1978; permits were issued for a single block comprising all GMUs in southeastern Arizona. In 1986, an October hunt was initiated which, along with the November hunt, was permitted with all 13 of southeastern Arizona's whitetail GMUs as 1 hunt area. For the December hunt, southeastern Arizona was split that year into an east and west half, which were then permitted separately (Fig. 1).

The following year (1987) the November hunt was also split into the east block/west block structure and permitted separately. In 1990, the west block was divided into individual GMUs for the December hunt. The following year, the October hunt in southeastern Arizona was

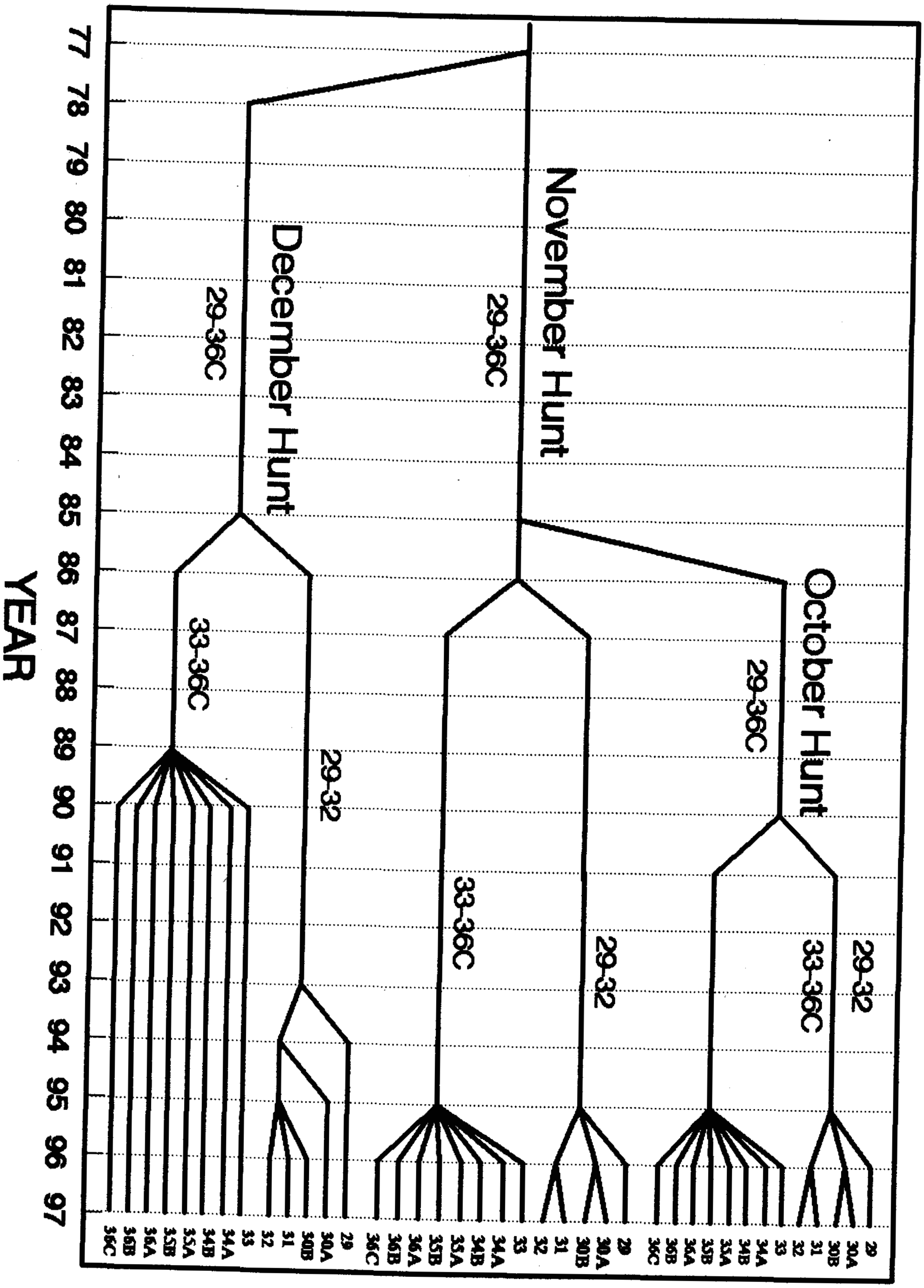

Figure 1. Graphic history of southeastern Arizona (Region V) whitetail hunt structure, 1977-97.

split into the east block/west block structure. The number of hunt areas that hunters had to choose on their applications continued to grow until 1997, when all whitetail hunts were permitted by individual unit, forcing hunters to choose among 3 season dates and 13 different hunt units for a total of 39 hunts.

The advantage to managing deer with smaller hunt areas is the ability to manipulate the hunter densities and harvest in localized areas, thereby allowing management at a finer resolution and smaller scale. Persistent recommendations from field personnel to control hunters and harvest by unit provided the impetus to most of the changes instituted in southern Arizona's whitetail management. In some cases though, hunt permits were reduced to alleviate hunter crowding in the areas with the highest whitetail densities and where most survey and harvest statistics were average or above average.

In 1991, the Arizona Game and Fish Department (AGFD 1991) conducted a survey of Arizona whitetail hunters to evaluate hunter opinions regarding the whitetail hunts. Only southeastern Arizona offers the October and November hunts, which comprise 82% of the whitetail permits in Region V. Permits, and therefore hunter densities, are kept low in December hunts in Region V to provide a quality hunt experience and because the bucks are more vulnerable during the rut. The results of the survey indicated that 69.1% of the October hunters and 74.4% of the November hunters felt hunter densities in the block hunts were "too low" or "about right." Unit 34A is considered to be 1 of the most crowded whitetail units in the state and 66.7% (16/24) of October and November hunters surveyed did not feel hunter densities were too high.

The number of hunters afield in the Region V October and November hunts has remained constant since that survey (Fig. 2). The trend in hunters afield has generally increased in the eastern half of the Region (east block hunt unit) and decreased in the western half because of a conscious shift of hunt permits to the east in 1988 to better distribute hunters and reduce concerns of hunter crowding in the west block. There

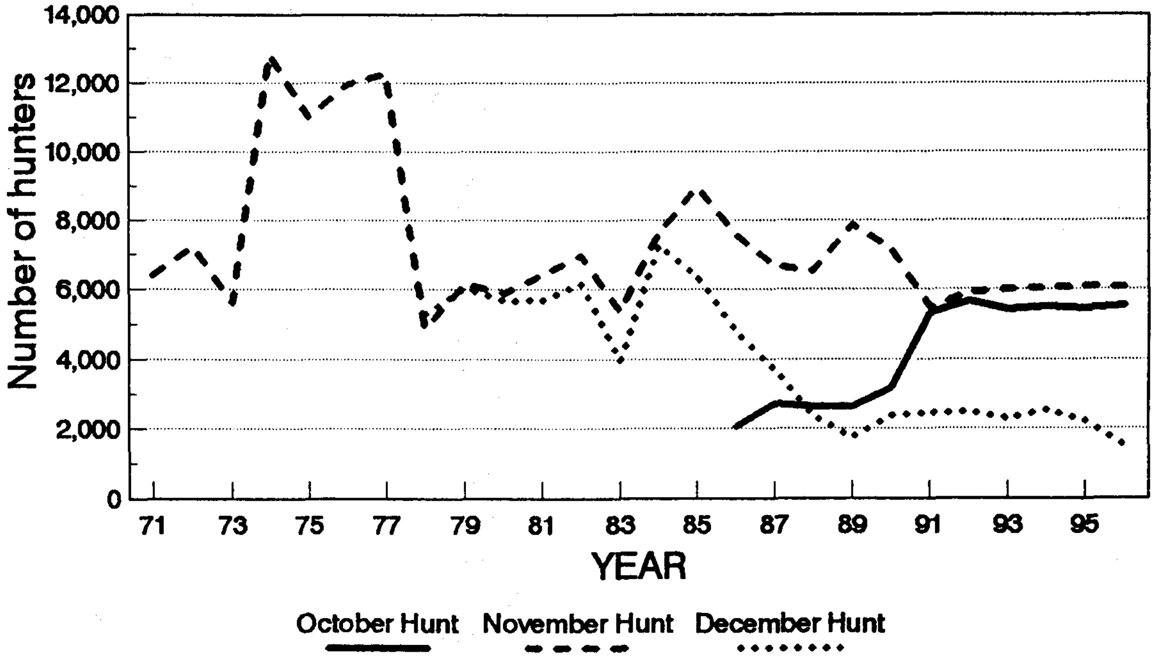

Figure 2. Number of whitetail hunters afield at 1 time in southeastern Arizona (Region V), 1971-96.

were 7,000 hunters afield in the November west block hunt in 1985, but by 1995 (the year before the block was split into individual GMU hunts) there were only about half as many west block hunters in the field at 1 time (3,656). Overall, whitetail hunter density in southeastern Arizona has been much less throughout the early 1990s than in the mid-1980s, due to changes in hunter management and a reduced deer population.

Permits have been reduced in some areas in response to a reduction in hunter access following the closure of roads on private land. Closures such as these concentrate hunters into the remaining open areas and exacerbate the problems which caused the original road closures. Threats by landowners to close additional access is also cited as a reason to reduce the number of deer permits authorized for that hunt unit. If hunter access to huntable habitat is a major problem in a particular area, it will be reflected in the percent of hunters who are successful (hunt success).

Hunters seemed to distribute themselves within the multi-unit block hunts in relation to deer abundance, densities, and hunter access. Data from an annual post-season hunter questionnaire support this. For example, in the 4 years previous to the splitting of the multi-unit block hunts (1992-95), the hunt success for October and November hunts in GMU 36B (25-35%) ranged above guidelines. The number of hunters choosing to go to this unit climbed at a steady rate throughout this period. The October hunters in 36B increased from 803 in 1992 to 1,113 in 1995 for an average annual increase of 12.9%. The number of hunters in the November hunts increased in parallel fashion from 954 to 1,153, for an average gain of 7% per year. In 1996, despite the bucks:100 does and fawn:100 does ratios within guidelines, and hunt success far above guidelines the number of hunters allowed in the field was reduced by 25.5% (October) and 23.2% (November) when the block hunt was divided into individual units.

On the other hand, Unit 35B had October and November hunt success (11-19%) below guidelines for the last 3 years of the block hunt structure (1993-95). In 1995, the number of hunters who chose that unit out of all units available to them in the block was 16.2% (October) and 29.5% (November) fewer than the previous 5-year average (1990-94).

The change to management by individual GMU allowed for the complete control over whitetail hunter distribution for the first time. Some shifts in permits were made (e.g., the reductions in GMU 36B), but the overall distribution Region-wide changed little (Fig. 3).

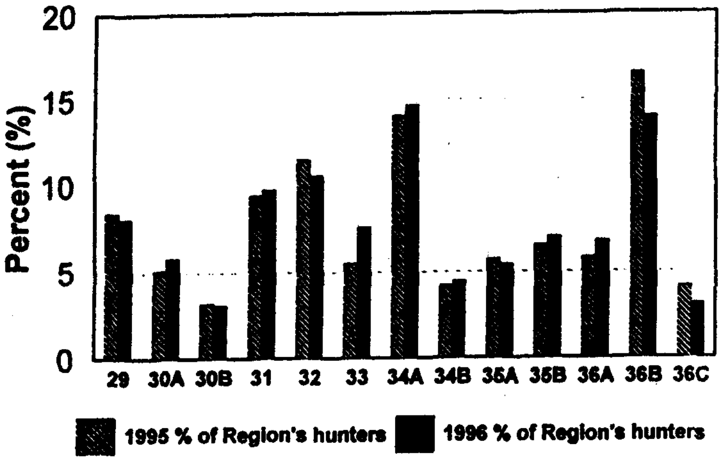

Figure 3. Distribution of whitetail hunters among Game Management Units (GMU) in southeastern Arizona (Region V) before (1995) and after (1996) splitting multi-GMU hunts to individual GMU hunts.

Deer management by smaller areas offers the opportunity to reduce buck harvest in localized areas to maintain the standards set in the hunt guidelines. Although the October and November hunts were in multi-GMU blocks in the western half of Region V, harvest could be regulated by changing permit levels in the December hunts which were prescribed individually in most (11/14) GMUs. December permits made up only 18% of the total permits but because hunt success was nearly twice as high as the earlier hunts, a much larger effect could be made on the total harvest by manipulating these hunts.

A desire to reduce harvest in GMU 34A has been a driving force for the splitting of the multi-unit block hunts. This GMU was considered by some Wildlife Managers to represent an over-exploited deer herd which would benefit from a reduction in harvest. GMU 34A contains the largest population of whitetails in the state. The density of deer in this unit, as indexed by deer observed per hour of helicopter flight (5-yr $\bar{x}$ = 112.9), is much higher than the Region V average (5-yr $\bar{x}$ = 32.6).

In southeastern Arizona, the age structure of the whitetail harvest shows a relatively mature buck population indicating past buck harvest levels have not been inappropriately high. The age structure of 687 whitetails field checked throughout Region V 1990-95 shows only 38.9% of that harvest sample was yearlings (267/687). A full 31.4% of the harvest was comprised of 3-5 and 6-8 year old bucks.

The age structure of 167 bucks harvested 1991-96 in Unit 34A was relatively mature for public land in the West with the 2.5-year olds (25.7%) and 3.5-5.5 year olds (37%) well represented. Yearlings made up only 35.9% of the harvest.

Antler classes (e.g., 1x1, 2x2, 3x3, etc.) observed from the post-hunt helicopter surveys in GMU 34A also indicate the population's age structure included older-aged bucks. Antler classes of bucks seen from the helicopter were recorded as a relative index to age structure 1991-95. In that time period, 111 bucks were classified by antler conformation with only 36.9% (*n* = 41) being 1x and 34.2% (*n* = 38) 2x (2x1s were tallied as "1x" and 3x2s counted as "2x"). A full 28.8% (*n* = 32) of the bucks observed on surveys were 3x3s or larger.

In addition, the hunt success in this GMU has been within or above Management Guidelines (20-25%) for the entire 1991-96 period, indicating that hunters are consistently finding and harvesting bucks at rates that met guidelines. GMU 34A hunters also harvested deer in fewer days (13 days/kill) than the Region V average (14) during this period.

The number of bucks:100 does from post-hunt surveys in Unit 34A has remained below guidelines during this period. This remains the only piece of contradictory information. When all data are considered the profile of this GMU is not indicative of an over-exploited whitetail population. A sufficient number of bucks have been surviving harvest and natural mortality factors to maintain a relatively old age structure. Additionally, hunters were as successful in this GMU, or more so, than the average Arizona whitetail hunter.

RAMIFICATIONS OF CHANGES

Biological

The disadvantages of an increasingly complex hunt structure are part biological and part sociological. Biological data used to make management decisions must be consistently gathered to provide useful trends. Changes to management boundaries (e.g., splitting a group of GMUs to be managed independently) break the unit history and compromise the long-term perspective that is critical for accurately monitoring herd responses to varying harvest intensities (Wisconsin Department of Natural Resources 1994). The AGFD frequently resists efforts made by outside entities to change their hunt boundaries for this reason. McCaffery and Ishmael (1995) stated that *"It is popularly believed that smaller Deer Management Units result in more precise management, but the opposite is usually true. Fragmentation of Deer Management Units reduces the precision of herd monitoring capability because sample sizes are smaller and subject to more inaccuracy."* Data analysis in Wisconsin showed that splitting a deer management unit has the minimum effect of increasing the imprecision of survey data by more than 40% (McCaffery and Ishmael 1995). Deer management units in Wisconsin are smaller in total size (approx. 1,036 km^2) than southeastern Arizona GMUs ($\bar{x}$ = 2,484 km^2), however, the average amount of whitetail habitat within Region V GMUs is actually less ($\bar{x}$ = 806 km^2) than Wisconsin units.

It has been suggested that managing in smaller units improves the quality of the harvest data collected via the post-hunt hunter mail questionnaire. An analysis of 1990 Arizona whitetail harvest data showed that confidence intervals would not improve if multi-GMU block hunts were split into individual GMU hunts (L. Piest, Arizona Game and Fish Department, unpubl. data).

Sociological

Perhaps the greatest detriment to more complex regulations is to the hunting public. Increasingly complicated hunt regulations can cause discontent and confusion among the hunters. Hunters supported the original permitting of the deer hunts statewide after several years of declining deer populations in the late 1960s where hunt success dropped to 16% (Supplee et al. 1997). However, out of 97,113 hunters in 1970, only 60,997 applied for the 77,437 permits authorized in 1971 (AGFD 1996). This 37.2% decrease is believed to be a reaction to the increased complexity of the permit system (Supplee et al. 1997). The number of 1st choice applicants slowly climbed back to 94,285 in 1980, decreased to 71,826 in 1983, and again climbed to 94,189 in 1995 (AGFD 1996). A similar decrease in the number of permit applicants was seen when the archery javelina seasons were permitted in Arizona (Heffelfinger and Olding 1997).

Arizona is 1 of the fastest growing states in the nation and the second most urban. Some of these new Arizona residents were hunters in their states of origin and accustomed to simpler deer hunting regulations. Many of these new potential hunters will be lost to the sport unless they can acclimate to the regulations and hunting environments in their new state (Bissell and Duda 1993:59). It is obvious that the simpler the regulations, the more potential hunters can be recruited and retained.

In addition to confusion by the hunting public, complex regulations also cause more confusion among the state wildlife agency staff who must assure that all regulations are accurate before they are printed and distributed. With increasing complexity, we have noted an increase in the number of errors which invariably slip past reviewers and into the printed regulations causing more confusion and lost revenue for reprinting or rectification.

Complex regulations can restrict hunters. For example, some felt splitting the Region V whitetail blocks into individual GMUs would not restrict hunters because questionnaire data indicated only 11.9% of the block hunters actually hunted more than 1 GMU in the block. Many hunters often have favorite hunting locations with which they are familiar. Under the block hunts a hunter who hunted in GMU 36A every year only had to draw 1 of the 4,000 permits in the west block hunt. When the hunt structure was changed to the issuance of permits by individual GMU, that same hunter must draw 1 of only 300 permits in 36A in order to hunt the same spot they have hunted for years. This has been even more critical since hunt applicants now outnumber permits nearly 2:1. Many wasted choices can be expended in low-permit individual units, resulting in applicants not being drawn at all.

These restrictions have a negative influence on hunter recruitment and retention (Bissell and Duda 1993:54-56). Enck and Decker (1990) found that confusing regulations was the most important impediment to waterfowl hunting participation in New York, with 39% of the ex-waterfowl hunters citing this reason for quitting. A 1995 survey of Arizona big game hunters found that 11% were definitely considering quitting big game hunting because of the permit drawing system and an additional 15% indicated they were thinking about quitting for that reason (Supplee et al. 1997).

DISCUSSION

Arizona's hunt regulations have grown from a mere pamphlet to a 67-page booklet in the last 2 decades. Much of this increased complexity was necessary to regulate the harvest of wildlife in the face of a growing human population. The origins of wildlife management in North America were based on simply reducing the unregulated harvest of wildlife. More recent efforts focus on an equitable distribution of the regulated harvest among various user groups. However, deer managers are sometimes too quick to make sweeping hunt structure changes which may not be necessary. These changes offer the appearance of better management because there is more control over hunters and harvest. Arizona's hunting public generally supports new regulation changes because the AGFD has earned their trust. Most hunters accept changes under the premise that it is necessary for the proper management of the wildlife resource.

Splitting the block whitetail hunts in southeastern Arizona may seem intuitively reasonable because of the mountain island physiogeography. However, the necessity of this increase in complexity does not appear to be supported by long-term survey, harvest, hunter density, and hunter satisfaction data. Survey and harvest data are collected by individual GMU and used to manipulate GMU permit levels. In a multi-GMU block, there will always be a GMU which, for a few years, may benefit from being separated from the block. The temptation to continually split management units into smaller and smaller portions persists even below the GMU level. Justifications could be made for splitting GMUs to the individual canyon level based on differences in survey and harvest data.

Supplee et al. (1997) speculated that "*Public acceptance of individual unit management of whitetail deer is perhaps evidence of the preference for managed opportunity over a more open system.*" This conflicts with public input received prior to that change in hunt structure where the public was overwhelmingly opposed to such a change.

Two public hunt meetings were held in southeastern Arizona prior to the change in 1995 to gather public input regarding the division of the multi-unit hunt blocks. Comments received from area hunters expressed overwhelming opposition to creating individual whitetail hunts by GMU. At 1 meeting in Willcox, Arizona, 2 hunters suggested that if a change was needed for biological reasons then they would rather cluster a few units together. At the Tucson public meeting a lively discussion ensued among a large crowd with no one expressing support for a change from the multi-GMU hunt structure which had been in effect since 1971.

A questionnaire was conducted in the summer of 1995 to determine hunter attitudes toward various potential management changes. No background information was given to respondents to avoid biasing the results. One question asked: *"Should whitetail block hunts be split up into single-unit hunts?"* To which 52.7% of the respondents replied "yes." Comments received at the Tucson public meeting indicated that some hunters may not have understood the ramifications of their "yes" answer.

The 1996 public open house in Tucson was attended by 25 people. Three hunters commented on the proposal to break up the multi-unit block hunts; all 3 were opposed. At the April Commission meeting, 3 different members of the public mentioned the whitetail block hunts in their comments to the Commission. All 3 were opposed to breaking up the multi-unit block hunts.

Deer managers must make a greater effort to take a close look at hunt structure changes they propose and ask if those changes are really necessary for the resource and/or public, and if the gains in control outweigh the disadvantages. It is instructive to look at what has been gained by the recent changes to the whitetail hunt structure in Arizona. Theoretically, management by individual GMU should allow for an increase in hunter opportunity because whitetail permit levels can be prescribed more precisely.

Trends in whitetail bucks:100 does, hunter success, days per kill, and deer observed per hour of helicopter flight in southeastern Arizona (Region V) have remained relatively stable for the last 4 years (Fig. 4). The statewide population estimate (based on the above harvest and survey data) also corroborates these trends, maintaining a relatively stable population 1994-96. During this 3-year time period, however, the number of statewide whitetail permits has decreased 9.5% (Fig. 5).

This loss of permits comes at a time when demand for deer hunting opportunity is high. In 1997, 92,323 deer hunt applicants competed for 53,150 deer tags. This resulted in more than 39,000 deer hunters not being able to go deer hunting in the Fall of 1997.

A survey of Arizona whitetail hunters in 1991 showed that the ability to deer hunt every year was by far the most important consideration (AGFD 1991). The stated Guideline Objective of the Species Management Guidelines for deer directs AGFD *"To maintain mule deer and white-tailed deer populations at levels which provide recreational opportunity to as many individuals as possible, while avoiding adverse impacts to the habitat."* As such, we should be striving to provide as much deer hunting opportunity as the resource will reasonably allow.

The public has entrusted management of the wildlife resource to trained, professional wildlife biologists employed by state wildlife agencies. We must be vigilant to ensure that the changes made are supported by data and are necessary for the benefit of both the resource and the public. AGFD has embraced Total Quality Leadership (TQL) in the past few years. In light of this, we need to ensure that management changes are the result of a complete analysis including informed and adequate public opinion.

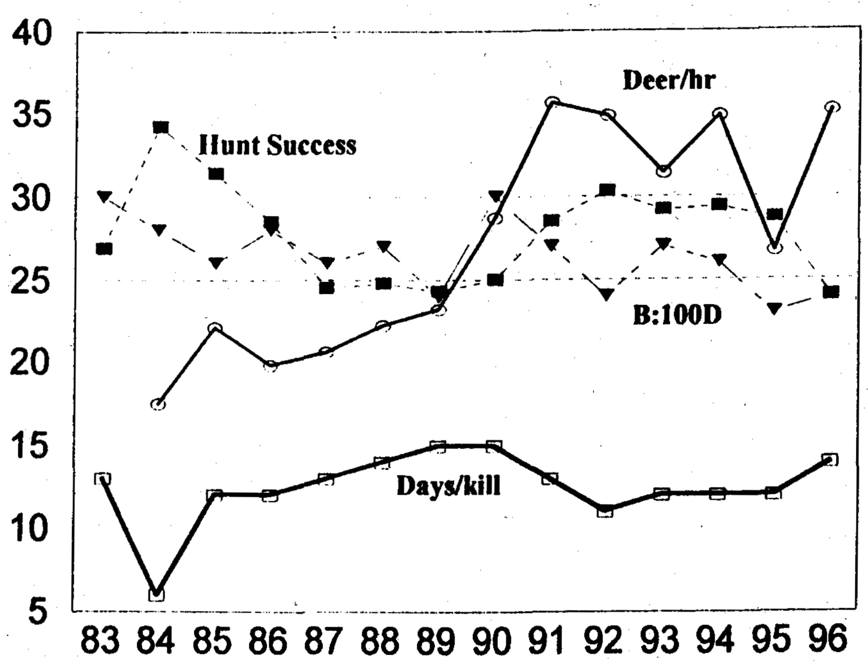

Figure 4. Trends in whitetail survey and harvest data in southeastern Arizona (Region V), 1983-96.

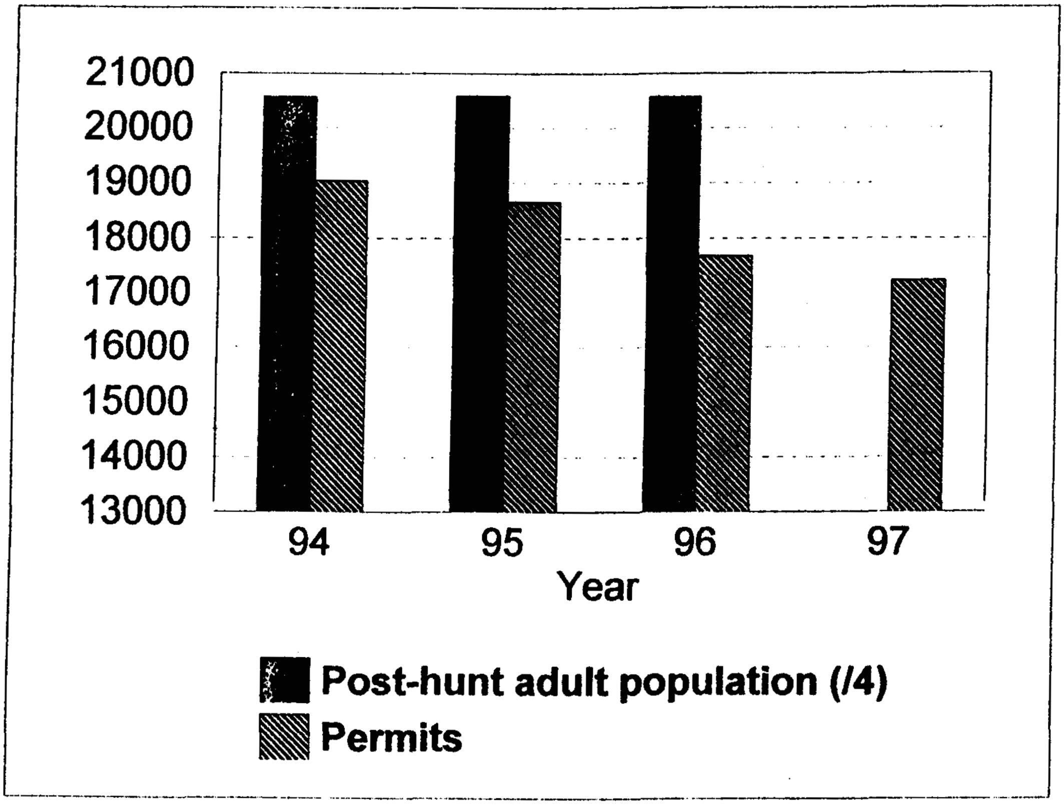

Figure 5. Trends in Arizona statewide adult whitetail post-hunt computer population estimate (/4) and whitetail permit levels, 1994-97.

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Density Dependence in Nevada Mule Deer

MIKE HESS
Nevada Division of Wildlife, PO Box 10678, Reno NV 89520

Abstract: Nevada deer data were examined for evidence of density dependence (DD). Data collected in 19 years of aerial survey showed a highly significant negative correlation ($r = -0.6668$, $P < 0.0019$) between the number of adults in the fall and the fawn-to-adult ratio during spring 3 months later and the hypothesis of DD occurring among deer in Nevada since 1978 was accepted. Nevertheless, severe winters disrupted DD for 2 years. Deer composition and kill data from the 26 years preceding the aerial censuses also provide evidence of DD when compared with the later data. Sustained yield (SY) harvest is possible and the existing monitoring capabilities are adequate to implement SY safely. Winter feeding, predator control, and habitat modification, among other strategies, should be reviewed critically based on their likely benefit to mule deer populations. Spring fawn-to-adult ratios are valuable for forecasting population trends.

Key words: census, density dependence, estimate, helicopter, model, mule deer, Nevada, *Odocoileus hemionus*, population, ratio, recruitment, sustained yield.

INTRODUCTION

The theory of population density dependence (DD) was originally published in 1798 by Thomas Malthus in *An Essay on the Principle of Population* (Berryman 1981). Broadly, DD is a change in birth, death, or migration rates resulting from intraspecific competition for resources. Mule deer (*Odocoileus hemionus*) were presumed DD (Dasmann 1964, Connolly 1981), but validating this hypothesis in wild populations has proven difficult. Mackie et al. (1990) concluded DD was not a reliable concept for managing 5 deer populations in Montana where environmental variability was a greater factor affecting population changes than DD. McCullough (1990) discussed the reasons for this difficulty and cautioned against discarding the DD hypothesis although abiotic factors and sampling biases often may obscure it. McCullough et al. (1990) and Bartmann et al. (1992) demonstrated DD in this species in limited spatial and temporal situations. DD has not been demonstrated for a large mule deer population over a long period. Nevada deer data were tested for DD relationships, focusing on the population composition data collected by helicopter since 1978.

STUDY AREA

Nevada contains an area of approximately 286,000 km^2. Biologists estimate deer winter ranges cover 29,400 km^2 with summer ranges being larger and sometimes overlapping. The Great Basin desert (Trimble 1989, Grayson 1993) occurs in the northern 3/4 of Nevada and most mule deer live in this portion of the state (Hall 1946). Mule deer habitat is found mostly in or next to the many small mountain ranges. The islands of deer summer range on the upper elevations of the mountain ranges are flanked by winter ranges in the foothills and on the bajadas. Elevations vary from 900 m in the valleys to over 3,000 m on many mountain crests.

Deer summer ranges are sagebrush (*Artemisia* spp.) and mountain brush habitats with mixtures of aspen (*Populus tremuloides*), conifers, and mountain mahogany (*Cerocarpus* spp.) (Papez 1979). Winter ranges are pinyon-juniper (*Pinus* spp., *Juniperus* spp.), juniper, sagebrush, and desert shrub vegetative types. Deer habitat quality ranges from poor to excellent, a function of the rain shadows of the Sierra Nevada and Cascade mountains.

Most mule deer populations reside wholly within the boundaries of Nevada, migrating altitudinally and often linearly between relatively distinct summer and winter ranges. The interstate populations shared with California, < 10% of the Nevada population, are the most notable exceptions, migrating to Nevada only in winter. Minor immigration (< 1%) occurs from Oregon, Idaho, and Utah. Delineating deer population seasonal ranges has been a major effort (Gruell and Papez 1963). This deer range identification continues, aided by evolving capture technology and telemetry. The original objective was matching deer populations with their ranges to enable additional harvest should deer range damage occur, but learning the limits of each population's migrations to improve population estimation and hunting quota recommendations with better data collection also became important. Present population area (PA) boundaries are thought to contain > 95% of all migratory movements. Winter deer numbers and relative distribution have not changed significantly in Nevada since they were identified in 1951 (Ritter 1952).

METHODS

All available deer composition, hunter kill, and population estimate data for Nevada were assembled for analyses and population modeling. Statewide deer estimates prepared annually were summations of the PA estimates prepared by the field biologists for their quota recommendations. These data are presently on file at the Nevada Division of Wildlife Headquarters in Reno.

Kill data were collected by a mail-in report card attached to the deer tag. Kill records from report cards began in 1929 (Hall 1946). Reporting has been mandatory since the late 1970s, with report rates averaging >70% before and >95% since.

Robinette collected the first reported composition ratios in Nevada from the Schell Creek Range beginning in 1943 (Robinette et al. 1977). The first systematic composition surveys of Nevada deer were conducted by county big game committees in the 1940s looking for symptoms of irrupting deer populations described by Leopold et al. (1947). Deer populations, not identified as irrupting in the 1940s, were not surveyed for herd composition until the late 1950s and early 1960s. Spring samples were not collected routinely in many populations until the 1970s. Before 1978, most surveys were conducted from the ground. Historically, bucks were classified by point class, and in recent years, biologists also were asked to classify yearling bucks. Does, adults in spring, and fawns were classified by size and by the allometric differences in body proportion, particularly in the muzzle.

Since 1978, major Nevada deer populations have been surveyed by helicopter twice per year (post-hunt and spring) to collect herd composition data. No significant differences in fawn-to-adult ratios were found in investigations comparing ground and aerial samples, although confidence intervals were smaller for aerial samples (Tsukamoto 1977). Twenty-two of 28 PAs were flown each year, which included >98% of the total deer population. These PAs were considered discrete populations based on marking studies. About 600 hours were scheduled to census deer annually, but the actual hours flown averaged 450 hours per year during the last 3 years. Helicopters used included Bell G-47 3B1s and Bell JetRangers. For the last 10 years, Nevada-owned JetRangers were flown exclusively. Two observers, unit biologists familiar with the unit, accompanied the pilot during surveys.

The aerial surveys were not random, but instead, were planned to classify as many deer as possible on all deer ranges in the PA within the scheduled survey time. With the recognition that composition ratios were often statistically imprecise (Alldredge et al. 1978), larger and presumably more accurate and representative samples were sought. Meeting the assumptions for change-in-ratio estimators (Caughley 1977) was the primary objective. The aerial samples were thought to represent the demography better than samples collected from the ground since all major deer ranges were flown, so habitats used differently by males and females (Bleich and Taylor *in press*) could be surveyed, and coverage was not limited to roads. Usually all high to moderate density deer ranges within a PA were flown, but low density ranges were also flown as time and weather permitted. If weather caused unusual shifts in deer distribution, the survey crew searched all known deer ranges until an adequate sample was obtained. Predetermined quadrants or transects were not flown.

Two helicopter crews were scheduled during the post-hunt and spring survey periods. The survey time scheduled for a unit corresponded with deer numbers and quotas, but public interest influenced scheduling as well. The post-hunt survey started after the hunting season, usually in the first week in November, and extended until early December. High winds, storms, and helicopter repairs or maintenance sometimes delayed survey flights. Because a primary goal was to survey as many PAs as possible for composition, crews moved to the next PA if too much delay occurred. When weather or other difficulties prevented comprehensive helicopter coverage in a PA, biologists surveyed from the ground to obtain composition samples from deer ranges in the PA not completed by aircraft. On occasion, the fall surveys continued until early January. This was avoided if possible because of antler drop. Spring surveys began the first week in March and were flown until mid-April.

Statistix for Windows (Analytical Software) was used for statistical analyses. Two-sample Student *T*-tests, 2x2 contingency tables, and simple linear regressions were used to compare these data. Populations were estimated using both a change-in-ratio estimator (Hess 1985) and the POP-II modeling program (Bartholow 1984). In the last decade, the POP-II computer modeling program, modified for Nevada's data and simulating >5 years of unit data preceding the forecast estimate, was used almost exclusively.

I evaluated PA estimates each year by comparing hunt quota objectives (post hunt buck ratio and kill) with the subsequent hunter reporting and the helicopter post hunt composition. I used 2x2 contingency tables to test for significant differences between the hunt objectives and the observed results. Quotas were intended to obtain a buck kill objective that in turn would yield a post-hunt buck ratio objective. For example, if the PA estimate was tracking the population, a buck kill that was significantly higher than expected should yield a post-hunt buck ratio that was proportionally lower than intended. If the population forecast by the model obviously did not track the actual population based on this testing, the PA model was reworked to fit the data as closely as possible for the next forecast. This estimate evaluation can be viewed as testing hypotheses about wildlife management activities as advocated by McNab (1983).

RESULTS

The Helicopter Data

Since helicopter surveys began in 1978, biologists classified a post-hunt mean of 36,386 deer and a spring mean of 40,853 deer (Table 1). The mean annual post-hunt fawn-to-adult ratio from the helicopter surveys was 0.483. The mean annual spring fawn-to-adult ratio for helicopter samples was 0.346.

For perspective, 17 PAs flown in the spring of 1997 yielded a sample of 28,334 deer classified on < 19,900 km^2 of winter range. Averaging by unit, 1,666 deer (n = 17, SE = 472.2) were classified on 1,171 km^2 (SE = 321.2). Low density units and interstate deer units were excluded from the preceding example. Deer numbers classified in each PA during the 19 years of aerial survey are correlated with the samples for all other PAs with equivalent data (P < 0.01), although the deer populations fluctuated markedly.

Population modeling resulted in estimated prehunt adult populations for Nevada ranging from 110,000 to 250,000 deer over the last 19 years, growing from a trough to a peak in 1988, then declining to a second trough in 1994. The annual mean estimate was 183,892 deer (SE = 5,059.8). The number of adults classified in the post-hunt surveys and the estimated populations were highly correlated ($x = 22{,}530 + 5.5805y$, $r = 0.6252$, $P < 0.005$). Collecting trend information during the aerial surveys was not intended, but the size of fall samples tracked density changes. Sample size was not used in developing either the CIR or POP-II estimates.

Buck kill and doe kill correlated with the estimates ($P < 0.005$) as expected, since quotas were based on the estimates. The buck kill averaged 11,821 (SE = 815.47) and the doe kill averaged 2,092 (SE = 815.47). Doe kill correlated with the number of does seen in the post-hunt surveys ($x = 17{,}591 + 1.0545y$, $r = 0.5997$, $P < 0.0067$). Buck kill did not correlate with the number of bucks seen post-hunt. This was predictable, given the higher rate of kill for a smaller segment of the population. About 35% of the bucks were killed each year during the hunting season compared to only 2% of the does during this period.

Table 1 Samples and fawn/adult ratios from surveys of Nevada mule deer from 1952 to 1996.

Survey	$\bar{x}$	SE	Minimum	Maximum
1952 - 1977				
Fall Sample	6,962	752.9	572	18,081
Fall Fawn/Adult	0.5296	0.0141	0.3803	0.6868
Spring Sample	5,502	670.7	575	14,287
Spring Fawn/Adult	0.4175	0.0222	0.261	0.6573
1978 - 1996				
Fall Sample	36,386	1,497.6	24,703	45,855
Fall Fawn/Adult	0.4834	0.0135	0.3267	0.5899
Spring Sample	40,853	1,664.3	33,338	57,290
Spring Fawn/Adult	0.3463	0.0149	0.1886	0.4785

The number of adults seen in the post-hunt surveys showed a negative correlation with the fawn-to-adult ratio of the spring composition sample collected 3-4 months later ($n = 19, x = 0.5748 - (9.29 \times 10^{-6})y, r = -0.6668, P = 0.0018$). This negative correlation is remarkably robust. It was assumed the spring fawn-to-adult ratio was equivalent to the population growth rate (r). The annual PA estimate hypothesis testing process corroborated this assumption. The hypothesis that the rate of fawn survival in the spring is negatively dependent on the adult deer density in late fall in Nevada was accepted. On a statewide basis, mule deer were DD during those 19 years.

Two winters in the 19 years were unusually harsh and resulted in the lowest spring fawn-to-adult ratios (0.189 in 1993 and 0.287 in 1982). The apparent fawn loss from comparing fall and spring ratios was highest for these 2 years. The spring fawn ratios in the 2 years immediately following these 2 harsh winters also were low (0.250 in 1994 and 0.312 in 1983). These 4 low fawn-to-adult ratios were < the lower 95% CI of 0.315 for the ratios, and their data points fell below the 95% CI of the regression line for fall adult sample and spring fawn ratio. After omitting these 4 outliers, a regression yielded a greater negative correlation ($n = 15, x = 0.5585 - (7.78 \times 10^{-6})y, r = -0.8492, P < 0.0001$). Harsh winters disrupted DD for more than 1 year, perhaps through their residual effects on rate of recovery of body condition among surviving females (Taylor 1996).

The composition data for 7 PAs also show significant negative correlations between fall adult numbers and spring fawn-to-adult ratios ($P < 0.05$), but individually none of these PAs showed correlations as robust as the statewide sample. These 7 DD PAs are in a contiguous block in northeast Nevada and contain the best deer ranges in the state. They represent an estimated 57% of the statewide population including the 5 largest deer populations (PAs). Estimated winter range density averaged 4.47 deer/km^2 (SE = 0.867) with a mean population size of 12,909 deer (SE = 3,448.5).

Nine PAs with composition samples that

Table 2. Deer kill from report cards for Nevada from 1952 to 1996.

Period	$\bar{x}$	SE	Minimum	Maximum
1952 - 1977				
Buck Kill	10,375	512.6	3,865	14,489
Doe Kill	6,973	728.1	0	13,149
1978 - 1996				
Buck Kill	11,821	3,554.6	5,803	18,801
Doe Kill	2,092	513.5	0	7,983

are comparable to the DD PAs do not show DD winter fawn survival. These 9 PAs not showing DD flank the 7 PAs showing DD on the west and south. With deer habitat of lesser quality, about 26% of Nevada deer occur in these non-DD PAs. Estimated mean winter range density averaged 1.7 deer/km^2 (SE = 0.48) with a mean population size of 4,683.6 (SE = 547.55). These means are both significantly lower ($P < 0.05$) than for the DD PAs.

Composition samples are not obtained regularly in most of the remaining 11 PAs. Deer densities are extremely low in these areas or, in the case of interstate deer populations, data collection methods have varied enough that comparisons cannot be made.

Reexamining the Earlier Ground Data

The composition data collected before aerial surveys were initiated in 1978 were analyzed for trends and for comparison with the aerial data. From 1952 to 1977, Nevada biologists classified annual means of 6,693 deer in post-hunt surveys and 5,502 deer in spring surveys. Over this period, the mean post-hunt fawn-to-adult ratio was 0.530 and the mean spring fawn-to-adult ratio was 0.418. Composition samples increased as the result of increasing sampling effort and coverage during the 26 years, not population changes. No correlations occurred between samples and fawn ratios.

The mean annual post-hunt fawn-to-adult ratio from the helicopter surveys (1978-1996) was 0.483. This ratio was significantly lower than the mean annual ratio from ground surveys ($X^2 = 10.17$, $P < 0.0015$) collected from 1952 to 1977. The mean spring fawn-to-adult ratio for helicopter samples was 0.346. This ratio was also significantly lower than the mean for the earlier ground samples ($X^2 = 18.64$, $P < 0.0001$). Higher mean ratios during earlier samples suggest that deer were at lower densities if DD were occurring.

The deer kill was quite different in the 2 periods (Table 2). The earlier mean annual buck kill was 10,375 ($n = 26$, SE = 512.6) and the mean annual doe kill was 6,974 (SE = 728.1). A 2-sample Student T-test comparing buck kills from 1952 to 1977 with buck kills from 1978 to 1996 showed no significant difference ($P = 0.2302$), but the corresponding doe kills were significantly different ($T = 5.95$, $P < 0.0001$). While the buck kills were equivalent, the earlier doe kills averaged >3X the doe kills in the last 19 years. This higher rate for female kills would be consistent with lower deer densities that are hypothesized to have existed.

Using the regression values from the post 1977 data, with the earlier mean fawn ratio, a population of 168,000 deer was projected. POP-II was used to model the Nevada deer population from 1952 to 1977 for a second estimate. The assumptions on sex ratios at birth, wounding loss, and various mortality rates that Nevada used successfully in POP-II to establish quotas since 1978 were used. The POP-II estimates that matched a CIR estimate series, the composition ratios, and the kill were much lower than expected. Modifying the assumptions to force the model population upward produced unrealistic changes in model population composition. The model yielded a mean estimate of 118,000 adults ($n = 26$, SE = 3,766.1) compared with a mean estimate of 184,000 adults in the last 19 years (SE = 5,059.8).

Despite their differences, both these estimates supported the hypothesis that the earlier, higher kills reduced adult densities and yielded higher recruitment rates. The earlier liberal harvest strategy sustained a higher yield of females, and a relatively higher yield of males.

DISCUSSION

Nineteen years of data collected during aerial surveys produced evidence of DD in Nevada mule deer. These data also provided a better basis for re-examining the 1952-1977 kill and composition data. Good support for the hypothesis that deer densities were lower in the 1950s and 1960s than in the 1980s was found. This hypothesis contradicted the dogma prevalent among deer hunters and deer biologists, that the 20th century mule deer population reached its apogee before the low population levels of the mid 1970s.

For 26 years, Nevada managed deer with a hunting program that produced a sustained yield. A population decline resulting from several successive severe winters initially went undetected, and later resulted in a drastic overhaul of hunting regulations and data collection in Nevada. The new hunting strategy was an ultraconservative quota hunt, with quotas based on prehunt estimates, post-hunt buck ratio objectives, and recent hunter success rates in each PA. Making an estimate each year that was subject to public review was an uncomfortable process for biologists.

Nevada overcompensated by emphasizing data collection. The statistical precision of kill and composition data improved with increasing sampling effort but consistent accuracy for better forecasting of pre-hunt populations with CIR remained elusive. CIR estimates were unsettlingly, and sometimes unrealistically variable. The POP-II model resolved the problem; it emphasized the less variable data, the fawn-to-adult ratios and the size of the kill. Collecting spring fawn ratios, and placing them in context with kill, allowed the construction of a model with realistic cohort sizes that was sensitive to trend but not hypersensitive to minute changes in buck ratios, which is true of the CIR used.

MANAGEMENT IMPLICATIONS

Demonstrating DD yearling recruitment, or compensatory mortality, among mule deer provided biologists with more realistic options in dealing with some recent management issues. Many of these issues originated in our folklore: DD provided good scientific arguments to counter anti-hunting, anti-predator, and anti-doe-hunting advocates.

Hunting, even at levels that significantly reduce densities, will not threaten mule deer populations. Managing for lower residual densities will increase management options (McCullough 1987). Winter starvation rates can be reduced by hunting. Winter feeding and predator control, except under catastrophic and atypical circumstances, likely will not help self-regulating deer populations, especially populations near carrying capacity. Sustained yield hunting can reduce the recent variation in hunter success. In the long-term, more hunters can hunt, and more can be successful. Habitat manipulations should be reviewed critically to ensure that projected gains will exceed those that simple manipulation of harvest can provide more cheaply. The trick, however, will be teaching the public what we have learned. Deer folklore, rather than sound science, is a powerful force that currently drives the management decision process in Nevada.

Spring composition surveys provide a good means to gauge the relative density of mule deer populations, barring complicating abiotic factors. These disruptive influences can be identified and monitored. In Nevada, the most disruptive factors are drought and winter severity.

More modest sampling strategies than intensive helicopter surveys and mandatory hunter reporting could provide data sufficiently accurate to forecast population trends. Forecasting can be uncomfortable, until it is recognized as a hypothesis testing process. The forecast population being the hypothesis and measuring results against management objectives of kill and composition being the testing process. A biased estimate is not a mistake but, instead is a test that helps refine the next hypothesis. Deer biologists and weathermen should be equally accurate, since both monitor aspects of the same chaotic system.

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Habitat Use by White-tailed Deer in a Tropical Forest

SALVADOR MANDUJANO
SONIA GALLINA
GERARDO SANCHEZ-ROJAS
GLORIA ARCEO
Depto. Ecología y Comportamiento Animal, Instituto de Ecología A.C., AP 63, Xalapa 91000, Veracruz, Mexico.

GABRIELA SILVA-VILLILOBOS, CUCBA
Universidad de Guadalajara, AP 39-82, Zapopan 45110, Jalisco, Mexico

Abstract: White-tailed deer in the tropical forest of "Chamela" in the state of Jalisco, Mexico, exhibit different spatial and temporal habitat use patterns. The heterogeneity of the understory of Chamela's tropical forest is determined by spatial (tropical dry forest and tropical semideciduous forest) and temporal (wet and dry seasons) variations in floristic composition, species richness and biomass, nutritional value, percentage of deciduous and evergreen species, and life form. During the wet season, white-tailed deer make greater use of the tropical deciduous forest. During this season the diet is less diverse. This greater selectivity in the diet is associated with an increase in foraging area, as greater distances are covered and the home-range is increased. In the dry period, low water and food availability is coupled with a decrease in cover to protect against climate and predators. White-tailed deer increases the diversity of its diet during this season. It also increases consumption of alternative food sources and water, such as fruits and flowers. Thus, habitat use is less selective in the dry season than in the wet season.

Key words: Habitat structure, habitat use, Mexico, *Odocoileus virginianus*, tropical forest, white-tailed deer.

INTRODUCTION

White tailed deer (*Odocoileus virginianus*) are found throughout all of Mexico except on the Baja California peninsula and in northern Sonora (Hall 1981). The species inhabits a wide variety of vegetation types, such as temperate forests, grassland, semi-arid land, and tropical forest (Leopold 1965). This deer supplements the diet of local ethnic groups (Mandujano and Rico-Gray 1991) and is 1 of Mexico's most important game species (Villarreal 1995).

Most studies of this species have been carried out in temperate forests and semi-arid zones of the United States, Canada, and Mexico (see Halls 1984). In contrast, few studies have been conducted in the tropical forests of Mexico, or in Central and South America (Vaughan and Rodriguez 1994). The present results are from a study of white-tailed deer (*O. v. sinaloae*) ecology in a tropical forest located in the state of Jalisco, Mexico, over a 6-year period (1989-1995). Our objectives were to determine basic life history information on population dynamics, activity patterns, and habitat use in a tropical environment noted for the marked seasonality of its available resources. The information contained in this paper is based on articles (Mandujano and Gallina 1993, 1995*a*, 1995*b*, 1996; Mandujano et al. 1994; Mandujano and Martinez-Romero *in press*; Sanchez-Rojas et al. 1997), theses (Mandujano 1992, Sanchez-Rojas 1995, Silva-Villalobos 1996, Arceo 1997), and recent information which is yet to be published. See these publications for details regarding methods, statistical analyses, and results discussed in a wider context.

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DESCRIPTION OF HABITAT

Study Site

This study was carried out at the Universidad Nacional Autonoma de Mexico's "Chamela" Station for Research and Biological Diffusion, located on the coast of Jalisco. The Station covers an area of 3,200 ha. The elevation ranges from 30 to 580 m, although most of the territory is not higher than 150 m. The topography is irregular with numerous systems of small basins, all of which have seasonal run-off. The greatest quantity of water falls in September (Bullock 1986). Depending on the amount of rainfall, there is frequently no water in the streams by the end of the dry season. Apart from these seasonal streams, there are only 3 permanent rivers in a 100 km radius of the Biological Station.

Climactic Pattern

Average annual precipitation from 1977 to 1993 was 73.55 cm. Monthly precipitation causes 2 seasons: wet (rainy) and dry. The wet season, which lasts an average of 126 days, begins in June, with 80% of the annual rain falling between July and November (Bullock 1986). Twenty percent of the annual rain falls during the dry season, which lasts an average of 158 days. From June to July, the Trade Winds play a role in the variability of annual rainfall; cyclones occur during August to October and greatly increase the likelihood of winter precipitation (Garcia-Oliva et al. 1991).

The mean annual temperature is 25 C, the hottest periods occurring between May and September (Bullock 1986). From June to November, the temperature was greater than 30 C on an average of 23 days (Mandujano and Gallina 1995*a*). From mid-December until mid-May, temperatures did not exceed 30 C. Insolation is highest in April. The maximum wind speed occurs from February to June and the minimum from August to December. The greatest evaporation occurs between March and June and the least between November and January. During the wet season dew was present for 7-15 days and between 5-12 days during the dry season (Gonzalez 1992).

Types of Vegetation

The dominant vegetation, covering 75% of the surface, is tropical deciduous forest (TDF). It is found on hills with shallow soils; the trees reach a height of 5 to 10 m and have a highly developed understory. Numerous tree and shrub species lose their leaves during the dry season (Lott et al. 1987). Some of the most common arboreal species are *Cordia alliodora* (Ruiz & Pav.) Oken, *Croton pseudoniveus* Lundell, *Lonchocarpus lanceolatus* Benth, and *Caesalpinia eriostachys* Benth. There is also tropical semi-evergreen forest (TSF), which grows along the principal streams in deep soils. The trees reach a height of 10 to 25 m. The most common tree species are *Thouinidium decandrum* (Humb. & Bonpl.) Radlk., *Astronium graveolens* Jacq., *Brosimum alicastrum* Sw, and *Sideroxylon capiri* A. DC. (Lott et al. 1987).

Understory Structure

In the wet and dry seasons during the period from 1989 to 1993, understory richness and biomass was measured in the TDF and TSF using permanent plots. The best represented families, genera, and species in the understory were Euphorbiaceae, Leguminosae, Sapindaceae, and Acanthaceae; *Acalypha* spp., *Croton* spp., *Lasiacis ruscifolia*, *Coursetia caribaea*, *Dicliptera resupinata*, *Forchhammeria pallida*, *Capparis verrucosa,* and *Elytraria imbricata*. In the TSF they were Euphobiaceae, Leguminosae, Bignoniaceae, Nyctaginaceae, and Sapindaceae; *Acacia rosei*, *Guapira macrocarpa*, *Croton pseudoniveus*, *Thounidium decamdrum*, *Clytostoma binatum*, *Paullinia cururu,* and *Capparis verrucosa*. During the wet season, 39% of the species were exclusive to the TDF, 43% to the TSF, and 18% are found in both vegetation types.

Average species richness during the dry season was 2 species/m^2 in the TDF and 4 in the TSF; during the wet season, richness was 9 species/m^2 in the TDF and 8 in the TSF. Average biomass during the dry season was 7 g/m^2 in the TDF and 18 in the TSF, while in the wet season it was 41 g/m^2 in both types of forest. There was a positive correlation between the precipitation and richness of both TDF and TSF and their biomass.

Availability of Potential Food in the Dry Season

Biomass availability for the species which deer consume in the TDF varied during the dry season from 2 to 12 g/m^2, depending on the year. This corresponds to an average of 23% of the standing biomass in the understory of this vegetation type (Mandujano and Gallina 1995*a*). In the TSF, availability was estimated at 1 to 10 g/m^2 for species which the deer consume; this corresponds to an average of 9% of the biomass for this type of vegetation.

Nutritional Value of the Vegetation

Using a proximal analysis, we found that the nutritional value of vegetation was greater during the wet season, as there was a higher percentage of crude protein and nitrogen free extract (NFE). Nutritional value decreased during the dry season, when there was a higher percentage of crude fiber and total polypyenols (Silva-Villalobos 1996). Plants in the TSF have a higher percentage of fiber, less protein, and less NFE throughout the year. Plants in the TDF had a high nutritional value during the wet season and a low value during the dry season.

Seasonal Fruit Production

Fruit production of arboreal species tends to occur mainly from February to early April and from July to August (Bullock and Solis-Magallanes 1990). Some species deer consume during the dry season are *Ficus* sp., *Brosimum alicastrum*, *Sideroxylon capiri*, *Opuntia excelsa,* and *Spondias purpurea.*

Characteristics of the *Spondias purpurea* Tree

Fruits from the *S. purpurea* are an important source of water for the deer at the end of the dry season because there are few of water sources. *S. pururea* is a dioecious arboreal species. The density of adult trees is 7.5/ha; approximately 50% are reproductive female trees, 38% of which produce more than 500 fruits (Mandujano et al. 1994). The average weight of fresh fruit is 7.5 g, and fruit production during 1991 was 14.9 kg/ha.

Chachalaca (*Ortalis poliocephala*) foraging on *S. purpurea* has important consequences for the deer. When chachalacas forage, they drop many fruits from their trees, making them available for the deer as well as for other terrestrial mammals. Exclusion experiments show that in the absence of this bird, the rate of *S. purpurea* fruitfall is very low (Mandujano and Martinez-Romero *in press*).

Water Availability

An estimate of the average availability of water for the deer was obtained using plant moisture content and the percentage of plants that the deer were known to consume in both types of forest during the dry seasons from 1990 to 1993. In the TDF, the average density of deer forage plants was 31/ha (ranging from 10-56/ha), while in the TSF the average was 28/ha (ranging from 4-50/ha) (Mandujano and Gallina 1995*a*). The average estimate of water in *S. purpurea* fruits was 10 L/ha in 1991.

HABITAT USE BY THE DEER

Biological Cycle

In the tropical forest of Chamela, the breeding season occurs between November and January (Mandujano 1992). Gestation occurs throughout the dry season, between December and June. The young are born between June and August.

Group Size

In this habitat, the white-tailed deer do not form large herds (Mandujano and Gallina 1996). Solitary individuals are frequently seen throughout the year. Females and their offspring comprise the most common social groups. Males are not known to form groups. This group size strategy is related to the availability of food, and to the density of cover in the understory that provides protection against predators.

Population Dynamics

Population density was estimated using a direct count of animals on line transects. Population density was estimated between 10 and 14 deer/km^2 (Mandujano and Gallina 1993, 1995*b*), and did not change over a 5-year period. The birth rate is 1.5 fawns per female, however, the mortality rate is high from the fawn to yearling category. Mortality is higher for males than for females. We propose that the period between May and June is the "bottle-neck" for deer population increase in this tropical habitat.

Feeding Habits

Using microhistological fecal analyses, 129 species of 29 families were eaten by deer (Arceo 1997). The most important families were Euphorbiaceae, Leguminosae, and Convolvulaceae throughout the year, Malvaceae during the wet and transition seasons, and Anacardiaceae during the dry season. The deer selected 36, 55, and 44 species during the wet, transition, and dry seasons, respectively. But on average, only 5 species represent 50% of the seasonal diet. *Acalypha* spp. was the most important food item in the wet and transition season. Overall, *Acalypha langiana*, *Cardiospermum halicacabum*, *Coursetia caribaea*, *Croton* sp., *Abutilon* sp., *Spondias purpurea*, and *Ayenia micrata* were the more important species in the diet. Deer diets became more diverse from wet to dry season, and the plant parts consumed changed in this period. Leaves and twigs were the most important plant parts in the annual diet, but in the dry season fruits and flowers, particularly fruits of red mombin (*Spondias purpurea*), constituted 30% of its diet. Overall, shrubs and vines were the most important life forms in the diet year-round, with trees being most important in the dry season. Perennial plants with deciduous leaves were dominant in the diet year-round. Plant species from TDF comprised a greater percentage of the diet, principally in the dry season, than those species from the TSF.

Water Demand

The deer population's need for water was estimated using the following factors: daily water demand for 1 individual, average weight, the percentage of each age group represented, annual population density, and consumption over 30 days at the end of each year's dry season (Mandujano and Gallina 1995*a*). Minimum and maximum individual demand was estimated at 1.9 and 3.9 L/day, respectively, for adult deer, 1.4 and 2.8L/day for young deer, and 0.8 and 1.7L/day for fawns.

Use of Vegetation Types

Through direct observations of deer and pellet group counts from 1989 to 1994, we found that the TDF is used more frequently throughout the year than the TSF. In particular, in the wet season the TDF is used more during the morning hours, while in the dry season it is used more in the afternoon. The TSF, in contrast, is used during the morning in the dry season and very little during the day in the wet season. Deer prefer the hillsides with northern exposure in the dry season.

From 1992 to 1994, radiotelemetry of 1 male (*n* = 122 locations) and 1 female (*n* = 479) indicated that females preferred hillsides more than areas near streams (Sánchez-Rojas 1995). Specifically, the doe favored hillsides facing NE or NW during the wet season and SW during the dry season. The male, on the other hand, made less use of hillsides facing NW and SE and preferred low areas.

Activity Patterns

The radiotracking of 2 deer provided the following data. In the dry season, the female exhibited more movement at dawn (0500-0800 hours) and at dusk (1700-2000 hours). In the wet season, she remained active throughout the day, slowing down notably at night (2100-0400 hours). Male activity during the dry season was higher at dusk and at night. The distance covered by the female was 1.5 km/day in the dry season and from 2.5 km/day in the wet season. The male covered 2.5 km/day in the dry season of 1994. Estimates of female home-range were 11 ha during the dry season and between 24 and 44 ha in the wet season (Sánchez-Rojas 1995). Figures for the male were 26 ha in the dry season of 1994.

Predation

At Chamela, the jaguar (*Panthera onca*), puma (*Puma concolor*), and ocelot (*Leopardus pardalis*) are the principal predators of white-tailed deer (Lopez-Gonzalez et al. 1995). Like other studies (Main et al. 1996), it is very probable that the deer's habitat use is influenced by the risk of predation. Tracks of these felines are common along the streams of the study area.

IMPLICATIONS

Results indicate that the deer's foraging strategy during the wet season is to make greater use of the TDF because of its high nutritional value (higher percentage of protein and NFE and less fiber), greater richness and increased production of biomass of understory species as compared to the TSF. During this season the diet is less diverse, which indicates that the deer selects fewer species, principally those of the Euphorbiacea, Convolvulacea, and Leguminosae families, to cover its nutritional requirements. Deer get more energy and nutrients from these species, thus permitting the accumulation of fat reserves for the mating season and for the critical dry season. This greater selectivity in the diet could be associated with an increase in the foraging area, as greater distances are covered and the home-range is increased.

In the dry period, low water and food availability is coupled with a decrease in cover to protect against climate and predators. The deer's strategy is to select, from low species richness and biomass, those plants and plant parts which are more nutritious and that have lower concentrations of fiber. Thus, the white-tailed deer increases the diversity of species and families in its diet during this season. It also increases consumption of alternative sources of nutrients and water, such as fruits and flowers, especially *Spondias purpurea*, *Ficus* spp., and *Brosimum alicastrum*. Thus, habitat use is less selective in the dry season than in the wet season. Apparently, the distribution of fruiting trees plays a role here. During the dry season, deer show a clear preference for hillsides with northern exposure where the solar radiation is lower and humidity higher. Also, deer cover less distance, decreasing their home-range which could be a strategy to diminish energy demand and protect against predators.

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Movements and Mortality of Mule Deer in the Wallowa Mountains

PATRICK E. MATTHEWS
VICTOR L. COGGINS
Oregon Department of Fish & Wildlife, 65495 Alder Slope Road, Enterprise, OR 97828

Abstract: Understanding movement and mortality patterns for migratory and resident mule deer is important when defining populations, and provides managers information necessary for selecting appropriate management schemes. From January 1992 through December 1994, 57 mule deer were radiocollared and monitored in the Wallowa Mountains of northeast Oregon. Twenty-five percent of the radiomarked deer were not migratory. Migration between winter and summer ranges averaged 25.3 km. Deer showed high fidelity to summer and winter ranges; 100% of the adults used the same range each year they were monitored. Annual mortality rate from natural causes was 31% and 13% for males and females, while hunter kill accounted for an annual rate of 19% and 2%, respectively. Cougar predation was the leading cause of all mortality.

Key words: Cougar, migration, mortality, movements, mule deer, natural mortality, Oregon.

INTRODUCTION

In Oregon, wildlife management units have been established to administer hunting seasons for deer and other game species. Management objectives for total wintering deer and adult sex ratios are also managed by unit. Ideally a management unit would contain a distinct deer herd or population whose seasonal ranges occur within the unit boundary. However, unit boundaries have been described primarily for administrative purposes and do not account for deer movement between units.

It is well known that many mule deer (*Odocoileus hemionus hemionus*) populations are nonmigratory (Wallmo and Regelin 1981, Eberhardt et al. 1984) while others contain both migratory and nonmigratory deer (Kufeld et al. 1989, Wood et al. 1989, and Brown 1992). Gruell and Papez (1963) reported deer using a discrete winter range may migrate to several distinct summer ranges. Migratory mule deer have been reported to travel through summer or winter ranges used by other populations enroute to their seasonal ranges (Brown 1992).

Population models can be a helpful tool to evaluate total population size, age, and sex ratios. Herd composition information needed to build models is often obtained during winter and spring surveys, and may not accurately reflect late summer and early fall population size and composition in a given area or unit. To better use this type of information for modeling, knowledge of seasonal movements and distribution are important in identification of seasonal ranges, migration routes, and determining interchange between management units.

This paper reports the results of a 3-year management project examining the year-long and seasonal ranges used by mule deer from 3 separate winter ranges, and adult mortality associated with these individuals . Specific objectives were to gain a better understanding of: (1) proportion of migratory and nonmigratory deer wintering in the unit, (2) timing, fidelity, and distance between seasonal ranges, (3) rate and principle causes of adult mortality.

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PROJECT AREA

The project area encompassed 1,030 km² of the Wallowa Mountains and adjacent lower elevation ranges south and west of Enterprise, Oregon. Elevations within the area varied between 860 and 3,000 m. Climate is typical of the mountainous West with warm summers and cold winters. Mean annual precipitation varies from 28 cm on lower ranges to 114 cm at upper elevations.

Mid to lower elevation ranges are characterized by moderate to steep slopes containing bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), and Sandberg's bluegrass (*Poa sandbergii*) mixed with timber stands containing ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies grandis*), and western larch (*Larix occidentalis*). Upper elevation ranges are characterized by U-shaped glaciated valleys, alpine basins, rugged precipitous terrain, and numerous avalanche chutes. A wide variety of grasses, forbs, and shrubs occur throughout upper elevations with subalpine fir (*Abies lasiocarpa*) and whitebark pine (*Pinus albicaulis*) the primary conifer species.

The project area contains 3 major mule deer winter ranges and all lie within the Minam game management unit. An estimated 4,500 mule deer winter in the unit. The Minam unit contains 75% public land and is administered by the U.S. Forest Service. Winter ranges lie along the north portion of the unit and are primarily under private ownership. The summer range encompasses the southern two-thirds of the unit and includes the Eagle Cap Wilderness.

METHODS

During winters of 1992-94, 99 mule deer were captured using 3 methods. Sixty-nine percent were captured with panel traps, 23% were captured by net gunning, and 8% were captured by free-range darting with Captural-5. Capture efforts were concentrated on 3 major winter ranges; the Lower Minam, Bear Creek, and Lostine-Wade Flat, respectively. Blue plastic numbered alflex ear tags were attached to the right ear of all captured deer. Radiocollars (Telonics Inc., Mesa, Ariz.) were attached to 8 yearling (3 males, 5 females) and 49 adults (23 females, 26 males). Transmitters included mortality sensors. Adult male radiocollars were constructed of kydex plastic (Keister et al. 1988) to allow for neck expansion during the rut. Radiotracking was conducted from a Piper P.A. 125 Supercub or Cessna 180 aircraft with dual-yagi antenna configuration. Locations of radiomarked deer were obtained at 5-30 day intervals throughout the year, with additional ground locations obtained whenever possible. Mortalities of radiomarked individuals were investigated as soon as possible after death to determine cause. Procedures described by Wade and Browns (1983) were used to identify predator-related mortality. Annual mortality rates were calculated using the equation

$$R = \frac{d(12)}{m}$$

where R = annual rate of mortality, d = number of deaths, 12 = months in a year, and m = total months collared deer were monitored.

Movement data were separated into 4 categories: summer and winter movements within seasonal home-ranges, and spring and fall migrations. Summer range use was generally defined as those locations occurring between June 15 and September 15, with winter range use between December 15 and March 31. Seasonal home-ranges were constructed using all location data obtained during these time periods and were depicted as simple minimum convex polygons. A deer was considered to have initiated migration to summer range when it was located outside its area of winter use after April 1. Migration was considered complete when an individual was first located within its summer range area of use. Conversely, initiation of fall migration was considered when an animal was located out of its summer area of activity after September 15 and complete when first located within the winter range boundary. Boundaries of winter ranges were subjectively determined based on winter movements of all radiomarked deer.

Deer were considered migratory when an individual's summer area of use was located outside its documented area of winter use. Deer remaining within their documented area of winter use throughout the year or with summer locations overlapping winter range locations were considered nonmigratory. Fidelity of radiocollared deer to summer and winter ranges was assessed by examining the amount of overlap between an individuals seasonal home-range in consecutive years.

RESULTS

During the project, a total of 3 yearling and 23 adult females, 5 yearling and 26 adult males were radiocollared on the Lostine-Wade Flat, Bear Creek, and Lower Minam winter ranges (Table 1). Yearlings were 19-22 months old. From January 1992 through December 1994, 1,800 aerial and ground locations were obtained ($\bar{x} = 32$). Approximately 81% of the females and 45% of the males were monitored for ≥1 year, while 54% and 6% of the females and males were monitored 2-3 years, respectively. Eight males dropped their radiocollars, 1 transmitter failed prematurely, and 2 radiocollars were removed from females after 11 months. Four deer, 2 males and 2 females, died before seasonal migration commenced.

Nonmigratory Deer

Nonmigratory deer occurred on all 3 winter ranges and accounted for 25% (*n* = 13) of the 53 radiomarked deer alive prior to migration. Summer and winter home-ranges partially or completely overlapped and were similar in size, about 3.6 km^2.

Table 1. Number of yearling and adult mule deer radiocollared on 3 separate winter ranges in the Wallowa Mountains, Oregon, 1992-94.

Winter range	No. of females		No. of males	
	Adult	Yearling	Adult	Yearling
Lostine	7	1	6	4
Bear Creek	7	1	8	0
Minam	9	1	12	1
Total	23	3	26	5

Four deer were monitored for 2 or more consecutive years on summer ranges and 4 were monitored for 2 or more consecutive years on winter ranges. All individuals used greater than 75% overlapping summer and winter home-ranges during each year, although areas of greatest activity varied between years. Each year during the month of April, 3 individuals moved 4-6.5 km outside of their respective winter and summer range to lower elevation ranges during spring green-up. A radiomarked yearling female captured on the Lostine range remained there the rest of the winter then moved 23 km to the Lower Minam range where she remained for 12 months until hit by a vehicle and killed.

Migratory Deer

Distances traveled between winter and summer ranges varied from 4.5 to 61 km for 40 migratory individuals ($\bar{x}$ = 25.3 km). Mean distance traveled between summer and winter ranges for females was 26.7 km (range 6.4 to 56 km). Mean distance for males was 24.5 km (range 4.8 to 61 km). Timing of migration to seasonal ranges varied slightly between years and sexes. Females generally commenced migration to summer ranges in early May and were on summer ranges by late May (Fig. 1). Males moved later than females; 68% did not begin movement to summer ranges until early June. Movements to winter ranges occurred over a wide period from late September through late November (Fig. 2). The majority of individuals, male and female, began moving by mid-October. Radiomarked individuals of both sexes migrated through summer ranges used by other radiomarked deer en route to their seasonal ranges. Two males and 1 female migrated through winter ranges used by other deer. Most (90%) of the deer (n = 36) moved generally south from low elevation winter to higher elevation summer ranges. Three males (7%) moved in an east direction and 1 female moved north to summer. Thirteen percent (4 males, 1 female) of the deer migrating to summer ranges summered outside of the Minam unit.

Twenty-three migratory deer (14 females and 9 males) were monitored for 2 or more consecutive years on both summer and winter ranges. One male was monitored for 2 consecutive years on winter range only. Fidelity to summer ranges was 100% for both males and females. All females returned to winter in the same area in consecutive years. Ninety percent of the males used overlapping winter home-ranges each year. One male, radiomarked as a yearling, wintered 21 km from the winter home-range used the previous year.

Mortality

Twenty-five of 57 radiomarked deer died during the 3-year project. Males suffered higher mortality (n = 17) than females (n = 8) (Table 2). Eight deer died from cougar (*Felis concolor*) predation, 7 from hunter harvest, 5 unknown causes, 3 winter kills, 1 vehicle collision, and 1 from capture injuries. Annual mortality rate during the 3-year period was 28% overall, excluding the capture related death. Annual mortality rate was 15% for females and 50% for males. Annual mortality rates due to natural causes was 31% and 13% for males and females, respectively. Mortalities occurred throughout the year, with most taking place during the October hunting season followed by the mid- to late-winter period (Fig. 3). Cougar predation was the primary cause of mortality for females (38%), and secondary cause of mortality for males (31%), accounting for 33% of all deaths, and 47% of all deaths outside of hunting.

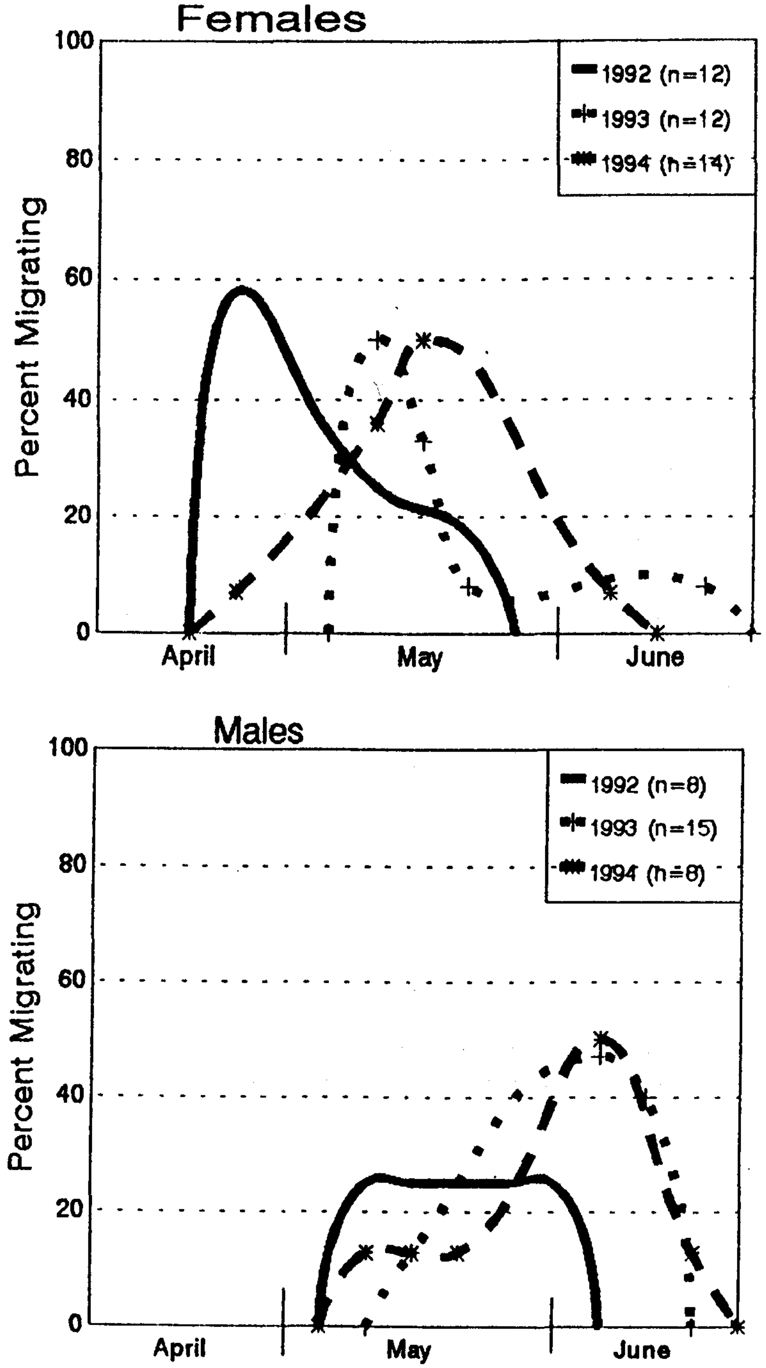

Figure 1. Timing of spring migration by male and female mule deer in the Wallowa Mountains, Oregon, 1992-94.

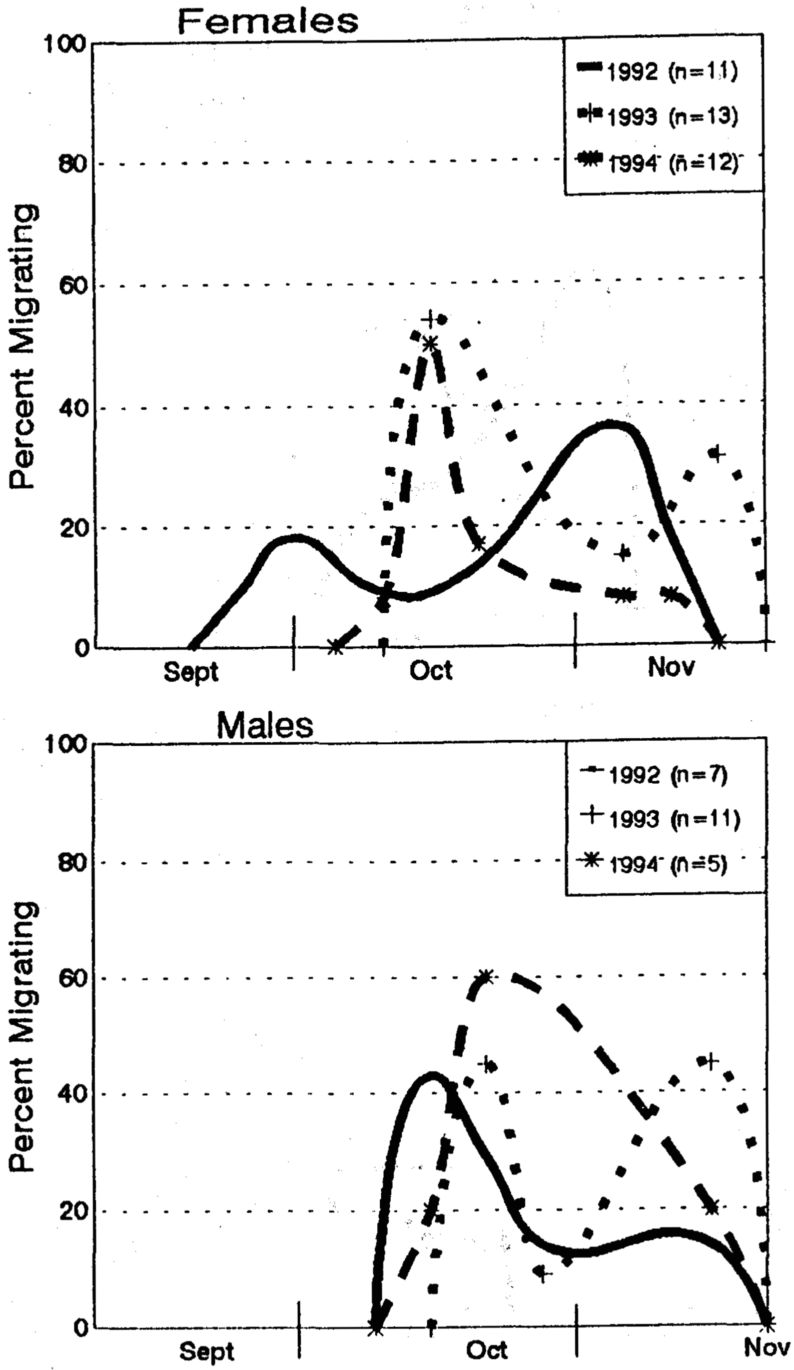

Figure 2. Timing of fall migration by male and female mule deer in the Wallowa Mountains, Oregon, 1992-94.

Table 2. Sex, estimated age, and cause of mortality of radiomarked mule deer in the Wallowa Mountains, Oregon, 1992-94.

Date trapped	Sex	Estimated age (yrs.)	Date dead	Months monitored	Cause of death
1/5/92	Female	7	4/3/92	3	Unknown
1/5/92	Female	1	6/24/93	18	Vehicle
1/7/92	Female	4	3/25/92	2	Cougar
1/8/92	Male	1	10/5/93	22	Hunter
1/8/92	Male	1	10/7/92	10	Hunter
1/12/92	Male	6	2/11/92	1	Capture
1/15/92	Female	7	10/24/94	34	Cougar
1/16/92	Male	3	4/26/94	27	Cougar
1/17/92	Male	6	12/1/92	10	Unknown
1/17/92	Male	2	2/12/92	1	Cougar
1/20/92	Female	5	6/27/94	30	Cougar
2/8/92	Male	6	3/5/93	13	Winter
2/9/92	Female	2	4/15/93	14	Winter
2/13/92	Female	2	10/1/94	33	Hunter
3/29/92	Female	6	3/5/93	11	Unknown
3/29/92	Male	7	3/30/93	12	Winter
3/29/92	Male	1	8/21/92	5	Cougar
2/8/93	Male	3	10/2/93	7	Hunter
3/27/93	Male	3	10/6/93	6	Hunter
4/3/93	Male	2	9/20/94	17	Unknown
4/3/93	Male	5	9/29/93	5	Unknown
4/10/93	Male	6	5/25/94	13	Cougar
4/10/93	Male	8	10/10/93	6	Hunter
3/26/94	Male	5	12/19/94	9	Cougar
6/1/94	Male	1	10/10/94	4	Hunter

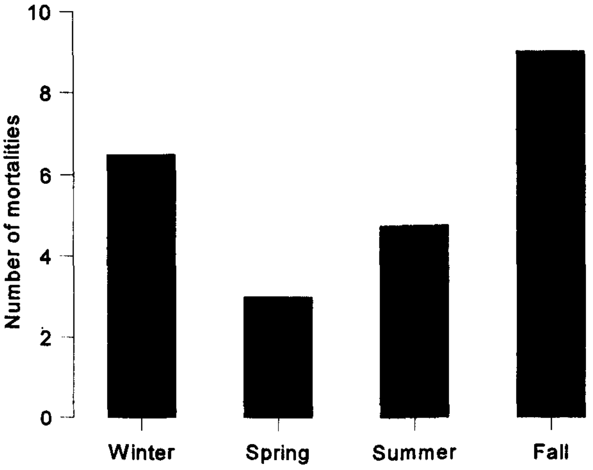

Figure 3. Number of adult mule deer mortalities by season in the Wallowa Mountains, Oregon, 1992-94.

Annual mortality rate due to hunting was 19% for males and 2% for females. During the 3-year period, 6 of 37 radiomarked adult males alive prior to legal hunting season were harvested. Percent of radiomarked males harvested varied by year with 1 of 8 (13%) harvested in 1992, 4 of 17 (24%) in 1993, and 1 of 12 (8%) during 1994. One radiomarked female was accidentally shot by a hunter in 1994.

DISCUSSION

Migrational patterns exhibited by radiocollared deer in this project were multidirectional and similar to those patterns reported by Gruell and Papez (1963), Zalunardo (1965), and Brown (1992). Migrational routes were not always oriented by drainage. Each of the 3 winter ranges contained deer which migrated to summer ranges that geographically were in closer proximity to other winter ranges. One male from the Bear Creek and 2 males from the Lower Minam traveled greater than 51 km to summer on ranges in adjacent management units that were within 13-20 km of winter ranges in Baker County. Mean distances traveled between winter and summer ranges were greater than those reported by Carpenter et al. (1979), Wood et al. (1989), and Brown (1992). Distances were less than those reported by Thomas and Irby (1990) and by Garrott et al. (1987). Distance traveled between winter and summer ranges were nearly the same for males and females which is typical of migratory mule deer populations (Carpenter et al. 1979, Ackerman et al. 1984, Thomas and Irby 1990, Brown 1992).

Fidelity

Migratory mule deer typically exhibit high fidelity to summer ranges (Ackerman et al. 1984, Garrott et al. 1987, Kufeld et al. 1989, Wood et al. 1989). Brown (1992) reported all females and 92% of radiomarked males used overlapping summer home-ranges during consecutive years. Monitoring of adult males and females in this project indicated high fidelity to summer home-ranges with 100 % of the marked individuals returning to the area used the previous years. Telemetry locations were not accurate enough to determine if areas of highest use varied within individual home-ranges between years. Garrott et al. (1987) reported consecutive summer center of activities varying ≤ 1 km for 85% of the females monitored in their study.

Fidelity to winter home-ranges was also high for adult deer. Adults returned to the same wintering locations in successive years, however, some radiomarked individuals left winter home-ranges and moved up to 6.5 km to use spring green-up on nearby ranges prior to spring migration. During fall migration, 2 males moved 10 and 14 km beyond their respective winter ranges and spent 3-4 weeks during the rut period in adjacent wildlife units, then returned to winter home-ranges in early December. This movement pattern was observed both years that these animals were monitored. One yearling male captured on the Lostine winter range wintered 21 km to the west on the Lower Minam range the following winter. Young individuals (primarily yearling and 2-year olds) often demonstrate erratic movements as they likely have not developed a tradition for previously used ranges. This type of movement behavior may also allow deer to pioneer new or lightly used ranges. The strong fidelity to summer and winter areas demonstrated may result in a loss of some traditional migration routes or areas of summer use when population numbers are reduced. Rate of reoccupying or pioneering these areas will likely depend on level of annual yearling recruitment.

Most radiomarked deer remained inside

the Minam management unit boundary the entire year. Nine percent ($n = 5$) spent summer months outside of the unit boundary. Only 1 radiomarked female summered outside the Minam unit boundary. This female moved north through the Sled Springs and Wenaha units and summered across the state line in the Tucannon Wilderness of Washington. This was the only radiomarked deer that moved north to summer. Fourteen percent ($n = 4$) of all radiomarked males summered outside Minam unit boundaries. Although the total number of radiomarked males in this project was small, it does indicate that a proportion of males wintering in the Minam unit are not available for harvest in this unit. The Minam unit shares high elevation summer range with the Pine Creek, Keating, and Catherine Creek units, all of which contain winter ranges where deer are surveyed. Migrational movement patterns should continue to be delineated to better understand interchange between units and assist managers with hunting season strategies and tag allocations.

Timing of Movements

Movement to summer ranges occurred rapidly with individuals normally covering the distance within 1 week. Females migrated earlier than males and may do so to reach summer ranges prior to fawn drop. One radiomarked female migrated 28 km to her summer home-range in mid May during 1992 and 1994, however, in 1993 she did not move until early July. This may be an example of a female which gave birth prior to migration and did not migrate until her fawn was strong enough to travel the distance. Whether or not this hypothesis is true needs further study since Riley and Dood (1984) reported mule deer fawns capable of extensive movements at an early age. Males moving to summer ranges later than females may likely be a result of generally poorer body condition at the end of winter, hence, they remain longer on lush lower elevation ranges to improve their body condition prior to migration.

Studies have reported that fall migration to winter range was caused by snowfall (Richens 1967, Gilbert et al. 1970), however, during this project some individuals moved to winter ranges prior to snowfall, while others did not move until snow began to accumulate on summer ranges. Individual deer monitored in consecutive years exhibited a strong tendency to migrate during the same time period each year regardless of weather conditions. This suggests that deer movement was perhaps a result of an individuals learned tradition triggered by photoperiod, snow accumulation, or possibly a change in forage quality resulting from freezing temperatures. Since many of the radiomarked deer in the Minam unit began fall migration by mid-October, managers should be cautious when designing hunting season framework to avoid over harvest as deer begin to congregate near winter ranges.

Mortality Rates

Mortality rates reported in this paper represent mortality observed for the radiomarked deer in this project, and may or may not represent the mortality rate for unmarked deer in the population. However, we do not have reason to believe these rates differ from the rest of the population; therefore, we discuss them in that context. Males suffered a considerably higher mortality rate than females. This difference between sexes is expected in hunted populations where hunting pressure on males is greater than for females. However, aside from losses due to hunting, male mortality was still more than twice the annual rate of females. Cougar predation was the principal cause of mortality for females, yet annual rate of mortality from cougar predation was higher for males than females. Confirmed cougar kills nearly equaled that of hunter harvest for radiomarked adult males during the 3-year period. These findings coincide with information published by Robinette et al. (1959), Hornocker (1970), and Dixon (1982) who reported cougar taking greater numbers of adult male mule deer than females, and Knipe (1977) reported cougar preyed on adult Coues white-tailed deer (*Odocoileus virginianus couesi*) with bucks killed more often than does. Although we were unable to determine cause of death for 5 radiomarked individuals, cougar predation was suspected for 3 of the 5 individuals (2 males, 1 female). Previous studies of cougar predation on mule deer herds reported cougar predation not negatively impacting deer numbers (Richens 1967, Hornocker 1970, Robinette et al. 1977, Shaw 1977). Although cougar numbers vary by location, it is accepted that their numbers have increased in most areas throughout the West during the past 20 years. With increased densities and distribution, the effect cougars have on present day mule deer herds needs new attention and study.

Mule deer numbers in the Minam unit have declined considerably during the past 2 decades. Information from hunter harvest, sightings, and damage complaints indicate cougar numbers have increased in the Minam and adjacent wildlife units in recent years and continue to do so. If adult mortality rates observed in this project are representative of the population, it is unlikely that we will see a return to higher population levels observed in the 1960s and 1970s. Future population modeling and research should be conducted to further evaluate the relationship between mule deer and cougar population dynamics in the Minam unit.

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Coues White-tailed Deer Dietary Overlap with Cattle in Southern Arizona

RICHARD A. OCKENFELS
CHARLES H. LEWIS[1]
Arizona Game and Fish Department, Research Branch
2221 W. Greenway Road, Phoenix, AZ 85023

Abstract: Competition for forage between Coues white-tailed deer and domestic cattle is a concern in the Southwest. We investigated seasonal diets of deer and cattle in southern Arizona during 1987-89 to determine dietary overlap. Coues white-tailed deer diet shifted seasonally between forbs, shrubs, and trees; forb abundance seemed the primary factor influencing diet. Overall, shrubs (50.8%), forbs (29.8%), and trees (14.7%) comprised most of the deer diet; cattle diets were dominated by grasses (>70%), except during late summers when new forb growth was abundant. Seasonal dietary overlap was typically less than 20%. Individual plant species were seldom used by both deer and cattle. We did not find evidence of competition under moderate livestock grazing.

Key words: Arizona, cattle, competition, Coues, deer, diet, dietary overlap, forage, grazing, *Odocoileus virginianus couesi*

INTRODUCTION

This paper presents dietary overlap data between Coues white-tailed deer (*Odocoileus virginianus couesi*) and cattle in southern Arizona to examine whether forage competition occurs under moderate livestock stocking rates. Competition occurs when ≥2 species use a limited resource and survival or reproduction is adversely affected for ≥1 of the species in question (Birch 1957); it does not occur simply because different species are using the same abundant resource. Nonetheless, concern about competition between livestock and Coues white-tailed deer has been expressed by resource managers in the Southwest.

In Arizona, Coues white-tailed deer inhabit most southeastern and central mountain ranges below the Mogollon Rim, primarily in mixed-oak (*Quercus* spp.) woodlands and higher elevation semidesert grasslands (Knipe 1977). They also occur locally in high-desert scrublands, along riparian corridors, and in pine forests (Hoffmeister 1986).

White-tailed deer are often classified as "browsers" because of their high consumption of plant material from woody species (Harlow 1984). However, woody material consumed can range from nearly zero (Cross 1984, Gavin et al. 1984, Verme and Ullrey 1984) to virtually all browse (Erickson et al. 1961, Allen 1968).

White-tailed deer cannot digest highly lignified forage as well as cattle (Verme and Ullrey 1984), and a diet high in woody material reduces survival. Cattle are better able to use coarser plant materials, such as cured grasses, than small deer subspecies (Clutton-Brock and Harvey 1983). Thus, white-tailed deer are classed as selective foragers (Verme and Ullrey 1984), eating the most palatable parts of plants first. Cattle are a non-selective, grass-roughage feeding type (Henke et al. 1988).

Dietary overlap between Coues white-tailed deer and cattle has been studied in Arizona (Day 1964) and Mexico (Gallina et

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[1] Present address is Bureau of Indian Affairs, PO Box 10, Phoenix AZ 85001

al. 1981, Gallina 1993). For other white-tailed deer subspecies, diet overlap studies have occurred in Idaho (Kingery et al. 1996), Louisiana (Thill 1984, Thill and Martin 1990), Oklahoma (Jenks et al. 1990), and Montana (Allen 1968). In general, their conclusions indicated that livestock grazing pressure primarily affected dietary overlap, with overlap highest under heavy grazing compared to moderate or light grazing.

Further, cattle, being larger animals and requiring more forage volume than deer, are more strongly influenced by seasonal forage availability (Clutton-Brock and Harvey 1983). Diet switching by cattle possibly results in direct competition with white-tailed deer for browse and forbs in dry periods (Knipe 1977).

We hypothesized that forage competition between Coues white-tailed deer and cattle was not occurring under rest-rotation, moderate grazing in southern Arizona. We defined competition as seasonal dietary overlap >50% by plant species.

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STUDY AREA

The Santa Rita study area (SRSA) was located in the foothills of the Santa Rita Mountains in southeastern Arizona, adjacent to the town of Patagonia. SRSA encompassed 123 km² of mixed ownership lands. Elevation ranges from 1,200 m in the southeast portion to 1,675 m in the northeast corner. Topography was moderately steep, with long ridges dissected by small canyons.

Climate was mild, with Patagonia lying in a temperature belt ranging from 4-7 C in January to 21-24 C in July (Sellers and Hill 1974). May-June tended to be hot and dry, and accounted for only 2.8% of annual precipitation, whereas July-August monsoons typically provided half the annual rainfall (43.9 cm for Patagonia). Snowfall (3.0 cm) was generally ephemeral on SRSA.

Vegetation on SRSA was classified overall as Madrean evergreen woodland (Brown 1982), but was diverse due to elevation, broken topography, and uneven precipitation. Communities studied ranged from semidesert grasslands to evergreen shrublands. The mountains were rich in species diversity because of biseasonal rainfall, variety of geological features, and elevation changes (McLaughlin and Bowers 1990). There was a sequence of overstory dominance that changed altitudinally (Brady and Bonham 1976), and a north versus south-facing slope vegetative dichotomy on much of SRSA. North-facing slopes were dominated by trees and shrubs, while grasses, succulents, and forbs were more plentiful on drier south-facing slopes.

Portions of 3 cattle rest-rotation systems made up SRSA. Range analysis of the area (USFS unpubl. documents) showed ridge tops and drainage bottoms in fair to poor condition, with slopes in good condition. Allotments were grazed below specified carrying capacity under existing management plans; Temporal allotment, more than 50% of SRSA, took a 20% non-use reduction in forage animal unit months (AUMs) to help historically heavily grazed areas improve faster. Water distribution systems were maintained in conjunction with the rest-rotation schedules.

METHODS

We summed daily rainfall by week and averaged values over a 7-year period (1981-1987) to establish seasonal patterns; weekly rainfall was graphed and examined for breakpoints. Five seasons (winter: Dec-Feb, spring: Mar-Apr, early summer: May-Jun, late summer: Jul-Sep, fall: Oct-Nov) were established.

We collected fecal samples from white-tailed deer during the 5 seasons from each of 5 different vegetative types scattered throughout SRSA. We collected a minimum of 5 pellets from 15 different deer pellet groups during each season, then labeled and froze samples for future analysis.

Frozen samples were transferred to the Range Analysis Lab of University of Arizona for microhistological examination (Sparks and Malechek 1968). Density data by plant species and 6 plant groupings (grasses, forbs, shrubs, trees, cacti, and other) were summarized and relative percentage use for species and plant grouping was calculated. Plant names followed Soil Conservation Service reference (USDA 1982) and Kearney and Peebles (1973).

We attempted to normalize percentages by arcsine square root transformations (Zar 1984). We tested for differences in annual deer diet composition by one-way analysis of variance (ANOVA). Plant category and seasonal diet interaction were tested by two-way ANOVA. We combined data from grasses, cacti, and other categories for ANOVA tests, because of problems with zero data.

Small pieces of 20-25 cattle droppings were collected in the same sampling scheme as were deer pellets. Cattle droppings were also sent to the Analysis Lab for examination. Percentage diet was calculated the same as for Coues white-tailed deer.

We computed deer dietary overlap with cattle by the niche overlap index of Morista (1959), following review by Smith and Zaret (1982). Diet overlap values range from 0 to 1, with 0 indicating no overlap by composition grouping and 1 reflecting total dietary overlap by plant grouping. If plant grouping data overlapped substantially (>50%), we then determine if individual plant species were used by both deer and cattle.

RESULTS

We identified a total of 11 grasses, 22 forbs, 21 shrubs, and 4 trees used by Coues white-tailed deer. Only 1 cactus, prickly pear (*Opuntia* spp.), was identified in fecal samples, as was 1 fern (*Notholaena parrya*). Few species dominated the diet of Coues white-tailed deer; only 6 species accounted for more than 5% individually (Table 1). Shrubs accounted for over half the overall diet (50.8%), whereas forbs and trees comprised 29.8% and 14.7%, respectively. Grasses (1.1%), cacti, and ferns were relatively minor dietary components.

We found no ($F = 0.01$, 12 df, $P < 0.989$) effects on deer diets due to annual variation. However, Coues white-tailed deer diets were influenced substantially ($F = 73.49$, 3 df, $P < 0.001$) by plant category (i.e., forb, shrub, tree, or other). We also found an interaction ($F = 10.92$, 12 df, $P < 0.001$) between percentage use of plant category by deer and season collected. The primary shift in deer diet occurred between forbs and shrubs (Fig. 1). Seasonally, shrub use was high when forb use was low and low when forb use was high.

Samples of cattle diet for fall of 1989 were unusable because slide identifying information was lost at the lab. Several other slides for both deer and cattle were

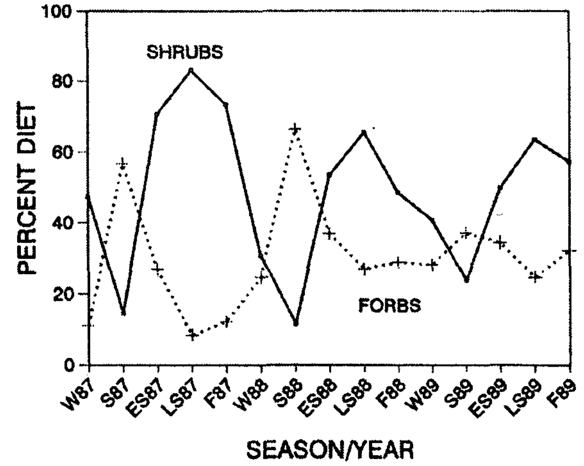

Figure 1. Percent of diet by season (W = winter, S = spring, ES = early summer, LS = late summer, F = fall) of shrubs and forbs by Coues white-tailed deer in the Santa Rita Mountains, Arizona, 1987-89.

also unusable because seasonal dates were lost. Cattle dietary composition was dominated (>70%) by grasses, except during late summer of 1988 and 1989 (Fig. 2). Forb and shrub use by cattle increased during these seasons. Cattle used trees more than shrubs, except during late summer periods.

Calculated dietary overlap between white-tailed deer and cattle was generally low (Fig. 3), with values less than 0.20 (i.e., 20%), except during late summers of 1988 and 1989. Only in late summer of 1989 did diet overlap by plant group exceed 50%.

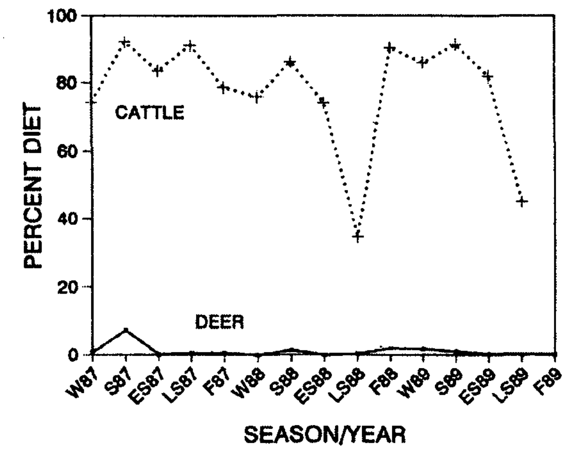

Figure 2. Percent of diet by season of grasses by Coues white-tailed deer and cattle in the Santa Rita Mountains, Arizona, 1987-89.

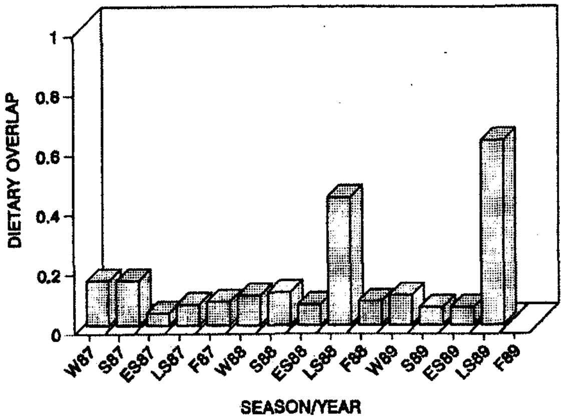

Figure 3. Seasonal dietary overlap between Coues white-tailed deer and cattle in the Santa Rita Mountains, Arizona, 1987-89.

Overlap for fall of 1989 could not be calculated because of missing cattle data. During late summer 1989 and late summer 1988, deer and cattle did not forage for the same species of forbs or shrubs.

DISCUSSION

With the typically low dietary overlap values obtained and lack of use of the same forb and shrub species during late summers, we accepted our null hypothesis that continous competition between Coues white-tailed deer and cattle did not occur under the seemingly moderate grazing pressure that existed on SRSA during 1978-89. Similar to the results of Day (1964), Gallina et al. (1981), and Gallina (1993), we found little support that forage competition between deer and cattle exists under moderate grazing and "normal precipitation." Based on climate records, drought conditions did not occur during 1987, 1988, and 1989. Therefore, we could not test Knipe's (1977) contention that cattle compete with deer under drought conditions. We found, as predicted, that cattle diets were predominately grass and deer diets were predominately browse or forbs.

As expected, mainstay forage plants for Coues white-tailed deer were shrubs, and to a lesser extent, trees (White 1961, Anthony 1976, Knipe 1977). These are available year round and seasonally provide new growth. Well over one-half (65.7%) the diet on SRSA was of these 2 groups. Gallina et al. (1981) also found that shrubs were the highest percentage (51%) of the Coues' year-round diet, and together with trees accounted for 83% of deer diets in Mexico. Browse also accounted for greater than 50% of white-tailed deer diet in Minnesota (Kohn and Mooty 1971) and Texas (Quinton and Horejsi 1977, Waid et al. 1984).

Grasses constituted only a minor part of deer diet on SRSA, but were the major components for cattle. However, grasses can be important to deer in spring (Cross 1984) and year round in certain areas (Everitt and Gonzalez 1979, Gavin et al. 1984), but generally amount to less than 5% of white-tailed deer diet (Kohn and Mooty 1971, McCulloch 1973, Quinton and Horejsi 1977, Krausman 1978, Everitt and Gonzalez 1979, Henry and Sowls 1980, Korschgen et al. 1980, Gallina et al. 1981).

We found no single forb to constitute a large proportion of Coues white-tailed deer diet on SRSA. Forb richness was high and many (>20 species, >10 genera greater than trace amounts) were used. We believe that forb seasonal abundance was the dominant factor influencing Coues white-tailed deer diet selection on SRSA. However, we had no quantitative estimates of seasonal plant abundance, simply our impression that forb use increased when forbs were an obvious feature of the landscape, but decreased when forbs dried. Nonetheless, forbs are the preferred plant group for white-tailed deer when available and green (McCulloch 1973, Cross 1984, McCullough 1985), and they provide more protein and phosphorus than woody plants (Urness et al. 1971). Noticeable changes in deer diet are generally related to increases or decreases in forb growth (Gallina et al. 1981). Unfortunately, forb abundance varies year to year, thus it is an unstable food resource (McCulloch 1972). During our study, forb abundance varied seasonally, and deer responded to those changes.

In Texas, Waid et al. (1984) found precipitation to be the main factor affecting abundance of forage. Shrubs, trees, and cacti generally do not vary seasonally in numbers, but instead vary mainly in amount of new growth.

Still, forage competition between white-tailed deer and domestic livestock remains an important concern for southwestern wildlife managers. Cattle are of particular concern because of their widespread distribution and often high stocking levels. Dietary overlap has been suspected to be high in Arizona during dry periods (Knipe 1977), when forage is scarce. Further research is warranted to determine if competition occurs under drought conditions. All we can claim is that competition, as defined, did not occur during our study period.

Seasons other than dry periods may also be important, as Allen (1968) found overlapping use of winter browse in Montana to be severe; heavy snow cover of grasses and reduced supplemental hay feeding of cattle contributed to the problem. As predicted, cattle switched their diet to be more similar to deer.

MANAGEMENT IMPLICATIONS

Dietary overlap values suggest no forage competition between Coues white-tailed deer and cattle on SRSA. The rest-rotation systems of the 3 allotments on SRSA did not seem to adversely affect vegetative composition, such that deer did not have available forage.

However, competition between deer and cattle can occur for non-forage resources. Vegetative type use patterns by Coues white-tailed deer were affected by livestock (M. Brown 1984), and heavy grazing prior to and during fawning periods may reduce hiding cover. Fawn survival is partially dependent on amount of hiding cover provided by perennial grasses; fawn survival is extremely important to deer abundance and is related to precipitation, which relates to vegetative cover (D. Brown 1984). We did not address these questions, but they need to be considered when discussing potential competition.

Nonetheless, grazing use should be based on actual current grass production (Thill 1984), instead of a set AUM allotment or a range analysis that is not indexed to climatic conditions prior to measurement. Levels for AUMs set during wet periods could easily be too high for drought. Coordination in monitoring grass use and forage switching by livestock is necessary for better white-tailed deer management.

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Desert Mule Deer Use of a Wildlife Movement Corridor

JOHN C. TULL
PAUL R. KRAUSMAN
RON J. POPOWSKI

School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721, USA

Abstract: We studied the efficacy of a "wildlife movement corridor" in the Avra Valley (26 km wide) between 2 mountain ranges in the Sonoran Desert. Our objective was to determine if desert mule deer used the Tucson Mitigation Corridor (11 km^2) to cross the barrier created by the Central Arizona Project (CAP) aqueduct. We monitored 17 radiocollared desert mule deer in the valley. Animal locations were spatially analyzed with a geographic information system. Eight deer entered the corridor; 3 deer crossed the canal via the corridor. Two deer crossed the canal outside of the mitigation corridor. Only 1 deer moved from the Roskruge to the Tucson Mountains. One female moved from the central to the west side of the valley but did not use the corridor. These data indicate that the corridor is used but not necessary for the movement of desert mule deer across Avra Valley. However, as the area around the canal is further developed the corridor may be of more value to wildlife.

Key words: Central Arizona Project, desert mule deer, home-range, radiocollar, Tucson Migration Corridor.

INTRODUCTION

Corridors have received recent attention in management and conservation of wildlife resources (Noss 1987, Simberloff and Cox 1987, Hobbs 1992, Simberloff et al. 1992, Hess 1994). A wildlife movement corridor can be defined as land that provides connectivity between 2 wildlife refuges or large-scale areas of wildlife use. For example, a corridor can be protected land within human-encroached landscapes, if it serves to link 2 wildlife management areas.

The Tucson Mitigation Corridor (TMC) provides natural areas for small-scale animal movement across the CAP, but engineered structures not designed for wildlife use also provide wildlife access across the CAP. Large-scale animal movements are possible from the Tucson Mountains to the Roskruge Mountains via a corridor system that is comprised of the TMC, conserved lands in Tucson Mountain Park and Saguaro National Park, and with currently undeveloped lands of the Tohono O'odham Nation's Garcia Strip. Although the TMC was designed and located on the assumption of large-scale animal movements across Avra Valley (deVos et al. 1983, deVos et al. 1985), the corridor system is untested.

We sought to determine if desert mule deer (*Odocoileus hemionus crooki*) were using the TMC to cross the CAP, and to determine if the TMC was used for large-scale movements across Avra Valley. We also assessed the effectiveness of the Tucson Mitigation Corridor versus unplanned crossing areas for providing access for desert mule deer and other wildlife across the CAP.

STUDY AREA

The study area was in Avra Valley, Pima County, Arizona and was bounded by the Tucson Mountains to the east and the Roskruge Mountains to the west (Fig. 1). Tucson is approximately 20 km east of Avra Valley. The CAP followed the eastern edge of Avra Valley and was proximate to

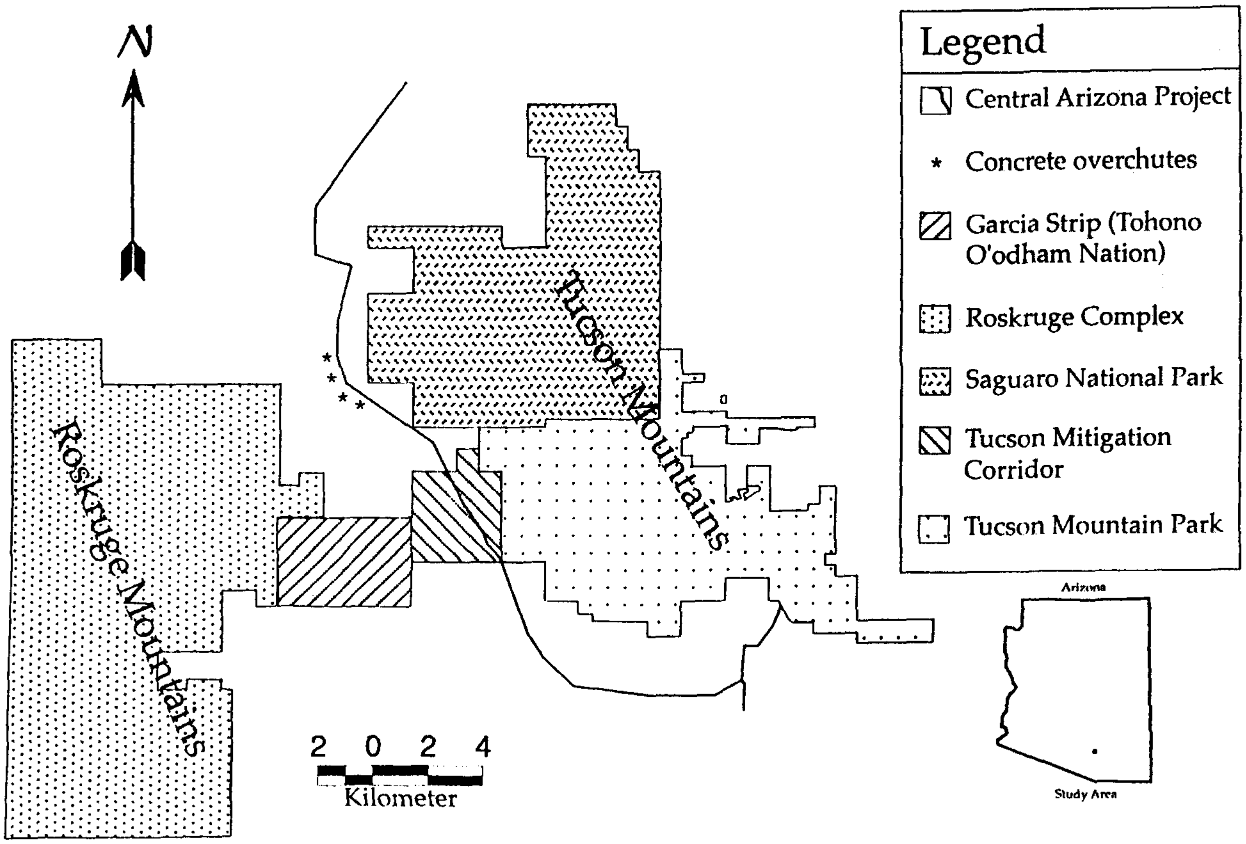

Figure 1. The desert mule deer study area in Avra Valley, Arizona, 1996-97. The Roskruge Complex (Tohono O'odham Nation, federal, and state lands) formed a reserve on the west, and Saguaro National Park and Tucson Mountain Park created a reserve on the east. The Garcia Strip and the Tucson Mitigation Corridor served as a wildlife movement corridor system.

Saguaro National Park and Tucson Mountain Park to the east. Elevations within the area ranged from 1,429 m at Wasson Peak in the Tucson Mountains to ıbout 610 m in north Brawley Wash. Vegetation in the area were common to the Sonoran Desert and included: 1) palo verde *Cercidium* spp.)-mixed cacti on bajadas; 2) reosote (*Larrea tridentata*)-bursage *Ambrosia* spp.) in undisturbed flats; 3) nesquite (*Prosopis velutina*)-burroweed *Isocoma tenuisecta*) in disturbed flats (i.e., bandoned agricultural lands); and 4) onwood (*Olneya tesota*)-canyon ragweed *Ambrosia ambrosioides*) in washes.

Precipitation is typically bimodal with most occurring during the July-September monsoon or occasional winter storms (Reitan and Green 1968). Precipitation in 1996 was 28.3 cm for Tucson, Arizona (National Climatic Data Center, unpublished data). Normal (1961-1990) precipitation was 30.6 cm; average normal seasonal temperatures were 24.3, 30.2, 16.6, and 13.6 C for spring (Apr-Jun), summer (Jul-Sep), autumn (Oct-Dec), and winter (Jan-Mar), respectively (National Climatic Data Center 1993). Seasons were defined based on weather patterns and biology of desert mule deer (Krausman 1985).

The TMC was an 11 km² parcel of land established to mitigate for lost habitats from CAP construction and to provide wildlife access to habitats on either side of the fenced CAP, which was a large-scale linear obstruction to wildlife movements. Lands for the TMC were purchased for $6,200,000 U.S. The placement of the TMC was based on research by deVos et al. (1983, 1985) performed prior to construction of the CAP. They examined telemetered peccaries (*Tayasu tajacu*, *n* = 11), coyote (*Canis latrans*, *n* = 7), gray fox (*Urocyon cinereoargenteus*, *n* = 7), desert mule deer (*n* = 5), bobcat (*Lynx rufus*, *n* = 5), and kit fox (*Vulpes velox*, *n* = 1) from March 1982 to March 1983.

Lands west of the TMC were developed for housing or were in the Tohono O'odham Nation (Garcia Strip). The east was bounded by Tucson Mountain Park, a permanent reserve. To the north, the boundary was adjacent to private land zoned for housing or state and federal lands. The land beyond the southern boundary was fallow ranch land. Extensive housing development occurred south and east of the TMC. Saguaro National Park was about 800 m beyond the northernmost extension of the TMC.

The CAP advanced generally northwest to southeast through the TMC with 7 wildlife crossing areas from 40-230 m wide spaced nearly evenly along the canal route. The aqueduct was underground and 1 wash was present at each crossing area. Vegetation in crossings was different than surrounding vegetation because of disturbances from canal construction, although grasses and shrubs were reclaiming the crossing sites and were structurally similar to the native plant community. Two catchments provided year round water to wildlife within the TMC. One was located east of the aqueduct near the northern boundary and the other was west of the canal near the center of the TMC.

Four wash overchutes (i.e., flumes) were present along the CAP. They were approximately 1 km apart beginning about 5 km north of the TMC. Flumes were engineered structures designed to allow water moving downslope across the landscape to pass over the canal. Saguaro National Park was within 1.2 km of all 4 flumes. Private, developed lands blocked direct access for each of the flumes, but undeveloped Bureau of Land Management lands provided indirect access to Saguaro National Park. Fallow fields and rangeland were west of the flumes with little or no development westward to the Roskruge Mountains. We defined these *a priori* as alternate crossing areas for deer. In addition, the CAP was underground for approximately 1 km from a pumping plant about 1.5 km north of the TMC to 500 m north of the TMC. This was also designated *a priori* as an alternate crossing area.

Saguaro National Park and Tucson Mountain Park abutted forming an extensive wildlife reserve (approx. 101 km²). The Roskruge Mountain lands were owned by the Tohono O'odham Nation, the Bureau of Land Management, and the state of Arizona (Roskruge Complex). The combined lands of the TMC and the Garcia Strip served as a movement corridor system (i.e., lands serving as a movement corridor but managed by non-cooperating stakeholders) linking the Roskruge Complex and the Tucson Mountain/Saguaro National Park reserve. The corridor system was 16.1 km in length and 1.6-3.2 km wide. A 2-lane highway bisected the 1.6 km shared boundary of the TMC and Garcia Strip.

METHODS

We captured a total of 17 desert mule deer (14 F, 3 M) with net-guns in November 1995 and February 1996 to obtain a representative sample of the population (Krausman et al. 1985). Each collar was color-coded to permit visual identification of individuals. We relocated each radiotagged deer by direct observation, triangulation, helicopter, or infrared camera 16 times/season to obtain seasonal home-range estimates following Mares et al. (1980) (Table 1). Locations on individually marked deer were taken 24 hrs apart and during daylight hours. Triangulated locations were determined from 2 single-observer directional locations taken within 5 minutes. We used a hand-held geographic positioning system (Magellan Systems Corp., San Dimas, Calif.) to obtain Universal Transverse Mercator coordinates for each location and estimated the seasonal home-ranges for each deer with the minimum convex polygon method (Southwood 1966). We estimated error of triangulation (White and Garrott 1990) under the assumption that deer were stationary during locations. Location data were placed into a geographic information system (GIS) for spatial analyses. We were able to identify movement patterns of radiocollared deer with the GIS and determine when and where deer moved across the CAP.

Table 1. Percent of each relocation method for radiocollared desert mule deer relocations in Avra Valley, Arizona, 1996-97.

Location method	%	n
Visual	54.5	520
Triangulation	31.3	299
Helicopter	13.7	131
Infrared camera	0.5	5
Total	100.0	955

RESULTS

We captured 17 deer (14 F, 3 M) providing a ratio similar to all deer observed in the study area from July 1996 to March 1997 (i.e., 29 M and 154 F). We obtained 177 radiocollared deer-months of data. Over half (54.5%; *n* = 954) of animal locations were visual observations, 299 (31.3%) were obtained by triangulation, 131 (13.7%) were located from helicopter, and 5 (0.5%) were captured by infrared cameras. Deer were moving during 35.3% of all visual locations. Error of triangulation for the remaining locations was estimated at 215.2 ± 28.9 (SE) m.

From our telemetry data, we had 41 of 957 total locations of deer inside the TMC. Of the 17 radiotagged desert mule deer, 5 crossed the CAP, and 2 of those crossings were outside the TMC (Table 2). One deer crossed the CAP and moved >500 m beyond the canal; the other 4 animals that crossed the CAP never ventured >500 m beyond the canal. Deer 4 had all her seasonal home-ranges abutting the CAP and used the TMC for habitats extensively. Animals 3 and 7 (male and female, respectively) ventured across the CAP from Saguaro National Park to the north, and both used the 1 km underground aqueduct to move to habitats on the opposite side of the canal route.

All canal crossings were short-duration (15 days) exploratory movements with the exception of 1 animal. Deer 18, a male, crossed the CAP at the onset of the winter season and moved east to the bajada and foothills of the western slope of the Tucson Mountains. He wandered Tucson Mountain Park for approximately 40 days during the rut (mid- to late-Jan), and returned west of the canal and toward his traditional home-range before being poached on February15, 1997. We located him in the foothills of the Roskruge Mountains in all other seasons, thus he made a large-scale movement across

Table 2. Desert mule deer crossings of the Central Arizona Project (CAP) in Avra Valley, Arizona, 1996-1997.

Animal no.	Sex	Approx. date (s) of crossing	Duration across CAP	Crossing location in Tucson Mitigation Corridor
3	M	Feb 5, 1997	1-11 days	No[a]
4	F	Oct 4, 1996	<1 day	Yes
		Jan 29, 1997	1-6 days	Yes
		Feb 17, 1997	1-8 days	Yes
7	F	Apr 6, 1996	<7 days	Yes[b]
17	F	Jul 24, 1996	3-15 ays	No
		Aug 1, 1996	<1 day	No
18	M	Jan 1, 1997	35-45 days	Yes[c]

[a] All crossings outside of the Tucson Mitigation Corridor (TMC) occurred across a 1-km stretch of underground aqueduct that begins approximately 500 m north of the TMC.

[b] The location point that places deer 7 across the canal is suspect because it is a triangulated location and was not visually located.

[c] Deer 18 was across the mitigation corridor until his last location on Feb 15, 1997.

Avra Valley and used the TMC for his crossing of the CAP.

DISCUSSION

Overall deer use of the Tucson Mitigation Corridor is low (<5%). Our data suggests that deer use the TMC for habitats, but not for the explicit purpose of crossing the CAP, with the exception of deer #18. This is excepted by the male deer that ranged the entire valley during the rut. When other deer crossed the CAP, they did not travel far beyond the crossing area.

We did not find deer on the opposite side of the CAP near flumes (i.e., radiocollared deer did not appear to cross the CAP via flumes). From ongoing research we have found that deer make use of flumes as CAP crossing sites. Preliminary results reveal that overall wildlife use of TMC crossing areas is not different from flume use, although deer use is lower for flumes than TMC crossings (R. J. Popowski and P. R. Krausman, unpubl. data). Forty percent of radiocollared deer canal crossings were outside of the TMC along a 1 km underground stretch of canal that was another engineered feature unintentionally aiding wildlife access across the CAP.

We have 1 example of a deer engaging in large-scale movements through Avra Valley via the TMC, thus the TMC aided large-scale wildlife movements across Avra Valley. We do not know if deer would travel across the valley if the TMC crossing areas were unavailable, but deer did make small-scale movements across the CAP outside of the TMC. The relatively short duration of the study and sample size limitations may have precluded us from gaining complete information on deer use of alternate crossing sites for large-scale movements across Avra Valley.

The future of a wildlife corridor system in Avra Valley is uncertain. The land ownership of the Roskruge Mountains is predominantly Tohono O'odham Nation and Bureau of Land Management, but the mountains are not a recognized reserve as are Tucson Mountain Park and Saguaro National Park on the east. Agricultural development is planned for the Garcia Strip and an aqueduct from the CAP is currently being created (United States Bureau of Reclamation 1988). Garcia Strip development would result in a truncation of the current movement corridor system. Under these circumstances, the TMC would serve as an extension of the reserved park lands east and north of the TMC. This may prove valuable to populations of plants and wildlife that do not require dispersal and large-scale movements to maintain panmixia, but it may result in less-frequent interchange among wildlife on the east and west sides of the CAP. Without the ability for wildlife to disperse across Avra Valley, the biological gains (Lande and Barrowclough 1987, Noss 1987, Hobbs 1992) of a movement route for wildlife would be lost. The primary intent of the TMC would no longer be met.

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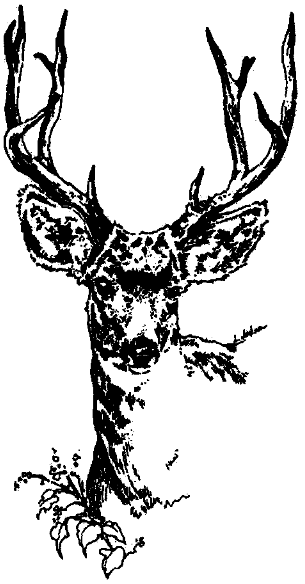

Mule Deer Management — What Should Be Monitored?

GARY C. WHITE
Department of Fishery & Wildlife Biology, Colorado State University, Fort Collins, CO 80523

RICHARD M. BARTMANN
Colorado Division of Wildlife, 317 West Prospect Road, Fort Collins, CO 80526

Abstract: For major mule deer populations in Colorado, Division of Wildlife biologists collect estimates of December age and sex ratios every 1-2 years, an estimate of total density in January every 3-5+ years, and estimates of harvest for antlered and antlerless segments every year. However, there are no estimates of survival rates for these populations. When building models to manage deer populations, model predictions are most sensitive to values of survival rates used. Further, radiocollaring of mule deer fawns in Piceance Basin in northwestern Colorado demonstrated considerable year-to-year variation of over-winter survival, whereas much less year-to-year variation was observed in recruitment. We suggest more effective monitoring can be accomplished by shifting resources from estimating recruitment to estimating over-winter survival in mule deer. The population variables that change most from year-to-year should be monitored more intensively, not variables that change little. We propose a monitoring system in which survival is estimated annually and recruitment and density less frequently. To accomplish this without increasing costs, only a few core areas would be monitored annually compared to the broader geographic coverage of the current monitoring effort. To obtain data for non-core, or satellite, areas, over-winter fawn survival would be monitored on a rotating basis. Over time, a covariance matrix of over-winter survival between the core and satellite populations would be developed so reliable inferences to satellite populations could be predicted from the core population. To evaluate this strategy, a realistic computer model of a set of deer populations would be built. This model would allow sampling modeled populations to determine which monitoring strategy best predicts the true population. For a fixed cost, the optimal sampling strategy could be determined.

INTRODUCTION

The Colorado Division of Wildlife (CDOW) has been a leader in development of methods for monitoring the status of mule deer (*Odocoileus hemionus crooki*) populations. Quadrat counts (Kufeld et al. 1980, Bartmann et al. 1986) conducted from helicopters during December-January provide population estimates, and December age and sex ratios, again determined from helicopters, provide estimates of recruitment and herd composition. Although annual estimates of these parameters would be desirable, costs are prohibitive, so population size is estimated every 3-5+ years and age ratios estimated every 1-2 years for major management units. Harvest estimates are obtained annually from phone surveys (White 1993, Steinert et al. 1994). From these data, population models are developed to project the population and establish harvest objectives for the coming year. Unfortunately, the 1 variable to which the model is most sensitive is survival, and no estimates of survival are routinely taken as part of monitoring procedures.

This paper has 2 objectives: 1) to present reasons why monitoring of survival is essential to project the trajectory of deer populations, and 2) to describe a monitoring system that includes estimates of survival and is within current budget constraints for state-wide deer monitoring. To implement these objectives, we first describe a simple population model. Then, the importance of the sensitivity of the model to parameter values and the importance of temporal variation to model predictions are explained. Finally, the need for a more complex "planning model" currently under development is described.

The crucial philosophy underlying this paper is that management decisions must be based on data. In other words, the management of mule deer in Colorado should not be based on model predictions where the model inputs are not provided from measurements made in the field. Complex models of mule deer dynamics may capture most of our knowledge of this system, but such models do not provide reliable predictions of year-to-year dynamics because of the lack of annual information on required inputs.

The issue of model complexity is better comprehended with an analogy to an auto trip from New York City to Los Angeles. No reasonable driver would start this trip with 7.5 minute USGS topographic quadrangles as his/her model. Certainly the topographic quadrangles contain all the necessary information, but the detail is considerably more than needed. A simpler model will suffice, such as state road maps, and is more likely to result in success. An even simpler model of just a single map of the Interstate highways would suffice, but would not provide all the details we might like. Unfortunately, costs usually limit the amount of information available, even though we may desire more.

The second crucial philosophy underlying this paper is that good data on a few mule deer herds are better than poor data on all the herds in Colorado. In other words, rigorous monitoring of a few herds provides better inferences to the herds not monitored than does inadequate monitoring on all the herds. Colorado's mule deer populations are managed as Data Analysis Units (DAUs) within which are 1 or more Game Management Units (GMUs). GMUs typically represent mule deer populations or a subset thereof. Population modeling and population objectives are conducted at the DAU level, whereas most monitoring and harvest estimation takes place at the GMU level.

MULE DEER POPULATION MODEL

To make this presentation explicit, a model of mule deer population dynamics is necessary. This model provides the framework to justify any population monitoring scheme, i.e., the model establishes what population parameters must be measured. The model is simple to economize the amount of input data necessary to use it. Yet, the model must adhere to biological authenticity so that it is useful in projecting mule deer population status. Mule deer population dynamics are much more complicated than the model portrays. However, routine measurement of a wider array of inputs required for a more complicated model is unrealistic. Thus, the model presented here is a reasonable trade-off between what can be measured practically and what is needed to predict mule deer populations for management purposes.

The model has only 2 age classes: fawns and adults. The gender of fawns will not be differentiated until they are 1-year old. Thus, we define 3 categories in the population: fawns (labeled Juveniles or *J*), females (*F*), and males (*M*). Fawns are recruited into the population in early December when the ratio of fawns to females is estimated. The number (*N*) of fawns on December 1 is computed as

$$N_J(t) = R(t)\ N_F(t)$$

where *R(t)* is the estimated ratio of fawns to yearling and adult females sampled in the population in year *t*. Total population size (N_T) in early December in year *t* is thus

$$N_T(t) = N_J(t) + N_F(t) + N_M(t)\ .$$

Total population size prior to the next hunting season is determined by multiplying December fawn and female population segments by over-winter survival rates followed by spring to fall female survival. Estimates of spring to fall survival rates are usually close to 1 so, for simplicity, we will ignore the small amount of mortality during that period. Further, we will assume a constant 50:50 sex ratio for fawns. The equations to project the population from December of year t forward to December of year $t+1$ and after harvest (H) in year $t+1$ are:

$$N_F(t+1) = S_J(t)\ 0.50\ N_J(t) + S_F(t)\ N_F(t) - H_F(t+1)\ ,$$

$$N_M(t+1) = S_J(t)\ 0.50\ N_J(t) + S_M(t)\ N_M(t) - H_M(t+1),$$

and

$$N_J(t+1) = R(t+1)\ N_F(t+1)\cdot$$

The fawn age class is the observed recruitment discussed above. The model contains 4 parameters that are year-specific: recruitment, juvenile survival, female survival, and male survival. Estimates of harvest could be inflated to account for wounding loss.

Other assumptions implicit in this model are that males and yearling females have the same survival as 2-year old females. We chose to not distinguish yearlings from older animals because data are not collected to support this additional complication. A more elaborate data collection operation would justify a more elaborate model. Given the insufficiency of current data collected by CDOW on mule deer, we opted for the simplest model possible.

WHY SURVIVAL ESTIMATES ARE CRITICAL TO MODELING MULE DEER POPULATIONS

The relative importance of a parameter in a mule deer population model must be evaluated from 2 perspectives. First is sensitivity of the model to the parameter. Second is how much variation from year to year takes place for each parameter.

Sensitivity

Sensitivity is defined as the amount of change of the model's output compared to the amount of change of the parameter, referred to as parameter sensitivity (Innis 1979). Thus, suppose the output from the model is rate of population change defined as $\lambda = N_{t+1}/N_t$. If adult doe survival (S_F) is increased 10% from 0.85 to 0.935, the change in λ for $S_F = 0.85$ to the new value of λ computed for $S_F = 0.935$ relative to the change in S_F is a measure of the sensitivity of λ to S_F. Technically, sensitivity is defined as the partial derivative of λ with respect to the parameter of interest. If S_F is increased by amount Δ, then

$$\text{Sensitivity} = \frac{\partial\lambda}{\partial S_F}\ ,$$

and is often presented as a percentage by multiplying by 100. The proportional sensitivity, or elasticity (Caswell 1989), of 2 or more parameters can be compared by multiplying the sensitivity of a parameter by the parameter value divided by λ. Elasticity gives the proportional change in λ resulting from a proportional change in the parameter. For S_F, the elasticity would be

$$\text{Elasticity} = \frac{S_F}{\lambda}\frac{\partial\lambda}{\partial S_F} = \frac{\partial\log\lambda}{\partial\log S_F}$$

Any ungulate model will have a very high sensitivity to adult female survival rates, while sensitivity for recruitment and juvenile survival is similar but considerably less than for adult survival rates. Intuitively, this is because adult survival occurs in the model multiple times for a single cohort of animals, whereas recruitment and juvenile survival only occur once per cohort.

For the model described above, an analytical expression can be derived for the rate of population change ($\lambda = N_{t+1}/N_t$) as a function of the survival and recruitment parameters from a Leslie matrix (Leslie 1945, Caswell 1989) formulation. The Leslie matrix for the above difference equations is

$$\begin{bmatrix} R\frac{S_J}{2} & RS_F & 0 \\ \frac{S_J}{2} & S_F & 0 \\ \frac{S_J}{2} & 0 & S_M \end{bmatrix},$$

with the dominant eigenvalue of this matrix λ, so that

$$\lambda = \frac{RS_J + 2S_F}{2},$$

where the value 2 is the result of the even sex ratio. Note that adult male survival rate does not affect population growth rate (and does not appear in this equation), as only females give birth. With this equation, we can compute sensitivity directly, as described above, plus we can compute sensitivity analytically by taking the partial of λ with respect to each of the parameters (i.e., R, S_J, and S_F). Taking the numerical values of $R = 0.64$, $S_J = 0.40$, and $S_F = 0.85$ (Table 1), the resulting value of λ is 0.978. When a 10% increase is made in each of the 3 parameters, 1 at a time, the estimates of elasticity are 0.1309, 0.1309, and 0.8691, respectively, for R, S_J, and S_F. That is, a 10% increase in either R or S_J results in a 1.309% increase in λ, whereas a 10% increase in female survival results in an 8.691% increase in λ. The resulting values of λ are 0.9908 for R and S_J, and 1.063 for S_F.

These results suggest that a precise estimate of female survival must be used in the model, or else population projections will be seriously biased. Much more bias (about 6.6 times) will result in projections from a 10% error in S_F than from a 10% error in either R or S_J.

Although the model used to obtain these results is not complex, conclusions will be essentially the same regardless of how much more complex the model is structured. Adult survival will always be the most sensitive parameter in a reasonable mule deer population model. Recruitment and over-winter fawn survival will have identical sensitivities (unless sex ratio or sex-specific survival rates are used) and be much lower than adult survival.

Temporal Variation

The second perspective on the relative importance of parameters in the model is year-to-year variability of the parameters, often labeled temporal variation or environmental variation. How much do each of the 3 parameters vary from year to year? Although computing the variance of a series of estimates of recruitment or survivals would seem appropriate, such is not the case. Variation of the true, but unknown, population parameters is of interest. True survival or recruitment rates are not observed. Rather, we make estimates of these parameters. Thus, total variance of the series of estimates includes both sampling variance (because only estimates are available) and temporal variation of the true process. To properly estimate temporal variation of the series, the sampling variance of the estimates must be removed. To further understand this concept, consider 2 studies to compute juvenile survival over a 10-year period on

Table 1. Estimates of recruitment (fawns/100 adult females), over-winter fawn survival, and annual adult female survival in DAU D-7 in northwestern Colorado.

	Recruitment		Fawn Survival		Adult Female Survival	
Year	Estimate	SE	Estimate	SE	Estimate	SE
77	76.4	2.73				
78	72.6	2.30				
79	72.9	2.17				
80	78.6	2.78				
81	78.1	2.04				
82	75.5	1.96	0.32	0.09	0.80	0.13
83	62.9	1.53	0.07	0.05	0.78	0.11
84	58.7	1.71	0.20	0.08	1.00	0.00
85	73.4	1.86	0.54	0.07	0.92	0.05
86	61.5	1.53	0.43	0.06	0.72	0.09
87			0.24	0.08	0.82	0.12
88	63.0	1.20	0.27	0.08	0.86	0.13
89	63.9	0.97	0.78	0.08	0.83	0.08
90	62.1	1.33	0.32	0.09	0.97	0.03
91	55.6	1.12	0.46	0.11	0.72	0.07
92	49.7	1.38	0.11	0.04	0.72	0.07
93	47.1	1.40	0.55	0.06	0.90	0.04
94	54.9	1.38	0.70	0.05	0.85	0.05
95	47.6	3.04	0.62	0.06	0.97	0.03
Average	64.14	1.80	0.40	0.07	0.85	0.07
SD	10.55		0.22		0.10	

the same study area. One study uses only 10 radios/year, whereas the other uses 100/year. The study with the small sample size will have considerably more variation in the series of estimates because of larger sampling variation, while temporal variation for both studies is identical. Thus, to estimate temporal variation properly, we must remove the sampling variation. In this section, we describe a procedure to remove sampling variance from a series of estimates to obtain an estimate of the underlying process variation (which might be temporal or spatial variation). The procedure is explained in Burnham et al. (1987:260-278).

Consider the example of estimating over-winter survival rates for a deer population annually for 10 years. Each year, the true survival rate is different from the overall mean because of snow depth, cold weather, etc. Let the true, but unknown, overall mean be S. Then the survival rate for each year can be considered to be S plus some deviation attributable to temporal variation, with the expected value of the e_i equal to zero:

Environmental Variation

i	Mean	Year i	Year i
1	S	$S + e_1$	S_1
2	S	$S + e_2$	S_2
3	S	$S + e_3$	S_3
4	S	$S + e_4$	S_4
5	S	$S + e_5$	S_5
6	S	$S + e_6$	S_6
7	S	$S + e_7$	S_7
8	S	$S + e_8$	S_8
9	S	$S + e_9$	S_9
10	S	$S + e_{10}$	S_{10}
Mean	S	S	S

The true population mean S is computed as S:

$$\bar{S} = \frac{\sum_{i=1}^{10} S_i}{10} ,$$

with the variance of the S_i computed as:

$$\hat{\sigma}^2 = \frac{\sum_{i=1}^{10} (S_i - \bar{S})^2}{10} ,$$

where the random variables e_i are selected from a distribution with mean 0 and variance σ^2. In reality, we are never able to observe the annual rates because of sampling variation or demographic variation. For example, even if we observed all the members of a population, we would still not be able to say the observed survival rate was S_i because of demographic variation. Consider flipping 10 coins. We know the true probability of a head is 0.5, but we will not always observe that value exactly, i.e., get 5 heads from 10 flips. Further, imagine if you flip 11 coins -- the true value is not even in the set of possible estimates. That is, the only possible estimates are 0/11, 1/11, ..., 11/11, with none of the estimates equal to 0.5. The same process operates in a population as demographic variation. Even though the true probability of survival is 0.5, we would not necessarily see exactly ½ of the population survive on any given year. Hence, what we actually observe are the quantities:

Environmental Variation + Sampling Variation

i	Mean	Truth Year i	Observed Year i
1	S	$S + e_1 + f_1$	$\hat{S}_1$
2	S	$S + e_2 + f_2$	$\hat{S}_2$
3	S	$S + e_3 + f_3$	$\hat{S}_3$
4	S	$S + e_4 + f_4$	$\hat{S}_4$
5	S	$S + e_5 + f_5$	$\hat{S}_5$
6	S	$S + e_6 + f_6$	$\hat{S}_6$
7	S	$S + e_7 + f_7$	$\hat{S}_7$
8	S	$S + e_8 + f_8$	$\hat{S}_8$
9	S	$S + e_9 + f_9$	$\hat{S}_9$
10	S	$S + e_{10} + f_{10}$	$\hat{S}_{10}$
Mean	S	S	$\bar{\hat{S}}$

where the e_i are as before, but we also have additional variation from sampling variation, or demographic variation, or both, in the f_i.

The usual approach to estimating sampling variance separately from temporal variance is to take replicate observations within each year so within-cell replicates can be used to estimate sampling variance; whereas the between cell variance is used to estimate the environmental variation. Years are assumed a random effect, and mixed model analysis of variance procedures are used. This approach assumes that each cell has the same sampling variance. Classical analysis of variance methodology assumes the variance within cells is constant across a variety of treatment effects. This assumption is often not true, i.e., the sampling variance of a binomial distribution is a function of the binomial probability. Thus, as the probability changes across cells, so does the variance. Another common violation of this assumption is caused by the variable of interest being distributed lognormally, so that the coefficient of variation is constant across cells and the cell variance is a function of the cell mean. Further, the empirical estimation of the variance from replicate measurements may not be the most efficient procedure. Therefore, the remainder of this section describes methods that can be viewed as extensions of the usual variance component analysis based on replicate measurements within cells. An estimator of the temporal variation is provided for the situation where the within cell variance is not estimated by the method of moments estimator based on replicate observations.

Assume that we can estimate the sampling variance for each year, given a value of $\hat{S}_i$ for the year. For example, an estimate of the sampling variation for a binomial is

$$\hat{\text{var}}(\hat{S}_i | S_i) = \frac{\hat{S}_i(1 - \hat{S}_i)}{n_i},$$

where n_i is the number of animals monitored to see if they survived. Then, can we estimate the variance term due to environmental variation, given that we have estimates of the sampling variance for each year?

If we assume all the sampling variances are equal, the estimate of the overall mean is still just the mean of the 10 estimates:

$$\bar{\hat{S}} = \frac{\sum_{i=1}^{10} \hat{S}_i}{10},$$

with the theoretical variance being

$$\text{var}(\bar{\hat{S}}) = \frac{\sigma^2 + E[\text{var}(\hat{S}|S)]}{10},$$

i.e., the total variance is the sum of the environmental variance plus the expected sampling variance. This total variance can be estimated as

$$\hat{\text{var}}(\bar{\hat{S}}) = \frac{\sum_{i=1}^{10} (\hat{S}_i - \bar{\hat{S}})^2}{10(10 - 1)}.$$

We can estimate the expected sampling variance as the mean of the sampling variances

$$\hat{E}(\text{var}(\hat{S}|S)] = \frac{\sum_{i=1}^{10} \hat{\text{var}}(\hat{S}_i | S_i)}{10},$$

so that the estimate of the environmental variance obtained by solving for σ^2

$$\hat{\sigma}^2 = \frac{\sum_{i=1}^{10} (\hat{S}_i - \bar{\hat{S}})^2}{(10 - 1)} - \frac{\sum_{i=1}^{10} \hat{\text{var}}(\hat{S}_i | S_i)}{10}.$$

However, sampling variances are usually not all equal, so we have to weight them to obtain an unbiased estimate of σ^2. The general theory says to use a weight, w_i

$$w_i = \frac{1}{\sigma^2 + \text{var}(\hat{S}_i | S_i)},$$

so that by replacing $\text{var}(\hat{S}_i|S_i)$ with its estimator $\hat{\text{var}}(\hat{S}_i|S_i)$, the estimator of the weighted mean is

$$\bar{S} = \frac{\sum_{i=1}^{10} w_i \hat{S}_i}{\sum_{i=1}^{10} w_i},$$

with theoretical variance (i.e., sum of the theoretical variances for each of the estimates)

$$\text{var}(\bar{S}) = \text{var}\left(\frac{\sum_{i=1}^{10} w_i \hat{S}_i}{\sum_{i=1}^{10} w_i} \right) = \frac{1}{\sum_{i=1}^{10} w_i},$$

and the empirical variance estimator

$$\widehat{\text{var}}(\bar{S}) = \frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{\left[\sum_{i=1}^{10} w_i \right] (10 - 1)}.$$

When the w_i are the true (but unknown) weights, we have

$$\frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{\left[\sum_{i=1}^{10} w_i \right] (10 - 1)} = \frac{1}{\sum_{i=1}^{10} w_i},$$

giving the following

$$\frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{(10 - 1)} = 1.$$

Hence, all we have to do is manipulate this equation with a value of σ^2 to obtain an estimator of σ^2.

To obtain a confidence interval on the estimator of σ^2, we can substitute the appropriate chi-square values in the above relationship. To find the upper confidence interval value, $\hat{\sigma}_U^2$, solve the equation

$$\frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{(10 - 1)} = \frac{\chi^2_{10 - 1, \alpha_L}}{10 - 1},$$

and for the lower confidence interval value, $\hat{\sigma}_L^2$, solve the equation

$$\frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \bar{S})^2}{(10 - 1)} = \frac{\chi^2_{10 - 1, \alpha_U}}{10 - 1}.$$

As an example, consider over-winter fawn survival data from mule deer fawns in Piceance Basin in northwest Colorado (Table 1). Survival rates are from the staggered entry Kaplan-Meier estimator (Pollock et al. 1989). The standard deviation of the 14 survival estimates is 0.22. When sampling errors are removed (mean SE = 0.07), the standard deviation of temporal variation is estimated as $\hat{\sigma} = 0.21$ (95% confidence interval 0.15 to 0.35). This confidence interval represents the uncertainty of the estimate of temporal variation, i.e., the sampling variation of the estimate of temporal variation. Note that the temporal variation estimate is only slightly smaller than the overall standard deviation, as the sampling variation of the estimates is relatively small. Similar results are shown for adult survival and recruitment (Table 2).

For mule deer in DAU D-7, which includes Piceance Basin, in northwestern Colorado, the relative variability of recruitment rates, and juvenile and female survival have been measured with the coefficient of variation, defined as the standard deviation of temporal variation ($\hat{\sigma}$) divided by the mean of the parameter estimates. From Table 2, we see there is much more variation of over-winter fawn survival than of either recruitment or adult survival. Even though the model is most

Table 2. Estimates of temporal variation in recruitment (fawns/100 adult females), over-winter fawn survival, and adult female survival in DAU D-7 in northwest Colorado.

Parameter	Mean	Temporal Variation	95% Confidence Interval	Coefficient of Variation
Recruitment	64.1	10.3	7.6 - 15.7	16%
Over-winter Fawn Survival	0.40	0.21	0.15 - 0.35	52%
Adult Female Survival	0.85	0.078	0 - 0.14	9%

sensitive to adult survival, this parameter varies little from year to year.

Thus, we conclude a precise estimate of S_F must be obtained. In contrast, the model is not terribly sensitive to S_J, but this parameter varies considerably from year to year and thus must be estimated each year. Recruitment (R) is not particularly variable, nor is the model particularly sensitive to R. Thus, we don't need to put nearly as much effort (dollars) into estimating recruitment as into estimating survival.

PROPOSED MONITORING SCHEME

Current CDOW monitoring places all effort into measuring recruitment and occasionally population density, and none into estimating juvenile or female survival rates. Thus, we conclude current monitoring efforts are wasteful because the variable being measured most often is likely the least important to measure annually. As a result, CDOW lacks the necessary information to properly monitor mule deer populations (R. M. Bartmann, Colo. Div. Wildl., unpubl. rep.). In this section, a monitoring scheme that shifts emphasis from monitoring recruitment to monitoring survival is developed.

An obvious reason why survival is not monitored is that it is more expensive to measure than recruitment. To rigorously estimate age-specific survival, the fate of a sample of marked animals must be determined. The most direct approach is via radiotracking, but mark-resight or banding analysis methods are also possible (van Hensbergen and White 1995). However, mark-resight or mark-recapture (e.g., Burnham et al. 1987, Lebreton et al. 1992) and banding methods (Brownie et al. 1985) are indirect in that additional parameters (resighting probability or band recovery probability) must be estimated. These parameters are nuisance parameters in the sense that they are not the real parameters of interest. However, precision of survival estimates is greatly affected by the precision with which nuisance parameters are estimated. As a result of the increased number of parameters, a larger sample size is required with indirect methods than with radiotracking methods. For example, White and Bartmann (1983) estimated survival of mule deer banded during winter. Even though 1,923 animals were banded over a 5-year period, annual survival estimates had coefficients of variation averaging over 32% for juvenile survival and over 19% for female survival. Had radiocollars been used, the average coefficients of variation would have been approximately 14% and 5% for juvenile and female annual survival rates, respectively.

However, an even bigger problem with using banding or mark-resight methods for monitoring annual survival rates is that estimates are not obtained for the current year, but only for intervals prior to the current year. This phenomenon occurs because the survival parameter and the recovery or resight parameter are confounded for the last survival interval of the data set. This confounding is removed only by adding another year of marking and recovery or resighting data. Thus, these methods are not useful for monitoring because estimates of survival will not be available until after the current year's harvest.

White et al. (1996) developed a method to estimate adult and juvenile over-winter survival based on age ratios of the population prior to and after winter, and the age ratio of animals dying during the winter. However, the assumptions of this method are unlikely to be met and the potential for biased estimates is considerable. They suggest radiotracking is generally more appropriate for estimating survival of juvenile and adult female cohorts unless special circumstances exist.

Therefore, we conclude radiotracking is the most economical method to estimate survival even though initial costs are high. Additional benefits of radiotracking are that cause of death can be determined so insights into the mechanisms affecting population dynamics may be gained.

Considering the standard error of the survival estimate as a function of the number of radioed animals (n) for various survival rates, approximately 50 animals must be marked to achieve survival estimates with reasonable precision (Fig. 1). The variance of a survival estimate is a function of both sample size and true survival. Variance is symmetrical about 0.5, with the maximum variance at 0.5 [see White and Garrott (1990) for a review of estimating survival with radioed animals]. This requirement is regardless of the size of the unit or the density or number of deer, because the fraction of the population sampled with radios is too small to affect finite population correction. As shown in Fig. 1, the magnitude of the survival rate does affect the standard error of the estimate.

If a sample of 50 radios are needed to estimate over-winter fawn survival adequately, approximate costs can be determined. Assuming \$350/fawn for capture (helicopter netgunning) and \$200/radio, \$27,500 will be needed to initiate monitoring. Additional costs are incurred for monitoring. Assuming \$160/hour for tracking via fixed-wing aircraft and 10 flights of 4-hours

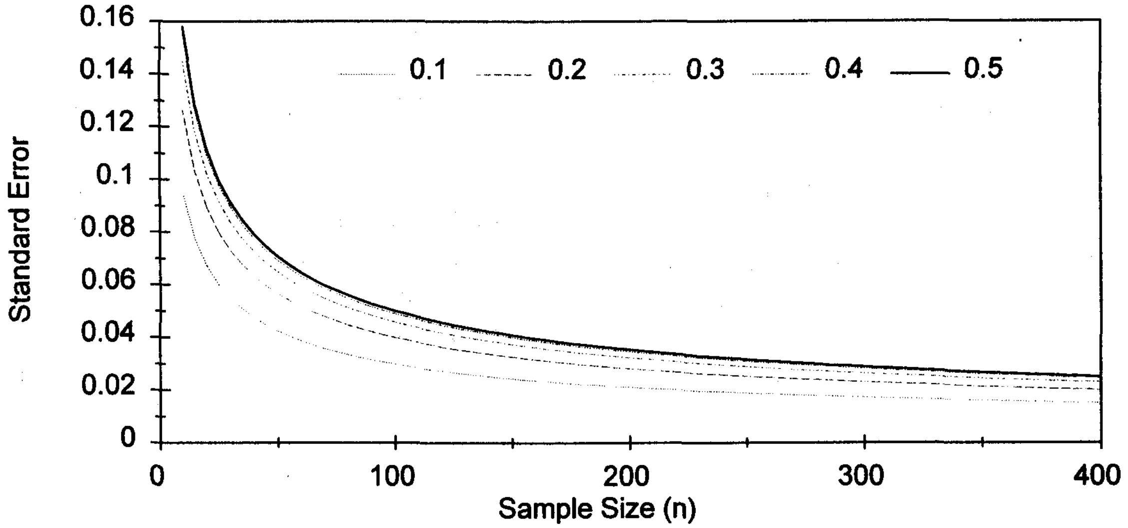

Figure 1. Standard error of the estimate of survival ($\hat{S}$) for a radiotracking study with n radiomarked animals. The 5 lines portray the SE for $\hat{S}$ = 0.5, 0.4, 0.3, 0.2, and 0.1 from highest to lowest.

duration each to determine live/dead status of each animal, an additional $6,400 is required. Thus, approximately $34,000 (exclusive of personnel costs) is required to monitor over-winter fawn survival for a single population or DAU.

Obviously, monitoring fawn survival in all 53 DAUs in Colorado is impractical. Instead, we suggest the CDOW annually monitor over-winter fawn survival in a subset of DAUs around the state, labeled core DAUs here. This core subset should represent larger mule deer populations and different habitats. Presumably, estimates from core DAUs would be representative of surrounding, or satellite, DAUs, thus providing estimates of survival in DAUs similar in nature to 1 of the core DAUs. An objective approach to deciding on which DAUs to include in the core subset would be to perform a cluster analysis of DAUs based on available information such as harvest rates, recruitment, habitat, and elevation.

However, using estimates from a core DAU to manage a satellite DAUs is risky and this approach should be evaluated. A random sample of satellite DAUs could be selected each year for monitoring along with the core units. Through time, a correlation between the core DAUs will be developed with each satellite DAU. The validity of inferences from core units to any satellite DAU will thus be able to be tested over time.

Instead of DAUs, more effective and efficient monitoring might be provided by GMUs. In the past, CDOW biologists have not consistently collected monitoring data for entire DAUs. Instead, some subset of GMUs within DAUs may be sampled. This practice leads to estimates of population parameters that are not comparable across years because different portions of a DAU are sampled in different years (R. M. Bartmann, Colo. Div. Wildl., unpubl. rep.). The reason for monitoring 1-2 GMUs within a DAU is that the GMUs generally represent distinct mule deer populations or population subsets which are unlike a DAU where a potpourri of populations may be represented. Thus, GMUs may provide more practical and useful data than DAUs.

So far, we have focused on over-winter fawn survival. This is because over-winter fawn survival was found highly variable from year to year and necessitated annual monitoring. Adult survival is also critical in that the model is most sensitive to this parameter. However, because of little annual variation in adult survival, this parameter can be estimated with data collected across a series of years. Thus, we propose that core units have an initial sample of adults included in the monitoring program. Female fawns could be fitted with expandable collars so that survivors of their first winter would contribute to estimating adult female survival rates during ensuing years. The annual effort needed to monitor adult survival can be considerably less than for fawns because data can be pooled across years. A sample of at least 20 adults in each core unit, as well as any satellite units, should be maintained.

Ideally, recruitment and density should probably be monitored annually in core units and in each randomly selected satellite unit. However, we have not determined the optimal allocation of effort between monitoring over-winter fawn survival, adult survival, recruitment, and population size, or the costs associated with each scenario. Based on the analysis presented in this paper, we assume that an adequate monitoring system requires annual survival information on fawns. Information on recruitment and density will also be required, but how often and what quality of information will be needed in the core units? How much effort (meaning dollars) should be diverted from monitoring survival to monitoring recruitment and/or density?

An objective approach to determine monitoring intensities and intervals for fawn and adult survival, recruitment, and density is to develop a simulation model of a mule deer population that includes random temporal variation. The model we have developed allows the user to sample the modeled population to mimic monitoring procedures. The optimal strategy for monitoring requires allocating effort to the monitoring of the various parameters as a function of the cost of collecting data and the temporal and sampling variability of each parameter. Estimates of cost for the various monitoring procedures are used to set the amount of data collected for each parameter monitored. From these data, harvest levels are set to maintain the population at a herd objective as is currently done for real populations. Because the true population is known, an evaluation of performance can be made. For a fixed cost, different allocations of monitoring effort can be compared relative to the mean squared error between the true population and the herd objective population size, i.e., minimize $\sum (N_{\text{True}} - N_{\text{Objective}})^2$ where the summation is over years. Specifically, we would want to find the relative amount of effort for sampling age ratios and population density across time versus the relative amount of effort for sampling survival with radiotracking. Can better management be achieved for the same cost by monitoring survival frequently and recruitment and population size intermittently than by monitoring all 3 at the same level annually?

Alternatively, instead of a optimizing results from a computer model, possibly analytical solutions can be developed to allocate effort optimally to monitoring the different population parameters. However, at this time, we do not understand how to derive such analytical relations.

Our model to develop an optimal sampling strategy assumes that December herd composition (and thus recruitment) and population density can be sampled simultaneously during the same helicopter survey. Randomly selected quadrats are counted and classified to provide the data. The biological parameters in the model are taken from Table 2, except that fawn survival was increased to 0.6 and recruitment increased to 0.691 so that the population has $\lambda > 1$, requiring harvest to maintain the population at a specified objective. An initial population of 10,000 animals was assumed, with the population objective of 5,300 adult females. Costs associated with monitoring are \$600/hr of helicopter time, with 1/4 hr required to count and classify a quadrat, and \$600/animal to capture and radio an animal to determine its fate. The hypothetical DAU sampled contains 665 quadrats. The budget for sampling is assumed to be \$30,000/yr. Radios on adult females were assumed to last 4 years, thus, most adult radios provide data beyond the year in which the radio was put on the animal. Fawn radios were assumed to drop off after 1 year.

Based on these inputs, the optimal sampling strategy to minimize the squared deviation of the true population size from the desired objective is to spend approximately 18 hours of helicopter time each year performing herd composition and population counts, and split the remaining \$19,200 evenly between collaring fawns and adult females to measure survival (Fig. 2). Note that changes in the input values will change these results somewhat. However, the optimal allocation of radios between fawns and adults generally is close to 50:50.

The final step to evaluate the proposed change in monitoring strategy is to demonstrate that adequate correlations exist in over-winter survival between the core units and the satellite units. These correlations must be estimated from field data, so this evaluation will take many years to complete. Without reasonably good correlations, the lack of monitoring in the satellite units would lead to inadequate information for management. Thus, the proposed monitoring procedure can be considered adaptive management (Walters 1986, Hilborn and Walters 1992) in that the validity of using core units to manage satellite units will be

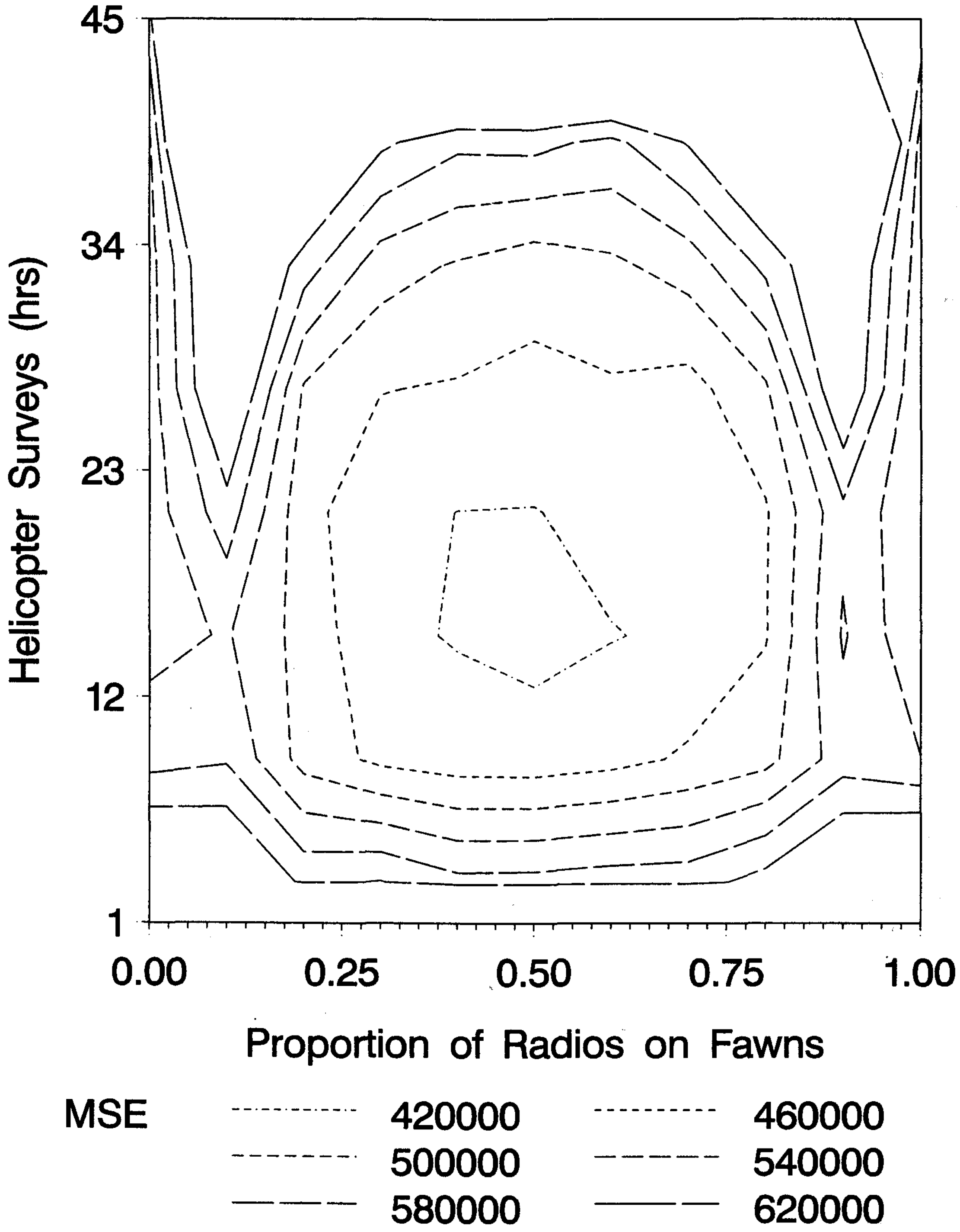

Figure 2. Contour plot of the mean squared difference of true population size and the desired population size as a function of allocation of effort between helicopter surveys, and fawn and adult female radiocollars to monitor survival.

evaluated through time. Likely, the set of core units may change as we gain more information on the similarity of parameters across units.

A final caveat must be offered. Monitoring mule deer populations does not provide cause and effect relationships that govern the population dynamics. Monitoring will suggest that the population is changing. However, to understand the mechanisms that are causing the change, designed experiments must be conducted. Thus, a sound monitoring program does not remove the need for a sound research program.

In summary, the following steps must be taken to implement the proposed monitoring scheme.

1. Select a set of core units for monitoring that are representative of the mule deer populations in Colorado.

2. Determine the optimal allocation of effort for monitoring of over-winter fawn survival, adult female survival, recruitment, and population size on core units. This allocation of effort will likely change as more data become available, and will vary depending on costs for the particular unit being monitored.

3. Monitor core units annually, always including over-winter fawn and adult female survival as part of this monitoring.

4. Monitor a randomly selected subset of satellite units annually so correlations between satellite units and core units can be developed to evaluate the effectiveness of the monitoring scheme.

5. Evaluate the effectiveness of the monitoring scheme annually to determine if a more efficient scheme can be developed.

CONCLUSION

Current CDOW monitoring procedures for mule deer populations are inadequate, because the parameters most important in projecting mule deer population status are not measured. A monitoring scheme that includes over-winter fawn survival and adult female survival is proposed. To evaluate this monitoring scheme, and to initiate it objectively, a simulation model of mule deer management has been developed. Results from this model suggest that annual helicopter surveys of herd composition and population density and over-winter fawn and adult female survival are required. Further, a key assumption of the proposed monitoring scheme is that correlations exist in basic population parameters between similar units. This assumption can only be tested with field data, not through simulation.

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ELK MANUSCRIPTS

Thinking Too Small - Managing Mule Deer And Elk Habitat Using Ecological Sites in The Great Basin

DONALD J. ARMENTROUT
Eagle Lake Resource Area, BLM, Susanville, CA 96130

GARY D. BRACKLEY
Natural Resources Conservation Service, Nevada State Office, Reno, NV

RAYMOND J. BOYD
National Applied Resource Sciences, BLM, Denver, CO 80225 (Retired)

Abstract: Wildlife biologists involved in management of mule deer and elk have applied ecological succession concepts to forest habitats for at least 50 years. Applying this same approach to rangeland habitats has several shortcomings. Because of their complex habitat needs, mule deer and elk habitat management requires a landscape approach rather than an individual unit approach. Mule deer and elk habitat is best described in terms of current vegetation cover, structure, diversity, and forage availability. Ecological sites are described using current vegetation biomass in relation to established potentials. Wildlife biologists must describe the desired habitat condition in terms important to wildlife (cover, structure, diversity) and relate these elements to landscape potential.

Key words: ecological site concepts, elk, Great Basin, habitat, mule deer.

INTRODUCTION

Leopold (1950), while discussing forest plant succession, referred to mule deer (*Odocoileus hemionus*) as an early successional species. Elk (*Cervus elephus*), were referred to as a late seral species. Wildlife biologists working with rangeland habitats began to apply the same terminology in defining elk and mule deer habitat. Approximately 20 years ago it became obvious that habitat analysis and management for elk and mule deer required a landscape approach (Black et al. 1976, Thomas et al. 1979, Skovlin et al. 1982, and Boyd et al. 1986). Because the major habitat managing agencies, the Bureau of Land Management (BLM) and the USDA Forest Service (FS), are using their versions of the Rangeland Inventory Methods developed by the Natural Resources Conservation Service (NRCS), the practice of referring to elk and mule deer habitat requirements in successional terms continues focusing discussions on individual habitat units rather than the whole of their habitat (USDA 1976, 1991, and USDI 1990).

Skovlin (1982) listed 4 basic habitat elements which must be considered for elk. These include landscape features, food supplies, cover characteristics, and water availability. Black et al. (1976) found that elk habitat across the landscape should consist of 20% hiding cover, 10% thermal cover, 10% either thermal or hiding cover. Strohmeyer and Peek (1996) found elk home-range and movement patterns in a sagebrush-cropland-rangeland mosaic were closely tied to aridity, juxtaposition of habitat components, and human disturbance. Human disturbance and habitat component patterns are both landscape features.

Leckenby et al. (1986) recommended a ratio of 40% cover to 60% forage areas for mule deer habitat in the Great Basin of southeastern Oregon. Thermal cover should be at least 0.8-2.0 ha in size, hiding cover can be as small as 2-10 ha, and fawn rearing cover can comprise approximately 160 ha. Optimum distribution of hiding cover consists of continuous, interconnecting zones and scattered patches with canyons and ravines supplementing and enhancing vegetation cover (Leckenby et al. 1986).

STUDY AREA AND METHODS

The floristic Great Basin, a subdivision of the Intermountain Region (Cronquist et al. 1972), is the study area with a primary focus on that portion of the Great Basin in southeastern Oregon and Nevada. Covering approximately 508,000 km^2 it is shaped like a shield that is approximately 770 km wide and 840 km tall (Fig. 1). Portions of 9 Major Land Resource Areas (MLRAs) are within the Great Basin. MLRAs are defined by major climatic, physiographic, geomorphic, and vegetation differences (USDA 1981). Range or ecological sites are described within their respective MLRA (USDA 1976).

Maser et al. (1986) consolidated 29 plant communities described by Dealy et al. (1986), into 16 plant communities, added 5 special habitats, and developed wildlife habitat relationship matrices for 341 vertebrate species. We used those relationships relevent to elk and mule deer (Table 1). Applied across a landscape these 23 plant communities and special habitats should be referred to as landscape elements. Landscape elements are defined by Foreman and Godron (1986) as *the basic, relatively homogeneous, ecological unit, whether of natural or human origin, on land at the scale of a landscape*. Because ecological sites can be several individual habitat units within landscape elements we refer to them as tessera; *the smallest homogeneous unit visible at the spatial scale of a landscape* (Foreman and Godron 1986).

To illustrate the importance of structural layers within vegetation landscape elements we developed Table 2 from the Maser et al. (1986) wildlife habitat relationship matrices. Sixteen vegetation landscape elements were consolidated into 5 overstory types and listed with 3 understory components. Tables 1 and 2 illustrate plant community and structure importance to feeding and reproductive activities. Importance of plant communities and their structure for hiding and thermal cover can added to the information presented by wildlife biologists for their areas of concern.

In order to illustrate the comparison between habitat values important to elk and mule deer (cover) versus the production information used in describing rangeland ecological succession we chose 1 representative site from each of 5 MLRAs (Fig. 1). These sites are found in mule deer or elk habitat, or habitat for both species within the Great Basin. Percent production and crown cover for key species was prepared for each seral stage of each site using ecological status data gathered during the 80+ years of our combined field experience. These approximations have been duplicated on-the-ground, and provide an average description of the seral stage within each ecological site (Tables 3-7).

RESULT

Seventeen of the 23 landscape elements listed on Table 1 are of primary importance for mule deer feeding activities, reproductive activities, or both. Nine of the 23 are of primary importance for elk. This indicates that diversity across the landscape is more important than any individual landscape element or tessera. Table 2 illustrates the importance of structure in limiting the usefulness of vegetation elements on the landscape. The combination of vegetation element diversity and structure increases the complexity of mule deer and elk habitat requirements. Add to this combination the limiting factor of habitat patch size (Leckenby et al. 1986), and the diversity and spatial complexity extends beyond the individual element or tessera.

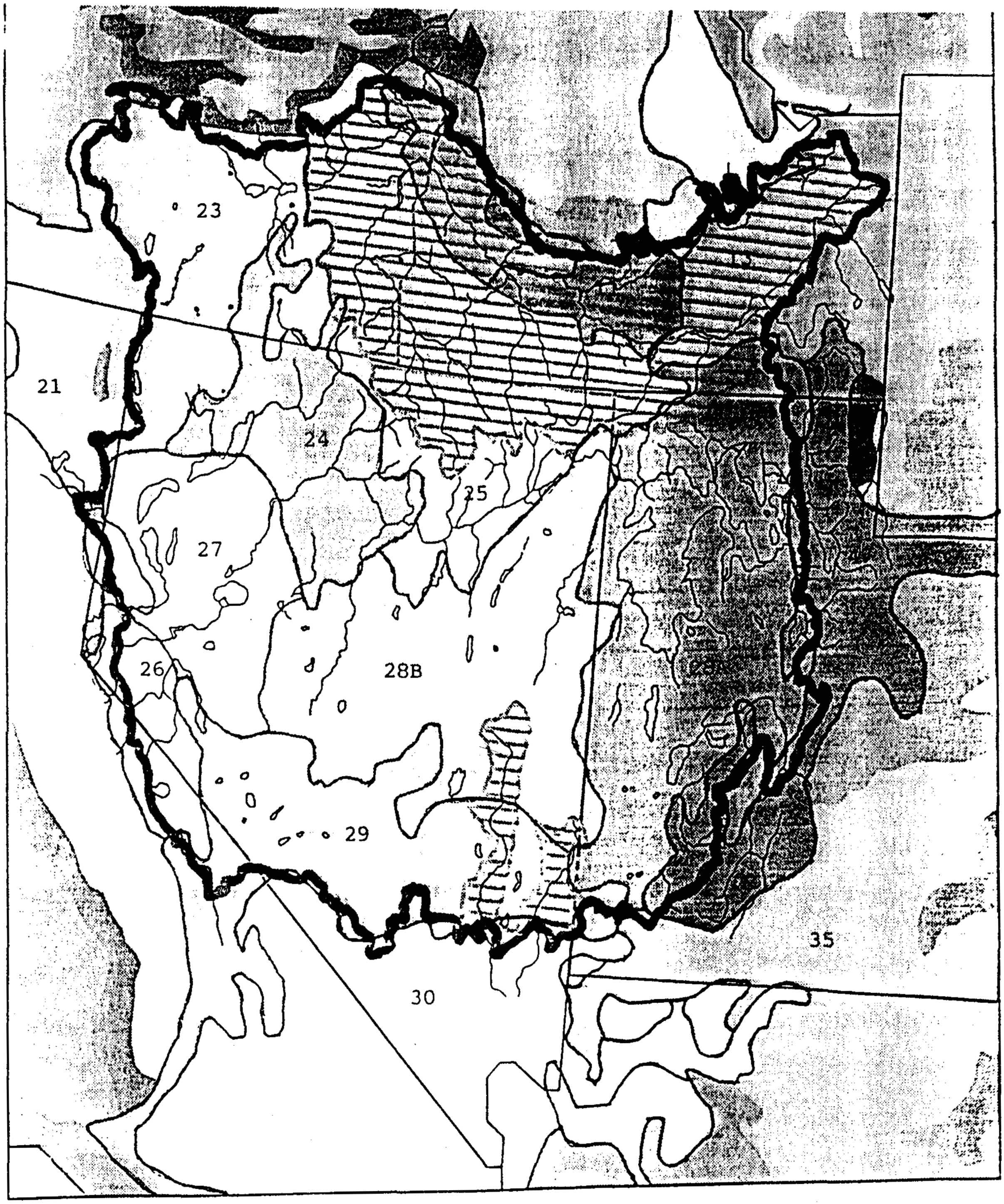

Figure 1. Floristic Great Basin boundary and included Major Land Resource Areas (MLRAs). Note: The horizontally hatched areas delineate portions of the hydrologic Great Basin within the floristic Great Basin.

Table 1. Landscape element importance for meeting mule deer and elk feeding and reproduction habitat needs in the Great Basin. (From Maser et al. 1986)

Plant communities	Mule Deer	Elk
Crested wheatgrass	f	
Subalpine bunchgrass	F	
Permanent wet meadow	F	
Seasonally wet meadow	F	
Shadscale saltbush/bunchgrass	F	
Low sagebrush/bunchgrass	F	
Black greasewood/grass	F	
Tall sagebrush/bunchgrass	F,R	
Squaw apple/bunchgrass	F	
Curleaf mountain mahogany/bunchgrass	F,R	F
Curleaf mountain mahogany/pinegrass	F,R	F
Curleaf mountain mahogany/shrub	F,R	F
Juniper/sagebrush/bunchgrass	F,R	F
Quaking aspen/grass	f	F,R
Quaking aspen/Mountain big sagebrush/bunchgrass	F	F,R
Riparian	F	F,R
SPECIAL HABITATS		
River, Creek, Stream	F	F,R
Lake, Reservoir, Ponds	F	f
Marsh, Bog, Swamp	F	
Standing, Slow-moving water	f	F,R
Geomorphic and/or Edaphic	f,r	

F = Primary, ≥ 40% use for feeding activity
f = Secondary, < 40% use for feeding activity
R = Primary, ≥ 40% use for reproductive activity
r = Secondary, < 40% use for reproductive activity

Table 2. Importance of vegetation structure (overstory-understory combinations) to feeding and reproductive activities of mule deer and elk in the Great Basin. (From Maser et al. 1986)

Overstory and understory combinations	Mule Deer	Elk
Grass - Forb		
- bareground		
- annuals	F	
- bunchgrass	F	
Low shrub		
- bareground		
- annuals	F	f
- bunchgrass	r	f
Tall shrub		
- bareground		
- annuals	F	f
- bunchgrass	R	f
Tree		
- bareground		
- annuals	F	F
- bunchgrass	F	F
Tree/shrub		
- bareground		
- annuals	F	R
- bunchgrass	R	R

F = Primary, ≥ 40% use for feeding activity
f = Secondary, < 40% use for feeding activity
R = Primary, ≥ 40% use for reproductive activity
r = Secondary, < 40% use for reproductive activity

Table 3. Ecological Site: Loamy 14-15" Precipitation Zone MLRA 23

Ecological Condition Classes by Crown Cover and Production

	PNC		Late Seral		Mid Seral		Early Seral	
Plant Species	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)
mtn. big sagebrush	10	200	17	350	25	450	30	650
antelope bitterbrush	8	100	12	200	10	150	-	-
Utah serviceberry	2	50	2	25	1	T	-	-
mtn. snowberry	1	25	3	50	7	100	11	150
Idaho fescue	7	350	4	150	1	25	-	-
bluebunch wheatgrass	7	400	4	175	1	25	-	-
bluegrass	1	25	3	50	3	50	2	25
cheatgrass	T	T	T	50	3	50	5	100
perennial forbs	4	100	5	100	4	75	1	25
TOTAL PRODUCTION		1,250		1,150		950		950

[1] Total crown (foliar) cover, vertical projection.
[2] Air-dry weight.

Table 4. Ecological Site: Loamy Slope 12-14" Precipitation Zone MLRA 24

Ecological Condition Classes by Crown Cover and Production

	PNC		Late Seral		Mid Seral		Early Seral	
Plant Species	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)
mtn. big sagebrush	5	100	18	325	23	350	T	T
rabbitbrush	T	T	1	25	7	125	17	350
Utah serviceberry	3	75	3	75	T	T	-	-
mtn. snowberry	3	50	3	50	4	75	3	50
Idaho fescue	6	300	4	175	1	25	-	-
bluebunch wheatgrass	12	450	5	200	T	15	-	-
bluegrass	2	25	3	50	5	75	3	50
cheatgrass	T	25	1	50	2	25	17	450
perennial forbs	8	125	5	75	5	125	3	50
TOTAL PRODUCTION		1,150		1,025		815		950

[1] Total crown (foliar) cover, vertical projection.
[2] Air-dry weight.

Table 5. Ecological Site: Loamy Slope 12-16" Precipitation Zone MLRA 25

Ecological Condition Classes by Crown Cover and Production

	PNC		Late Seral		Mid Seral		Early Seral	
Plant Species	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)
mtn. big sagebrush	5	75	16	200	25	400	30	500
antelope bitterbrush	5	75	8	135	15	175	5	75
Utah serviceberry	3	50	6	100	6	80	T	T
mtn. snowberry	1	20	5	80	7	100	15	250
Idaho fescue	10	280	8	100	1	25	-	-
bluebunch wheatgrass	9	505	5	175	1	25	-	-
bluegrass	1	20	3	75	5	125	T	T
cheatgrass	-	-	T	T	T	T	T	T
perennial forbs	5	125	7	170	2	50	2	50
TOTAL PRODUCTION		1,150		1,035		980		875

[1] Total crown (foliar) cover, vertical projection.

[2] Air-dry weight.

Table 6. Ecological Site: Loamy 12-14" Precipitation Zone MLRA 26

Ecological Condition Classes by Crown Cover and Production

	PNC		Late Seral		Mid Seral		Early Seral	
Plant Species	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)
mtn. big sagebrush	15	275	17	300	23	375	12	250
antelope bitterbrush	20	175	20	175	12	125	10	100
green ephedra	1	15	1	15	2	25	3	40
mtn. snowberry	1	25	3	50	3	50	5	75
slenderbush eriogonum	1	15	4	75	7	150	12	250
needlegrass	10	425	6	225	1	50	-	-
bluegrass	3	75	3	75	1	25	T	T
cheatgrass	-	-	-	-	1	25	2	45
perennial forbs	5	135	6	175	6	150	3	75
TOTAL PRODUCTION		1,140		1,090		975		835

[1] Total crown (foliar) cover, vertical projection.

[2] Air-dry weight.

Table 7. Ecological Site: Granitic Slope 12-14" Precipitation Zone MLRA 27

Ecological Condition Classes by Crown Cover and Production

	PNC		Late Seral		Mid Seral		Early Seral	
Plant Species	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)	Cover[1] (%)	Prod.[2] (#/ac)
mtn. big sagebrush	20	300	20	300	10	175	3	50
Utah juniper	T	T	8	75	15	150	40	250
green ephedra	1	15	3	50	2	25	1	15
mtn. snowberry	2	50	2	50	4	100	1	25
Anderson peachbrush	T	-	2	75	2	75	1	35
needlegrass	8	400	5	250	2	50	-	-
bluegrass	5	75	5	75	2	50	T	T
cheatgrass	-	-	T	T	2	50	1	25
perennial forbs	5	100	6	125	3	50	1	25
TOTAL PRODUCTION		940		1,000		700		425

[1] Total crown (foliar) cover, vertical projection.
[2] Air-dry weight.

There is no direct correlation between crown cover and production (Table 3-7). A simple statement of successional status for an individual site does not provide adequate wildlife habitat information to determine the value of the tessera for any wildlife species. In order to use an ecological site's seral stage as an indicator of habitat condition, the wildlife biologist must determine at what sere the ecological site provides the cover and structure needed. At present, this requires additional vegetation analysis by the wildlife biologist beyond that performed during an ecological site inventory. Species diversity applicable to forage availability analysis can be taken directly from ecological site inventory data. We note that the NRCS is presently revising their standards for ecological site inventories to include information such as cover and structure.

DISCUSSION

Managing elk and mule deer habitat requires an ability to predict landscape potential. This ability is built through understanding the sum potential of landscape parts (elements and tessera) present. To simply state we want early, late, or mid seral status has been shown to be inadequate. Once we can equate habitat requirements to ecological site succession we are better prepared to address the entire landscape. We must also understand the successional forces at work.

Current ecological status ratings are based on the concept of well-defined, predictable, and reversible changes along a linear successional gradient that holds for all or the majority of rangelands. This linear theory implies that a site that has regressed can recover if the process is reversed (Weaver and Clements 1938, Dyksterhuis 1949). Most recently (Archer 1989, Friedel 1991, Laycock 1991, Noss and Cooperrider 1994, and Committee on Rangeland Classification 1994) have introduced the alternative, state and transition model. Rather than succession being a continuum, the state and transition model indicates there is a point where existing succession may breakdown. This point is a threshold which is defined as a boundary in space and time between 2 ecological states. Thresholds differ from other changes from 1 state to another because they are not reversible on a practical time scale without human intervention (Committee on Rangeland Classification 1994). We are, therefore, required to have the capability to identify thresholds and determine actions necessary to move past them.

CONCLUSION

Mule deer and elk habitat requires management at a landscape scale using the patterns, elements, and functions of landscapes as the basis for habitat decision making. Habitat requirements must be described and analyzed using factors important for species survival such as current structure, cover, diversity, and production. Ecological sites (tessera) on the landscape which have similar potential should be combined into broader landscape elements to better describe landscape potential.

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Diet Selection and Importance of Management Indicator Species to Elk and Domestic Sheep in a North-central Utah Aspen Ecosystem

JEFFREY L. BECK [1]
Utah Division of Wildlife Resources, Price, UT 84501

JERRAN T. FLINDERS
Department of Botany and Range Science, Brigham Young University, Provo, UT 84602

DEANNA R. NELSON
U. S. Forest Service, Uinta National Forest, Provo, UT 84601

CRAIG L. CLYDE
Utah Division of Wildlife Resources, Springville, UT 84663

H. DUANE SMITH
Department of Zoology, Brigham Young University, Provo UT 84602

PERRY J. HARDIN
Department of Geography, Brigham Young University, Provo, UT 84602

Abstract: Concerns over forage competition and range degradation caused by an expanding elk (*Cervus elaphus*) herd on historical domestic sheep range in north-central Utah were the impetus for this cooperative study. Dietary relationships of elk and domestic sheep determined from summer 1994 feeding site analyzes are examined. The influence of 8 plant species identified as indicators of rangeland health on elk and domestic sheep diet selection are discussed. It is recommended that these plants be monitored to assess the health of this aspen (*Populus tremuloides*) ecosystem. A similar protocol is recommended to manage other forests and rangelands used jointly by elk and livestock.

Key words: competition, diet, domestic sheep, elk, rangeland health, Utah.

INTRODUCTION

Willow Creek is situated in a semi-roadless aspen park ecosystem in north-central Utah. Domestic sheep have been grazing the Willow Creek drainage for about 100 years. Elk were reintroduced to the area and have increased dramatically in the past 2 decades (Beck et al. 1996*a*).

Sheep operators permitted to graze in Willow Creek and surrounding areas expressed concerns to Forest Service and Utah Division of Wildlife Resources personnel regarding increases in this elk population. These concerns were centered around (1) possible forage competition, and (2) watershed impacts at certain sites within the drainage. A cooperative study was thus conducted from 1993-1994 to determine elk and domestic sheep resource use and overlap in the Willow Creek Demonstration Area, Uinta National Forest.

Data sets from this study include: dietary overlap, preference, and similarity; animal unit equivalents; forage use ratios; feeding site selection; utilization of herbaceous and browse forage; habitat use; elk population estimates; elk herd composition; elk migration patterns; influence of biting flies on elk

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[1] Present address: Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844-1136

movements; and the importance of natural mineral licks and human-placed salt to elk and sheep (Beck 1996, Beck et al. 1996*a*, *b*).

This paper will discuss several of the most important findings in regards to dietary overlap and interactions of elk and domestic sheep for forage selection. We will focus on the importance of 8 plants selected as management indicator species (MIS) for the Willow Creek drainage. These plants are indicators of ecosystem health and are important elk and sheep food sources in this system.

STUDY AREA

The Willow Creek study area lies southeast of Strawberry Valley in north-central Utah and consists of 100.1 km^2 of lands administered by the Heber Ranger District, Uinta National Forest. Willow Creek and tributaries serve as the drainage for this watershed. Willow Creek flows northeast for about 17.7 km from its point of origin on Willow Creek Ridge to its confluence with the Strawberry River. Elevation ranges from approximately 2,400 m to 3,000 m (Beck et al. 1996*a*). Major vegetation types include: aspen (38.2%), mixed shrub/perennial grass (28.1%), mountain shrub (11.9%), mountain fir (7.7%), and aspen-conifer (6.6%). Snow water equivalents as of April 1 (indicating yearly snowpack) were 51.3 cm in 1993 (U. S. Soil Conservation Service 1993) and 21.6 cm in 1994 (U. S. Natural Resources Conservation Service 1994).

The entire Willow Creek study area is used as summer and early fall range for domestic sheep. During the study, sheep grazing was administered on 8 allotments throughout the drainage by the Uinta National Forest.

METHODS

Joint elk and sheep herbivory were compared in summer and fall seasons. Information on fall elk herbivory in Willow Creek was limited as elk began a migration to winter ranges by September 1 (Beck et al. 1996*a*). Dietary component data from 1993 consisted of only herbaceous species. A method was developed in 1994 to ascertain the relative importance of woody species in elk and domestic sheep diets.

Herds of elk and bands of domestic sheep were randomly located in sheep grazing allotments throughout the study area. A random digits table was used to select 1 individual elk or sheep from each herd for focal animal sampling (Altmann 1974). Feeding sites were designated when focal animals were observed ingesting woody or herbaceous plant material. Feeding sites were sampled no later than 1 week after initial observation of the foraging focal animal (Beck et al. 1996*a*).

The percent of available herbaceous biomass consumed by elk or sheep was determined visually and the remaining plant biomass by species was clipped and weighed. A similar method was used to determine the amount of available woody biomass by species eaten by elk and sheep. Plant samples were then dried in an oven and weighed. Dry specimens of plants that contributed to at least 90% of elk and domestic sheep diets were ground. These samples were nutritionally analyzed by the Brigham Young University Soil and Plant Analyses Laboratory. Dried plant weights were used to compute statistics including standing herbaceous crop, percent dietary composition, and biomass utilization by plant species and feeding site (Beck et al. 1996*a*). Plant nomenclature follows that of Welsh et al. (1993).

Similarity of the proportion of vegetational biomass in elk and sheep diets (seasonal relative dry weight consumed at feeding sites) and the proportion of seasonal relative dry standing biomass at elk and sheep feeding sites were calculated using Kulczynski's mathematical expression of similarity (Oosting 1956, Flinders and Hansen 1972, Beck et al. 1996*a*).

Ivlev's electivity index (Ivlev 1961) was used to compute values indicating elk and/or sheep forage preference or avoidance for 142 plant species. Forage electivity values (dependent variables) for those species constituting at least 90% of elk and sheep diets in summer 1994 were regressed on nutritional fractions (independent variables) of these forages.

Multiple regression analyses were performed to predict patterns of feeding site selection by elk and domestic sheep. Environmental variables (independent variables) measured at feeding sites were regressed with percent consumption of the standing crop (dependent variable) (Beck et al. 1996*a*).

The best estimates of elk and sheep dietary overlap are from summer 1994 when all plant fractions (forbs, graminoids, and woody species) were considered in dietary calculations. Data presented in this paper will focus on results from summer 1994.

RESULTS AND DISCUSSION

Dietary overlap based on the average similarity of dietary fractions was 36.4 ± 32.8% in summer 1994. A Spearman's rank correlation comparing these dietary fractions revealed these data were positively correlated ($r_s = 0.63$, $P = 0.000$) (Beck et al. 1996*b*). This correlation showed that dietary incorporation of similar forage species by elk and sheep increased at the same time.

Animal unit equivalents (AUEs) that included dietary overlap (Flinders 1988) were calculated for adult elk and ewe sheep in the study area. These calculations resulted in an AUE of 1:6.6 in summer 1994, or it took 6.6 average-sized ewes in Willow Creek to consume the same amount of biomass from those plants eaten in common as 1 average-sized adult elk (Beck et al. 1996*a*).

It was found that summer 1994 elk preference was best related to Ca to P ratios (Ca:P), percent crude protein (CP), percent nondigestible carbohydrates (ADF), percent water (H_2O), and percent soluble carbohydrates (TNC) ($R^2 = 0.87$, df = 10, $P = 0.030$). Sheep forage preference in summer 1994 was implicated with percent TNC and percent Mg in forages ($R^2 = 0.25$, df = 20, $P = 0.073$) (Beck et al. 1996a).

Elk and sheep clearly demonstrated differences in forage preference. In 1994, the major portion (≥90%) of diet biomass consisted of fewer species for elk (spring = 11, summer = 11, and fall = 7) than sheep (summer = 21, and fall = 12) (Beck et al 1996*b*). Mineral supplements (primarily Na) placed for sheep in the drainage were used by elk and sheep. Elk, which were free-ranging and wild used natural mineral licks in the drainage. Sheep, which were herded, did not normally access these mineral sources. Sheep obtained mineral requirements from forage and granulated salt supplements consisting largely of Na (93-98%) (Beck et al. 1996*a*). Water and Na were abundant in the area and were never selected as variables implicated with forage preference in summer 1994 (Beck et al. 1996*a*).

Animals grazing in spring need Mg as optimal forage conditions (high succulence) create a scenario wherein animals experience low blood serum Mg levels (Robbins 1993). This condition is often referred to as grass or magnesium tetany. In summer 1994, Mg was selected only by sheep as an independent variable predicting forage preference. Magnesium concentrations were the third highest in sheep salt supplements (0.06-0.18%) and normally the third highest mineral fraction in 9 natural mineral licks analyzed in the study area. Magnesium concentrations in forb and browse species were typically higher (>0.18%) than Mg levels in sheep salt supplements, while Mg levels in graminoids were typically equivalent (0.06-0.18%) to Mg levels in sheep salt supplements (Beck et al. 1996*a*). One reason that sheep diets consisted of more species than elk may have been due to a lack of Mg in their diets. Sheep selected those plants (forbs and browse) containing the highest Mg concentrations.

Feeding site selection was best related to forage conditions as well. Elk feeding site selection in summer and fall (1993 and 1994 combined) was best related to topographic (aspect, elevation, distance to ridgetop, and slope) and vegetative conditions (grams of herbaceous biomass, percent vegetative ground cover, and season and year [differences in vegetative production between seasons and 1993 and 1994]) ($R^2 = 0.59$, df = 29, $P = 0.007$). Domestic sheep feeding site selection in summer and fall (1993 and 1994 combined) was attributed to sheepherder movement patterns (aspect, elevation, grams of herbaceous biomass, distance to sheepherder, and distance to salt placements) ($R^2 = 0.51$, df = 18, $P = 0.068$) (Beck et al. 1996*a*). Sheep selected plants presented to them through herding practices while elk moved to optimal areas to select preferred plants. It can be demonstrated in the Willow Creek study area that elk used natural as well as human-placed sources of minerals and subsisted on fewer plant species than sheep to obtain adequate nutrition.

Overall use of herbaceous biomass by elk and domestic sheep in the study area was light (combined mean use in 1993 = 17.8%; 1994 = 13.8%). However, elk and sheep concentrated use on several key species. For example, combined foraging on red elderberry (*Sambucus racemosa*), exceeded Forest Service allowable use standards (40 [unsatisfactory condition range] to 60% [satisfactory condition range]) (U.S. Forest Service 1993) on 4 feeding sites analyzed in fall 1994 (Beck et al. 1996*b*).

Eight plant species including red elderberry and aspen were designated as indicators of rangeland health in this ecosystem (Table 1). These plant species were defined as those comprising ≥5% of sheep and elk diets during at least 1 season of 1 year (Beck et al. 1996*a*:64). Overall, the 8 MIS species comprised 61.8% of the standing crop at elk feeding sites and 55.1% of the standing crop at sheep feeding sites in summer 1994. These species also contributed to 72.1% of elk and 49.0% of domestic sheep diets in summer 1994. In summer 1994, mean botanical composition at elk and sheep feeding sites was 42.1 ± 30.2% similar and elk and sheep diets were 51.3 ± 37.2% similar (Table 1).

Correlations on the relative proportion of each botanical species in elk and sheep diets with the relative proportion of those species in elk and sheep feeding sites revealed that elk and sheep were consuming forage in relative proportion to its availability (elk [$r_s = 0.76$, $P = 0.000$]; sheep [$r_s = 0.89$, $P = 0.000$]) (Table 2). This differs with the findings of Alexander et al. (1983) who studied domestic sheep summer food habits in southeastern Montana. They reported negative Spearman's rank correlation coefficients suggesting that sheep were seeking plants (certain grasses and sedges) that were not abundant on the graminoid-dominated (96%) rangeland they studied. The diversity in plant communities (31) and food options (188 plants) available to elk and sheep in our study (Beck et al. 1996*a*) allowed herbivores more diet opportunities than sheep in the Alexander et al. (1983) study.

The 8 designated MIS species formed the majority of elk and sheep feeding choices and diets in Willow Creek (Table 1). Plants such as aspen, red elderberry, and mountain snowberry (*Symphoricarpos oreophilus*) were functional components of most plant communities in the study area. Any reduction in regeneration of these species leads to impairment of the health and productivity of this aspen ecosystem. Although combined forage use was light, key plants were consumed at elevated levels. Consequently, current ungulate populations are probably inducing disclimax changes in Willow Creek plant communities.

Aspen plant community types comprised 44.8% of study area vegetation and provided

Table 1. Percent of management indicator species in the botanical composition of elk and domestic sheep feeding sites and in diets of elk and domestic sheep, Willow Creek study area, summer 1994. Kulczynski's similarity (sim) index provided for comparison.

		% Feeding site			% Diet		
Species	Scientific name	Elk	Sheep	%	Elk	Sheep	% Sim
Forbs							
Tall bluebell	*Mertensia arizonica*	6.2	1.7	43.0	20.3	6.37	47.6
Grasses							
Mountain brome	*Bromus carinatus*	10.9	2.5	37.3	8.88	2.97	50.1
Slender wheatgrass	*Elymus trachycaulus*	7.1	2.9	58.0	2.34	2.60	94.7
Smooth brome	*Bromus inermis*	0.0	5.5	0.0	0.00	21.92	0.0
Browse (shrubs and trees)							
Aspen	*Populus tremuloides*	7.8	10.3	86.2	10.1	3.04	46.0
Mountain snowberry	*Symphoricarpos oreophilus*	9.5	32.0	45.8	13.3	11.33	91.7
Red elderberry	*Sambucus racemosa*	0.1	0.2	66.7	0.51	0.76	80.3
Wolf's willow	*Salix wolfii*	20.2	0.0	0.0	16.4	0.00	0.0
Total Composition %		61.8	55.1	94.3	72.1	48.99	80.9
$\bar{x}$		7.7	6.9	42.1	9.01	6.12	51.3
SD		6.4	10.7	30.2	7.58	7.32	37.2

Table 2. Comparison of the importance of management indicator species in overall use of available forage for food by elk and domestic sheep. These relationships expressed through Kulczynski's index of similarity and Spearman's rank correlations (r_s). Calculations performed using percent diet composition with percent botanical composition of plant species sampled at elk and domestic sheep feeding sites, Willow Creek study area, summer 1994.

		% Similarity		Spearman's	
Elk	*n*	$\bar{x}$	SD	r_s	P^b
MIS[a] only	7	68.8	23.8	0.36	0.382
No MIS	42	31.5	32.1	0.65	0.000
Total	49	36.8	33.6	0.76	0.000
Sheep					
MIS[a] only	7	58.7	23.8	0.61	0.137
No MIS	71	49.4	34.7	0.87	0.000
Total	78	50.2	33.8	0.89	0.000

[a] MIS = management indicator species. Those forage species that comprised ≥5% of sheep and elk diets during at least 1 season of 1 year.

[b] Significant correlations ($P < 0.05$).

up to 1,525 kg/ha of seasonal herbaceous forage. In summer 1994, elk consumed 13.3% and sheep 11.8% of available aspen biomass and elk and sheep browsed on 59.8% and 58.9%, respectively, of aspen stems present in feeding sites. Most aspen stands in Willow Creek are even-age and mature, or overmature (Beck et al 1996*a*). These conditions render existing aspen stands vulnerable to future declines in abundance and productivity. Aspen regeneration is of utmost importance in maintaining functional plant communities that will provide food and cover to wildlife and livestock in the future.

MANAGEMENT IMPLICATIONS

Future range trend studies conducted by the Forest Service in Willow Creek will assist in acquiring knowledge on component parts of disclimaxes as well as monitoring the 8 designated MIS species. Other forests and rangelands used to provide habitat for elk and livestock could likewise be managed by identifying plant species of special concern. Resource managers could then monitor such species and direct projects intended to regenerate and/or protect identified indicator species. For example, Wydeven and Dahlgren (1983) recommended monitoring 4 key elk forage species in their study of elk food habits in Wind Cave National Park, South Dakota. They reported that monitoring the condition and abundance of these plants was needed to determine elk stocking levels and forage use in consideration of other sympatric ungulates.

Eight management recommendations were set forth in detail in Beck et al. (1996*a*). All recommendations will assist in promoting rangeland health and productivity of the 8 indicator species described in this paper. Recommendations are: (1) road closures, (2) aspen regeneration projects, (3) riparian habitat restoration, (4) weed control and maintenance of native plant communities, (5) improved placement of sheep salt supplements, (6) maintenance and use of stock water developments, (7) protection of natural mineral licks, and (8) elk hunting.

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Non-Narcotic Capture of Cow Elk

ARTHUR F. FULLER
Arizona Game and Fish Department, 5325 N. Stockton Hill Road, Kingman, AZ 86401

NEIL LAWSON
Arizona Game and Fish Department, 2221 W. Greenway Road, Phoenix, AZ 85023

Abstract: Non-narcotic immobilization of 6 adult cow elk was accomplished for the purpose of radiomarking. Target animals were called or stalked to within 15 m using camouflage clothes and a mouth call. A Pneu-Dart model 178B projector (Sheradin Blue Streak Pump Model) was used to propel 3 cc and 4 cc "P" Pneu-Darts with 3.2-cm wire-barbed needles. For undisturbed animals, 800 mg of powdered Telazol® dissolved in 320 mg liquid xylazine provided satisfactory immobilization. All animals were reversed with 8 mg (4cc) of yohimbine (2mg/ml) by either intramuscular (IM) injection or slow intravenous (IV) injection, 30-60 minutes after initial immobilization. All animals were located monthly. Six months after capture, no mortalities were detected.

Key words: Arizona, capture, *Cervus elaphus*, elk, immobilization, non-narcotic, Telazol®, xylazine, yohimbine.

INTRODUCTION

In 1927, a train loaded with elk (*Cervus elaphus*) from Yellowstone National Park arrived in north-central Arizona at the town of Williams. The train was met at the station by cattlemen with guns, so it continued west to Kingman where the elk were unloaded and herded to the Hualapai Mountains 11 km east of town. The Hualapai Mountains rise to 2,440 m above sea level and are surrounded by Mohave Desert Scrub at 760 m elevation. A small population of less than 100 elk has survived in this mountain range since their introduction. Currently a few archers and muzzleloader hunters hunt the elk with ≤5 hunting permits issued each year.

In the last 5 years, people in the Pine Lake subdivision have begun feeding the elk. Since this housing development is within a county park, the elk are protected. As the elk became conditioned to the presence of people, problems, such as illegal take and incidents of elk entangled in fences, have spawned increasing complaints to the Arizona Game and Fish Department (AGFD). The AGFD responded by holding educational meetings with the local homeowners association, publishing articles in the local newspaper designed to reduce the feeding of elk and deer, and submitting an application to the Rocky Mountain Elk Foundation to fund an elk study.

Funding was obtained in July 1996 to radiomark and monitor 8 elk in the Hualapai Mountains. This 2-year study will determine elk seasonal movements, habitat selection, reproductive success, and mortality rates. The objective of this paper is to summarize elk captures that were made using the non-narcotic drug Telezol®.

METHODS

We captured elk with clover traps and by remote chemical injection from the ground. One yearling female was captured in a Clover trap baited with hay and apple pomace. Two adult elk caught in the traps escaped by bending the trap frames or ripping through old-age netting. Darting was used as a secondary capture method because of potential risks to the public while capturing elk near, or in, a county park. To offset this concern, we selected Telazol® to immobilize elk because this non-narcotic substance is less dangerous than etorphine (M99) and carfentanil, which can be lethal to humans in very small amounts.

Telazol® is a non-narcotic, non-barbiturate injectable anesthetic agent composed of equal parts of tiletamine hydrochloride and zolazepam hydrochloride. Telazol® is sold as a lyphilized powder in 5-ml sterile vials containing 500 mg of active drug. Telazol® is rapid acting and produces a state of dissociative anesthesia resulting from interruption of sensory inputs to the brain.

We selected a drug cocktail of powdered Telezol® dissolved in liquid xylazine based on recommendations by Dr. Hunter, an Idaho Fish and Game veterinarian with experience capturing elk using this drug combination (Idaho Fish and Game Newsletter 1996). He recommended a dosage for a cow elk of 1,000 mg of powdered Telazol® (2 500-mg vials) dissolved in 400 mg liquid xylazine (4 ml at 100 mg/ml). When mixed, the total volume is about 4.8 ml. We selected a reduced dose for 3 reasons: we believed female elk in the Hualapai Mountains to be smaller in body size than comparable Idaho animals, we planned to dart elk with minimal chase time or disturbance, and we wanted to utilize the lightest possible dart. A 4-cc Pneu-Dart filled with the above mixture contained approximately 800 mg Telazol® and 320 mg xylazine. This Telazol®/xylazine combination was estimated to be 25-30% less drug than the 4.6 mg/kg recommended for elk capture using Telazol® alone (Schobert 1987).

A Department employee, experienced with calling elk using a mouth call, was able to approach and call cow elk to his position successfully. Elk were darted using a compressed-air rifle, Pneu-Dart Model 178B projector. Average range was 17 m. The gun was sighted in using 8 pumps of the gun-charging lever. When darted in this manner, elk were often not alarmed, sometimes moving less than 100 m before immobilization.

RESULTS AND DISCUSSION

Cow elk number 1 was darted in the left shoulder at 1400 hours on December 9, 1996. The animal showed some response within 5 minutes and was immobilized after 20 minutes (Table 1). After the radiocollar and eartag were installed, the elk was monitored for recovery. After 1.5 hours from initial darting, the animal's respirations were getting shallow and the pulse rate continued to decline. Because the elk never observed the shooter, we believed very little adrenaline was released into the elk's blood before immobilization. We felt without reversal the animal might die. Therefore, 4 ml yohimbine (2 mg/ml) were hand injected IM in the right shoulder. The cow began to recover within 10 minutes. The shooter remained with the recovering animal keeping it upright on its brisket. When the animal recovered enough to see the shooter, it stood up prematurely, lost balance, and tumbled 30 m down a steep hillside. After an additional 10 minutes of recovery, the elk was able to walk away, sustaining minor cuts and scrapes.

Although this elk's response suggested the dosage may be excessive for radiocollar installation, we decided to continue using the same dosage for capturing animal #2. This adult cow was darted in the left shoulder on December 12. It had some response within 5 minutes and was immobilized after 12 minutes. After the ear tag and radiocollar were installed, 4 ccs of yohimbine were administered IM and the elk recovered and walked away after 40 minutes. The shooter remained hidden this time throughout the recovery period because he had earlier propped the elk up on it's brisket with the aid of terrain features.

We reduced the dosage for animal #3 to 3 ml (600 mg Telazol® and 240 mg xylazine). When darted, the elk laid down in 25 minutes, but when approached was able to stand and walk away. The animal was darted again with another 3 cc dart 50 minutes after initial injection (Table 1). Response to the second injection occurred in 5 minutes and immobilization in 10 minutes. Elk #3 was injected IM with yohimbine and recovered in 30 minutes. The 3-ml dose was apparently insufficient for complete immobilization.

Animals 4, 5, and 6 were darted using the original drug dosage. Response time was 5-10 minutes with immobilization in 10-15 minutes. Yohimbine was administered, followed by recovery in 10 minutes to an hour (Table 1).

In summary, we feel 4 ml of Telazol-xylazine (800 mg/320mg) is a safe and effective dose for immobilization of undisturbed adult cow elk. The elk should be allowed to metabolize the Telezol® for 30-45 minutes after complete immobilization before reversing the xylazine with yohimbine. The elk should be reversed in an area with minimal disturbance to minimize injury to the elk or the capture crew. The researcher must judge when to inject yohimbine into a vein or a muscle. Intravenous injections can result in an immediate recovery. In very steep terrain, this can be dangerous to the elk, as it may have not regained total coordination. In steep terrain, intramuscular injections are more prudent. Intravenous injections should be used in gentler terrain, or when falling temperatures threatens hypothermia.

The original recommended dose of 1,000 mg of Telazol plus 400 mg of Xylazine was not tested, and may still be the best option for cow elk which are darted in a more excited state.

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Table 1. Data for Capture/Recovery of 6 Cow Elk, 1996-97

Animal number	Telazol/xylazine combination (mg)	Time to immobilization (min)	Time to recovery (min)
1	800/320	20	20
2	800/320	7	40
3	600/240 (x2)	60[1]	30
4	800/320	15	10
5	800/320	10	45
6	800/320	10	60

[1] 10 minutes after 2nd dart.

Drive Counts of Tule Elk at Point Reyes National Seashore, California

DALE R. MCCULLOUGH
Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management, and Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720-3110

Abstract: Drive counts to census the tule elk population at Point Reyes National Seashore in Marin County, California were conducted in Fall 1995 and 1996. This population occurs on Tomales Point peninsula and is contained behind a fence enclosing 1,052 ha. Drive crews were composed of students and faculty from the University of California, Berkeley. The October 28, 1995 drive count crew consisted of 35 people organized into 2 crews (each responsible for part of the area), and a count of 274 elk was obtained. This was the highest count among several census methods applied to the area, and thought to be the most accurate because duplicate counting was unlikely. It was apparent that a greater number of people should be used, and that they should be organized into 3 crews. The October 12, 1996 drive count crew consisted of 50 people divided into 3 crews, and a count of 381 was obtained. This was similar to a systematic ground count of 380, and an aerial count of 385. About 50 people are sufficient for the drive, but in the future they should be divided into 4 crews to increase efficiency. Adult sex composition was obtained reliably in both years. However, the number of calves was not reliably determined in 1995, and was determined for only the northern cow-calf herd in 1996. Video tapes taken during the drive in 1996 allowed accurate classification of the northern herd, but were not of sufficient quality to classify the southern cow-calf herd. Better use of camcorders in the future should solve this problem. Drive counts appear to give accurate, cost-effective estimates to monitor this population.

Key words: California, census, *Cervus elaphus nannodes*, drive count, Point Reyes National Seashore, tule elk.

INTRODUCTION

Probably the best known long-term application of drive counts to monitor a population of ungulates is the white-tailed deer (*Odocoileus virginianus*) on the George Reserve in southeastern Michigan. This 464-ha fenced area was censused by drive count almost every year (a few were missed during World War II) between 1933 and 1987 (McCullough 1979, 1982). I conducted the drive counts from 1966 to 1987. Thanks to independent estimates of the population by age structure reconstruction, the failings of the drive count were identified, and corrected over time (McCullough 1982). By the 1980s, the drive counts were quite accurate; for 4 years running the number of marked (radiocollared) animals known to be in the population matched exactly the number reported in the drive count. At that time, drive counts were more reliable than reconstruction methods because of the failure of cementum age determination when the population was greatly reduced (McCullough 1997). Using my experience, I obtained a successful drive count of black-tailed deer (*O. hemionus columbianus*) on Angel Island in San Francisco Bay (Mayer et al. 1995).

In this paper I report on drive counts of tule elk (*Cervus elaphus nannodes*) on Tomales Point in Point Reyes National Seashore conducted in 1995 and 1996. The tule elk is a subspecies endemic to California that underwent a severe decline to low numbers. It has been the object of a recovery program for over 120 years; currently it occurs in 22 subpopulations (McCullough 1969, 1978; McCullough et al. 1996). The Point Reyes herd on Tomales Point is 1 of the populations established in the recovery program. The drive crews were composed of students and faculty of the Department of Environmental Science, Policy, and Management at the University of California, Berkeley. Most of the students were involved in a course exercise. The purpose of the drive was not just as a class exercise, but to obtain a reliable count of elk in this population. Aerial counts have proven unreliable despite what would appear to be a favorable situation for aerial counts. The population can be assessed reliably from the ground by rapid, intensive, coordinated search (Ray 1981, Gogan 1986, Wahome 1995, Judd Howell, USGS-BRD, pers. commun.). This is the most cost-effective census method if experienced personnel are available. However, its effectiveness as the population grows is unknown, because a larger population will cause increasing problems of movement and double counting. Drive counts hold promise of yielding reliable estimates so long as a suitable crew can be assembled.

THE STUDY AREA AND POPULATION

The study area is on Point Reyes National Seashore, managed by the National Park Service. Tomales Point is a peninsula between the Pacific Ocean and Tomales Bay, which was created by the underlying San Andreas Fault. It is characterized by a central ridge top with the hillsides sloping away on either side to the water. Some steeply-cut canyons occur, mainly on the south end of the peninsula. The climate is Mediterranean with mild temperatures, winter rainfalls, and summer droughts. The summers are somewhat modified from the inland conditions by frequent coastal fogs. The vegetation is a mixture of open grassland and coastal scrub, which forms thick brush fields in some areas (Fig. 1).

Elk are contained on Tomales Point by water on 3 sides, and a fence that crosses the peninsula to partition off 1,052 ha. The fence was completed and 10 tule elk (2 bulls and 8 cows) were introduced to a small enclosure from San Luis Island National Wildlife Refuge in March 1978. Seven calves were born in the enclosure before the animals were released (Ray 1981). An additional 3 bulls were introduced from Owens Valley in 1981, but they promptly disappeared, and apparently did not contribute to the subsequent population growth (Gogan 1986).

At first this population declined due to the severe condition of the range because of grazing by domestic cattle, and an apparent copper deficiency problem (Gogan 1986). The elk also contracted Johne's disease (paratuberculosis, *Mycobacterium paratuberculosis*) from the cattle and showed clinical symptoms for several years (Gogan 1986). This is a density-dependent disease, showing clinical symptoms when the population is stressed, but not when conditions are favorable. These clinical symptoms disappeared and have not been seen since 1981; cattle were removed in 1980, and the elk population began to grow with subsequent recovery of the range. However, 100 fecal samples tested in 1993 had 4 positives, showing the population still harbors the disease in subclinical levels.

Relatively rapid growth of the population thereafter caused concerns about overpopulation and led, in 1993, to the appointment of a review committee to assess the situation. The committee noted that the population was showing signs of natural regulation since the growth rate was declining (McCullough et al. 1993). From projected population growth, carrying capacity was estimated at 346 elk. No reliable estimate of carrying capacity could be made from measurements directly on the vegetation. Although the range showed clear impacts of use by the elk, and the brush fields were being opened up by trails, overall the range looked in good condition—in fact, far better than most of the ranges on the Seashore still grazed by domestic livestock, and infinitely better than when the elk were first introduced.

On a small scale, the elk on Tomales Point pose many of the same questions about natural regulation of an ungulate population in a national park setting as does the northern Yellowstone elk herd. The scale of the problem, however, is much more manageable for a test of the natural regulation hypothesis. Furthermore, artificial control of the herd will, in all likelihood, initiate an unending program of control. There seems little doubt that a program could be put into place to maintain the population artificially at some prescribed level. The more profound question is what is this level, and is the program consistent with other objectives of park management?

The questions about regulation of the elk herd, and the consequences of the outcome for park management highlight the importance of good population estimates of this elk herd, particularly for a method to reliably monitor the population over the long term. Drive counts are 1 such possible method. The review committee viewed natural regulation with considerable trepidation, and noted that the population growth over the next few years would be important in the evaluation. However, 2 things happened that complicated the picture. First, the 1995 drive count reported here gave the highest count to date. Because double counting was not thought to have occurred, this result suggested that *ad hoc* estimates since Gogan (1986) may have been systematically low. Second, a particularly large population increase occurred in 1996. Was this an outlier—the consequence of a particularly good year—or was it evidence that the natural regulation hypothesis did not hold?

Elk are in good condition and show no clinical signs of Johne's disease, which would be expected if the population were under food stress; in fact, high calf recruitment is strong evidence that the population was on a good nutritional plane. Still, such a circumstance would be consistent with a time lag overshoot of carrying capacity, and that possibility can not be ruled out. Only more years of data will answer the question.

Notably, the range still looks to be in good condition. There is considerable residual in the herbaceous layer, particularly in the grassland habitat. The major impact has been on the woody shrubs where the extensive brush fields are being opened up by elk use. Poison oak (*Rhus toxicodendron*) especially is showing the impacts of elk browsing. In the Mediterranean climate of coastal California, use of woody browse is important mainly in the summertime when the lack of rain results in the drying out of the herbaceous layer. Furthermore, although the estimates of black-tailed deer on Tomales Point are poor, general observations suggest that their numbers are declining as tule elk increase.

RESULTS

1995 Drive Count

The first drive count was conducted on October 28, 1995 using 30 students and 5 faculty organized into 2 crews. An organizational session was held at the assembly place at Upper Pierce Ranch (Fig. 1), at which the 2 crews were given their instructions, and then lined up from 1 side of the peninsula to the other. The basic instructions are to maintain a straight line by keeping in constant contact with the people on either side, to move left or right to keep the line intact, to pass instructions back and forth to slow or speed up the sections to keep a straight line, and to tally and report all elk passing to the rear through the line on their right (except the left end person who tallies elk on both sides). If by chance elk pass through the line from back to front they are tallied as a negative number to avoid double counting.

Each crew was then individually instructed in how to split the line to go around

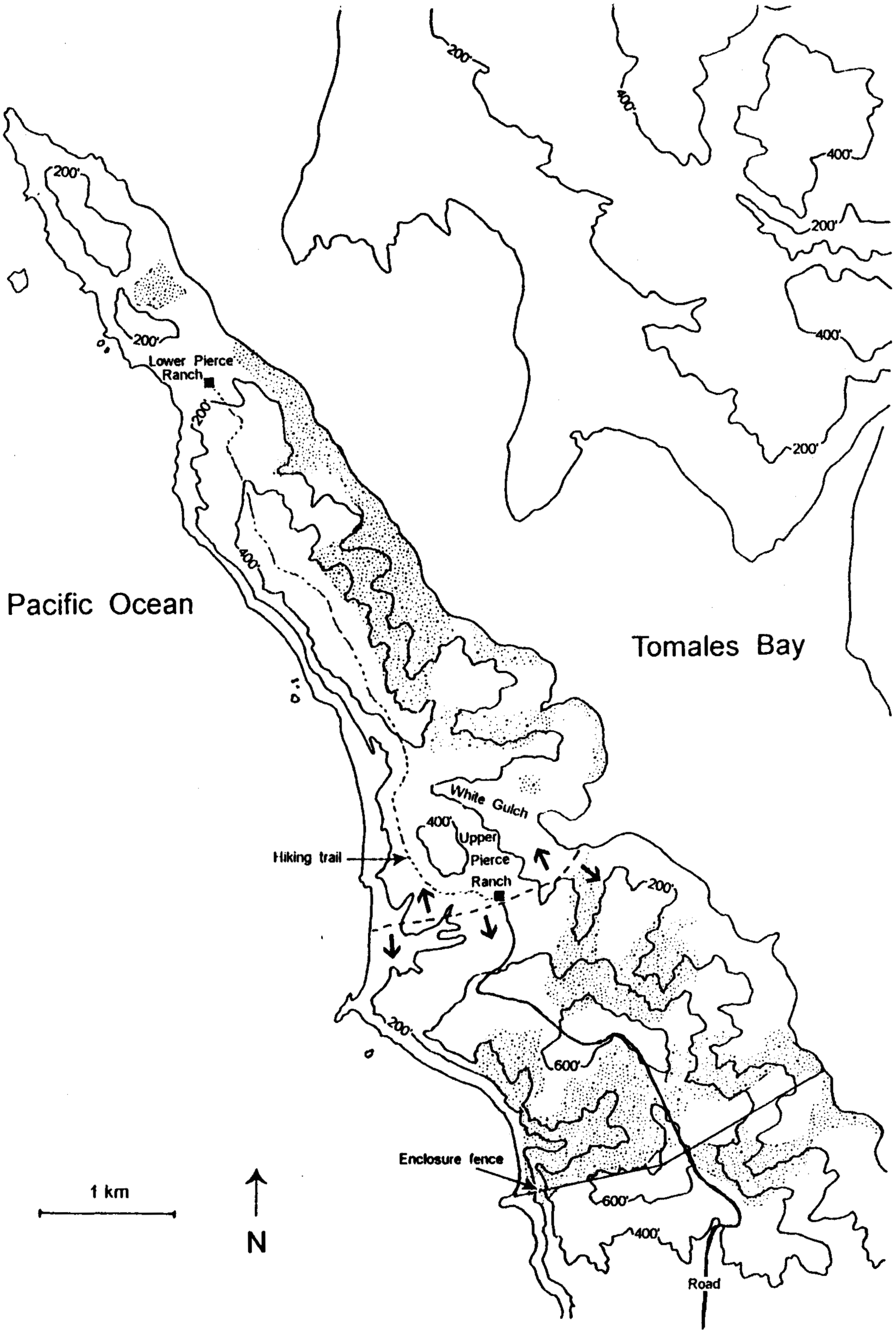

Figure 1. Tomales Point tule elk enclosure, Point Reyes, National Seashore, California. Stippled areas indicate brush fields. Arrows indicate position and direction of the 2 drive crews in the 1995 census.

impassable canyons or brush fields, and how to envelope large elk herds without pushing them away from the area of their original location. One crew covered the area from Upper Pierce Ranch southeastward to the fence, whereas the other covered the area from Upper Pierce Ranch northwestward to the end of the point (Fig. 1). After the completion of the drive count the captains and lieutenants of the 2 crews gathered and went over the tallies of their crews, and discussed possible errors of commission and omission, problems conducting the drive, and any changes helpful for future drives.

The south crew reached the fence about an hour after the drive began. They tallied 42 antlered bulls, 3 spike bulls, and 1 cow for a total of 46 elk. This was thought to be all of the elk with no duplication, although there was some question about 1 group. Changes needed were more people to keep the line connected, and better placement of people as the line enveloped canyons and brush fields to be more certain of an accurate and unduplicated tally.

The north crew drive took 4 hours to complete, and encountered many more problems. The east end of the line bogged down when it encountered thick brush fields, a steep slope, and a difficult creek crossing, and was lost to the rest of the crew. Eventually I reorganized the remainder of the crew and continued the drive with a more thinly spread line. Nevertheless, the reduced crew worked well together, and we managed to complete the remainder of the drive without serious difficulty. We tallied 221 cows, calves, and spike bulls, and 21 antlered bulls for a total of 242 elk. I observed all but 9 of these elk myself. The grand total for the drive count was 288. The herd estimate in use at the time was 220.

Although the number of antlered bulls was correct, the rest of the north drive herd composition was not reliably determined. The problem was that most of the cows, calves, and spike bulls occur in 2 large herds in White Gulch and Lower Pierce Ranch (Fig. 1). In the confusion of the milling animals, it was imperative to get a correct total count first, and a composition second, if possible. It proved difficult to funnel these 2 herds back through the line as planned. The loss of part of the crew disrupted the procedure in White Gulch, and after line reorganization, the herd was being funneled when 2 tourists (not part of the drive crew) appeared in the gap, and caused the herd to flee back ahead of the drive line. Fortunately, cows and calves resist being moved from their areas of occupation, and they ran back through the line, but at high speed and in a not very favorable location for counting. We accomplished a good total count (132), but had no time for classification by sex and age. The Lower Pierce Ranch herd contained 89 animals, and a reliable composition again was not obtained.

The south crew also reported seeing a mountain lion (1 has been observed in this area in the past and may be a resident animal), and coyote sign was abundant. Thus, these predators are present on the area. One dead elk was found. Few deer were seen.

It was apparent from this experience that successful drive censuses could be made of the Tomales Point elk population. However, changes would be needed in future drives to increase their reliability (particularly reduction of the possibility of double counting), and to improve their efficiency.

1996 Drive Count

The 1996 drive count was conducted on October 12, 1996 with a crew of 50, including 4 faculty and 46 students. More wildlife graduate students were incorporated in the crew as lieutenants to give better coordination. A pre-drive orientation was held to reduce the time to instruct the crew members on the procedures. The drive was organized into 3 crews. The south crew was as in 1995, but the north crew was split into 2, 1 (north crew) which hiked to the end of the point and moved south, and the other (central crew) that started from Upper Pierce Ranch and moved north. The 2 crews met near Lower Pierce Ranch. The rough section where the crew got lost in 1995 was covered from both sides. In addition, each crew carried a small camcorder to attempt to record the large cow-calf herds to aid in determining herd composition.

The south section drive went well. One part of the line covered the western portion of the section, and then set up a picket line in a gap between brush-filled canyons. The eastern part of the drive line then pushed elk past the picket line where the animals could be counted. A total of 54 elk was tallied (Table 1).

The central drive tallied 215, but the video of the White Gulch herd was taken from a distance, and sex and age composition of this group was not reliable. Calves were surprisingly large and difficult to distinguish from a distance. Miscommunication between parts of the line again resulted in the herd not coming through the line at the expected place, and that made classification and counting of this group difficult. However, a good video count agreed to within 1 animal of the count tallied by the person where the elk went back through the line. The White Gulch herd contained 187 animals by video count. Two coyotes were sighted, and few deer were seen. I personally saw 12 deer, all but 2 of which were bucks.

The total drive count in 1996 was 381 elk (Table 1). This was nearly identical to a systematic ground count of 380 elk made from horseback as part of an ongoing research project on the elk population (Judd Howell, USGS-BRD, pers. commun.), and was similar to the 385 elk counted in a fixed-wing aerial census (with still photos of large groups) conducted by the California Department of Fish and Game (Jon Fischer, pers. commun.). Photos taken from the air were not sufficient to determine herd composition. It is not known which of the censuses, if any, was absolutely correct. For practical purposes, however, differences between the results were trivial.

DISCUSSION

The 2 drive counts at Tomales Point show that this elk population can be reliably censused by this method. The next drive count can be further improved by splitting the central drive crew into 2, resulting in 4 crews total. The new crew would cover White Gulch from the ridge top eastward downhill. It would require few people to count and videotape this herd because of the open

Table 1. Tule elk drive count at Point Reyes National Seashore, October 12, 1996.

Area	Adult bulls	Spike bulls	Cows	Calves
South (fence to Upper Pierce Ranch)	44	3	7	0
Central (Upper to Lower Pierce Ranch)	24	3	160	28
North (Lower Pierce Ranch to point)	4	4	86	18
Total	72	10	253	46
Grand Total				381

valley. This would also solve the problems with funneling the herd back through the line on north-south drives, and cause less disruption of the herd, as well as being less subject to intrusion by tourists.

There are advantages and disadvantages of all 3 methods for censussing this population. Ground counts require few, but very experienced personnel, and are more easily rescheduled if ground fog in this coastal area interferes with the census. Drive counts can be run with inexperienced people. Aerial counts have been particularly subject to the frequent fogs of this area, and rescheduling has been difficult. Furthermore, tallying numbers accurately is difficult in the 2 very large groups of cows and calves. In the past, aerial counts of this herd have yielded implausibly low numbers for these, and probably other unknown reasons. Problems of herd classification in both the drive count (inexperienced personnel) and aerial counts (difficulty of obtaining sufficiently clear and sharp views) may be solved by better technique with video and still camera equipment.

Ground counts may be less efficient in brush fields, where the greater number of people in drive counts are more likely to flush lone animals or small groups. Areas in steep canyons cannot be traversed by either method, and one has to hope that elk in those areas can be seen from 1 side or the other. Elk are commonly seen from across canyons, and observing them in these areas seems a less difficult problem than flushing them from brush fields on more gentle terrain near the end of the point.

As all 3 methods are applied, they serve as cross-checks on each other, and each can be refined and improved. Hopefully, future censuses by different methods can be conducted as closely in time as possible to be comparable. Aerial counts could be conducted the same day as either the ground count or drive count, but the latter 2 methods probably should not be done the same day because of disruption and interference with each other.

In future drives, greater effort will be made to assess deer numbers because of a possible inverse relationship of numbers of the 2 species. It is reasonable to think this decline is due to the competition from elk, particularly for woody browse in the dry summer months in this Mediterranean climate, during which deer die-offs occur in late summer/early fall. There appears to have been a decline in the deer population concurrent with the increase in tule elk. Gogan (1986) estimated the Tomales Point deer population by line transect and pellet group counts to be 221 head. From my observations, I believe there are substantially fewer deer now. Indeed, I personally saw more deer in 1 drive capture effort in 1 canyon during Gogan's (1986) study than in either drive count.

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I thank faculty colleagues at U. C. Berkeley Barbara Allen-Diaz, John Battles, James Bartolome, Greg Biging, and Tom Kucera for help to run the drive counts. Although too numerous to mention individually, I gratefully thank the many graduate and undergraduate students of the Department of Environmental Science, Policy, and Management, U. C. Berkeley that composed the drive crews. Judd Howell of the U. S. Geological Survey Biological Resources Division and Jon Fischer of the California Department of Fish and Game kindly furnished me with the results of their censuses of the elk population. Costs of this project were covered by the University of California, Berkeley.

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Changes in The Selway Elk Herd After Five Decades: Evidence From a Repeated Pick-up Mortality And Classification Study

ERIK E. NORELIUS
Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071

ANTHONY L. WRIGHT
Hornocker Wildlife Institue, HC-83, Running Creek Ranch, Cascade, ID 83611

Abstract: Mortality plays an important role in shaping the age distribution and composition of wildlife populations. We conducted a repeat pick-up mortality and classification study in the Idaho portion of the Selway-Bitterroot Wilderness. We searched for, aged, and determined cause of death for carcasses of elk, mule deer, and white-tailed deer, and classified age/sex composition of herds repeatedly during December-April 1989-96. A similar, unpublished study had been conducted during 1936-37, when the cougar population was effectively suppressed. During the recent study 75% of female elk (total $n = 28$) were ≥ 7 years of age versus 64% (total $n = 11$) during the earlier study. Cougar predation replaced scabies as the major cause of elk mortality during the repeat study. Predation was the largest cause of deer mortality in both studies, but cougars replaced coyotes as the most important predator in the latter. Elk calf:cow ratios observed during the recent study ($\bar{x} =$ 19.2:100) were much lower than those of 1936-37 (63.0:100). An understanding of historic demographic change would improve attempts to model the effects of new predator introductions but is difficult to obtain with certainty. Regular collection of climate, landscape, vegetation, diet quality, and predator abundance data in addition to demographic and harvest data would be valuable to coming generations of wildlife biologists.

Key words: Cougar, elk, Idaho, mortality, mule deer, predation.

INTRODUCTION

The magnitude of wildlife population changes in wilderness areas is poorly documented both in the long- and short-term. For example, elk (*Cervus elaphus*) are a species of major interest in the Selway-Bitterroot Wilderness, however, the best available data consists of sightability estimates conducted at 3-4 year intervals beginning in 1988 (Kuck and Nelson 1991, see Appendix 1). In the long-term, it is unknown whether the species is indigenous to the area or originated from transplants of the Yellowstone herd (Bryant and Maser 1982). Both short- and long-term perspectives are valuable for designing harvest plans and forecasting effects of predator introductions. If demographic, habitat, and climate monitoring data were available for the past 100 years, one could answer questions such as: What are the current demographic characteristics of the herd and within what ranges have these varied? Does the area have low intrinsic productivity due to poor soils or nutrient deficiencies? Have severe winters become less frequent allowing large numbers of females to survive to age-classes with low natality rates? The best available information pertinent to such questions is an unpublished winter range study conducted in 1936-37 by the Idaho Department of Fish and Game (IDFG) and the U.S. Forest Service (USFS) (Maclay 1937, see Appendix 1). Several other studies in the 1930s report calf:cow ratios for the same general area (Landall 1935, see Appendix 1, Young and Robinette 1939). During 1989-96, we repeated pick-up mortality and age-sex classification surveys originally conducted by Maclay in 1936-37, and although not suitable for rigorous analysis, the results contribute to our understanding of herd demographics. Also, examination of regional climate data and historical documents allow us to hypothesize about the causes of this change.

STUDY AREA AND HISTORY

Maclay conducted his study on 101,215 ha comprising the lower elevations (825-1,980 m) of the Selway-Bitterroot drainage above Three Links Creek. We collected data in 1989-96 in the middle portion of this area from Bear Creek to Stewart Creek. The area consists of a mosaic of coniferous forests, brushfields, and open areas. Slope and aspect in the steep dendritic drainages and fire history play large roles in determining vegetation present on a given site. Some riparian areas support diverse deciduous vegetation. The extent and canopy coverage of forests have expanded since effective fire suppression began about 1935 (Habeck 1976). By 1970, increased shading by conifers caused a significant decline in redstem ceanothus (*Ceanothus sanguineus*), an important browse species, on north and east exposures (Leege et al. 1972, see Appendix 1). During the 20th century, plant communities of open rangeland below 1,700 m changed radically and repeatedly due to invasions by exotics such as cheatgrass (*Bromus tectorum*), goatweed (*Hypericum perforatum*), and spotted knapweed (*Centaurea maculosa*) (Wright and Kelsey 1997). A more complete description of vegetation is found in Wright and Kelsey (1997).

Diaries of homesteaders and USFS personnel (Pettibone 1916, Moe 1918, Parcell 1949, see Appendix 1) indicate elk were uncommon and limited to a few locales prior to 1917. Large fires in 1910 and 1919 may have initiated a major expansion of the elk herd that continued until the 1950s. There may have been several peaks in the population (Burns 1972, see Appendix 1) although no major mortalities were noted until the winter of 1948-49. Elk populations were generally high 1960-96, but perhaps not as high as in the 3 previous decades based on vegetative impacts described by local residents (K. Wolfinbarger pers. commun.).

Cougar (*Felis concolor*) and black bear (*Ursus americanus*) are the major predators of elk in the Selway-Bitterroot Wilderness (Schlegel 1976). Bounty hunting for cougars was effective at suppressing their population at the time of Maclay's research (Maclay 1937, see Appendix 1). Homesteaders relied on bear hides for a significant portion of their cash income (Pettibone 1916, Moe 1918, see Appendix 1) so black bear numbers may also have been lower at that time than in recent years.

METHODS

Pick-Up Mortality Sample

We were alert for the presence of cervid carcasses whenever in the field 1989-96. Most were discovered by watching the activities of ravens (*Corvus corax*), black-billed magpies (*Pica pica*), bald eagles (*Haliaeetus leucocephalus*), and golden eagles (*Aquila chrysaetos*) or through concentrations of cougar and coyote (*Canis latrans*) sign.

Preponderance of evidence was used to assign a cause of mortality if possible (Table 1). We collected a lower jaw, if possible, and examined the marrow of a long bone in both a front and rear leg if available and fresh. Maclay does not discuss how he determined causes of mortality, so we were not able to use exactly the same criteria. We combined all known causes other than predation, shooting, accident, and scabies (*Psoroptes* spp.) into a poor condition category in both the 1936 and recent data sets.

Table 1. Criteria used to assign mortality cause to cervid carcasses. Cause was listed as unknown unless at least 2 criteria were met except where noted.

Cause	Criteria
Shooting	• Antlers and canine incisors removed. • Only head, lower legs, and internal organs remain • Bullet damage or exit hole visible.[a] • Lower leg or jaw shattered or missing.[a]
Coyote predation	• Often in open area or on river ice. Hide and disarticulated skeleton widely scattered. Ribs mostly consumed. Physical trauma from attack, often on throat, neck, or head. • Numerous coyote tracks and loafing spots and no cougar tracks.
Cougar predation	• Usually in woodland or brush with cougar tracks repeatedly going to and from site. • Cougar sign present: droppings, bed, scrapes. • Carcass buried or partially buried if feeding has not terminated.
Poor condition	• Often bedded or mired in ice or deep snow. Adults often found shortly after green-up. Cougar tracks absent or make only 1 visit to site. • Extreme toothwear. • Emaciated, especially calves or fawns. • Marrow in some long bones "runny red jelly."

[a] Definitive single criteria.

Species of most carcasses was determined by gross examination. A few deer carcasses were assigned to species by characteristics of the metatarsal gland or lacrimal fossa (Baker 1984). Sex was determined by examination of skull, genitals, or pelvis (Larson and Taber 1980). Yearling elk, calf elk, and deer fawns were aged by tooth eruption (Murie 1951, Larson and Taber 1980).

Tooth cementum analysis was performed in accordance to Matson's protocol (1981) with the following deviations designed by the Wyoming Game and Fish Department Laboratory. We boiled jaws in water to extract the first incisor. The chemical composition of the AutoTechnicon™ baths and the stain used on the cementum samples were formulated by the Wyoming Game and Fish Laboratory. Deer teeth were also processed in the same manner except a frozen section technique was used in place of paraffin sections. The count of annuli plus a correction factor for the time of year death occurred gave the age of the animal.

The jaws aged by cementum were laid out according to age on a table. Jaws collected with incisors missing were aged by comparing wear on premolars and molars with known-age jaws. Jaws aged by wear in this manner were placed in the lower age in their age category due to possible grit in the forage (i.e., 5-6 years become 5 years).

Classification Surveys

Classification surveys were made several times weekly December-April 1990-96 and during other activities when possible (Wright and Kelsey 1997). Counts were not made in any area more often than once per week to avoid over-weighting more accessible portions of the herd. The exception to this occurred when the composition of the group was such that it clearly had not been counted earlier in that week. Mature bull elk were uncommon and distributed in remote parts of the 1989-96 study area and thus only the calf:cow ratio was adequately sampled. We also classified fawn and adult mule (*Odocoileus hemionus*) and white-tailed deer (*O. virgininanus*).

RESULTS

Pick-Up Mortality Sample

We identified 44 elk carcasses in the field from 1989-96. Females accounted for 63.7% (*n* = 28), males 13.6% (*n* = 6), and elk of undetermined sex 22.7% (*n* = 13) of the sample. Of the female elk whose age could be determined, 11% were calves and 29% were 13 years of age or older (Table 2). Of the females in the age class 7-12 years, 53.8% (*n* = 7) were 10-12 years of age. Maclay identified 25 elk carcasses in the field during 1936-37. Females accounted for 44% (*n* = 11), males 56% (*n* = 14). He aged 64% (*n* = 7) of the females as ≥ 7 years of age and 10% (*n* = 1) as a calf.

A total of 16 mule deer carcasses were identified during the recent study. Females comprised 50% (*n* = 8), males 31.3% (*n* = 5), and animals of undetermined sex 18.7% (*n* = 3) of the sample. Of the females, 25% (*n* = 2) were ≥7 years of age, 37.5% (*n* = 3) were 2-6, and 37.5% (*n* = 3) were ≤1. Maclay identified 48 mule deer carcasses; 35.4% (*n* = 17) were females, 2.1% (*n* = 1) males, 62.5% (*n* = 30) were of undetermined sex. Of the females, 5.8% (*n* = 1) were ≥7 years of age, 23.5% were 2-6, 5.8% (*n* = 1) were ≤1, and 64.7% (*n* = 11) were of unknown age.

Table 2. Age distribution (%) of female elk from pick-up mortality samples during 1936-37 (Maclay 1937, see Appenidx 1) and 1989-96 in the Selway-Bitterroot Wilderness, Idaho.

	Age (years)			
Time period	≤1	2-6	7-12	≥12
1936-37 (*n* = 11)	9	27	(---64 ---)[a]	
1989-96 (*n* = 28)	11	14	46	29

[a] % elk ≥7 years of age.

We identified 16 white-tailed deer carcasses. Females accounted for 43.8% (*n* = 7), males for 37.5% (*n* = 6), and animals of undetermined sex 18.2% (*n* = 3) of the sample. Maclay found only 2 white-tailed deer carcasses, a female fawn and a female of undetermined age. Maclay also located 11 additional deer carcasses of unknown species. We did not record data on deer we could not identify to species.

For elk, predation replaced scabies as the leading known cause of death in the repeat study (Table 3). Maclay observed mature bulls dying of scabies from early November through March, few cow mortalities (mostly of unknown cause), and only 1 instance of predation (a calf killed by coyotes). We observed no adult bull mortalities except during hunting season, cow deaths due to cougar predation and poor condition were common.

In both studies, predation accounted for most deaths of both deer species (78% and 62% in the earlier and later studies, respectively). Maclay recorded 53 instances of coyote predation on deer and 1 instance of

Table 3. Causes of death for elk carcasses found near the Selway River, Idaho during November-April 1936-37 and November-May 1989-96.

	Cause of death											
	Shot		Predation		Accident		Scabies		Poor condition		Unknown	
Years	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)	*n*	(%)
1936-37 (*n* = 25)	3	(12)	1	(4)	1	(4)	13	(52)	1	(4)	6	(24)
1989-96 (*n* = 46)	6	(13)	15	(33)	1	(2)	0	(0)	8	(17)	16	(35)

cougar predation. We observed 5 instances of coyote predation and 8 instances of cougar predation on deer.

Classification Surveys

Calf:cow ratios observed in the 1990s were much lower than those of the 1930s (Table 4). In contrast, during 1990-96 winter-spring ratios of fawn:adult mule deer ($\bar{x}$= 27.7:100 range 20.2 to 33.2) were moderately lower and white-tailed deer ($\bar{x}$= 26.0:100 range 17.8 to 29.8) were similar to those reported by Maclay (37:100 and 27:100, respectively).

DISCUSSION

In recent years, the Selway elk herd appeared to have many old cows and low recruitment. Of the cow mortalities found in the later study, 29% were greater than 13 years of age, perhaps old enough to exhibit reduced pregnancy rates (Flook 1970). Density dependent survival in calf elk, which has been demonstrated for red deer (Clutton-Brock et al. 1985) and elk (Sauer and Boyce 1983), could be acting with reduced fecundity to create the low calf:cow ratios recently observed. However, there was no direct evidence that elk density was high enough to impact calf survival, and this is only 1 of many possible explanations for low calf:cow ratios.

We could not construct a formal life table from our pick-up data for several reasons including small sample size, lack of data from summer range (especially for calf mortality), and uncertainty that a stable age distribution, and zero rate of increase could be assumed (Caughley 1977). However, the number of very old cows in the recent pick-up sample which approximates an age-at-death distribution, not a standing age distribution, was striking and likely reflected high survival of adult cows. Because calf:cow ratios reported during the 1930s were much higher, perhaps near feasible maximum sustained growth rate occurred (Eberhardt et al. 1996), and average age of cow elk was likely lower in those years.

Many characteristics of the habitat, physical environment, and management practices changed during the interval between the 2 studies. The degree of these changes and responses of the elk population warrant a speculative examination. Winter climate ameliorated beginning around 1980 as measured by the persistence of snow into the spring elevations above 1,070 m at nearby stations (Fig. 1). This may have permitted more cows to survive past their prime reproductive years.

Table 4. Ratios of calf to cow elk and fawn to adult deer in the Selway River drainage, Idaho, December through April except as noted. (*n*) = Number of animals classified including bull elk.

	Species		
Year	Elk	Mule deer	White-tailed deer
1934-35[a]	87.8:100 (718)		
1936-37[b]	63.0:100 (2,586)	36.9:100 (1,301)	28.4:100 (181)
1938[c]	74.0:100 (583)		
1949[d]	24.9:100 (2,667)		
1990-91	25.7:100 (1,819)	33.2:100 (417)	29.8:100 (257)
1991-92	18.6:100 (1,514)	26.3:100 (375)	17.8:100 (212)
1992-93	25.8:100 (1,453)	26.1:100 (406)	20.5:100 (223)
1993-94	14.8:100 (1,072)	35.3:100 (276)	29.2:100 (199)
1994-95	17.8:100 (1,226)	20.2:100 (184)	29.3:100 (194)
1995-96	12.5:100 (918)	25.0;100 (187)	29.7:100 (2.5)
Average year			
1990-96	19.2:100	27.7:100	26.0:100

[a] Data from Landall (1935) for November 1934-April 1935 study area same as 1990-96.

[b] Maclay (1937) for November 1936-April 1937.

[c] Young and Robinette (1939) for July-October 1938, Moose Creek area.

[d] Shaw and Neilson (1957) January 1949, Selway upstream from Moose Creek.

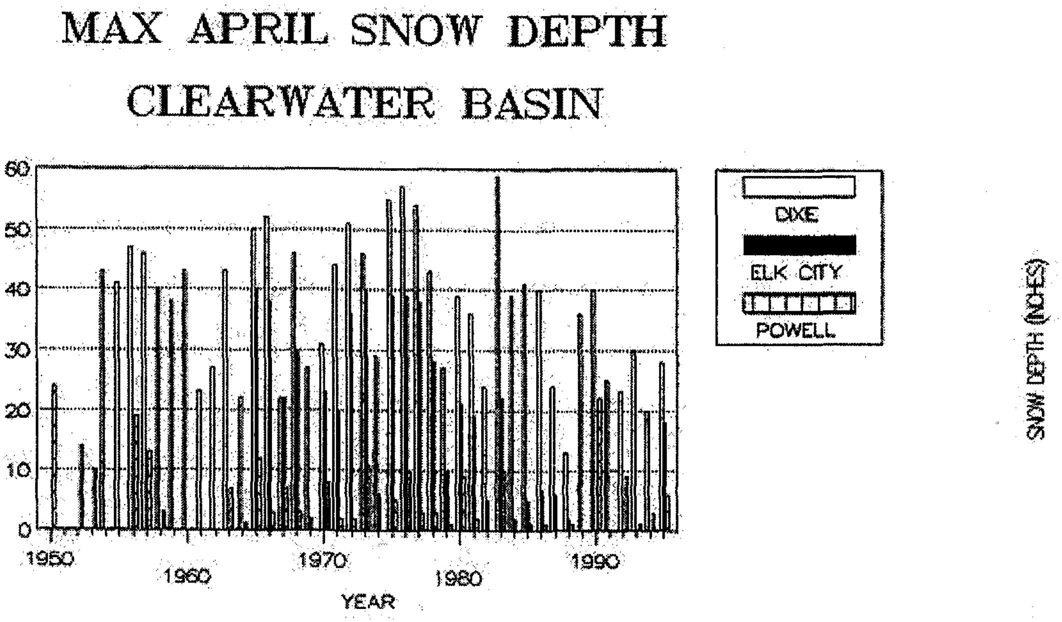

Figure 1. Maximum April snow depth in Clearwater Basin, Idaho, 1950-1995.

The preference of hunters has shifted from elk as food to elk as antler trophies. For example, during the open hunt of 1947, 149 bulls and 126 cows from the Selway were tallied at check stations (Biladeau 1949, see Appendix 1). In comparison IDFG estimated the harvest in the Selway unit in 1995 as 653 bulls and 8 cows. Large groups of bulls such as the 30 seen by Landall (1935, see Appendix 1) no longer occur in the study area, nor do scabies outbreaks. Low cow harvest also may play an important role in creating a large, unproductive, old-age cow segment of the population.

Cougar predation was apparently not an important mortality factor in the 1930s when an intensive effort was made to reduce numbers. If black bear predation was an important mortality factor on young cervids at that time, it was not recognized (Young and Robinette 1939:47). If the change in predator regime modified herd demographics, it has done so to a much lesser extent in the deer species, perhaps because efforts to reduce coyote numbers were unsuccessful (Maclay 1937). While Schlegel (1976) demonstrated intense black bear predation on elk calves, it remains unclear why the Selway should be unique in this respect. Increasing speculation that small calf size or asynchronous conception dates due to disruption of the rut by bugle hunters may be a contributing factor. (Squibb et al. 1986).

Suggestions that the granitic soils of the area are incapable of supporting a productive elk herd are refuted by the historic record. However, fire suppression and reduced salting for game and livestock (Landall 1935, Maclay 1937) may have made mineral requirements for reproduction more difficult for cervids to meet. Intense mineral craving, evidenced by many observations of bizarre behavior such as chewing of an antler immediately upon shedding (Landall 1935), prolonged bone gnawing, eating of plastic, gasoline-soaked soil, buildings, clothing, etc. (Wright pers. observ.), was exhibited by cervids in the Selway.

Negative impacts of fire suppression on browse availability were documented by Leege et al. (1972). Further carrying capacity reductions due to spotted knapweed infestation were not detected by Wright and Kelsey (1997).

Demographics of wildlife populations may change substantially, even in wilderness areas. We should expect more changes if predators such as the grizzly bear (*Ursus arctos*) and wolf (*Canis lupus*), are reintroduced or changes in human harvest occur. The results of these interventions complicate prediction efforts, which emphasizes the need for advancing monitoring capabilities. We suggest those data notably lacking during the past 50 years may be a good indication of what variables our data sets should routinely include now. If we hope to construct useful predictive models, we need to monitor not only demographics and harvest, but climate, landscapes, vegetation, diet quality, and predator populations.

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Habitat Potential Model for Rocky Mountain Elk

GARY J. ROLOFF
Timberland Resources, Boise Cascade Corporation
1111 West Jefferson Street, P.O. Box 50, Boise, ID 83728

Abstract: Habitat potential and effectiveness are 2 primary considerations of elk habitat assessment and management. Habitat potential is defined as the combination of ecological factors (e.g., existing vegetation, climate, landform) that influence the inherent ability of a landscape to produce and sustain elk in the absence of human disturbance. Habitat effectiveness is defined as the spatial use of potential habitat in the context of human disturbance. Knowledge of both components is necessary for resource planners to address 3 general questions: 1) can the planning landscape inherently support elk, 2) is elk use of potential habitat being limited, and 3) if elk use of potential habitat is being limited, what environmental factors are limiting? The model presented herein uses forage quality and quantity to index habitat potential. Subsequently, habitat effectiveness parameters are discounted from the potential. Key components of the model include an ecological classification system, forage quality and quantity relationships by season, effects of historic land use on forage condition, habitat juxtaposition, and roads. The model is designed as an expert system in that the assumptions, logic, and framework are provided herein but the derivation of quality indices are intended to be driven by local knowledge.

Key words: ecological classification, elk, habitat modeling.

INTRODUCTION

Elk (*Cervus elaphus*) population and habitat management have been primary considerations for resource decision-makers throughout the West during the last 25 years. With many landowners tending towards ecosystem and multi-resource management, the administration of elk harvests, habitat management, cattle grazing, and road closure programs have become increasingly complicated. Elk ranges typically contain multiple landowners with different ownership objectives, and although the goal of productive elk populations is generally consistent across ownerships, contributions toward and techniques for reaching that goal vary by landowner. Since land managers and planners can influence elk using a variety of management tools (e.g., harvest regulations, road closures, pasture rotations, the timing of domestic grazing, silvicultural prescriptions), habitat assessment techniques must be sensitive to a multitude of management alternatives.

Quantifying the effects of habitat modification over time at multiple spatial scales has necessitated the use of models in resource planning. Numerous elk habitat models have been developed with most efforts based on habitat relationships identified by Black et al. (1976), Thomas et al. (1979), Wisdom et al. (1986), and Thomas et al. (1988) (Table 1). Most existing models follow a general framework for habitat assessments by initially quantifying landscape potential and subsequently discounting the effects of direct human disturbance (e.g., road access, hunting). This model follows a similar procedure.

In this documentation, habitat potential is defined as the combination of ecological factors (e.g., existing vegetation, climate, landform) that influence the ability of a landscape to produce and sustain elk in the absence of human disturbance. Discounting the effects of human disturbance from habitat potential results in a *habitat effectiveness* index. Habitat effectiveness is the spatial use

Table 1. Summary (in chronological order) of common habitat models for Rocky Mountain and Roosevelt elk.

		Model Input Parameters						
Authors	Geographic location	Forage	Cover	Habitat spatial	Roads	Special	Migration	Others[2]
O'Neil and Witmer 1991	Central Idaho		√	√		√	√	√
Thomas et al. 1988	Blue Mountains (OR and WA)	√	√	√	√			
Brunt and Ray 1986	Vancouver Island, B.C.	√	√	√				
Harshman 1986	Western Oregon	√	√	√	√			√
Wisdom et al. 1986	Western Oregon	√	√	√	√			
Scharpf et al. 1986	Oregon Cascades	√	√			√		
Leege 1984	Northern Idaho	√	√	√	√			√
Witmer and deCalesta 1985	Western Oregon		√	√				√
Lyon and Jensen 1980	Western Montana	√	√	√				√
Lyon and Jensen 1980	Eastern Montana	√	√	√	√			
Thomas et al. 1979	Blue Mountains (OR and WA)	√	√	√	√	√		√
Black et al. 1976	Blue Mountains (OR and WA)	√	√	√	√			

[1] Includes delineation and quantification of winter range, meadows, and fawning areas.

[2] Includes quantification of poaching, elk access, livestock effects, and distance to water.

of potential habitat in the context of human disturbance. Consideration of both habitat potential and habitat effectiveness are necessary to make informed land management decisions relative to elk habitat.

Many localized (e.g., National Forest District) agency managers and planners accepted the habitat assessment framework proposed by Wisdom et al. (1986) and Thomas et al. (1988), and the models have received widespread use in forest planning. Most of the original models were designed to evaluate relative habitat conditions depicted as a function of forage, cover, and road densities during the non-hunting season (Table 1). To date, elk habitat models have not been designed to predict reproductive potential or elk densities (Leckenby et al. 1986). Since year-round forage quality and quantity have been demonstrated as critical determinants of elk fitness (Cook et al. 1996), I sought a framework that integrated forage condition into a resource-planning model. The model presented herein expands upon previous modeling efforts by incorporating forage quality and quantity dynamics relative to land classification system, season, and historic land use. Also, this model expands upon the spatial relationships between habitat components based on differences in habitat quality. Thanks are extended to Charles Meslow, Larry Irwin, John Cook, Robert

Riggs, Les Marcum, Richard Mackie, L. Jack Lyon, and Brian Gilbert for their reviews and input to drafts of this model and manuscript.

ELK HABITAT POTENTIAL MODEL OVERVIEW

General agreement exists among elk biologists regarding how habitat components should be compartmentalized for analysis, however, less knowledge and agreement exists as to how the variables interact to influence overall elk habitat potential (Thomas et al. 1988). The model presented herein uses a modular approach in the context of an ecological classification system to quantify important habitat components. Five modules are used: 1) foraging, 2) security cover, 3) integrating forage and security habitats, 4) special habitat requirements, and 5) road effects. The modules are systematically applied to portions of the planning landscape delineated by elk herd ranges for different seasons.

Model Partitions

Application of the model should correspond to the spatial extent of individual elk herds to ensure that the model is used at a scale biologically meaningful to the organism. The ability to approximately map herd ranges for both migratory and resident elk is a critical component for valid habitat assessments (Skovlin 1982, Thomas et al. 1988). For migratory herds, winter, transitional, and summer ranges typically vary by elevation and distinct ranges will be evident (R. Mackie, Wildlife Biologist, Belgrade, MT, pers. commun.; Fig. 1). Seasonal herd ranges for resident elk, in contrast, will overlap. In areas containing both resident and migratory animals, the different herd types will have overlapping ranges, however, range types for each individual herd should be computed separately. Within a herd's geographic space, seasonal habitat potential scores are calculated as they relate to life history period (Fig. 1).

Herd geographic space is partitioned into winter, transitional, and summer ranges (Fig. 1). The model also partitions the annual life history of elk into 4 life history periods: 1) winter survival; 2) spring movement, calving; 3) summer forage areas (Skovlin 1982); and 4) breeding, post-breeding (Fig. 1). Habitat potential scores are calculated for each life history period on the corresponding range type. For example, a winter survival score is calculated for winter range.

Model Validation

Ideally, a habitat potential model would provide an index to herd reproductive potential as expressed by cow elk fecundity (the number of female live births per female per year) or net reproductive rate (the survival of calves to reproductive age). The complex relationships between environmental and human induced factors that affect elk reproductive performance precludes controlling any 1 factor for model testing. Thus, elk and habitat response variables for model validation should be specific to each model component. For example, the response variables for foraging may include the amount of metabolizable energy, plant species composition, or biomass production (Elk Modeling Workshop 1996)[1]. Specific response variables should be identified for each seasonal life history period delineated in Figure 1 and tested against the corresponding habitat potential index.

FORAGING MODULE

Land Classification

Critical to the elk habitat potential model is an ecologically based land stratification that facilitates the prediction of forage and cover potentials (Skovlin 1982, Brunt and Ray

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[1] Elk Modeling Workshop 1996 involved approximately 15 elk biologists from the Pacific Northwest and Intermountain West that reviewed and discussed elk habitat relationships.

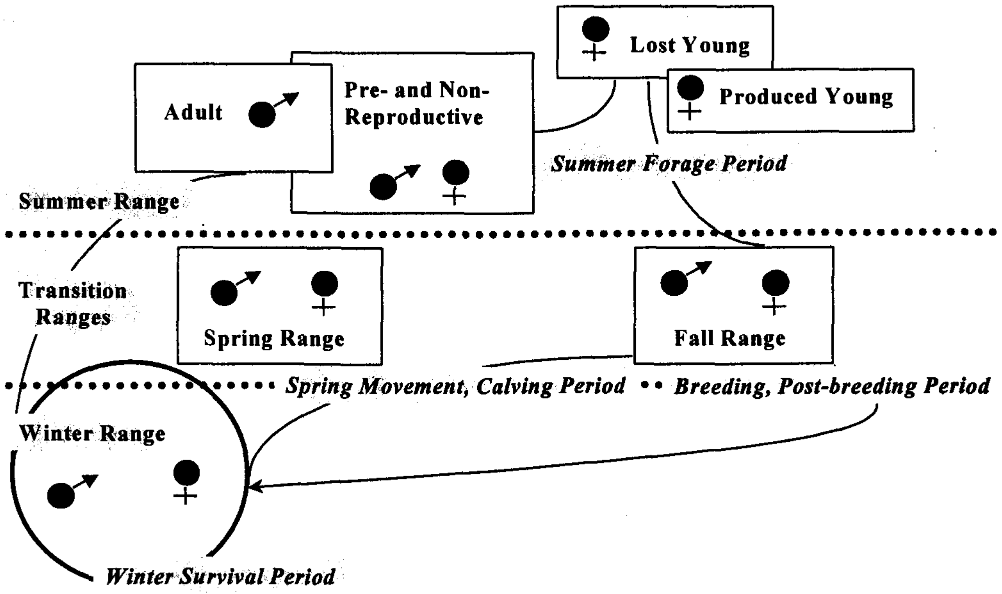


Figure 1. Partitioning of elk herd ranges and life history periods into modeling units.

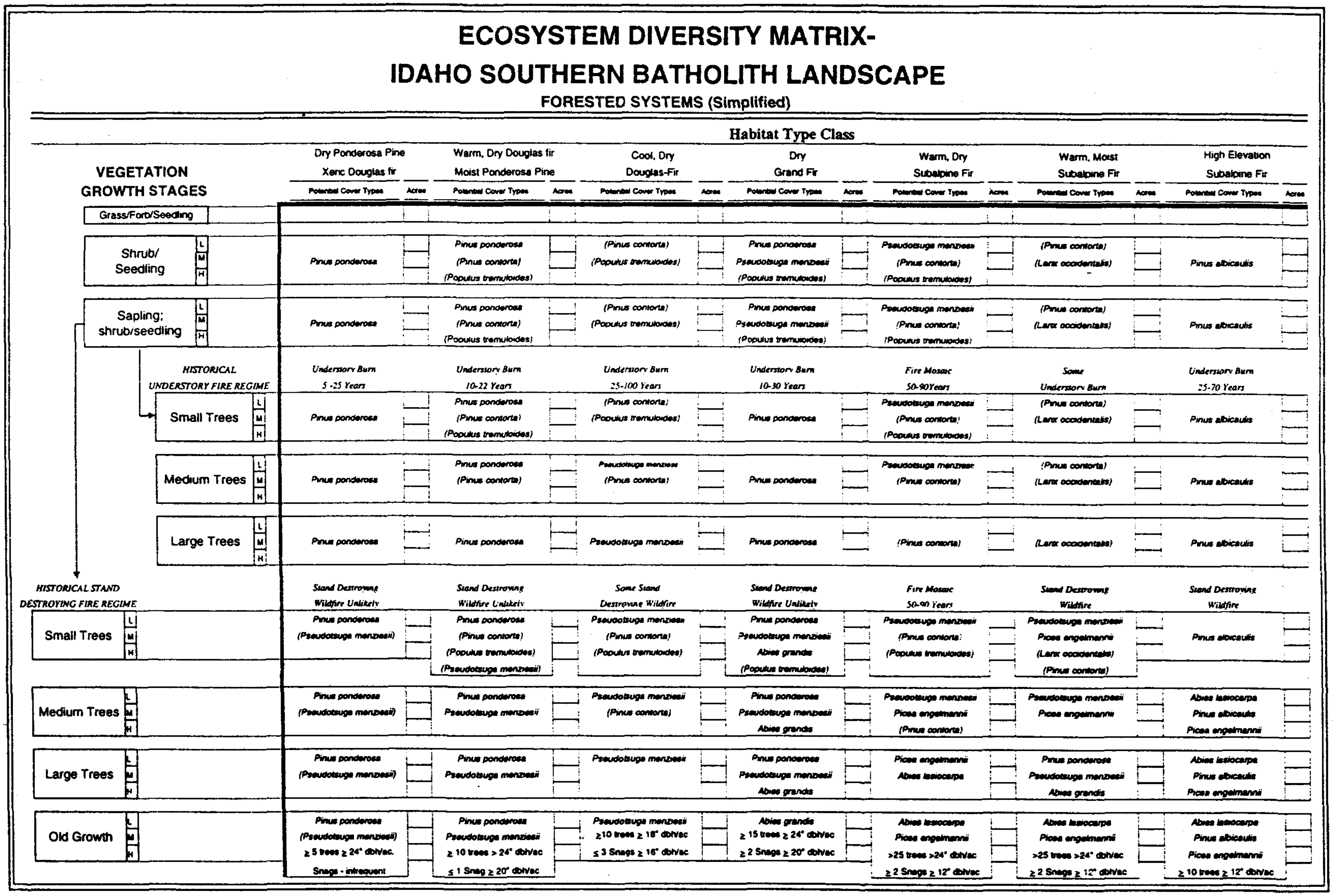
1986). An ecological classification system is a land stratification scheme that integrates existing vegetation conditions, site potentials, and predominant disturbance regimes in a temporal context (Haufler et al. 1996). Brunt and Ray (1986) explored 1 method of using ecological classification for elk habitat assessments and noted that seasonal elk habitat selection was accounted for by landscape physiography. Similarly, Skovlin (1982) noted that elk tended to avoid draws and canyon bottoms with nightly flows of descending cold air. Irwin and Peek (1983*a*) documented elk avoidance of cool-moist grand fir (*Abies grandis*) habitat types (herein, habitat type refers to the site classification of Daubenmire 1970) during late fall and early winter. Thus, relationships between elk habitat use and components of ecological classification systems have been documented. For purposes of this model, it is assumed that an ecological classification system integrates multiple factors including soils, landform, and geology and permits parameterization of plant assemblages expected on any individual site (Steele et al. 1981).

The first step in ecological land classification is to delineate the physiographic province that contains the elk range(s) of modeling interest. The purpose for delineating a physiographic province is to coarsely homogenize the landscape with respect to climate, geology, and inherent land processes (Haufler et al. 1996). Physiographic provinces tend to exhibit similar biogeoclimatic conditions that influence site potentials; similar historical disturbance regimes that influence vegetation structure and species composition, and are of adequate size to represent a diversity of vegetation or site potential types (Haufler et al. 1996). The United States Forest Service's National Hierarchy of Ecological Units provides a classification tool useful for physiographic province delineation (Ecomap 1993). Within the Forest Service hierarchy, preliminary data analyses lend support to using the Section or sub-Section levels (millions of hectares in size) to delineate planning landscapes (Haufler et al. 1996; see McNab and Avers 1994 for national delineation of physiographic units). Within and aquatic resources must be classified, however, the elk model presented herein will work on individual landscape components. Descriptions of the existing conditions should emphasize vegetation structure, species composition, and the ability to map each vegetation type. Site potentials must similarly be classified at a resolution conducive to describing predominant understory vegetation assemblages. Too coarse resolution will result in an inability to detect habitat quality differences, whereas too fine resolution becomes operationally impractical. By combining the existing vegetation with site potentials, within-mapped-strata variability is reduced, particularly for understory and ground layer vegetation attributes. This combination provides the ecological classification necessary to model elk habitat potentials and is recommended for most wildlife habitat assessments (Haufler et al. 1996). The resulting product is a map of ecological units and an associated ecosystem diversity matrix (Fig. 2; Haufler et al. 1996).

Forage Quality and Quantity

Forage quality and quantity are widely recognized as critical determinants of elk reproductive performance (see review in Nelson and Leege 1982; Irwin and Peek 1983*b*, Hobbs and Swift 1985, Marcum and Scott 1985, Cook et al. 1996). Thus, habitat evaluations and management practices that ignore forage considerations may be ineffective (Hobbs and Swift 1985, Cook et al. 1996). Although previous models (e.g., Wisdom et al. 1986, Thomas et al. 1988) recognized the importance of forage condition in assessing habitat potential, operational application of these models often ignore this component (Cook et al. 1996). A coarse-grained strategy for linking nutrition to elk reproductive potential was needed (Cook et al. 1996). The model presented herein relies on relationships between the ecological classification system, associated plant assemblages, and site responses to historic disturbances to provide a coarse index to forage quality and quantity across planning landscapes. Also, integration of an annual temporal component via partitioning elk life history into periods provides a means of indexing the effects of seasonal plant phenology on forage condition (Edge et al. 1988).

An evaluation of forage quality and quantity is estimated using characteristics of the ecosystem diversity matrix (i.e., elevation and moisture gradients, canopy closure, aspect, seral stage, site potential) to assign relative forage values to different ecological units (Fig. 3). For example, the ecological unit highlighted in Figure 3 can be characterized as a pine-and fir-dominated forest with a sparse understory that generally provides moderate to high forage value for elk. The value to elk varies according to season, topographic aspect, canopy closure, seral stage, and historic land use. To account for seasonal variation in forage quality and quantity, a forage potential matrix is developed for each elk life history period (Fig. 4). Subsequently, seasonal modifiers for each life history period are applied. For example, a snow modifier should be applied to the winter survival matrix for ecological units subjected to deep snows (Fig. 4). Similarly, forage scores for the "Spring movement, calving" period are weighted heavier than other seasons because of the annual spring flush of vegetation growth (Riggs et al. 1996) (Fig. 4). Although different site potential classes (i.e., columns in the matrix) often tend to reflect topographic aspect (Steele et al. 1981), each site potential class is divided into 2 categories of aspect (north/east and south/west) to account for differential plant phenologies. North and easterly aspects (320-140°) are assumed to have delayed plant phenology relative to south and westerly aspects (141-319°). Flat areas (i.e., no aspect effect) are assumed to

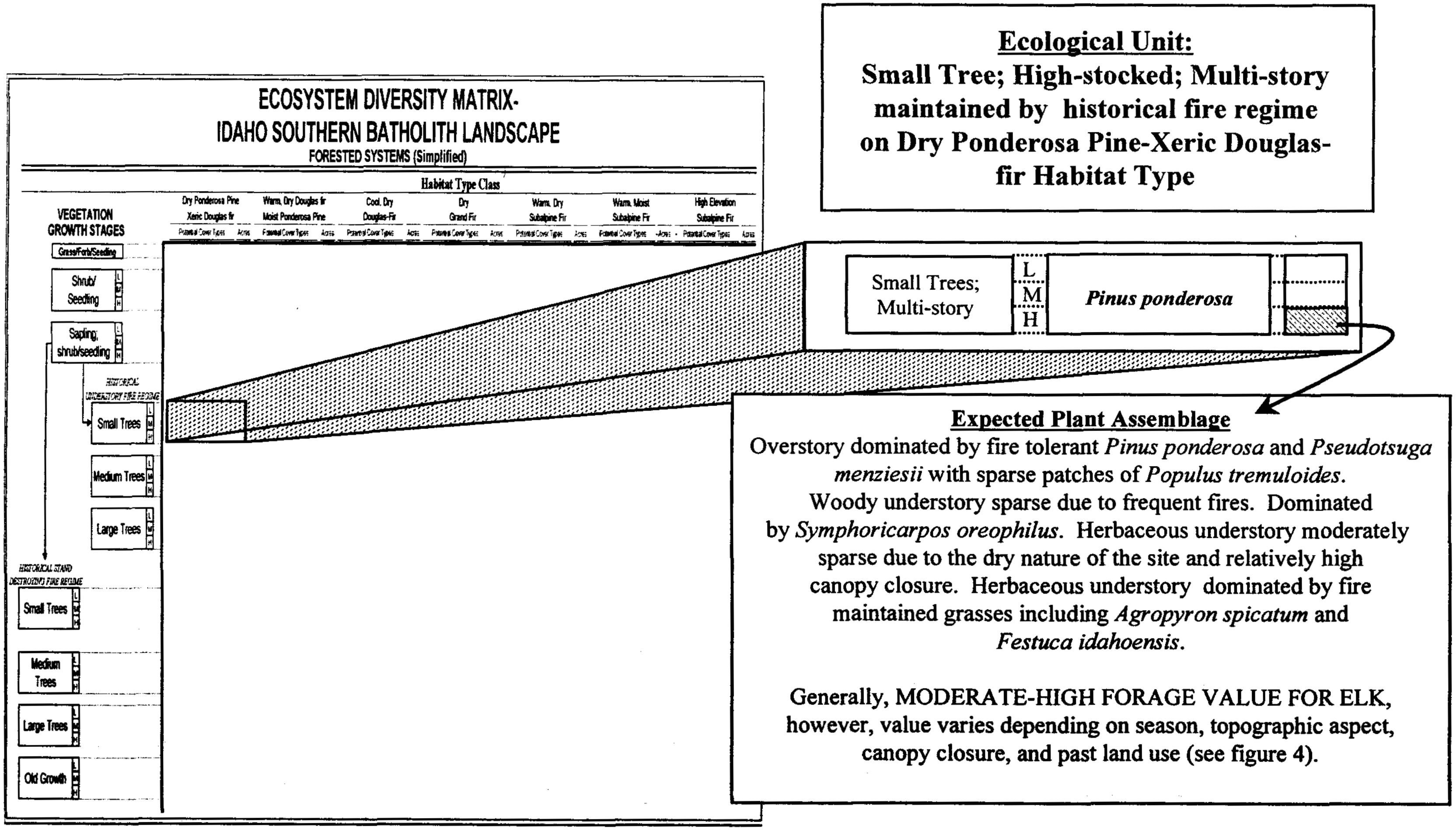


ECOSYSTEM DIVERSITY MATRIX-
IDAHO SOUTHERN BATHOLITH LANDSCAPE
FORESTED SYSTEMS (Simplified)

Habitat Type Class

VEGETATION GROWTH STAGES	Dry Ponderosa Pine Xeric Douglas fir		Warm, Dry Douglas fir Moist Ponderosa Pine		Cool, Dry Douglas-Fir		Dry Grand Fir		Warm, Dry Subalpine Fir		Warm, Moist Subalpine Fir		High Elevation Subalpine Fir	
	Potential Cover Types	Acres	Potential Cover Types	Acres	Potential Cover Types	Acres	Potential Cover Types	Acres	Potential Cover Types	Acres	Potential Cover Types	Acres	Potential Cover Types	Acres
Grass/Forb/Seedling														
Shrub/ Seedling L M H	*Pinus ponderosa*		*Pinus ponderosa* *(Pinus contorta)* *(Populus tremuloides)*		*(Pinus contorta)* *(Populus tremuloides)*		*Pinus ponderosa* *Pseudotsuga menziesii* *(Populus tremuloides)*		*Pseudotsuga menziesii* *(Pinus contorta)* *(Populus tremuloides)*		*(Pinus contorta)* *(Larix occidentalis)*		*Pinus albicaulis*	
Sapling; shrub/seedling L M H	*Pinus ponderosa*		*Pinus ponderosa* *(Pinus contorta)* *(Populus tremuloides)*		*(Pinus contorta)* *(Populus tremuloides)*		*Pinus ponderosa* *Pseudotsuga menziesii* *(Populus tremuloides)*		*Pseudotsuga menziesii* *(Pinus contorta)* *(Populus tremuloides)*		*(Pinus contorta)* *(Larix occidentalis)*		*Pinus albicaulis*	
HISTORICAL UNDERSTORY FIRE REGIME	*Understory Burn* *5 -25 Years*		*Understory Burn* *10-22 Years*		*Understory Burn* *25-100 Years*		*Understory Burn* *10-30 Years*		*Fire Mosaic* *50-90Years*		*Some* *Understory Burn*		*Understory Burn* *25-70 Years*	
Small Trees L M H	*Pinus ponderosa*		*Pinus ponderosa* *(Pinus contorta)* *(Populus tremuloides)*		*(Pinus contorta)* *(Populus tremuloides)*		*Pinus ponderosa*		*Pseudotsuga menziesii* *(Pinus contorta)* *(Populus tremuloides)*		*(Pinus contorta)* *(Larix occidentalis)*		*Pinus albicaulis*	
Medium Trees L M H	*Pinus ponderosa*		*Pinus ponderosa* *(Pinus contorta)*		*Pseudotsuga menziesii* *(Pinus contorta)*		*Pinus ponderosa*		*Pseudotsuga menziesii* *(Pinus contorta)*		*(Pinus contorta)* *(Larix occidentalis)*		*Pinus albicaulis*	
Large Trees L M H	*Pinus ponderosa*		*Pinus ponderosa*		*Pseudotsuga menziesii*		*Pinus ponderosa*		*(Pinus contorta)*		*(Larix occidentalis)*		*Pinus albicaulis*	
HISTORICAL STAND DESTROYING FIRE REGIME	*Stand Destroying* *Wildfire Unlikely*		*Stand Destroying* *Wildfire Unlikely*		*Some Stand* *Destroying Wildfire*		*Stand Destroying* *Wildfire Unlikely*		*Fire Mosaic* *50-90 Years*		*Stand Destroying* *Wildfire*		*Stand Destroying* *Wildfire*	
Small Trees L M H	*Pinus ponderosa* *(Pseudotsuga menziesii)*		*Pinus ponderosa* *(Pinus contorta)* *(Populus tremuloides)* *(Pseudotsuga menziesii)*		*Pseudotsuga menziesii* *(Pinus contorta)* *(Populus tremuloides)*		*Pinus ponderosa* *Pseudotsuga menziesii* *Abies grandis* *(Populus tremuloides)*		*Pseudotsuga menziesii* *(Pinus contorta)* *(Populus tremuloides)*		*Pseudotsuga menziesii* *Picea engelmannii* *(Larix occidentalis)* *(Pinus contorta)*		*Pinus albicaulis*	
Medium Trees L M H	*Pinus ponderosa* *(Pseudotsuga menziesii)*		*Pinus ponderosa* *Pseudotsuga menziesii*		*Pseudotsuga menziesii* *(Pinus contorta)*		*Pinus ponderosa* *Pseudotsuga menziesii* *Abies grandis*		*Pseudotsuga menziesii* *Picea engelmannii* *(Pinus contorta)*		*Pseudotsuga menziesii* *Picea engelmannii*		*Abies lasiocarpa* *Pinus albicaulis* *Picea engelmannii*	
Large Trees L M H	*Pinus ponderosa* *(Pseudotsuga menziesii)*		*Pinus ponderosa* *Pseudotsuga menziesii*		*Pseudotsuga menziesii*		*Pinus ponderosa* *Pseudotsuga menziesii* *Abies grandis*		*Picea engelmannii* *Abies lasiocarpa*		*Pinus ponderosa* *Pseudotsuga menziesii* *Abies grandis*		*Abies lasiocarpa* *Pinus albicaulis* *Picea engelmannii*	
Old Growth L M H	*Pinus ponderosa* *(Pseudotsuga menziesii)* ≥ 5 trees ≥ 24" dbh/ac. Snags - infrequent		*Pinus ponderosa* *Pseudotsuga menziesii* ≥ 10 trees > 24" dbh/ac ≤ 1 Snag ≥ 20" dbh/ac		*Pseudotsuga menziesii* ≥10 trees ≥ 18" dbh/ac ≤ 3 Snags ≥ 16" dbh/ac		*Abies grandis* ≥ 15 trees ≥ 24" dbh/ac ≥ 2 Snags ≥ 20" dbh/ac		*Abies lasiocarpa* *Picea engelmannii* >25 trees >24" dbh/ac ≥ 2 Snags ≥ 12" dbh/ac		*Abies lasiocarpa* *Picea engelmannii* >25 trees >24" dbh/ac ≥ 2 Snags ≥ 12" dbh/ac		*Abies lasiocarpa* *Pinus albicaulis* *Picea engelmannii* ≥ 10 trees ≥ 12" dbh/ac	

Figure 2. An example ecosystem diversity matrix for the Idaho Southern Batholith physiographic province (from Haufler et al. 1996).



Ecological Unit:
Small Tree; High-stocked; Multi-story maintained by historical fire regime on Dry Ponderosa Pine-Xeric Douglas-fir Habitat Type

Expected Plant Assemblage

Overstory dominated by fire tolerant *Pinus ponderosa* and *Pseudotsuga menziesii* with sparse patches of *Populus tremuloides*. Woody understory sparse due to frequent fires. Dominated by *Symphoricarpos oreophilus*. Herbaceous understory moderately sparse due to the dry nature of the site and relatively high canopy closure. Herbaceous understory dominated by fire maintained grasses including *Agropyron spicatum* and *Festuca idahoensis*.

Generally, MODERATE-HIGH FORAGE VALUE FOR ELK, however, value varies depending on season, topographic aspect, canopy closure, and past land use (see figure 4).

Figure 3. An example of using characteristics of the ecosystem diversity matrix to estimate plant assemblage.

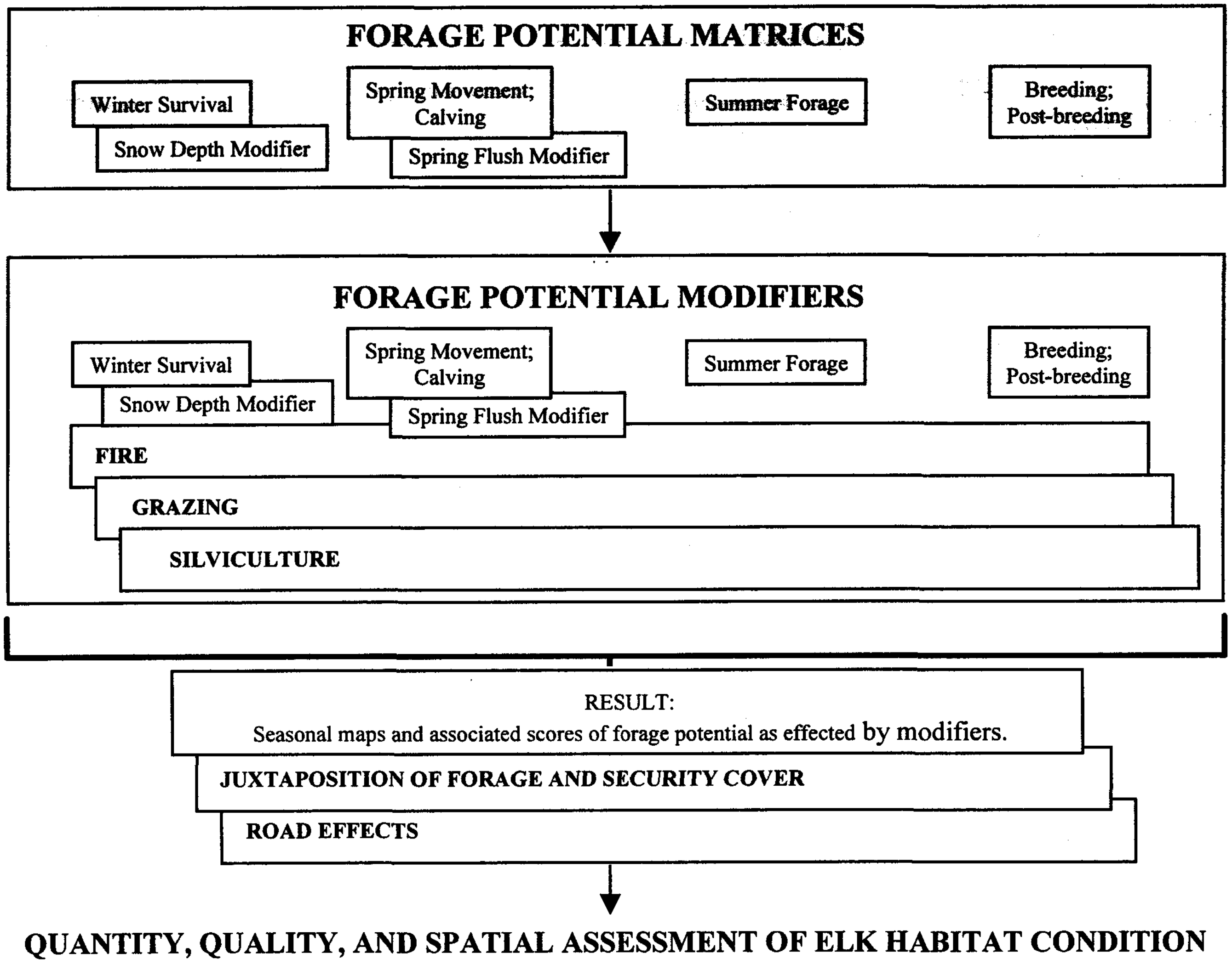


Figure 4. Schematic of the elk habitat potential model.

provide the same forage values as south and west aspects.

Each vegetation growth stage (rows in the matrix) is partitioned into 3 canopy closure classes (Fig. 3). Canopy closure is used to scale the effects of shading on understory and ground layer plant species with the general assumption that increases in canopy closure associate with a decrease in understory and ground cover (see review in Riggs et al. 1996). Also, shaded sites tend to exhibit a delayed plant phenology relative to unshaded areas. Seral vegetation growth stages are assumed to provide greater shrub cover (if shrubs were identified as a primary component of the ecological unit) and understory and ground cover are assumed to increase as canopy lift increases (more mature ecological units exhibit greater canopy lift). Single-storied, densely-stocked vegetation growth stages (e.g., small trees; Fig. 1) are assumed to have no shrub and tree regeneration. A culmination of these factors results in 4 forage potential matrices corresponding to each life history period (Fig. 4). In the absence of empirical information on digestibility and energy content by ecological unit, each matrix contains relative indices to forage potential. By linking the ecological units to a geographic information system, a spatial map of forage potential can be portrayed.

Although the ecosystem diversity matrix is a useful tool for coarsely quantifying plant assemblages across planning landscapes (Haufler et al. 1996), knowledge of historic land use is crucial to understanding plant ecology and associated forage value to elk at any individual site. The ability to integrate historic land use and forage potential is as much an exercise in geographic information system and database updates as it is in modeling. Historic land use is a spatial parameter that must be mapped, attributed, and continuously updated. For example, the effects of fire on winter survival forage scores will not modify the entire winter survival matrix (because these are average conditions expected to occur across the planning landscape), but rather, fire effects must be applied only to the spatial extent of the ecological units that were burned. Thus, fire effects on forage potential are spatially explicit. The proposed model framework may be used to integrate historic land use (e.g., fire, grazing, silviculture) by using modifiers on the forage potential matrices (Fig. 4).

In summary, approximations of forage condition can be made for numerous physiographic provinces throughout elk range. The foundation of the method is a well-founded ecosystem diversity matrix and an ability to approximate plant assemblages for each ecological unit. Considerable work has been conducted on classifying existing vegetation (see review in Grossman et al. 1997) and site potential guides and associated data exist for a variety of ecological regions [e.g., the Blue and Ochoco mountains (Johnson and Clausnitzer 1992), the Okanogan National Forest (Williams and Lillybridge 1983), the Mount Hood and Willamette national forests (Hemstrom et al. 1982, Halverson et al. 1986, Topik et al. 1988), the Gifford Pinchot National Forest (Brockway et al. 1983, Topik et al. 1986, Topik 1989), and much of Montana (Pfister et al. 1977)]. These tools provide the framework from which to construct a structured, defensible, spatially explicit perspective on forage quality and quantity.

SECURITY MODULE

Security cover is an important component of elk habitat for most life history periods, except perhaps for summer foraging (Skovlin 1982). Thomas et al. (1979) defined security cover as vegetation capable of hiding 90% of a standing adult elk from the view of a human at a distance ≤61 m. Generally, conifers begin providing this type of cover when they are 1.8 to 2.4 m tall and will continue to provide cover up to 6.4 m (Canfield et al. 1986). Brunt and Ray (1986) provided some guidance for delineating security cover by developing a model based on stand density and average diameter from tree growth and yield tables, however, they did not incorporate understory cover in their assessments. Security cover quality influences the spatial extent of elk use of adjacent forage areas.

Security cover quality varies according to stem density, conifer height, and understory cover (<3 m tall). For modeling purposes, a mathematical relationship between conifer height, stem density, and understory cover is used to index security cover quality on a scale of 0.00 to 1.00. Mapped polygons that provide some level of security cover (i.e., the index is >0.00) are subsequently evaluated for patch size. Brunt and Ray (1986) noted that security cover must be >120 m in width to function adequately, however, dense habitat patches may be functional at considerably shorter sight distances (Elk Modeling Workshop 1996). Witmer et al. (1985) presented a linear relationship between distance into cover and elk habitat use for forests west of the Cascade crest. Their relationship implied that all security cover provided some value no matter how low the quality. In the Idaho Southern Batholith, Roloff (1997) deemed highest quality security cover (i.e., index of 1.00) functional at 30 m into the security patch. As security cover quality decreases, it is assumed that elk must be further into the cover patch. The relationship between security cover quality and distance into the patch is determined according to physiographic province. For example, planning landscapes east of the Cascade crest undoubtedly have different security cover spatial relationships then landscapes west of the crest. In the Idaho Southern Batholith, the relationship was portrayed as a linear function with optimum security cover functional at 30 m and poor security cover (i.e., index of 0.01) functional at 120 m (Roloff 1997). Each map polygon identified as security cover (i.e., security cover score is >0.00) is internally buffered depending on the quality score to produce the portion(s) of the security cover polygons that are functional. For example, a polygon with a security cover score of 1.00 would be internally buffered by 30 m and the "core" is retained in the analysis as functional security cover.

Unique features of the landscape (e.g., topography, slash piles) may also provide functional security cover, though Thomas et al. (1979) noted that topography alone has not been demonstrated as a substitute for vegetation. Topography in combination with vegetation, however, can have a major impact on the value of a particular vegetation type (Thomas et al. 1979). The combinations of unique features that may provide functional security cover are infinite and quantification of these areas have been omitted from this model framework. Users of this model are recommended to identify, map, and assign attributes to unique cover features across their planning landscape so the model accounts for these areas in assessing habitat potentials.

The product of the security cover module is a map of internally buffered polygons and associated security cover index that represent functional security cover. The security cover map is used in conjunction with the maps and indices from the foraging module to rate overall forage quality for the planning landscape.

INTEGRATING FORAGE AND SECURITY HABITATS MODULE

Considerable work on the spatial relationships between suitable cover and forage has been conducted (see reviews in Thomas et al. 1979 and Thomas et al. 1988). Leckenby (1984) demonstrated that elk use of foraging areas decreased as distance from suitable security cover increased and Irwin and Peek (1983*a*) and Lyon and Jensen (1980) noted that elk use of different vegetation types for foraging was often tempered by the quality of security cover in adjacent forests. Wisdom et al. (1986) presented a distance band methodology for evaluating the effectiveness of habitats based on proximity to suitable cover for Roosevelt elk (*C. e. roosevelti*). Based on Leckenby's (1984) data, Thomas et al. (1988) developed similar forage quality modifier values based on proximity to security cover for the Blue Mountains of Oregon. It is important to note that the proximity of security cover has an impact on use of forage areas and not on forage quality. Vegetation types may be providing optimum forage potential, however, elk may not use the areas due to a lack of security cover (Elk Modeling Workshop 1996).

An overlay of the map outputs from the foraging and security modules produce 6 possible outcomes for individually mapped polygons:

Forage Score	Security Score	Relationship
>0.00	1.00[2]	Forage score = Forage score
0.00[1]	1.00[2]	Forage score = 0.00
>0.00	0.01 to 0.99[3]	Forage score = (forage score* security score)$^{0.5}$
0.00[1]	0.01 to 0.99[3]	Forage score = 0.00
>0.00	0.00[4]	Juxtaposition index (Thomas et al. 1988).
0.00[1]	0.00[4]	Forage score = 0.00

[1] No food. [2] Optimal. [3] Sub-optimal. [4] No cover.

For polygons containing food but not having any security cover (e.g., open meadows), the juxtaposition index applies as developed by Thomas et al. (1988). The Thomas et al. (1988) forage quality modifiers establish effective foraging bands into the foraging polygon based on the assumption that adjacent security cover was optimal. Thus, suitable foraging polygons (i.e., forage index >0.00) that do not overlap but are adjacent to optimal security cover are internally buffered at 91, 274, and 732 m resulting in 4 distance bands: 0-91, 92-274, 275-732, and 732+ (Thomas et al. 1988). The model presented herein expands upon Thomas et al. (1988) in that the buffer band widths are weighted according to the security cover index. For example, a security cover patch of 0.90 quality would influence the amount of adjacent forage habitat by reducing the effective foraging distance bands to 82 m (91 m x 0.90), 247 m (274 m x 0.90), and 659 m (732 m x 0.90). The "Integrating forage and security habitats" module produces 4 map products (1 for each season) that delineate effective foraging bands, functional security cover, and associated foraging and security quality index scores. In contrast to previous models that designated map polygons as either cover or forage (e.g., Wisdom et al. 1986, Thomas et al. 1988), this model recognizes that polygons can provide both forage and security value and offers a methodology to account for this phenomenon by season.

SPECIAL HABITAT REQUIREMENTS MODULE

Depending on the geographic region of model application, special habitat requirements may be a resource planning issue. For example, during the spring movement, the calving life history period in the Blue Mountains of Oregon, calving cover may be an important limiting factor (Thomas et al. 1979). During the calving period, optimal cover is apparently provided by forested stands dominated by shrubs or downed logs. Calving habitat is usually located on spring or fall ranges where slopes are relatively gentle (Thomas et al. 1979). In addition to delineating potential calving habitat based on vegetation inventory information, it is recommended that historical calving areas be mapped and attributed in the geographic information system so that these areas can be portrayed on the map products from the model.

Another special habitat requirement appears to be cover during the breeding, post-breeding period. Research has demonstrated that elk tend towards areas where large percentages of the surrounding vegetation types have >75% canopy closure during this period (Edge et al. 1987). Irwin and Peek (1983*a*) found that elk preferred pole-size vegetation types with >75% canopy closure, but avoided cool-moist grand fir and subalpine fir (*A. lasiocarpa*) habitat types. As the breeding, post-breeding period progresses, elk continue their selection for dense vegetation types and make little use of clearcuts, grass-shrub, or seral brush field types (Irwin and Peek 1983*a*). The selection of dense, closed canopy forest types is probably a function of 2 factors; an increase in succulent forage under closed canopies and an increase in human disturbance. Suitable breeding, post-breeding cover can be delineated based on vegetation attribute information (e.g., canopy closure exceeding 70%), or a minimum security index (computed in the security cover module) can be selected. A minimum security cover score of 0.70 was selected for the Idaho Southern Batholith example to ensure that all 3 vegetation attributes associated with the security cover computation are present for suitable breeding, post-breeding cover (Roloff 1997). The minimum of 0.70 was selected based on the mathematics used to combine the vegetation attributes of conifer height, stem density, and understory cover (≥3 m tall) in the Idaho example (Roloff 1997). For planning landscapes in which breeding, post-breeding cover is deemed a limiting factor, the security cover polygons with index scores >0.70 are used to delineate effective forage habitat (as opposed to the entire range of suitable security polygons, see module 3) for this life history period. Other effective foraging areas that were delineated in the security cover module are retained in the analysis (because elk tend to forage in open areas after the first frost [Elk Modeling Workshop 1996]), however, managers should strive for at least 40% of the breeding, post-breeding range in security cover with security cover scores in excess of the minimum threshold (e.g., ≥0.70 for the Idaho example; Roloff 1997).

ROAD EFFECTS MODULE

The primary factor affecting habitat effectiveness for deer and elk has been recognized as the presence, density, and human use of roads (Thomas et al. 1979, Lyon 1983). The effects of roads on elk habitat use has been reviewed extensively elsewhere (e.g., Thomas et al. 1979, Thomas et al. 1988). Road effects depend on the type of road, its location, and intensity of use. To properly apply the road module, a detailed road map layer, with associated attributes, is required. Ideally, a measure of vehicular traffic intensity, periodicity, and time of use for each road in the planning landscape should be used to index road effects on the spatial use of elk habitat (Elk Modeling Workshop 1996). In the absence of road use data, different indices have been developed based on road type. For example, Perry and Overly (1977) grouped roads into 3 classes and scaled road effects accordingly:

1) primary roads at least 1½ lanes wide that are improved, in good condition, are the main route of travel, and receive constant maintenance,

2) secondary roads that are at least 1½ lanes wide, somewhat improved such that they are in good to fair condition, and receive irregular maintenance, and

3) primitive roads that are 1-lane, unimproved in fair to poor condition, that are seldom maintained.

The assumption that road type is a suitable surrogate for road use has met considerable skepticism (Elk Modeling Workshop 1996) and users of the model should attempt to avoid this situation.

Historically, habitat effectiveness models have used the linear measure of roads per unit area (density) to modify habitat scores (e.g., Thomas et al. 1979, Wisdom et al. 1986, Thomas et al. 1988). The approach presented herein offers an alternative means for assessing road impacts based on the spatial arrangement of security cover relative to roads and the road use or intensity index.

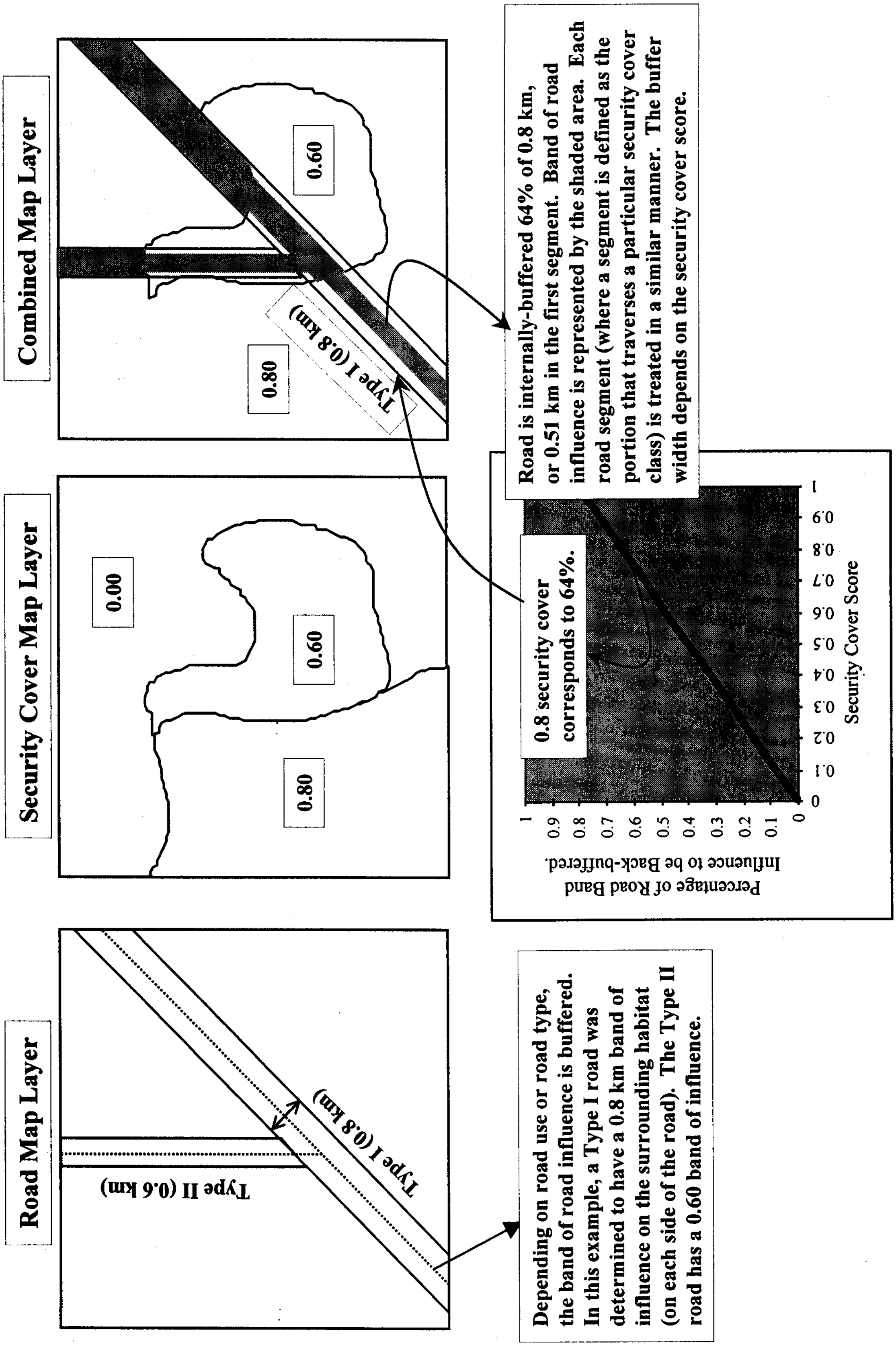
For each planning landscape, a band of road influence should be assigned. The first step in evaluating the effects of roads on habitat effectiveness of a herd range is to buffer the roads by these distance bands. Distance bands will vary according to planning landscape, road use or road type, and users of this model are encouraged to develop their own relationships. For example, Roloff (1997) used a simple methodology in an example for the Idaho Southern Batholith based on road type. Again, the intent of this model is to provide a system that permits local experts to input their knowledge into the habitat assessment thus avoiding the "one-size-fits-all" paradigm.

The juxtaposition of security cover and roads is factored into the habitat analysis. The road distance bands are overlaid with the security cover map generated from the security cover module (Fig. 5). The band of road influence is subsequently back-buffered (towards the road) based on the quality of adjacent security cover (Fig. 5). In the Idaho example, it was assumed that optimum security cover (i.e., security cover score is 1.00) provided protection 0.15 km from a primary road, or an 80% reduction in road band influence (Roloff 1997). The reduction in road band influence is applied to all roads to delineate the road influence map. The final step in the road effects module is to overlay the road influence maps with the habitat potential maps generated by the previous modules. The resultant maps denote areas of effective habitat that provide the spatially constrained view of habitat potential and several area-weighted habitat potential scores that index quality (Fig. 4).

SUMMARY AND CONCLUSIONS

Several products are generated from the elk habitat potential model including: 1) winter survival; spring movement, calving; summer forage; and breeding, post-breeding habitat potential maps and associated quality indices as modified by snow depth, spring vegetation flushes, and historic land use as appropriate, 2) functional security cover map and associated quality indices, 3) effective foraging map generated from integrating forage and security assessments, 4) maps of any special habitat requirements (e.g., calving areas), and 5) maps of road effects according to season. These products can then be used to evaluate elk habitat potential, habitat effectiveness, and to identify and manage limiting factors.

This model is currently being automated as an expert system in a geographic information system and database manager. This model is data intensive, requiring a commitment to describing and updating both map and vegetation inventory information. The complexity of elk habitat relationships warrants an extensive data commitment. Meaningful elk habitat assessments and effective management require these data and resource managers and planners should strive for timely and accurate information.



Depending on road use or road type, the band of road influence is buffered. In this example, a Type I road was determined to have a 0.8 km band of influence on the surrounding habitat (on each side of the road). The Type II road has a 0.60 band of influence.

0.8 security cover corresponds to 64%.

Road is internally-buffered 64% of 0.8 km, or 0.51 km in the first segment. Band of road influence is represented by the shaded area. Each road segment (where a segment is defined as the portion that traverses a particular security cover class) is treated in a similar manner. The buffer width depends on the security cover score.

Figure 5. Applying the road effects logic to an example landscape from the Idaho Southern Batholith (Roloff 1997).

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Applying GIS Technology to Test an Elk Habitat Effectiveness Model in North-Central Wyoming

H. HALL SAWYER
FREDERICK G. LINDZEY
BERT A. JELLISON
Wyoming Game and Fish Department, Sheridan, WY 82801

Abstract: We used Geographic Information System (GIS) technology to evaluate a summer habitat model for Rocky Mountain elk inhabiting the Bighorn National Forest (BNF) in north-central Wyoming. Model structure was based on elk habitat models developed in Washington and Oregon. Model variables included: 1) road density, 2) size and spacing of forage/cover areas, 3) cover quality, and 4) steepness of slope. We monitored 107 radiocollared elk (40 males, 67 females) from 1994-1996 to determine if any relationship existed between habitat variables and elk use in the BNF. Model variables were measured at 1994 and 1995 elk locations and then compared to model predictions. Results indicated elk on the BNF were more sensitive to road density and slope than predicted by the model. The model was adjusted accordingly, and tested using variables measured at 1996 summer elk locations. The adjusted model better reflected the relationship between elk and their habitats on the BNF.

Key words: *Cervus elaphus*, Geographic Information System (GIS), habitat effectiveness (HE) model, habitat use, Rocky Mountain elk, summer range.

INTRODUCTION

Determining the effects that different land uses have on elk (*Cervus elaphus*) habitat is a priority for wildlife agencies (Boyd et al. 1986). Various models have been developed to predict how wildlife species respond to habitat changes. Evaluation of habitat variables can be expressed in terms of habitat effectiveness (HE), which is defined as the proportion of achievement relative to an optimum condition, where conditions may range from optimum use (1.0) to minimum use (0.05) (Wisdom et al. 1986). Burcham and Jellison (1993) used Map and Image Processing Software (MIPS; MicroImages, Lincoln, Nebraska) and associated coverages (canopy closure, digital elevation model [DEM], vegetation, road networks) to develop a GIS-based summer HE model for elk in the BNF. Habitat models have been used extensively in the Pacific Northwest (Thomas et al. 1979, Witmer et al. 1985, Wisdom et al. 1986, Thomas et al. 1988) to assess changes in habitat and have served as a basis for models in other areas. Habitat variables and structure used in the BNF model were adapted from a model developed in western Oregon (Wisdom et al. 1986).

Wisdom et al. (1986) evaluated elk habitat based on the interactions of 4 variables: 1) density of roads open to motorized vehicles, 2) size and spacing of forage and cover areas, 3) cover quality (hiding, thermal, optimal), and 4) forage quality. The BNF model used the same variables with the exception of forage quality, which was replaced with a slope variable (Skovlin 1982). This modification better approximated habitat conditions on the BNF, where forage is not thought to be a limiting factor during summer. Although managers have little control over slope, the use of this variable emphasizes the importance of providing elk with habitat on gentler slopes.

Elk HE in the BNF was based on the following model (Burcham and Jellison

1993), where each variable consisted of a raster-based map with HE values assigned to 30 m x 30 m pixels:

HE = $V_1 \times (V_2 \times V_3 \times V_4)^{1/N}$
where V_1 = density of open road (miles of road/mi^2)
V_2 = sizing and spacing of forage and cover areas
V_3 = cover quality (hiding, thermal, optimal)
V_4 = steepness of slope (%)
$1/N$ = Nth root of the product taken to obtain the geometric mean

The specific relationship between road density and elk HE was defined by Lyon (1983). However, because elk use of habitat is strongly affected by road densities (Irwin and Peek 1979, Thomas et al. 1979, Witmer and deCalesta 1985, Grover and Thompson 1986, Edge et al. 1987, Edge and Marcum 1991, Lyon and Canfield 1991, Cole et al. 1997), considerably more weight (one-half of the cumulative HE score) was placed on this variable. Roads open to motorized traffic were digitized from Bureau of Land Management 1:100,000 maps and no distinction was made between primary, secondary, and tertiary roads. Refer to Wisdom et al. (1986), Burcham and Jellison (1993), or Sawyer (1997) for detailed descriptions of the V_2, V_3, and V_4 habitat variables.

Before HE models are applied to management situations they should be validated to determine which variables are more important in evaluating habitat quality (Edge et al. 1990, Holthausen et al. 1994). Unfortunately, little model validation is done because of time and budget constraints. The objective of this study was to evaluate the BNF summer elk model and modify it as warranted to better reflect elk habitat use patterns using GIS technology and locational data from radiocollared elk. Much of the work that the BNF elk model is based on uses standard measures, as opposed to the metric system. We used standard measures rather than metric to facilitate comparisons with the original BNF model and to be consistent with the research on which it was based.

STUDY AREA

The BNF was located in north-central Wyoming and encompasses 2,500 km^2, at elevations ranging from 1,200 - 4,018 m. Annual precipitation varied from 25 cm on the west side of the range, to 41 cm on the east, and to 72 cm at higher elevations. Vegetation was typical of the central Rocky Mountain region, with low-elevation juniper (*Juniperus osteosperma*), mid-elevation ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), with lodgepole pine (*Pinus contorta)* and spruce-fir (*Picea engelmannii* and *Abies lasiocarpa*) dominating the higher elevations. Aspen (*Populus tremuloides*) stands are present, but infrequent. The BNF was characterized by frequent large, natural openings and high-elevation gentle slopes, often dominated by big sagebrush (*Artemisia tridentata*) and/or Idaho fescue (*Festuca idahoensis*). Land-uses include livestock grazing, logging, and a variety of recreational activities. Despain (1973) provides a detailed description of vegetation, soils, geology, and climate of the Bighorn Mountains.

METHODS

Eighty mature (≥2 1/2 yrs) elk were captured with net-guns fired from helicopters and fitted with radiocollars during the winter of 1993-94. Seventeen elk were radiocollared during the winter of 1994-95, and another 10 in the winter of 1995-96. Elk captures were stratified proportionately to elk distributions on the winter ranges bordering the western and southern boundaries of the BNF.

Movements of radiocollared elk were monitored 1-2 times per month using a fixed-wing aircraft from 1994-1996. Relocation flights were conducted with a 160 horse-powered Arctic Tern; a small, 2-seat plane designed for low-level flying (20-25 m) and low air speeds (60-80 km/hr). Universal Transverse Mercator (UTM) coordinates were recorded from a Global Positioning System (GPS). Accuracy tests of GPS coordinates on known locations had a mean error of 53 m (SE = 11.4). An effort was made to visually locate elk at different times of the day to avoid biasing the sample toward crepuscular or diurnal habitat selection. Only locations within the BNF boundaries and between the dates of June 15 and August 17 were used in analyses.

Model evaluation/adjustment

Aerial locations of radiocollared elk from 1994 and 1995 were used to evaluate model performance by comparing actual elk-habitat relationships with those predicted by the model. Elk locations were assigned HE values for road density (V_1), size and spacing of cover/forage (V_2), cover quality (V_3), and steepness of slope (V_4) by overlaying UTM coordinates onto raster-based maps containing the HE values of each variable. The HE relationships constructed from these data were plotted to reflect actual elk use, and then compared with the HE relationships used in the original BNF elk model. When differences occurred, HE relationships of the model were replaced with those from the actual elk data. Two-sample *t*-tests (TWOT, MINTAB Ver.10, 1994) were used to detect significant ($P < 0.01$) differences between male and female elk data for each habitat variable. To validate changes made to the original model and assess the predictive power of the adjusted model, HE relationships for each habitat variable were calculated for 1996 elk locations and compared with those in the adjusted elk model.

RESULTS

Three hundred ninety-one (308 female, 83 male) aerial locations for 97 (30 males, 67 females) radiocollared elk from 1994 and 1995 were used to evaluate the HE relationships of variables in the original BNF elk model.

V_1: Road Density

Data suggested elk on the BNF were more sensitive to road density than those in western Oregon and Washington, on which Lyon's (1983) curve, used in the initial BNF elk model, was based (Fig. 1). Average road density on the BNF was 0.88 mi. rd./mi², but elk selected areas that averaged 0.43 mi. rd./mi². Road density did not differ ($t = 0.56$; 114 df; $P = 0.58$) between male and female elk locations. This model variable was modified by replacing Lyon's (1983) curve with the curve produced by the 1994 and 1995 elk locations.

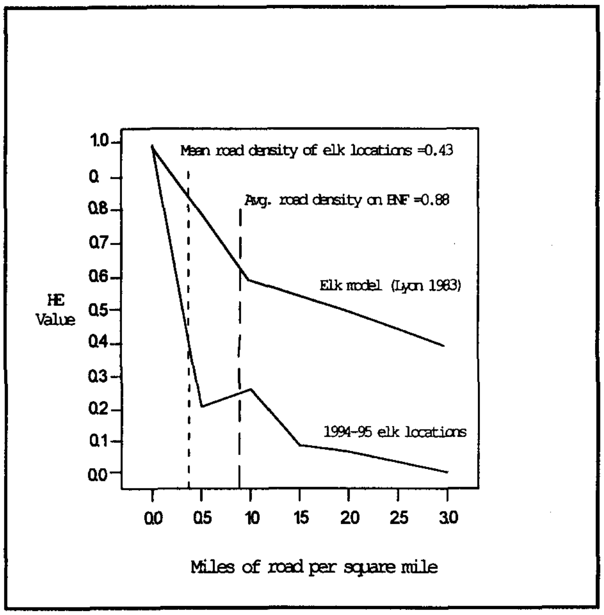

Figure 1. Comparison of Lyon's (1983) road density curve used in the original BNF elk model with the curve constructed from 1994-95 elk locations ($n = 391$) on the Bighorn National Forest, WY.

V_2: Size and spacing of forage and cover

Average HE value of the V_2 habitat variable at the 391 elk locations was 0.76 (SE = 0.15), while the average HE value on the entire BNF was 0.65. HE values at male and female locations did not differ ($t = 0.49$; 139 df; $P = 0.63$). These data suggested elk were selecting for areas along the forage-cover edge, adjacent to or within timber stands >200 m wide, as predicted by the HE relationship of size and spacing of forage/cover areas (Wisdom et al. 1986:14). No modifications were made to this habitat variable.

V_3: Cover quality

While Landsat™ image interpretation proved accurate for identifying timber types (B. Jellison, Wyoming Game and Fish Department, pers. commun.), it was not reliable for differentiating forest structure and successional stages necessary for assigning "hiding," "thermal," and "optimal" cover values to timber types. In its current form, this variable contributes nothing to the model and offers no insight into the evaluation of elk habitat.

A more reliable and straightforward method of evaluating cover quality is to eliminate the concepts of "optimal" and "thermal" cover, and simply rank timber types based on the amount of hiding cover they provide. There is increasing evidence that thermal cover, especially during the summer, is not critical to elk survival (Peek et al. 1982, McCorquodale et al. 1986, Groves and Unsworth 1993, Patterson 1996). Hiding cover appears to be more important for elk herds experiencing increased human disturbance (Peek et al. 1982, Edge et al. 1990). Other research indicates elk need security before feeding in an area (Knowles and Campbell 1982, Grover and Thompson 1986). Timber types were assigned the following HE values based on screening cover data collected by Sawyer (1997): spruce/fir = 1.0, Douglas fir = 0.9, early seral lodgepole = 0.8, lodgepole = 0.7, aspen = 0.7, and non-timbered areas = 0.5. A 0.1 drop in HE value reflects about a 10% decrease in the mean hiding cover value. In this form, V_3 emphasizes the importance of elk security and seemingly interacts well with V_2, giving foraging areas adjacent to better cover higher cumulative scores than those adjacent to poorer cover.

V_4: Slope

Although the average slope on the BNF was 98% (~43°), elk preferred slopes between 10% and 30% ($\bar{x} = 20$, SE = 0.52) (Fig. 2). Elk use of slopes over 30% decreased quickly. No elk use was recorded on slopes greater than 68%. Percent slope at male and female elk locations did not differ ($t = -1.22$; 112 df; $P = 0.23$).

This variable was modified by replacing the slope function in the BNF elk model with the function based on the 391 elk locations. Although elk use decreased on slopes between 0% and 10%, an HE value of 1.0 for this range was retained. We believe elk prefer gentler slopes, however, most flat areas in the BNF are roaded, which in turn limits elk use.

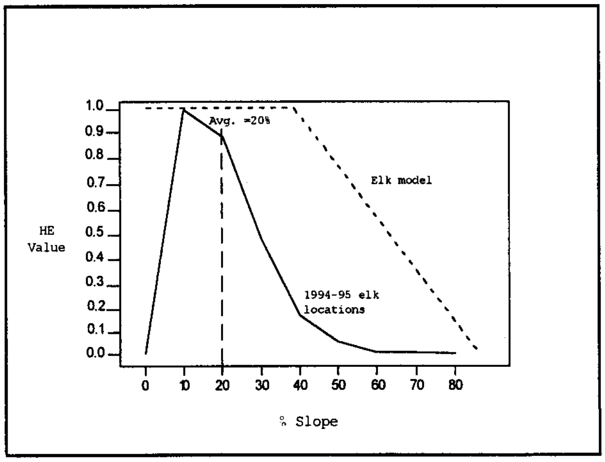

Figure. 2. Comparison of Skovlin's (1982) slope curve used in the original BNF elk model with the curve constructed from 1994-95 elk locations ($n = 391$) on the Bighorn National Forest, WY.

Evaluation of Adjusted Model

One hundred fifty-one (97 female, 54 male) aerial locations from 55 (17 males, 38 females) radiocollared elk between mid-June and mid-August 1996 were used to evaluate the HE relationships of the habitat variables in the adjusted model. Because many of the locations were from the same elk used in the 1994 and 1995 analyses, this was not a completely independent test. However, locations were from a different year and 10 new elk were included in the 1996 sample. Additionally, no significant ($P < 0.01$) differences were found between the 10 new elk and the other 45 elk in the 1996 sample in V_1 ($t = -0.43$; 58 df; $P = 0.67$), V_2 ($t = -1.56$; 83 df; $P = 0.12$), or V_4 ($t = 0.03$; 58 df; $P = 0.98$). HE curves based on the 1996 elk locations were plotted and compared with the curves used in the adjusted model for each of the 4 variables.

V_1: Road Density

The pattern of 1996 elk locations differed little from that predicted by the adjusted model. Elk selected areas that averaged 0.41 mi. rd./mi^2. Road density at male and female elk locations did not differ ($t = 2.05$; 79 df; $P = 0.04$). These data suggest that the adjustments made to V_1 were appropriate and the adjusted model accurately reflects how road densities affect elk use on the BNF.

V_2: Size and spacing of forage and cover

Average HE value of the V_2 habitat variable at 1996 elk locations was 0.75 (SE = 0.02), while the average HE value on the BNF was 0.65. HE values of male ($\bar{x} = 0.86$) and female ($\bar{x} = 0.68$) elk locations, however, differed significantly ($t = 3.72$; 147 df; $P = 0.0003$). Male elk apparently used areas along the forage-cover edge as predicted, while female elk used the forage-cover edge only in proportion to its availability.

V_4: Slope

Percent slope used by elk in 1996 was nearly identical to that predicted by the adjusted model. Again, elk preferred slopes between 10 and 30% ($\bar{x} = 20$, SE = 0.82). No elk use was recorded for slopes greater than 64%. Percent slope at male and female elk locations did not differ ($t = -0.74$; 128 df; $P = 0.46$).

DISCUSSION

Although testing and modifying models based on empirical data is generally an accepted approach, caution should be used when adjusting model parameters. Modification of model variables need to be justified and underlying assumptions understood. Adjustments made to the BNF model were supported by habitat selection patterns of elk in 1996. Although the 1996 data set was not strictly independent of the 1994-95 data sets on which model adjustments were made, the 10 new elk in the sample did not differ from the other elk in their habitat use.

The most influential change made to the original BNF elk model was the adjustment of the road density variable (V_1). Because of the low road densities on the BNF, most areas were assigned a V_1 HE value of 1.0 in the original elk model. Thus, not only was the original V_1 of little value in evaluating elk habitat, it also misinterpreted how elk on the BNF responded to road density. Data from 1994-95 indicated elk were more sensitive to road density than predicted by the model, rarely using areas where road densities exceeded 0.5 mi. rd./mi^2. The 1996 data supported replacement of Lyon's (1983) road density/HE curve in the original model with the curve generated from the 1994-95 elk relocation data.

Elk maximize forage intake and minimize their energy expenditures when forage and cover areas are of adequate size and in close proximity (Wisdom et al. 1986). The size and spacing of forage and cover areas variable (V_2) predicts HE decreases as the distance from the forage-cover edge increases, given that cover stands are at least 200 m in width. (Witmer et al. 1985, Wisdom et al. 1986, Thomas et al. 1988, Burcham and Jellison 1993). Elk on the BNF appeared to select for areas along the forage-cover edge and respond to (V_2) as the model predicted, by selecting for areas with above average HE values. Van Horne and Wiens (1991) also emphasized the importance of patch size and other landscape mosaic effects in the development of habitat models.

Modifications made to the cover quality variable (V_3) were intended to simplify the variable and emphasize the importance of hiding cover. Adjustments assume that cover types are accurately classified and updated to account for silviculture treatments and natural disturbances. As remote sensing techniques improve, other measures which describe the structure and successional stages of forest types may be better indicators of cover quality than simply screening cover. However, hiding cover will likely be the dominant characteristic of cover selected by elk during the summer (Sawyer 1997).

The slope variable (V_4) was adjusted to reflect elk use on the BNF. This modification was made assuming GIS slope measurements were as precise as those used in development of the Skovlin (1982) curve. However, it is possible that different methods used to calculate slope produce different results. The Skovlin (1982) curve was based on studies carried out in the 1970s, when slope was measured using a clinometer or estimated ocularly. Recent advances in computer technology allow slope to be calculated from DEMs using GIS software. Precision of these measurements depends on the resolution of the DEM. Whether these differences in methodology exist or not, it was desirable to use a curve developed from DEM data because this will undoubtedly be the method used to calculate slope in future models.

Assuming proportionate elk use is an accurate indicator of habitat quality, the modified BNF elk model should be an improvement over the original model because relationships between elk use and each variable are known. The modified model, while lowering HE values across the BNF, should have greater utility for management purposes because it identifies a broader range for potential habitat improvements. The modified BNF model is more sensitive than the original model, with road densities and slope characteristics now contributing to cumulative HE scores. The original model apparently would have resulted in erroneous conclusions about the effects of roads and slope on summer elk habitat in the BNF. In its modified form, for example, the model makes it more obvious how habitats may be improved by differing road management practices. Further, the modified model more accurately reflects the influence of slope and the quality of cover in cover-forage edges.

MANAGEMENT IMPLICATIONS

Management of public lands has become an area of considerable debate, as increasing demands are being placed on our natural resources. It is important to understand impacts of different land uses on animal populations and identify possible alternatives that may minimize the impact of habitat perturbations. The BNF elk model will provide agencies and industry with a tool to help assess the impacts of proposed activities on summer elk habitat and identify the best options. Further, GIS capabilities in conjunction with the elk model, allow different spatial scales (e.g., hunt area, watershed, diversity unit, forest-wide) to be examined such that cumulative effects and mitigation opportunities can be identified forest-wide, rather than simply at the scale of the proposed activity.

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Movements and Home-Ranges of Elk in Eastern Arizona

MARK C. WALLACE
Department of Range, Wildlife, and Fisheries Management
Texas Tech University, Lubbock, TX 79409-2125

PAUL R. KRAUSMAN
School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721

Abstract: Rocky Mountain elk near the southern limits of their distribution may respond to environmental conditions or use seasonal habitats differently than populations in the Northwest. We identify seasonal use areas and migration routes of Rocky Mountain elk on the White Mountain Fort Apache reservation in eastern Arizona. Yearly home-ranges in this population were large; 639 ± 465 (SE) km^2 for males and 386 ± 313 km^2 for females. Distances elk moved/day varied seasonally. Habitats were not represented in proportion to their availability in seasonal home-ranges. In summer, males selected spruce forests and associated clearcuts while females selected mixed-conifer associations. In winter, males selected juniper sites and sites where juniper had been removed. Females selected juniper and cleared sites but also used meadows and mixed-conifers greater than their availability.

Key words: Behavior, *Cervus elaphus nelsoni*, habitat, seasonal range, sexes.

INTRODUCTION

Rocky Mountain elk (*Cervus elaphus nelsoni*) populations in Arizona represent the southwestern extent of the species' distribution. Information about daily and seasonal movements of elk at the southern margins of their range is not available. Seasonal range use and migration routes are not delineated for most elk herds in Arizona (Arizona Game and Fish Department [AGFD] 1986), and no literature exists about elk that summer on the White Mountain Fort Apache Reservation (reservation). Our objectives were to identify and map seasonal use areas, migration routes, and home-ranges of elk in the White Mountains, Arizona in relation to sex and forest types.

Funding for this project was provided by the White Mountain Apache Game and Fish Department (WMGF), and the University of Arizona, School of Renewable Natural Resources. J. Jojolla and M. Brown helped with elk captures and data collection. We also thank Drs. R. W. Mannan, W. J. Matter, W. W. Shaw, and M. J. Zwolinski for their comments on earlier drafts of this manuscript.

METHODS

Our study in the White Mountains, Arizona (approx. 57° 5' N, 109° W) covered 5,107 km^2 of land, including the east half of the reservation and the adjacent portions of the Apache-Sitgreaves National Forest (ASNF), state, and private lands. Climate was sub-humid and supported 9 biotic communities (Brown 1982), from interior chaparral and Plains and Great Basin grasslands at the lower elevations (1,200-2,300m) to Rocky Mountain subalpine conifer and alpine tundra at the higher elevations (2,600-3,475m).

Elk were trapped on the reservation from October 1983 through July 1984 using a modified Clover trap (Clay et al. 1980). All captured elk were classified as yearling or adult and sex was recorded before being fitted with a color-coded collar and a numbered ear tag. Some captured elk were fitted with standard radio transmitters (MOD-500) with mortality sensors (model HP) (Telonics, Inc., Mesa, Ariz. transmitter wt = 255 g). Radiocollared elk were located 2X/month 1984-1986, from a Maule (Model E-5) aircraft using equipment and techniques described by Krausman et al. (1984). Ground observations of each radiocollared elk were made twice every 30-45 days. A radiocollared elk was located before 1200 and followed until dark. It was then relocated before sunrise the following day and followed until 1200. We tried to observe and follow radiocollared elk without disturbing normal movement patterns or behaviors. If observation disturbed our subject elk we made 1 attempt (after waiting 30 min) to locate and observe the animal again. No data from elk disturbed ≥1 time/day were used for our analyses of movements or home-range.

We mapped seasonal use areas and migration routes used by elk herds in the White Mountains from successive locations of radiocollared individuals and other marked and unmarked elk during aerial winter elk surveys and summer ground counts conducted by the WMGF (J. Jojolla, unpublished report, WMGF, 35pp. mim. 1984).

Seasonal home-ranges were determined from aerial and ground radio locations of elk (1 day apart). Only the first ground location for any elk observation period was included in home-range estimation. Although only initial locations from elk tracking periods were used in home-range calculations, these were compared to locations representing entire tracking periods to verify that they represented use areas from all times of day. We tested for independence of locations using Schoener's (1981) T^2/r^2 statistic following Swihart and Slade (1985). We used Minimum Convex Polygon (MCP) area observation (AO) curves (Odum and Kuenzler 1955) on MCP estimates to evaluate home-range sample adequacy. Sampling was considered adequate when mean increase over the last 5 successive locations was ≤1% of the home-range area.

Core areas of intensive use within the home-range and mean centers were determined using the harmonic mean (HM) method (Dixon and Chapman 1980, Boulanger and White 1990). Home-range MCP and HM estimates were calculated using the McPAAL software package (M. Stuwe and C.E. Blohowiak, Conserv. Res. Cent., Natl. Zool. Park, Smithsonian Inst., Front Royal, Va., 1985).

Home-range fidelity, the between-years overlap of an individual's estimated (MCP) home-range, was examined using methods described by Edge et al. (1985), though we chose Jaccard's measure of association (Hubalek 1982) and only included elk with adequately sampled home-ranges in ≥2 years. We used Mann-Whitney U to test differences in indices of home-range fidelity between sexes or seasons.

Distances traveled and individual elk movement data were determined entirely from ground observation data. Individual movement data were included only from undisturbed observations of elk during tracking periods ≥4 hours long. Individual daily use areas were obtained by combining observations of the same elk from consecutive days tracking periods.

The boundaries of this study were delimited by the outer bounds of all telemetry locations of all radiocollared elk during the entire study period. We assumed that this area represented the total habitat available to individual radiocollared elk during the study. Winter habitat was arbitrarily defined as areas <2,316 m elevation (the mean winter snow level) Mean winter snow level was determined from recorded snow accumulation values from 7 weather stations ranging in elevation from 1,547 m to 3,048 m on the study area. Transition (spring and fall) habitat included areas ≥2,316 m and ≤3,048 m. Summer habitats were areas ≥2,316 m elevation. Cliffs, lakes, and permanent human habitations were excluded, following Krausman et al. (1989), from determinations of elk habitat availability.

We estimated habitat availability on the study by placing 0.64-cm square grids randomly over forest type maps or aerial photos. Forest type maps, derived from aerial photos, were available for the reservation (Bureau of Indian Affairs, Whiteriver, Az.). We systematically recorded habitat as the forest types at the corners of grid squares (n = 2,218) following McCorquodale et al. (1989). Habitats included within seasonal home-ranges of elk were determined by plotting individual elk home-ranges on the same maps. Percentages of habitats within home-ranges were then estimated.

We used replicated goodness-of-fit tests (Thomas and Taylor 1990) to examine the null hypothesis that seasonal elk home-ranges include habitats in proportion to their availability. All hypotheses were tested at the 0.05 significance level.

Results

We marked 179 elk (143 with colored collars and ear tags and 36 [11M, 25F] with radiocollars) between October 1983 and July 1984. We mapped seasonal use areas and migration routes (Fig. 1) using 1,397 elk locations. Summer use areas were contiguous or overlapped. We identified 10 separate winter use areas. We defined these as areas with ≥1 individual radiocollared elk whose MCP winter home-range estimates were non-overlapping with elk using other areas. Winter use areas delineated included substantial transitional use area (habitats between 2,316 and 3,048 m elevation) because elk made elevational movements during late winter and spring each year. All seasonal use areas delimited were based on >15 locations. All winter use areas identified were used ≥2 years by ≥1 radiocollared elk except Faught Ridge, lower Diamond Creek, and Black River which were each used by only 1 radiocollared elk.

Distances between summer and winter harmonic mean centers varied from 11.2 to 32.6 km ($\bar{x}$ = 16.8 ± 3.4 km [SE]). Movements to winter use areas were related to heavy snowfalls. Half the observed elk movements (51%) were ≤2 days after the first major snowfall to holding areas at 1,980-2,377 m elevations where they remained until heavier snows pushed them to lower elevation <2,316 m winter use areas. Nearly one-third (32%) of movements were directly to wintering areas, while other animals (17%) moved back and forth between winter use and summer use areas throughout the winter. Movements to winter use areas did not differ between sexes (Wilcoxon T^+ = 22, n = 7, P = 0.11). Mean interval between locations of elk in winter was 9.1 ± 5.1 days. Mean duration of snow cover >5 cm on winter and lower transition use areas during the study was 6.3 ± 1.4 days. However, each year 3-5 major winter storms pushed elk back onto lower winter use areas. Elk-days of use on winter and transitional use areas was inversely correlated with snow depth (r^2 = 0.62). Elk moved off winter use areas earlier during the mild winters in 1983-84 and 1985-86 and used large portions of transitional use areas during the winter months. Elk spent more days on winter use areas off the reservation than they did on winter use areas on the reservation (Wilcoxon T^+ = 24, n = 7, P = 0.04).

We combined ground and aerial locations to estimate home-range size. We had adequate sampling to describe yearly home-ranges for 18 (5M, 13F) elk (Table 1). Mean number of observations to meet AO sampling criteria was 41.4 ± 13.2. Successive locations within seasons were independent (P > 0.05). However, when we combined seasonal observations to estimate yearly

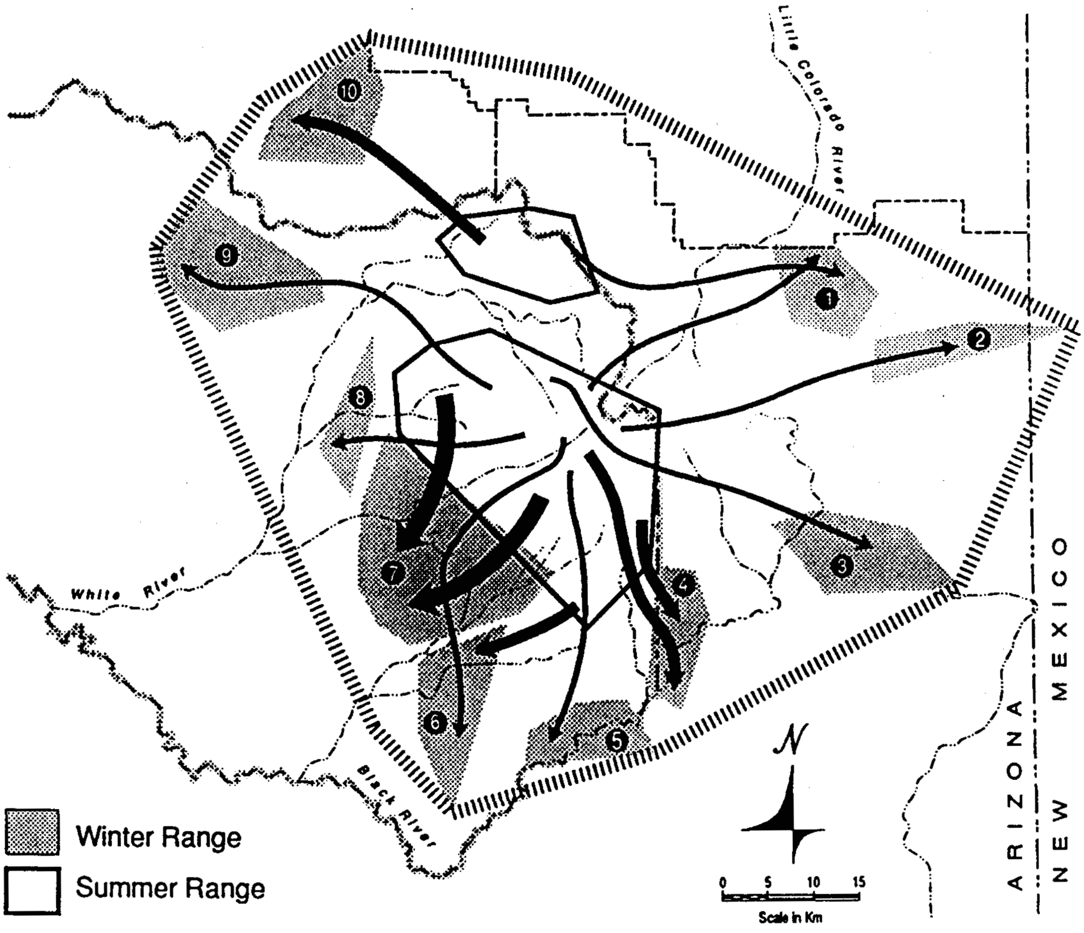

Figure 1. Seasonal ranges and migration routes mapped from locations of radiocollared elk in the White Mountains, Arizona 1983-86. Broad hatched line indicates boundaries of study, shaded dotted line marks boundary of the White Mountains Apache reservation, narrow hashed line marks U.S. National Forest Boundaries. Thickness of arrow denotes relative number of radiocollared elk using that route. Winter ranges: 1 = Milligan Creek, 2 = Escudilla Mountain, 3 = Campbell-Blue River, 4 = Turkey Mountain, 5 = Black River, 6 = Maverick-Poker Mountain, 7 = Corn Creek Plateau, 8 = lower Diamond Creek, 9 = Faught Ridge, 10 = Porter-Sponseller Mountain.

Table 1. Home-range sizes (km^2) for 5 male and 13 female elk using minimum convex polygon (MCP), and harmonic mean (HM); 95, 75, 50 % contour intervals (HM95, HM75, HM50) estimates, respectively in the White Mountains, Arizona 1983-1986.

		Home-range estimate							
Season		MCP	SE	HM95	SE	HM75	SE	HM50	SE
Males									
Spring	11[a]	301.40	344.21	126.72	88.95	44.49	33.45	15.22	9.82
Summer	10	30.89	23.29	6.76	10.68	2.50	3.92	0.82	0.53
Fall	10	162.06	73.98	76.01	42.80	29.49	15.01	6.35	4.13
Winter	12	194.72	333.21	82.89	153.50	28.82	52.36	9.12	5.92
Yearly	42	638.90	465.23	445.51	339.85	155.82	102.74	50.41	32.45
Females									
Spring	13	126.58	73.46	103.13	70.97	37.29	24.53	14.17	9.65
Summer	12	20.31	16.84	9.85	8.32	4.62	3.71	1.04	0.86
Fall	11	137.57	105.39	67.62	47.41	28.42	21.93	5.29	3.52
Winter	13	111.69	150.59	73.56	145.72	27.03	43.51	7.84	12.53
Yearly	48	385.68	313.11	271.49	191.78	99.65	64.15	29.29	16.09

[a] Median number of observations/animal/season.

home-ranges they showed significant autocorrelation ($P = 0.05$), illustrating the migratory nature of elk home-range use in this area, and temporal concentrations in seasonal use areas. Spring and fall home-ranges were large with widely scattered to bimodally-grouped observations.

Elk wintering east of the reservation had larger ($\bar{x} = 860 \pm 99$ km^2, $F = 10.76$, 4 df, $P = 0.005$) home-ranges than those wintering west or south of the reservation ($\bar{x} = 329 \pm 81$ km^2). Summer ($\bar{x} = 20 \pm 5$ km^2) and winter ($\bar{x} = 48 \pm 11$ km^2) range sizes, with the exception of 1 east herd female that moved between 2 areas in mid-winter each year, were not different ($t = -1.63$, 34 df, $P = 0.12$) between herds. Controlling for east-west herd differences and excluding the 1 female noted above, seasonal home-range size differences were apparent between the sexes. Males had larger ($F = 4.56$, 3 df, $P = 0.05$) yearly home-ranges than females, but spring was the only season when male home-ranges were significantly larger ($t = 2.24$, 16 df, $P = 0.04$) than female home-ranges. Spring ($\bar{x} = 147 \pm 41$ km^2) and fall ($\bar{x} = 141 \pm 23$ km^2) ranges were larger ($F = 5.84$, 3 df, $P = 0.001$) than summer and winter ranges ($\bar{x} = 24 \pm 5$ km^2, and $\bar{x} = 70 \pm 21$ km^2, respectively), though winter home-range size was extremely variable.

Indices of yearly home-range fidelity ranged from 0.42 to 0.52. Seasonal home-range fidelity was low. Mean distance between HM centers of activity (Dixon and Chapman 1980) for seasonal home-ranges was 6.2 km ± 1.5 (Table 2). Spring and summer home-range fidelity was greater than fall and winter home-range fidelity. There

Table 2. Mean distances (km) between harmonic mean home-range centers for elk with adequate observations to estimate seasonal home-ranges in ≥2 years, White Mountain Fort Apache Reservation, Arizona, 1983-86.

Season[a]	No. comparisons[b]	No. elk[c]	Distance	SE
Spring	42	22	5.88	0.91
Summer	23	23	2.25	0.44
Fall	42	21	9.51	1.16
Winter	36	18	7.18	0.55
Year-long	143	18	6.75	6.57

[a] Spring = Mar-May, summer = Jun-Aug, fall = Sep-Nov, winter = Dec-Feb.

[b] An individual elk could provide as many as 3 comparisons (e.g., spring 1984 vs. 1985, spring 1985 vs. 1986, and spring 1984 vs. 1986).

[c] No. individual elk compared.

was no difference ($U = 48.5$, $P = 0.35$) in home-range fidelity between sexes for any season. Between-year overlaps of winter and of summer home-ranges coincided with core areas identified by HM analyses. There were no significant differences in distances between seasonal home-range HM centers related to sex of elk in any season ($P = 0.49$).

Distance traveled and time of day movements occurred varied among elk. Mean daily distances traveled differed between seasons ($F = 12.57$, 3 df, $P < 0.001$). Summer ($\bar{x} = 7{,}537 \pm 324$ m) and fall ($\bar{x} = 6{,}506 \pm 475$ m) distances traveled/day were not different, but winter ($\bar{x} = 3{,}171 \pm 166$ m) and spring ($\bar{x} = 3{,}990 \pm 315$ m), distances traveled/day were less than those in summer and fall ($P < 0.05$). Distances moved/hour in relation to time of day (Fig. 2) showed a crepuscular activity pattern. After controlling for variation due to the number of minutes of elk observation, both time of day ($F = 2.73$, 13 df, $P = 0.001$) and season ($F = 16.94$, 3 df, $P < 0.001$) affected distance moved/hour. Distances moved/hour were greater near sunrise and sunset and decreased during mid-day. Mid-day movements were lowest in fall and winter. Daily movements also differed among seasons. Elk movements in winter frequently showed a daily pattern of movement to and from the same forage and bedding areas. Spring, summer, and fall daily movements were more nomadic. Elk wandered, often foraging along the way, through many habitats without returning to specific sites to feed or bed. In late spring and early summer, however, elk often stayed close to open mesic foraging areas throughout the day.

Male summer use areas were at higher elevation (summer use area harmonic mean center ($\bar{x} = 2{,}782.1 \pm 88.4$ m) than were females ($\bar{x} = 2{,}433.5 \pm 66.1$ m) ($U = 239$, $P < 0.05$). Elevation of winter harmonic mean centers of males and females were not different ($U = 103$, $P > 0.05$).

Wallace et al. (in press) describes elk habitats for this study area more completely including species compositions, forest stand structure, cover, and topographic features. Summer and winter home-range habitat selection (Fig. 3) show differences between the sexes. Habitats available in male summer ranges were dominated by spruce, ponderosa

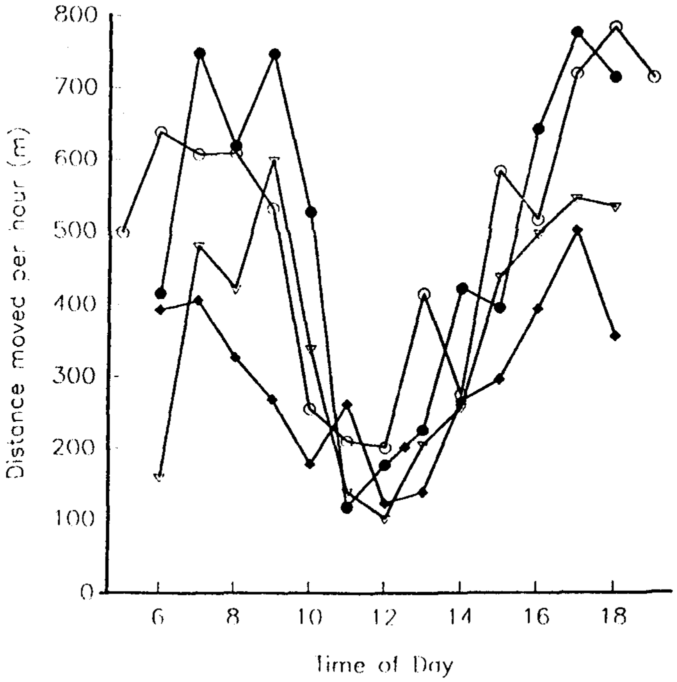

Figure 2. Distances moved (m) per hour during the day by radiocollared elk in spring (solid circles), summer (circles), fall (triangles), and winter (diamonds) in the White Mountains, Arizona, 1984-86.

pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*) types, but males selected for spruce (*Picea* spp.) habitats and the associated clearcuts and selected against ponderosa pine habitats. Summer ranges of females were dominated by ponderosa pine, Douglas fir, and spruce, but females selected for mid-elevation Douglas fir, clearcuts and large burns in ponderosa pine, and included lower elevation ponderosa pine habitats in proportion to their availability. In summer, home-ranges of males included meadows proportionally to their availability, while females selected against them. This reflects the later phenology and more mesic conditions in higher elevation meadows that were used by males in late summer (Wallace et al. 1997). Winter ranges of males were dominated by ponderosa pine and pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) habitats, but males selected for pinyon-juniper and artificial openings and against open (<10% crown density) and ponderosa pine types. Home-ranges of males included pinyon-juniper stands with old clearings or seral brushfields associated with old burns. Winter ranges of females were dominated by ponderosa pine and pinyon-juniper types. Females selected for pinyon-juniper clearings. But, they also selected north faces, riparian Douglas fir stands, and open meadow associations more than did males.

DISCUSSION

Home-ranges estimated from only 2-3 years of an elks life may not represent all resources required for the individual's long-term survival and reproduction. We used MCP and HM home-range methods to describe the use patterns of elk in the White Mountains. We believe that our careful evaluation of sample size and sample point

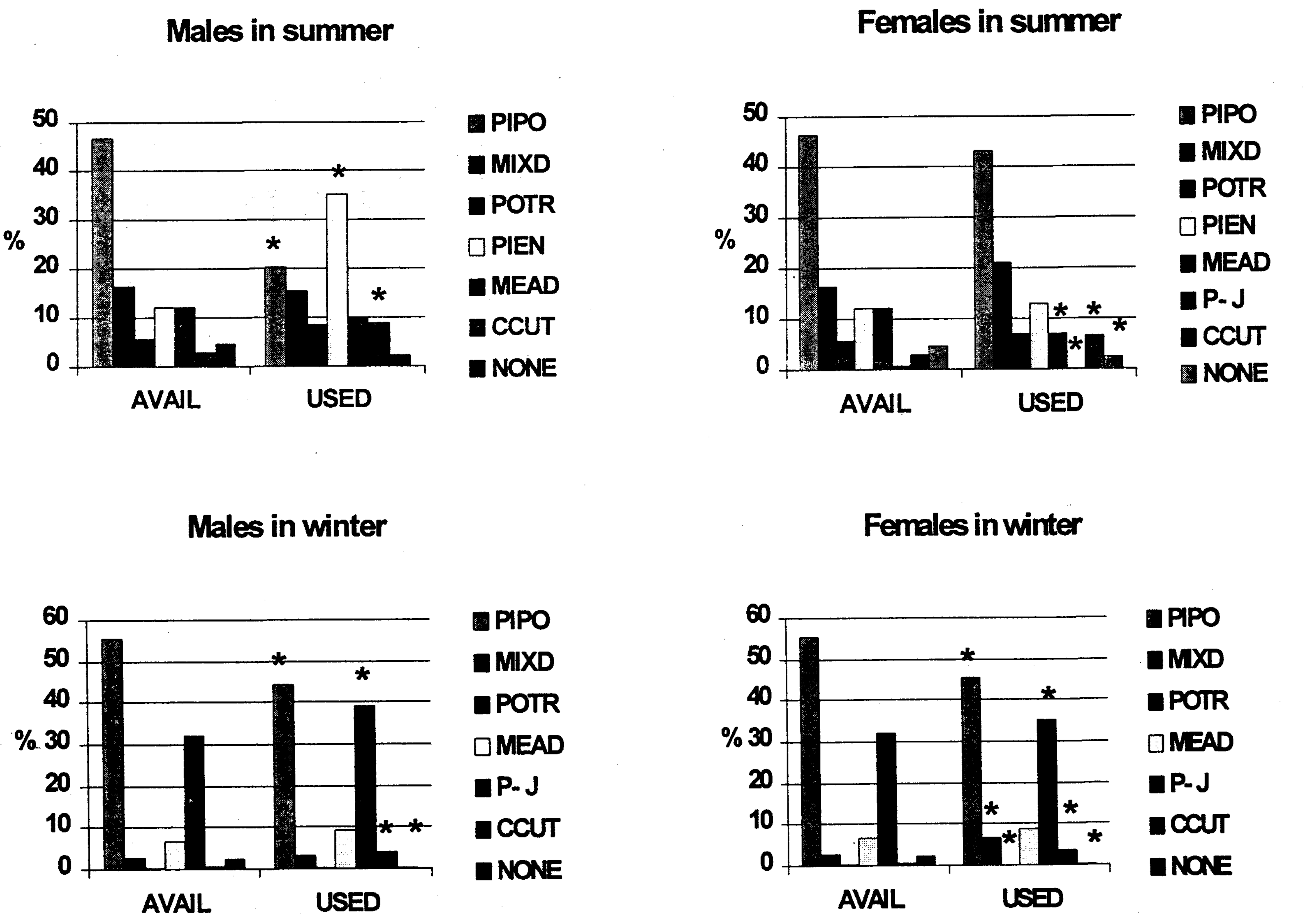

Figure 3. Differences between habitats within male and female elk home ranges by season in the White Mountains, Arizona, 1984-86.

independence reduced the effects of biases inherent in these techniques (Dunn and Gipson 1977, Swihart and Slade 1985, Boulanger and White 1990). Minimum convex polygon estimates provided ready comparison to other studies.

We identified 10 separate wintering areas used by elk summering on the reservation. We also identified major migration routes and spring-fall transition areas (Hershey and Leege 1982). Elk in this study did migrate seasonally, similar to elk reported by Adams (1982) and Hershey and Leege (1982), though distances moved reflect the topography of the study area. East herds moved farther than west herds because suitable low elevation winter ranges were more distant. Duration of elk use of wintering areas varied widely. Other elk herds show similar movements (Brazda 1953, Sweeney 1975, Hershey and Leege 1982). Time spent on wintering areas differed among years, due to winter snows. Snow depths have influenced migrations of other elk herds (Sweeney 1975, Hershey and Leege 1982). Time spent on wintering areas also differed among areas. This probably was due to the number of radiocollared elk sampled ($n = 10$) that used the severely overgrazed Corn Creek winter use area on the reservation (J. Jojolla, unpubl. rep. WMGF, 35pp. 1984). There was very little available forage (J. Jojolla, White Mountain Tribal Game and Fish Department, pers. commun.) on the lower portions of the Corn Creek winter use area. Elk wintering on that use area moved to transition areas quickly when snow melted. Spring movements also were similar to those reported elsewhere (Brazda 1953). However, spring movements began earlier and were more gradual than those reported for more northern herds (Craighead et al. 1972, Sweeney 1975, Adams 1982, Hershey and Leege 1982).

Home-ranges were larger than those reported for other migratory elk (Craighead et al. 1972, McCorquodale et al. 1989) and red deer (*Cervus elaphus*) (Georgii 1980, Georgii and Schroder 1983). Summer home-range sizes were similar to those reported by Franklin et al. (1975), Georgii (1980), Georgii and Schroder (1983), and McCorquodale et al. (1989). Other seasonal use areas were large and reflect the elevational movements of elk in the White Mountains in relation to snow levels during fall through spring.

Yearly home-range fidelity was comparable to that reported by Edge et al. (1985), but seasonal home-range fidelity was low. Despite low home-range area overlaps, 75% of elk observed ≥2 years returned to within 2 km of the same wintering areas and 95% to within 2 km of the same summer areas.

Daily movements show diurnal and seasonal patterns similar to those reported by Georgii (1980), Georgii and Schroder (1983), and Green and Bear (1990). Elk traveled less at mid-day than during the major feeding periods in the crepuscular hours. However, there was movement throughout the day in all seasons unlike the mid-day resting reported by Altmann (1952). Diurnal winter movements were less than those of other seasons. Georgii and Schroder (1983) and Green and Bear (1990) reported similar activity patterns in winter areas close to human disturbance. Red deer that were distant from human disturbance in the Alps were more active at mid-day (Georgii 1981, Georgii and Schroder 1983). We did not observe elk on winter areas distant from human disturbance in this study.

Elevational differences accounted most for different habitat selection by the sexes at the home-range level (Johnson 1980). Males moved to higher use areas in summer did than females. Females remained at mid-elevations in May-June to have their calves (Wallace and Krausman 1991). Males selected spruce and small- to moderate-sized clearcuts in spruce associations and against ponderosa pine in summer home-ranges. Males used Douglas fir, aspen, and meadow associations in summer home-ranges in proportion to their availability. Females selected for Douglas fir and small burns and clearcuts in ponderosa or Douglas-fir associations on summer home-range. They selected against large meadows that dried out at mid-elevations by summer. Females selected against pinyon-juniper associations on summer use areas and they used ponderosa pine, aspen, and spruce associations in proportion to their availability. Edge et al. (1987) reported similar use in Montana and DelGuidice and Rodiek (1982) and Wallace and Krausman (1987) reported similar habitat occupation by elk elsewhere in Arizona.

Winter habitat selection in home-ranges was different for males and females. Pinyon-juniper and ponderosa pine dominated home-ranges of both sexes. But females selected Douglas-fir stands, meadow openings, pinyon-juniper, and pinyon-juniper treatment areas, while males selected only for the pinyon-juniper and treatment areas. Peek and Lovaas (1968) also documented differential habitat use by sexes on winter range in Montana.

Management of elk on a herd-unit basis requires knowledge of elk use areas and movement patterns. We identify some of the major seasonal use areas and migration routes used by elk in eastern Arizona. Male and female elk showed different seasonal movement patterns and used areas differently by seasons. Males use high elevation summer use areas more than females do.

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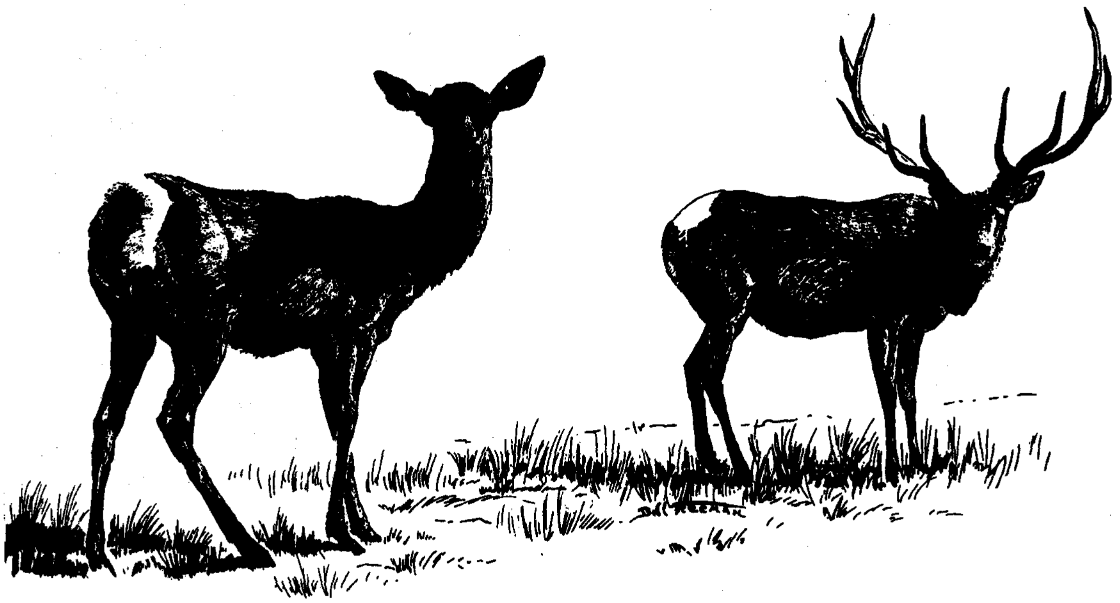

Elk Food Habits in Southern Piñon-Juniper Woodlands of the Gila National Forest

V. W. HOWARD, JR.
Department of Fishery and Wildlife Sciences, New Mexico State University,
Las Cruces, NM 88003

LAURA K. MANGOLD
Department of Fishery and Wildlife Sciences, New Mexico State University,
Las Cruces, NM 88003

Abstract: Piñon-juniper woodland encroachment into native rangelands has been viewed as a management problem for livestock grazers and wildlife managers for >4 decades. Removal or thinning of piñon and juniper trees to facilitate growth of grasses, forbs and browse species have been common remedial management techniques. Elk use of these modified areas has been studied in the past to determine use in modified vs. unmodified areas, season of use, and distance of use from suitable cover. This study reports on seasonal elk diets, primarily in or near mechanically disturbed areas, as determined by microhistological analysis of feces. All samples were processed in the laboratory using standard microhistological techniques. Results showed greater percentages of browse in the diets of elk for all seasons, years, and areas, except for spring/summer 1994 when grasses slightly exceeded trees/shrubs. Elk were selecting for forbs on all study areas whenever these plants were available. Grasses were an important component of elks' diets during spring/summer, but did not comprise 50% of their diets on any area during any year or season.

Key words: elk, food habits, piñon-juniper, seasons, years

INTRODUCTION

Piñon-juniper (*Pinus* sp.-*Juniperus* spp.) woodlands cover approximately 243,000 km^2 of the United States (Short et al. 1977). In 1981, it was estimated that there was 9.3 million ha of piñon-juniper habitat in New Mexico, covering approximately 29% of the state (Garrison and McDaniel 1982). The encroachment of piñon-juniper woodlands upon native rangelands has caused problems for many livestock grazers throughout the southwestern United States since the beginning of the 20th century (Arnold et al. 1964, Williamson and Currier 1971, Burkhardt and Tisdale 1976, Springfield 1976). The main reasons for piñon-juniper invasion have been fire suppression, overgrazing, and climatic changes (Leopold 1924, Nichol 1943, Branscomb 1958, Humphrey 1962, Johnson 1962, Blackburn and Tueller 1970, Burkhardt and Tisdale 1976).

As piñon and juniper trees increase in density and abundance, plants that provide forage for livestock tend to decrease (Arnold and Schroeder 1955, Arnold et al. 1964, Reynolds 1964, Bedell and Bunch 1977, Short et al. 1977, Short and McCulloch 1977, Schott and Pieper 1985, Armentrout and Pieper 1988). The main reasons for this decrease in understory vegetation are shade, competition for water, precipitation interception, litter accumulation, and phytotoxic root exudates (Jameson 1966, Jameson 1967, Schott and Pieper 1985). The removal of piñon and juniper trees to facilitate the growth of forage suitable for grazing has been the common management technique used to remedy this problem. The mechanisms used to eradicate the trees have been mechanical disturbances, prescribed fires, and chemical treatments (Aro 1971).

Livestock grazing has been the focus of these management techniques in the past (Short et al. 1977, Short and McCulloch 1977). However interest in piñon-juniper woodlands as a source of multiple recreational uses has increased greatly in the past few years (Choate 1966). The impacts of these management techniques on elk (*Cervus elaphus nelsoni*) and mule deer (*Odocoileus hemionus*) have become a concern because of their importance as leading big game species and because of their increasing noncumsumptive importance (Short et al. 1977, Reynolds 1964). Elk and mule deer are an important economic asset to the state of New Mexico. Therefore, it is essential to consider these impacts on mule deer and elk when manipulating range habitats.

Considerable data have been collected on elk and mule deer use of this manipulated habitat over the past 10 years. However, there are few data available concerning how manipulation of the piñon-juniper woodlands effects forage availability for these ungulates. If the manipulation of piñon-juniper woodlands is to improve the habitat for deer and elk, there must be an increase in forage production while retaining suitable cover (Short et al. 1977, Nelson and Leege 1982). Therefore, it would follow that knowledge of elk and mule deer food habits would be essential in improving management techniques that would be beneficial to all herbivores.

This lack of data dictated the need for a food habits study. Because of time constraints, this study was concerned only with seasonal diets of elk in the mechanically disturbed and adjacent undisturbed areas of Fort Bayard and North Star Mesa in the Gila National Forest of New Mexico. Elk diets were determined through analysis of fecal material. Fecal analysis was chosen because it is inexpensive, practical, and accurate for evaluating diet compositon of large herbivores in the arid Southwest (Anthony and Smith 1974, Sanders et al. 1980, Johnson and Pearson 1981, Kessler et al. 1981, Alipayo et al. 1992, Mohammad et al. 1995).

The objectives of this study were to: 1) determine diets of elk in disturbed areas vs undisturbed areas, 2) determine seasonal differences in diets in disturbed and undisturbed areas, and 3) determine differences in elk diets between years.

STUDY AREAS

The Gila National Forest is located in western New Mexico and consists of 1,343,100 ha. Nearly one-fourth of the Gila National Forest has been designated as a wilderness area. Elevations range from 1,372 m in the desert to almost 3,353 m in the alpine life zone. The rugged mountainous terrain helps create a diversity of plant and animal communities.

Piñon-juniper woodlands occupy approximately 34% of the Gila National Forest (Springfield 1976). The piñon-juniper woodlands within New Mexico occur at elevations of 1,350 m to 1,890 m (Aro 1971, Ffolliot and Gallina 1981) and are associated with a semi-arid climate (Ffolliot and Gallina 1981). Annual precipitation can vary in piñon-juniper woodlands from 30 to 60 cm depending on elevation and year (Ffolliot and Gallina 1981). Piñon-juniper woodlands occur mostly on soils derived from basalt, limestone, and sandstone (Aro 1971, Ffolliot and Gallina 1981).

Fort Bayard and North Star Mesa study sites are located in Grant County within the Gila National Forest. The sites were chosen because of evidence of elk use recorded by previous studies. The following site descriptions are from Cosper (1989) and Casady (1995).

Site Descriptions

Fort Bayard A & B

The Fort Bayard study site is located just east of Silver City, New Mexico at an elevation of 1,980 m. The site consists of approximately 4,152 ha. The main tree species occurring on Fort Bayard are Colorado piñon pine, alligator juniper (*Juniperus deppeana*), one-seed juniper (*Juniperus monosperma*), and oak species (*Quercus* spp.). Mountain mahogany (*Cercocarpus montanus*), Wright's silktassel (*Garrya wrightii*), Brickellia (*Brickellia* spp.), and skunkbrush sumac (*Rhus trilobata*) occur among the other woody species. The primary grasses found on Fort Bayard were blue grama (*Bouteloua gracilis*), threeawn (*Aristida* spp.), sideoats grama (*Bouteloua curtipendula*), and wolftail (*Lycurus phleoides*). The major forb species occurring on the site were globemallow (*Sphaeralcea* spp.), trailing four o'clock (*Mirabilis multiflora*), and buffalo gourd (*Cucurbita foetidissima*).

Fort Bayard consisted of 2 disturbed areas, area A and area B, and 1 undisturbed area. Both disturbed areas were treated in 1970. In area A, there was complete mechnical removal of the trees by bulldozer and the resultant debris was cleaned up by a controlled fire. Then in 1993, the site was subjected to a prescribed burn. In area B, there was partial removal of the trees by bulldozer with the exception of the northeast slopes that were greater than 15%. The slash was left on the site.

North Star Mesa

Northstar Mesa is located north of Mimbres, New Mexico, at an elevation of 2,225 m. The site consists of approximately 1,062 ha. The main woody species found on North Star Mesa are Colorado piñon pine, alligator juniper, and oak species. Blue grama, mat muhly (*Muhlenbergia richardsonis*), and wolftail were the primary grasses occurring on the site. Major forb species occurring on the site were (*Dalea* spp.), desert marigold (*Baileya* spp.), and red-stemmed filaree (*Erodium circutarium*).

North Star Mesa study area consists of 1 disturbed and 1 undisturbed site. The disturbed area was cut for fuelwood in 1977. The slash was piled on the stumps and later burned. The site was retreated in 1990 when seedlings and stump sprouts were removed by hand.

MATERIALS AND METHODS

Field Techniques

Collection of Elk Pellet Groups

Five elk pellet groups were collected from disturbed and undisturbed areas on Fort Bayard and North Star Mesa to determine the diets of elk utilizing these areas. Pellet groups were collected in September to determine spring/summer diets and in April to determine fall/winter diets. Wherever possible, pellet groups were collected from within plots along pellet group transects that were established for a previous study (Cosper 1989). Resampling by collecting pellets from previously sampled groups and collecting old pellet groups was avoided by either removing or marking the pellets with Eco-Spot® orange tree marking paint. If no pellet groups were found on the plots, groups were collected near the transects. Color was used to estimate the age of the pellet groups so that old pellet groups were not collected (Freddy 1983). Each sample collected was placed in a labeled bag and dried in an oven in the laboratory.

Vegetation Availability

Permanent vegetation transects were established in 1987 by Cosper (1989) in a random direction off of 2 of the 5 stakes located on each pellet group transect within each disturbed and undisturbed area for all sites. The line-point method, as described by Pieper (1978), and a steel tape suspended by aluminum poles, as described by Howard (1966), was used to sample vegetation availability. Vegetation data were recorded as a plant species, bare ground, or litter at 30.5 cm intervals along a 30.5 m transect. Data were collected in September at the end of the growing season during alternate years from 1988 to 1996.

Collection of Reference Plants

Plants commonly encountered, and plants reported to constitute elk foods (Nelson and Leege 1982) were collected from Fort Bayard and North Star Mesa. Collecting began in the spring of 1996 and continued through the summer until the end of the growing season in the fall. Two specimens of each species were collected. One specimen was placed in a plant press in the field for later identification and the other specimen was dried in an oven in the laboratory. Plants were identified by referencing Parker (1972), Spellenberg (1979), Niehaus et al. (1984), Allred (1993), and Anderson (1996). Those plants that could not be located in the reference books were identified by Dr. Kelly Allred, Department of Animal and Range Sciences, New Mexico State University.

Microhistological Laboratory Techniques

Slide Preparation

Aqueous Kaiser glycerine jelly was used as the mounting medium in the preparation of the slides. To prepare the mounting medium, 8 g of gelatin were mixed with 52 ml of water in a small jar and allowed to soak for 2 hrs. Then 50 ml of glycerine and 0.01 g of thimerosal preservative were added to the aqueous solution. The mixture was heated by placing the jar in a water bath for about 10-15 min. until a homogenous jelly formed.

Each of the previously collected pellet groups were ground through a 1 mm (20 mesh) screen in a Wiley mill to reduce the pellets to fragments of equal size. Slides were prepared from the fragments according to the techniques described by Sparks and Malechek (1968), and modified by Holechek (1982). The oven-dried reference plants were ground and mounted on slides using the same techniques. Each ground pellet sample and each reference plant sample was soaked in boiling water for 10-15 min. and then rinsed in a 120-mesh sieve with warm tap water for 5 min. to remove dirt and fine plant particles. The sample was then soaked in 20 ml of bleach for 5 min. to remove plant pigments, and stain, and were again rinsed in the sieve with warm tap water until the odor of the bleach was gone. Excess water was removed from the sample by pressing it against the bottom of the sieve.

Slide Mounting

Once preparation was complete, each sample was mounted onto 5 separate microscope slides. An aluminum slab with a 5 mm hole drilled into it was placed onto a slide and the sample was packed into the hole until the fragments were flush with the top of the slab. The sample was pushed through the hole onto the slide. This ensured that equal amounts of each sample were mounted onto the slides. The Kaiser glycerine jelly was heated in a water bath until liquified. Fourteen to 18 drops of the jelly were placed onto the slide and mixed with the sample until the fragments were distributed uniformly. A 24 mm X 50 mm glass cover slip was placed over the mixture. Once the mounting medium dried, the cover slip was sealed by applying a thin coat of clear fingernail polish around all sides.

Plant Fragment Identification

The botanical compositions of elk diets from Fort Bayard and North Star Mesa were determined by the identification of plant fragments found in the feces. Plant fragments were identified by the characteristics of the epidermal tissues and appendages. Diagnostic characteristics included: 1) stomata size, shape, orientation, and associated guard or subsidiary cells; 2) trichrome presence or absence, and structure; 3) epidermal cell morphology; 4) silica cell presence, size, shape, and placement; 5) cork cell size, shape, and bases for trichromes (Stebbins and Kush 1961, Zyznar and Urness 1969, Esau 1977, Howard and Samuel 1979, Fahn 1982, Dabo et al. 1986).

To ensure that the plant fragments in the pellet groups were identified accurately, L. Mangold was trained following techniques described by Holechek and Gross (1982*a*). Simulated diets were prepared from different combinations of reference plants, unknown to her, previously reported to be eaten by elk (Nelson and Leege 1982). Tests using these simulated diets were conducted until the mean similarity index was above 90%, and an approximate 1:1 ratio of actual:estimated botanical composition was observed using Kulczinsky's formula (Oosting 1956). Once a test was passed, she began quantifying the botanical composition of the elk diets.

Botanical Composition of Elk Diets

Analysis of the pellet group slides followed a procedure similar to that described by Sparks and Malechek (1968). Twenty microscope fields were located systematically on each slide using 100X magnification. Each plant species identified by epidermal tissues using 100X-200X magnification within each field was recorded. If a plant fragment could not be identified to genus or species, it was recorded as belonging to one of the following five categories: 1) trees/shrubs; 2) grasses; 3) forbs; 4) cactus/yucca; or 5) unknown. If a plant fragment could not be identified as belonging to one of the categories, but was clearly a specific structure it was recorded as unknown. Two slides were read for each pellet group. With the total number of frequency observations for each slide being at least 20, 2 slides were an acceptable number to achieve identification of major and some minor plant species (Holechek and Vavra 1981).

Data Analysis

Vegetation Data

Data collected from the vegetation transects was used to compute percent composition by species and vegetative classes for the undisturbed and disturbed areas of each study site. The total number for each species identified along each vegetation transect was obtained. Totals were then converted to percent vegetative composition for each transect. A single vegetation transect was made up of 2 100ft. line-point transects associated with each pellet group transect. Mean percent composition was obtained by averaging the percent composition values for each transect. The same procedure was used to obtain the mean percent composition of vegetative classes. Confidence intervals for the mean percent vegetation composition data for 1994 were not calculated because data were not available (Casady 1995). However, 95% confidence intervals were calculated for the mean percent vegetation composition data for 1996 using Dowdy and Wearden (1991).

Botanical Composition of Elk Diets

The frequency addition procedure (Holechek and Gross 1982*b*) was used to determine the percent composition of each species and vegetative class found in the pellet groups from each undisturbed and disturbed area for spring/summer and fall/winter. The following formula was used for the frequency addition procedure:

$$\%\ \textbf{composition} = \frac{\textbf{\# of occurrences of a species (veg. class)}}{\textbf{total occurrences of all species (veg. class) in the diet}} \times 100$$

Because there was no replication in study sites, no statistical procedures could be performed. Therefore, the results presented are strictly descriptive.

RESULTS AND DISCUSSION

Vegetation Availability

North Star Mesa

1994

The highest percentage of vegetation available in the undisturbed area fell into the class of trees/shrubs (93%) (Fig. 1). Species constituting the majority of the vegetative composition in the undisturbed area were *Juniperus deppeana* (53%), *Pinus edulis* (30%), and *Quercus* spp. (10%). Grasses (61%) were the primary vegetative class available on the disturbed area (Fig. 1). The most abundant grasses were *Bouteloua gracilis* (56%), *Muhlenbergia richardsonis* (4%), and *Lycurus phleoides (1%).* No forbs were found on the transects in the undisturbed area. Forbs made up only 1% of the vegetative composition in the disturbed area (Fig. 1).

1996

Trees/shrubs (95%) were the vegetative class with the highest percent composition in the undisturbed area (Fig. 2). The primary tree species were *Juniperus deppeana* (53%), *Pinus edulis* (34%), and *Quercus* spp. (7%). In the disturbed area, trees/shrubs (47%) were the most plentiful followed closely by grasses (43%) (Fig. 2). The species with the highest vegetative composition were *Bouteloua gracilis* (33%), *Juniperus deppeana* (29%), and *Pinus edulis* (17%). Few grasses (2%) were available on the undisturbed site. Forbs comprised 3% and 10% of the vegetation available in the undisturbed and disturbed areas, respectively (Fig 2). The major forb species in the undisturbed area were *Chamaesyce* spp. (1%), *Cologania longifolia* (1%), and *Allium* spp. (1%). In the disturbed area, *Portulaca oleracea* (3%), *Ambrosia* spp. (2%), and *Chamaesyce* spp. (2%) were the primary forbs.

Fort Bayard

1994

Tree/shrubs (96%) were the primary vegetative class in the undisturbed area (Fig. 3). Major species were *Juniperus deppeana* (51%), *Cerocarpus montanus* (23%), and *Garrya wrightii* (13%). Few grasses (4%), and no forbs were identified on the undisturbed area (Fig. 3).

Grasses made up the majority of the vegetative composition in disturbed area A (79%) (Fig. 3). *Bouteloua* spp. (57%), and *Aristida* spp. (10%) were the primary grasses found in area A. Disturbed area A contained few trees/shrubs (12%). Grasses (49%), and trees/shrubs (46%) were the primary vegetative classes in disturbed area B (Fig. 3). The species most commonly encountered were *Bouteloua* spp. (40%), *Brickellia* spp. (11%), *Garrya wrightii* (10%), *Quercus* spp. (9%), and *Cercocarpus montanus* (8%). No forbs were found on the undisturbed area. Forbs contributed 9% and 5% in disturbed areas A and B respectively. (Fig. 3).

1996

In the undisturbed area, trees/shrubs were most abundant (87%) (Fig. 4). The main species were *Juniperus deppeana* (26%), *Cercocarpus montanus* (24%), and *Juniperus monosperma* (22%). Few forbs (9%), and grasses (4%) were found on the undisturbed area (Fig. 4).

Disturbed area A contained few trees/shrubs (9%). Forbs were encountered the most on area A (Fig. 4). *Portulaca oleracea* (17%), *Chamaesyce* spp. (8%), and *Kallstroemia parviflora* (8%) were the major forb species found on area A. Area B consisted mostly of trees/shrubs (39%), and forbs (38%) (Fig. 4). Primary species were *Brickellia* spp. (10%), *Quercus* spp. (9%), and *Chamaesyce* spp. (8%). Grasses (23%) on area B (Fig. 4) were primarily *Bouteloua* spp. (20%).

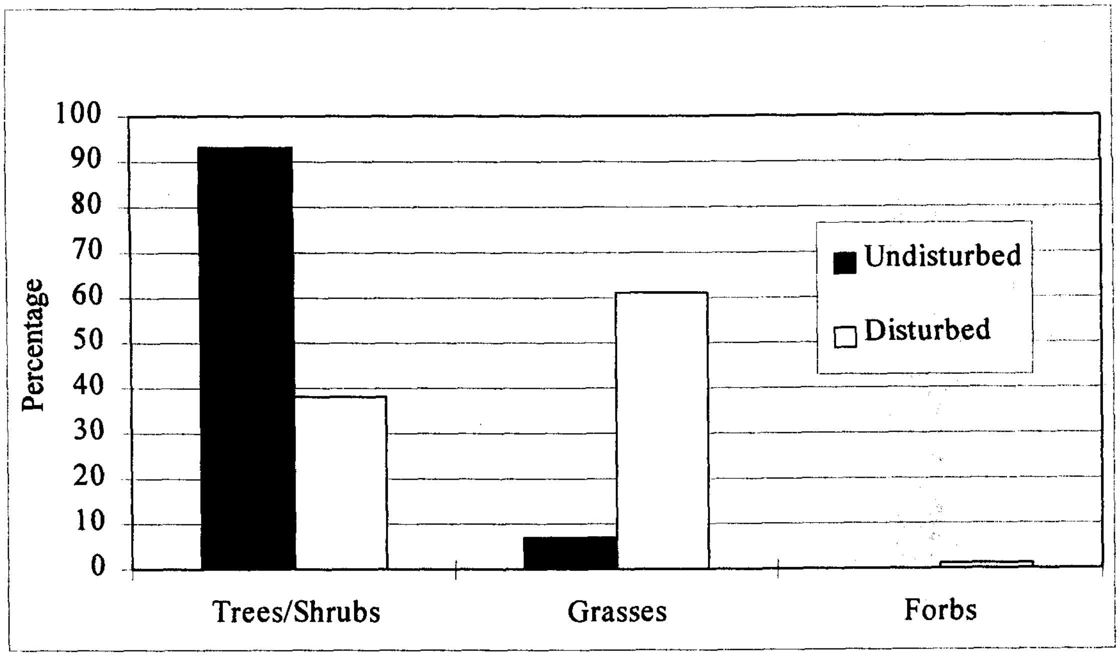

Figure 1. Mean percent composition of vegetation on North Star Mesa, 1994.

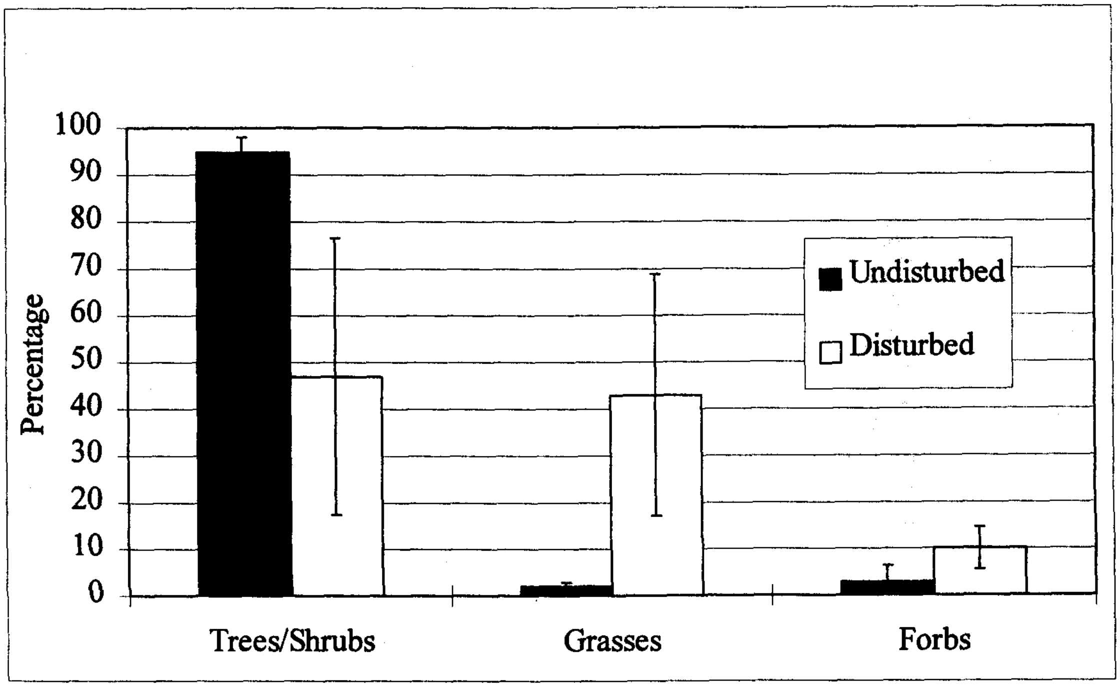

Figure 2. Mean percent composition of vegetation on North Star Mesa, 1996, with 95% confidence intervals.

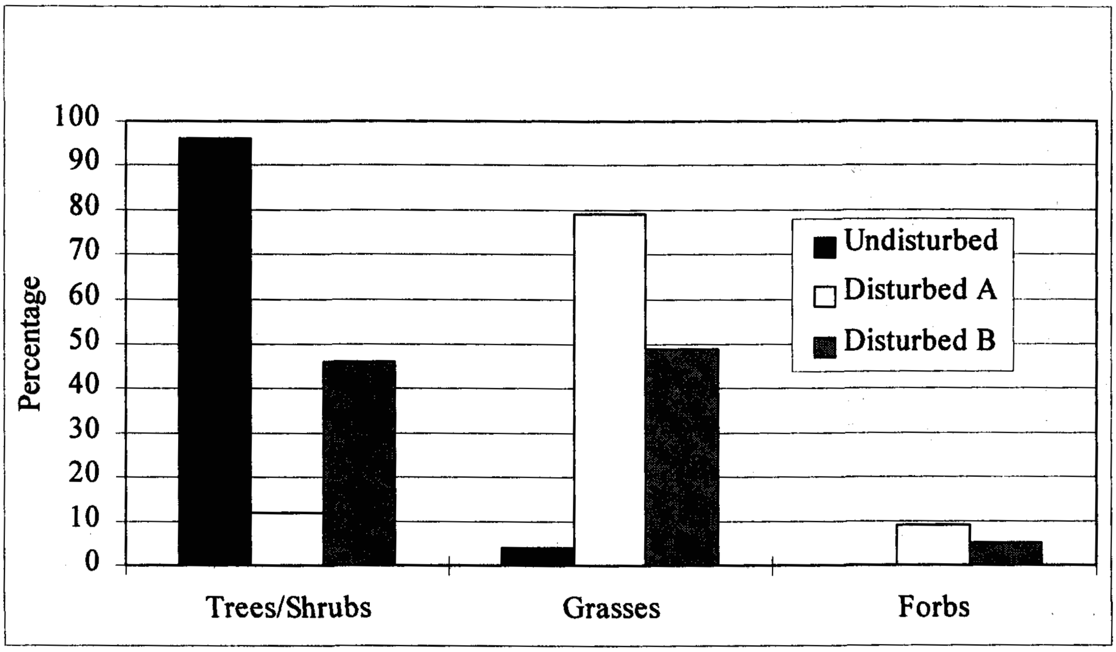

Figure 3. Mean percent composition of vegetation on Fort Bayard, 1994.

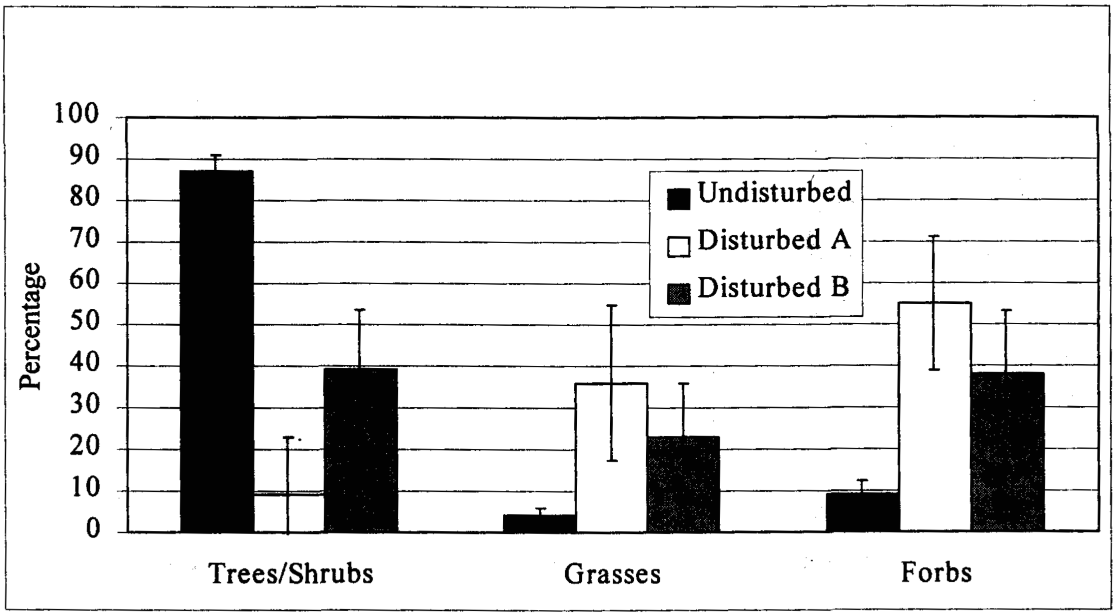

Figure 4. Mean percent composition of vegetation on Fort Bayard, 1996 with 95% confidence intervals.

Seasonal Food Habits

North Star Mesa

Elk diets did not vary between the undisturbed and disturbed areas on North Star Mesa. The primary reason for this was the close proximity of the 2 areas. Elk tend to use edges where both cover and forage are readily available (Skovlin 1982). Therefore, elk could have been foraging and defecating in both areas producing equivalent food habits results. Because elk diets did not differ, the data from the undisturbed and disturbed areas were combined and further analyzed.

During spring/summer 1994, elk diets consisted mostly of grasses (44%). The percentage of trees/shrubs found in elk diets also was high (38%). Fall/winter 1994-1995 showed an increase in the percentage of trees/shrubs (68%), and a decrease in the percentage of grasses (22%), consumed by elk (Fig. 5). *Quercus* spp. and *Juniperus* spp. were the primary woody species consumed during all seasons, and *Leptochloa* spp., *Bromus* spp., and *Bouteloua* spp. were the primary grasses. The amount of forbs consumed during all seasons in 1994-1995 was high compared to availability. Spring/summer months (15%) showed a slightly higher percentage over the fall/winter months (9%) (Fig. 5). The primary forbs found in elk diets were *Sphaeraclea* spp., *Cologania longifolia*, and *Xanthocephalum sarothrae*. Traces of *Opuntia* spp. also were present in the diets.

The data reveal that elk on North Star Mesa were browsing more than grazing in 1994-1995. Elk are typically considered to be year-round grazers with a slight increase in browsing during the winter months when grasses and forbs become less available, and nutritive quality decreases (Morris and Schwartz 1957, Hansen and Clark 1977, Collins et al. 1978 , Hobbs et al. 1981, Baker and Hobbs 1982, Nelson and Leege 1982, Wydeven and Dahlgren 1983, Kasworm et al. 1984). However, food habits of elk are extremely variable depending on where in the United States they are found and what type of forage is available (Nelson and Leege 1982). Forage availability is in turn dependent upon weather conditions. The Gila is an area susceptible to drought. The average rainfall on North Star Mesa was 56% and 39% below the long-term average from April through September for 1994 and 1995, respectively. Because of this, grasses and forbs may have been less available than in other years and elk were forced to increase browse intake even during spring/summer months. Geist (1982) states that *"elk are opportunistic and will take advantage of locally abundant food sources brought about by ecological and climatic factors"*. Short et al. (1977) found similar results when conducting a food habits study in the piñon-juniper woodlands on Fort Bayard.

Spring/summer 1995 showed an increase in the amount of trees/shrubs consumed when compared to spring/summer 1994 (Figs. 5 & 6). Trees/shrubs exceeded all other vegetative classes found in elk diets during spring/summer 1995 (63%) (Fig. 6). Fall/winter showed an even greater amount (88%) in trees/shrubs (Fig. 6). The amount of grasses consumed was low for spring/summer (16%), and fall/winter (9%) months when compared to availability (Fig. 6). The amount of forbs consumed during the spring/summer months of 1995 (20%) exceeded the amount of grasses consumed during the same months (16%) (Fig. 6). The percentage of forbs found in elk diets during fall/winter was only 2% (Fig. 6). The primary woody grass and forb species consumed by elk remained the same between years. Traces of *Opuntia* spp. were present during the fall/winter months only. The years 1995 and early 1996 on North Star Mesa remained dry causing elk to continue browsing. The average rainfall was only 61% of the long-term average.

The data for all seasons between 1994-1996 on North Star Mesa suggests that the elk were not feeding strictly on the study site. A

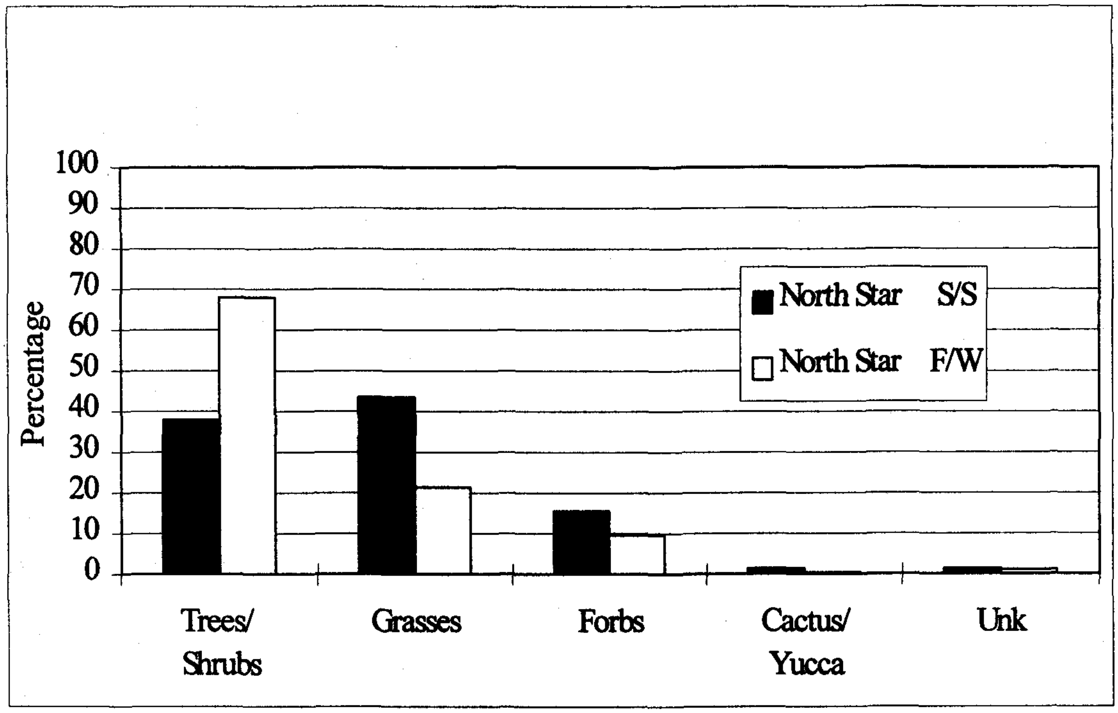

Figure 5. Percent composition of elk diets from undisturbed and disturbed areas combined on North Star Mesa, 1994-1995.

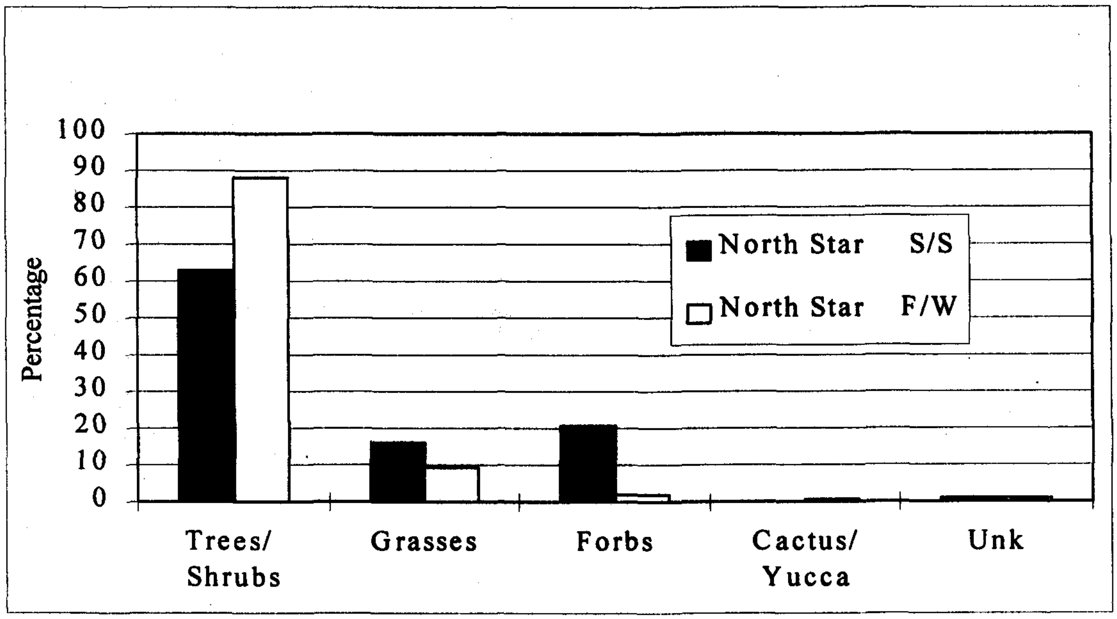

Figure 6. Percent composition of elk diets from undisturbed and disturbed areas combined on North Star Mesa, 1995-1996.

good indication of this was the presence of green sprangletop (*Leptochloa dubia*) in elk diets. This grass was never found on the study site. Another indication that the elk were feeding somewhere other than the study site was the fact the percentage of forbs found in elk diets exceeded estimated forage availability during all seasons except fall/winter 1995-1996 (Figs. 1 & 2, and Figs. 5 & 6). *Cologania longifolia* was one of the major forb species found in elk diets. This species occurred only sparsely in the wetter areas on the study site. Elk were either selecting for forbs or a particular species of forb found on the study site, or they were feeding in the wet areas located below North Star Mesa where forbs were more plentiful.

Because elk are such wide ranging animals and the study site is small in comparison, it is highly probable that the elk were foraging somewhere else. Without being able to follow the movements of the elk, it was impossible to tell exactly where they were feeding. Since elk are considered opportunistic, they were probably feeding in the wetter areas below the study site where the new growth was more available. The time of throughput (period between the first ingestion of a plant and its first appearance in the feces) in ruminants is approximately 20-30 hours, and the time of elimination is about 5-6 days (Stewart 1967). It may be longer or shorter depending on the type of forage consumed (Stewart 1967). Therefore, the elk could have been feeding in an area outside the study site, and travelling to North Star Mesa 20-30 hours or even days later and defecating. When they were feeding on North Star Mesa, the plants consumed may have been eliminated several miles away.

Fort Bayard

Elk food habits on Fort Bayard showed similar results to those on North Star Mesa. The data showed small differences between the undisturbed an disturbed areas. The spring/summer diets showed the most difference. This was probably the result of a greater variety of plants being available during the spring/summer months. The study areas at Fort Bayard also were in close proximity to each other. Therefore, the elk were most likely foraging and defecating in both areas producing equivalent food habits results. As with the data from North Star Mesa, the sites were combined and further analyzed.

Elk diets consisted primarily of trees/shrubs during spring/summer (53%) of 1994 and fall/winter (83%) of 1994-1995 (Fig. 7), and spring/summer (51%) of 1995, and fall/winter (87%) of 1995-1996 (Fig. 6). As expected, the percentages of trees and shrubs (Figs. 7 & 8) in diets from fall/winter months exceeded those from spring/summer months. The primary woody vegetation consumed was *Quercus* spp., *Garrya wrightii*, and *Cerocarpus montanus* with some *Juniperus* spp. present in diets from the spring/summer months.

As on North Star Mesa, elk were browsing more than grazing. This corresponds with vegetation availability (Figs. 3 & 4). Average rainfall on Fort Bayard from 1994-1996 was 76% of the long-term average. This lack of rain kept the availability of forbs and grasses on the study site low. These results were similar to those found in the study conducted by Short et al. (1977) on Fort Bayard. His data revealed that elk diets consisted of 74% trees/shrubs during the fall/winter, and 71% during the spring/summer.

In 1994-1995, and 1995-1996, fewer grasses were consumed than were available (Figs. 3 & 4 & Figs. 7 & 8). More grasses were found in the diets during the spring/summer months than during the fall/winter months (Figs. 7 & 8). The main grass species consumed by elk during all seasons from 1994-1996 on Fort Bayard were *Leptochloa dubia*, and *Bouteloua* spp. During the fall/winter months, *Bromus* spp. was

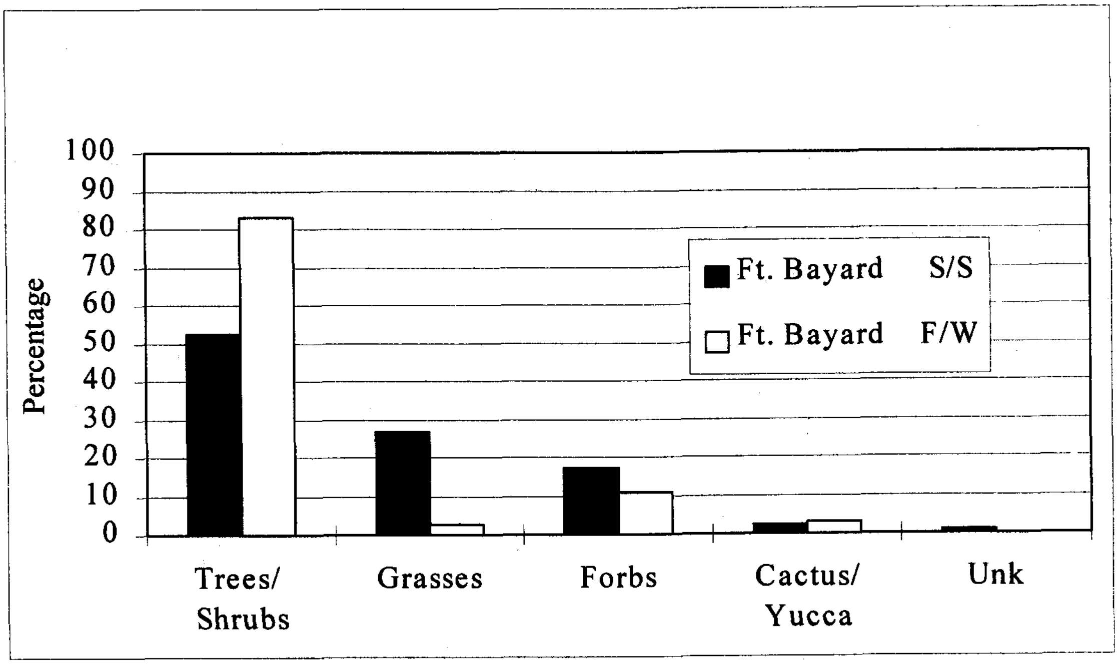

Figure 7 Percent botanical composition of elk diets from undisturbed and disturbed areas combined on Fort Bayard, 1994-1995.

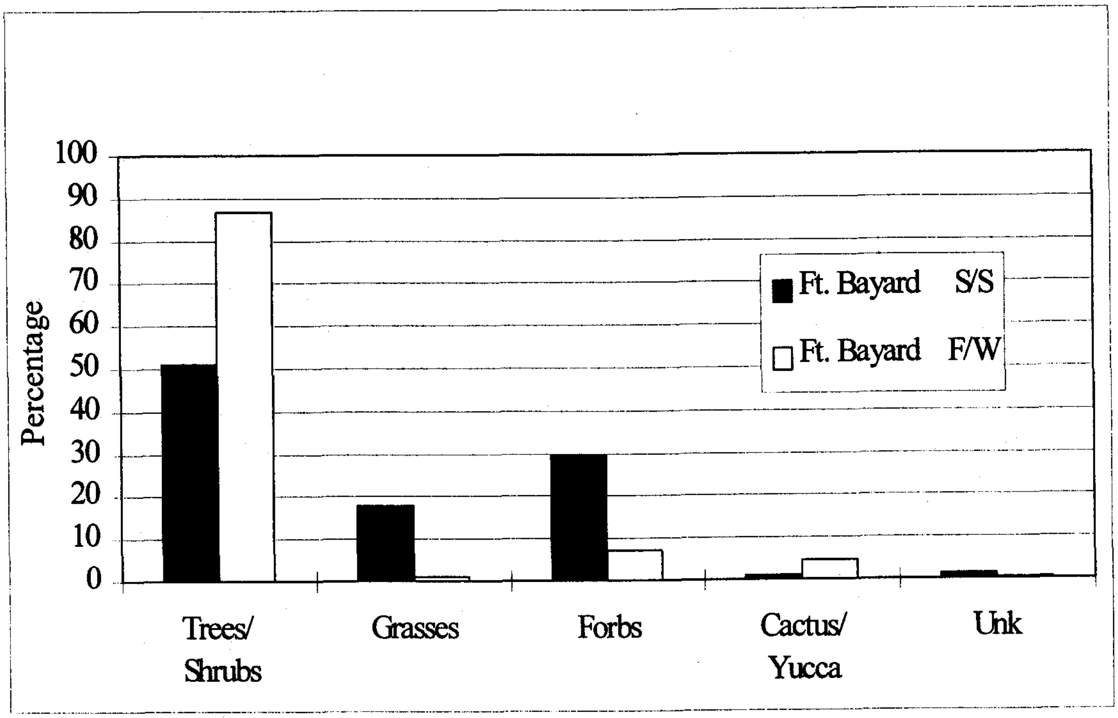

Figure 8. Percent botanical composition of elk diets from undisturbed and disturbed areas combined on Fort Bayard, 1995-1996.

plentiful in elk diets, and during the spring/summer months, traces of *Sporobolus* spp., *Aristida* spp., and *Muhlenbergia* spp. were found in the diets. The presence of the green sprangletop (*Leptochloa dubia*) in the elk diets during all seasons revealed that the elk on Fort Bayard were feeding somewhere other than the study site as this species was not found along any of the vegetation transects.

More forbs were consumed during the spring/summer months of 1994 (17%) than were available (14%) (Figs. 3 & 7). During the spring/summer of 1995, more forbs were consumed (30%) than grasses (17%) (Fig. 8). These results correspond with vegetation availability. The primary forbs found in the diets for all seasons from 1994-1996 were *Marrubium vulgare* and *Sphaeralcea* spp. During the spring/summer months *Lotus* sp. was also a primary species in the diets, while during the fall/winter months, *Commelina dianthifolia* was present. Traces of *Opuntia* spp. were greater during the fall/winter months than the spring/summer months.

Possible Biases Associated with Fecal Analysis

Evaluating diet composition of large herbivores such as elk by fecal analysis may be biases by several important factors. One factor is differential digestion of various plant species (Anthony and Smith 1974, Dearden et al. 1975, Vavra et al. 1978, Holechek et al. 1982). The amount a plant species is digested is dependent upon the plant form, and the growth stage of the plant (Mohammad et al. 1995). Herbaceous species such as forbs are likely to be digested more thoroughly than woody species. Because of this, fecal analysis may be biased toward the tree/shrub category (Anthony and Smith 1974). Several studies reported that grasses often were overestimated and forbs were underestimated because the resistance of grasses to digestion was greater (Vavra et al. 1978, Havstad and Donart 1978, Vavra and Holechek 1980, McInnis et al. 1983, Bartolome′ et al. 1995).

Some species may become unidentifiable after going through the digestive track and therefore misrepresented (Smith and Shandruk 1979). Other species with dense stellate hairs or trichromes may be overestimated (Sanders et al. 1980). Large plant fragments in the feces also may cause misrepresentation of a species. The frequency of the species may be low, but because of the size of the fragments, the species may contribute more to the estimate than many other plant fragments (Storr 1961). Species may be differentially fragmented so that the proportion of the plant consumed does not equal the proportion of the fragments observed in the feces (Owen 1975, Holechek et al. 1982).

Other factors that may cause biases are: observer error and training (Holechek and Gross 1982*a*, Holechek et al. 1982, Alipayo et al. 1992, Bartolome′ et al. 1995), sample preparation (Vavra and Holechek 1980, Holechek 1982), calculation procedures for analysis (Holechek and Gross 1982*b*), microscope magnification levels (Holechek and Valdez 1985), presence of woody material (Holechek and Valdez 1985), and sample size (Anthony and Smith 1974). Because of these biases, food habits results should be interpreted carefully.

Despite these limitations, fecal analysis is a useful technique for studying diets of large herbivores such as elk. This technique allows for practically unlimited sampling (Anthony and Smith 1974). Sampling can be done when killing the animals and utilization techniques are not practical (Johnson and Pearson 1981). Fecal analysis involves no interference of normal habits of the animals, it has particular value where several herbivores occupy the same range, and it is the only feasible procedure to use for studying rare, endangered, or secretive animals (Anthony and Smith 1974, Vavra et al. 1978).

MANAGEMENT RECOMMENDATIONS

When managing these areas, wildlife managers should take into consideration the potential for competition of food items between deer and elk. Since elk are consuming so much browse on North Star Mesa and Fort Bayard, there may be considerable diet overlap with the mule deer also found on these sites. Boeker et al. (1972) reported that 75% of the total diet of mule deer on Fort Bayard was woody browse. Collins and Urness (1983) concluded that there was considerable potential for exploitative competition between mule deer and elk (that favors elk). They determined that elk were less selective of plant species, and that deer could not digest some forages as efficiently as elk (Collins and Urness 1983).

Similarly, Cliff (1939) found elk and deer became competitors when they occupied the same range, and 1 or both of them exceeded carrying capacity in the Blue Mountains of Oregon. He concluded that under unfavorable range conditions, elk were more productive than deer. Cliff (1939) stated that in the Blue Mountains, deer could not compete successfully with elk when food was a limiting factor because elk could browse higher than deer.

Since there is potential for diet overlap between elk and mule deer, especially under severe drought conditions, managers need to monitor both populations. If 1 or both exceed carrying capacity, populations may need to be reduced.

Because elk prefer to use edges (Skovlin 1982), are known to use both undisturbed and disturbed areas (Casady 1995), and are consuming a lot of browse on North Star Mesa and Fort Bayard, disturbed areas interspersed among undisturbed piñon-juniper woodlands may be the best way to improve elk habitat. According to Short et al. (1977) clearing of large areas of piñon-juniper woodlands decreased elk use; therefore, the clearings should be small. Short et al. (1977) and Casady (1995) recommended clearings that are long narrow strips so that escape cover is readily accessible.

On North Star Mesa, *Quercus* spp. were the most important forage followed by *Juniperus* spp. Therefore, when managing for elk in this area, *Quercus* spp. should be maintained with some *Juniperus* spp. interspersed throughout. On Fort Bayard, *Pinus edulis,* and *Juniperus* spp. could be sacrificed from the standpoint of food contribution while maintaining *Quercus* spp., *Garrya wrightii*, and *Cercocarpus montanus*. Removal of the overstory trees should enhance the growth of the more important shrub species.

Further food habits research for mule deer and elk in the piñon-juniper woodlands of the Gila National Forest needs to be conducted. Future studies should not be concerned so much with comparing diets between undisturbed and disturbed areas. They should take a broader scope and sample the many different habitat types interspersed throughout the piñon-juniper woodlands. The study area should be expanded to include elk and mule deer home-ranges. It would also be beneficial to monitor elk movements while collecting samples to get a better idea of where the elk are foraging. The attainment of this knowledge would give wildlife managers more information on how to improve elk and mule deer habitat in piñon-juniper woodlands and provide a biological basis for management strategies for these important ungulates.

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POSTER SUMMARY

Inheritability of Breeding Dates For Female White-tailed Deer

BOB K. CARROLL
Texas Parks and Wildlife Department, 3852 Pine Ridge Road, La Grange, Texas 78945

Abstract: The Texas Parks and Wildlife Department has trapped and transplanted thousands of white-tailed deer during the past 40 years. Breeding chronology data indicates a wide difference in conception between ecological types. This study was designed to determine if breeding dates are altered by translocating deer from one ecological area to another. Data collected thus far suggests that translocated deer retain their original breeding dates. Wildlife managers should consider this information before moving deer between ecological types.

Key words: breeding dates, inheritability, *Odocoileus virginianus*, Texas, Texas Parks and Wildlife Department, translocation, white-tailed deer.

INTRODUCTION

The Texas Parks and Wildlife Department has trapped and transplanted thousands of white-tailed deer (*Odocoileus virginianus*) during the past 40 years. The majority of deer were trapped in south-central Texas and released in the eastern part of the state without consideration for possible differences in breeding and fawning dates between the source and destination herds. In a 3-year study, Williams et al. (1995) reported the earliest breeding date in the western counties of the South Texas Plains was November 29 and the latest breeding date was February 1. The mean breeding date for each year of this study was December 21, 22, and 28. The data collected in Colorado County during this study indicated the earliest breeding date was September 28, and the latest was November 22. The mean breeding dates for Colorado County in 1991 and 1992 were October 28 and October 24, respectively. The objective of this study was to determine if breeding dates are altered by translocating deer from 1 ecological area to another. A better understanding of how white-tailed deer breeding dates are impacted could influence state policies on translocation. This study is supported by Texas Parks and Wildlife Department state funds and Crier Creek Ranch.

STUDY AREA

The study was conducted on a 121.4 ha deer-proofed ranch in the Post Oak Savannah ecological area of Texas. The study site was located in Colorado County, 14.6 km northwest of Columbus. The wooded areas consisted primarily of post oak (*Quercus stellata*) interspersed with live oak (*Q. virginiana*), water oak (*Q. nigra*), and eastern red cedar (*Juniperus virginiana*). Grasses found on the study area included broomsedge bluestem (*Andropogon virginicus*), King. Ranch bluestem (*A. ischaemum*), brownseed paspalum (*Paspalum plicatulum*), and threeawns (*Aristida* spp.).

METHODS

There were 14 bucks, 52 does, and 10 female fawns trapped and ear-tagged in the South Texas Plains ecological area and relocated to the 121.4 ha deer-proofed study site in the Post Oak Savannah ecological area. Attempts were made to eradicate native deer within the study site enclosure prior to the February 1994 introduction.

In 1994, 32 male and 27 female fawns were captured on the study area and ear-tagged with color-coded ear tags which would be used to identify these doe for study collection in following years. A total of 18 male and 27 female fawns were tagged in 1995. In February and/or March of 1995, 1996, and 1997 does were collected and embryos measured to determine breeding dates on a fetal scale developed by Hamilton et al. (1985).

RESULTS

In February and March of 1995, 5 ear-tagged South Texas doe were collected and the breeding dates were December 9, 15, 25, and 31, 1994, and January 24, 1995. In March of 1996, 6 ear-tagged doe were collected and the breeding dates were December 13, 24, and 29, 1995, and January 4, 6, 1996. In February and March of 1997, 4 female deer of the first generation of deer born to introduced doe and 4 does of the second generation were collected. The 4 first generation does had breeding dates of December 9, 11, 13, and 17, 1996. The 4 second generation does had breeding dates of December 4, 14, and 16, 1996, and January 13, 1997. Mean breeding dates for the study area deer herd in 1995, 1996, and 1997 were January 1, December 25, and December 26, respectively.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Data collected thus far suggests that breeding dates of the introduced does and 2 succeeding generations of does have remained consistent with the source herd. Williams et al. (1995) indicated that breeding dates vary from 1 ecological area to another. Based on this information care must be taken when translocating deer from 1 ecological region to another. A translocated deer herd could have lower survivability due to varying conditions between regions.

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A Selective Overview of State Status Reports

RAYMOND M. LEE
Arizona Game and Fish Department, Phoenix, AZ 85023

Evaluating various aspects of wildlife management programs of the western states and provinces is always an entertaining proposition. Just for starters, it is entertaining to find just how difficult it is for well-trained wildlife professionals to follow relatively simple instructions - particularly when they are provided with a "fill-in-the-blanks" computer disk. It could be that wildlifers are a particularly independent lot, who don't want to be restricted with form questions - "I'll just fill this in any damn way I want." This could help explain the divergent evolution of the various game management programs.

For example, lets look at something rather simple - like, what is your state's definition of a legal animal? Answers varied somewhat. A legal mule deer was identified as being: "any deer with 1 antler at least 5" long;" "any antlered deer with a least 1 antler >3;" "deer having at least 1 antler;" "buck with a visible antler;" "a deer with hardened antler protruding through the skin;" "having an antler fully erupted through the skin and capable of being shed;" and, "antlers over 5" in length." There were, of course, variations on this: "4 points or greater buck - with the latter referring to any buck having at least 4 tines, excluding the brow tine, on 1 antler;" "a 3 point buck or less;" "deer with 2 points or less per side;" "antlerless (no antlers or antlers < 2);" and finally, "the legal animal is 1 fork-antlered deer - the fork-antlered deer is further defined as possessing antlers, 1 of which has a definite fork showing 2 or more distinct points."

Okay, that was simple enough. Now how much does it cost to hunt 1 of these legal animals? From state to state, resident hunting license and tag fees for mule deer ranged from $15 to $49, while non-resident hunting license and tag fees ranged from $75 to $328, with Idaho being the proudest of their deer (Table 1). This does not include the various application fees and conservation permits. The non-resident/resident cost ratios also varied widely. From 4.6X in Arizona to Idaho's 18.2X.

Similar differences were seen in the cost of elk hunting. Resident hunting license and tag fees ranged from a low of $17 in Montana to $134 in Nevada (Table 2). Non-resident fees ranged from $150.00 in British Columbia to Nevada's $621. California closes their elk hunting to non-residents, except for special fund-raising tags which typically cost in the $1,000s. Non-resident/resident cost ratios ranged from Nevada's 4.6X to Idaho's 17.8X.

Wildlife populations have varied greatly in recent years. The apparent increases in elk numbers and the concurrent decreases in mule deer numbers have led many people to assume that the former is causing the latter. Assuming that there is at least some correlation between the number of animals harvested under an effective wildlife management program and their population, respondents were asked to provide population estimates for 1985 (a period of relatively high wildlife population levels in many states) and for 1995 (a period with more depressed wildlife levels). The change in mule deer harvest ranges from +3% for Montana to -59% for Idaho (Table 3). On average, mule deer numbers have declined 33%. Elk harvest, conversely, ranged from a 265% increase in New Mexico to a 52% decrease in Alaska (Table 4). The average increase for elk harvest was 67%.

Table 1. The relative costs for resident and non-resident hunters for mule deer hunting license and tag fees in the various western states and provinces. Values are in U. S. dollars.

State/Province	Total Resident Hunt Fees	Total Non-resident Hunt Fees	Resident/Non-resident Hunt Fee Ratio
Arizona	$ 35.50	$ 164.00	4.6
British Columbia	15.00	75.00	5.0
Nevada	49.00	266.00	5.4
California	44.90	257.25	5.7
Washington	33.00	210.00	6.4
Colorado	20.25	150.25	7.4
New Mexico	23.00	180.00	7.8
Wyoming	17.00	150.00	8.8
Oregon	26.00	229.00	8.8
Montana	28.00	298.00	10.6
Texas	19.00	250.00	13.2
Idaho	18.00	328.00	18.2

Table 2. The relative costs for resident and non-resident hunters for elk hunting license and tag fees in the various western states and provinces. Values are in U. S. dollars.

State/Province	Total Resident Hunt Fees	Total Non-resident Hunt Fees	Resident/Non-resident Hunt Fee Ratio
Nevada	$ 134.00	$ 621.00	4.6
Arizona	81.00	388.50	4.8
British Columbia	25.00	150.00	6.0
New Mexico	75.00	465.00	6.2
Utah	50.00	328.00	6.6
Washington	39.00	270.00	6.9
Colorado	30.25	250.25	8.3
Oregon	41.00	344.00	8.4
Wyoming	28.00	350.00	12.5
Montana	17.00	245.00	14.4
Alaska	25.00	385.00	15.4
Idaho	24.00	428.00	17.8

Table 3. Mule deer harvest and % change between 1985 and 1995 for the various western states and provinces.

State/Province	Total Harvest (1985)	Total Harvest (1995)	% Change
Montana	74,411	76,936	3
Washington	40,487	37,765	-7
Colorado	58,243	51,899	-11
Oregon	34,228	28,450	-17
Texas	4,745	3,845	-19
British Columbia	27,550	21,214	-23
New Mexico	25,931	14,944	-42
California	32,190	17,273	-46
Arizona	17,968	9,410	-48
Wyoming	61,483	31,935	-48
Utah	61,955	26,012	-58
Nevada	19,520	8,118	-58
Idaho	48,950	19,990	-59

Table 4. Elk harvest and % change between 1985 and 1995 for the various western states and provinces.

State/Province	Total Harvest (1985)	Total Harvest (1995)	% Change
New Mexico	2,862	10,443	265
Arizona	3,959	10,125	156
Nevada	82	183	123
California	49	108	120
Utha	2,862	10,443	103
Colorado	23,332	36,171	55
Idaho	15,500	22,400	45
Montana	17,635	21,961	25
Oregon	14,534	16,985	17
British Columbia	3,763	2,897	-23
Washington	8,970	6,429	-28
Alaska	200	96	-52

Along with this change in animal numbers, the relative status of mule deer and elk has also changed. In Arizona, for example, as late as 1984, there were more than twice as many deer applicants as there were elk applicants. By 1996, these numbers were much closer, with mule deer holding only a slight edge in applicant pressure (Fig. 1). Due to the differential in fee structure, in 1994 elk surpassed deer as the number 1 big game revenue generator (Fig. 2).

Respondents were also asked about the occurrence of "Special Status Seasons." In this case, we weren't looking for the common archery-only, or muzzleloader-only seasons - we were looking for something different - an even thinner slicing of the hunter pie. We found seasons for seniors (65+) and for Advanced Hunter Education Graduates. "Differentially-able" individuals, defined as either wheel-chair bound, quadriplegic, or meeting challenged hunter access mobility requirements, ranged from having no special seasons to incentives such as increased bag limits, or extended seasons. Most states offered incentives to junior hunters (though definitions ranged from 10-14 to under 19) with Oregon having a particularly interesting twist. There, a junior hunter is guaranteed to receive 3 controlled tags when they are between 12 and 17 years of age. If a youth is unsuccessful in a drawing, they can select a hunt and receive a tag.

One of the benefits to taking on the task of compiling state status reports is that you get to ask questions that interest you. Therefore, among others, the following questions were proffered:

Are non-resident hunters encouraged in your state/province?

This question was asked to determine whether any agencies were actively competing for hunters, or whether they were following the trend to limit the number of non-residents, and as a result their revenue, to appease their resident hunters. Was that non-biased enough? Again, the responses were quite varied. Some stated that "the Department has no programs to encourage non-resident hunters" others mentioned that non-residents were "benignly neglected." Several states indicated that "non-resident hunters must be accompanied by a licensed local guide." New Mexico has a newly enacted, and recently challenged, law requiring non-residents to use a registered guide/outfitter. This effectively limits the number of non-residents since there are only a limited number of guides registered with the state. Most states have non-resident caps of 5-10% on their controlled permits. Washington's response was perhaps the most interesting, "we have no programs to promote non-resident hunters; we have too many hunters already."

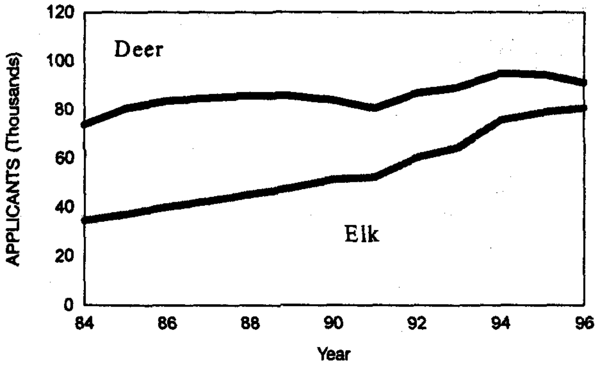

Figure 1. Historical comparison between the number of elk applicants and the number of deer applicants for hunting opportunities in Arizona.

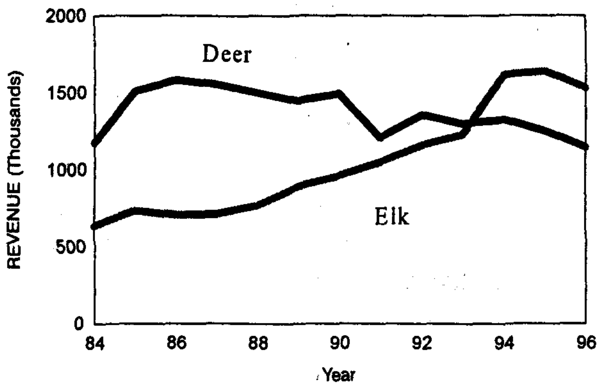

Figure 2. Historical comparison between the revenue generated from the purchase of elk hunting licenses and tags and deer hunting licenses and tags in Arizona.

On the other hand, Nevada offers a special guided hunt catering directly to non-residents. Wyoming sets aside 20% of the year's limited quota deer and 16% of the limited quota elk licenses for non-residents.

Does your state/province have a Special Tag program (Governor's tag) to generate revenue?

While some states and provinces do not use these "special tag" programs, or limit them to only a few species, there are a number of jurisdictions which use these programs for fundraising purposes. Again, each agency puts its own particular spin on this concept. California, for example, has a "Golden Opportunity Tag" which is good for all open areas for a 7-month period. An "Open Zone Tag" allows the hunter to hunt in any open zone during the normal season. Oregon raffles 9 and auctions 8 deer and elk tags each year. Texas's Grand Slam, offered for the first time in 1996, generated $70,000 - $10 at a time. This drawing allowed the successful person 4 fully-guided hunts in Texas.

Wyoming may be the most aggressive state in the allocation of special tags, if not in the generation of revenue. Each year the Governor is allocated 20 complimentary hunting licenses (as well as 20 fishing licenses) to use at his or her discretion. The licenses are usually donated to charitable organizations for raffle or auction (the Department does not receive any of the revenue from these tags). In addition, each of the 7 members of the Commission can issue, at cost, 8 big game licenses per year to nonprofit charitable organizations. The Department does not receive any revenue beyond the initial fee for the sale of these licenses.

Each of these programs bring in varying amounts of revenue, with Arizona's being perhaps the most successful. In 1984, Arizona was given legislative authority to auction or raffle 2 tags for each big game species each year for fundraising purposes, with the revenue received to be spent for the benefit of that species. To date, that program has generated over $4,500,000. In 1996, the 4 deer and 2 elk tags brought in $268,960.

If, after listening to this rehash of the information provided in the state status reports, you are still interested in the detailed information provided, you will find the reports printed in your registration book. I, personally, find the information very interesting. I find the names and numbers of the contact persons invaluable.

EDITOR: James C. deVos, Jr.

REVIEWERS

KELLY ALTENDORF
Idaho State University
Campus Box 8007
Pocatello ID 83209

VERN BLEICH
California Department of Fish & Game
407 W Line St
Bishop CA 93514

SUE BOE
Arizona Game & Fish Department
2221 W Greenway Rd
Phoenix AZ 85023

TOM BRITT
Arizona Game & Fish Department
3500 S Lake Mary Rd
Flagstaff AZ 86001

LEN CARPENTER
Wildlife Management Institute
4015 Cheney Dr
Ft Collins CO 80526

WILLIAM CARREL
Arizona Game & Fish Department
2221 W Greenway Rd
Phoenix AZ 85023

ALAN CLARK
US Fish & Wildlife Service
Box 566
Cathlamet WA 98612

MICHAEL COFFEY
National Park Service
1201 Oak Ridge Dr
Ft Collins CO 80525

LEON FISHER
USDA Forest Service
8416 Julian Robles NE
Albuquerque NM 87122

SANTIAGO GONZALES
New Mexico Department of Game & Fish
PO Box 25112
Santa Fe NM 87504

JOHN GOODWIN
Arizona Game & Fish Department
3500 S Lake Mary Road
Flagstaff AZ 86001

CHUCK HAYES
New Mexico Department of Game & Fish
PO Box 25112
Santa Fe NM 87504

JIM HEFFELFINGER
Arizona Game & Fish Department
555 N Greasewood Rd
Tucson AZ 85745

BOB HENRY
Arizona Game & Fish Department
9140 E County 10 ½ St
Yuma AZ 85350

DOUG HUMPHREYS
Texas Parks & Wildlife Department
1600 W Highway 90
Alpine TX 79830

RICK KAHN
Colorado Division of Wildlife
317 W Prospect St
Ft Collins CO 80526

PAUL KRAUSMAN
University of Arizona
PO Box 238
Oracle AZ 85623

JOHN LAUNDRÉ
Idaho State University
Biological Sciences
Pocatello ID 83209

RAYMOND M. LEE
Arizona Game & Fish Department
2221 W Greenway Rd
Phoenix AZ 85023

FREDERICK LINDZEY
Wyoming Cooperative Research
Box 3166, University Station
Laramie WY 82071

BRUCE LUBOW
Colorado Cooperative Fish & Wildlife
Research
Colorado State University
Ft Collins CO 8052

KEN MAYER
California Department of Fish & Game
8819 Liscarney Wy
Sacramento CA 95828

CHARLES MESLOW
Wildlife Management Institute
8035 NW Oxbow
Corvallis OR 97330

TERRY MESSMER
USU/UMC-5210
Department of Fish & Wildlife
Utah State University
Logan UT 84322-5210

BILL MILLER
Arizona State University
3617 S Siesta Ln
Tempe AZ 85282

PAT O'BRIEN
Arizona Game & Fish Department
2221 W Greenway Rd
Phoenix AZ 85023

HAL SAWYER
Wyoming Cooperative Research
Box 3166 University Station
Laramie WY 82071

GENE SILOVSKY
US Forest Service
Pacific Northwest Region
11461 SW 98th
Tigard OR 97223

VASHTI SUPPLEE
Arizona Game & Fish Department
2221 W Greenway Rd
Phoenix AZ 85023

BOB VAHLE
Arizona Game & Fish Department
HC 66 Box 577201
Pinetop AZ 85935

GARY WHITE
Colorado State University
3928 Buckskin
Laporte CO 80535

LAUREL WILEY
US Fish and Wildlife Service
PO Box 1306
Albuquerque NM 87059

JIM WITHAM
Arizona Game & Fish Department
5325 N Stockton Hill Rd
Kingman AZ 86401