

THE STARKEY PROJECT:

A synthesis of long-term studies of elk and mule deer

Michael J. Wisdom, Technical Editor



Featuring Forewords by Forest Service Chief Dale Bosworth
and Former Chief Jack Ward Thomas

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Jennifer Rahm, General Editor
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Featuring Forewords by
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To Scott Feltis (deceased), whose dedication and perseverance
in helping establish the Starkey facility will always
be remembered (a.k.a, *Scotty's Gate*)

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Preface:

The Starkey Project—A Long-Term Endeavor

The Starkey Project is a unique program that has combined long-term research with multi-disciplinary, multi-partner involvement. The research was, and still is, designed to answer management questions. Even studies designed as basic research have been conducted in a manner that could identify mechanisms relevant to management. What is particularly noteworthy is that this research approach has resulted in a wide array of information critical to the management of elk, mule deer, cattle, forests, and rangelands. Importantly, results have provided a better understanding of the many interactions among the three species and human uses of forests and rangelands.

The original Memorandum of Understanding developed for the Starkey Project reflected a long-term commitment by the Forest Service's PNW Research Station and the Oregon Department of Fish and Wildlife. Other partners who have been essential to the success of the Project include Boise Cascade Corporation, National Council for Air and Stream Improvement and the Eastern Oregon Agricultural Research Center of Oregon State University. Over 40 other partners, including federal and state agencies, universities, tribal nations, and private organizations have participated in the Project.

Four major themes of research were identified when the Starkey Project began in the mid-1980s. Elk herd productivity was being recognized as a major issue of herds in the Northwest. Intensive timber harvest and concomitant increases in road density and traffic related to both logging and recreation were recognized as having a substantial effect on deer and elk distributions across landscapes. Competition for forage among cattle, deer, and elk had long been a contentious issue among sportsmen, stockmen and wildlife managers. These four major issues—elk herd

productivity, intensive timber management effects on deer and elk, roads and traffic effects on deer and elk, and competition for forage among elk, deer, and cattle—formed the basis for the project from 1989 through the late 1990s. Several complementary studies also were developed, such as the influence of late summer nutrition on elk cow and calf survival, and elk thermal cover needs. Again the long-term commitment of diverse research partners provided the opportunity to address critical information through a variety of studies beyond the original research themes.

The long-term commitment of the research partners is evident throughout this book. The manuscripts provided here synthesize the four major research themes and the many subsequent, complementary studies conducted in response to managers' continued requests for additional information. These synthesized manuscripts are based largely on peer-reviewed articles that have appeared in scientific publications, and we encourage readers to examine those articles for more details.

Importantly, the long-term commitment of partners in the Starkey Project continues today, and many new manuscripts have recently been submitted for publication in scientific journals. These new articles reflect changing research directions that address the effects of ungulate herbivory on ecosystem patterns and processes; the dynamics of habitat-nutrition-predator relations with ungulate condition and population performance; the effects of forest management designed to reduce fire risk on forage and habitat use by ungulates; and the effects of human recreation on elk and mule deer populations. Many of these studies are being conducted not only at the Starkey Experimental Forest and Range, but also on industrial forestland and national forests in the western United States. The new stud-

ies maintain the same high degree of integrity exemplified by the research partnerships of past studies.

We believe that readers will find the information presented here interesting, informative, and of high utility for management. We commend the many partners and scientists who have made this synthesis possible. The continued need for

new and better knowledge of ungulate relations with forest and rangeland management has made the investment in the Starkey Project a prudent one, and one that we believe will continue to provide benefits to habitat and population managers of elk and mule deer, as well as public users of these resources, well into the future.

Bruce K. Johnson
Starkey Project Leader
Oregon Department of Fish and
Wildlife
November 10, 2004

Martin Vavra
Starkey Project Leader
Pacific Northwest Research Station

Foreword: The Starkey Project—In the Beginning

In 1989, The Forest Service (FS) Research Work Unit ("Range and Wildlife Habitat Research") that I headed in La Grande, Oregon, was preparing a new 10-year research plan—known in FS research circles as a "Problem Analysis." In contrast to most research units that conducted "basic" research, this unit had traditionally focused on "applied" research on habitat relationships between mule deer, elk, and livestock.

Applied research is directed to attaining answers to management questions. By contrast, basic research seeks to develop knowledge on underlying processes, with no immediate focus on the ultimate "usefulness" of that understanding.

That approach made our research unit popular with user groups and somewhat less so with those who directed FS research. Past cooperative work with the Oregon Department of Fish and Wildlife gave us a leg up. The group that had most recently focused on deer-elk-cattle interactions was composed of Larry Bryant and myself, of the Forest Service's Pacific Northwest Forest and Range Experiment Station, and Donavin Leckenby and Leonard Erickson of the Oregon Department of Fish and Wildlife (ODFW).

The previous decade had produced some crisis events for public land managers that came to bear as we thought about a new decade of research effort. In 1973, the supervisors of the Umatilla, Wallowa-Whitman, and Malheur National Forests were faced with dealing with the aftermath of a severe outbreak of Douglas-fir tussock moth that included a massive effort to salvage the dead and dying timber. The relatively new requirements for environmental assessment that had arisen from the National Environmental Policy Act and planning coming from the National Forest Management Act presented a problem.

The supervisors approached the La Grande research unit to lead a "crash effort" to develop a "manual" that would provide the basis for dealing with wildlife

issues. The resultant effort (*Wildlife Habitats in Managed Forests—The Blue Mountains of Oregon and Washington*) included guidance and models to evaluate various salvage operations relative to their effects on mule deer and elk (Thomas 1979 and Thomas et al. 1979). This "manual" was quickly adopted and adapted for use in planning for national forests across the range of elk in the United States, with additional use in the western regions of Canada. This widespread use took place in spite of the criticism that the authors were "guessing" as they patched together the models.

The critics had a point. But, the models were a place to start and, we thought, considerably better than simply throwing up one's hands and playing dumb. However, there was a responsibility for the researchers who led this effort to, as quickly as possible, test the hypotheses upon which this management guidance was based. Joint efforts to test these hypotheses were headed by Donavin Leckenby and Leonard Erickson of the ODFW and Ed Dealy of FS research. Their work built on earlier elk research by ODFW biologist Richard Pedersen, who later moved to the FS and continued to provide scientific support for the elk models and research. Work by Leckenby, Erickson, and Dealy was a valiant effort and produced considerable information on elk habitat use but lack of experimental controls was a serious drawback.

For example, two of the assumptions, or working hypotheses, upon which managers were making decisions that were particularly troublesome were the "thermal cover hypothesis" (Thomas et al. 1979) and the "animal equivalency hypothesis" (Stoddard and Smith 1955). The thermal cover hypothesis was based on observations of how deer and elk behaved in forested habitats when faced with very cold temperatures, particularly when low temperatures were coupled with wind. These forest patches were assumed to allow the animals using them to

"thermo regulate" or use such cover to conserve energy. Forest plans included preserving such stands from timber harvest or thinning to provide patches of such cover. Such actions could impose significant costs on timber programs.

In the case of the "animal equivalency hypothesis" managers assumed that there was direct and complete competition for forage between mule deer, elk, cattle, and sheep. "Consumption equivalency" (Davis 1952) was computed on the basis of a 454-kilogram (1,000 pound) "animal unit" (Stoddard and Smith 1955) whereby 5 deer = 5 sheep = 2 elk = 1 cow of 454 kilograms (1,000 pounds). This simple concept was widely applied and resulted in exaggerated estimates of competition. Obviously, this could only be correct when various species were in the same place, at the same time, and consuming the same plants in the same proportions. But, by and large, those assumptions were accepted.

In the meantime, Dixie Smith, then staff director for wildlife and range research in the Forest Service's Washington Office, was increasingly concerned that the bulk of the research budget for wildlife was being directed to the "charismatic megafauna" that included mule deer, white-tailed deer, elk, moose, and turkeys. He championed the idea that all available information on those species be collected, summarized, and interpreted before any additional commitments of scarce research dollars and personnel were directed to those species. Senior FS research scientists were assigned to organize an approach—and recruit authors—to synthesize the information on those species to provide guidance to managers for immediate use in management and guide researchers to important problems for research scientists to address.

I was given the lead role to deal with elk as part of my duties as research scientist at the Forest Service's La Grande Laboratory. I recruited a fresh-faced wildlife biologist, Dale Toweill, just out of school, to assist in that effort. The prize-winning *Elk of North America—Ecology and Management*, developed in associa-

tion with the Wildlife Management Institute including the overall editorial assistance of Richard E. McCabe and Laurence R. Jahn, was the result (Thomas and Toweill 1982). Almost simultaneously, FS scientist O. Charles Wallmo (1981) and associates came out with *Mule and Black-tailed Deer of North America*—also produced in cooperation with the Wildlife Management Institute.

Armed with these massive efforts at synthesis regarding elk and mule deer, we sought out managers concerned with range and wildlife (federal, state, and private) to get ideas of what our next efforts should entail. Four questions came up over and over—particularly from the National Forest System and state fish and wildlife departments.

1. How did elk, mule deer, and cattle divide use of mutually occupied habitats? It was assumed that the animals were in direct competition for food. "Animal units" were determined on the basis of weight (one cow = two elk = six deer). Managers knew this would be so only if the various species were in the same place, at the same time, eating the same diet.
2. How did the three species utilize space relative to habitat features such as cover/opening edges, various canopy closures, and—most especially—roads and the traffic rate on those roads? Managers had ideas from various studies but were uneasy basing essentially irrevocable management decisions on such "hints."
3. Did the age of breeding male elk (bulls) influence herd reproductive performance? State after state, in response to increasing numbers of hunters, had allowed unrestricted kill of bulls, which resulted in the vast majority of bulls during breeding season being 2.5 years of age or younger. There were suspicions that this situation was resulting in lowered herd recruitment. But, data of sufficient quantity and quality was not available to give agencies the backup to make unpopular decisions to more stringently regulate the number of hunters to in-

crease the number of mature bulls surviving after hunting season.

4. How would elk respond to intensively managed forests that might occur in the future? Preliminary studies indicated that elk avoided portions of forests that were being more intensively managed—i.e., roaded and logged. But, what would happen if elk were forced to respond to a situation that would likely be the condition at some time in the future as managed forests became pervasive in the landscape?

As we considered these questions, we could come up with no other approaches than those that had already been taken and provided less than definitive answers. Managers needed better information if changes were to be instituted.

Over and over, we kept returning to the need for controlled experiments of adequate scale in space and time, and adequate data sets with sufficient predictive power and broad inference space. Over and over, we rejected the notion due to potential cost, non-existence of required technology, political difficulties related to such an endeavor, and the high risk of failure. Such an endeavor would require:

1. A fenced enclosure of adequate size, say 40 square miles, that would contain deer and elk;
2. A radio telemetry system that would track a suitable sample size (several hundred) of deer, elk, and cattle; provide accurate locations at the rate of one per 15–20 seconds, and, then, log these locations in a computer for later manipulation;
3. A means of concentrating deer and elk in the winter (the study area would be summer range), feeding them a standard diet to maintain a winter condition that would mimic natural winter weights, and handling the animals so that they could be fitted (and refitted) with radio collars, blood tested for disease, age determined, and health assessed on a yearly basis.

In a fit of irrational enthusiasm, we decided it could be done. Our immediate supervisor was appalled—likely scared wit-

less—and withheld support. That whetted our appetite. We had the bit in our teeth. We were convinced that these problems would have to be addressed, and in a new way using controlled experiments, or they would forever confound forest and range managers.

The first rule of trying something new and bold—and likely very expensive—is to look around to see what existing knowledge and technology can be brought to bear on the problem at hand. After all, reinventing the wheel has limitations.

We knew that ranchers and farmers in New Zealand were successfully raising red deer (the same species as elk but a different subspecies) in captive situations, which required experience and developed technology in fencing and repeatedly handling animals. So, my associate in FS research, Larry Bryant (having won a bitterly contested coin toss), was off to New Zealand to observe the fencing and the handling facilities used in the business of farming red deer. In retrospect, Bryant was the “key player” that made the whole thing work. He simply would not give up on the dream—and he wouldn’t let me give up either. It seemed that his favorite line was, “I can do that. Give me a chance.” He got chance after chance and he never failed in his mission. Sometimes I was convinced that he had landed on his head too often during his paratrooper days—but in the end he carried the day.

The Kiwis had developed a new twist in the matter of fencing to enclose red deer. This fencing was high tensile with a modification that provided a spring-like effect with a two-fold benefit. Once stretched, it remained taught for years and provided “give” when an animal ran into it. Instead of ending up with a deer with a broken neck, the animal was bounced back—sometimes upside down and backwards—but otherwise intact. And, elk, being quite intelligent and quick learners, usually took on a fence only once. Further, they seemed to learn from seeing others of their kind take on the fence and were dissuaded otherwise.

Bryant, on his own hook, and with the disarming “aw shucks” demeanor of his eastern Oregon upbringing as a rancher’s son, negotiated a deal with the New Zealand company—and the New Zealand government (who wanted to get their fencing into the United States)—to provide the fencing at cost. Then, in order to sweeten the deal just a bit, Bryant talked them into throwing in the shipping costs to a U.S. port.

We didn’t know it then, but this sweetheart of a deal required approval by the State Department. We were assured, by the purchasing folks in the FS, that such approval could never be attained—and, even if it was, it would take years. We refused, one more time, to give up. So, with more than a tad of political support from some high-level Oregon elected officials whom we had gotten to know over the years on “show me” trips and an occasional “back country inspection trip,”—State Department approval was attained in a matter of a few weeks.

While in New Zealand, Bryant traveled from one red deer farming operation to another and then another studying the various handling facilities including corals, chutes, loading facilities, etc. The New Zealanders had worked these facilities out, with modification after modification, over many years of trial and error. That experience and the knowledge gained were shared freely with us and undoubtedly saved us years—and many dollars—in time and experimentation in learning how to handle the animals with minimal injury and trauma to both man and beast.

Now, we could say, “so far—so good,” and go the next step—the radio telemetry system that we had to have to make the dream a reality. Bryant sought out, and worked with, a research and development outfit in Texas (the only ones of the half dozen or so that we contacted who would even talk to us and not intimate that, perhaps, we were more than a little punch drunk from our experiences thus far) to develop the automated radio telemetry system. We had figured out, or so we thought, that such a system could

play off the Long Range Aid to Navigation (LORAN) system that was in place to serve as a navigational aide for aircraft and ships at sea and was operated by the U.S. Government. Every group we consulted—except this one—advised that the scheme would not work or, equally discouraging, that our ideas were simply too much of a “small potatoes” operation for them to concern themselves with. These sorts of folks, after all, were used to dealing with the Department of Defense.

Because the Research Division of the Forest Service had limited resources, we turned to the folks with the problems that had stimulated our efforts thus far—the National Forest System. John Butruille, Regional Forester in the Pacific Northwest Region, pledged help. Lamar Beasley, the Deputy Chief of the FS for Administration in Washington, undertook the task of finding the money necessary to back the dream. We were on a roll—a bit on the outside of the system—but on a roll nonetheless.

Then, reasonably enough, we were asked to consult with FS engineers in the regional office in Portland, to get them to sign off on our fence design and cost estimates. When the engineers looked at the fence design we had imported from New Zealand—with a few of our own modifications thrown in—they announced that our estimates of construction costs were off by a factor of four or more. They based their assessment on what they knew of building fences to exclude deer and elk from “seed orchards” for trees.

We stuck to our estimates and convinced Butruille and Beasley that we were right—or, at least, right enough to keep plowing ahead. We found a partner in a local logging contractor that was a personal friend of mine and got caught up in our dream. Gari Price was a dreamer—and an innovator—in his own right. No one else would even bid on the job.

After he got the bid, Price essentially designed and built a machine that would drill postholes in basalt rock and move over rugged terrain. Part of the secret to success was the realization, and the agreement with the Forest Service Dis-

strict Ranger Jeff Blackwood, who oversaw management of the site, that it was not ordained from above that a fence doesn't necessarily have to go in a straight line—a mostly straight line will do. That flexibility allowed Price, working with Dick Partney, another local supporter of the Project, to take the tracked drilling machine up and down through ravines that would have been otherwise impossible to negotiate. It was just one more crashout that came up "sevens." Scott Feltis, a determined FS technician (now deceased) who worked for Bryant, worked closely with Price and Partney in overseeing the contract for building the enclosure in the span of a few short months in 1987—on time and within cost.

After a series of fits and starts, and with incredible innovations and modifications, our friends in Texas came through with the radio telemetry system upon which everything depended. The pieces were falling into place.

Now, there were mounting political problems to overcome. This 40 square mile, 8-foot-high, fenced enclosure sat smack-dab in the middle of an elk and mule deer migration corridor and some of the most powerful environmental advocates in the area didn't like our proposal one bit. And, some hunters who had hunted on the Starkey Experimental Forest and Range for many decades were bumped from their accustomed hunting grounds—and they really didn't like that.

Again, supporters in the National Forest System came to the rescue. Hugh Black, Jr., then the Fish and Wildlife Director for FS Region 6, recruited an outstanding young biologist from the Bureau of Land Management, Michael Wisdom, to handle the public relations aspects of the operation. Wisdom held repeated informational meetings in every town and community within a 100-mile radius of Starkey. He was, seemingly, ever present in the press, in magazines, and on television and radio. He organized and conducted hundreds of tours for interest groups of all kinds—ranchers, foresters, hunters, environmentalists, science classes, service clubs, and anyone else he

could snatch off the streets. And, as a result, the tide of public opinion slowly turned from opposition to support—with some significant exceptions.

Four groups encountered signs posted on the Starkey Experimental Forest that proclaimed "Jack Ward Thomas—Communist American!" Another sign was a circle surrounding a "Red Star" that proclaimed—in Russian script—"Kill a Communist for Christ!" Others presented my face in the cross hairs of a rifle scope. To address these views, known opponents of the Project were contacted directly and shown the facility first-hand. As a result, opposition to the Project eventually subsided among these strongest of local detractors in rural communities of northeast Oregon.

Further support, however, was needed at regional and national levels. In response, Robert "Bob" Munson of the fledgling Rocky Mountain Elk Foundation—headquartered in Missoula, Montana—offered substantial and essential help. The organization was new and struggling, but Munson came through with a little money—but a significant portion of what they had in the sock—and a lot of endorsement. He took a gamble, and it paid off with increased national support from those interested in elk management on the public lands.

The permittees that ran cattle on Starkey had to adjust to the new circumstances and were, understandably, apprehensive. But, they had been dealing with FS researchers for nearly half a century and gave us their support—with a bit of trepidation. With the help of Martin Vavra and Tim DelCurto of Oregon State University's Eastern Oregon Agricultural Research Station, the permittees agreed to adapt their cattle grazing operations to the new research goals. The permittee's cattle, along with those provided by Vavra and DelCurto from Oregon State University, thus were incorporated into the new research.

At this point, we had the enclosure, the handling facilities, the radio telemetry system, and support where it counted most. Now, all we needed was the per-

sonnel and the operating money to conduct the planned studies. It was quickly made clear by our bosses in FS research that in terms of personnel and operating dollars “what you see is what you’ve got”—i.e., there was to be no increase in personnel or funding. So, our long-term research partners stepped in to provide the scientific staffing not available from the FS budgets. Key leaders of ODFW stepped in—Northeast Regional Director Warren Aney, Big Game Director Rod Ingram, and Director Randy Fisher—to commit a full staff of ODFW scientists to the new Project. Leckenby and Erickson of ODFW had moved on but were replaced by an outstanding scientist staff of Bruce Johnson, Jim Noyes, Scott Findholt, Priscilla Coe, and Rosemary Stussy. In particular, Bruce Johnson, long-time Starkey Project Leader for ODFW, provided the leadership, dedication, and scientific credibility that ultimately saved the Project during the extremely lean budget years experienced by the FS during the mid- and late 1990s. Without the contributions of these scientists from ODFW, particularly those from Johnson, the Project would likely have come to an unfulfilling end in the 1990s.

The National Council on Air and Stream Improvement (NCASI) also stepped up and provided personnel to carry out the studies related to the “thermal cover hypothesis.” Larry Irwin helped us obtain the services of John Cook, and later Rachel Cook, to head up that research and follow-on studies of elk birth date-nutrition interactions. John Cook provided an extremely high standard of scientific performance and dedication in carrying out these essential studies. Boise Cascade Corporation lent their support through in-kind contributions to fence construction and implementation of the timber management study. Boise also hired biologist and range scientist Bob Riggs, who has worked as an extremely effective and scholarly collaborator with the Project to this day.

The National Forest System provided further support through detailing of range and wildlife personnel to the Project dur-

ing the early 1990s, when research staffs of the FS were given a number of other technical assignments that took time away from the Starkey Project. Moreover, the PNW Research Station allowed Bryant to make an astute hiring of Brian Dick in 1990, who oversaw the increasingly complex management of the new facility and technologies at Starkey. Dick was further assisted by the hiring of Jack Nothwang, Ryan Kennedy, and Cheryl Borum, who played important roles in the establishment and management of the new facilities. Norm Cimon was assigned as data analyst for the Project, and established and maintained complex data collection and storage systems essential to the Project’s success. Alan Ager of the Umatilla National Forest stepped in and provided new software needed for managing and analyzing the complex data sets as they became available. Mary Rowland, then a consulting biologist and now a PNW scientist, wrote a series of publications outlining the rationale, objectives, technologies, and methods of data collection for the Project. These needed personnel were recruited during the tenure of PNW Station Leader Charlie Philpot, and were further supported by subsequent Station Leaders Tom Mills and Tom Quigley.

Within a few short years of the Project’s conception, what seemed an impossible dream had come true thanks to persistence, luck, skill, and a lot of help from our friends in the National Forest System, ODFW, and NCASI. Even today, I look back and marvel that it all actually came to pass. And, when I look at the results and the changes in wildlife and land management that have occurred as a result, it was clearly time and money well spent.

The Starkey facility is like nothing else that has ever existed in the world of natural resources research—or is likely to exist in the future. The opportunities it presents for new research are enormous—but the opportunity is not being exploited to anywhere near its potential.

Detailed long-term research often receives short shrift from both land and wildlife management agencies. But, in the

end, such research and the underpinnings it provides to actually effect adaptive management is essential. Good research is meticulous, slow, methodical, and expensive. But, when push comes to shove in the management arena there is simply no substitute for such a foundation.

The research results that make up this book are the payoff for those who pursued and facilitated the realization of what seemed, at times, an impossible dream. Sometimes, and most fortunately in my view, the “Don Quixotes” of the world do succeed.

The facility at Starkey and the research background that exists there is unique in all the world. Current upgrades in facilities and a new and improved radio telemetry system will continue to provide unparalleled opportunities to investigate new and previously intractable questions such as how grazing animals—wild and domestic—influence the trajectory of plant community development and other related questions.

If you are impressed with the research results reported in the rest of this volume, it is likely that “you ain’t seen nothing yet!” But, the realization of that potential depends on continued support from the Forest Service and its partners. Chief Dale Bosworth is to be commended for his interest and personal support for the promise that Starkey holds to provide critically needed understanding of ecosystem function and dynamics. I can only hope, and trust, that others will follow his lead.

More, much more, good research lies ahead. But, so much more could be done. Once before, we built “a field of dreams” with confidence in the whispers in our heads—“build it and they will come.” We were not wrong in our faith then. I

don’t think we will be wrong this time either.

And so it was—in the beginning.

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Jack Ward Thomas

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September 15, 2004

Foreword: The Starkey Project—A Research Model for the Future

Throughout my career, I can point to key programs and people who kept national forest management ahead of the curve. Such is the case with the Starkey Project and its scientists.

The project was born of a typical controversy in national forest management: How do we balance uses such as timber harvest, livestock grazing, road access, and hunting in relation to the needs of elk and mule deer? The stakes were high, given that elk and mule deer provide recreational opportunities for millions of national forest users. Typically, the voices were shrill on both sides, yet we knew little about the tradeoffs.

Then some enterprising scientists had a bold idea: Why not find out for sure what the tradeoffs are? And why not do it in a way that national forest managers could use to help them make better decisions on the ground?

The Starkey Project was born. Jack Ward Thomas and Larry Bryant of the Forest Service, along with Donavin Leckenby of the Oregon Department of Fish and Wildlife, helped found the project and initiate its research in the 1980s. Since then, more than a hundred researchers from more than 40 state, federal, private, university, and tribal organizations have provided definitive, scientifically credible information on mule deer and elk on national forest land. Although the project has produced more than 140 publications, the information they contained has influenced management actions long before it appeared in technical journals or the popular press—frequently months or even years before. The Starkey Project set a new standard for cooperation between Forest Service Research and National Forest System management, a shining example for researchers and managers today.

In spring 2004, I saw it for myself when some visiting Starkey scientists told me about their research. They were studying how mule deer and elk were affected

by off-highway vehicles (OHVs), fire risk management, and the spread of invasive plants. Barely a year before, I had first spoken publicly of OHVs, fire and fuels, and invasive species as major threats to national forest management. Yet Starkey had already begun related research a good two years earlier. For a long-time land manager, seeing research ahead of the curve like that is deeply refreshing. I've always expected scientists to address relevant management issues in a credible and compelling way, but to do so with the anticipation and foresight shown by the Starkey scientists is truly extraordinary.

This book testifies to Starkey's foresighted influence on land management. For example, results from the breeding bull study on elk have led to changes in state and provincial hunting regulations across western North America. Similarly, findings from the elk–thermal cover study have prompted changes in national forest standards and guidelines across the western United States, as have findings from studies on deer and elk in relation to roads, traffic, livestock grazing, and timber harvest. Moreover, recent findings on mule deer and elk responses to all-terrain vehicles have already been incorporated into national direction set forth by the Forest Service for improving management of OHVs. These are just a few examples of the Starkey Project's long-term success in providing relevant and timely information to land managers—sometimes before they even knew they had a problem.

The Starkey Project is a model for applied research in the Forest Service. I commend the project's various partners for making the model an unqualified success. This book documents Starkey's accomplishments, and I expect it to become a standard reference on mule deer and elk management for many years to come.

Dale N. Bosworth
Chief, USDA Forest Service
September 29, 2004

The Starkey Project: Long-Term Research for Long-Term Management Solutions

Thomas M. Quigley and Michael J. Wisdom

INTRODUCTION

The Starkey Project is a unique, long-term research program designed to study the effects of key resource uses of National Forests on mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) habitats and populations. Located at the Starkey Experimental Forest and Range (Starkey), the purpose of the Project was to fill key knowledge gaps that posed difficult impediments to effective management of ungulates, and to facilitate transfer of this knowledge in mediums most useful to managers. The original studies were completed in the 1990s, but research to understand the effects of emerging resource uses on deer and elk continues today. In addition, new studies are underway to understand the role of these ungulates as disturbance agents that can dramatically alter the ecological patterns and processes in forest ecosystems.

The following papers at this special session of the 69th North American Wildlife and Natural Resources Conference address this evolution of research topics by the Starkey Project and associated research programs. This research now has a 22-year history. With this history is a compelling array of scientific accomplishments made possible through long-term commitments from a wealth of scientists and partners.

In our introductory paper, we summarize the long-term commitments of the Starkey Project, and acknowledge the many partnerships that made this research possible. We also describe what we consider to be the key “ingredients” of a successful, long-term research program, using the Starkey Project as a case example. Finally, we discuss the accomplishments and credibility that result from long-term research involving diverse partnerships and public interests.

INGREDIENTS FOR SUCCESSFUL, LONG-TERM RESEARCH

Long-term research is rare and invaluable. Few research programs have the opportunity to operate, without interruption, for five years, let alone 10, 15, or 20 years. The history of the Starkey Project is one such exception. Born of controversy over management of timber, grazing, roads, and hunting, the planning stage alone took four years (1982–1985) (Wisdom et al. 2004a). Another four years (1986–1989) were required to establish the research facility (Rowland et al. 1997). Finally, the original studies took five to seven years to complete (1990 through mid-1990s).

Today, the research at Starkey (Wisdom et al. 2004a) continues to flourish as it diversifies (Thomas and Wisdom 2004). Known as the Starkey Project since inception (Rowland et al. 1997), the research was designed to address the most contentious problems regarding management of mule deer and elk on National Forests in the western United States. While the original issues were addressed in research during the 1990s, a myriad of new issues have emerged. As a result, the Starkey Project has evolved to address these new issues, with continued focus on studies designed to gain a better understanding of the role of ungulates in managed ecosystems (Vavra et al. 2004).

The record of the Starkey Project provides a convincing example of what defines an effective, long-term research program. Our examination of its history (Rowland et al. 1997, Wisdom et al. 2004a) and achievements (Thomas and Wisdom 2004) led us to identify four key ingredients of the Project’s success: (1) diverse, stable partnerships, (2) long-term commitment, (3) high relevance to man-

agement, and (4) effective technology transfer.

Diverse, Stable Partnerships

From inception, the Starkey Project sought support and involvement from all groups with strong interests and investments in management of National Forests in the western United States. These interests included state wildlife agencies, federal land management agencies, timber companies, livestock associations, tribal nations, and conservation groups. University partners became increasingly involved as the diversity of research topics increased and opportunities for involvement of graduates studies was enhanced. Over 40 groups ultimately played an active role in planning and implementing the research (Table 1). Importantly, the distribution of different groups has been relatively even, with highest number of partners having private, university, and federal affiliations (Figure 1).

The diverse partnerships provided strong ownership in the research and subsequent results. Over 100 scientists, representing more than 40 partners, have participated in the publication process (Figure 1). (See the following web link for a complete list of authors: http://www.fs.fed.us/pnw/starkey/publications/by_author/index.shtml). The strong ownership and subsequent trust among so many partners has resulted in rapid and effective use of findings (Thomas and Wisdom 2004).

An additional benefit of the diverse partnerships has been the long-term stability that comes with a variety of funding sources. For example, federal and state budgets have fluctuated across the many budget cycles experienced by the Starkey Project, but the two lead agencies—the Oregon Department of Fish and Wildlife and U.S. Department of Agriculture Forest Service—have invariably found ways to match resources with other partners in a cost-effective manner. Moreover, the diverse partnerships have provided a stable base of support, helping minimize undesired changes in funding and research focus that can occur with dynamic budgets

of any one partner or small group of partners.

The many partners also have contributed a variety of research skills, enhancing the scientific credibility of publications and subsequent management products. One example is the development of a model to allocate forage among ungulates for allotment management planning on public lands (Ager et al. 2004). Scientists involved with this work included field biologists, computer programmers, research analysts, ungulate specialists, and landscape ecologists. Another example is the birth date-nutrition study of elk (Cook et al. 2004) that involved scientists with expertise in natural history, population genetics, ungulate ecology, manipulative experiments, animal nutrition, and animal husbandry.

Long-term Commitment

The Starkey Project has a long and productive history. The research facility was formally established in 1987 with the completion of one of the largest ungulate-proof enclosures ever constructed (Rowland et al. 1997). The facility became operational in 1989 with the installation of a novel, automated radio-telemetry system that could track the movements of more than 100 radio-collared ungulates accurately, frequently, and regularly, 24 hours a day (Rowland et al. 1997). Since then, more than 50 studies have been conducted, with more than 140 publications completed or in press (Thomas and Wisdom 2004).

A central and vital benefit from this long-term commitment has been the accelerating production of scientific publications (Figure 2). During the late 1980s and early 1990s, the number of publications in peer-reviewed journals was low, owing to the need to focus on large capital investments in the facility and to develop, test, and implement a series of innovative research designs (Rowland et al. 1997). As the original studies were completed during the 1990s, the number of publications increased substantially (Figure 2). This accelerating pace in publication rate has become particularly ap-

TABLE 1. Research and management partners and their roles in the Starkey Project, 1982–2004

Partner	Role
Oregon Department of Fish and Wildlife	Lead state agency in Starkey research from time of inception to the present.
U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station	Lead federal research branch in Starkey Project research from time of inception to the present.
U.S. Department of Agriculture, Forest Service, Region 6	Lead federal management branch supporting the establishment of Starkey Project telemetry system, other technologies, and the technology transfer program.
Boise Cascade Corporation	Private company that provided the means to harvest timber as part of construction of the Starkey enclosure and as an experimental treatment for the intensive timber management study. Ongoing partner in research through its staff of scientists. Led research on ungulate herbivory effects in Blue Mountains.
National Council of the Pulp and Paper Industry for Air and Stream Improvement	Private nonprofit organization that has participated as a major research partner since inception of the Starkey Project. Led research on elk thermal cover and nutrition.
Oregon State University	Major academic partner in Starkey Project research. Oregon State University's Eastern Oregon Agricultural Research Center has led the cattle-related studies of the Starkey Project since inception. Graduate students have completed, or are in the process of completing, a myriad of different studies used in eight Master Theses.
Rocky Mountain Elk Foundation	National non-profit organization that has provided key logistical, funding, and technology transfer support for Starkey research from time of inception to the present.
Wallowa-Whitman National Forest and La Grande Ranger District	Provided major funding and staffing in support of installation, maintenance, and repairs of infrastructure required for the Starkey Project. Helped collect needed data on traffic counts and other field variables in support of original studies.
U.S. Department of Agriculture, Forest Service, Washington Office	Provided majority of funding for establishment of Starkey Project enclosure and other technologies to launch the start of the Project.
Umatilla National Forest	Provided critical analytical and software support for the Starkey Project since inception, with support continuing to the present. Have provided funding and helped plan various studies for the Starkey Project as part of the Blue Mountains Elk Initiative.
Oregon Department of Parks and Recreation	State agency that provided major research funding for study on effects of off-road recreation, and helped design the study.
Ochoco and Malheur National Forests	Helped plan various studies for the Starkey Project as part of the Blue Mountains Elk Initiative.
University of Alaska-Fairbanks	Major partner in recent research on the role of mule deer and elk in ecosystem processes. A Ph.D. student has completed this research, with multiple publications produced, in press, or submitted.
University of Idaho	Major partner in a variety of studies. Graduate students have completed, or are in the process of completing, multiple studies that include two Master Theses and two Ph.D. Dissertations.

TABLE 1. Continued

Partner	Role
University of California-Berkeley	Provided major analysis and design for studies of diffusion modeling of animal movements with use of Starkey Project data. Graduate student is participating in study of effects of off-road recreation on mule deer and elk.
Purdue University	Partner in DNA-breeding studies of elk.
University of Minnesota	Partner in research on nutritional indices and condition for elk, using Starkey Project's tame elk.
University of Montana	Partner in research on effects of intensive timber management at Starkey. Graduate student completed a Master Thesis in support of this study.
Washington State University	Participated in the design of new herbivory research at Starkey, and have provided long-term veterinary care for tame deer and elk as part of Starkey Project.
Washington Department of Fish and Wildlife	Major partner in elk diet selection grazing trials, using Starkey Project's tame elk.
Eastern Oregon University	Provided field and office support for the Starkey Project since its inception, in the form of biological interns under the Student Employment Training Program, and in collaborative research efforts between faculty and Starkey Project staff.
Oregon State Police, Game Division	Provided law enforcement during the 58 hunting seasons conducted in support of research since inception.
Idaho Department of Fish and Game	Major partner in research to validate and refine methods of aerial survey for elk.
Alaska Department of Fish and Game	Loaned and demonstrated the use of equipment for Starkey research.
La Grande Animal Health Center	Provided critical veterinary care for deer and elk used in Starkey Project research since inception.
Confederated Tribes of the Umatilla Indian Reservation	Helped design and participated in tribal hunts conducted in support of Starkey research. Helped plan various studies for the Starkey Project as part of the Blue Mountains Elk Initiative.
Nez Perce Tribe	Helped plan various studies for the Starkey Project as part of the Blue Mountains Elk Initiative.
Confederated Tribes of Warm Springs Indian Reservation	Helped plan various studies for the Starkey Project as part of the Blue Mountains Elk Initiative.
Oregon Hunter's Association	Provided funding and helped plan various studies for the Starkey Project as part of the Blue Mountains Elk Initiative.
U.S. Department of the Interior, Bureau of Indian Affairs	Helped design tribal hunts at Starkey as part of the research. Helped plan various studies for the Starkey Project as part of the Blue Mountains Elk Initiative.
U.S. Department of the Interior, Bureau of Land Management	Helped plan various studies for the Starkey Project as part of the Blue Mountains Elk Initiative.
Oregon Cattlemen's Association	Helped plan and provide support for the animal unit equivalency study at start of Starkey Project.
Dick Snow Ranch	Participated in cattle research as part of the Starkey Project since inception.
Trimble, Incorporated	Provided major technologies needed for the Loran-C automated telemetry system.
Tracor, Incorporated	Provided major technologies needed for the Loran-C automated telemetry system.
Partney and Sons, Incorporated	Established the ungulate enclosure with use of innovative drilling technology.

TABLE 1. Continued

Partner	Role
West, Incorporated	Provided major statistical analyses in support of Starkey Project research.
Statistical Services, Incorporated	Provided major statistical analyses in support of Starkey Project research.
David Marx Consulting	Provided major statistical analyses in support of Starkey Project research.
U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station	Provided major analysis support for study of effects of off-road recreation on deer and elk at Starkey, and for studies of diffusion modeling of animal movements.

parent during the past six years, signaling a compelling return from the long-term investment. The publication rate for the Starkey Project now exceeds 12 peer-reviewed publications per year (not including published abstracts, tours, workshops, symposia, videos, magazine articles, television features, and other popular media). This publication rate surpasses many other state or federal research projects of similar size and budgets.

Importantly, the large number of peer-reviewed publications produced during the past six years also reflects an increasing depth of study. Since 1998, most publications of the Starkey Project contained results from data collected over a period of four to five years. By contrast, our examination of publications appearing in the *Journal of Wildlife Management* dur-

ing 2003 indicated that less than 5 percent of the articles were based on data collected over a period of four years or longer.

Research implemented over long time periods is invaluable because results are robust to short-term anomalies that can confound results. For example, long-term results minimize the confounding effects of seasonal, annual, and climatic variation that can overwhelm and bias results of short-term studies. Long-term studies provide valuable opportunities to validate the findings and hypotheses that emerge from the early years of research; that is, portions of larger data sets, collected over a longer period of time, can be "held out" to validate initial findings of a given

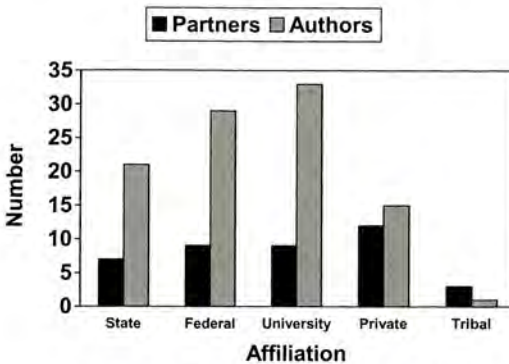


FIGURE 1. Number of partners in the Starkey Project and number of authors of Starkey publications, by affiliation (state agencies, federal agencies, universities, private groups, and tribal nations).

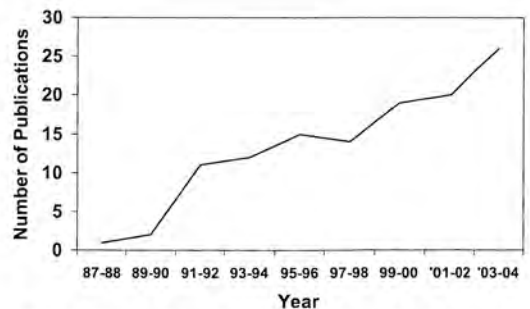


FIGURE 2. Number of Starkey Project publications since 1987, summed by two-year periods through early 2004. Only peer-reviewed publications appearing in journals, books, and graduate theses and dissertations are included (i.e., the summary excludes all published abstracts, "white papers," popular news and magazine articles, and other "gray literature").

study. Moreover, long-term data provide opportunities for a variety of follow-on analyses not planned under the original study objectives.

An example is the 2004 release of a voluminous data set by the Starkey Project (Kie et al. 2004). These data are now available for use by students, educators, and scientists as a complement to past uses by the Starkey Project. Kie et al. (2004) and Wisdom et al. (2004a) describe these data and their original uses in Starkey Project studies.

High Relevance to Management

The Starkey Project was designed to address key knowledge gaps identified as impediments to effective management of ungulates on National Forests in the western United States. The Project operates under the concept of adaptive management (Holling 1984, Walters 1986). The scientific basis for adaptive management uses the following process: (1) managers identify knowledge gaps that prevent desired improvements in targeted resources, (2) managers and scientists jointly develop testable hypotheses to address the knowledge gaps, (3) scientists design and implement studies to test the hypotheses, (4) managers and scientists interpret and disseminate results from the studies for management use, (5) managers and scientists identify additional knowledge gaps and hypotheses for testing, based on study results and ensuing questions that arise from the results, and (6) the cycle is repeated one or more times, if desired, using knowledge gained from earlier phases of study.

An example of the Starkey Project's use of adaptive management is the study of breeding efficiency of bull elk (Noyes et al. 2004). This study was jointly designed by managers and scientists to address the issue of whether hunter harvest of bull elk needed modification to improve survival of older bulls and enhance their breeding performance. The study was conducted from 1989 through 1993, as implemented over the entire elk population in the 19,180-acre (7,768-ha) Main Study Area. Hunting by the public

was used to implement the research, with hunters working closely with scientists to achieve desired harvest and collect needed data. Managers then used results from the study to redesign harvest regulations for bull elk in many states and provinces in western North America. In turn, validation tests were conducted by repeating the study for another five years at Starkey. Results from the validation provided strong support for earlier changes in hunting regulations that were made in response to findings of the original study (Noyes et al. 2004).

Use of adaptive management continues in current research. For example, an emerging, national issue is the use of all-terrain vehicles (ATVs) on public lands. Land managers and public interests at national, regional, and state levels worked closely with Starkey scientists in 2002 to design and implement new landscape research to evaluate effects of ATVs on deer and elk as compared to hiking, mountain bike riding, and horseback riding. Initial findings are now available (Wisdom et al. 2004b). Importantly, the findings are already being considered by managers, interest groups and Starkey Project scientists to devise appropriate management applications. Given the high level of controversy surrounding off-road recreation on public lands, new study proposals are being drafted by managers and Starkey scientists to validate aspects of the initial findings, and expand upon this study in future research.

Effective Technology Transfer

The Starkey Project was one of the first research programs in the Forest Service with full-time support from a technology transfer scientist (Rowland et al. 1997). This position functioned as part of the Starkey Project staff from 1987 to 1994, and served as the primary liaison between management and research. During this time, the Starkey Project shared technologies and results with more than 200,000 recipients encompassing local, regional, national, and international organizations, groups, and agencies. Transfer mediums included field tours, presentations, work-

shops, symposia, news releases, newspaper features, magazine articles, radio interviews, and television coverage. This work helped garner widespread public acceptance and support of the Project and its initial results (Rowland et al. 1997, Thomas and Wisdom 2004).

Today, the Starkey Project continues to actively share results and technologies with a wide range of resource managers. Scientists have averaged more than 15 field tours and more than 20 meeting presentations per year during the past decade. These communication mediums, beyond the formal scientific publications, have played an important role in Starkey's technology transfer program.

CHALLENGES FOR LONG-TERM RESEARCH

Many obstacles prevent successful implementation of long-term research. Short-term priorities, budget fluctuations, large capital investments, changing political agendas, and impatience with the lack of immediate scientific production are example impediments. The Starkey Project has overcome these obstacles because of diverse partnerships, long-term investments, high relevance to management, and effective delivery of results. Continued emphasis on these key ingredients will enable the Starkey Project to continue its success in serving land and population managers of deer and elk in the western United States.

Key to this continued success will be the Project's reliance on adaptive management and effective synthesis of results in forms useful for management. Maintenance of healthy and diverse partnerships is imperative. Considering the wealth of completed and ongoing studies, success of partnerships, and the utility of the research facility, the future of the Starkey Project appears bright. The many papers presented at the 69th North American Wildlife and Natural Resources Conference attest to the Project's accomplishments and relevance to resource management over the past 20 years.

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We thank C. West, E. DePuit, A. Christensen, and M. Vavra for reviewing our paper, J. Boyd for editing and production of figures, and the many partners (Table 1) who have made the Starkey Project an effective and exceptional research program for more than 20 years. We particularly thank Donavin Leckenby and Jack Ward Thomas for their innovative ideas and proposals in initiating the Starkey Project, and for their perseverance in establishing the facility and implementing the original studies.

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Overview of the Starkey Project: Mule Deer and Elk Research for Management Benefits

Michael J. Wisdom, Mary M. Rowland, Bruce K. Johnson, and Brian L. Dick

INTRODUCTION

Managers have long been concerned about the welfare of mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) on public lands in the western United States. These two species generate millions of dollars annually to state wildlife agencies from sales of hunting licenses, and elk viewing generates millions of additional dollars to local and regional economies (Bolon 1994, Bunnell et al. 2002). By contrast, the potential for elk and mule deer to compete with livestock, to damage agricultural crops, and to modify plant succession make the two species obvious sources of controversy among private and public land managers.

In the 1980s, wildlife managers began to focus on the potential effects of timber management, livestock grazing, road use, and ungulate harvest strategies on mule deer and elk. At the same time, land managers were concerned about constraints associated with these management activities, based on the perceived needs of the two species. In particular, timber harvest, livestock production, road construction, and motorized traffic were dominant and pervasive uses of public lands during the 1980s and earlier decades, but their effects on deer and elk were uncertain and widely debated. In addition, the dichotomy of managing for productive habitats (i.e., high biomass and quality of forage) versus secure habitats (i.e., dense cover and minimal human disturbance) was highly debated, with management trade-offs that were unclear (Lyon and Christensen 2002). As an outgrowth of these concerns and the lack of empirical data, the Starkey Project was initiated in the mid-1980s at the U.S. Department of Agriculture, Forest Service's Starkey Experimental Forest and Range (Starkey) in

northeastern Oregon (Figure 1). The Project was designed to evaluate mule deer and elk responses to the most common management activities occurring on National Forests in the western United States.

In this paper, we provide an overview of the Starkey Project, as an introduction for the papers that follow. Additional details about the Starkey Project and the Starkey Experimental Forest and Range are found in Rowland et al. (1997, 1998), Skovlin (1991), and at the Starkey Project web site: (<http://www.fs.fed.us/pnw/starkey/>).

CONTROVERSIES OF UNGULATE MANAGEMENT: BEGINNING OF THE STARKEY PROJECT

The Starkey Project was born from contentious debate about how best to manage habitats and populations of mule deer and elk in the western United States, and the degree to which traditional management practices on public lands needed modification to accommodate the two species' needs. The most prominent issues of debate related to (1) road and traffic management, (2) intensive timber production and thermal cover, (3) competition between wild ungulates and cattle, and (4) breeding efficiency of male elk in relation to population productivity. These four issues became the foundation of the Starkey Project's original studies that began in 1989 and ended during the 1990s (Table 1).

The issue of road management revolved around the uncertainty of whether mule deer and elk avoided roads open to motorized traffic, and whether the rate of motorized traffic influenced ungulate dis-

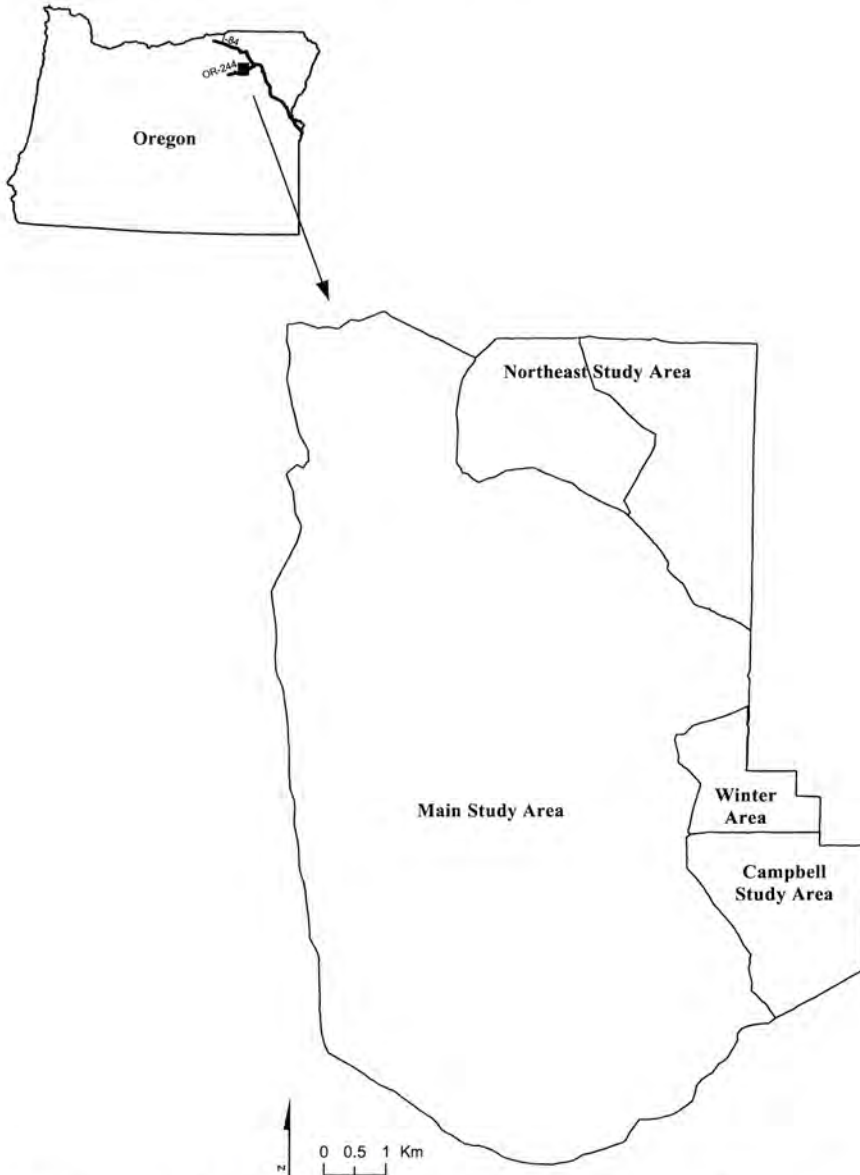


FIGURE 1. Location of Starkey Experimental Forest and Range in northeastern Oregon, 28 miles (45 km) southwest of La Grande (upper left), and boundaries of the ungulate-proof enclosure, internal ungulate fences, and study areas (bottom). The 3,590-acre (1,453-ha) Northeast Study Area and 19,180-acre (7,768-ha) Main Study Area are the two study sites where research occurs from April through early December on free-ranging ungulates. The 655-acre (265-ha) Winter Area is the site of winter feeding and handling of deer and elk. The 1,537-acre (622-ha) Campbell Study Area is used in support of ungulate breeding and grazing studies.

tribution (Rowland et al. 1997). To address these issues, vehicle travel by the public was monitored with traffic counters during the 1990s in the Main Study

Area (Figure 1) from May through December of each year (Table 1). Radio-telemetry locations of ungulates were collected and analyzed in relation to road

type (open, closed, restricted) and traffic rate (zero, low, moderate, high, very high). The result has been a set of compelling findings about deer and elk distributions in relation to distance to roads of varying traffic rates (Wisdom 1998, Wisdom et al. 2004b), and elk distance to open roads (Rowland et al. 2000, 2004). Results are now used for management of roads and access throughout western North America (Thomas and Wisdom 2004).

Considerable controversy also existed about the effects of timber management on mule deer and elk (Hieb 1976, Rowland et al. 1997). Consequently, ungulate response to intensive timber production was assessed in the Northeast Study Area of Starkey (Figure 1). Radio-collared cattle, deer, and elk were monitored from 1989–1996, spanning periods before, during, and after timber harvest (Table 1). Over half of the forested area was subjected to intensive logging, combined with a doubling of road density. Animal responses were monitored in a variety of ways (Rinehart 2001, Wisdom et al. 2004c). Results provided little evidence of negative effects on ungulates from activities or changes brought about by intensive timber harvest on summer range during non-hunting periods (Wisdom et al. 2004c).

Throughout the 1980s, some studies documented high use of dense forests by elk (Leckenby 1984), and others postulated that elk were selecting these sites for thermal cover (Thomas et al. 1988). These ideas generated considerable debate about how forests should be managed and why elk were selecting dense cover. To address this issue, an experimental study was conducted at Kamela, Oregon, approximately 30 miles (48 km) northeast of Starkey (Cook et al. 1998). Here, the nutritional condition of tractable elk maintained in pens was monitored in relation to four treatments: (1) dense thermal cover, (2) moderately dense thermal cover, (3) no cover, and (4) a combination of no cover and thermal cover. Results indicated no positive benefits to animal condition from thermal cover. Instead, a

negative effect was associated with high levels of cover (Cook et al. 1998, 2004a). These results have changed the way that managers think about and plan for maintenance of elk thermal cover across western North America (Thomas and Wisdom 2004), in balance with the need to maintain dense cover for elk security, especially during hunting seasons (Lyon and Christensen 2002).

The issue of whether mule deer and elk compete with cattle for available forage on summer range was addressed by a long-term study of ungulate interactions in the Main Study Area (animal unit equivalency study, Table 1). By evaluating the spatial distributions, resource selection patterns, and behavioral interactions of the three ungulates as cattle were rotated through livestock pastures on summer range (Coe et al. 2001, 2004; Stewart et al. 2002), scientists were able to devise a realistic allocation of forage among the ungulate species by month and season (Johnson et al. 1996, Ager et al. 2004). Based on these results and a subsequent study of diet overlap among the three species (Findholt et al. 2004), a new forage allocation model is now available for beta testing as part of allotment planning on National Forests of the interior western United States (Ager et al. 2004).

The issue of whether elk productivity is affected by age of breeding bulls also was addressed in the Main Study Area (Table 1). From 1989 to 1993, breeding male elk were allowed to increase in age, beginning as 1.5 year-old (yearling) bulls in 1989. During each of these five years, this single cohort of male elk functioned as the only breeders in the study population. As bulls grew older, conception dates in female elk were earlier and more synchronous (Noyes et al. 1996). As a result, calves were born earlier and over a shorter time period each spring, which may provide a number of survival benefits (Noyes et al. 2004). Results have caused substantial changes in hunting regulations for bull elk across many states and provinces in western North America (Thomas and Wisdom 2004).

TABLE 1. Chronology of major research activities of the Starkey Project, 1982–2004 (from Rowland et al. 1997 and updated to early 2004)

Year	Research activity
1982–1985	Initial discussions regarding the Starkey Project take place among scientists from the Oregon Department of Fish and Wildlife and U.S. Department of Agriculture, Forest Service Pacific Northwest Research Station, resulting in proposals for the original studies.
1986	Environmental Assessment is completed and approved for construction of the Starkey research facility.
1987	Twenty-seven miles (43 km) of New Zealand woven-wire fence is completed to enclose 24,962 acres (10,110 ha) of the Starkey Experiment Forest and Range (Figure 1), encompassing summer range populations of mule deer and elk.
1988–1989	- Over 65 traffic counters are installed at intersections of open roads in the Main Study Area for the roads and traffic study. - The 655-acre (265-ha) Winter Area and handling facility is completed (Figure 1). - Loran-C automated telemetry system (ATS) becomes operational in Northeast Study Area, allowing ungulates to be radio-collared and monitored remotely to start the intensive timber management study. - Limited entry hunting of deer and elk begins in support of breeding bull study in the Main Study Area.
1990	- Timber harvest contract is awarded for intensive timber management study in the Northeast Study Area. - Loran-C ATS is completed for the Main Study Area, making the telemetry system operational in all areas of Starkey, and allowing the start of the animal unit equivalency and roads and traffic studies.
1991	- Elk thermal cover study begins at Kamela, 30 miles (48 km) northeast of Starkey. - Starkey's Institutional Animal Care and Use Committee is formed under new regulations promulgated from the federal Animal Welfare Act, formalizing the existing procedures for humane care and treatment of ungulates used for research (Wisdom et al. 1993). - Road construction and logging begins late in the year in Northeast Study Area as part of intensive timber management study.
1992	- Campbell Study Area (1,537 acres [622 ha]) is established (Figure 1) in support of new breeding bull study. - Study of ungulate herbivory effects on plant succession and nutrient availability begins at exclosures established >25 years ago throughout northeastern Oregon.
1993	- Loran-C ATS is upgraded, resulting in improved accuracy of animal locations. - Logging is completed early in the year in Northeast Study Area; over 7 million board feet is harvested. - Elk breeding bull efficiency study is completed in Main Study Area. - Performance tests of Loran-C ATS are initiated.
1994	Animal unit equivalency study is completed in Main Study Area.
1995	- Prototype forage allocation model is built, tested, and published as part of animal unit equivalency study (Johnson et al. 1996). - Validation phase of elk breeding bull study begins in Main Study Area. - Roads and traffic study is completed in Main Study Area. - Elk thermal cover study is completed at Kamela study site.
1996	- Results from the elk breeding bull study are published (Noyes et al. 1996). - Intensive timber management study is completed and elk-ecosystem processes study is designed for Northeast Study Area.

TABLE 1. Continued

Year	Research activity
1997	• New fuels reduction study is designed for Main Study Area. • Cross-fencing of Northeast Study Area into east (1,500 acres [608 ha]) and west (2,090 acres [846 ha]) pastures is completed to start new research about elk-ecosystem processes.
1998	• Results from elk thermal cover study at Kamela are published (Cook et al. 1998). • Performance tests and bias corrections for ATS are published (Johnson et al. 1998). • Results from the traffic study are summarized in a Ph.D. dissertation (Wisdom 1998).
1999	• Manipulative experiment to validate results from traffic study begins in Main Study Area.
2000	• Fuels reduction study begins in Main Study Area. • Results from elk-roads study are published (Rowland et al. 2000). • Results from study on ungulate herbivory effects on plant succession are published (Riggs et al. 2000). • Additional results from the animal unit equivalency study on mule deer and elk are published (Johnson et al. 2000). • Manipulative experiment to validate results from traffic study is completed in Main Study Area.
2001	• Elk-ecosystem processes research in Northeast Study Area is completed. • Results from the intensive timber management study for elk are summarized in a Master's thesis (Rinehart 2001). • Additional results from the animal unit equivalency study of cattle-deer-elk interactions are published (Coe et al. 2001). • Symposium held at Eastern Oregon University to summarize findings of 10-plus years of research of the Starkey Project; attended by more than 150 scientists and managers from western North America.
2002	• Results from the validation phase of the elk breeding bull study are published (Noyes et al. 2002). • New study on effects of off-road recreational activities on deer and elk begins in the Northeast Study Area. • Construction of two ungulate exclosures, each 18 acres (7.3 ha) in size, is completed in the Main Study Area to begin new research on ungulate herbivory effects on ecological processes. • Replacement of the Loran-C ATS with a new GPS-based telemetry system is identified as a key need, with initial design and cost estimates completed.
2003	• Three additional 18-acre (7.3-ha) ungulate exclosures are built in support of new herbivory research in Main Study Area. • New GPS-based radio collars are used on 16 elk in the Northeast Study Area as part of study on effects of off-road recreation. • Study to validate Starkey elk resource selection patterns begins at Sled Springs demonstration area on Boise Cascade Corporation lands in northeast Oregon.
2004	• Off-road recreation study is completed in Northeast Study Area and preliminary results are published (Wisdom et al. 2004a). • Field sampling begins for new herbivory research in Main Study Area. • Treatments for fuels reduction study are completed in Main Study Area. • Over 10 years of research findings from the Starkey Project are summarized in a set of 20 papers presented at the 69th North American Wildlife and Natural Resources Conference, and subsequently published in the Conference Transactions and reprinted in a book by Allen Press. • Results from elk birth-nutrition study are published (Cook et al. 2004b).

CONTINUED NEED FOR INFORMATION DRIVES ADDITIONAL STUDIES

The original studies at Starkey were completed during the mid- and late 1990s (Table 1) and used by management agencies soon after publication (Thomas and Wisdom 2004). Results also spurred follow-on research, such as validation tests of the original breeding bull study (Noyes et al. 2002) and original traffic study (Wisdom et al. 2004b). Results from the original studies also were the catalyst for subsequent studies on the interactions of nutrition and bull age in affecting elk condition (Cook et al. 2004b) and the assessment of ungulate diets (Findholt et al. 2004) to realistically allocate forage among cattle, mule deer, and elk (Ager et al. 2004).

New research continues today to further complement the original research. While past studies focused on mule deer and elk responses to management, new research also considers the effects of these ungulates on the ecosystem (Riggs et al. 2004, Vavra et al. 2004). In addition, new research has recently been completed, or is nearing completion, regarding deer and elk responses to off-road recreation (Wisdom et al. 2004a), fuels reduction (Vavra et al. 2004), hunting (Johnson et al. 2004), breeding-nutrition interactions on elk condition (Cook et al. 2004b), and fine-scale movement patterns of deer and elk (Ager et al. 2003).

New research also is underway on non-federal ownerships near Starkey to complement past and current studies at Starkey. As an example, the resource selection models derived at Starkey for the animal unit equivalency study (Johnson et al. 2000) are being validated at the Sled Springs study area, on land owned by Boise Cascade Corporation (Coe 2003). This research at Sled Springs will strengthen and expand the inference space for the Starkey forage allocation model (Ager et al. 2004) to improve its use across larger areas of the western United States (Coe 2003).

NEW TECHNOLOGIES SUPPORT THE STUDIES

The main goal of the Starkey Project has been to measure the habitat, behavioral, and population responses of mule deer and elk to intensively managed forests and rangelands at the landscape scales at which management occurs. Meeting this goal for the plethora of studies that have taken place required innovative technologies and a unique research environment with the following characteristics:

1. a closed system to ungulates, with defined ungulate populations whose responses to management experiments on spring, summer, and fall ranges could be measured accurately;
2. an expansive area over which the experiments could be implemented, allowing inferences to be made at landscape scales used for management;
3. an animal tracking system capable of accurate and continuous monitoring of animal movements;
4. a network of traffic counters for close monitoring of human activities and movements;
5. a winter facility, where mule deer and elk could be fed to minimize the confounding effects of winter weather;
6. a database and mapping system capable of storing and displaying a comprehensive set of environmental variables in relation to animal movements and human activities; and
7. an effective strategy of hunter management and mule deer and elk harvest, using limited entry hunts, to achieve desired management treatments on ungulate populations, to collect data from harvested animals to meet research goals, and to evaluate ungulate responses to varying levels and types of hunting pressure.

Establishing these technologies and the needed research facility at Starkey required innovation, persistence, and persuasion on the part of the founders of the Project (Rowland et al. 1997). Scientists Jack Ward Thomas and Donavin Leck-enby, then with the Forest Service's Pa-

cific Northwest Research Station and the Oregon Department of Fish and Wildlife, developed novel study plans not conceived in past wildlife research. The plans called for the most intensive radio-telemetry monitoring of ungulate populations ever attempted, and for novel experimental treatments and controls for evaluating animal responses to management activities at landscape scales not considered possible.

Thomas then convinced Regional Forester John Butruille of the worth of the proposed studies. Butruille responded by committing millions of dollars from the management branch of the Forest Service to establish the needed technologies and research facility. Larry Bryant, another scientist with the Pacific Northwest Research Station at the time, then directed the development, acquisition, and implementation of every major technology and facility improvement during the late 1980s, each of which is still in use today in support of Starkey research.

Ungulate-proof Enclosure

Forty miles (64 km) of 8-foot-high (2.4 m), New Zealand woven-wire fence were constructed in 1987 to establish the Starkey ungulate enclosure (Bryant et al. 1993). An additional 27 miles (43 km) of internal fence were constructed to establish three separate areas (Figure 1): the Main Study Area (19,180 acres [7,768 ha]), Northeast Study Area (3,590 acres [1,454 ha]), and Winter Area (655 acres [265 ha]). Later, in 1992, the 1,537-acre (622-ha) Campbell Study Area was built to accommodate additional research needs (Figure 1, Table 1).

The total area of 24,962 acres (10,110 ha) functions as one of the largest ungulate research enclosures in the world. Its completion established a closed but ecologically extensive system for ungulates. The result was a research environment that provided ungulates with unconstrained habitat choices over expansive areas commensurate with the size of their spring, summer, and fall ranges in the western United States, but also forced the

ungulates to respond to the management experiments (Rowland et al. 1997).

Importantly, the New Zealand woven-wire fence was designed as an effective but humane barrier to ungulates. When ungulates run into the fence, it acts as a trampoline, pushing animals away from the fence without injury (Bryant et al. 1993). The fence was designed to function more than 30 years before major repairs are needed.

Automated Telemetry System

Long Range Navigation (LORAN-C) technology developed by the United States Coast Guard for ship and airplane navigation was adapted by Starkey scientists to establish an automated telemetry system (ATS) in 1989 (Dana et al. 1989, Table 1). The Starkey ATS can generate up to one animal location every 20 seconds, 24 hours a day, from April through December each year. The frequency and order of obtaining animal locations is programmable, such that more than 100 radio-collared animals can be relocated at a frequency of approximately one location for each radio-collared animal/hour (Rowland et al. 1997, Kie et al. 2004). Or, a subset of animals can be relocated more frequently, such as one location for a given animal every minute, depending on the sampling schedule required to meet research needs.

Locations from the ATS have a mean accuracy of 164 feet (50 m) of the true location (Findholt et al. 1996). This location accuracy allows for reliable estimation of resource selection patterns and spatial distributions of ungulates in time and space to meet Starkey research goals (Findholt et al. 2002). Performance of the ATS has been well documented (Johnson et al. 1998, Garton et al. 2001). Over 2 million locations of elk, mule deer, and cattle have been collected since 1989, with location data used in a variety of Starkey publications. Example uses include Johnson et al. (2000), Rowland et al. (2000), Garton et al. (2001), and Leban et al. (2001). See complete list of Starkey Project publications at <http://>

www.fs.fed.us/pnw/starkey/publications/by_author/index.shtml.

Winter Feeding and Handling

Mule deer and elk traditionally migrated to winter range at lower elevations far from Starkey. Construction of the Starkey enclosure in the summer and fall of 1987, however, surrounded the populations of mule deer and elk on their spring, summer, and fall range, preventing migration to traditional winter range. Consequently, a 655-acre (265-ha) Winter Area (Figure 1) was established to feed animals, and in the process, minimize the confounding effects of winter weather and foraging conditions on deer and elk responses to the summer range experiments (Rowland et al. 1997).

Mule deer and elk are baited to the Winter Area or live-trapped and moved to the site each December. Deer and elk are fed alfalfa pellets and hay, respectively, from December through March, and then released back into the study areas for another year of research. This ration is fed *ad libitum*, thus reducing potential variation in physical condition of animals owing to variation in winter weather.

The Winter Area also has an elk handling facility that allows scientists to handle animals humanely and efficiently to check their condition and equip them with radio collars (Wisdom et al. 1993). Handling in December and January includes tests for pregnancy and disease, and measurements of percent body fat and weight, for analysis of these data in relation to the summer range experiments.

Network of Traffic Counters

Over 65 traffic counters were installed at open road intersections throughout the Main Study Area in 1989 as part of the roads and traffic study (Table 1). The counters record the number of motorized vehicles that pass over an inductive loop buried underneath the road, as summarized by 15- or 30-minute intervals, 24 hours a day, from May through December of each year.

The counts have been used to estimate

the rate of motorized traffic (number of vehicles per unit time) on each road at Starkey, as summarized by time of day for each season of each year. The traffic rates were used to evaluate mule deer and elk distributions in relation to distance from roads with varying rates of motorized traffic in the Main Study Area (Wisdom 1998, Wisdom et al. 2004b).

Use of Hunting for Research

From 1989 through 2003, 58 limited entry hunts of deer or elk have taken place in support of Starkey research goals (see Rowland et al. 1997 and the Starkey web page). These hunts are used to maintain population characteristics (e.g., sex and age ratios) for mule deer and elk similar to those outside Starkey, so that results are relevant to extant populations. Rowland et al. (1997:31) listed five additional reasons for use of hunting as part of Starkey research: (1) to collect data on animal condition, (2) to obtain baseline population data from harvest statistics, (3) to provide traditional recreational opportunity, (4) to provide data for input into a model of elk vulnerability to harvest, and (5) to subject animals to hunting pressure and disturbance similar to that outside the enclosure. The incorporation of hunting as part of the Starkey research also has allowed scientists to evaluate deer and elk responses to being hunted, as measured in terms of energy expenditures, changes in spatial distributions and resource selection patterns, and harvest rates in relation to hunter density (Johnson et al. 2004). Finally, the use of hunting as part of the research has facilitated detailed studies of hunters' willingness to pay for a variety of harvest opportunities and hunting experiences (Fried et al. 1995).

Data Collection and Mapping of Environmental Variables

Data for more than 100 environmental variables have been collected and mapped for Starkey research (Rowland et al. 1998). Example variables include slope, aspect, elevation, convexity, canopy clo-

sure, ecoclass, distance to water, and distance to open roads (Kie et al. 2004). These variables have been used in a variety of Starkey publications, such as those as described here and in Table 1. Example uses include evaluation of resource selection patterns (Johnson et al. 2000, Coe et al. 2001); effects of roads (Rowland et al. 2000, 2004), traffic (Wisdom 1998, Wisdom et al. 2004b), and timber harvest (Rinehart 2001, Wisdom et al. 2004c); and forage allocation modeling (Johnson et al. 1996, Ager et al. 2004).

NEW TECHNOLOGIES SUPPORT RESEARCH BENEFICIAL TO MANAGEMENT

Use of the innovative technologies at Starkey allowed the original and subsequent studies to be completed during the 1990s (Table 1). Findings from the many studies are diverse and compelling. Highlights of key findings from the original studies are summarized here as an example of what has been learned. Details can be found in the papers cited.

- Elk avoid roads open to traffic, validating observational studies from the 1970s and 1980s that first identified this relation (Rowland et al. 2000, 2004).
- Elk avoidance of roads increases with increasing rate of traffic, providing further evidence that elk are not reacting to roads per se, but the activities associated with roads (Wisdom 1998, Wisdom et al. 2004b).
- Mule deer generally do not avoid roads, and show increasingly strong selection toward areas near roads with increasing rate of traffic (Wisdom 1998, Wisdom et al. 2004b). This pattern is a result of mule deer avoiding elk, rather than deer selecting particular habitats near roads and traffic (Johnson et al. 2000, Coe et al. 2001).
- Elk avoid cattle and mule deer avoid elk, but the degree to which interference competition is operating is less clear (Johnson et al. 2000, Coe et al. 2001, Stewart et al. 2002). Elk may have ample opportunity to select a variety of habitats where cattle are not present, owing to rotation of cattle through a series of livestock pastures (Coe et al. 2001). Mule deer may not have these same habitat choices when avoiding elk, owing to the presence of elk throughout their summer range.
- Diets of cattle, mule deer, and elk differ substantially during early summer, with cattle diets containing a higher composition of grasses, deer diets containing more shrubs and forbs, and elk diets intermediate to those of cattle and deer (Findholt et al. 2004). Diets of the three ungulates become increasingly similar during late summer, when forage biomass and quality decline with the onset of summer drought, suggesting increased potential for exploitative competition.
- During the fall rut, the date of conception in female elk becomes progressively earlier and synchronous with increasing age of male breeders (Noyes et al. 1996, 2002, 2004). Breeding by yearling (1.5 year-old) bulls results in the latest dates of conception and highest variation in conception dates; breeding by mature (5.5 year-old) bulls results in earliest dates of conception. Earlier and closely synchronous dates of conception allow calves to be born earlier in spring and over a compressed time period, with potential benefits to survival (Noyes et al. 2004).
- In the absence of hunting, elk and cattle do not appear to be negatively affected by intensive timber harvest (Rinehart 2001, Wisdom et al. 2004c), but timber harvest increases the vulnerability of elk to hunting (Wisdom et al. 2004c).
- Elk do not require or benefit from thermal cover to ameliorate their thermoregulatory requirements in response to extreme weather during winter and summer (Cook et al. 1998). Instead, a mix of open and closed-canopy habitats results in superior animal performance compared to homogeneous stands of thermal cover. Importantly, elk appear to select dense forest for se-

curity during both hunting and non-hunting seasons (Ager et al. 2003, Johnson et al. 2004).

STARKEY'S FUTURE APPEARS BRIGHT

The Starkey Project now has one of the most voluminous and intensive data sets ever collected on ungulates. Over 140 publications have been produced, with more than 50 studies underway or completed (Thomas and Wisdom 2004). More than 100 scientists have conducted the research, with support from the timber industry, livestock industry, hunting groups, conservation organizations, and state and federal agencies (Quigley and Wisdom 2004). Results have been used widely to improve management of timber, grazing, roads, and recreation in relation to the needs of mule deer and elk (Thomas and Wisdom 2004).

The future of ungulate research at Starkey and associated, non-federal sites appears bright. A unique set of technologies and research facilities remain in place, allowing scientists to investigate a wide range of management issues related to ungulates. Continued focus on studies to integrate the needs of mule deer and elk with economic, social, and recreational interests in western North America represents an ongoing, compelling need that will continue to be addressed by the Starkey Project.

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The Starkey Databases: Spatial–Environmental Relations of North American Elk, Mule Deer, and Cattle at the Starkey Experimental Forest and Range in Northeastern Oregon

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INTRODUCTION

The Starkey Project was initiated in the late 1980s to study interactions among North American elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and domestic cattle at the Starkey Experimental Forest and Range in northeastern Oregon. As part of the Starkey Project, an automated radio telemetry system was developed to collect an unprecedented volume of location data on both wild and domestic ungulates (Rowland et al. 1997). That radio telemetry system was based on rebroadcast Long Range aid to Navigation- (LORAN-) C signals. In this paper, we provide an overview of the databases resulting from this effort.

LORAN, which stands for LONG Range aid to Navigation, is a marine radio-navigation system that was well-established before widespread use of the Navstar Global Positioning System (GPS). LORAN-A was the earliest version developed during World War II, while today LORAN-C serves the civilian community and LORAN-D is used by the military (Logsdon 1992, West and Pittman 1993). LORAN operates by measuring the difference in arrival times of a radio signal broadcast at 100 kHz directly from a master station and after being relayed through several secondary stations. The time differences of arrival among the signals routed through the various secondary stations allow a LORAN receiver to determine its location on several hyperbolic lines-of-position. Where those lines cross is the estimate of the actual

location of the receiver (Logsdon 1992, West and Pittman 1993).

The automated radio telemetry system at Starkey consists of a central computer base station, seven radio relay stations located throughout Starkey Forest, and radio collars placed on individual elk, mule deer, and cattle. Every 20 seconds, the base station pages one of the many radio collars deployed at any given time (Figure 1). As many as 150 animals have been included in the user-defined paging list simultaneously. When a particular animal is paged, a LORAN-C receiver inside the collar responds by collecting raw LORAN data, which are then retransmitted via a VHF radio link to one of the radio relay stations. The relay towers then transmit the data back to the central computer, where the raw data are decoded and information on the animal's location is stored electronically for future analysis (Figure 1). This LORAN-C system has a mean locational accuracy of about 55 yards (50 m), although some errors can exceed 219 yards (200 m), particularly in the east-west direction (Findholt et al. 1996, 2002).

The Starkey Project has collected information on well over 2 million animal locations since 1989. All animal data were collected following approval of protocols by an Institutional Animal Use and Care Committee (Wisdom et al. 1993). This telemetry database represents one of the largest data sets of large-animal locations ever compiled. A variety of studies have been completed based on these data. Examples include research on ungulate interactions and resource selection

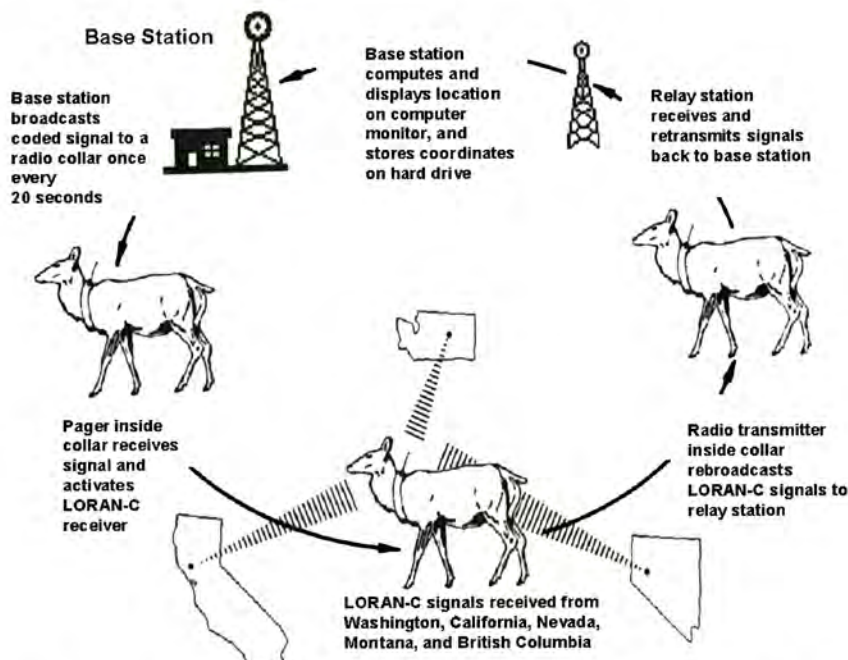


FIGURE 1. Automated, rebroadcast LORAN-C radio telemetry system used to collect location data on elk, mule deer, and cattle at Starkey Experimental Forest and Range (from Rowland et al. 1997).

(Johnson et al. 2000, Coe et al. 2001, Stewart et al. 2002), effects of roads (Rowland et al. 2000) and traffic (Wisdom 1998) interactions of elk, mule deer, and cattle, and their spatial and temporal patterns of habitat use (Ager et al. 2003), effects of sample size on estimates of resource selection (Leban et al. 2001) and home range (Garton et al. 2001), and development of ungulate forage allocation models (Johnson et al. 1996).

To facilitate new analyses by other research wildlife biologists, we are providing access to a portion of the Starkey Project telemetry database over the world wide web at <http://www.fs.fed.us/pnw/starkey/data>. The telemetry database includes locations of animals in the Main Study Area at Starkey Forest (Wisdom et al. 2004) recorded during spring and summer between 1993–1996, along with associated metadata. In addition, we are providing relevant Geographic Information System (GIS) layers such as habitat types, soils, a digital elevational model, and the forest road network in a second,

habitat database. The public release of these data will allow other scientists to formulate and test hypotheses that are best analyzed with comprehensive information about animal locations such as that provided by the Starkey data set.

STARKEY UNGULATE TELEMETRY DATABASE

Records in the telemetry database consist of elk, mule deer, and cattle locations (total $n > 287,000$) collected in the 19,180 acre (7,762 ha) Main Study Area at Starkey Forest (Wisdom et al. 2004) during spring and summer (April to mid-August) from 1993–1996 (Table 1). Animal locations are provided both as a point estimate in Universal Transverse Mercator (UTM) coordinates (UTMEasting and UTMNorthing, all in UTM Zone 11) and also placed in the center point of each 33 by 33 yard (30 by 30 m) pixel that encompasses the point estimate (UTMGrid, UTMGridEast, UTMGridNorth). All UTM coordinates are given in North

TABLE 1. Synthesized metadata description of variables included in the telemetry database of locations of elk, deer, and cattle collected in Main Study Area, Starkey Experimental Forest and Range, spring and summer, 1993 through 1996

Variable name	Variable definition	Units	Storage type ^a	Codes	Code definitions	Range (min, max)	Data format ^b
UTMGrid	Universal Transverse Mercator (UTM) Coordinates that identify the center point of each 33 by 33 yard (30 by 30 m) pixel within Starkey (Rowland <i>et al.</i> 1998); first six digits represent the UTM zone 11 easting; second seven digits represent the UTM Zone 11 northing. Example: 373695 5014530 are the easting and northing coordinates, respectively, that identify the center point of a given 33 by 33 yard (30 by 30 m) pixel at Starkey.	Meters	Character	—	—	373695 5014470, 381885 5007540	Fixed (14)
UTMGridEast	Coordinates in UTM Zone 11 easting Example: 373695 are easting coordinates.	Meters	Numeric (long integer)	—	—	373695, 381855	Variable
UTMGridNorth	Coordinates in UTM Zone 11 northing Example: 5014530 are the northing coordinates.	Meters	Numeric (long integer)	—	—	5005110, 5019120	Variable
ID	Unique alpha-numeric identification code assigned to each ungulate that was radio-collared. Example for deer: 890224E04 Example for elk: 930318D01 Example for cattle: OSUX83041	—	—	—	—	—	Fixed (9)

TABLE 1. Continued

Variable name	Variable definition	Units	Storage type ^a	Codes	Code definitions	Range (min, max)	Data format ^b
Starkey time	Cumulative number of seconds that have elapsed since the Greenwich Mean Time of 00:00:00 on 31 December 1987, which represents a starting point of the Starkey Ungulate Research. Example: Starkey time equals 1 at Greenwich Mean Time of 00:00:01 on 31 December 1987.	Seconds	Numeric	—	—	168825628, 272245926	Variable
GMTime	Greenwich Mean Time expressed as Hour:Minutes:Seconds; 8 hours ahead of Pacific Standard Time Example: 18:31:47 is 31 minutes, 47 seconds after hour 18 in the 24-hour cycle, as set on GMTime.	Hour:Minutes:Seconds	Character	—	—	00:00:00, 23:59:59	Fixed (8)
GMDate	Date associated with the Greenwich Mean Time, expressed as Year/Month/Day Example: 19930526 is 26 May 1993	Year/Month/Day	Character	—	—	19930507, 19960815	Fixed (8)
LocDate	Date synchronized in relation to Pacific Standard Time, which is 8 hours behind Greenwich Mean Time, LocDate is expressed as Year/Month/Day and is set for the Pacific Time Zone. Example: The Pacific Standard Time of 19:59:27 has an associated date for the Pacific Time Zone of 19930512, or 12 May 1993. However, the commensurate Greenwich Mean Time of 03:59:27 has an associated date of 13 May 1993.	Year/Month/Day	Character	—	—	19930506, 19960815	Fixed (8)

TABLE 1. Continued

Variable name	Variable definition	Units	Storage type ^a	Codes	Code definitions	Range (min, max)	Data format ^b
LocTime	Pacific Standard Time, which is 8 hours later than Greenwich Mean Time. No adjustment is made for Pacific Daylight Savings Time. Example: 19:59:27 is 59 minutes, 27 seconds after hour 19 of a 24-hour cycle, as set on Pacific Standard Time, which is commensurate with 03:59:27 of Greenwich Mean Time.	Hour:Minutes:Seconds	Character	—	—	00:00:00, 23:59:59	Fixed (8)
RadNum	Unique identification code assigned to a given radio-collar. Note that a given radio-collar could be worn by one or more animals within or across years, and thus should not be confused with the unique identification code for each radio-collared animal, or ID.	—	Numeric	—	—	8, 450	Variable
Species	Species of ungulate associated with the animal location, where C = cattle, D = deer, and E = elk.	—	Character	C, D, E	C = cattle, D = deer, and E = elk.	—	Fixed (1)
UTME	Coordinates in the Easting Direction. Constitutes the x coordinate of the point estimate of the animal location.	Meters	Numeric	—	—	373705, 381853	Fixed (6)
UTMN	Coordinates in the Northing Direction. Constitutes the y coordinate of the point estimate of the animal location.	Meters	Numeric	—	—	5005110, 5019118	Fixed (7)
Year	Year in which the animal location was collected.	Year	Numeric	—	—	93, 96	Fixed (2)

TABLE 1. Continued

Variable name	Variable definition	Units	Storage type ^a	Codes	Code definitions	Range (min, max)	Data format ^b
Grensunr	Time of sunrise at Starkey for a given date, expressed in Greenwich Mean Time. See GMT variable.	Hour:Minutes:Seconds	Numeric	—	—	12:05:00, 13:35:00	Fixed (8)
Grensuns	Time of sunset at Starkey for a given date, expressed in Greenwich Mean Time. See GMT variable.	Hour:Minutes:Seconds	Numeric	—	—	02:23:00, 03:49:00	Fixed (8)
Obswt	Correction to the bias in observation rate of an animal location, where observation rate is defined as the probability of obtaining an animal location from a radio-collared animal, when an animal location is requested by the Loran-C telemetry system. Application of Obswt (1 divided by the observation rate) increases the number of locations for a given area, according to the degree of bias in observation rate associated with that area (Johnson et al. 1998). Example: An Obswt of 2 would place twice the weight on a given animal location, whereas an Obswt of 1.5 would place 1.5 times the weight on a given animal location. These weights correct for animal locations in a given UTMGrid that were not observed, given the bias in observation rate among pixels (Johnson et al. 1998).	—	Numeric	—	—	1.14, 3.5	Variable

^a Refers to way in which data is entered, such a character (text), long integer, or floating point.^b Refers to whether data is of fixed or variable length; for fixed variables, maximum number of characters is displayed.

TABLE 2. Synthesized metadata description of variables included in the habitat database for Main Study Area, Starkey Experimental Forest and Range

Variable name	Variable definition	Units	Storage type ^a	Codes	Code definitions	Range (min, max)	Data format ^b
UTMGrid	Universal Transverse Mercator (UTM) Coordinates that identify the center point of each 33 by 33 yard (30 by 30 m) pixel within Starkey (Rowland <i>et al.</i> 1998); first six digits represent UTM Zone 11 easting; second seven digits represent the UTM Zone 11 northing. All coordinates are given in NAD83. Example: 373695 5014530 are the easting and northing coordinates, respectively, that identify the center point of a given 33 by 33 yard (30 × 30 m) pixel at Starkey.	Meters	Character	—	—	373695 5014470, 381885 5007540	Fixed (14)
UTMGridEast	Easting coordinate in UTM Zone 11.	Meters	Numeric (long integer)	—	—	373695, 381855	Fixed (6)
UTMGridNorth	Northing coordinate in UTM Zone 11.	Meters	Numeric (long integer)	—	—	5005110, 5019120	Fixed (7)
SoiDpth	Soil depth to the restrictive layer (obtained from the Wallowa-Whitman National Forest soils resource inventory [SRI])	Centimeters	Numeric	—	—	9, 60	Variable

TABLE 2. Continued

Variable name	Variable definition	Units	Storage type ^a	Codes	Code definitions	Range (min, max)	Data format ^b
PerSlope	Percent slope (Rowland et al. 1998)	—	Numeric	—	—	0, 84	Variable
SINAspet	Sine of aspect (Rowland et al. 1998)	—	Numeric	—	—	−1, 1	Variable
COSAspet	Cosine of aspect (Rowland et al. 1998)	—	Numeric	—	—	−1, 1	Variable
Convex3	Convexity (Rowland et al. 1998)	—	Numeric	—	—	465.86, 524.64	Variable
DistCWat	Distance to the nearest water source from within a cattle pasture, including class I through III streams and water point sources such as stock ponds and springs	Meters	Numeric	−99	−99 denotes 33 by 33 yard (30 by 30 m) pixels in the pasture that are not available to cattle. These pixels should be excluded from any analyses of cattle distance to water.	−99, 2714	Variable
Canopy	Total canopy closure (%) of all trees >1 inch (2.5 cm) diameter at breast height)	—	Numeric	—	—	0, 85	Variable
Elev	Elevation (Rowland et al. 1998)	Meters	Numeric	—	—	1121, 1500	Fixed (4)
DistEWat	Distance to the nearest water source form within an ungulate-proof pasture (e.g., Main Study Area), including class I through III streams and water point sources such as stock ponds and springs	Meters	Numeric	—	—	0, 1188	Variable

TABLE 2. Continued

Variable name	Variable definition	Units	Storage type ^a	Codes	Code definitions	Range (min, max)	Data format ^b
EcoGener	General ecoclass description; modified from the original ecoclass variable (Rowland <i>et al.</i> , 1998) to include only the dominant forest canopy species.	—	Character	AB	Buildings, structures, roads	—	Fixed (10)
				CD	Douglas-fir		
				CJ	Juniper		
				CL	Lodgepole pine		
				CP	Ponderosa pine		
				CW	White fir, grand fir		
				GB	Bunchgrass vegetation		
				MD	Dry meadow ^c		
				MM	Moist meadow ^d		
				MW	Wet meadow ^e		
				NR	Rocky land		
				SD	Dry shrubland ^f		
				WR	Running water (stream, river, creek, ditch)		
DistOPEN	Distance to the nearest open road (Rowland <i>et al.</i> 1998)	Meters	Numeric	—	—	0, 2419	Variable
DistRSTR	Distance to the nearest restricted access road (Rowland <i>et al.</i> 1998)	Meters	Numeric	—	—	0, 2315	Variable
DistCLSD	Distance to the nearest closed road (Rowland <i>et al.</i> 1998)	Meters	Numeric	—	—	0, 2208	Variable
DisEFnc	Distance to the nearest ungulate-proof fence (Rowland <i>et al.</i> 1998)	Meters	Numeric	—	—	0, 4243	Variable

TABLE 2. Continued

Variable name	Variable definition	Units	Storage type ^a	Codes	Code definitions	Range (min, max)	Data format ^b
CowPast	Cattle pasture (Rowland et al. 1998)	—	Character	BEAR HORSE SMITH-BALLY HALFMOON MDWCRK NE STRIP	Meadow Creek Northeast Narrow strip of land between Campbell and Bear Pastures; formerly includ- ed in Campbell Pasture	—	Fixed (11)
ForgProd	Forage production (bio- mass of understory spe- cies considered forage for ungulates: Hall 1973)	Kilograms/ Hectare	Numeric	—	—	0, 2200	Variable
DistEdge	Distance to nearest edge, based on the EcoGener polygons used for eco- classes	Meters	Numeric	—	—	0, 426	Variable

^a Refers to way in which data are entered, such as character (text), long integer, or floating point.
^b Refers to whether data is of fixed or variable length; for fixed variables, maximum number of characters is displayed.
^c Water table available part of the season.
^d Water table available all growing season.
^e Surface moist or wet all of growing season.
^f Includes sagebrush and non-forest zone shrubland; not desert.

TABLE 3. Habitat layers in Arc Info export for Main Study Area, Starkey Experimental Forest and Range

Habitat layer name	Layer type	Description
vegetation_ecoclass	grid	Map of vegetation ecoclasses; 33 by 33 yard (30 by 30 m) cells
soils	grid	Map of soil types; classified by soil series and depth; 33 by 33 yard (30 by 30 m) cells
DEM	grid	Digital elevation model for Starkey; 33 by 33 yard (30 by 30 m) cells
Black_hole_corrections	grid	Black-hole corrections for spatial differences in telemetry observation rates (Johnson <i>et al.</i> 1998); 33 by 33 yard (30 by 30 m) cells
canopy closure	grid	Canopy closure of overstory trees
vegetation_forest_stands	polygon	Map of forest stands; classified by ecoclass
roads	line	Map of all roads on and immediately adjacent to Starkey; classified by road type
streams	line	Map of all stream drainages; classified by stream class, presence or absence of running water
game_proof_fences	line	Map of game-proof fences only
all_fences	line	Map of all fences, including barbed-wire cattle fences and exclosures
water_points	point	Location of water point sources such as stock troughs

American Datum 1983 (NAD83). Animals are uniquely identified by ID and were assigned a specific radio-collar number (RadNum) each year. The user should be aware that a given radio-collar number could be worn by different animals in different years. Time and date of each observation is provided in Greenwich Mean Time (GMTTime) and in local time (LocTime in Pacific Standard Time; no adjustments were made for daylight savings time). Time is also provided in a variable called Starkey Time, representing seconds from an arbitrary zero point at 0000 hours on 31 December 1987. Starkey Time is useful in determining elapsed time between any two observations. Sunrise and sunset times are given based on GMTTime (Grensunt, Grensuns). Finally, a correction factor is provided to account for spatially-dependent observation rates as discussed by Johnson *et al.* (1998). The observation rate is defined as the probability of obtaining an animal location as a function of its location at Starkey. The correction factor (Obswt), defined as the inverse of the observation rate ($1/\text{observation rate}$), can be used to

weight locations for assessing patterns of spatial use.

STARKEY HABITAT DATABASE

Spatial layers for various features are provided in the habitat database (Table 2). Each record in the database is identified by UTM coordinates, and represents a unique 33 by 33 yard (30 by 30 m) pixel in Main Study Area, Starkey Experimental Forest and Range. All UTM coordinates are given in North American Datum 1983 (NAD83). Values for variables such as ecoclass, soil depth, and canopy closure are provided. Details of the habitat database are available in Rowland *et al.* (1998).

In addition to providing habitat information in database form, habitat layers are included ArcInfo (Environmental Systems Research Institute, Inc., Redlands, California, USA) interchange format (e00; Table 3). Raster files include ecoclass, soils, a digital elevational model, canopy closure of overstory trees, and black hole corrections for differences in telemetry observation rates as per John-

son et al. (1998). A polygon file is provided showing forest stand boundaries. Line files include roads, streams, and fences (game-proof fences and barbed-wire cattle fences). Water sources are given as a point coverage.

PUBLICATIONS

Additional information about the Starkey Project is available on the web at <http://www.fs.fed.us/pnw/starkey/>. Two publications from the Starkey Project helpful in interpreting the telemetry and habitat databases are available there in PDF format: a general history of the Starkey Project which contains information about telemetry data (Rowland et al. 1997), and details of the Starkey Habitat Database (Rowland et al. 1998). A complete list of Starkey Project publications, many available as full-text PDF files can be found at <http://www.fs.fed.us/pnw/starkey/publications>.

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Effects of Roads on Elk: Implications for Management in Forested Ecosystems

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The effects of roads on both habitat and population responses of elk (*Cervus elaphus*) have been of keen interest to foresters and ungulate biologists for the last half century. Increased timber harvest in National Forests, beginning in the 1960s, led to a proliferation of road networks in forested ecosystems inhabited by elk (Hieb 1976, Lyon and Christensen 2002). Among disturbances to elk habitat, roads have been viewed as a major factor influencing distributions of elk across the landscape (Leege 1984, Lyon 1984, Lyon et al. 1985, Roloff 1998, Lyon and Christensen 2002, Wertz et al. 2004). Evidence from a variety of studies, such as those conducted at the Starkey Experimental Forest and Range (Starkey) in northeastern Oregon, has corroborated this view (Lyon 1983, 1984; Witmer and deCalesta 1985; Cole et al. 1997; Johnson et al. 2000; Rowland et al. 2000; Ager et al. 2003). (See Rowland et al. [1997] for a general description of the Starkey Project and the Starkey environment.)

Early studies of elk were among the first to address effects of roads on wildlife, establishing a precedent for subsequent research on a wide range of terrestrial and aquatic species. These early elk-roads studies included those reported in a symposium on the topic in 1975 (Hieb 1976), the seminal studies of Jack Lyon in Montana and northern Idaho (Lyon 1979, 1983, 1984), the Montana Cooperative Elk-Logging Study (Lyon et al. 1985), and work by Perry and Overly (1977) in Washington and Rost and Bailey (1979) in Colorado.

As research and analysis techniques have become more sophisticated, particularly with the advent of geographic information systems (GIS) and high-resolution remote imagery, the study of ef-

fects of roads on terrestrial and aquatic communities has evolved into a unique discipline of “road ecology” (Forman et al. 2003). Road effects are far more pervasive than originally believed and include such disparate consequences as population and habitat fragmentation, accelerated rates of soil erosion, and invasion of exotic plants along roadways. Indeed, “in public wildlands management, road systems are the largest human investment and the feature most damaging to the environment” (Gucinski et al. 2001:7). Summaries of the effects of roads on wildlife habitats and biological systems in general have been compiled by Forman and Alexander (1998), Trombulak and Frissell (2000), Gućinski et al. (2001), Forman et al. (2003) and Gaines et al. (2003).

Well-designed research that furthers our understanding of road effects and road management on key species, such as elk, and their habitats is critical for enhancing the long-term functioning of ecosystems impacted by the vast network of roads in North America. Moreover, addressing effects of roads on elk and elk habitat often is mandated on public lands, e.g., through standards and guidelines developed for National Forests.

Our goals in this paper are three-fold: (1) to describe current knowledge about effects of roads on elk, emphasizing results of research conducted at Starkey, (2) to describe an example in which a distance-band approach, rather than the traditional road density method, was used to evaluate habitat effectiveness (HE) for elk in relation to roads, and (3) to discuss the broader implications of road-related policies and land management with regard to elk.

EFFECTS OF ROADS ON ELK IN FORESTED ECOSYSTEMS—WHAT DO WE KNOW?

Effects of roads on elk can be divided into two broad categories: indirect effects on habitats occupied by elk, and direct effects on individual elk and their populations. Effects of roads in forested ecosystems in general have been well summarized (Gucinski et al. 2001, Gaines et al. 2003). With regard to elk habitat, the primary effect of roads may be habitat fragmentation; heavily roaded areas may contain few patches of forest cover large enough to function effectively as habitat for elk, especially where elk are hunted (Leege 1984, Rowland et al. 2000). The total loss of elk habitat from road construction is unknown; a rough estimate of 5 acres per linear mile (1.4 ha/km) of road is often applied (Forman et al. 2003). Across the United States, the area occupied by public roads and associated corridors is estimated to be 27 million acres (10.9 million ha); these numbers do not include private roads or "unofficial" roads on public lands (Forman et al. 2003). Roads may also exert more subtle influences on habitat, for example by facilitating the spread of exotic vegetation (Gelbard and Belnap 2003) which may subsequently reduce quality and abundance of forage available to elk. Gaines et al. (2003) listed five road-associated factors in relation to elk: hunting, poaching, collisions, displacement or avoidance, and disturbance at a specific site.

The direct impacts of roads and associated traffic on elk, in addition to outright mortality from collisions with motorized vehicles, can be summarized as follows:

1. *Elk avoid areas near open roads.* A plethora of studies have demonstrated an increasing frequency of elk occurrence or indices of elk use, such as pellet groups, at greater distances from open roads (defined here as any road where motorized vehicles are allowed). This response varies in relation to traffic rates (Wisdom 1998, Johnson et al. 2000, Ager et al. 2003), the extent of forest canopy cover adjacent to roads

(Perry and Overly 1977, Lyon 1979, Wisdom 1998, Wisdom et al. 2004b), topography (Perry and Overly 1977, Edge and Marcum 1991), and type of road (e.g., improved versus primitive; Perry and Overly 1977, Lyon 1979, Witmer and deCalesta 1985, Marcum and Edge 1991, Rowland et al. 2000, Lyon and Christensen 2002, Benkobi et al. 2004), which also correlates with traffic rates. Responses may also differ between sexes, with bull elk demonstrating a stronger avoidance of areas close to roads than do cow elk (Marcum and Edge 1991). Shifts in distribution of elk away from roads may occur across a range of temporal and spatial scales. For example, elk at Starkey were generally farther from open roads during daytime, but moved closer to roads during nighttime (Wisdom 1998, Ager et al. 2003). This pattern was also observed in South Dakota (Millspaugh 1999). In addition, both daily movements and size of home ranges of elk may decrease when open road density decreases. These reductions could lead to energetic benefits that translate into increased fat reserves or productivity (Cole et al. 1997). On a larger scale, entire ranges can be abandoned if disturbance from traffic on roads and the associated habitat loss and fragmentation exceed some threshold level. The ultimate effect of displacement of elk, by motorized traffic as well as other disturbances, is a temporary or permanent reduction in effective habitat for elk. Concomitant with loss of effective habitat are reduced local and regional populations (Forman et al. 2003).

2. *Elk vulnerability to mortality from hunter harvest, both legal and illegal, increases as open road density increases.* Many factors affect elk vulnerability to hunter harvest, but the evidence is compelling that survival rates of elk are reduced in areas with higher road density (Leege 1984, Lepitch and Zager 1991, Unsworth et al. 1993, Gratson and Whitman 2000a, Weber et al. 2000, Hayes et al. 2002, McCorquodale et al. 2003). Closing

roads offers more security to elk and may decrease hunter densities (fewer hunters may be willing to hunt without vehicle access). Also, poaching losses may decrease when roads are closed (Cole et al. 1997).

3. *In areas of higher road density, elk exhibit higher levels of stress and increased movement rates.* Higher levels of physiological indicators of stress, such as fecal glucocorticoids, have been observed in elk exposed to increased road density and traffic on roads (Millspaugh et al. 2001). In addition, the energetic costs of moving away from disturbance associated with roads may be substantial (Cole et al. 1997). Research to estimate such costs to elk in relation to recreational use on roads is underway at Starkey (Wisdom et al. 2004a). Conversely, elk may conserve energy by traveling on closed roads to avoid woody debris and down-fall (Lyon and Christensen 2002).

Knowledge has been gained not only about elk response to roads, but also about modeling this relationship. Results from research at Starkey suggested that a road-effects model based on distance bands provides a more spatially explicit and biologically meaningful tool than a traditional model based on road density (Rowland et al. 2000). This analysis, based on more than 100,000 radiolocations of cow elk during spring and summer, found no relation between numbers of elk locations and HE scores based on open road density in 15 elk "analysis units." (We define habitat effectiveness as the "percentage of available habitat that is usable by elk outside the hunting season" [Lyon and Christensen 1992:4].) However, elk preference increased strongly (as measured by selection ratios) as distance to open roads increased. Such distance-to-roads analyses are readily accomplished using widely available spatial data layers in a GIS.

Despite the wealth of information about how roads and motorized traffic affect elk and their habitats, gaps in our knowledge remain. For example, while we know that elk response to roads gen-

erally varies depending on the level and type of motorized traffic, we have little knowledge about the precise levels of such disturbance that elicit a response, and the duration of that response. Research at Starkey has demonstrated threshold rates of traffic above which a response by elk is elicited, but below which open roads are functionally equivalent to closed roads (A. A. Ager, personal communication 2003; Wisdom et al. 2004b). Measurements of traffic rates and elk response to these rates are needed in other locations to better understand these thresholds. Though more costly to obtain than maps of roads, information about traffic rates can be used to improve management of roads in elk habitat in ways that are both cost-effective and beneficial to elk. Further research also is needed to better understand the interaction of roads, topography, and forest cover in affecting elk distributions, primarily in relation to providing security for elk.

Also needed is a better understanding of the effectiveness of road closures; examples abound about the lack of effectiveness of closures on public lands, especially when few resources are made available for enforcement (Havlick 2002, Wertz et al. 2004). More than half of 802 road closures inventoried on National Forests in Idaho, Montana, Washington, and Wyoming were found to be ineffective, even after accounting for administrative use (Havlick 2002). In Idaho, elk mortality was positively correlated to densities of both closed roads and open roads, suggesting that road closures were ineffective in reducing mortality from hunting (Hayes et al. 2002). Systematically collected data on use by all motorized vehicles, including off-highway vehicles, of closed roads would benefit management of elk and other resources (e.g., soils) affected by vehicle traffic on roads. And last, HE models for elk, including the roads variable, need further validation. Beyond the Starkey research (Rowland et al. 2000) and a few other studies (e.g., Roloff et al. 2001, Benkobi et al. 2004), such validation has not been conducted, especially of the most com-

monly applied models (Wisdom et al. 1986, Thomas et al. 1988). Given the continued widespread use of elk HE models in land-use planning on National Forests and other lands occupied by elk, such validation is a critical research need.

A final cautionary note: much of what has been learned about elk and roads to date has resulted from field studies that had no experimental component and thus no sound basis from which to infer cause-effect relations. Experimental studies underway at Starkey, in which road densities and traffic rates are manipulated according to strict sampling protocols, and distributions of elk are closely monitored, will greatly enhance our understanding of elk response to roads (Wisdom et al. 2004b).

CURRENT MANAGEMENT APPROACHES TO ELK-ROADS ISSUES

In light of the deleterious effects of roads on elk as described above, both ungulate biologists and land managers have developed methods to address their respective concerns. During the 1970s and 1980s, biologists created a suite of models, based on empirical data, to predict effects of land management activities on habitat effectiveness for elk (e.g., Lyon 1979, 1983; Thomas et al. 1979, 1988; Leege 1984; Wisdom et al. 1986). All of these models incorporated a road-density component. In addition to the more general elk HE models, specific habitat guidelines were written related to roads. For example, guidelines developed in Montana specified that elk security areas be located more than 0.5 miles (0.8 km) from open roads (Hillis et al. 1991). Elk habitat models that include a roads component also have been used to evaluate the suitability of sites for restoration of elk populations (Didier and Porter 1999). Further, ungulate biologists have constructed resource selection models that include a roads variable to predict spatial distributions of elk (Cooper and Mills-paugh 1999, Johnson et al. 2000).

Land managers in turn have incorporated concerns about elk and roads into for-

mal planning processes through the application of standards and guidelines. How management agencies address elk-roads issues varies widely, however, both within and across agencies. For example, elk are designated as a Management Indicator Species (MIS) within some National Forests but not others. This designation, or lack thereof, subsequently affects how elk habitat is addressed in forest planning and environmental assessment.

Forest plans for many National Forests contain specific standards and guidelines for elk HE, using one or more of the various elk HE models that have been developed. For example, the forest plan for the Wallowa-Whitman National Forest in northeastern Oregon provides direction to maintain HE >0.5 during timber sale planning in management area 1 (MA1; timber production emphasis), but only "where this can be done without reducing timber harvest volumes" (U.S. Department of Agriculture, Forest Service 1990b:4–57). (Habitat effectiveness scores range from 0 to 1.0 in most HE models.) Furthermore, the plan assumes that in the long-term, elk HE will be maintained at 0.62 in MA1. Open road density in this management area is targeted not to exceed 2.5 miles per square mile (1.6 km/km²) in general, but no more than 1.5 miles per square mile (0.9 km/km²) in selected elk summer and winter ranges. In the adjacent Umatilla National Forest, elk HE is projected to range between 0.67 and 0.70, and open road density from 2.0–2.2 miles per square mile (1.2–1.4 km/km²), forest-wide during the five decades beyond 1990 (U.S. Department of Agriculture, Forest Service 1990a). In addition, the standard for elk HE on big game winter range is 0.70 (U.S. Department of Agriculture, Forest Service 1990a). Generally, if habitat for elk is identified as an issue for a proposed management activity, such as timber restoration, or if elk have been identified as a Management Indicator Species, evaluation of elk habitat is mandated during the environmental assessment process. Such evaluation commonly entails the application of an elk HE model to the affected area under the various alternatives, with

the results incorporated into an "effects analysis" for evaluation of alternatives.

A more recently developed approach is to incorporate evaluations of habitat effectiveness for elk into the initial stages of forest planning, rather than using HE models to evaluate effects of single management activities, such as timber harvest (Bettinger et al. 1999). This approach incorporates elk HE into the objective function of a mathematical forest-planning model. Various scenarios can be simulated, with maximization of elk HE scores, timber output, or both. Likewise, Roloff et al. (1999) developed a decision support system that allows evaluation of effects of various management strategies on habitat for elk and other wildlife within the context of forest planning models.

APPLYING A DISTANCE-BAND MODEL OF ELK-ROAD EFFECTS IN FOREST PLANNING: A CASE EXAMPLE

A method to evaluate effects of roads on elk using a distance-band approach has been suggested both by Roloff (1998) and by Rowland et al. (2000), as described above. Based on radiolocations of elk at Starkey, Rowland et al. (2000) found no relation between number of elk locations and HE based on open road densities. By contrast, the authors found a strong, linear increase in selection ratios of elk as distance to roads increased. For this analysis, elk locations were assigned to 109-yard (100-m) wide bands away from open roads. Roloff (1998) also developed a road-effects module in which habitat adjacent to roads was buffered into distance bands in a GIS. Habitat effectiveness in the bands was adjusted according to level of security cover, as well as road use or road type. Regardless of the exact approach selected, ongoing planning efforts within National Forests and other lands that provide habitat for elk may benefit from consideration of a revised, spatially explicit road-effects variable.

The mechanics of calculating HE related to roads (HE_R) using distance bands

are similar to those for another variable in elk HE models—the size and spacing of cover and forage (HE_S). Both variables involve buffering out from a linear feature—either roads, for HE_R , or the cover: forage edge, for HE_S —to create distance bands. Each band is assigned a weight, with lower weights corresponding to lower HE. A weighted average is then calculated, based on the proportion of the analysis area in each of the bands and the weight of the appropriate band (see Hitchcock and Ager 1992 for details of calculating HE_S using this method). The sum of these products yields the final HE value, which cannot exceed 1.0.

To examine how the method of calculation (i.e., the traditional road-density method versus distance bands) might affect HE_R for elk, we applied both methods in an evaluation of the effects of a timber sale in the Wallowa-Whitman NF in northeastern Oregon. The Dark Meadow Restoration Project was proposed to "restore and enhance ecosystems" within the project area, through thinning, prescribed fire, and mechanical fuels-reduction treatments over the next 10–15 years (U.S. Department of Agriculture, Forest Service 2003). Project goals include reductions in fuel loading, promotion of old-growth habitat, improvement in big game habitat, and initiation of tree regeneration. Under the two "action alternatives" of the project, open road density will be lower than that under the "no action" (existing condition) alternative (Table 1, Figure 1).

The Dark Meadow analysis area encompasses 17,700 acres (7,169 ha) of the Blue Mountains and is completely contained within the Starkey Game Management Unit. The elk population in this unit is estimated to be at the objective (5,300) set by Oregon Department of Fish and Wildlife. The area functions primarily as summer range for elk, with smaller portions used as transitional or winter range. Lack of elk security habitat was identified as a key issue in planning for the Dark Meadow project; thus, roads were a primary consideration in the crafting of alternatives (U.S. Department of Agriculture, Forest Service 2003).

TABLE 1. Comparison of two methods for modeling effects of roads on elk habitat effectiveness (HE) under three alternatives in the Dark Meadow Restoration Project, Wallowa-Whitman National Forest, northeastern Oregon

Variable	"No action" alternative ^a	Alternative 1	Alternative 2
Total miles (km) of open roads in analysis area ^b	138.1 (222.2)	114.2 (183.7)	106.5 (171.4)
Open road density in miles /mi ² (km/km ²)	4.99 (3.09)	4.13 (2.56)	3.85 (2.39)
HE _R -ORD ^c	0.20	0.28	0.31
HE _R -DB ^c	0.17	0.19	0.20
HE _C ^d	0.60	0.59	0.61
HE _S ^e	0.84	0.79	0.80
Total HE (ORD method) ^f	0.47	0.51	0.52
Total HE (DB method)	0.45	0.46	0.47

^a This alternative is the existing condition.

^b Open roads include any road available to motorized traffic; these are roads officially designated as open as well as closed roads that have no promulgation. See text for details.

^c Habitat effectiveness for roads (HE_R) based on open road densities (ORD); HE_R-DB uses distance bands (DB) to calculate HE_R. See text for details.

^d Habitat effectiveness as related to cover quality; see Thomas et al. 1988 for details.

^e Habitat effectiveness as related to size and spacing of cover and forage areas; see Thomas et al. 1988 for details.

^f Total habitat effectiveness, which is the geometric mean of HE_R, HE_C, HE_S, and HE_F. HE_F (habitat effectiveness as related to forage quality and quantity) was not derived empirically for this analysis; rather a default value of 0.5 was input for this variable.

To calculate HE_R for elk in Dark Meadow, all roads open to motorized vehicles were counted. No traffic rate data were available; thus, roads were not weighted according to level of use. We defined open roads as those officially designated as open, as well as closed roads for which no promulgation was planned. Promulgated road closures are those for which the Code of Federal Regulations is applied; such closures are legal and enforceable. In the Wallowa-Whitman Forest Plan, closed roads were assumed to be physically impassable to full-sized vehicles, and also assumed to be seldom traveled by off-highway vehicles (U.S. Department of Agriculture, Forest Service 1990b). Roads designated as "closed" but not promulgated, however, are often traveled by off-highway vehicles (Havlick 2002).

The HE_R variable based on open road densities (hereafter referred to as HE_R-ORD) was then calculated with the equations of Hitchcock and Ager (1992), for the existing condition and the two action alternatives (Table 1). To calculate HE_R based on distance bands (HE_R-DB), all open roads were buffered in a GIS. The

analysis area was partitioned into five bands, each 394 yards (360 m) wide, with the sixth band containing any area greater than 1,969 yards (1,800 m) from an open road. This distance (i.e., 1,969 yards) is equivalent to that at which elk response to open roads diminished markedly at Starkey (Rowland et al. 2000). Each band was assigned a weight, reflecting a linear increase in elk selection ratios as distance from open roads increased at Starkey; band 1–0.17, band 2–0.33; band 3–0.50; band 4–0.67; band 5–0.83; and band 6–1.0. HE_R-DB was then calculated as a weighted average, with the proportion of the analysis area in each band multiplied by the appropriate weight. Finally, we calculated total HE for the analysis area, based on all four variables of the elk HE model, with only HE_R differing between the two calculations (Table 1).

Open road density in the Dark Meadow area was relatively high under all three alternatives, and HE_R-DB was consistently lower than HE_R-ORD (Table 1). However, this difference was more pronounced with lower open road densities; under the "no action" alternative, HE_R-DB was only 15

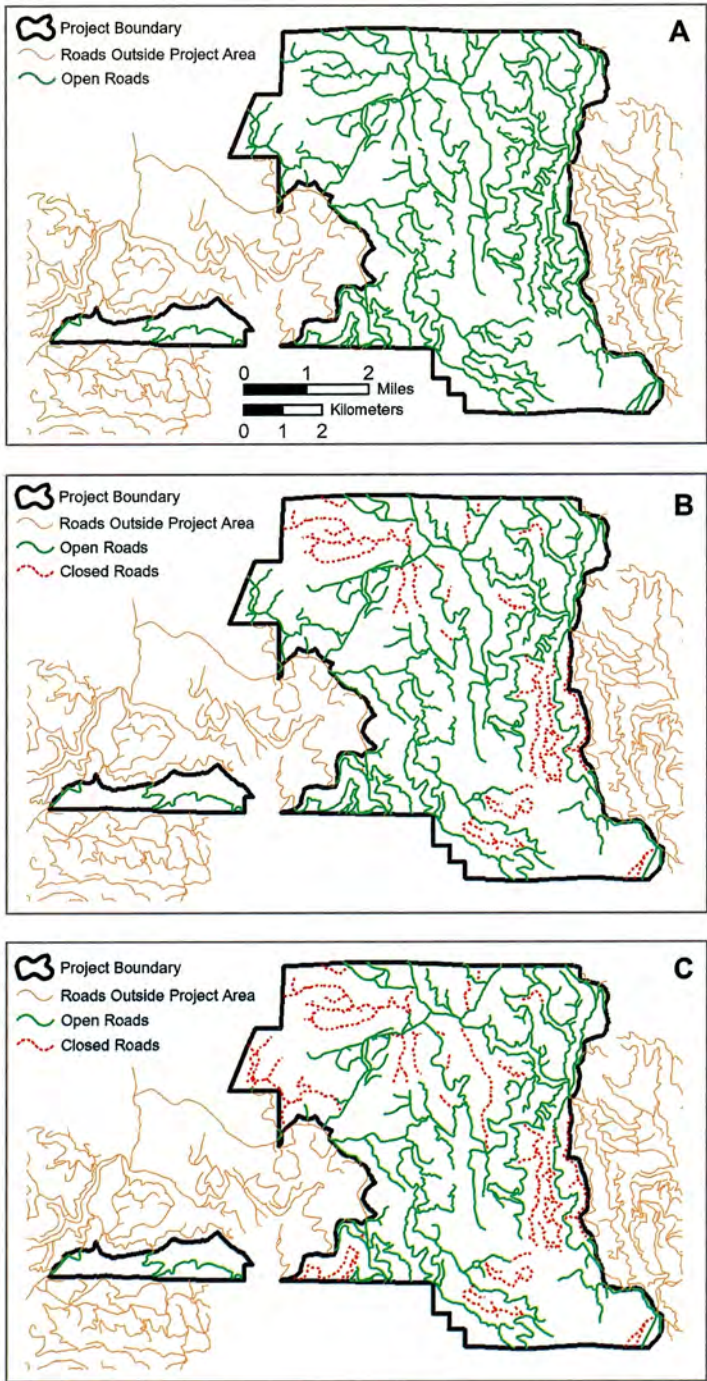


FIGURE 1. Roads under three alternatives of the Dark Meadow Restoration Project, Wallowa-Whitman National Forest, northeastern Oregon: the “no action” alternative (A); Alternative 1 (B); and Alternative 2 (C). Open roads were defined as any road available to motorized traffic, including roads officially designated as open and closed roads that have no promulgation.

percent less than HE_R -ORD, but under the two action alternatives this difference increased to 32–35 percent (Table 1). Compared to the “no action” alternative, the density of open roads declined 17 and 23 percent, respectively, under Alternatives 1 and 2. Concomitant with this decline in road density were increases in HE_R -ORD of 40 and 55 percent for the two action alternatives, respectively; however, HE_R -DB increased only 12 and 18 percent (Table 1). These results suggest that the spatial arrangement of remaining open roads was such that the amount of effective habitat for elk improved only marginally (Figure 1). Thus, HE_R -ORD may overestimate habitat effectiveness for elk under certain conditions.

Because total HE is the geometric mean of all four input variables, differences in total HE between the two methods were not as substantial as were those for HE_R alone (Table 1). Among the four variables used to calculate HE, all of which are equally weighted in computing the mean, values for HE_R were substantially lower than those of the other three variables (Table 1). Thus, in the Dark Meadow project area, the relatively high open road densities were largely responsible for the low total HE scores. These scores exceeded only slightly the recommended standard of 0.5 for total HE in timber planning on the Wallowa-Whitman, and only when HE_R -ORD was used for the roads variable (Table 1). By contrast, when HE_R -DB was used, total HE was below the standard for all alternatives (Table 1).

We did not alter band weights, or “back buffer” them, based on the level of security cover in each band (see Roloff 1998). This additional refinement may be warranted in situations where cover quality varies widely across the analysis area, or is predicted to vary under proposed management alternatives. In addition, band weights could be adjusted by accounting for topographic relief, such that areas providing topographic barriers to human disturbance would have weights adjusted upward, or by traffic rates, if such data were available (e.g., Wisdom *et al.* 2004b).

IMPLICATIONS FOR MANAGEMENT AND POLICY INVOLVING ELK-ROADS ISSUES

Road management inevitably involves tradeoffs between the benefits of increased access that roads provide versus the ecological and economic costs associated with roads (Gucinski *et al.* 2001, Forman *et al.* 2003). Because the U.S. Department of Agriculture, Forest Service (Forest Service) manages about 10 percent of the public road system in the United States (Forman *et al.* 2003), road-management decisions made by that agency strongly influence current road systems. The Forest Service policy regarding road closures and construction continues to engender controversy, exemplified by the multi-year debate over the national Roadless Rule. The rule, first published in the Federal Register in January 2001 (U.S. Government 2001), has been challenged by at least nine lawsuits in federal district courts. Decisions about roads, including construction, reconstruction, closure, obliteration, or decommissioning, are complex because they affect a multitude of resources, not just wildlife. All resource values in a watershed must be evaluated when making decisions about roads; these may include human safety (e.g., access to combat wildfires), soils, recreation, commercial timber harvest, and restoration activities. In addition, decisions about roads are closely tied to available funding. Expenses are involved both in constructing and maintaining roads and in decommissioning roads and enforcing road closures (Forman *et al.* 2003). Complicating the issue of evaluating effects of roads is that roads in forested ecosystems currently are not well inventoried (Gucinski *et al.* 2001).

The potential implications of road-related policies for elk management are diverse and complex. Benefits of road closures may include:

- Decreased energy expenditure by elk, a result of less frequent disturbance by motorized vehicles, with potential improvements in animal performance.
- Increases in total amount of effective

habitat for elk in the area affected by the closures.

- Increased hunting opportunities on public lands, when roads are closed on public lands adjacent to comparatively less-roaded private lands, thereby enticing elk to remain on public lands rather than moving to private lands where hunting may not be allowed or is prohibitively expensive (Wertz et al. 2004).
- Decreased damage to crops and haystacks from elk on private lands, due to decreased disturbance from traffic on public land, which in turn causes elk to remain on public land longer during the fall and winter seasons.
- Improvements in diet quality when elk are able to forage undisturbed in areas previously avoided due to excessive motorized traffic; these changes may translate into improvements in animal fitness and population performance.
- Increased hunter satisfaction from the opportunity to hunt in a roadless area or the use of all-terrain vehicles on closed roads or other "off-highway" sites (Gratson and Whitman 2000b).
- Decreased vulnerability of elk during hunting seasons, due to fewer hunters willing to hunt without a vehicle or able to access the area.

Road closures alone may not be effective in eliminating effects of roads and traffic on elk because of inadequate enforcement. For this reason, the Forest Service may promulgate road closures in addition to designating roads as closed, as in the Dark Meadow project discussed above. Careful assessment of how roads are being used, rather than their official status, is important to credibly evaluate effects of roads on elk and other wildlife. Likewise, judicious closing of certain road segments, particularly road spurs (Forman et al. 2003), may retain or create blocks of habitat that serve as security areas for elk while allowing sufficient road access for other management needs. Spatially explicit models and tools are currently available to aid in evaluating among road closure alternatives.

Elk continue to exert tremendous impact on local economies, through their

status as a premier game species, and on forested ecosystems, through their role as abundant, widespread, large herbivores. Given the indisputable effect of roads on distribution of elk, roads and their management will undoubtedly remain, as stated by Lyon and Christensen (2002:566), "central to elk management on public and private lands."

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Spatial Partitioning by Mule Deer and Elk in Relation to Traffic

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INTRODUCTION

Elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) have overlapping ranges on millions of acres of forests and rangelands in western North America. Accurate prediction of their spatial distributions within these ranges is essential to effective land use planning, stocking allocation, and population management (Wisdom and Thomas 1996). Many habitat variables influence the distributions of the two ungulates, making predictions a challenging and sometimes daunting task for resource managers (Johnson et al. 1996, Ager et al. 2004).

Distance to roads open to motorized vehicles has been identified as a significant predictor of deer and elk distributions (Thomas et al. 1979). Elk in particular have shown disproportionately less use of areas near roads open to motorized traffic (Lyon 1983; Rowland et al. 2000, 2004). As a result, extensive road closures have been implemented in the western United States in an attempt to mitigate the presumed reduction in elk use of habitat near open roads. Often, road closures are implemented under the presumption that any road open to traffic, regardless of its construction standard or traffic flow, will cause avoidance by elk, and that closing such roads will mitigate the avoidance (Wisdom et al. 1986, Thomas et al. 1988). Moreover, mule deer have been assumed to avoid roads in the same manner as elk (Thomas et al. 1979), although empirical support for this assumption is limited and imprecise (see Perry and Overly 1977 versus Rost and Bailey 1979).

Despite the assumption that any road open to traffic elicits avoidance, researchers have suspected that the rate of traffic influences the magnitude of potential

avoidance, especially by elk (Lyon and Christensen 2002). This was confirmed indirectly by Perry and Overly (1977), Rost and Bailey (1979), and Witmer and deCalesta (1985), among others, who found less elk use of areas near primary or main roads than use observed near secondary or primitive roads, presumably due to a higher rate of traffic on primary roads and a higher level of human activity associated with the traffic. In addition, Rowland et al. (2000, 2004) found that elk showed increasingly strong selection toward areas with increasing distance from roads open to motorized traffic at the Starkey Experimental Forest and Range (Starkey). This research was especially compelling, owing to the large number of radio-collared elk and telemetry locations on which results were based during three years of study.

Until recently, however, no research has examined the explicit relationship of mule deer and elk distributions with traffic rates on jointly occupied range. Johnson et al. (2000) included roads with varying traffic rates as part of their analysis of resource selection by mule deer and elk at Starkey during spring. Such data are needed by resource managers charged with answering a myriad of questions about population and road management for these ungulates. For example, what traffic rate, if any, elicits avoidance? Is the response the same for the two species, and the same during day versus night? Answers to these questions are needed to justify and guide efforts to mitigate any negative effects. Moreover, if traffic causes ungulate avoidance of areas near roads, the reduction in carrying capacity could be biologically significant (Johnson et al. 1996, Wisdom and Thomas 1996).

In this paper, we build on the earlier analyses by Johnson et al. (2000) at Starkey to further explore the spatial patterns of mule deer and elk in relation to roads of varying traffic rates and management. We specifically relate traffic rate with areas selected by mule deer and elk on spring and summer range. Our objectives were to (1) assess the degree to which mule deer and elk may avoid areas near roads based on variation in rates of motorized traffic; (2) examine differences in response of mule deer versus elk to traffic, as an explicit test of the assumption made by earlier investigators that mule deer avoidance of open roads is similar to that of elk; (3) describe the implications and potential uses of results for management.

STUDY AREA AND TECHNOLOGIES

Our study took place in the Main Study Area of Starkey in northeast Oregon (see Figure 1 in Wisdom et al. 2004). Starkey features an automated telemetry system (ATS) that has been used to monitor the movements of a large percentage of female deer and elk (12–25% of females/species) in the Main Study Area since 1991 (Findholt et al. 1996, Rowland et al. 1997). Monitoring with the ATS has occurred during April–late December each year.

Starkey's Main Area was designed to facilitate large-scale studies of resource selection by deer and elk under population, habitat, and human activity conditions that mimic conditions in National Forests on spring, summer, and fall ranges in the western United States. These design features are described in detail by Rowland et al. (1997) and Wisdom et al. (2004).

METHODS

Deriving Traffic and Road Variables

Over 50 traffic counters were placed throughout the Main Area along roads not physically blocked to vehicle traffic. Each counter was associated with a unique road

segment. Counters were located immediately beyond a segment's intersection with other roads, providing an explicit count of traffic for that segment. Each counter automatically tallied the number of vehicles passing over the associated road segment at 15-minute intervals, 24 hours a day, throughout the study. Rowland et al. (1997) described details about the counters and their use in collecting traffic data.

We used the counts of traffic to characterize the rate of traffic on each road segment for spring (mid-April to mid-June) and summer (mid-June to mid-August), 1993–1995, with the following steps. First, we summed the counts of traffic/counter for each hour of each day, and summed these counts across like hours for each counter/season/year. Second, we used the summed counts to identify the 12-hour period of highest traffic frequency versus the 12-hour period of lowest traffic frequency for a generalized 24-hour day for each counter/season/year; we did this by calculating the ratio of traffic counted for all possible pairs of 12-hr periods for each counter/season/year, using a 12-hour moving window analysis, with each 12-hour window advancing in 30-minute intervals. Third, for a given season and year (season-year period), we defined day as being the 12-hour portion of the generalized 24-hour day that had the highest 12-hour ratio of traffic counts for the majority of counters, and defined night as the opposite 12 hours. Starting times for the 12-hour portion defined as day ranged from 0530 to 0700, Pacific Standard Time, among season-year periods. And fourth, for each season-year period, we examined the frequency distributions of traffic counts for day and for night among counters, and identified distinctive breaks in the distributions that resulted in five categories of traffic rate during day and three categories during night (Table 1). Traffic rates were substantially higher during day versus night, thus accounting for the larger number of traffic categories for day versus night (Table 1).

Each segment of road was then assigned to one of the five categories of

TABLE 1. Definitions of 11 traffic and road variables and mean nearest distance of 86,000 pixels to each traffic and road variable, for each of six season-year periods encompassing spring (mid-April to mid-June) and summer (mid-June to mid-August), 1993–1995, Main Study Area, Starkey Experimental Forest and Range, northeast OR. Values of mean nearest distance were used as estimates of the area available to deer and elk (V_{AVAIL} , as defined in text) for MANOVA and ANOVA tests of selection in relation to traffic and road variables.

Traffic or road variable (no. vehicles/12 hours)	Nearest distance of pixels to traffic or road variable (m)					
	Spring 1993	Summer 1993	Spring 1994	Summer 1994	Spring 1995	Summer 1995
D5 (>10 day vehicles)	2005	1557	4310	1560	4310	4310
D4 (>4 day vehicles $\leq$ 10)	2114	1225	1665	1491	1658	1658
D3 (>1 day vehicles $\leq$ 4)	1033	1493	909	1136	928	944
D2 (>0 day vehicles $\leq$ 1)	870	883	872	946	901	820
D1 (0 day vehicles)	280	280	269	280	279	280
N3 (>1 night vehicles)	1785	761	4471	1388	4471	4470
N2 (>0 night vehicles $\leq$ 1)	701	713	585	531	597	591
N1 (0 night vehicles)	236	280	242	263	232	237
Open (All rates possible)	638	638	638	638	638	638
Restr. (All rates possible)	408	408	408	408	408	408
Closed (All rates possible)	398	398	398	398	398	398

traffic rate for day and one of the three categories for night, based on the category that was associated with that segment's traffic counter. The Main Area was then subdivided into 86,000 0.22-acre (30- by 30-meter) pixels, and spatial analysis software (Ager and McGaughey 1997) used to calculate the distance of each pixel to the nearest road of each of the categories of traffic. Because segments of road often changed categories across season-year periods, the mean distance of the 86,000 pixels to the nearest road of each category of traffic often was unique for each season-year period (Table 1). Rowland et al. (1997, 1998) described additional details about the spatial database and the methods used to derive distance estimates for the traffic variables.

In addition to the traffic variables, we calculated the distance of each pixel to the nearest road open to motorized vehicles; nearest road closed to motorized vehicles; and nearest road restricted to administrative traffic (Table 1, Rowland et al. 1997, 1998). Estimates of these road variables were an important complement to the traffic variables because such road variables are used as imprecise but presumably unbiased indices of traffic rate on National Forests in northeast Oregon, as well as in large areas of the western

United States, as part of road management for deer and elk. Thus, we wanted to determine how well the patterns of ungulate selection accounted for by the traffic variables might also be indexed by the road variables. Unlike the dynamic nature of the traffic variables, whose distance estimates changed across season-year periods with shifts in traffic rate across road segments, the mean distance of the 86,000 pixels to nearest road of each type remained static across all season-year periods (Table 1).

Monitoring Animal Movements

We used the ATS during spring and summer, 1993–1995, to collect more than 160,000 locations from 12–31 radio-collared females/species/season-year period. Animals were systematically located approximately once every 3–4 hours ($\bar{x}$ = 3.7 hours among season-year periods, SE = 0.6), which generated an average of 447 locations/female/season-year period (SE = 69).

The ATS computed each animal location in Universal Transverse Mercator (UTM) coordinates. Point estimates of these locations were placed within the center of the nearest 0.22 acre (30- by 30-meter) pixel. Location accuracy of the

ATS was ± 58 meters ($\bar{x} = 53$ meters, $SE = 5.9$) (Findholt et al. 1996). Findholt et al. (1996), Johnson et al. (1998), and Rowland et al. (1997, 1998) described additional details about use of the ATS to collect animal locations.

Assessing Deer and Elk Selection in Relation to Traffic and Road Variables

Calculating use and availability

For each season-year period, use for a given radio-collared animal for a given traffic or road variable was calculated as the mean of all distance values for the variable taken across all pixels in which the animal was located. Each location was weighted by a spatially-explicit algorithm that corrected for spatial differences in the rate at which telemetry locations were successfully obtained (Johnson et al. 1998). Estimates of use (i.e., mean distance values) for all traffic and road variables for each animal in each season-year period were then placed in a use vector, defined as V_{USE} .

Similarly, availability of each traffic and road variable for each season-year period was calculated as the mean of all distance values for the variable taken across all 86,000 pixels (Table 1). Estimates of availability for all traffic and road variables for each season-year period were then placed in an availability vector, defined as V_{AVAIL} . Each vector of availability was unique to each season-year period (Table 1) due to the dynamic nature of traffic rates across seasons and years.

Within-species selection

For each season-year period, we calculated a selection vector (V_{SELECT}) of use minus availability of all traffic and road variables for each radio-collared animal. Specifically, V_{SELECT} was calculated as a difference vector of selection values (use minus availability) of all traffic and road variables resulting from V_{USE} minus V_{AVAIL} for each animal and period. Each selection vector for a radio-collared animal

in a season-year period was used as the unit of observation, or statistical replicate, to evaluate patterns of within-species selection by the population of deer or elk in relation to the traffic and road variables.

We used a two-step process to evaluate within-species selection. First, we used a fixed-effects, factorial Multivariate Analysis of Variance (MANOVA) (Type III Sum of Squares (SS), Generalized Linear Procedure (PROC GLM), SAS Inst., Inc. 1990), with season and year as factors, to initially test whether within-species selection differed by season, year, or both. This MANOVA was described in detail by Wisdom (1998).

Second, with the finding of a significant factor effect ($P < 0.05$) of season, year, or their interaction, we examined each individual Analysis of Variance (ANOVA) to identify which traffic and road variables contributed to these effects in a biologically significant manner. We defined a biologically significant effect as any traffic or road variable that was statistically significant ($P < 0.05$) for a given factor, and whose mean value for that factor was inconsistent in sign. For example, if use minus availability by season for the open roads variable was statistically significant and had a positive sign for spring (suggesting selection of areas farther from open roads than available) but a negative sign for summer (suggesting selection of areas closer to open roads than available), results for the two seasons were presented separately. Simple main effects (individual season-year periods analyzed separately) and partial main effects (some season-year periods pooled) were reported for any variable having biologically significant effects due to season, year, or both.

All traffic and road variables deemed not to contribute to season, year, or interaction effects in a biologically significant manner were then brought forward to test the main effects of within-species selection, all seasons and years pooled. This test was conducted using a one-sample, fixed-effects, completely randomized MANOVA (Hotelling's T^2 , No Intercept

Option, Type III SS, PROC GLM, SAS Inst., Inc. 1990), as described by Wisdom (1998).

Because we had an unequal number of radio-collared replicates among seasons and years, we used the Least Square Means Option (Lsmeans, PROC GLM, or equivalent programming in PROC MEANS, SAS Inst., Inc. 1990) for all ANOVAs so that variation from radio-collared replicates for each season-year period contributed equally to univariate tests. We also weighted radio-collared replicates within each season-year period such that within-species variation by trap location (radio-collared animals trapped in Main Study Area versus winter feed ground) was represented equally. Because of large differences in categories of traffic by day versus night, we conducted separate MANOVAs for day and for night.

Between-species selection

We also evaluated patterns of between-species selection by deer versus elk in relation to traffic and road variables. We used a fixed-effects, factorial MANOVA (Type III SS, Proc GLM, SAS Inst., Inc. 1990), with season, year, between-species selection, and their interactions as factors, as outlined by Wisdom (1998).

With the finding of a significant interaction ($P < 0.05$) between any factors in the MANOVA, we examined the individual ANOVAs to identify which traffic and road variables contributed to the interaction in a biologically significant manner. Biologically significant interactions were defined as any statistically significant interaction that also contained "crossing" (Kirk 1982:356–359) of the treatment level means for between-species selection, and whose treatment level means for between-species selection were inconsistent in sign and direction. For example, if the interaction of between-species selection and season for the open roads variable was statistically significant and indicated that elk were closer than deer to open roads during spring but farther from open roads during summer, results for the two seasons were presented separately.

As done for tests of within-species se-

lection, we used the Least Square Means Procedure (Lsmeans, PROC GLM, SAS Inst., Inc. 1990) so that variation from radio-collared replicates from all season-year periods contributed equally to ANOVA tests of main effects and all interactions for between-species selection.

RESULTS

The vector of traffic and road variables selected (V_{SELECT}) by mule deer and by elk was significantly different ($P < 0.05$) from zero, both day and night, for the main effects of within-species selection (Wisdom 1998). Moreover, MANOVA tests of difference in selection between the two species also were significant ($P < 0.05$), as described in detail by Wisdom (1998). Univariate contributions of each traffic and road variable to the significant main effects and to the biologically significant interactions are described below for all within-species and between-species MANOVAs.

Within-Species Selection: Deer

Both day and night, mule deer selected areas closer to roads that had day rates of >4 vehicles/12 hours (D4 and D5, Figure 1a, b), closer to roads that had night rates of >1 vehicles/12 hours (N3, Figure 1c, d), and closer to roads open to motorized traffic (Open, Figure 1e, f). Mule deer also selected areas closer to roads that had day rates of >1 but ≤ 4 vehicles/12 hours except during summer, when selection was not significant (D3, Figure 1a, b).

The magnitude of selection toward D5, D4, N3, and D3 roads appeared to increase with increasing rate of traffic: roads with the highest rate—D5—had the greatest mean difference of use versus availability, followed by N3, D4, and D3. The consistency of selection toward these roads also appeared to increase with increasing rate of traffic: roads with the highest rates—D4 and D5—had no significant season or year interactions.

In contrast to selecting areas closer to open roads and to roads that had higher rates of traffic, mule deer selected areas

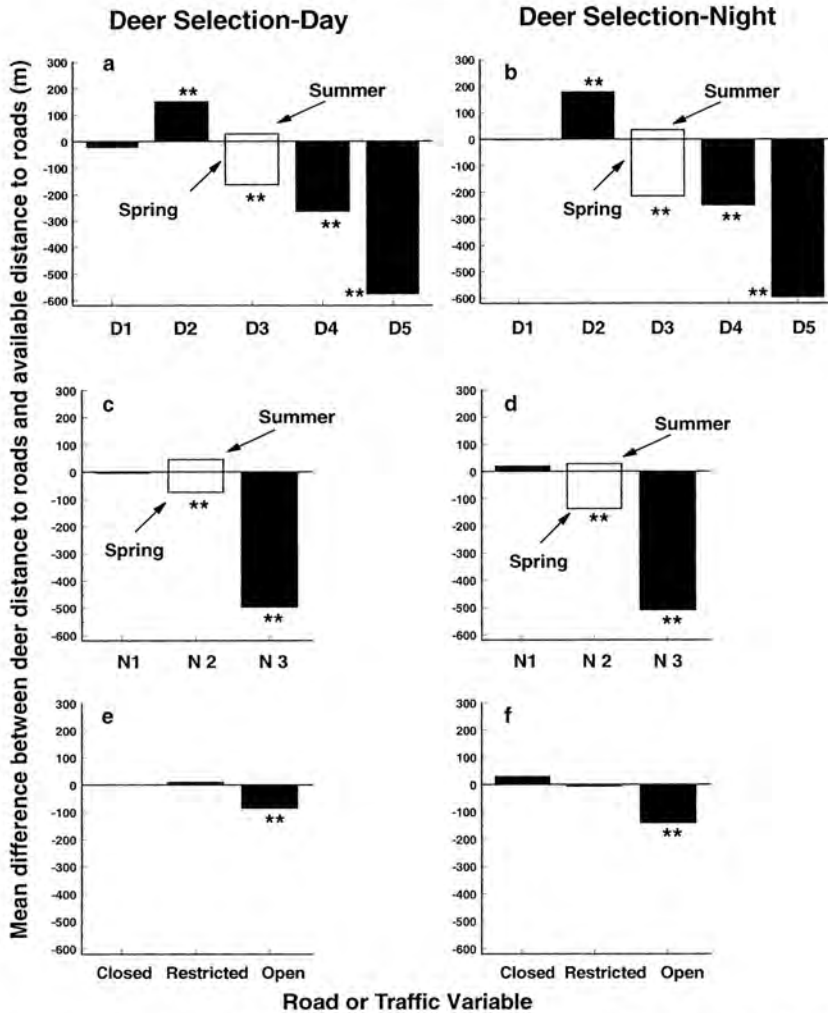


FIGURE 1. Areas selected by mule deer during day (a, c, e) and night (b, d, f) in relation to roads of different rate of traffic (D1 through D5, N1 through N3) and type (closed, restricted, or open to vehicles). D1, D2, D3, D4, and D5 were roads with 0, > 0 but ≤ 1, > 1 but ≤ 4, > 4 but ≤ 10, and > 10 vehicles/12 hours during day. N1, N2, and N3 were roads with 0, > 0 but ≤ 1, and > 1 vehicles/12 hours during night. Main effects (all seasons and years pooled) are shown in black and partial main effects (some seasons and years pooled) shown in white. Partial main effects are shown for variables whose parameter estimates could not be pooled across certain seasons or years due to interactions by season, year, or both. Significant differences in selection are shown with asterisks (* = $P < 0.05$, ** = $P < 0.01$). Positive differences indicate selection away from roads. Negative differences indicate selection toward roads. Descriptive and test statistics are provided by Wisdom (1998).

farther from roads that had day rates of >0 but ≤1 vehicles/12 hours (D2, Figure 1a, b) but selected areas closer to roads that had night rates of >0 but ≤1 vehicles/12 hours during spring (N2, Figure 1c, d). Finally, mule deer showed no se-

lection in relation to roads that received no traffic (D1, Figure 1a, b; and N1, Figure 1c, d) and no selection in relation to roads that were closed to vehicles or restricted to administrative traffic (Closed and Restricted, Figure 1e, f).

Within-Species Selection: Elk

Both day and night, elk selected areas farther from roads that had day rates of >1 vehicles/12 hours (D3, D4, and D5, Figure 2a, b). Elk also selected areas farther from roads that had night rates of >1 vehicles/12 hours (N3, Figure 2c, d) and farther from roads open to motorized traffic (Open, Figure 2e, f). During night, summer 1995, however, elk showed no selection in relation to roads having night rates of >1 vehicles/12 hours (N3, Figure 2d). Elk also showed no selection during night in relation to open roads for spring, all years (Figure 2f).

The consistency of elk selection away from roads appeared to increase with increasing rate of traffic: roads with the highest rates—D3, D4, and D5—had no significant season or year interactions. Roads with the highest rate of traffic—D5—also had greatest mean difference between use and availability.

In contrast to typically selecting areas farther from open roads and farther from roads that had higher rates of traffic, elk generally selected areas closer to roads that had little or no traffic. However, the pattern was not consistent among all season-year periods. Specifically, elk were closer to roads that had day rates of >0 but ≤ 1 vehicles/12 hours (D2, Figure 2a, c, except for spring 1994 during day), closer to roads with no traffic (D1, Figure 2a, b, except for spring 1993; and N1, Figure 2c, d, except for spring 1993) and closer to roads that were closed (Closed, Figure 2e, f). However, elk showed either an opposite or an inconsistent pattern of selection, day versus night, in relation to roads that had night rates of >0 but ≤ 1 vehicles/12 hours (N2, Figure 2c, d). During day, elk also selected areas farther from roads restricted to administrative traffic (Restricted, Figure 2e) but selected areas closer to these same roads during night (Restricted, Figure 2f).

Between-Species Selection: Deer Versus Elk

Both day and night, elk were farther than deer from roads that had traffic rates

of >1 vehicles/12 hours (D3, N3, D4, and D5, Figure 3a, b, c, d) and farther than deer from open roads (Open, Figure 3e, f). By contrast, deer generally were farther than elk from roads that had lower traffic rates or that were restricted or closed, especially during night. Specifically, deer were farther than elk from roads having day rates of >0 but ≤ 1 vehicles/12 hours (D2, Figure 3a, b), farther than elk during night from roads having night rates of >0 but ≤ 1 vehicles/12 hours (N2, Figure 3d, except for summer 1993), and farther than elk during night from roads that were restricted or closed (Restricted, Closed, Figure 3f). During day, however, deer were closer than elk to N2 roads (Figure 3c, except for summer 1993) and closer than elk to restricted roads during spring, all years (Restricted, Figure 3e). Finally, we found no difference in deer versus elk selection in relation to roads with zero traffic (D1, N1, Figure 3a–d), except during night, when deer were farther than elk (N1, Figure 3d). We also found no difference in deer versus elk selection during day in relation to closed roads (Closed, Figure 3e).

DISCUSSION

Selection Patterns

A number of strong and surprising patterns emerged from our results. First, deer and elk selected areas in opposite ways in relation to rate of traffic, with the magnitude of difference increasing with increasing rate of traffic. Second, thresholds existed for both species in terms of direction in selection: elk were generally farther from roads with traffic rates >1 vehicles/12 hours, both day and night, while deer were closer; by contrast, selection by both species was inconsistent in relation to roads with little or no traffic (≤ 1 vehicles/12 hours). Third, the type of road often correctly indexed the direction in selection shown by both species in relation to rates of traffic; that is, elk were farther from and deer were closer to roads that were open to all vehicular travel, which agreed with the overall direction in selection shown by both species in rela-

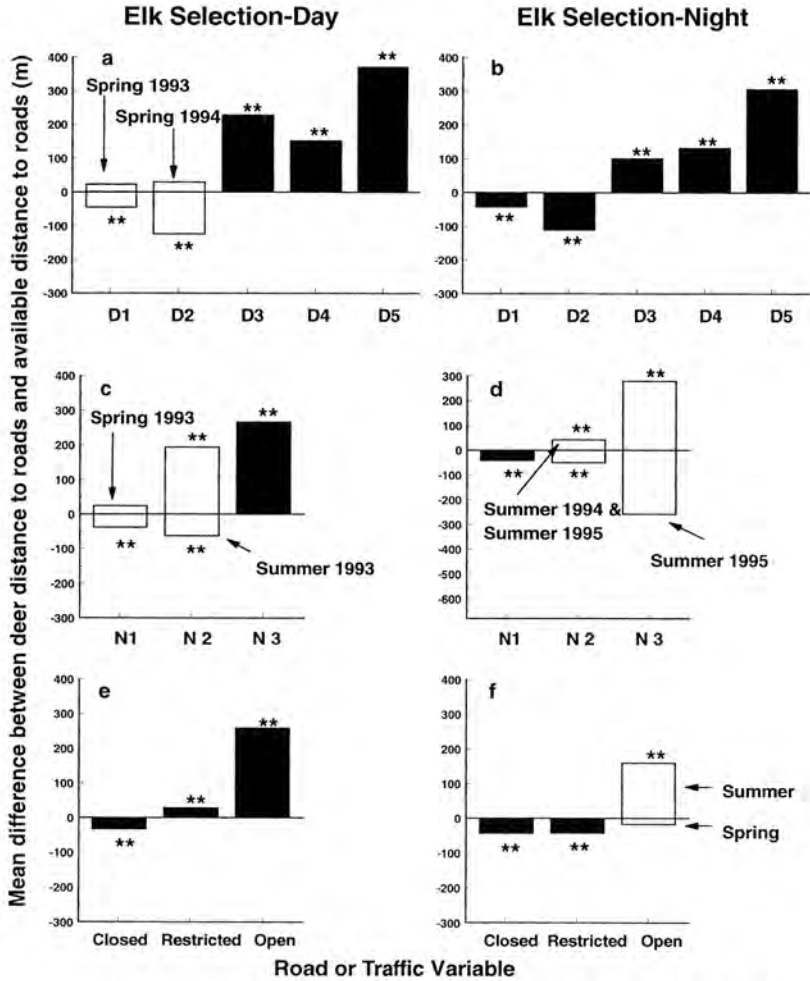


FIGURE 2. Areas selected by elk during day (a, c, e) and night (b, d, f) in relation to roads of different rate of traffic (D1 through D5, N1 through N3) and type (closed, restricted, or open to vehicles). D1, D2, D3, D4, and D5 were roads with 0, > 0 but ≤ 1, > 1 but ≤ 4, > 4 but ≤ 10, and > 10 vehicles/12 hours during day. N1, N2, and N3 were roads with 0, > 0 but ≤ 1, and > 1 vehicles/12 hours during night. Main effects (all seasons and years pooled) are shown in black, partial main effects (some seasons and years pooled) shown in white. Partial main effects are shown for variables whose parameter estimates could not be pooled across certain seasons or years due to interactions by season, year, or both. Significant differences in selection are shown with asterisks (* = $P < 0.05$, ** = $P < 0.01$). Positive differences indicate selection away from roads. Negative differences indicate selection toward roads. Descriptive and test statistics are provided by Wisdom (1998).

tion to most roads that had non-zero rates of traffic (i.e., all roads having >1 vehicles/12 hours). Moreover, both species showed a weak or inconsistent pattern of selection in relation to closed or restricted roads, which agreed with the inconsistent pattern of selection shown by both species in relation to roads with little or no

traffic (≤1 vehicles/12 hours). And fourth, the type of road sometimes failed to index the magnitude of selection in relation to the traffic variables. For example, mule deer were approximately 100–150 yards (91–137 m) closer to open roads than available, yet deer were more than 250 yards (229 m) farther from roads

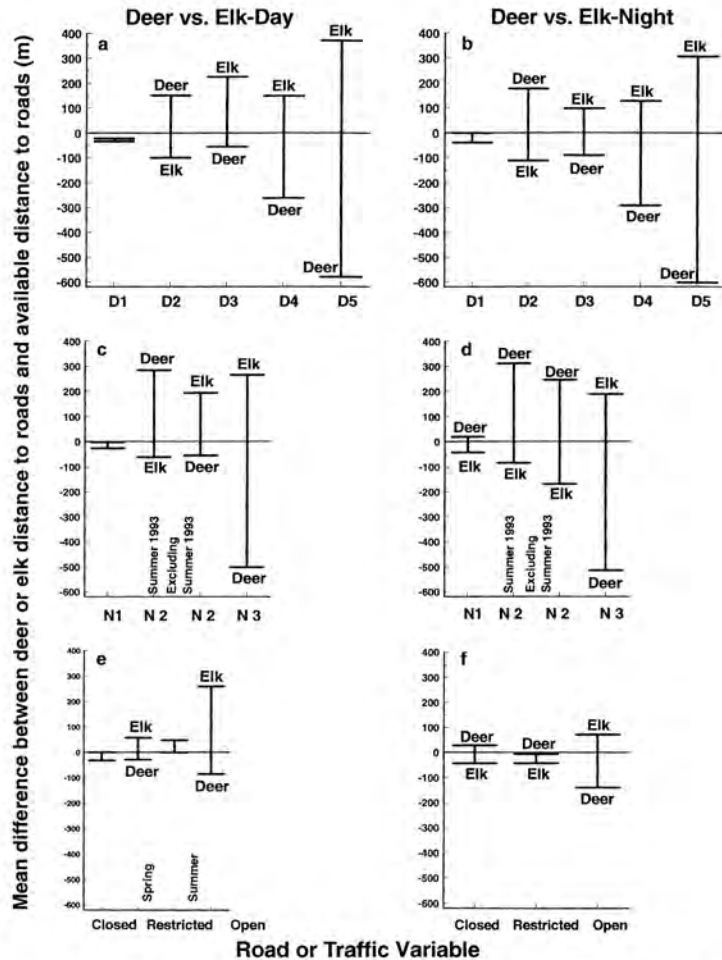


FIGURE 3. Differences in areas selected by mule deer versus elk during day (a, c, e) and night (b, d, f) in relation to roads of different type (closed, restricted, or open to vehicles) and rate of traffic (D1 through D5, N1 through N3). D1, D2, D3, D4, and D5 were roads with 0, > 0 but ≤ 1 , > 1 but ≤ 4 , > 4 but ≤ 10 , and > 10 vehicles/12 hours during day. N1, N2, and N3 were roads with 0, > 0 but ≤ 1 , and > 1 vehicles/12 hours during night. Main effects (all seasons and years pooled) are shown except when parameter estimates could not be pooled due to interactions by season, year, or both. In such cases, partial main effects (some seasons and years pooled) or simple main effects (specific season-year periods analyzed separately) are shown and explicitly identified. Significant differences ($P < 0.05$) in selection are denoted by the names of each species above and below the bar. The species whose name is above the bar indicates it was significantly farther from a road than the species named below the bar. Descriptive and test statistics are provided by Wisdom (1998).

of second-highest traffic rate (D4), and more than 550 yards (505 m) farther from roads of highest traffic rate (D5).

Implications for Roads and Habitat Models

Our results have direct bearing on a number of key assumptions and relation-

ships contained in habitat models for elk. First, our results support the inclusion of an open roads variable in spring-summer habitat models, such as done in models by Thomas et al. (1979), Leege (1984), Lyon et al. (1985), Wisdom et al. (1986), and Johnson et al. (1996). Second, our results corroborate the assumption by some

elk habitat modelers (e.g., Thomas et al. 1979, Wisdom et al. 1986) that increasing rate of traffic exerts an increasingly strong effect on elk selection; this implies that accuracy of elk habitat models could be improved by substituting a variable on traffic rate for the currently-used variable on open roads. Third, our findings do not support the assumption (Thomas et al. 1979) that selection by mule deer is similar to that by elk in relation to traffic and road variables; instead, our findings suggest that separate modeling terms are needed for each species. And fourth, our results call into question the use of carrying capacity models that are strictly nutrition- or forage-based, such as those by Nelson (1984), Cooperrider and Bailey (1984), Van Dyne et al. (1984), and Schwartz and Hobbs (1985), due to the strong effect that traffic and traffic-indexed human activities may have on modeling results. In contrast to these models, our findings provide compelling justification for the inclusion of traffic variables as a potential decrement to any projections of carrying capacity for both species.

Our results would be particularly useful when considered as part of "distance band" assessment of roads, as recently proposed by Rowland et al. (2004). Under such an assessment, all roads open to traffic are mapped, and the associated landscape is subdivided into distance intervals or bands, according to the distance of each band to the nearest open road. The probability that elk will use each distance band, based on prior research on elk distributions in relation to distance from open roads (Rowland et al. 2000), is then assigned to each band. These probabilities are then weighted by the area of each distance band occurring on the landscape being evaluated, and an overall probability calculated. If open roads could be further characterized by traffic rates, that probabilities of elk use by distance to nearest road of each rate could be considered. This refinement in the road-distance band assessment deserves further consideration in future modeling of elk habitat

use at landscape scales such as watersheds.

Are Elk Displacing Deer?

Perhaps our most intriguing finding relates to the hypothesis of interference or disturbance competition, where "the mere presence of an animal intimidates or annoys another animal into leaving the area" (Nelson 1982:416). In the past, this hypothesis has been tested in relation to potential displacement of wild ungulates by domestic livestock. For example, many studies have shown that elk avoid or decrease their use of areas with the onset of cattle grazing (Knowles and Campbell 1982, Lonner and Mackie 1983, Wallace and Krausman 1987, Frisina 1992, Yeo et al. 1993, Coe et al. 2001, 2004), suggesting that interference competition may be operating.

The interference competition hypothesis, however, has not been tested rigorously between sympatric species of wild ungulates in North America. In potential support of this hypothesis in relation to mule deer and elk, a number of researchers (Cliff 1939, Mackie 1981, Nelson 1982) inferred that elk may out-compete and potentially displace mule deer on winter ranges that are limited in size and available forage. Nelson (1982) also believed that mule deer may leave or avoid areas of heavy use by elk, even if forage is abundant and dietary overlap with elk is low. Wisdom and Thomas (1996) also suggested that elk may displace mule deer on jointly occupied ranges when elk exist at moderate to high densities, due to a number of behavioral and physiological advantages that elk presumably have over deer. Finally, Cowan (1950:582), working in western Canada, inferred that "mule deer and moose have decreased since elk became abundant, and the causal nature of the two events, though not established, seems probable."

Lack of direct, cause-effect evidence, however, limits firm conclusions. On the other hand, an additional analysis at Starkey (M. J. Wisdom, unpublished data) supports the assumption that mule deer change their distributions within our

study area in relation to opposite changes in distribution by elk. In this additional analysis, elk were significantly farther ($P < 0.05$) from roads that had highest rate of traffic (D5) during summer 1994 (use minus availability = 338 yards), while mule deer were closer (use minus availability = -412 yards). During a one-month, either-sex bow season on elk that immediately followed summer 1994, however, elk shifted their distributions significantly closer to these same roads (use minus availability = -227 yards) while deer moved significantly farther away (use minus availability = 388 yards). Simultaneous with the shift by elk toward the D5 roads during the bow-hunt was the inclusion of the D5 roads within a no-hunting area that extended 400 yards outward from these roads. Thus, the most plausible, logical explanation for these distributional shifts is that elk are sensitive to traffic but more sensitive to hunting pressure, and that mule deer are sensitive to the presence of elk. The results, we believe, are distributions of mule deer and elk that exist and shift in dynamic, opposite ways, both in direction and magnitude, in agreement with the interference competition hypothesis.

Similar findings and inferences were made from earlier analyses of mule deer and elk interactions at Starkey by Johnson et al. (2000), Coe et al. (2001, 2004), and Stewart et al. (2002). In each of these analyses, investigators found strong evidence, although observational, that mule deer were avoiding elk. For example, Johnson et al. (2000) found that the strongest coefficient in explaining resource selection by mule deer was resource selection by elk. While mule deer occupied areas largely avoided by elk, the opposite was not true. That is, resource selection by elk could not be explained by selection patterns of mule deer.

Although such discussion is compelling, manipulative experiments are needed to formally test and validate the interference competition hypothesis under varying levels of deer and elk densities and rates of traffic, under the presumption that certain ungulate densities and certain

traffic rates work together to cause elk to avoid areas near roads, and to cause mule deer to select areas near roads as a means of avoiding elk. Ideally, such manipulative experiments should be designed to measure effects on population performance of both species. To date, analyses of the effect of vehicle access on survival (such as Unsworth et al. 1993 and Cole et al. 1998 for elk) and reproduction of both species on jointly occupied range has not been conducted.

It also is important to note that some researchers have speculated that mule deer are attracted to areas near roads when roadsides have been seeded with nutritious grasses and forbs (Wallmo et al. 1976). However, attraction to forage along roadsides would not plausibly account for the large differences in mule deer selection that we observed in relation to varying rates of traffic. Moreover, the distributional shifts described above for mule deer versus elk before versus during the 1994 bow-hunt provide compelling support for the interference competition hypothesis, which does not accommodate the notion that mule deer selected areas near roads due to superior roadside forage.

LIMITS OF INFERENCE

Our findings particularly are relevant to spring and summer ranges that are jointly occupied by deer and elk under conditions of moderate to high densities of elk. These are the conditions under which our study was conducted. However, these conditions are common across large areas of western North America. By contrast, inferring results from our study to other areas where mule deer are common and elk are absent or sparse, would be inappropriate and likely unreliable. Inferring results of our study to spring and summer ranges occupied solely by mule deer, in particular, could be especially unreliable, given the high potential for mule deer distributions in our study area to be affected strongly by selection patterns of elk. In the absence of moderate or high densities of elk, mule deer may exhibit different distribution and selection patterns in re-

lation to roads and traffic than we observed at Starkey.

MANAGEMENT IMPLICATIONS

Differences in selection by mule deer and elk in relation to traffic could be considered in the management of motorized vehicles and traffic-related human activities on spring-summer ranges where both species occur, and where elk exist at moderate to high densities. Our results suggest that spring-summer habitat models for elk may not account for patterns of resource selection by mule deer on jointly occupied range, and that resource needs of each species must be addressed separately.

Our results also suggest that inclusion of road or traffic variables in habitat models is essential to accurate portrayal of selection patterns for both species. Forage- or nutrition-based habitat models that exclude road or traffic variables have the potential to be highly inaccurate, given the large magnitude of difference in selection shown by sympatric populations of deer and elk in relation to rates of traffic and types of roads. Manipulative experiments are needed to validate the presumption that rate of traffic acts as a mechanistic cause for differences in selection patterns between mule deer and elk, and to validate these selection patterns across a diversity of environments in which both species occur.

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Effects of Off-Road Recreation on Mule Deer and Elk

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Norman J. Cimon, and Bruce K. Johnson

INTRODUCTION

Off-road recreation is increasing rapidly in the United States, especially on public lands (Havlick 2002, U.S. Department of Agriculture Forest Service 2004). An expansive network of roads provides easy access to many public lands, which facilitates off-road uses in the form of all-terrain vehicles (ATVs), horses, mountain bikes, and foot traffic. No research, however, has evaluated effects of these off-road activities on vertebrate species in a comparative and experimental manner (see review by Gaines et al. 2003). One recent study (Taylor and Knight 2003a) evaluated bison (*Bison bison*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*) responses to mountain biking and hiking. This study, however, did not include ATV or horseback riding, nor did it include experimental controls needed to assess cause-effect relations.

To address these knowledge gaps, we initiated a manipulative, landscape experiment in 2002 to measure effects of off-road recreation on mule deer and elk (*Cervus elaphus*), two charismatic species of keen recreational, social, and economic interest across western North America. Our objectives were to (1) document cause-effect relations of ATV, horseback, mountain bike, and hiking activities on deer and elk, using these off-road activities as experimental treatments and periods of no human activity as experimental controls; (2) measure effects with response variables that index changes in animal or population performance, such as movement rates, flight responses, resource selection, spatial distributions, and use of foraging versus security areas; (3) use these response variables to estimate the energetic and nutritional costs asso-

ciated with each activity and the resultant effects on deer and elk survival; and (4) interpret results for recreation management.

Our research began in 2002 and ended in 2004. In this paper, we present findings from 2002 to address parts of objectives 1, 2, and 4. We specifically focus on changes in movement rates and flight responses of mule deer and elk in relation to the off-road activities, as compared to periods of no human activity. We then describe potential uses of the results for recreation management.

We present findings from our first year of study because of the urgent need for timely management information to address the rapid growth in off-road recreation (U.S. Department of Agriculture Forest Service 2004). For example, ATV use on public lands has increased sevenfold during the past 20 years, and many conservation groups are calling for widespread restrictions on ATV travel (U.S. Department of Agriculture Forest Service 2004). Yet no studies have evaluated the role of ATVs compared to other off-road activities, such as mountain biking and horseback riding, which also are increasing rapidly. Without comprehensive studies of ATV effects in relation to other recreation, the debate over ATV is likely to intensify. Our study was designed to measure a variety of ungulate responses to address this debate, such that results can be used to identify compatible mixes of different off-road recreational opportunities in relation to deer and elk management.

Throughout our paper, we refer to off-road recreation, both motorized and non-motorized, as that occurring on trails, primitive (unpaved) roads, or areas without trails or roads. This definition complements the term "off-highway vehicle

(OHV) use," which refers to motorized vehicle use on any surface beyond highways (U.S. Department of Agriculture Forest Service 2004), but which does not include other forms of non-winter recreation that typically occur on primitive roads and trails, such as hiking, horseback riding, and mountain biking.

STUDY AREA AND TECHNOLOGIES

We conducted our research at the Starkey Experimental Forest and Range (Starkey, Figure 1) in northeast Oregon, a facility equipped to evaluate real-time and landscape-level responses of deer and elk to human activities under controlled experimentation (Rowland et al. 1997, Wisdom et al. 2004a). The facility encompasses spring, summer, and fall ranges typical of those used by mule deer and elk in the western United States. Timber harvest, livestock grazing, motorized traffic, hunting, camping and other public uses of Starkey also are managed like those on National Forests in the western United States, thus providing a large inference space for research findings (Rowland et al. 1997, Wisdom et al. 2004a).

An essential research component at Starkey is the ungulate-proof enclosure, one of the largest in the world, which allows scientists to evaluate ungulate responses to human activities over large areas and under controlled conditions (Bryant et al. 1993, Rowland et al. 1997). Another key technology is the automated tracking system (ATS), which can generate up to one animal location every 20 seconds, 24 hours a day, from April through December each year (Rowland et al. 1997, Kie et al. 2004). Additional technologies include maps and databases of more than 100 environmental variables to relate animal movements to the landscape experiments, as well as supporting methods and software to analyze these data (Rowland et al. 1997, 1998).

IMPLEMENTING THE RECREATION TREATMENTS

To meet our objectives, a network of off-road transects was established and run

in 2002, using ATV, horseback, mountain bike, and hiking activities as experimental treatments in the 3,590-acre (1,453-ha) Northeast Study Area (Figure 1). Approximately 20 miles (32 km) of transects were established (Figure 1), over which ATV, horseback, mountain bike, and foot traffic was experimentally applied from mid-April through October. Locations of each transect were established with Global Positioning System (GPS) units (Figure 1). Transects were located on flat or moderate terrain typically used by off-road activities. Primitive roadbeds, like those often established by off-road vehicles (U.S. Department of Agriculture Forest Service 2004), were included in the transects. Use of roadbeds and trails to implement human activities is referred to as a "tangential" experimental approach because animals are not targeted directly by the activities (Taylor and Knight 2003b). This is in contrast to a direct experimental approach, such as testing the reaction of nesting birds to designed encounters with humans at nest sites.

A sufficient number and length of transects were established to encompass all portions of the Northeast Study Area (Figure 1). Each off-road activity was run on a given transect twice daily, once in the morning and once in the afternoon, during a 5-day period; this daily frequency of activity corresponds to traffic frequency on Starkey roads that produced an avoidance response by elk in earlier research (Wisdom 1998, Wisdom et al. 2004b).

A particular activity for a given morning or afternoon was completed by one to three people who rode ATVs ("four-wheelers" or "quads"), mountain bikes, or horses, or hiked as a group. On most days, group size consisted of two people moving as a pair; that is, by two people hiking or each riding ATVs, mountain bikes, or horses. A group size of two, with a range of one to three people, often is typical for these recreation activities in non-wilderness portions of National Forests (D. Barrett, personal communication 2002). Group size can vary substantially, however, with larger groups of 5–10 ATV

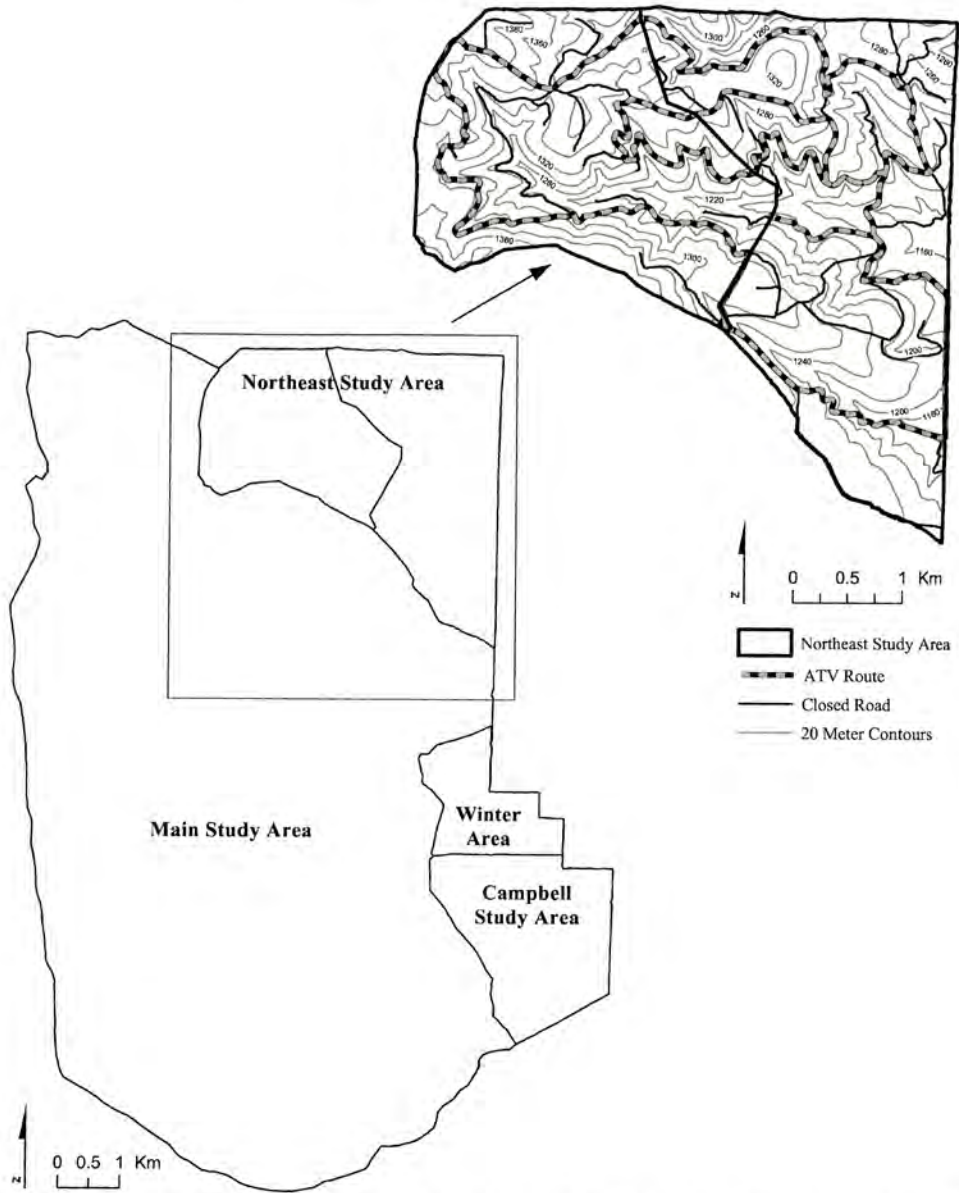


FIGURE 1. Boundaries of ungulate-proof enclosures at the Starkey Experimental Forest and Range in northeast Oregon (bottom left), and location of transects used for ATV activities in the 3,590-acre (1,453-ha) Northeast Study Area (upper right), site of the off-road recreation study. Transects were similar in length and location for mountain biking, hiking, and horseback riding as that shown here for ATV activities.

riders or horseback riders, for instance. We had neither the resources nor the experimental options to include these larger groups as treatments in our study. Moreover, group size of mountain bikers and hikers often does not approach 5–10 peo-

ple, and we wanted to maintain approximately the same group size across all four activities. A group size of two people, with a range of one to three people, provided this consistency.

For ATV travel, a pair of riders could

easily cover the 20 miles (32 km) of transects during a given morning or afternoon. A pair of mountain bike riders, however, could cover about 50 percent of the 20 miles (32 km) in a morning or afternoon. Horseback riders and hikers could cover about 30 percent. Because we wanted to standardize the experiment by the same number of transect runs or "passes" (twice daily) among all four off-road activities, two different groups of mountain bikers, and three groups of horseback riders or hikers, were used to obtain complete coverage of transects for a given morning or afternoon. For mountain biking, the transects were divided in half, with each of the two groups assigned to ride a different half of the 20 miles (32 km) in a morning or afternoon. Similarly, three groups of horseback riders or hikers, each assigned to travel a different third of the transect length, were used for each morning and afternoon to obtain complete coverage of transects.

Each of the four off-road activities was implemented under an "interrupted" movement design, where humans were allowed to momentarily stop to view animals for less than 1 minute when animals were observed. This is in contrast to a "continuous" movement design, where human activities are not delayed or stopped when animals are observed (Taylor and Knight 2003b).

Each 5-day period of off-road activity was followed by a 9-day control period, during which no human activities occurred in the study area. This pattern was followed from mid-April through October, resulting in three replicates of each of the four off-road activities. Each 5-day replicate of an off-road activity thus was paired with a 9-day control period that immediately followed the replicate. Only one type of off-road activity (ATV, horseback, mountain bike, or hiking) occurred on transects during a given 5-day replicate. The chronological order of each off-road activity, in terms of which activity occurred during the first 5-day replicate in late April, versus the next 5-day replicate in early May, and so on, was randomly chosen.

Throughout the experiment, all human entry beyond the four off-road activities, including administrative use of roads, was prohibited to eliminate the confounding effects of other human activities with animal response to the off-road activities. Consequently, human activities such as timber harvest, road traffic, camping, and hunting did not occur during the study because of their confounding effects.

MEASURING ANIMAL RESPONSES

To monitor animal responses, 12 female mule deer and 12 female elk were radio-collared among a larger population of approximately 25 female deer and 100 female elk present in the Northeast Study Area in early April. Movements of these radio-collared animals were monitored with the ATS (Rowland et al. 1997). During periods of off-road activity, locations of each radio-collared deer or elk were generated at approximately 10-minute intervals. Locations of humans engaged in each off-road activity were generated at approximately 1-minute intervals, using GPS units carried by one of the persons in each group of hikers or riders of ATVs, horses, or mountain bikes. Use of the automated telemetry system to track animal movements, combined with the use of GPS units to track human movements, provided real-time, unbiased estimates of the distances between each ungulate and group of humans.

Our method of estimating distances between ungulates and humans contrasts strongly with the use of direct observation, using rangefinders or other devices, to measure distances. Direct observation as a means of estimating distances between ungulates and humans is likely to be biased by the proportion of deer or elk whose reactions to human activities cannot be observed because such reactions are different than those of animals that can be observed. For example, some animals may run from human activity at distances beyond the view of observers, while other animals may react at close distances to, and in view of, observers. This bias in observed distances would re-

sult in underestimation of the true distance at which animals react to the human activity. In other cases, animals may flee from humans at close distances, but not be viewed because such animals seek dense cover during flight; this bias would result in overestimation of distances. We avoided such biases with the use of our automated telemetry system and GPS units to continuously monitor the movements of ungulates and humans throughout our study.

We also located radio-collared animals during the 9-day periods of no human activity, or control period. Approximately two locations of each radio-collared animal were obtained every hour during control periods, to establish baseline information about areas of deer and elk use, habitat selection, movement rates, and flight responses in the absence of human activities. For this paper, we analyzed two types of animal reactions: (1) movement rate and (2) probability of flight response. We evaluated movement rate and probability of flight response because both can ultimately be used to estimate the energetic costs of animal reactions to off-road activities (see Conclusions and Interpretations).

Estimating Movement Rates

We defined movement rate as the speed of animal movement (yards moved/minute), as estimated hourly, 24 hours per day, for a given species, treatment, and control period. We calculated the speed of animal movement for each radio-collared deer or elk for each pair of successive locations; that is, the horizontal distance between two successive locations divided by the elapsed time between locations (Ager et al. 2003). Each measurement of animal speed for a given radio-collared animal was assigned to the time recorded for the first location of each pair of animal locations used in the calculation.

Only successive locations with consistent elapsed times were included in the calculation of movement rates to eliminate the bias of excessively short and long elapsed times. Short elapsed times (less than 5 minutes) between locations

falsely inflate the movement rate because of random location errors in the ATS over such short time periods (Findholt et al. 1996, 2002). Long elapsed times (e.g., greater than 35 minutes) between locations allow animals to move back and forth between the documented locations, thus biasing the estimate of movement rate downward (Ager et al. 2003).

To estimate overall patterns of movement rates for each species, rates calculated for each individual radio-collared animal were averaged among all animals, for mule deer and for elk, by hourly interval, for each off-road treatment and the paired control period that immediately followed that treatment. For this analysis, we minimized random variation by summarizing results across each 5-day treatment and across each subsequent 9-day control. We did this after exploratory plots of data provided no evidence of change in movement rates of animals from day 1 through day 5 of each treatment period, or for day 1 through 9 of each control period, as examined on an hourly basis. We then pooled hourly results for each species across the three replicates of each off-road activity, and across control periods, after finding no evidence of differences in like replicates across time, or in control periods across time.

Estimating Probabilities of a Flight Response

We used a stimulus response model to estimate the probability of a flight response by a deer or elk with changing distance between each animal and off-road activity. We defined a flight response as the speed of animal movement, or movement rate, that exceeded the 95th percentile of all deer or elk speeds calculated for each hour from data collected during the control periods. Specifically, a flight response was any animal movement for a given hour of day that exceeded the 95th percentile of all deer or elk speeds calculated for that same hour of day during the paired 9-day control period that immediately followed a given 5-day period of off-road activity. Thus by defini-

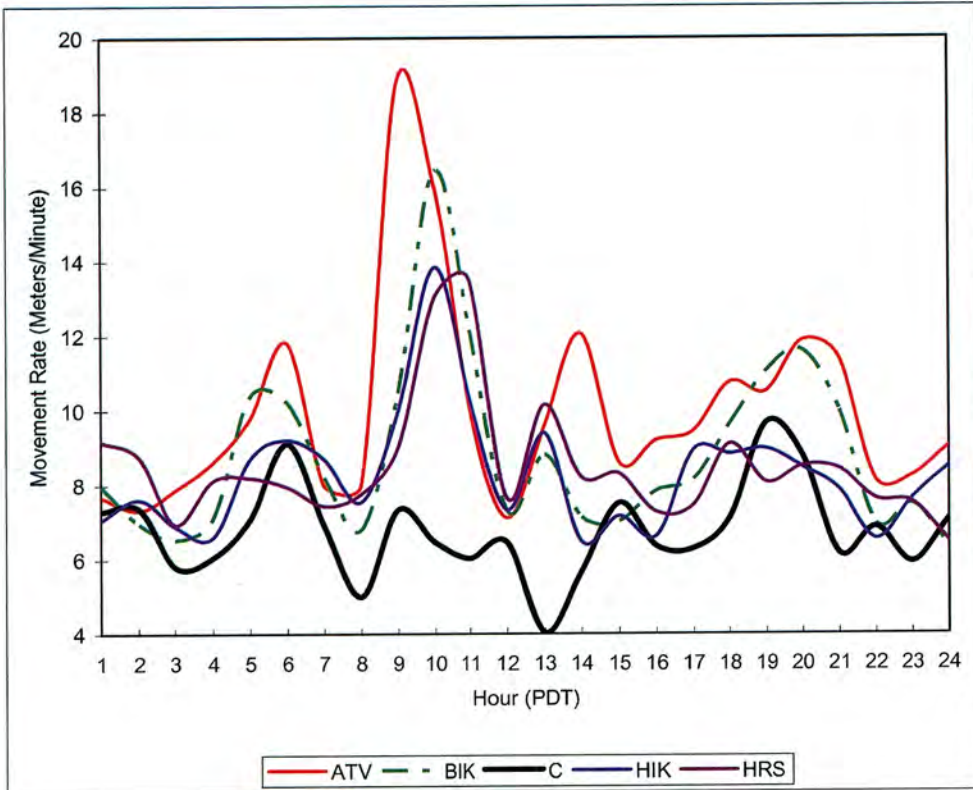


FIGURE 2. Mean movement rate (speed, meters/minute) of elk, estimated hourly on a 24-hour basis, Pacific Daylight Time (PDT), during periods of no human activity (C) versus periods of ATV activity (ATV), hiking (HIK), mountain bike riding (BIK), and horseback riding (HRS), from April through October, 2002, in Northeast Study Area of Starkey.

tion, when no stimulus was present (no human activity), a deer or elk would register a response (i.e., travel at speeds greater than the 95th percentile of all deer or elk speeds for that hour during the control period) 5 percent of the time. Probabilities of response were estimated using logistic regression within the generalized additive model framework (Hastie and Tibshirani 1990).

Each estimated probability of a flight response for a given radio-collared animal was linked to the estimated distance between that animal and each group of humans conducting an off-road activity, thus allowing an examination of how probabilities changed with distance between animals and humans. As with our analyses of movement rates, we pooled the probability data for each species across the three replicates of each off-

road activity, and across control periods. We pooled data after initial analyses showed that results for deer and elk were similar across the three replicates of each off-road activity, and across all control periods.

MOVEMENT RATES OF ELK

Movement rates of elk were substantially higher during periods of all four off-road activities as compared to periods of no human activity (Figure 2). Responses of elk to the morning and afternoon runs were clearly evident, with the most pronounced increase in movement rates observed during the hours when each off-road activity occurred (Figure 2). For example, our morning pass on transects began between 0830 and 0930 Pacific Daylight Time (PDT), and highest movement

rates for elk occurred in the hours immediately after, from 0900–1100, during all four activities (Figure 2). Moreover, lunch break for participants in the experiment occurred at or near noon, and movement rates for elk dipped to their lowest level at noon during all activities. Finally, we resumed each activity at 1230–1300 PDT, and movement rates for elk substantially increased immediately after (Figure 2).

Movement rates were substantially higher for elk during the morning pass compared to the afternoon pass for all four activities (Figure 2). Movement rates of elk during the afternoon pass, however, stayed well above the rates observed during the periods of no human activity (control period, Figure 2). Movement rates during the afternoon pass declined after 1500 PDT, when afternoon activities ended.

For the morning pass, movement rates of elk were highest during ATV riding, second-highest during mountain bike riding, and lowest during hiking and horseback riding (Figure 2). Movement rates of elk also stayed higher, over a longer period, during the afternoon ATV run, compared to lower rates during afternoon horseback riding, mountain bike riding, and hiking. Peak movement rates of elk during the morning pass were highest for ATV riding (21 yards/minute [19 m/min]), followed by mountain bike riding (17 yards/minute [16 m/min]) and horseback riding and hiking (both about 15 yards/minute [14 m/min]). For the afternoon run, movement rates of elk again were highest during ATV riding (13 yards/minute [12 m/min]), followed by horseback riding (about 11 yards/minute [10 m/min]) and hiking and mountain bike riding (about 10 yards/minute [9 m/min]).

By contrast, peak movement rates of elk during the control periods did not exceed 9 yards/minute (8 m/min). Moreover, peak movement rates during the control periods stayed below 8 yards/minute (7 m/min) during daylight hours of 0800–1500, the comparable period of

each day when off-road treatments were implemented.

Interestingly, movement rates of elk also were higher than control periods at times encompassing sunrise and sunset for the days in which an off-road activity occurred, even though humans were not present at these times of day (Figure 2). These higher movement rates near sunrise and sunset suggest that elk were displaced from preferred security and foraging areas as a result of flight behavior during the daytime off-road activities. In particular, movement rates of elk at or near sunrise and sunset were higher during the 5-day treatments of mountain bike and ATV activity (Figure 2). This finding will be studied in detail in future analyses.

FLIGHT RESPONSES OF ELK

The estimated probability of elk flight from a human disturbance was highly dependent on distance. When elk and humans were close to one another, the maximum probability of a flight response was approximately 0.65 during ATV, mountain bike, and hiking activity, and 0.55 during horseback riding (Figure 3). Higher probabilities of flight response occurred during ATV and mountain bike activity, in contrast to lower probabilities observed during hiking and horseback riding (Table 1). Probability of a flight response declined most rapidly during hiking, with little effect when hikers were beyond 550 yards (500 m) from an elk. By contrast, higher probabilities of elk flight continued beyond 820 yards (750 m) from horseback riders, and 1,640 yards (1,500 m) from mountain bike and ATV riders (Figure 3).

MOVEMENT RATES OF DEER

In contrast to elk, mule deer showed less change in movement rates during the four off-road activities compared to the control periods (Figure 4). During the period of day from 0800 to 1500 when off-road activities occurred, movement rates of deer during ATV riding were similar to rates during control periods. By contrast, daytime movement rates of deer were

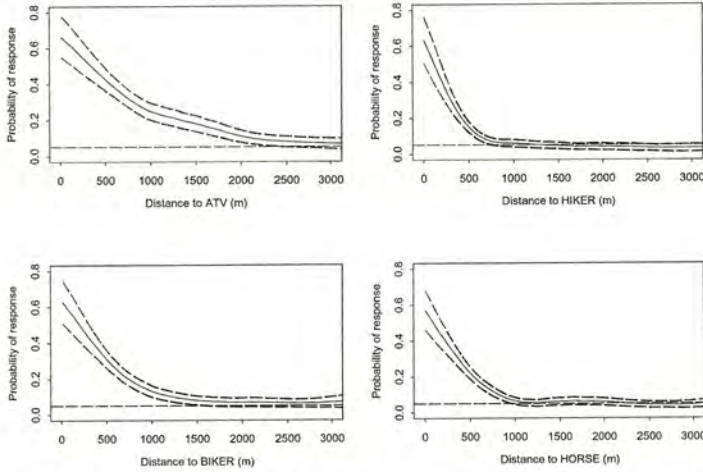


FIGURE 3. Estimated probability (solid line encompassed by dashed lines of the approximate 95 percent pointwise confidence interval) of a flight response by elk during 2002 in relation to distance (meters) from humans riding ATVs, mountain bikes, horses, or hiking. A flight response is defined as an animal movement with a speed exceeding the 95th percentile of speeds observed during periods of no human activity (control period). The horizontal dashed line at the bottom of each graph is the probability of a flight response by elk during periods of no human activity, and this line represents the background or “null” condition, above which significant elk response to the off-road activities exists.

higher, as compared to control periods, during mountain bike riding, horseback riding, and hiking, especially in the morning (Figure 4).

Interestingly, the increased movement rates observed for elk near sunrise and sunset also were evident for mule deer. Movement rates at these times were particularly high during all four activities as well as during the control periods, suggesting that these times were peak foraging periods (Ager et al. 2003).

FLIGHT RESPONSES OF DEER

Estimated probabilities of flight response for mule deer were similar among all four activities versus control periods (Table 1, Figure 5). These probabilities were nearly identical among all four activities and not significantly different than the null probability of 0.05 set for control periods, suggesting that deer were not exhibiting the same tendency for flight as shown by elk in relation to off-road activities (Table 1).

CONCLUSIONS AND INTERPRETATIONS

Elk

Movement rates and probabilities of flight response for elk were substantially higher during all four off-road activities compared to control periods of no human activity. Consequently, off-road recreational activities like those evaluated in our study appear to have a substantial effect on elk behavior. The energetic costs associated with these treatments deserve further analysis to assess potential effects on elk survival. For example, if the additional energy required to flee from an off-road activity reduces the percent body fat of elk below 9 percent as animals enter the winter period, the probability of surviving the winter is reduced (Cook et al. 2004). Animal energy budgets also may be adversely affected by the loss of foraging opportunities during periods when animals are responding to off-road activities, both from increased movements, and from displacement from for-

TABLE 1. Estimated probabilities (and approximate 95 percent Confidence Limits) of a flight response by elk and mule deer as a function of distance between animals and humans riding all-terrain vehicles (ATV), mountain bikes (BIKE), horses (HORSE), or hiking (HIKE). On average there were 128 deer or elk locations obtained during a given day of each off-road activity (treatment periods). During periods of no human activity (control periods), the null probability of a flight response is 0.05 (see text). Thus, any values >0.05 reflect an increased probability of a flight response in relation to an off-road activity

Distance ¹	ATV	BIKE	HORSE	HIKE
100 meters (109 yards) from elk	0.62 (0.52–0.73)	0.58 (0.46–0.68)	0.50 (0.40–0.59)	0.52 (0.42–0.64)
500 meters (545 yards) from elk	0.43 (0.36–0.49)	0.31 (0.26–0.35)	0.22 (0.19–0.26)	0.15 (0.12–0.18)
1000 meters (1090 yards) from elk	0.25 (0.20–0.30)	0.13 (0.10–0.16)	0.07 (0.05–0.08)	0.06 (0.04–0.08)
All distance from elk	0.19 (0.17–0.21)	0.14 (0.12–0.16)	0.11 (0.09–0.12)	0.08 (0.07–0.10)
100 meters (109 yards) from deer	0.06 (0.01–0.11)	0.08 (0.02–0.14)	0.11 (0.03–0.19)	0.10 (0.04–0.17)
500 meters (545 yards) from deer	0.05 (0.02–0.07)	0.07 (0.04–0.10)	0.05 (0.03–0.07)	0.04 (0.02–0.05)
1000 meters (1090 yards) from deer	0.03 (0.01–0.06)	0.06 (0.03–0.08)	0.04 (0.02–0.06)	0.04 (0.02–0.06)
All distance from deer	0.03 (0.02–0.05)	0.05 (0.04–0.07)	0.04 (0.03–0.05)	0.04 (0.03–0.06)

¹ Distance between an animal and human during each off-road activity.

aging habitat. These potential effects will be evaluated as part of future analyses.

Our results from 2002 also show clear differences in elk responses to the four off-road activities. Elk reactions were more pronounced during ATV and mountain bike riding, and less so during horseback riding and hiking. Both movement rates and probabilities of flight responses were higher for ATV and mountain bike riding than for horseback riding and hiking.

Interestingly, the maximum probability of flight was approximately 0.65 for the treatments, meaning that about 35 percent of the time elk did not exhibit a flight response when close to an off-road activity. Most likely the response depends on local topography, cover, and other factors that we have not yet analyzed as part of our flight response model. Future work will include terrain and vegetation measures as covariates in the probability models to examine whether these effects can be detected and quantified (per recommendations and discussion by Taylor and Knight 2003b).

It is important to note that designing our study to maintain the same number of daily passes on transects among all four activities required most effort for hiking and horseback riding, and least effort for ATV riding. Specifically, to accomplish two runs per day required three groups of hikers or horseback riders (with each group hiking approximately 33 percent of transect length), but only one group of ATV riders. By contrast, accomplishing two runs per day required two groups of mountain bikers (with each group covering approximately 50 percent of transect length).

Our results for elk might be different had we designed the study to test animal response to an equal number of groups, or equal density, of people engaged in the four off-road activities (i.e., the same number of groups of people engaged in each activity, regardless of the number of passes that could be accomplished), rather than testing for effects of equal saturation of the study area (i.e., two daily passes

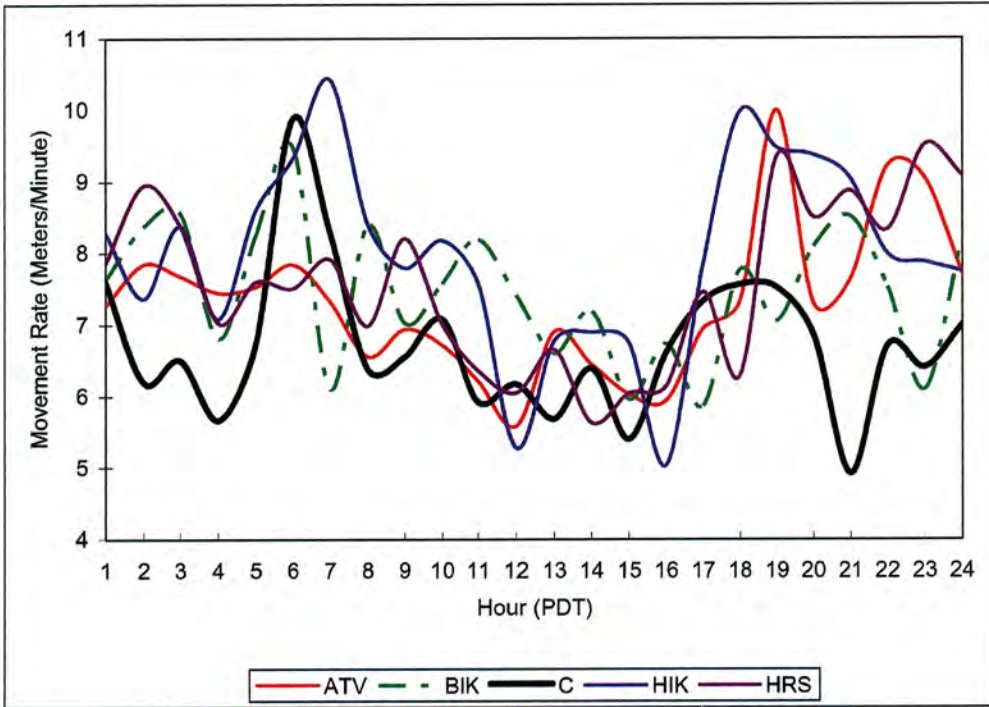


FIGURE 4. Mean movement rate (speed, meters/minute) of mule deer, estimated hourly on a 24-hour basis, Pacific Daylight Time (PDT), during periods of no human activity (C) versus periods of ATV activity (ATV), hiking (HIK), mountain bike riding (BIK), and horseback riding (HRS) during 2002 in Northeast Study Area of Starkey.

on transects for all four activities). In future analyses, we plan to explore the use of the amount of time spent by each off-road activity as a covariate, and possibly weight the movement rates and probabilities of flight response by the inverse of time spent by each of the four off-road activities. This weighting would help account for differences in effort required among the four activities to achieve equal saturation of the study area.

Our results may also change if elk eventually become “habituated” to some or all of the off-road activities. We will evaluate this possibility in future analyses by formally testing for replicate and year effects under a random effects model, with repeated measures taken on radio-collared animals over time (Kirk 1982). Analyses to test for animal habituation to the off-road activities will be possible when all three years of data are collected.

Mule Deer

In contrast to elk, mule deer showed little measurable response to the off-road treatments. Movement rates increased slightly, however, during periods of all four off-road activities except ATV riding. Deer may well be responding to the treatments with fine-scale changes in habitat use, rather than substantial increases in movement rates and flight responses.

For example, it is possible that deer may respond to an off-road activity by seeking dense cover, rather than running from the activity. If mule deer are spending more time in dense cover, in reaction to any of the off-road activities, this could result in reduced foraging opportunities, and a subsequent reduction in opportunities to put on fat reserves during summer that are needed for winter survival. Such potential responses will be evaluated as part of future analyses.

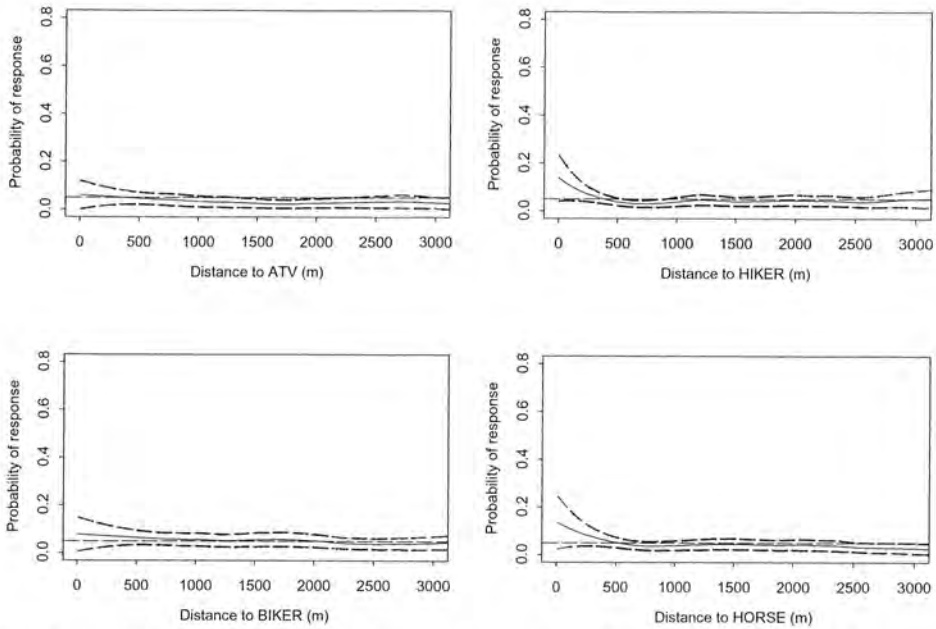


FIGURE 5. Estimated probability (solid line encompassed by dashed lines of the approximate 95 percent pointwise confidence interval) of a flight response by mule deer during 2002 in relation to distance (meters) from humans riding ATVs, mountain bikes, horses, or hiking. A flight response is defined as an animal movement with a speed exceeding the 95th percentile of speeds observed during periods of no human activity (control period). The horizontal dashed line at the bottom of each graph is the probability of a flight response by deer during periods of no human activity, and this line represents the background or “null” condition, above which significant deer response to the off-road activities exists.

Utility of Response Variables

Taylor and Knight (2003b) defined a variety of terms for measuring animal responses to human activity. Neither movement rate nor probability of a flight response was defined, however, because these types of animal responses apparently have not been measured in past research. We measured these two responses to human activity because both variables can ultimately be used to estimate the energetic costs of animal reactions to human activities. For example, movement rate can be used as a background index of the rate of animal speed without human activities, versus periods of human activities, to estimate the additional energetic costs of increased movement, if any, in relation to human activities (Ager et al. 2003).

Similarly, the probability of a flight response indicates how likely an animal is

to move at high speed in relation to its distance from a human. This probability indicates how likely an animal is to run from a human activity, and thereby disrupt the animal’s activities related to energy acquisition (foraging) or energy conservation (resting). Any movement away from an area in relation to human activity has the potential disrupt these foraging and resting patterns, and thereby cost energy (Johnson et al. 2004).

Future analyses will focus on the energetic costs, if any, to mule deer and elk from exposure to each off-road activity. Additional analyses also will include estimates of (1) the distance moved by an animal, given a flight response; (2) the time required for an animal that exhibits a flight response to return within a specified distance of the animal’s location before the flight; (3) the change in space use by an animal, during or following periods

of human activity, which may suggest or reflect an animal seeking greater refuge from the human activity, as compared to background or "null" use of space during periods of no human activity; and (4) the degree to which animals spend time in forage areas, gaining energy, versus time spent in non-foraging areas, during each off-road activity versus control periods.

IMPLICATIONS FOR RECREATION MANAGEMENT

Laws and policies of public land management emphasize multiple resource uses. Management of timber, grazing, roads, minerals, and wilderness are examples of traditional uses on lands administered by the U.S. Department of Agriculture Forest Service (Forest Service) and U.S. Department of Interior Bureau of Land Management (BLM), the two largest federal landowners in the United States. Public land managers now face the additional challenge of serving a variety of off-road recreational uses that are increasing rapidly, and that can be difficult to accommodate on the same land area at the same time (Taylor and Knight 2003a).

New planning approaches are now underway in the Forest Service to accommodate increasing off-road recreational demands while mitigating the negative effects on species like elk (U.S. Department of Agriculture Forest Service 2004). These approaches could consider two related concepts: (1) off-road use rates and (2) off-road recreational equivalents. We define off-road use rates as the number of passes per unit time on a given linear route (primitive road or trail that we referred to as transects) traveled by an off-road activity. Our results show that one pass per day by any of the four off-road activities causes increased movement rates and flight responses by elk.

We define off-road recreational equivalents as the ratio of ATV riders, mountain bikers, horseback riders, and hikers that results in approximately the same effect on a given resource, given the same off-road use rate. In the case of elk, movement rates and probabilities of flight were highest during ATV riding and low-

est during horseback riding and hiking. These effects were a result of one group of ATV riders, two groups of mountain bikers, and three groups of horseback riders or hikers required to complete one pass on the transects each morning or afternoon. Consequently, the stronger effects posed by ATV riding, combined with differences in the number of groups required of each activity to achieve one pass on the transects, suggest that recreational equivalents would exceed three groups of horseback riders or hikers to every group of ATV riders, and exceed two groups of mountain bike riders to every group of ATV riders.

While the formal methods of calculating the specific recreational equivalents could be a subject of lengthy debate, the idea that different levels of each off-road activity are required to approximate the same effect on a given resource is logical and defensible. Accordingly, off-road use rates and recreational equivalents could be tested as potential concepts in helping allocate recreational activities within and across watersheds on a given National Forest or BLM Field Office. These concepts may be particularly relevant when derived from a combination of response variables or resource uses. For example, effects of each off-road activity on water quality, soil productivity, invasion of exotic plants, and species sensitive to human activities could be considered in deriving use rates and recreational equivalents.

Such an approach would demand a substantial increase in research on effects of off-road activities. For management of elk, results from our study will be most useful when estimates of the energetic costs, if any, are derived for each of the four off-road activities in terms of use rates and recreational equivalents. Energetic costs to elk from one pass per day on a given linear route traveled by a given off-road activity could be estimated, and the equivalent energetic costs, given the same use rates, could be estimated among all off-road activities.

Although these details are not yet available, managers could begin to con-

sider holistic management strategies for all off-road activities based on our current findings. Some watersheds might feature opportunities for ATV or mountain bike riding, for example, while other watersheds might focus on opportunities for horseback riding or hiking. Importantly, the watersheds identified for horseback riding or hiking could accommodate a substantially higher number of groups engaged in these off-road activities before realizing the same effects on elk as would be expected in watersheds where ATV or mountain bike riding are featured. This type of holistic management of different mixes of all off-road activities contrasts with management approaches that focus on a single off-road activity, without consideration of all off-road uses and their cumulative effects.

Other strategies for watershed planning might simply focus on restricting each recreational activity to specified trails or roads. In this case, our results suggest that the effectiveness of such a strategy would depend on how much area is affected by the network of trails or roads allowed for use. If the linear distance of trails or roads open to recreation is small relative to the total area of the watershed, the effect on elk is likely to be minor or negligible. If the linear distance is large relative to the size of the watershed, the negative effect on elk could increase substantially. The specific effects could be analyzed in the same manner as outlined for estimating effects of motorized road traffic on elk, as done with "distance band" models (Rowland et al. 2004).

Effective and defensible strategies to meet off-road recreation demands, while also mitigating negative resource effects, are likely to require a substantial increase in budgets of public land agencies for research, management, and monitoring of these activities. Managers currently have little knowledge with which to develop effective strategies in partnership with the many public recreation users. Without such knowledge, the debate about off-road recreation is likely to intensify, with few scientifically based options for resolution in relation to mitigating potential

negative effects on species like elk that are sensitive to human activities.

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Issues of Elk Productivity for Research and Management

Bruce K. Johnson, Michael J. Wisdom, and John G. Cook

INTRODUCTION

Elk (*Cervus elaphus*) populations in western North America have been intensively managed for the past century. The species' popular appeal as an animal for hunting and viewing, and its potential to damage agricultural crops and compete with livestock make it a species that is closely scrutinized by managers and many public interests. Today, elk continue to have significant ecological, cultural, and economic values. For example, the species provides substantial revenue for rural communities from hunting and viewing (Bolon 1994). Since the 1960s, elk in some areas of the western United States caused economic damage to farming and ranching operations. Elk managers spent considerable effort to maintain populations at levels compatible with these private land uses, while also striving to provide sufficient hunter opportunities on public lands to meet recreational demands.

More recently, concern about elk has changed from how to manage increasing populations to that of population maintenance. Elk recruitment, defined here as number of calves per 100 females that survive to one year of age, has declined in many areas of the western United States. Elk recruitment gradually declined since the 1960s in areas of northeast Oregon (Oregon Department of Fish and Wildlife 2003) from more than 50 calves per 100 females to fewer than 20 calves per 100 females in some areas during the 1990s, resulting in lower elk populations and fewer hunting tags issued. In Wallowa County of northeast Oregon, the number of antlered elk tags was reduced from 7,030 in 1995 to 4,620 in 2000 and from 4,140 to 350 for hunting antlerless elk (Oregon Department of Fish and Wildlife 2001). Elk populations declined

25 percent in the Clearwater Basin in Idaho, 50–70 percent in the North Rainier, 30–50 percent in the South Rainier, and 30 percent in the Blue Mountains elk herds in Washington during the late 20th century, and most of these declines were concurrent with low recruitment (Cook et al. 1999).

The focus of our paper is to describe biological factors that affect elk population dynamics and focus on some potential causes of recent declines in elk recruitment. We identify interacting factors that may explain recent declines in elk recruitment, and describe the most likely hypothesis as a combination of several factors. We provide this discussion as context for the many subsequent papers that focus on elk productivity or related issues as part of research conducted by the Starkey Project and its partners.

FACTORS AFFECTING ELK RECRUITMENT AND POPULATIONS

The question of what regulates elk productivity is of practical interest because effective management depends on understanding how the multitude of factors may limit or interact to affect populations. Questions have centered on whether factors that most affect ungulate productivity are density dependent or density independent and if predation can limit elk populations. Following Skogland (1991), we define regulation as any positive density-dependent (effects increase as density increases) process that tends to stabilize population numbers over time. Any process that causes changes in population size is termed limitation. Limitation processes normally operate independently of density and thus do not stabilize populations. Both regulatory and limitation factors have been proposed to explain the

long-term decline in elk recruitment. Factors that are usually listed as regulating include food, disease, and perhaps other key habitat resources that may be in short supply as populations increase. Changes in elk population characteristics such as reproduction and survival have been correlated with changes in population size (or density) (Houston 1982). Factors that are often listed as limiting ungulate populations include human harvest, stochastic events (usually weather related), and predation. Predation effects can be density dependent, density independent, or inversely density dependent (Messier and Crête 1985, Skogland 1991, Messier 1994). Because territoriality of predators will restrict their density at some point, there should be a point at which predation should no longer be positively density dependent as prey populations increase (Skogland 1991). Messier (1994) identified three scenarios where predation can have varying effects on ungulate populations. Predation can be (1) density dependent at low prey densities when predation rates increase as prey density increases, (2) density independent when predation rates remain constant, and (3) inversely density dependent when predation rates decrease as populations increase often at higher prey densities (Messier and Crête 1985).

Density independent and density dependent factors affect population parameters (e.g., rates of birth, growth, fertility, mortality), and the statistics that quantify these parameters are vital rates (Caswell 2001). Temporal variation in vital rates have a major effect on population growth (λ) of elk. Eberhardt et al. (1996) estimated a maximum rate of increase (λ) of 1.33, or about 27 percent per year. Survival of adult female elk is the most important vital rate for long-term stability of populations (Nelson and Peek 1982, Wisdom and Cook 2000, Garrott et al. 2003) followed by fecundity of prime-aged adults, fecundity of primiparous females, and finally juvenile survival (Gaillard et al. 2000). In practice, however, survival of juveniles is an important component of ungulate

population dynamics even though this vital rate has disproportionately less effect on population growth than other vital rates (Gaillard et al. 1998, 2000; Eberhardt 2002).

How might density independent and density dependent factors act separately or interactively to control vital rates and growth of ungulate populations? The literature contains theoretical and empirical works that address ungulate productivity and are often contradictory when read in the absence of a broad examination of the issue. For example, within the Serengeti, smaller ungulate species were controlled by predation, and available resources controlled larger species (Sinclair et al. 2003). Moreover, density dependent and density independent factors may act simultaneously, such that effects of density independent factors (drought or severe winter) increase with higher population density (Gaillard et al. 2000).

A related concept to density dependence is that of compensatory versus additive sources of mortality. Compensatory sources of mortality are those that have little influence on population growth, because other factors interact or negate their effect (e.g., Bartmann et al. 1992). By contrast, additive sources of mortality are direct, minimally influenced by other factors, and cause a predictable increase in mortality and reduction in population growth. Predation can be an additive source of mortality when density dependent effects are minimal but compensatory at high population densities if food is limiting (Messier 1994). Hunting also can have an additive effect in heavily exploited populations (Dusek et al. 1992).

Density Dependent Effects

Effects of density dependence on population growth are well-documented in theoretical and experimental work (Holling 1959; Fowler 1981, 1987). Density dependence in ungulates has been most evident in isolated populations, often on islands, and in predator-free or nearly predator-free environments (Grubb 1974, McCullough 1979, Coulson et al. 1997, Gaillard et al. 2000, Garrott et al. 2003,

but see Houston 1982, Lubow et al. 2002, Taper and Gogan 2002 for exceptions with elk). Density dependent regulation evidently was caused by intraspecific competition for food that decreased reproductive performance, increased juvenile mortality rates, and in some cases increased adult mortality rates. Density dependent changes in vital rates were most obvious in ungulates when populations are close to carrying capacity (Fowler 1981). Eberhardt (2002) summarized how density dependent regulation of ungulates manifests itself via four sequential steps as populations approach carrying capacity: (1) juvenile mortality increases, (2) age at first reproduction increases, (3) reproductive rate of adult females decreases, and (4) mortality of adults increases.

Nutrition fundamentally controls reproduction in ungulates, with effects that can carry over from one season or year to the next. Inadequate nutrition of cow elk in winter and spring reduced calf weight and survival at birth (Thorne et al. 1976). Reduced spring ambient temperature also reduced calf birth weight (Smith and Anderson 1996). Poor condition of moose (*Alces alces*) cows resulted in low birth mass of their calves (Keech et al. 2000). Nutrition in summer has marked effects on growth and development of deer fawns (Holter and Hayes 1977, Verme and Ozoga 1980) and elk calves (Cook et al. 1996, 2004). Steinheim et al. (2002) found that lifetime reproductive performance of free-ranging domestic sheep (*Ovis aries*) was related to body mass at birth: ewes with an initial low body mass produced fewer offspring at first and second parturition. Summer nutrition influenced black-tailed deer (*Odocoileus hemionus*) body fat and weight dynamics (Parker et al. 1999) and probability of survival in winter (Mautz 1978, Parker et al. 1999, Cook et al. 2004). This effect might be most pronounced in ecosystems occasionally or frequently experiencing relatively harsh winters.

Nutritional demands of lactation during late spring through early autumn can affect pregnancy rates in autumn because nutritional condition (e.g., body fat) of

cow elk is the prime determinant of successful breeding (Trainer 1971, Kohlmann 1999, Cook et al. 2001c, Cook et al. 2004). The energetic demands of lactation are high, and if the digestible energy in summer forage is low or marginal relative to requirement, cow elk may not rebuild sufficient body reserves by autumn to enter estrous. However, Cook et al. (2004) found that if the cow loses its calf early after parturition she can accumulate sufficient fat reserves to successfully breed in autumn even when forage quality in summer is markedly inadequate for lactating cows. Trainer (1971) suggested that at a kidney to fat ratio (KFI) < 60 [9 percent body fat (Cook et al. 2001a)], probability of pregnancy was reduced. Cook et al. (2004) also found that female elk in poor condition would not conceive and suggested that 8–9 percent body fat was a threshold for cow elk in autumn, below which pregnancy rates decline.

It is not clear about the degree to which density-dependent nutritional effects in winter versus those in summer most influence populations. Density dependent mortality has been well-established in Yellowstone as a function of elk density on winter range (Houston 1982, Taper and Gogan 2002). Lubow et al. (2002) also concluded that density dependence on winter range regulated the elk herd in Rocky Mountain National Park. Beuchner and Swanson (1955) suspected density dependent influences on primiparity of young cow elk in southeast Washington. Merrill and Boyce (1991) reported significant correlations between elk calf survival and abundance of green phytomass during summer in Yellowstone. Crête and Huot (1993) reported marked effects of nutrition during summer on reproductive processes in caribou at relatively high herd density.

Whatever the case may be regarding seasonal influences, it follows that as elk populations approach carrying capacity, recruitment should decrease because increased intraspecific competition for high quality forage lowers nutrition. Moreover, selective grazing at high herbivore den-

sity may effectively erode the nutritional value of plant communities available to herbivores, enhancing the food-based density effect over time (Irwin et al. 1994, Riggs et al. 2000). Forest succession patterns also may exacerbate density dependent effects despite little or no change in animal numbers, because amount of forage may decline markedly from early-successional stages to advanced stages in forest ecosystems (Hett et al. 1978, Peek et al. 2001). Such influences might be pronounced where wild-fire and logging have been reduced and precipitation is adequate to support high rates of forest succession. These effects may require many years to develop and thus may be hard to document with typical short-term studies (but see Peek et al. 2002). Finally, nutrition may be inadequate at low animal densities, simply because available forage, no matter how abundant, may not adequately satisfy requirements. This density independent aspect of nutritional influences is rarely recognized, but may be important in some ecosystems (Cook et al. 2004).

Density Independent Effects

Climate is typically identified as having a density independent effect on ungulates (Gaillard et al. 2000) that can limit populations. Effects of climate, however, can be more severe when populations are close to carrying capacity (Garrott et al. 2003). Variation in climate caused juvenile survival to vary widely even though adult survival was high (Gaillard et al. 1998). Sæther (1997) argued that climate is the most important density independent variable in the absence of predation. In temperate and montane habitats, climate is characterized by distinct warm and cold seasons, with corresponding variation in forage quality and quantity. During late spring and early summer, forage typically is abundant and high in quality, but in winter quality is low and abundance may be low.

Among seasons, temperature and precipitation may be highly variable, resulting in summer drought or severe winter conditions. Summer drought can decrease

forage quantity and quality (Vavra and Phillips 1980), thus reducing fat accumulations in yearling and lactating cow elk that can delay or cancel estrus (Cook et al. 2004). The result can be lower pregnancy rates of yearling cow elk (Bruce Johnson, unpublished data, 2003) and prime-aged elk, and increased susceptibility to harsh winter conditions. Variation in winter severity can cause wide variation in survival of elk calves but have little affect on survival of prime-aged females (Garrott et al. 2003). Severe winter climate followed by cold, wet springs that delayed green up of vegetation lowered survival of neonate caribou (*Rangifer tarandus*) (Adams et al. 1995) and caused higher predation on neonates in semi-domestic reindeer (Tveraa et al. 2003).

Diseases and parasites can infect elk (Thorne et al. 2002); however, most of the common livestock diseases do not affect elk recruitment. The one exception is brucellosis that can reduce pregnancy rates up to 12.5 percent annually (Thorne et al. 2002). Elk populations in Oregon have been monitored for brucellosis and the disease has not been detected in any sample. In general, elk populations are little affected by parasites, and problems are often restricted to local situations (Thorne et al. 2002).

Predation

Predation can have highly variable effects on ungulate population growth, and in many areas of western United States, predator populations are increasing (Mech et al. 2001, Keister and Van Dyke 2002). Predator to prey ratios are not sufficient to describe the effects of predation on ungulate populations because the functional response of predation may vary with prey density (Messier 1994). Manipulative experiments with ungulates and predators can be difficult to accomplish because of the long time periods required. Several manipulative or correlative studies, however, have been conducted. Sinclair et al. (2003) described a 40-year experiment in Africa where small to medium sized ungulate populations increased when pred-

ators were poached or poisoned in the Serengeti from 1980–1987. When predator populations were allowed to return to previous levels, the ungulate populations returned to their former levels. Jedrzejewski et al. (2002) found that wolf (*Canis lupis*) predation had an inverse density dependent effect, in that predation limited red deer (*C. e. elaphus*) numbers but did not regulate the population; by eliminating a large portion of the juvenile age class, wolves dampened the rate of deer population growth. Jedrzejewski et al. (2002) also summarized the effects of wolf predation on red deer in temperate forests of Poland from 1850 to the present. Wolves were extirpated twice. During both periods of wolf extirpation, populations of red deer increased dramatically to the point where density dependent effects were obvious. When wolf populations were reestablished, deer populations decreased in proportion to the increase in wolf populations.

Hayes et al. (2003) manipulated wolf densities across 10 sites in Canada to evaluate the population responses of woodland caribou (*R. t. caribou*), moose, and Dall sheep (*Ovis dalli*) and found that predation lowered caribou and moose recruitment and adult moose survival. Populations of Dall sheep, however, did not respond to changes in wolf density. Kunkel and Pletscher (1999) found that when wolves colonized a study area in northern Montana, survival of white-tailed deer (*Odocoileus virginianus*) and elk decreased and concluded that wolf predation was an additive mortality.

Predation does not necessarily affect sympatric prey species in the same manner (Hayes et al. 2003). Robinson et al. (2002) compared recruitment parameters and cause-specific mortality factors for sympatric white-tailed deer and mule deer (*Odocoileus hemionus*). While there were no differences in fetuses per female or fawn survival between the species, survival of adult white-tailed deer was higher. Predation by cougar (*Puma concolor*) was the major source of adult mortality for each species but predation rates on adult mule deer were two times higher

than on white-tailed deer. As a result, the mule deer population was about 30 percent lower than that of white-tailed deer.

Further complications with interpreting effects of predation on ungulates involve sources of alternative prey and multiple predators on one prey species. Messier and Crête (1985) and Messier (1994) suggested that wolf predation of moose was less pronounced when multiple species of prey were present. If a second predator was present, however, effects of predation may increase. By contrast, Wakkinen and Johnson (2001) suggested that woodland caribou numbers were declining in the Selkirk ecosystem because of predation by cougar. They hypothesized that the dependable, alternate prey source provided by the expanding white-tailed deer population allowed the cougar population to remain high, which in turn, resulted in increased predation on caribou. Kunkel and Pletscher (1999) found that the survival of moose increased when white-tailed deer and elk were present when cougars, grizzly bears (*Ursus arctos*), wolves, and black bears (*Ursus americanus*) were sympatric with the three prey species. Finally the degree of seasonal migration may affect the extent to which predation acts on prey populations (Crête and Huot 1993).

The composite picture from these studies suggests that effects of predation can operate in multiple ways, depending on the suite of prey species present and the number and abundance of predator species. Prey population responses to predation can vary, and few, if any conclusions can be drawn without site-specific information on the predator and prey species that occur. Skogland (1991) stressed that although predators may limit prey populations, there is little evidence that predators regulate prey populations. Territoriality of predators may place upper limits on predator densities, potentially precluding predation as a regulating factor (Skogland 1991).

Hunting

Hunting can have an important influence on ungulate populations, diminish-

ing the evidence of density dependence by reducing density below carrying capacity. For example, Swihart et al. (1998) evaluated the nutritional condition and pregnancy rates of white-tailed deer from areas with and without hunting. In areas without hunting, pregnancy rates, body size, and body fat were lower than in areas where hunting controlled deer numbers. In addition, Swihart et al. (1998) found that pregnancy rates varied inversely with density among the five sites evaluated. Messier and Crête (1985) warned that ungulate populations appearing to be healthy (high recruitment) may change if human exploitation increases in the presence of predator populations. If predator to prey ratios change, predation can shift from inverse density dependence to density dependence, resulting in a further decrease in ungulate density and resulting in predation being sufficient to keep ungulate populations suppressed (Messier and Crête 1985). In recognition of such effects, Hayes et al. (2003) suggested hunter harvest of moose and caribou populations be set at low levels (2–5 percent) in areas where wolf and bear populations were high.

Pervasive Human Disturbances

Recreational activities on public lands are increasing as human populations increase, and may decrease animal fitness or expose animals to higher rates of mortality (Knight and Gutzwiller 1995). Since the 1950s, road construction on public lands of the western United States has provided access, resulting in increased use of areas that were previously undisturbed (Trombulak and Frissell 2000). Examples of increased recreational activities include mushroom and berry picking, fire wood gathering, mountain biking, all terrain vehicle use, cross country skiing, back packing, camping, and snowmobiling. Elk have responded by moving away from roads open to the public (Rowland et al. 2000, 2004), especially roads with higher rates of traffic (Wisdom 1998). Elk have also moved away from off-road recreation activities, especially ATV and mountain bike riding

(Wisdom et al. 2004). Conner et al. (2001), Vieira et al. (2003), and Wertz et al. (2004) found that displaced animals moved to areas where disturbance was minimal.

During hunting seasons, energetic consequences of the increased disturbance include increased energetic costs associated with movements (Johnson et al. 2004) and perhaps shifts to habitats where foraging conditions are diminished (J. G. Cook, unpublished data, 2003). Disturbance during parturition and calf rearing resulted in higher calf mortality (Phillips and Alldredge 2000) or decreased reproductive performance of mule deer in the following year (Yarmoloy et al. 1988). These added energy costs could lead to higher winter mortality rates as animals deplete stored fat reserves to avoid human activities.

COMPETING HYPOTHESES TO EXPLAIN DECLINES IN ELK PRODUCTIVITY

Several factors or hypotheses may explain long-term decline in elk recruitment across large areas of the northwestern United States. Each factor is plausible but not likely to operate independently of other factors. Exact mechanisms causing declines likely vary from location to location depending on habitat, climate, and predator populations. We hypothesize that recent declines in elk productivity are a result of a combination of factors that interact in both density dependent and independent ways. Our hypothesis is built on the following assumptions:

1. Intraspecific competition for forage.—Elk populations have gradually increased concomitant with reductions in forage biomass and quality over the last six decades in much of western United States. In turn, this may have increased intraspecific competition for nutritious forage, resulting in lower pregnancy rates and higher mortality rates of elk. Effective fire suppression on forestlands over the last 60 years has had a substantially greater, negative effect on forage production than

the counteracting, positive benefits of wildfire, timber harvest, and insect-caused mortality of trees that has occurred in the last two decades. The effect in total may be a slow erosion of carrying capacity on many elk ranges. For example, the elk populations increased dramatically in the 1980s and subsequently declined in the late 1990s following the volcanic eruption at Mount St. Helens in Washington.

2. Decrease in highly palatable forage.—Elk may exert strong and highly selective grazing pressure on the forage species that are relatively palatable and available, especially if animals are displaced because of human activities. Coupled with increasing density, nutritional limitation occurs, reducing population parameters.
3. Increase in predator populations.—Cougar, black bear, and wolf populations have increased substantially during the past four decades, resulting in lower recruitment of elk.
4. Summer drought and winter severity.—Abiotic factors of summer drought and winter severity may not be operating in the traditional, density independent manner. Instead, these factors may increase the vulnerability of elk to predation or increase winter mortality due to nutritional constraints.
5. Legal and illegal hunting.—In situations where recruitment is lowered due to predation, cow elk hunting has an additive and substantial effect on growth rate of elk populations.
6. Human activities.—Human disturbance activities have increased across all elk ranges, and may be exerting a negative effect on elk populations not observed in the past. The energetic costs of elk avoiding pervasive human disturbances can be substantial, and have been overlooked as affecting elk nutritional condition.

Considering the above assumptions together, we hypothesize that the underlying basis for elk productivity is nutrition and that predation, hunting, weather variation, and human disturbance factors currently are additive in their effects on the

decline in productivity, and that the relative effects of each may vary among herds. Where limiting factors are prevalent, density dependent effects may not be apparent. Ratios of predators to prey are critical in understanding how the several factors outlined above result in increasing or decreasing rates of population growth. At high levels of nutrition and appropriate (but unknown) predator to prey ratios, we hypothesize that effects of predation, human disturbance, and hunting would reduce but not limit population growth. That is, elk recruitment would respond positively even with these sources of mortality under high levels of nutrition, thus providing an inherent resilience to population change. If, however, predator to prey ratios were shifted dramatically due to reduction of elk populations due to hunting, severe winter mortality of elk, or increases in predator populations, then predation could keep elk at a lower equilibrium such that elk populations and recruitment remain low. The point at which mortality factors tip the balance between growth and decline of the prey population should vary along a gradient of nutritional adequacy.

CHALLENGES TO RESEARCH AND MANAGEMENT

We believe our hypothesis deserves careful examination within a research framework. Obviously, no single factor can explain either the variability or the long-term decline in elk recruitment across the northwestern United States. Several factors are interacting, in different ways in different areas, making it difficult to impose any one management strategy that can ensure recovery of elk populations.

One of the principal goals of the Starkey Project was to examine management activities that affected elk productivity. The original studies of the Starkey Project were directed at understanding how single factors affected elk fitness, distribution, or reproduction (e.g., Cook et al. 1998, Rowland et al. 2000, Noyes et al. 2002). Subsequent research at Starkey and associated study sites was then expanded to examine how two or more fac-

tors might interact to affect elk reproduction, survival and recruitment (e.g., Cook et al. 1999, 2004; Johnson and Jackson 2001). The next step is to further expand research to address the full complexity of factors and their interactive effects on elk productivity and population growth.

We suggest three complementary approaches to gain better knowledge about elk productivity: (1) adaptive management, (2) retrospective and meta analysis, and (3) simulation modeling. Under adaptive management, research would be designed and tested as manipulative experiments in real-world conditions (Walters 1986). Researchers and managers would jointly develop hypotheses for testing and implementing treatments, and work together to measure and interpret the results. For example, a set of watersheds could be selected for intensive habitat improvements and subsequent reduction in human disturbances, and another set of similar watersheds used as controls. Researchers could measure and compare a variety of population responses of elk to the habitat improvements and reduction in human disturbances. On the other hand, predator populations could be reduced, and responses of prey populations monitored, probably providing a more rapid assessment that would not require waiting on habitat changes.

Retrospective and meta analysis provide alternative analyses of potential value. Meta analysis could be used to analyze the multitude of studies that have evaluated the effects of nutrition, predation, and weather on population dynamics of ungulates as case studies (e.g., Messier 1994, Linnell et al. 1995, Sæther 1997, Unsworth et al. 1999, Gaillard et al. 2000, Hayes 2002). The synthesis of many studies of elk recruitment (Schlegel 1976, 1983; Smith and Anderson 1996; Singer et al. 1997; Myers et al. 1998; Gratson and Zager 2000; Jedrzejewski et al. 2002; Zager and White 2003, and unpublished results from the region) could yield general, predictive patterns about the interactive effects of various factors on ungulate productivity and population dynamics. However, most of these studies

had no measure of nutritional condition of the prey populations or imprecise estimated of predator populations, making analysis and interpretation more difficult.

Simulation modeling also can provide insights about the potential interactions of factors that affect elk productivity and growth rates of populations. For example, a series of models could be constructed under different competing hypotheses, and each model run under a set of standard simulations to gain a more formal understanding of potential effects. Model parameters could reflect empirical data, but also hypothesized data, to further understand the range of potential effects, and to identify the most plausible effects and outcomes. The challenge will be to link habitat conditions, prey populations, and predator populations, an undertaking that has rarely been attempted. Hobbs (1989) and Weisberg et al. (2002) provided examples of models that link weather and habitat conditions with animal population characteristics, but neither incorporated predation effects. Typical predatory-prey models (Skogland 1991) rarely explicitly addressed contributions of habitat and nutrition. Further, if simulation models are to consider habitat/nutritional conditions on summer ranges in forest ecosystems, then plant succession patterns following disturbance and the interaction of herbivore numbers and plant succession patterns will be key elements of models.

Without these types of new research, managers face the difficult challenge of dealing with the high uncertainty about the proximate and ultimate causes of declines in elk recruitment. Even then, long-term monitoring of elk recruitment, survival, and nutritional condition are critical to understanding when predation, weather variation, and hunting may be limiting and nutrition is regulating. Nutritional condition of elk populations can be measured inexpensively by using cow elk hunters to collect reproductive tracts, suitable indices of condition, and mammary tissue for animals harvested in autumn (Kohlmann 1999; Cook et al. 2001a, b). In situations where hunter collections are inadequate to satisfy research/monitoring

objectives, nutritional condition of live elk can be assessed reliably (Cook et al. 2001a, b).

When elk recruitment is low or declining, managers will need to gain insights about how density dependent factors, long-term vegetative successional trends, variation in summer precipitation and winter severity, hunting, and predation may be interacting. If nutritional characteristics and climatic variability are implicated, then management alternatives to address habitat conditions; where hunting or predation appear to be limiting recruitment, then alternative actions may be required to increase recruitment. Public acceptance of predator management evidently is waning, creating challenges for managers to meet the social and economic needs of the various public groups interested in wildlife. Consequently, a strong partnership between managers and researchers, with the use of modeling and adaptive management approaches, appears to be the most suitable strategy increasing understanding and for effectively dealing with emerging challenges of declining elk productivity.

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Influence of Age of Males and Nutritional Condition on Short- and Long-Term Reproductive Success of Elk

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INTRODUCTION

Rocky Mountain elk (*Cervus elaphus*) populations in some areas of northeast Oregon have experienced declines in spring calf: cow ratios of nearly 80 percent over the last 40 years. Among the potential causes of these declines, the effects of age of male sires and nutritional condition of females on conception dates and pregnancy rates have received the most attention from biologists and wildlife managers. Reliance on younger males as primary breeders can result in later conceptions and a prolonged rut period (Follis 1972; Hines and Lemos 1979; Noyes et al. 1996, 2002). Mechanisms involved with delayed conception due to male age have included late maturity of young males (Hines et al. 1985), female preference for older males (Gibson and Guinness 1980, Squibb 1985), and delayed timing of estrus in the absence of older males (Komers et al. 1999). The rate of conception (pregnancy), rather than the timing, does not appear to depend on the presence of older male sires (Follis 1972; Noyes et al. 1996, 2002).

Female nutritional condition during breeding influences date of conception (Trainer 1971, Mitchell and Lincoln 1973) and pregnancy rate (Trainer 1971, Albon et al. 1986). The importance of nutritional condition applies to males as well as females. It has been shown that age at puberty (Hines et al. 1985) and annual or long-term reproductive success of males depends on body size and dominance, both of which are influenced by birth date and nutritional condition (Green and Rothstein 1993, Komers et al. 1999). Although age of male sires, nutritional condition of females (and males to

a lesser extent), predation, and other determinants of ungulate productivity have been examined in many studies, their interactions in Rocky Mountain elk have only recently been addressed (see Cook et al. 2004 for a thorough literature review).

We conducted a study in two trials, from 1989 to 1993 and from 1995 to 1999, to assess the effects of male age and female nutritional condition on conception dates and pregnancy rates of female elk in northeast Oregon (Noyes et al. 1996, 2002). Results of both trials showed a significant influence of male age on conception dates but not on pregnancy rates. Results from the interaction of male age and female nutritional condition pooled across trials likewise verified the importance of male age in affecting conception dates across a range of nutritional conditions.

The most commonly referenced manifestations of skewed sex ratios and nutritional limitations on elk reproduction are short-term (annual) differences in conception dates, pregnancy rates, and calf survival. Beyond their short-term effects on calf survival, early conceptions and birth dates may be of greater significance in affecting long-term reproductive success and herd demographics. Benefits of early births may include higher lifetime reproductive success in female red deer [*C. e. elaphus*, Clutton-Brock et al. 1987)], bison [*Bison bison*, (Green and Rothstein 1993)], and moose [*Alces alces*, (Saether et al. (2003))]. Understanding the importance of maintaining older males in elk populations, in conjunction with knowledge of nutritional condition and their interactions should assist wildlife managers

in making informed, effective decisions about harvest management.

STUDY AREA

We conducted our study within a 30 square mile (78 km²) study area at the U. S. Forest Service Starkey Experimental Forest and Range (Starkey) in northeast Oregon, about 21 miles (35 km) southwest of La Grande. Elevation ranged from 3,680 feet (1,116 m) to 4,960 feet (1,502 m). Vegetation was a mixture of grasslands, regenerating forests, and older forest stands. Grand fir (*Abies grandis*), Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) dominated the north aspects and higher elevations; ponderosa pine (*P. ponderosa*) was the dominant forest vegetation at lower elevations. Bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*) typically dominated grassland vegetation. Mean annual precipitation was 20 inches (50.8 cm), and average mean temperatures were 24.8° Fahrenheit (−4° C) in January and 64° Fahrenheit (18° C) in July. Starkey was enclosed by a game-proof fence 8 feet (2.6 m) tall that allowed us to adjust the population size and structure of a free-ranging elk herd. Further descriptions of the study area can be found in Noyes et al. (1996) and Rowland et al. (1997).

METHODS

Herd Management

We managed the elk population during both trials to allow a single cohort of males to function as principal herd sires as they matured from one to five years of age. We estimated our elk population size with a model described in greater detail in Noyes et al. (1996).

We maintained a bull:cow ratio of the study cohort between 16:100 and 21:100 during both trials to minimize the effects of numbers of males. We conducted hunts for yearling male elk in early August (except 1989 and 1995) to reduce the number of yearling males prior to the breeding season. Males that were younger than

the study cohort were trapped annually and released outside of Starkey.

We fed a maintenance ration of alfalfa hay to those elk that moved to the winter feed ground. Elk were returned to the study area in similar nutritional condition each year to minimize the influence of variable winter severity on elk reproduction. Noyes et al. (1996, 2002) provide further descriptions of herd management. Our research was conducted under approved animal welfare protocols (Wisdom et al. 1993).

Reproductive Data

We collected reproductive tracts (uteri and ovaries), udders, lower incisors, and kidneys with associated fat from female elk killed by hunters in early December. We determined conception dates, pregnancy status, lactation status, and female age and nutritional condition (KFI) as described by Trainer (1971). We conducted blood tests for leptospirosis (*Leptospira* spp.) and brucellosis (*Brucella abortus*) to identify presence of diseases that may have affected elk reproduction.

Statistical Analysis [See Noyes et al. (1996, 2002) for detailed explanations of the following analyses]

Conception date

We compared conception dates of females among male ages (years) in each trial with analysis of variance and accounted for female nutritional condition with analysis of covariance. We compared conception dates of lactating and nonlactating females older than or equal to three years old with *t*-tests. We used stepwise multiple regression to predict conception date.

Pregnancy rate

We excluded females younger than age 3 or older than age 13 when summarizing pregnancy rates pooled by male age across trials because of age and lactation status effects.

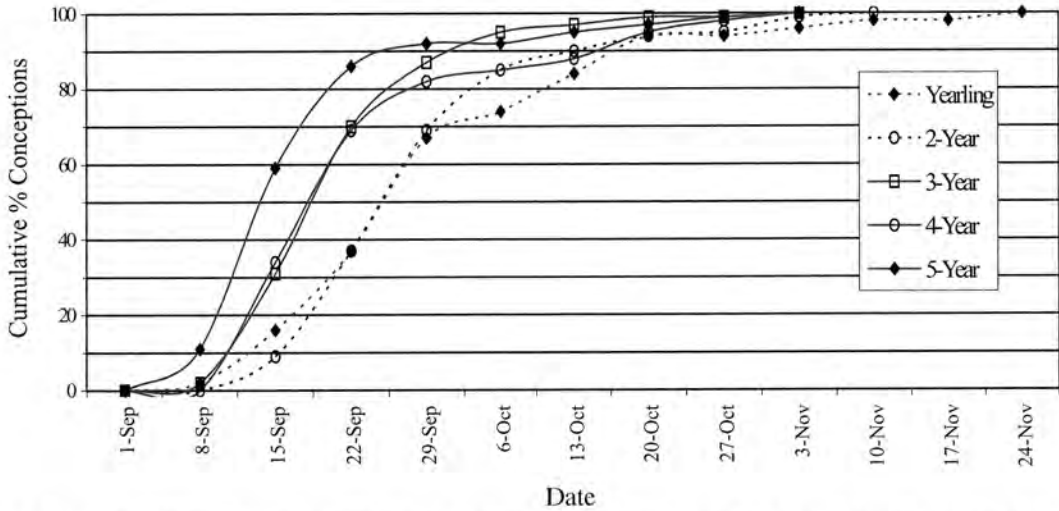


FIGURE 1. Cumulative percent conceptions for adult female elk (≥ 2 years old) bred by males of five different ages at Starkey Experimental Forest and Range, Oregon, 1989–99. Data were pooled from two identical five year trials. Age of sires increased each year from yearlings to 5-year-olds.

Female nutritional condition

We used analysis of variance to compare KFI among years for females greater than or equal to two years old and compared KFI of lactating and nonlactating females greater than or equal to three years old with *t*-tests. We also used *t*-tests to evaluate nutritional condition of lactating and nonlactating females between the two trials. We tested for correlation between KFI for all females and May to August precipitation.

RESULTS

Conception date

Conception dates varied with age of male sires in both trials and also when conception dates were pooled among trials and adjusted for female nutritional condition. The largest differences in mean breeding dates were between 5-year-old sires and yearling or 2-year-old sires. Females bred by males older than or equal to three years of age conceived earlier than females bred by younger males in both trials and had similar conception dates. Median dates of conception for females bred by yearling males were ap-

proximately two weeks later than when 5-year-old males were sires. Lactating females conceived about nine days later than nonlactating females.

Conception dates became more synchronous as male age increased (See Figure 1 in Noyes et al. 1996 for the chronology of conceptions, which applies to both trials). The duration of the rut differed by an average of 31 days between years with yearling and 5-year-old male sires (Noyes et al. 1996, 2002). We discarded the latest 10 percent of conceptions in each year to reflect that portion of the annual reproduction with the most management relevance. The date by which 90 percent of pregnant females were bred by yearling males was approximately three weeks later than when 5-year-old males were the sires. The cumulative percent of conceptions moved toward earlier dates as male age increased (Figure 1).

Pregnancy rate

Pregnancy rates of females greater than or equal to two years old did not differ by male age in either trial. Pregnancy rates of females 3–13 years of age pooled

across trials ranged between 89 percent and 94 percent (from Noyes et al. 1996, 2002). Pregnancy was related to KFI, but not male age, in pooled trials.

Female nutritional condition

The KFI of adult females differed among years and was significantly greater in 1989 and 1995, when yearling males were the primary herd sires. The KFI for all adult females during the second trial was less than KFI during the first trial. Pregnant, lactating adult females were in especially low nutritional condition in both trials when breeding was by 4-year-old males. KFI was lower in lactating females than in nonlactating females. KFI was correlated with May to August precipitation and precipitation during those months was lower in the second trial than recorded in the first trial.

DISCUSSION

We acknowledge the complex interactions among variables affecting reproduction in elk, but for the purposes of this paper we will emphasize the contribution of the age of male sires to differences in calf survival and long-term reproductive success.

We demonstrated the importance of mature males as sires to achieve early and synchronous conception in female elk, but we found no relationship between age of males and pregnancy rates. In our study, female nutritional condition was significantly higher during the two years that immature males were sires than during the other years. Because of this, we were not able to determine if pregnancy rates of females bred by immature males might be lower if nutritional conditions were comparable to the other years. Holland et al. (2003) assessed the effects of skewed sex ratios and male age structure on calving rates of female reindeer (*Rangifer tarandus*) in excellent condition, and also questioned how the results might vary if females were in poor condition.

Early breeding by older male sires has been documented for elk [Follis (1972), Hines and Lemos (1979)], moose (Saether

et al. 2003), fallow deer (Komers et al. 1999), and reindeer (Holland et al. 2003). Conception dates for females in both of our trials were strongly influenced by the age of male sires across a range of nutritional conditions. After adjusting conception dates for differences in female nutritional condition, conception dates became increasingly earlier as male sires matured from yearlings to 5-year-olds.

Another influence of male age results from conception synchrony and its effect on female reproductive success and neonate survival. The significance of synchronous births on survival of neonates likely depends on the strategy for optimizing neonate survival employed by different species (Geist 1982, Clutton-Brock et al. 1987, Kiltie 1988).

For a discussion on the effects of male age on calf survival and long-term reproductive success, we will assume a constant gestation length and consequently will consider the terms birth date and conception date to be interchangeable. Results of previous research on the length of the gestation period in ungulates and the ability of females to adjust the length vary depending on the species, nutritional condition of females, supplemental feeding, the effects on calf weight and survival, and perhaps a host of other unknown factors. No consistent patterns between nutritional condition and gestation length appear to be available. Guinness et al. (1978) stated that differences in calving time are likely due to factors affecting the time of conception, and we will make the assumption that early and late conceptions are reflected in early and late births.

Birth date has been closely linked to the probability of offspring survival. Late calving and reduced survival has been associated with lower body weight in autumn in reindeer (Holland et al. 2003) and in winter in moose (Saether et al. 2003). Delays in breeding as a result of highly skewed sex ratios and subsequent delays in birthing may reduce survival of offspring. Winter survival of red deer was related to birth date and population density (Guinness et al. 1978, Loison and Langvatn 1998). Cook et al. (2004) sug-

gested that winter survival of captive-reared calves under varied nutritional condition was not related to birth date, but indicated that other potential causes of mortality (e.g. predation) were not present. Clutton-Brock et al. (1987) reported that mortality of red deer calves increased by 1 percent for each day the calf was born after the median birth date. Captive red deer hinds that bred much later than normal did not lactate normally following the late births, and Guinness et al. (1978) suggested that their calves in the wild would quickly die.

The ability of young ungulates to exhibit compensatory growth is an important variable that should be considered in assessing the relationship between birth date and survival. Research has shown conflicting patterns of compensatory growth in ungulates. Late-born captive calf elk on low or medium quality diets reached weights in winter similar to early-born calves, while late-born calves on a high quality diet had significantly lower weights than early-born calves during the first year of a study (Cook et al. 2004). Compensation in the low and medium nutrition groups may have been influenced by growth rate differences between sexes; late-born calves were composed of 62 percent males compared to 31 percent in early-born calves. This pattern of compensatory growth was reversed during the second year, however, and the advantage of early birth was present in the low and medium nutrition groups, but not in calves in the high nutrition group. Guinness et al. (1978) observed a relationship between winter weights and birth dates of red deer under high nutritional conditions. Late-born calves had lower weights, further illustrating the difficulty in assessing the presence of compensatory growth under sometimes widely different conditions. Holand et al. (2003) reported that late calving in reindeer was associated with lower body weight in autumn, but suggested caution when applying results from enclosure experiments to wild, free-ranging populations.

The relative importance of birth date differences resulting from age of male

sires and their interaction with nutritional condition varies among studies and whether they involve wild or penned ungulates. Ginsberg and Milner-Gulland (1994) reported that breeding delays of one estrous cycle (18 days) in red deer can result in a 36 percent decline in reproductive success of females. Cook et al. (2004) suggested that birth date differences of three weeks (the effect of male age differences in our study) were insufficient to influence winter survival of calves under captive conditions. Mean differences of one week or less may be biologically significant for reindeer in environments with short seasons (Holand et al. 2003).

Perhaps more important than the effects of birth date and nutrition on survival of young are the long-term, cumulative effects on herd productivity. Most studies are short-term and thus are not able to determine these effects. Green and Rothstein (1993) conducted a 9-year study to evaluate the relationship between birth date, long-term growth, and reproductive success in bison. They documented beneficial effects of early birth that endured for the length of the study. Early-born females had significant fitness advantages and were more fecund during their first 9 years (Green and Rothstein 1993). Body weight differences related to birth date persisted throughout the study in females, suggesting that adult body size is enhanced by early birth. Links between birth date and body mass of moose calves in winter have been reported by Saether et al. (2003), who suggested that there may be long-term consequences of skewed sex ratios. Early births enhanced the probability that females would give birth in the succeeding year; late births increased the likelihood of subsequent reproductive failure.

To illustrate the range of interpretation of research results, Cook et al. (2001) stated that marginally deficient nutrition was responsible for delayed breeding of prime-aged lactating females despite high pregnancy rates. In our study, of 17 prime-aged lactating females in deficient nutritional condition (less than 9 percent

body fat), pregnancy rate was 94 percent and conception dates were not delayed. This is another indication that age of male sires is an important influence on pregnancy rates and conception dates and is implicated in herd demographics due to reduced survival of late-born calves.

A longer, slower trend toward lower productivity in ungulate populations may exist with late conceptions because hinds that conceived early or produced heavy calves had higher lifetime success (Clutton-Brock et al. 1983). Several mechanisms are plausible to explain reduced long-term reproductive success. Delayed births may not allow females to recover from the demands of lactation in order to ovulate early in the rut or at all (Laflamme and Connor 1992). Female red deer that have delayed conception by one estrous cycle (18 days) may experience a 36 percent decline in reproductive success. In bison (Green and Rothstein 1993) it has been shown that the effects of late birth and the resulting decreased body mass may have lasting consequences that are likely not evident from the results of annual reproductive performance.

Reproductive success of males is related to body mass. Early-born bison calves are socially dominant to late-born calves and may have increased reproductive success (Lott 1979 in Green and Rothstein 1993). Many life history characteristics are closely related to body mass of young females (Saether et al. 2003), which in moose is related to their body mass as calves, which is related to birth date. Because of this same relationship in male calves, the effects of late births result in reduced body mass of yearling males, which again can result in lower reproductive success. We could speculate that this pattern might function as a mechanism by which a subtle cycle of later births, lower body mass, and decreased reproductive success is repeated to the long-term detriment of elk productivity.

The age of male sires can also influence reproductive dynamics and survival by means other than dates of conception. Young males may be either socially (behavior) or physiologically immature dur-

ing the rut period. Female fallow deer avoided sub-adult males more than mature males (Komers et al. 1999). Females with subadult males lost more weight (4.2 percent) during the rut than females with mature males (1.9 percent), and reduced body reserves could compromise female survival. Male moose in Norway exhibited a long-term decline in mean body mass as the proportion of adult males decreased (Solberg and Saether 1994). They also found that the oldest male age groups experienced the largest declines. The relationship between body mass in males and reproductive success has been reported for red deer and bison. Early birth affects the social dominance status and breeding success in male bison.

Young females may be especially sensitive to skewed sex ratios (Solberg et al. 2002 in Saether et al. 2003). In our study the behavioral immaturity of yearling males might help to explain the reproductive performance of 2-year-old females. There were approximately equal numbers of 2-year-old females for each of the five age classes of male sires (60 females total). Pregnancy rates were similar, ranging from 82 percent to 100 percent and nutrition was significantly higher when yearling males were sires. Because very few 2-year-old females were pregnant as yearlings, there were no effects of lactation on dates of conception. However, conception dates of 2-year-old females were again about 3 weeks different between immature and mature male sires.

MANAGEMENT IMPLICATIONS

Effective management of elk populations might involve providing mature males necessary to obtain early and synchronous conceptions, and to interact with nutritional condition to enhance the survival of calves and long-term productivity. The importance of dates of conception might also be to "set the stage" for the influences of female nutritional condition. Without early conception, high nutritional condition of females cannot solely determine the probability of calf survival. We have restricted our discussion to interactions among male age and the

nutritional condition of females and males. The nutritional condition of elk herds can be reduced for reasons other than habitat quality. Preliminary results from ongoing studies evaluating the energetic effects of recreational use (Wisdom et al. 2004), and increased movements related to hunting seasons (Ager et al. 2004) indicate energetic costs that also may affect herd demographics. Preliminary results from four years of a 6-year study evaluating archery disturbance during the rut indicate lower pregnancy rates and asynchronous conceptions (J. H. Noyes, unpublished data, 2003).

We have identified several variables and their interactions that affect elk reproduction in slightly different ways. The challenge to wildlife managers is to provide the conditions that will allow the most opportunities for increased production over the greatest range of conditions. Managing for mature bulls through harvest regulations is much more straightforward than predicting precipitation and annual forage production. The presence of mature males in ungulate populations may be warranted for reasons other than their effects on short-term productivity. The significance of mature males in elk populations, regardless of the interpretations of research results, should not be ambiguous because of the evolutionary doctrine that states natural selection operates to provide conditions that enhance the survival of species. Mature bulls ordinarily function as principal sires of polygamous harems (Bubenik 1982). We seek to understand some of the complex interactions that are present today under conditions that have been greatly altered. Wildlife managers might consider all variables affecting the productivity of elk herds (male age, nutritional condition, predation, human disturbance, and others). Challenges lay in adapting management options to the variety of social and environmental conditions that currently exist.

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Nutritional Condition Indices for Elk: The Good (and Less Good), The Bad, and The Ugly

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INTRODUCTION

Research on captive ruminants has clearly established the role of nutrition on virtually all aspects of individual and herd productivity, but assessment of nutritional effects on population dynamics of free-ranging ungulates is rare. Understanding influences of nutrition on wild ungulate herd demographics has been limited by a lack of practical, reliable, and cost-effective techniques for monitoring elk condition and nutrition (Cook 2002). Assessing nutritional quality of forage is difficult, unreliable, and expensive, whereas assessing nutritional condition of animals has been impractical in the field, inaccurate, or inadequately tested (Robbins 1983, Harder and Kirkpatrick 1994, Saltz et al. 1995).

The most rigorous approach to test the value of condition indices involves comparing various indices to actual fat and protein levels of the homogenized carcass. Statistical analysis of indices generally involved correlation between the indices and a body component, usually ingesta-free body fat. Non-linear relationships often were transformed to facilitate analysis using general linear models (e.g., Finger et al. 1981, Watkins et al. 1991). The final value of indices usually was determined via comparison of correlation coefficients or coefficients of determination. However, these methods of analysis often are incomplete, leaving unanswered questions related to reliability, sensitivity, and applicability of such indices across space and time.

Moreover, past studies often failed to clarify between indices appropriate for nutritional assessment versus those appropriate for evaluating nutritional condition. Nutrition is defined as the rate of ingestion of assimilable energy and nutrients,

and nutritional condition is the state of body components (e.g., fat, protein) which in turn influence an animal's future fitness (Harder and Kirkpatrick 1994).

Cook et al. (2001a) used captive-raised cow elk (*Cervus elaphus nelsoni*) fed a variety of diets to induce a wide range of body conditions to develop predictive models of body fat. For live animals, they assessed serum and urine chemistry, a body condition score, thickness of subcutaneous rump fat, and bioelectrical impedance analysis. For dead animals, they assessed femur and mandible fat, two carcass scoring techniques, and three different kidney fat indices. They assessed relations between indices and percent fat and developed models to predict nutritional condition. Cook et al. (2001b) also evaluated range of usefulness, bias, precision, and sensitivity to small changes in body condition for each model deemed to be most useful by standard methods. Herein we summarize these findings and report major results.

METHODS

Seventeen 1.5-year-old, 19 2.5-year-old, and 7 adult (5- or 7-year-old), non-gravid cow elk were housed in pens near Kamela, Oregon. These elk originated from wild stocks in northeast Oregon and were either bottle- or dam-raised in captivity (Cook, J. G. et al. 2004). Pens were devoid of vegetation and contained a barn designed for individual feeding and collection of blood, urine, and fecal samples.

Within each age group, we randomly assigned elk to one of three processing dates, mid-September, late-December, or mid-March, which corresponded with times that managers most often handle ungulates in the wild. Beginning 2.5 months before each processing date, we

subdivided animals within each age group into three nutrition treatments to create divergent condition levels. Dietary manipulation involved varying quantity and quality of food rations using alfalfa, mixed-grass hays, and pellets (Cook et al. 2001a). A high nutrition diet was designed to maintain high nutritional condition during the 2.5-month feeding trial. We formulated medium and low diets to induce average body-mass losses of 8–10 percent and greater than 15 percent. We placed all animals on identical diets 7 days prior to data collection to alleviate potential confounding from effects of short-term nutritional influences on relations between condition indices and percent fat. We fed all elk a 35:65 ratio of high quality pellets:high quality hay at a maintenance level.

At the end of each 7-day period, we collected urine samples via a galvanized metal pan placed under each stall's floor. The next day, animals were brought into the barn and anesthetized with xylazine hydrochloride. Blood samples were obtained within 10 minutes of the drug injection by jugular venipuncture. Seven urine and 23 serum variables were included in the analysis (Cook et al. 2001a).

We collected all live-animal measurements while elk were anesthetized. We used a body condition scoring (BCS) system which involved averaging three separate scores derived from palpation of the ribs, withers, and rump areas (scoring criteria described by Cook 2000). We calculated a body reserve index ($BCS \times$ body mass; Gerhardt et al. 1996) and followed methods of Farley and Robbins (1994) for bioelectrical impedance analysis. Subcutaneous rump fat thickness (MAXFAT) was measured using ultrasonography (Stephenson et al. 1998).

Elk were then euthanized via jugular injection of sodium pentobarbital. Carcass fat, musculature, and visceral fat were visually scored via the Kistner score (Kistner et al. 1980) and the Wyoming Index (Lanka and Emmerich 1996), both of which were developed for deer (*Odocoileus* spp.) and modified for elk by Cook et al. (2001a).

Cows were eviscerated and weighed. We halved each carcass from nose to tail along the vertebrae (Stephenson et al. 1998). One half of the carcass, along with the hide and hair, was sectioned, stored at -2 degrees Fahrenheit (-20 degrees Celsius) and later homogenized to determine body composition. The other half was used as a source for collection of the femur and the mandible for bone marrow analysis.

We trimmed perineal fat according to Riney (1955), and weighed the kidneys, remaining fat, and trimmed fat. We evaluated total kidney fat mass (kg) and calculated kidney fat indices (KFI) based on total fat mass (KFI_{full}) and trimmed fat mass (KFI_{trim}). For all analyses, we estimated KFIs separately for each kidney and calculated the average. We combined the removed organs and blood with the trachea, larynx, diaphragm, esophagus, and all contents of the pleural and peritoneal cavities, exclusive of the ingesta, weighed, and stored them frozen.

Half carcasses and viscera were homogenized separately in a whole-body grinder (Autio 801 B with a Falk 50 hp grinder) at the University of California (Davis). We collected two samples of each ground tissue and stored them frozen until chemical analysis of fat, protein, ash, and water content (see Cook et al. 2001a for assay descriptions). Body components were converted to a whole body, ingesta-free basis for subsequent analyses.

Statistical Analysis

Data were linear transformed when necessary and all indices with a coefficient of determination less than 0.25 with body fat were excluded from further analyses. We then assessed influences of age and season on relationships between each index and ingesta-free body fat using analysis of covariance (ANCOVA), general linear model procedure [PROC GLM], Statistical Analysis System (SAS) Institute 1988) with season and age as covariates. This identified the need for separate equations for each level of the two factors. If not significant, one equa-

tion was generated across all ages or seasons.

Second, we created two single-variable indices from arithmetic combinations of two original indices, each with different ranges of predictive ability. As described for deer (Connolly 1981), we combined femur marrow fat and KFI to form the CONINDEX. We combined the variables BCS and MAXFAT in a similar manner to produce a new variable: LIVINDEX (Cook et al. 2001a). We also combined MAXFAT and only the rump portion of the BCS in the same manner to produce rLIVINDEX. We then developed single variable predictive models for ingesta-free body fat with an accompanying coefficient of determination.

Evaluation of range of usefulness and sensitivity

To address some of the criticisms of past validation studies (see Robbins 1983, Hobbs 1987, Cederlund et al. 1989, Harder and Kirkpatrick 1994), we evaluated usefulness of 18 models having a coefficient of determination greater than or equal to 0.70 (Cook et al. 2001b). Our evaluation consisted of two types of analyses reflecting criteria of Robbins (1983) and Hobbs (1987); (1) a range of usefulness evaluation to identify specific types of relations between indices and body fat (i.e., identify biological relations that provide insights for what levels of condition the models apply); (2) an analysis of model sensitivity to test variation in the index relative to variation in the dependent variable.

To compare the range of usefulness among indices (i.e., identify biological relations that provide insights for what levels of condition the models apply), we graphed levels of fat with a depletion ratio (DR) of each index. We inserted percent fat (y-values) into each single-variable predictive equation for each index (see Figure 1 for general equations) and solved for x, providing index values we refer to as "IN." DR was then calculated as:

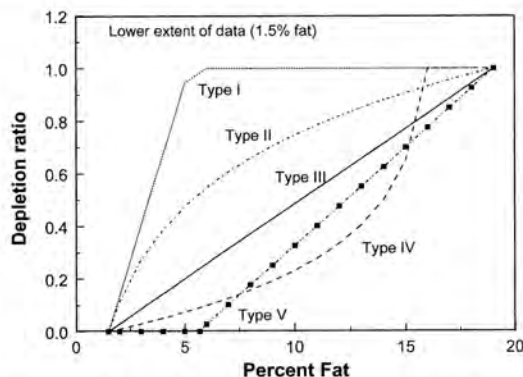


FIGURE 1. Depletion patterns of condition indices evaluated in the elk body composition study of 1998–1999. Each curve represents a different type of relation to body fat: Type I, almost asymptotic; Type II, power ($y = ab^x$); Type III, linear ($y = bx + a$); Type IV, logarithmic ($y = a[1 - e^{-bx}]$); and Type V, linear but truncated. Depletion ratios were standardized across indices (with one being the highest value attained for that particular index for the range of condition in this study [no depletion], and zero being the lowest value attained for that particular index for the range of condition in this study [complete depletion]). Although we presented the curves with actual fat values, these should be used as relative values only. Within a type, individual curves vary due to different equation coefficients.

$$DR = \frac{(IN - LV)}{(HI - LV)},$$

where

IN = value of index for any given level of fat;

LV = value of index at lowest value of fat in our data set (1.5 percent fat);

HI = value of index at highest value of fat in our data set (19 percent fat).

This equation standardized the depletion ratios across indices, with one being the highest value attained for that particular index for the range of condition found in this study (no depletion) and zero being the lowest value attained for that index (complete depletion). Differences in depletion patterns among indices were then compared graphically. Steep

slopes represented hypersensitivity (i.e., large changes in the index relative to small changes in condition); shallow slopes represented hyposensitivity (i.e., small changes in the index relative to large changes in condition); and a slope of zero indicated no predictive capability.

Next, we compared variation associated with the indices relative to variation in the dependent variable (percent fat) for this set of models. We wanted to determine whether a seemingly good predictive model generated from data with a large range of condition (e.g., among seasons) could accurately assess condition within smaller ranges typically found within seasons (see Hobbs 1987). We estimated within-season range of fat levels of wild elk to be 7 percentage-points from condition data collected during early November and late March (1998, 1999) from an elk herd in the Cascade Mountains, near Enumclaw, Washington. We randomly selected 26 subsets from our captive elk data, each with a 7 percentage-point range of body fat, and regressed percent fat on the index for each subset of data. Model performance was based on the average coefficient of determination of the 26 regressions and the percent of them that had 95 percent confidence levels that did not overlap zero.

RESULTS

Total body fat ranged from 1.6 to 19.0 percent and protein ranged from 16.6 to 24.8 percent of the ingesta-free body. Live mass ranged from 297 to 539 pounds (135 to 245 kg) and mass change ranged from +1.0 to -21.5 percent across the 2.5-month feeding period. These characteristics fell within ranges found in wild elk populations (Bender *et al.* undated, Cook, R. *et al.* 2004).

Of the total 50 single-variable models evaluated, most indices, particularly serum and urine, related poorly to percent fat ($r^2 < 0.25$). Twenty-four indices each accounted for greater than or equal to 25 percent of the variation in body fat. Of these, 12 were significantly correlated with body fat (see Cook *et al.* 2001a for predictive equations and coefficients of

determination). Cow age influenced relations between percent fat and mandibular marrow fat (Figure 2), as did season, on relations between percent fat and two serum variables: insulin-like growth factor-1 and thyroxine (Figure 2).

For live animals, LIVINDEX (calculated from either the whole BCS or only the rump portion) accounted for the most variation in percent fat ($r^2 = 0.90$; Figure 2). Both BCS (using the entire score [$r^2 = 0.87$] or only the rump portion [$r^2 = 0.86$]) and rump fat thickness separately ($r^2 = 0.87$) were highly related to body fat (Figure 2). Body mass alone was poorly related to percent fat ($r^2 = 0.44$; Figure 2) and failed to increase the correlation of BCS when they were combined into a body reserve index ($r^2 = 0.79$). Thyroxine and insulin-like growth factor-1 were the only single serum or urinary indices useful in predicting body fat ($r^2 \leq 0.82$), but this predictive ability was restricted to early and late winter (Figure 2).

For dead elk, the modified Kistner Score ($r^2 = 0.92$; Figure 2) and the Kistner subset score ($r^2 = 0.90$) using only the heart, pericardium, and kidney scores (Figure 2) were most related to percent fat. The Wyoming Index was moderately related to body fat ($r^2 = 0.69$; Figure 2) but is limited in use to when subcutaneous fat is present. Kidney fat mass ($r^2 = 0.86$; Figure 2) alone was superior to KFI_{full} ($r^2 = 0.77$; Figure 2), and KFI_{full} was superior to the traditional method of trimming ($r^2 = 0.74$; KFI_{trim}). Although CONINDEX worked moderately well ($r^2 = 0.70$), it was linear only at low to moderate levels of condition (less than 12.5 percent fat; Figure 2) but had no predictive ability at higher levels of condition. Femur marrow fat produced an r^2 of 0.89 using an inverse transformation of the dependent variable ($-1/y$). Mandible marrow fat was less curvilinear, but our estimate of the relationship for adults is tentative because of the confounding effect of age (Figure 2).

Range of Usefulness

We observed five types of depletion patterns (Figure 1), each with substantial

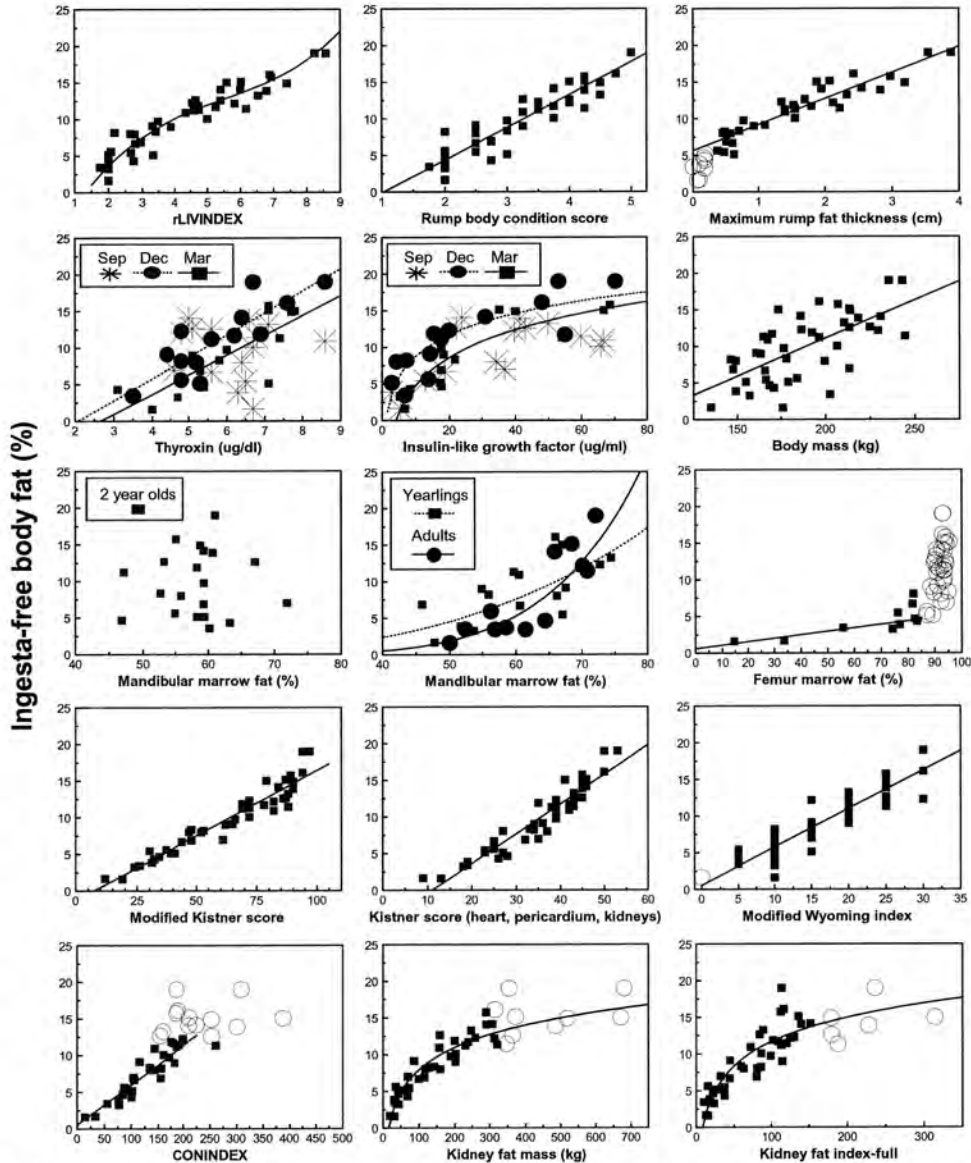


FIGURE 2. Relations of 14 nutritional condition indices with total body fat (percent) for 43 captive-raised cow elk. Seasonal or age trends are shown for thyroxin, insulin-like growth factor, and mandibular marrow fat. Open circles represent the range where an index loses predictive ability (e.g., maximum rump fat thickness, femur marrow fat, Wyoming Index, CONINDEX, and kidney fat indices).

differences in range of usefulness. Type I was derived from an almost asymptotic relation (femur marrow fat). Type II was derived from a power relation (mandibular marrow fat). Type III was derived from a linear relation (body condition scores, LIVINDEX, rLIVINDEX, Kistner scores,

body reserve index, body mass, thyroxin). Type IV was derived from a logarithmic relation (kidney fat indices, insulin-like growth factor-1). Type V was derived from a linear relation but with an abruptly truncated range of usefulness (rump fat thickness, Wyoming index).

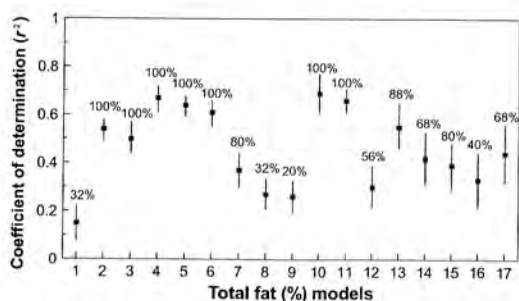


FIGURE 3. Sensitivity of 17 elk condition models was evaluated by subjecting each to 26 regressions within a restricted range of condition (7 percentage points of body fat representing within-season variation of condition of wild elk in western Washington; unpublished data, $n = 50$). The average coefficient of determination ($\pm$ SE) and the percent of time the model was significant over the seven-point ranges are presented. Models used were (1) body mass; (2) body condition score; (3) rump body condition score; (4) maximum subcutaneous rump fat thickness; (5) an arithmetic combination of body condition score and maximum subcutaneous rump fat thickness (LIVINDEX); (6) an arithmetic combination of the rump body condition score and maximum subcutaneous rump fat thickness (rLIVINDEX); (7) body reserve index; (8) insulin-like growth factor-1; (9) thyroxine; (10) Kistner score; (11) Kistner subset score (heart, pericardium, and kidney scores); (12) Wyoming index; (13) kidney fat mass; (14) kidney fat index_{full}; (15) kidney fat index_{trim}; (16) femur marrow fat; and (17) an arithmetic combination of kidney fat index_{full} and femur marrow fat (CONINDEX).

Model Sensitivity

When restricted to within-season ranges of condition, coefficients of determination generally were lower than for among-season ranges (Figure 3). Body condition score (Model 2), rump BCS (Model 3), MAXFAT (Model 4), LIVINDEX (Model 5), rLIVINDEX (Model 6), Kistner score (Model 10), Kistner subset score (Model 11), and kidney fat mass (Model 13) were significantly related to body fat ($P \leq 0.05$) for greater than 80 percent of the 26 data subsets. However, body mass (Model 1), body reserve index (Model 7), insulin-like growth factor-1 (Model 8), thyroxine (Model 9), Wyoming

index (Model 12), kidney fat index_{full} (Model 14), kidney fat index_{trim} (Model 15), femur marrow fat (Model 16), and CONINDEX (Model 17) were significantly related to body fat ($P \leq 0.05$) for ≤ 80 percent of the 26 data subsets. Body mass (Model 1), insulin-like growth factor-1 (Model 8), thyroxine (Model 9), and femur marrow fat (Model 16) were markedly insensitive; they were significantly related to body fat for less than 50 percent of the 26 data subsets.

DISCUSSION

Past studies evaluating nutritional condition indices for ungulates have rarely addressed issues of reliability, sensitivity, and applicability across space and time. Many have referenced these assessment limitations (e.g., Robbins 1983, Hobbs 1987, Cederlund et al. 1989, Harder and Kirkpatrick 1994) and have offered criteria that should be used to evaluate the value of an index (Robbins 1983, Hobbs 1987). Useful indices of condition should: (1) be linearly related to condition over the entire range of condition (Robbins 1983); (2) be insensitive to a variety of confounding influences, such that specific relations developed for one area, time, or diet, are applicable to others without bias (Robbins 1983, Hobbs 1987); (3) share a biological relation with condition rather than just a significant statistical correlation (Robbins 1983); (4) exhibit low to moderate variation relative to the variation in the dependent variable (Hobbs 1987); and (5) be reasonably practical for field application. By using these criteria, our analyses indicate that many indices that were significantly related to percent fat exhibited non-linear relations and were insensitive to small changes in condition. These indices often are those most utilized in the field today.

Range of usefulness generally is a function of linearity of relations between indices and nutritional condition. Transforming such data to make them linear is a common approach that facilitates analysis with linear statistical models. However, attempting to produce good statistical fit via this approach masks important

biological attributes and shortcomings of indices (Robbins 1983:222). Non-linearity of many condition indices often results from sequential patterns of fat mobilization across various areas of the body (Harder and Kirkpatrick 1994). As animals decline in condition, fat mobilization is believed to occur in subcutaneous depots first, viscera, including the kidneys next, and finally in the marrow (Cederlund et al. 1989).

The different type curves of Figure 1 generally reflect this sequence of fat mobilization and, in turn, identify patterns of range of usefulness. Indices exhibiting Types I and II curves have little sensitivity at high levels of condition, and probably are of value only in winter and spring. Indices with Type V curves are marginally useful at low levels of condition and probably are of value only in summer and autumn. Indices with Type IV curves are most valuable at moderate levels of condition, and optimum season of use will depend on fat characteristics of the herd. Indices that are linear across the entire range of condition (Type III) greatly facilitate comparisons among herds, among seasons, and across time. This analysis indicated that range of usefulness of indices based on only one fat depot will be limited to some extent, and that range of usefulness will be greatest for indices that include measurements of more than one fat depot or muscle.

Our sensitivity analysis revealed that models with even small differences in coefficients of determination differed in their ability to predict across within-season ranges of percent fat (Figure 3). In general, indices with moderate relations to body fat, curvilinear relations, or indices based on a relatively small number of categories provided poor predictive capability when restricted in this manner. With these conclusions in mind, we rank the condition indices available to biologists from good to ugly.

The Good

This category includes indices that can be used with high precision across all seasons, ages, and ranges of condition. For

live animals, rLIVINDEX (displaying a slightly curvilinear relation; Figure 2) was the most correlated to percent fat of any live animal index. Combining the rump BCS and rump fat thickness reduces potential subjectivity over moderate and high levels of condition where rump fat is more effective, and relies solely on BCS only on the low end of condition (the range where BCS appears to be least subjective; Cook, unpublished data, 2000). Despite its precision, two potential drawbacks may limit the use of this technique: (1) extensive training is necessary for both the ultrasound technique and the body condition score to ensure consistency in data collection, and (2) it may be expensive if live animal capture has to be done with helicopters.

Carcass/musculature scores have produced strong correlations to condition, particularly the Kistner score (Kistner et al. 1980, Watkins et al. 1991). We also found a tight linear relationship between the modified Kistner score and percent fat. In addition, by using only the heart, pericardium and kidney scores (the most easily attainable and identifiable parts of the Kistner score), we were able to predict percent fat almost as well as the whole score across the entire range of condition.

The Less Than Good

This category includes indices that can be reliably used only for limited ranges of body fat. Thus they may be of poor or no value during certain seasons or even for certain herds in any season if their fat levels exist outside the range of usefulness. Kidney fat indices have a long history of use in elk studies (e.g., Trainer 1971, Kohlmann 1999) despite a well-recognized non-linear relation to body fat (e.g., Finger et al. 1981, Depperschmidt et al. 1987). Problems with prediction typically were believed to be mostly at the low end of condition (Harder and Kirkpatrick 1994). However, our data indicate that kidney fat indices also are of marginal value above moderate levels of condition (greater than 13 percent body fat). In addition, though kidney fat indices result from quantitative measurements

of fat mass (versus more subjective visual scores, e.g., Kistner scores), consistency and accuracy may be compromised, particularly when samples are collected by untrained personnel or hunters, because complete removal of only the fat associated with kidneys can be subjective.

Combining femur fat and kidney fat indices into the CONINDEX may correct for poor predictive ability of kidney fat at low levels of condition for deer (Connolly 1981), but this index failed to predict higher levels of body condition of elk accurately (Figure 2).

The subcutaneous rump fat index covered the greatest range and the highest range in condition (more than 6 to 19 percent body fat) of the fat-based indices we examined, supporting the contention that the last depot of fat accretion is subcutaneous. Unlike the other fat indices, rump fat thickness declines linearly as body fat decreases until it is depleted and thus, range of usefulness was two to three times greater. Even so, the value of this index may be limited, particularly during winter and spring.

The Bad

This category includes indices that can be used as measures of condition, but have the most restricted range of usefulness or display season/age effects. Femur fat was the most non-linear index we assessed. It demonstrated good predictive capability when body fat was below 6 percent, but it had no predictive power above this value. However, when we did a linear transformation, femur fat had one of the highest correlations with body fat of any index we assessed, illustrating vividly the danger of transformations to enhance statistical relations. Mandible fat has been offered as an easy-to-collect alternative to femur fat (Harder and Kirkpatrick 1994). Although mandible fat appears somewhat more linear, suggesting a greater range of usefulness, significant age effects and lower correlations cast doubt about its value for elk (Figure 2).

The Ugly

We found serum and urine indices to be of little value for assessing nutritional condition. Only thyroxine and insulin-like growth factor-1 produced significant correlations with body components, but both were greatly limited when restricted to evaluating small changes in body condition. They also displayed seasonal variations that limited their use as well (Figure 2). We suspect many of these serum and urine indices are rate variables, or more reflective of short-term nutritional status. Nutritional condition is a state variable, and cannot be measured in terms of rates (Saltz *et al.* 1995).

RESEARCH AND MANAGEMENT IMPLICATIONS

Despite over four decades of intensive research on western elk herds, very little is known about the nature and extent of nutrition's influences on most wild elk populations. Elk populations were generally increasing in much of their range during this period (Christensen *et al.* 1999) which probably helped foster a perception that nutrition was not very limiting (Cook, J. G. *et al.* 2004). Declines in productivity and population numbers in elk herds, a phenomenon that is becoming increasingly severe and widespread in the Northwest (Johnson *et al.* 2004), suggest that a new era with different challenges await elk biologists. Of those habitat attributes with the potential to influence productivity and demographics of large herbivore populations, nutrition is probably the most important (Parker *et al.* 1999, Cook, J. G. *et al.* 2004). Clearly, a better understanding of how nutrition influences elk populations is needed.

Suitable tools available to biologists for evaluating nutritional adequacy of habitat are limited (Harder and Kirkpatrick 1994, Cook 2002). General surveys of forage abundance and quality across landscapes are expensive and difficult to conduct, and interpreting their relevance to herd performance is problematic. A long history of serum and urine analyses has identified techniques that have poten-

tial at least for monitoring short-term nutritional status, but even the best and most studied of these remain controversial (Cook 2002). In contrast, estimates of nutritional condition are compelling because they reflect cumulative energy balance of the animal, thereby integrating the separate effects of nutritional adequacy of their environment with their nutrient demands, and because condition can strongly influence reproductive success and survival probability (Cook, J. G. et al. 2004). However, direct estimation of nutritional condition, either via dilution techniques (e.g., Torbit et al. 1985) or laboratory assays of samples from homogenized carcasses, is largely impractical for evaluations of free-ranging animals. Various condition indices potentially offer a solution to problems of practicality, but our data indicate many pitfalls with their indiscriminate use, and those indices that require dead animals can limit research and monitoring designs and are increasingly less acceptable to society.

Our data identify several new techniques and infrequently-used older techniques that are sensitive across wide ranges of nutritional condition, are robust across animal age and season, and are reasonably practical. The rLIVINDEX index which combines a body condition score with ultrasound rump-fat measurements for live animals and the Kistner scores for dead animals proved superior in our analysis. These in particular can help open the door to a variety of research designs useful for evaluating nutrition's effect on populations. Foremost among potential applications may be an initial screening to evaluate the need for more detailed and expensive nutritional evaluations. Live-animal indices also provide opportunities for monitoring nutritional status among unhunted herds, during seasons in which hunting is precluded, or among unhunted segments (e.g., females) of populations. Thresholds linking nutritional condition with animal performance have now been developed for elk (Cook, J. G. et al. 2004) that provide criteria useful for relating animal condition to performance of elk cows, yearlings, and

calves. Additional applications for nutritional condition data on wild or captive elk populations include evaluations of: (1) relative degree of limitations among seasons and ranges by taking repeated measurements on the same animal across the yearly cycle, (2) relations between condition and productivity (Cook, J. G. et al. 2004), (3) predisposition to predation and starvation, (4) wildlife-habitat relations that are animal-productivity explicit (e.g., relations between home range characteristics and nutritional condition), (5) top-down versus bottom-up contributions to population dynamics and trends, and (6) the potential for herd augmentation (Bender et al. undated). Finally, modeling of carrying capacity and simulation modeling of population dynamics may require or benefit from estimates of nutritional condition (e.g., Hobbs et al. 1982, Hobbs 1989, DelGiudice et al. 2001).

Many of the above applications rely on use of live-animal indices for collecting nutritional condition data because they may require flexible collection dates and, in some cases, sequential data on individual animals. In many situations, acquiring such data will require expensive helicopter time. Thus, the nature and extent of data required to address key management issues must be carefully considered in the context of costs of collecting data and interpretive value and reliability associated with each potential condition index and various research designs. Reduced costs up front are of little value if the data collected fail to address important issues. As stated by Hobbs (1987), the necessity of reliability should always precede the need for applicability because unreliable predictions can be misleading no matter how easily obtained.

A significant hurdle for using condition results from past studies emanates from the multitude of techniques used and in particular, the units associated with each. For example, it is nearly impossible to link condition results from studies reporting kidney fat indices to those reporting body condition scores or femur fat and so on. Reporting nutritional condition in standard units whenever possible would greatly fa-

cilitate comparisons, and we suggest percent body fat of the ingesta-free body (Farley and Robbins 1994, Stephenson et al. 1998). For elk, our study provides equations (Cook et al. 2001a) to convert measures of nutritional condition from a variety of indices into estimates of percent body fat (though always accounting for limitations associated with each index). These equations facilitate comparisons among elk studies, and provide a means to standardize data from long-term historical trends where different techniques were used or where changes to new and better techniques are being considered.

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Nutrition and Parturition Date Effects on Elk: Potential Implications for Research and Management

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INTRODUCTION

Understanding and managing those mechanisms that affect population dynamics comprise perhaps the most fundamental aspect of wildlife management (Caughley 1977). Biologists generally categorize these mechanisms as either top-down (predator-driven) or bottom-up (habitat and/or animal density driven). Bottom-up influences involve imbalances between increasing animal density and key habitat resources. For large ungulates, abundance and nutritive value of forage are commonly thought to be the primary mediators of bottom-up regulation (Caughley 1979, McCullough 1984). Certainly, nutritional deficiencies can have extensive and often acute effects on reproduction, growth and development, and survival (Verme and Ullrey 1984, Cook 2002).

Much research has focused on nutritional effects, particularly for livestock (National Research Council 1984) but also for deer (*Odocoileus* spp.) (Verme and Ullrey 1984, Parker et al. 1999), caribou (*Rangifer tarandus*) (Thomas 1982, Cameron et al. 1993, Cameron 1994, and many more), and moose (*Alces alces*) (Schwartz and Renecker 1998). A research emphasis on nutrition has been largely lacking for elk (Cook 2002), except to some extent in Colorado (e.g., Hobbs et al. 1982) and in relation to game-farming in Canada (Haigh and Hudson 1993). Moreover, nutrition has largely been discounted in national forest models used to reconcile elk habitat quality with other land management concerns (Edge et al. 1990). This reflects an apparent perception that nutrition is not par-

ticularly important factor affecting most elk herds. It may also reflect uncertainty regarding how to evaluate nutritional resources across large landscapes in a manner relevant to ungulate populations.

Despite increased attention to non-forage aspects of habitat such as roads and cover, productivity and population size are declining in a number of Northwestern elk herds (Irwin et al. 1994, Gratson and Zager 1999, Ferry et al. 2001). This has spurred a reconsideration of the broader range of factors that may be contributing to herd demographics. Beyond nutritional limitations, low numbers of mature bulls (e.g., less than 5 bulls: 100 cows, Schommer 1991) was considered a potentially important cause of declines. Noyes et al. (1996, 2002) demonstrated that such low numbers of mature bulls can delay breeding up to two or three weeks, thereby delaying and de-synchronizing parturition. Ultimately such effects might reduce calf survival due to a variety of proximate causes, primarily through winter mortality and perhaps through predation.

Despite a perception that nutrition on summer range is rarely limiting in the western U.S. (e.g., Marcum 1975, Wallmo et al. 1977, Lyon 1980, Nelson and Leege 1982, Leege 1984, Christensen et al. 1993, Unsworth et al. 1998), we opted in our research to investigate the potential for summer-autumn nutrition to contribute to bottom-up regulation. Nutritional requirements are appreciably elevated to support key summer-autumn life processes, such as lactation, juvenile growth and development, and recovery of mass lost during winter (Verme and Ullrey 1984,

Oftedal 1985, Cook 2002). Forage quality and quantity may be greatest during the growing season, but it may nevertheless be insufficient to consistently satisfy high nutritional requirements during summer and autumn (e.g., see Julander et al. 1961, Pederson and Harper 1978, Verme and Ullrey 1984, Merrill and Boyce 1991, Crête and Huot 1993, Parker et al. 1999, Alldredge et al. 2002).

This study was conducted from summer 1995 through spring 1998 using a captive herd of 57 cow elk to achieve three primary goals. First, we wanted to estimate the extent to which summer-autumn nutrition and parturition date could each influence reproduction and survival, and also to explore the extent to which these two factors might exert interactive influence as well. Second, we wanted to quantify the nutritional requirements of lactating cows with calf. Third, we wanted to quantify the relationship between magnitude of nutritional restriction and magnitude of reduction in reproduction and survival.

We tested hypotheses regarding influences of summer-autumn nutrition and birth date, specifically including those that pertain to direct effects of summer-autumn nutrition and birth date on reproduction and those that pertain to carry-over effects, across seasons, of nutrition and birth date on subsequent reproduction and survival. Herein, we briefly review findings of the study and discuss their implications.

STUDY AREA AND ELK HERD

The study site was 20 miles (30 km) west of La Grande in the Blue Mountains of northeast Oregon in forest zones at 4,200–4,400 feet (1,300–1,350 m). Facilities consisted of two pen complexes. The primary complex housed the cows year-round and consisted of six 1.85-acre (0.75 ha) pens. Small barns with stalls were built in each pen and used for individualized feeding, weighing, and handling. A smaller complex was used to hold the calves after they were weaned. It consisted of three 1-acre (0.4 ha) pens that were devoid of vegetation.

We used two cohorts of bottle-raised female elk captured from wild stock in Northeast Oregon, the first born in 1991 ($n = 22$) and the second in 1993 ($n = 35$) (Cook et al. 1996). All bulls used for breeding were from wild stock at the Starkey Experimental Forest and Range and were at least three years old.

METHODS

The study consisted of three primary experiments to evaluate relations between nutrition, birth date, and reproduction-survival.

1. Cows and their calves were fed three levels of digestible energy (DE) *ad libitum* (Figure 1) from late June through early November in 1996 and 1997. These levels of nutrition were selected to represent dietary DE levels identified on elk summer ranges in Northeast Oregon.
2. Early and late birthing treatments were induced in spring 1996 by placing a bull with half the cows in September and with the other half in October 1995. Early and late parturition was included in the summer experiments of 1997 based on post-birth stratification rather than by inducing breeding dates as during the rut of 1995.
3. Influences of summer-autumn nutrition levels and birth date on winter survival of calves were evaluated by feeding during winter a sub-maintenance ration, assumed to mimic that likely to be realized under harsh winter conditions, and monitoring number of days survived from early December through mid-March during winters 1996–97 and 1997–98.

Additionally, we conducted several supplementary experiments to further evaluate nutrition effects.

1. During summer 1997, cows that failed to breed the previous autumn were separated into two nutrition groups, one receiving the high nutrition, the other the low nutrition level, identical to those fed to lactating cows in the primary summer-autumn nutrition ex-

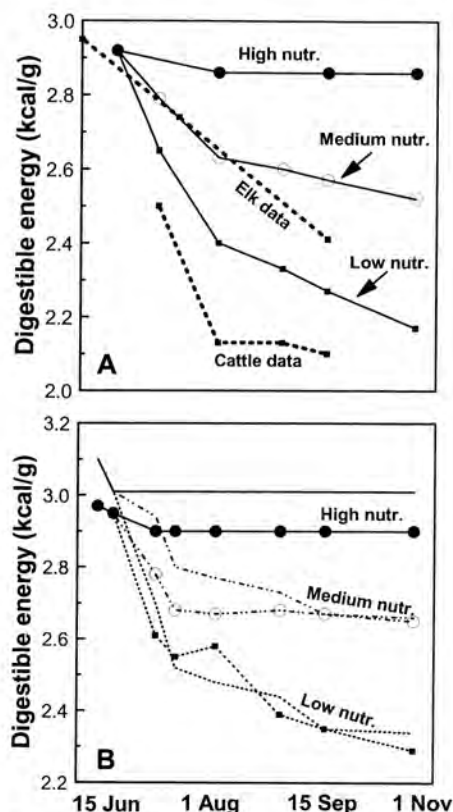


FIGURE 1. In graph A, target digestible energy (DE) content of food offered to cow elk and their calves from late June through early November, 1996 and 1997. Dashed lines labeled "Elk" and "Cattle" were dietary DE levels of elk (J. G. Cook, unpublished data, 1995) and cattle (Holechek *et al.* 1981) determined during dry years at moderate to low elevations in forest zones in the Blue Mountains of northeast Oregon. The average of these two DE levels set the target for the low nutrition treatment group. In graph B, actual DE content of food consumed by cows and calves from late June through early November, 1996 (lines without circles and squares) and 1997 (lines with circles and squares).

periment of the same year. This provided insights of the potentially different effects of summer nutrition on lactating versus non-lactating cows.

- From early December through early March 1997–98, all pregnant cows were stratified into three winter nutrition levels, with the intention of comparing winter nutrition and late-au-

tumn nutritional condition (i.e., ingesta-free body fat) influences on fetal survival. Results of the experiment also allowed an assessment of winter nutrition and late-autumn condition on cow survival.

Response variables included mass change of cows, calves, and yearlings, nutritional condition of cows as indexed by percent fat of the ingesta-free body (determined using the LIVINDEX score described by Cook *et al.* 2001a), pregnancy rates and timing of breeding of cows and yearlings, number of days of winter survived by calves during the calf winter survival experiments, and survival of cows and their fetus during the cow winter nutrition experiment. The winter experiments were designed to determine survival without actually allowing animals to die. Threshold criteria were established based on percent mass loss, body temperature, behavior, and appearance from which to proclaim the animals to be "dead". They were then removed from the experiments and provided care and abundant food (a total of 5 elk actually died of 110 used in these trials). During the two winters preceding both summer nutrition experiments, pregnant cows were fed a moderately sub-maintenance diet to induce about 10 percent body mass (BM) loss, to mimic mass loss assumed representative of that during mild to normal winters. In March of both years, elk were placed on ad libitum diets of high quality food to eliminate nutritional restriction on fetal development during the third trimester.

In all cases, statistically significant results refer to P values ≤ 0.05 .

RESULTS

Summer-autumn Nutrition, Parturition-date Experiments

The induced breeding periods of autumn 1995 provided 40 pregnant cows with two parturition pulses for the summer experiments: 26 May (range = 12 May–10 June) and 19 June (range = 11 June–29 June). Breeding in autumn 1996 provided 30 pregnant cows for the sum-

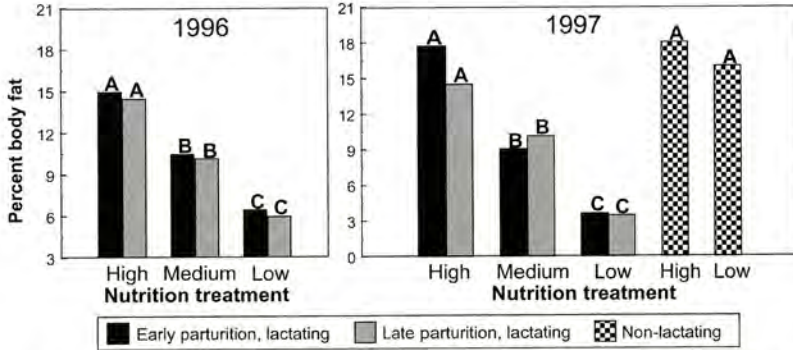


FIGURE 2. October ingesta-free body fat levels of cow elk across three levels of summer-autumn nutrition and two levels of parturition date. Within years, vertical bars with different letters differ significantly.

mer experiments. Post-birth stratification of birth date provided early-late parturition treatments of 1 June (range = 20 May–9 June) and 20 June (10 June–8 July).

In summer-autumn 1996, parturition date and nutrition significantly affected cow BM changes, but to a markedly different degree. At the end of the experiment, cows on the high nutrition treatments averaged 5 and 10 percent heavier, approximately 25 pounds (12 kg) and 50 pounds (23 kg) heavier, than cows in the medium and low nutrition treatments, respectively. The parturition date increment amounted to 2–3 percentage points, a mass difference of about 10 pounds (5 kg). Mass dynamics followed a similar trend during the second summer experiment of 1997. Body fat also was significantly related to summer-autumn nutrition levels in both summer experiments, but was unrelated to parturition date (Figure 2). The marked effects of the high versus low nutrition levels evident for lactating cows was not evident for non-lactating cows fed the same two dietary levels (Figure 2), indicating a substantial interaction between lactation status and summer-autumn nutrition on body fat accretion in cow elk.

The low nutrition treatment effectively precluded pregnancy by most cows (~80 percent of these cows failed to become pregnant), and the medium nutrition treatment significantly delayed timing of breeding, whereas parturition date failed

to influence either pregnancy or timing of breeding in either year (Figure 3A, B). Pregnancy failure resulted from a failure to enter estrus (Cook et al. 2001b). Body fat during the rut was significantly related to breeding probability and timing of breeding, and provided a basis for prediction equations for both of these responses (Figure 3C).

Body size of calves by late June, when nutrition treatments were implemented, was significantly inversely correlated to their birth date and positively correlated to their birth mass. Both variables together accounted for about 90 percent of the variation in late-June BM. Results demonstrate the “head-start” advantage of early birth, and also indicated that daily growth rate of calves larger at birth was greater than that of smaller calves at birth. Growth starting at the time nutrition treatments were implemented in late June was profoundly influenced by nutrition (Figure 4) in both years. Body mass of calves at the end of autumn was a function of summer-autumn nutrition and, inconsistently, their birth date. Late-born calves in the low and medium nutrition groups overcame their “late-start” mass disadvantage, and caught up with their early-born counterparts in their respective nutrition groups in 1996 (Figure 4A). In 1997, late-born calves, but only in the high nutrition group, also caught up with their early-born counterparts (Figure 4C).

Pregnancy of yearling cows ($n = 21$) was significantly correlated to both their

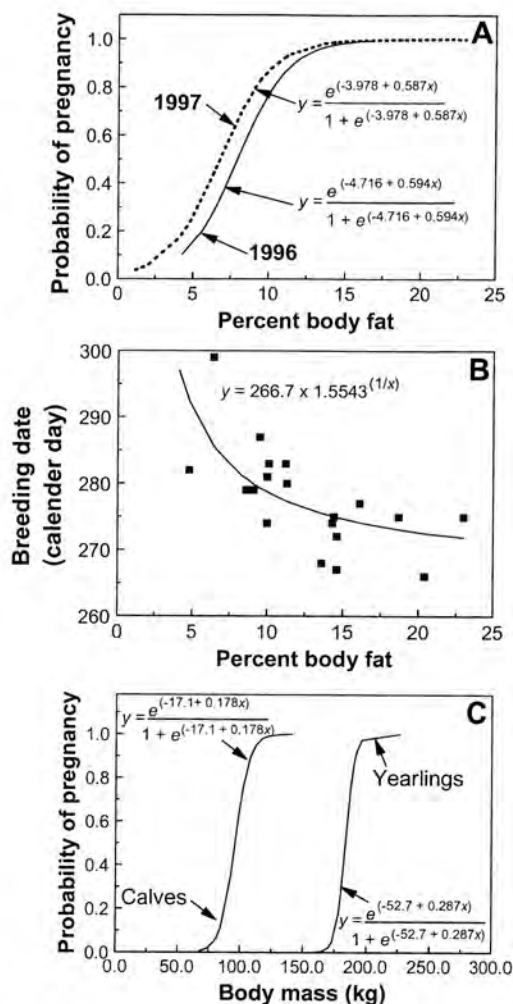


FIGURE 3. In graph A, logistic relations between ingesta-free body fat during the breeding season and pregnancy probability of adult lactating cows in 1996 and 1997. In graph B, non-linear relations between body fat during the breeding season and timing of breeding of lactating cows during 1997. In graph C, logistic relations between probability of breeding for yearlings in 1997 based on their body mass during the rut in 1997 and their body mass when calves the previous autumn (1996).

size as calves the previous autumn (1996) and to their size in autumn 1997 (Figure 3C). All 5 yearling cows in the previous-year high summer-autumn nutrition group, 3 of 7 in the previous-year medium group, and only 1 of 7 in the previ-

ous-year low nutrition group bred (i.e., the summer-autumn nutrition treatment these yearlings received when they were calves).

Calf Winter Survival Experiments

Forty calves in winter of 1996–97, with BM ranging from 135–310 pounds (61–140 kg) (mean = 212 pounds [96.3 kg]) and 30 calves, with BM ranging from 125–290 pounds (57–131 kg) (mean = 222 pounds [101 kg]) in winter of 1997–98 were available for these experiments. We varied feeding regimes of calves between the two winters. In the first winter, the magnitude of deficiency was increased gradually to about half of maintenance by mid-February. In the second, the magnitude of deficiency was increased relatively abruptly to half of maintenance by early January and held constant through the rest of winter.

In both winters, BM of calves was significantly correlated to the number of days of winter they were able to survive (Figure 5A, C). Smaller calves lost BM at a faster relative rate than did larger calves (Figure 5B, D), indicating the mechanism accounting for reduced tolerance of smaller calves to winter undernutrition. Differences in feeding regime between the two winters probably accounted for the different functional responses of calves in the two winters (i.e., non-linear in 1996, linear in 1997, Figure 5A versus 5C). Additional analyses indicated that their nutrition level of the previous summer-autumn, but not their birth date, was significantly related to number of days that calves survived in winter (Cook *et al.* 2004).

Winter Survival of Cows and Fetuses

This experiment was conducted with 40 pregnant cows in 1998 divided equally among four treatment groups, high summer-autumn nutrition and high (45 percent of maintenance), moderate (55 percent of maintenance), and low (65 percent of maintenance) winter nutritional depri-

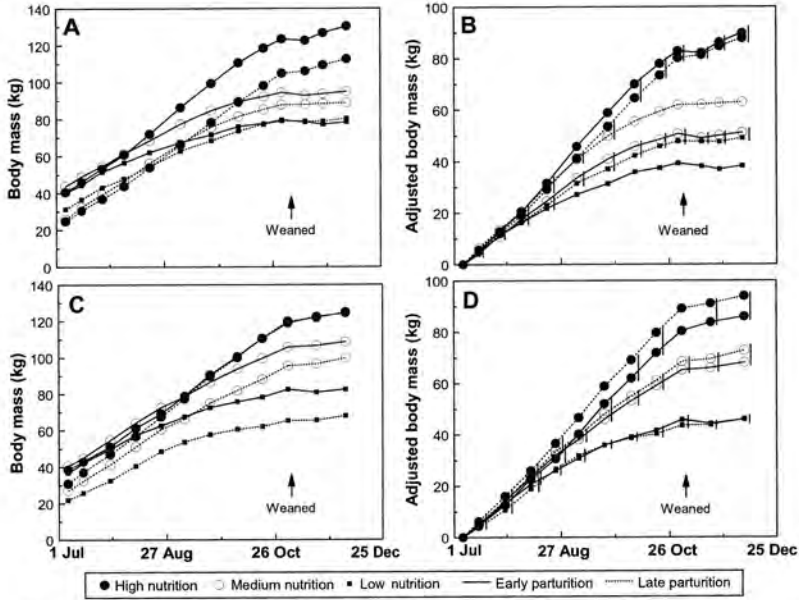


FIGURE 4. Body mass of elk calves during summer and autumn 1996 (A,B) and 1997 (C,D) across three levels of summer-autumn nutrition and two periods of birth date. Actual body mass is presented in graphs A and C. In B and D, body mass was adjusted to remove effects of birth date and birth mass, by subtracting mass at the start of the time period (early July) from all subsequent mass estimates. Data values not connected by vertical lines differ significantly within weekly periods.

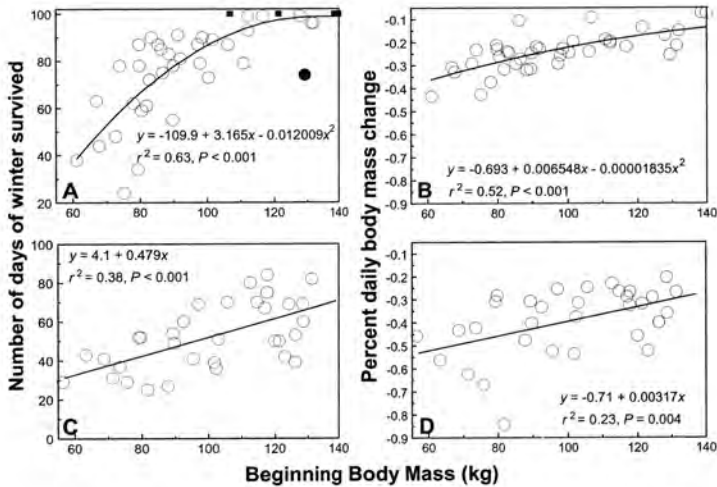


FIGURE 5. Number of days of winter survived (A, 1996–97; C, 1997–98) and rate of body mass loss (B, 1996–97; D, 1997–98) of elk calves as a function of their body mass at the start of winter. In A, the four solid squares are data for calves that survived the entire winter experiment, and the solid circle indicates a data point treated as anomalous and excluded from calculating the regression equation (but not the associated statistical parameters).

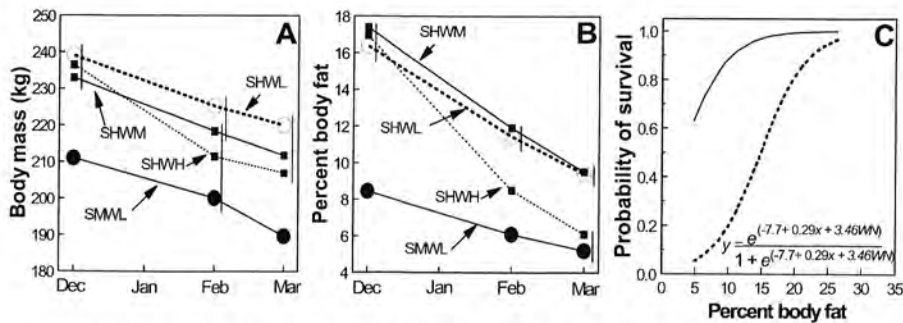


FIGURE 6. Body mass (A) and ingesta-free body fat (B) of pregnant cow elk during winter (1997–98) across four summer-autumn and winter nutritional deprivation treatments: SHWL = high summer-autumn nutrition, low winter nutritional deprivation; SHWM = high summer-autumn nutrition, moderate winter nutritional deprivation; SHWH = high summer-autumn nutrition, high winter nutritional deprivation; and SMWL = medium summer-autumn nutrition, low winter nutritional deprivation. Within monthly time steps, data points not connected by vertical lines differ significantly. These data were used to calculate logistic relations (C) between probability of winter survival and late-autumn body fat ($P = 0.073$) at two levels of winter nutritional (WN) deprivation ($P < 0.05$) (low-to-moderate = solid line; high = dotted line). In the logistic equation, WN is an ordinal variable with values of one for high winter nutritional deprivation and two for low-to-moderate winter nutritional deprivation.

vation, and medium summer-autumn nutrition, low winter nutritional deprivation.

Summer-autumn nutrition and winter nutritional deprivation significantly influenced end-of-winter BM and fat levels (Figure 6A, B). Body fat of cows on the high winter nutritional deprivation treatment plummeted, such that they ended winter with body fat equivalent to that of cows in the medium-summer-nutrition, low-winter-deprivation treatment group, indicating important interactive influences of summer and winter nutrition. One cow died and five particularly emaciated cows were removed from the study to prevent death. Four of these cows were in the high-summer-nutrition, high-winter-deprivation group; the other two were in the medium-summer-nutrition, low-winter-deprivation group. No cows lost their fetus prior to their removal from their study, but two aborted two weeks to two months after their removal and refeeding had been initiated. Both of these were in the medium-summer-nutrition, low-winter-deprivation group. Although limited, these data suggest elk cows may typically die before they abort. The “mortality” data provided an opportunity to develop a logistic model comparing effects of body fat in late autumn and the winter

nutrition levels we implemented on survival probability (Figure 6C). This model probably is specific to our experimental setting, and should not be considered robust across a wide variety of winter range conditions.

DISCUSSION

Our results show that relatively small differences in DE content of food consumed by elk in summer and autumn can have very strong effects on fat accretion, timing of conception, probability of pregnancy of lactating cows, calf growth, yearling growth (see Cook *et al.* 2004), and yearling pregnancy rates. Effects of summer-autumn nutrition on fat accretion of cows and growth of calves significantly influenced their survival probability under harsh winter conditions.

Earlier birth often resulted in larger size of calves in late autumn, but we were unable to document significant, consistent effects of parturition date on any other reproductive or survival attribute we evaluated. Despite a clear “head-start” growth advantage for calves due to early birth, our data suggest that delays in parturition, expected due to a very low ratio of mature bulls to cows (two to three

weeks [Noyes et al. 1996, 2002]), are of insufficient magnitude to appreciably affect reproduction and survival in elk (see also Bender et al. 2002). To some extent, this finding may reflect accelerated growth of some (but not all) late-born calves that eliminated the "head-start" advantage of early birth. These faster-growing calves tended to be heavier at birth and/or were male, both of which contributed to faster growth and both of which occurred more frequently late in the parturition period. Additionally, Cook et al. (2004) reported some evidence indicating that delays in breeding did not necessarily result in similar delays in parturition, and Berger (1992) reported that late-breeding bison (*Bison bison*) in good condition shortened gestation by up to 15 days, synchronizing births with other females. Thus, much can occur to compensate for delayed breeding on the resulting calf crop by the time calves are six months old, just prior to their first winter, thereby obscuring the implications of moderately-delayed breeding. But we note a potentially important caveat. Because our captive animals were not subjected to predation, this study could not evaluate the effect of parturition synchrony on predation-related mortality (see Keech et al. 2000), and thus it may be possible that delayed and desynchronized parturition effects are realized through a predation-mediated mechanism even where calf growth and survival is not constrained by nutrition directly.

That nutrition affects reproduction and survival was hardly surprising, but it was surprising the extent to which relatively small differences in DE content of food (a maximum of 20 percent between the high and low nutrition levels, Figure 1) induced large differences in animal performance. This finding confirmed the "multiplier-effect" noted by White (1983)—it occurred due to the combination of reduced DE concentration in food and the effect of reduced food quality on daily dry matter intake, evidently a result of reduced digesta passage rates. Ruminants cannot be expected to compensate appreciably for poor forage quality sim-

ply by eating more; they instead eat less as quality declines (see also Minson and Wilson 1994, Grey and Servello 1995). Thus, wild ungulates can be limited by nutritional quality of their forage even in the face of what might appear to be abundant food quantity (Riggs et al. 1996).

In addition to marked effects on calf growth, probably the greatest effect of summer-autumn nutrition on animal performance during this season was reductions in pregnancy rates. Our data indicated a marked threshold effect of about nine percent body fat, below which the probability of breeding declines precipitously. However, our study also demonstrated what has been supposed (e.g., Mautz 1978) and remains a suspicion of some (Parker et al. 1999:38), that effects of nutritional deficiencies occurring in summer-autumn often appear after summer-autumn, particularly during the subsequent winter and spring if winter conditions are sufficiently harsh. Although observations of winter mortality at first glance may implicate winter conditions as the limiting factor (e.g., the bottleneck of winter range, Wallmo et al. 1977), the potentially predisposing contributions of summer-autumn nutrition to winter mortality should not be categorically discounted without reliable collaborative data.

Additionally, high pregnancy rates of cows should not necessarily be considered proof that summer-autumn nutrition is adequate and thus is of little concern for management. Summer-autumn nutrition that is just adequate to support high pregnancy rates is not necessarily adequate to avoid predisposition of cows to winter starvation, and is inadequate to (1) support high growth rates of calves and yearlings, (2) preclude predisposition of calves to winter starvation, and (3) support high levels of breeding by yearling cows. Moreover, prime-aged animals in herds existing on marginal levels of summer nutrition levels just adequate to support high pregnancy rates in most years may be small-bodied (see Crête and Huot 1993), and such herds might be prone to substantial year-to-year variation in vital

TABLE 1. Estimated levels of performance expected for elk in temperate ecosystems as a function of dietary digestible energy (DE) from mid-summer through mid-autumn.^a Animal performance estimates are based on late-October and November measurements. For adults, levels apply to prime-aged, roughly 3–12 years old, lactating cows

Sum-aut nutritional status ^b	Dietary DE (kcal/g of food)	Calf mass (kg)	Yearling cow mass (kg)	Lactating adult cow fat (percent)	Yearling pregnancy (percent)	Adult pregnancy (percent)	Adult cow breeding date
Excellent	>2.90	125–145	195–230	16–25	≥90	≥90	≤30 Sep
Good	2.75–2.90	105–125	180–195	12–16	30–90	≥90	≤5 Oct
Marginal	2.40–2.75	90–105	160–180	8–12	5–30	70–90	≤10 Oct
Poor	<2.40	<90	<160	<8	<5	≤70	≥10 Oct

^a Caveats and suggestions for proper use of these guidelines are described in detail by Cook *et al.* (2004).

^b “Excellent” is defined as summer-autumn nutritional levels in which there are virtually no nutritional limitations. “Good” is defined as summer-autumn nutrition levels that exert minor limitations on performance, but the magnitude of this effect probably is too small to be of practical relevance. “Marginal” pertains to nutrition levels that may influence reproduction or survival (e.g., enhanced probability of death in winter, delayed breeding, delayed puberty). “Poor” pertains to nutrition levels that markedly affect reproduction and reduce survival probability.

rates due to annual variation in weather. Under these marginal nutritional conditions, how habitats are managed may have particularly important influences on population dynamics.

A goal of this study was to identify nutritional requirements for various levels of performance. Our findings indicate DE levels of at least 82 kilocalories per ounce (2.9 kcal/g) of food over summer into early autumn are required by adult lactating cows for levels of performance approaching the genetic maximum for adult elk. Such a level resulted in daily DE intake of 162–172 kilocalories per pound of $BM^{0.75}$ (400–425 kcal/kg of $BM^{0.75}$). This level simultaneously satisfies requirements for lactation and recovery from previous-winter mass loss, although it (82 kilocalories per ounce, 2.9 kcal/g) might be slightly deficient for supporting maximum growth of juveniles (Verme and Ozoga 1980) and yearlings (Cook *et al.* 2004). Elk in our medium nutrition treatment approximately maintained body fat levels at a constant level through early autumn (see Cook *et al.* 2004) and thus provided an estimate of “maintenance” for lactating cows during this period. Digestible energy content of their food ranged between 75–78 kilocalories per ounce (2.65–2.75 kcal/g) of food, resulting in daily DE intake of 131–152 kilocalories per pound of $BM^{0.75}$ (325–375

kcal/kg $BM^{0.75}$). This estimate agrees closely with that presented by Haigh and Hudson (1993), when converted to a $BM^{0.75}$ basis, and the estimate calculated using a factorial approach by Cook (2002). However, it is markedly greater than previously estimated for elk by Nelson and Leege (1982, see Cook 2002). Their estimate (75–78 kilocalories per ounce, 2.65–2.75 kcal/g) may satisfy maintenance (i.e., constant body fat levels) of adult lactating cows, but definitely will retard growth of calves and yearling cows (Cook *et al.* 1996, 2004), and probably will preclude recovery by adult cows of all mass lost the previous winter if the winter is harsh (Cook 2002). Occasional reproductive pauses (Cameron 1994) by individuals might occur in elk herds existing on such a “maintenance” plane of nutrition.

It is clear that nutritional “requirement” should be considered as a gradient, along which different levels of performance can be expected. Thus, nutritional requirements are most relevant in the context of animal performance targets, which of course is largely a function of what the public and wildlife managers expect or desire. One value of our research is to provide standards of performance (Table 1) with which to gauge the likelihood of nutritional limitation and to relate animal performance to nutritional resources in

management settings. We mention several precautions for these guidelines. First, they are intended to apply to lactating cows, because we assume that game managers are concerned primarily with productivity of their cows, not merely the maintenance of non-reproductive cows. Second, high mortality of juveniles particularly in summer and early autumn can mask inadequate nutrition, because adults are spared to some extent the nutritional demands of raising an offspring (Verme and Ullrey 1984). It may be that overall fat levels of cows in herds experiencing high juvenile mortality in summer are greater than those in herds with low mortality, despite identical nutritional environments for both. Finally, our finding that seemingly small differences in DE content of forage have large effects on the performance of elk suggests some cautions for forage quality surveys. The ability of herbivores to select diets significantly greater in quality than generally available (Schwartz and Hobbs 1985) restricts the interpretive value of general forage quality surveys. Also, field and laboratory techniques that cause even a small bias of estimated DE in forage (just 10 percent) also might lead to important misinterpretations of nutritional adequacy.

RESEARCH AND MANAGEMENT IMPLICATIONS

Our study did not directly test the hypothesis that forage conditions in summer and autumn do, in fact, exert strong limiting influences on free-ranging elk. The extent to which our findings are indeed relevant to management largely depend on how well our nutrition treatments represent the range of forage quality consumed by free-ranging elk. This caveat is particularly important for the low nutrition treatment because its effect was so debilitating. This low level was based on the actual dietary quality of cattle (Holeček et al. 1981) and elk (J. G. Cook, unpublished data, 1995) determined in low- to-moderate elevation, forest zones during dry years in the Blue Mountains of northeastern Oregon. Also, based on

the review of Cook (2002), DE content of wild herbivore diets typically ranges from 71–92 (2.5–3.25) in early summer, 64–85 (2.25–3.0) in mid-summer, 62–71 (2.2–2.5) in late summer, 57–74 (2.0–2.6) in mid-autumn, and 36–57 kilocalories per ounce (1.25–2.0 kcal/g) in late autumn, based on western U.S. and Canadian studies ($n = 20$). If these studies provide reasonable estimates of actual diets for wild elk, then (1) the DE levels in our high nutrition group generally exceeded that of free-ranging elk by late summer, (2) our medium nutrition level generally mimicked the higher range of these estimates after mid-summer, and (3) our low nutrition level fell within these ranges by late summer. If so, it may be reasonable to speculate that marginally adequate to inadequate summer-autumn nutritional conditions prevail in many areas of the West. Where this is in fact the case, some of the consequences that can be expected include low or declining herd productivity, reduced hunting opportunity, increased severity of die-offs in relatively harsh winters, and perhaps increased damage by wild ungulates on agricultural lands.

Elk herd declines in the Northwest are becoming a markedly contentious issue in the region, spawning (1) a plethora of newspaper articles decrying reduced hunting opportunity, calling for widespread predator control, and accusing mismanagement by state wildlife departments, (2) new, expensive research to identify causes, and (3) even state-level legislative directives. These declines, along with the more widespread and recognized declines in mule deer populations (Carpenter 1998), are creating serious new challenges for large-ungulate biologists in the 21st century. Causes of declines are being debated (see Johnson et al. 2004), and contributions of nutrition (among other factors) have been postulated, acting through density-dependent mechanisms (McCullough 1984, Fowler 1987, Irwin et al. 1994) or via advancing forest succession in some areas (Gill et al. 1996; Bomar 2000; Peek et al. 2001, 2002) following years of fire suppression,

and more recently, curtailment of timber harvest on federal lands.

Despite a rich history of elk research over the last three decades, there has been little focus on influences of nutrition on elk herd abundance, productivity, and demographics, and on how management's influence on forage quality and quantity might affect these population attributes. Similarly, nutrition's role has been discounted in most of the habitat models and habitat evaluation procedures used by federal and state land and wildlife management agencies to manage vast areas on behalf of elk (Edge et al. 1990). Findings of our study and others indicate that nutritional attributes of habitat are at least as important for habitat modeling and planning as those habitat attributes (e.g., thermal cover, hiding cover, distance to roads, and other such factors) typically included in these models and procedures. This is true whether elk herds are declining or not. Parker et al. (1999) noted that nutrient requirements, foraging and digestive efficiencies, and forage characteristics provide functional cause-and-effect relations that influence nutritional condition and body mass dynamics, and ultimately, reproduction and survival, and that most interrelations among them are quantitatively predictable. Thus, nutritional ecology "offers the prospect of a quantitative, predictive, and general theory of key relations between" large ungulates and their habitat (Parker et al. 1999:6). A number of efforts exist to model nutritional influences and nutrition-based carrying capacity for elk (e.g., Hett et al. 1978, Hobbs et al. 1982, Hobbs and Swift 1985, Roloff et al. 2001). But the explicit objectives and approaches of these efforts to consider nutrition were never incorporated into the Habitat Effectiveness/Habitat Suitability approaches routinely applied on behalf of elk by most state and federal agencies in the West. We think that nutritional ecology provides a compelling basis for large-scale habitat evaluation procedures, and that the need for incorporating nutrition into habitat evaluation procedures is heightened by new challenges presented

by declining ungulate herds. Moreover, we think that a growing body of literature provides a compelling case for evaluations of nutrition on summer-autumn range, in addition to that on winter range in many ecosystems. Reliable, nutrition-explicit, and large-scale habitat planning and management, however, undoubtedly will require a new research emphasis that links fine-scale nutritional attributes of habitat to population dynamics of elk herds.

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Photo by F. Vanni



Photo by M. Wisdom



Ungulate-proof fence

Map by B. Naylor

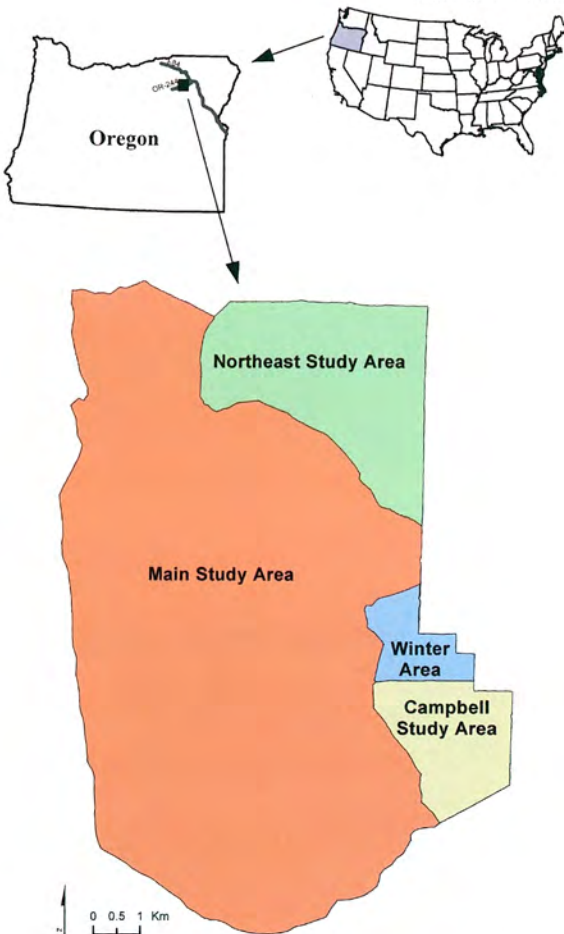


Photo by M. Wisdom



Aerial view of fence line

The USDA Forest Service Starkey Experimental Forest and Range (Starkey), located in northeast Oregon, is the site of a 25,000-acre, ungulate-proof research enclosure (bottom left). Established in 1987 with the construction of over 40 miles of 8-foot-high, New Zealand woven-wire fence (right), the enclosure consists of four separately fenced areas (bottom left) for long-term studies on elk, mule deer, and cattle.

Photo by F. Vanni



Summer

Photo by M. Wisdom



Winter

Photo by R. Cook



Elk

Photo by G. Zahm



Mule deer

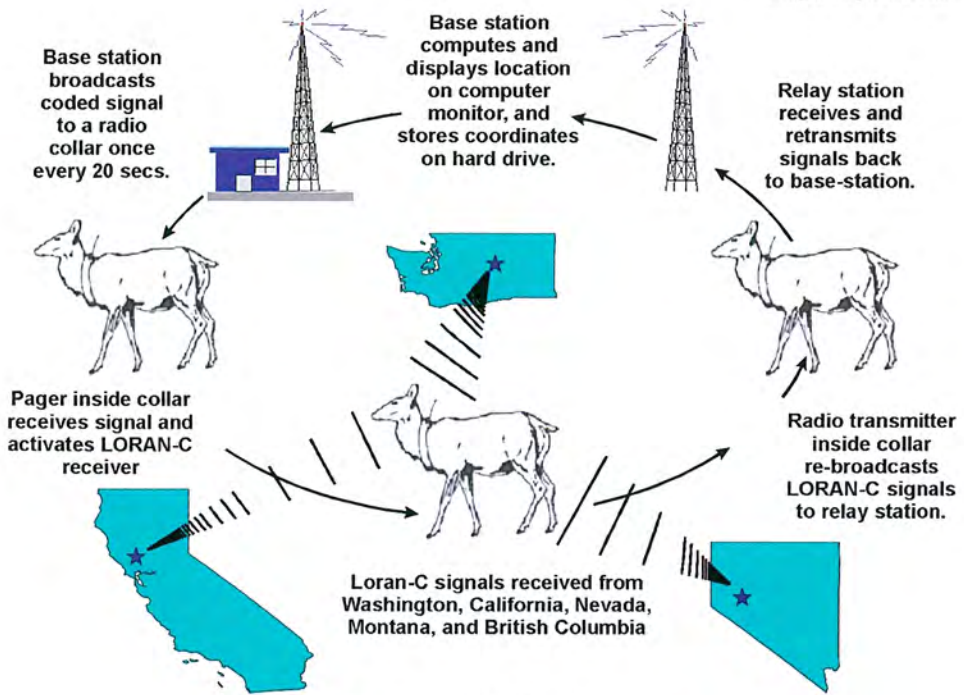
Photo by M. Wisdom



Cattle

The Starkey landscape is a mosaic of forests and rangelands typical of National Forests in the interior western United States. Ponderosa pine, Douglas-fir, and grand fir forests are intermixed with bunchgrass and meadow communities, providing summer range for elk, mule deer, and cattle. Winter snow pack at Starkey usually ranges from 2–4 feet, precluding use as ungulate winter range. Consequently, ungulate research at Starkey occurs from mid-April to mid-December of each year.

Diagram by J. Abcitta



Loran-C automated telemetry system

Photo by L. Naylor



Loran-C (left) and GPS (right) radio collars on Starkey elk

Photo by D. Johnson



Starkey Base Station

Long Range Aid to Navigation (LORAN-C) technology developed by the United States Coast Guard for ship navigation was adapted by Starkey scientists to establish an automated telemetry system (ATS) in 1989. The frequency and order in which radio-collared elk (bottom left), deer, and cattle are relocated can be programmed with hardware and software at the Starkey Base Station. Animal locations can be generated as frequently as every 20 seconds, 24 hours a day, and viewed in real time at the Base Station. A new ATS based on global positioning system (GPS) technology will be installed at Starkey in 2005 to replace the LORAN-C technology.

Photo by M. Wisdom



Winter feeding with alfalfa hay

Photo by M. Rowland



Elk in handling chute

Photo by M. Wisdom



Elk handling facility

Photo by M. Rowland



Bull elk in pen at handling facility

Photo by B. Johnson



Deer released from portable trap after handling

Elk and mule deer are fed from mid-December to late March at the 655-acre Winter Area to minimize the confounding effects of winter weather and foraging conditions on animal responses to the summer range experiments. The Winter Area's elk handling facility allows for pregnancy and disease testing, and for measurements of percent body fat and weight, all of which are analyzed as response variables as part of the summer range experiments. Similar tests and measurements are completed for mule deer with the use of portable traps.



Road construction



Timber felling



Log loading



Log hauling

Photo by J. Boyd

Photo by D. Johnson



Post timber harvest



Radio-collared cattle on post-harvest site

Cattle and elk responses to intensive timber harvest were studied in Starkey's Northeast Study Area, and elk responses to varying levels of thermal cover were studied at the Kamela research site. Elk vulnerability to hunting increased in the open, post-timber harvest landscape at Starkey, but cattle and elk performance (summer weight gains) was not affected. At Kamela, elk performance was higher in treatment sites with no thermal cover, or a mix of openings and thermal cover, in contrast to treatment sites with thermal cover only.



Cattle rotation into new pasture

Photo by S. Findholt



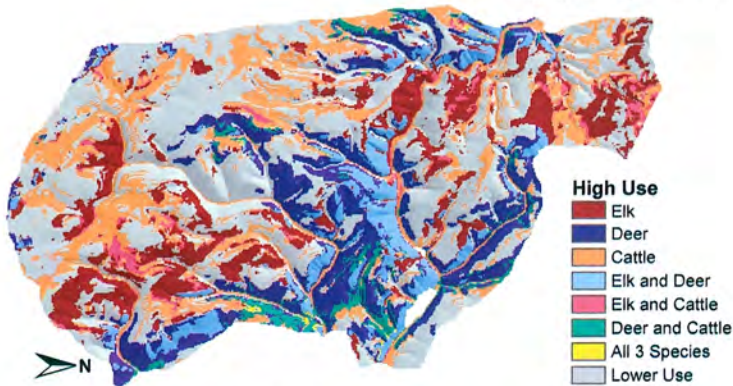
Diet selection study—cattle

Photo by S. Findholt



Diet selection study—mule deer

Map by B. Naylor and J. Boyd



Spatial separation and overlapping use areas among elk, deer, and cattle

The forage allocation study at Starkey evaluated diet selection and spatial distributions of elk, mule deer, and cattle under a deferred rotation grazing system for cattle. Results showed that diets and spatial distributions among the species were distinctly different in early summer and became more similar in late summer and early fall. Results indicated that the late summer-early fall period, when forage biomass and nutritive content is low, is likely to be the primary time period of potential competition.

Photo by E Vanni



Mature bull elk at Starkey

Photo by M. Wisdom



Starkey elk hunter

Photo by M. Wisdom



Hunters check maps at
Starkey Hunter Check Station

Photo by M. Wisdom



Hunter at Starkey Hunter
Check Station

Photo by M. Wisdom



Tooth extraction from harvested
elk at Starkey to estimate
age

The breeding bull study of elk at Starkey used hunters as part of the research, specifically to maintain the desired age classes of male elk to meet study goals. Results from the study showed that conception dates in female elk were earlier and more synchronous as age of breeding bulls increased. The most efficient breeders were mature (5-year-old) bulls. Based on the results, state and provincial wildlife agencies in western North America now protect a higher percentage of older bulls from hunter harvest to enhance breeding efficiency.

Photo by D. Johnson



All-terrain vehicles pass by traffic counter

Photo by M. Wisdom

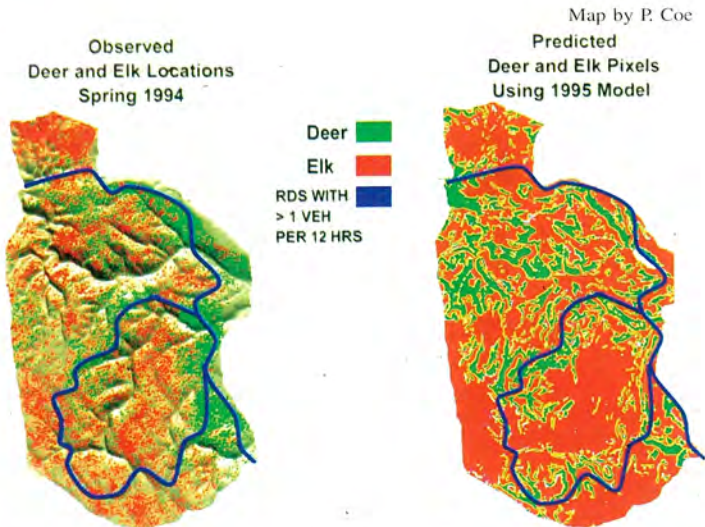


Road closed to motorized traffic

Photo by M. Wisdom



Traffic counter



Observed and predicted spatial separation between elk and mule deer in relation to traffic

Elk and mule deer distributions in relation to closed versus open roads, and to roads with varying rates of motorized traffic, were evaluated in Starkey's Main Study Area. Traffic was estimated with counters placed along roads open to public and administrative use. Results showed that elk avoided open roads, with avoidance increasing with rate of traffic. Additional analyses suggested that mule deer were avoiding elk when selecting areas near open roads and roads with higher traffic rates.

Photo by K. Munday



ATV rider

Photo by M. Wisdom



Mountain biker

Photo by D. Johnson



Horseback rider and elk

Photo by M. Wisdom



GPS unit on
recreationist

Effects of all-terrain vehicle (ATV), mountain bike, horseback, and hiking activities on elk and mule deer were evaluated in Starkey's Northeast Study Area. Recreationists followed transect routes and carried Global Positioning System (GPS) units that were used to estimate human locations. Elk and mule deer responses to each activity were measured by estimating movement rates, flight responses, and other reactions of radio-collared animals. Movement rates and flight responses of elk were higher during ATV riding and mountain biking than during hiking and horseback riding, but elk showed increased reactions to all four activities compared to control periods when no humans were present. Mule deer showed no measurable response to the activities.

Photo by R. Stussy



Elk calf

Photo by M. Wisdom



Rearing tame elk

Photo by M. Wisdom



Loading tame elk for transport

Photo by S. Findholt



Diet-nutrition study with tame elk

Photo by B. Johnson



Evaluating animal condition of elk populations

Studies of elk nutrition at Starkey and associated sites have used tame elk, reared from birth and trained to work in close proximity to humans, to assess diet selection, diet quality, and nutritional plane of animals in relation to varying environmental conditions. Studies of elk nutrition also have evaluated nutritional plane of wild elk routinely captured to estimate pregnancy rates, presence of disease, percent body fat, and other measures of animal condition. A variety of studies led by Starkey partners, particularly the National Council for Air and Stream Improvement, have demonstrated substantial differences in elk condition as affected by varying levels of diet quality and associated habitat conditions.

Photo by M. Wisdom



Fire-suppressed stand with high fuel loads

Photo by M. Vavra



Mechanical thinning to reduce fuel loads

Photo by M. Vavra



Prescribed burning after mechanical thinning

Photo by M. Wisdom



Two years of grazing exclusion (right side of fence) just after mechanical thinning and prescribed burning

Photo by M. Vavra



Aspen and Ceanothus recovery (green area) two years after wildfire and grazing exclusion in northeast Oregon.

New research at Starkey evaluates effects on cattle, deer and elk from fuels treatment reductions (mechanical thinning and burning) to reduce fire risk in fire-suppressed stands. Additional research seeks to understand potential effects of grazing by cattle and elk on vegetation in the resulting thinned and burned sites.

Photo by M. Wisdom



Larry Bryant (center) with Russian scientists

Photo by M. Wisdom



Jim Barrett (foreground) with National Forest managers at Starkey

Photo by M. Wisdom



Starkey tour led by Jack Ward Thomas

Photo by G. Ernst



Public tour at entrance to Starkey enclosure

Starkey scientists share research results with the public, fellow scientists, and resource managers on a regular basis. A variety of communication mediums have been used to complement scientific publications. Over 200,000 people, encompassing local, regional, national, and international groups and agencies, have toured Starkey or heard a presentation. Additional communication mediums have included workshops, symposia, news releases, newspaper features, magazine articles, radio interviews, and television coverage at regional and national levels.

Elk and Mule Deer Responses to Variation in Hunting Pressure

Bruce K. Johnson, Alan A. Ager, James H. Noyes, and Norman J. Cimon

INTRODUCTION

Hunting can exert a variety of potential effects on both targeted and non-targeted ungulates, and animals usually either run or hide in response to hunting pressure. If animals successfully elude hunters by running, the energetic cost may deplete fat reserves needed for survival during winter in temperate regions. If animals successfully elude hunters by hiding, there also may be an energetic cost from lost foraging opportunities.

Most studies of ungulate responses to hunting have focused on changes in habitat selection. Ungulates typically respond to hunting by seeking areas of security (Irwin and Peek 1979, Knight 1970, Edge and Marcum 1985, Naugle et al. 1997, Millsaugh et al. 2000), altering activity patterns (Naugle et al. 1997), adjusting home ranges (Kufeld et al. 1988, Root et al. 1988) or moving long distances (Conner et al. 2001, Vieira et al. 2003). However, the difficulty of monitoring hunter density and elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) populations on large landscapes has prevented the collection of sufficient data to develop models of energetic costs associated with hunting or other recreational activities. Variation in weather, hunter density, herd dynamics, and seasonal conditions can likely bring about changes in the interactions between hunters and animals, making generalizations tenuous at best. Quantitative relationships between levels of hunting pressure and energy expenditure can be used to evaluate potential secondary effects of activities on nutritional condition of ungulates. For instance, frequent human disturbance that results in high energy expenditure by ungulates could adversely affect animal weight dynamics in winter when forage is scarce,

or in summer when energy requirements are high for lactation and rebuilding body mass following winter (Cook et al. 2004).

In this study, we examine the effects of hunter density and associated motorized traffic on movement and habitat use by elk and mule deer over 10 years during 21 rifle and 2 archery hunting seasons at the Starkey Experimental Forest and Range (Starkey). Our goal was to quantify the relationship between levels of hunting pressure, as measured by hunter density and traffic counts, and changes in movement and habitat use patterns. These relationships were then used to estimate effects from variation in hunting pressure and type of hunt on daily and seasonal energy budgets of elk and mule deer.

STUDY AREA

Starkey Experimental Forest and Range covers 40 square miles (101 km²) on the Wallowa Whitman National Forest, 21 miles (35 km) southwest of La Grande, Oregon (45°15'N, 118°37'W). Our study was conducted in Main Study Area (30 square miles, 77.6 km²), which was enclosed with 7.9 feet-(2.4-m) tall woven-wire fence (Bryant et al. 1993) and has been used for studies on Rocky Mountain elk, mule deer, and cattle since 1989 (Rowland et al. 1997). Starkey contained habitat for elk and mule deer typical of summer range conditions in the Blue Mountains. A network of drainages in the project area created a complex and varied topography. Vegetation at Starkey was a mosaic of coniferous forests, shrublands, wet meadows, riparian areas, and grasslands.

Approximately 37 percent of the study area had forest canopy more than 40 percent, and about 4 percent had forest canopy greater than 70 percent. Traffic lev-

els, recreational activities (including hunting), cattle grazing, and timber management were representative of adjacent public lands. About 500 cow-calf pairs of domestic cattle grazed Main Study Area on a deferred rotation system through four pastures within the study area between 15 June–15 October (Coe et al. 2001). Our study area at Starkey was three to four times larger than typical summer home ranges of elk in the Blue Mountains (7.7–11.2 square miles (20–29 km²)) (Leckenby 1984), providing study animals with large-scale habitat choices commensurate with free-ranging herds. Details of the study area and facilities are available elsewhere (Wisdom et al. 1993, Noyes et al. 1996, Rowland et al. 1997).

MATERIALS AND METHODS

Hunt Sample

We analyzed 13 rifle hunts for elk, 8 rifle hunts for mule deer, and 2 archery hunts for elk, all conducted between 1991 and 2000 (Table 1). Elk rifle hunts were 5–9 days long with 75–175 tags issued to hunters and deer rifle hunts were 7–12 days long with 25 tags. Archery hunts were 30 days long with 85 tags. We staffed a hunter check station starting the day before the opening of each hunt through the end of the hunt for all elk rifle hunts and through the first three days of the deer hunts and intermittently during the rest of the deer seasons. We staffed the archery check station during most days with project personnel or volunteers. For each hunter, we recorded number of days hunted and success. Prior to any hunts, the yearling and adult elk populations were estimated between 313 and 443 females and 78 to 153 males (Noyes et al. 1996, 2002), and the mule deer population was estimated between 262 and 342 (Rowland et al. 1997). Densities of adult elk and deer in the study area were similar to those on adjacent public lands (Johnson et al. 2000).

Animal Locations

We determined animal locations with an automated telemetry system that uses

retransmitted Long-range aid to navigation signals (LORAN-C) (Dana et al. 1989, Findholt et al. 1996, Rowland et al. 1997). Each radiocollared elk was used on average 1.6 years, while each mule deer was used about 1.9 years. We monitored between 25–60 elk and 12–33 deer during the hunts. Locations were assigned to Universal Transverse Mercator coordinates of associated 98.4 by 98.4-foot (30 by 30-m) pixels containing habitat information stored in a geographic information system (GIS). Locations had a mean error of 175 ± 19 feet (53 ± 5.9 m SE, Findholt et al. 1996).

Vehicular Traffic

We measured traffic throughout the year from a network of 71 traffic counters (Rowland et al. 1997, 2000). Preliminary analysis of traffic counter data showed that data collected at the counter located 0.15 miles (0.24 km) inside the main gate were highly correlated with data obtained at the other counters located throughout the study area. For this analysis, we used the daily counts of vehicles that passed over the Starkey main entrance counter as an index to total traffic activity. In addition, by using a single counter the application of our results to areas with limited traffic data is made more feasible.

Habitat Variables

We selected 10 variables that were significant in resource selection models for elk or mule deer in previous studies at Starkey (Johnson et al. 2000, Table 1). However, we used distance to open roads rather than distance to roads of various traffic rates, because during hunting seasons daily use of open roads was greater than the minimum value associated with roads with high traffic rates (more than 4 vehicles per 12 hours). Additional details can be found in Johnson et al. (2000) and Rowland et al. (1998).

Data Analysis

We used day as our sampling unit and required a minimum of 10 locations from

TABLE 1A. Summary of elk (E) hunts included in the study held in Main Study Area (30 square miles [77 km²]) at the Starkey Experimental Forest and Range

Hunt label	Date	Days of elk velocity data	Days of deer velocity data	Days of elk habitat data	Days of deer habitat data	Number of hunters/day	Traffic counts/day	Elk locations	Deer locations	Available dependent variables for elk telemetry H = habitat V = velocity	Available dependent variables for deer telemetry H = habitat V = velocity	Available independent variables [both deer and elk] Hu = hunters T = traffic
E3 ¹	15–23 Aug 92	6	Na ⁶	8	Na	19–168	65–245	904	0	HV		HuT
E4 ²	5–12 Dec 92	3	Na	4	Na	24–73	59–103	753	0	HV		HuT
E5 ¹	14–22 Aug 93	3	5	6	6	50–117	74–164	1855	771	HV		HuT
E6 ³	27 Aug–25 Sep 94	30	20	30	30	2–53	26–66	6368	4146	HV	HV	HuT
E7 ¹	26–30 Oct 94	5	5	5	5	74–113	87–116	1552	1122	HV	HV	HuT
E8 ⁴	5–13 Nov 94	9	9	9	9	25–130	42–168	3407	2054	HV	HV	HuT
E9 ⁵	19–27 Nov 94	7	7	7	7	7–63	25–106	2264	1588	HV	HV	HuT
E10 ¹	18–25 Aug 96	9	1	9	4	15–134	Na	2632	318	HV		Hu
E13 ²	29 Nov–5 Dec 97	5	5	5	5	12–69	Na	3972	2106	HV	HV	Hu
E15 ²	5–11 Dec 98	4	5	4	5	13–46	2–25	1496	723	HV	HV	HuT
E18 ¹	1–5 Aug 00	3	4	4	4	33–122	Na	859	712	HV	HV	Hu
E19 ³	25 Aug–24 Sep 00	29	28	30	30	12–52	1–33	9709	5993	HV	HV	HuT
E21 ²	3–9 Dec 94	3	3	3	3	51–82	76–105	890	634	HV	H	HuT

¹ Rifle spike-only elk hunt² Rifle antlerless elk hunt³ Archery any elk hunt⁴ Rifle any elk hunt⁵ Rifle antlered elk hunt⁶ Data not available due to sample size restrictions of 10 animals each with 10 locations, missing traffic counts, or missing hunter number.

TABLE 1B. Summary of mule deer (D) hunts included in the study held in Main Study Area (30 square miles [77 km²]) at the Starkey Experimental Forest and Range

Hunt label	Date	Days of elk velocity data	Days of deer velocity data	Days of elk habitat data	Days of deer habitat data	Number of hunters/day	Traffic counts/day	Elk locations	Deer locations	Available dependent variables for elk telemetry H = habitat V = velocity	Available dependent variables for deer telemetry H = habitat V = velocity	Available independent variables [both deer and elk] Hu = hunters T = traffic
D1 ¹	28 Sep–4 Oct 91	5	Na ²	7	Na	Na	48–85	842	0	HV		T
D2 ¹	3–9 Oct 92	4	Na	4	Na	Na	58–145	1042	0	HV		T
D3 ¹	2–8 Oct 93	7	4	7	6	2–16	33–71	2272	878	HV	HV	HuT
D4 ¹	1–12 Oct 94	10	4	10	10	Na	14–54	2040	1322	HV	HV	T
D7 ¹	30 Sep–11 Oct 97	8	7	8	7	3–12	Na	4294	2079	HV	HV	Hu
D8 ¹	3–14 Oct 98	12	7	12	12	0–24	10–100	4225	1615	HV	HV	HuT
D9 ¹	2–13 Oct 99	11	Na	12	12	Na	11–43	3515	1412	HV	HV	T
D10 ¹	30 Sep–11 Oct 00	Na	10	12	12	Na	55–158	4363	2410	H	HV	T

¹ Rifle antlered deer hunt.

² Data not available due to sample size restrictions of 10 animals each with 10 locations, missing traffic counts, or missing hunter numbers.

each of at least 10 animals of a species per day. Choice of minimum sample sizes was based on previous analyses (Ager *et al.* 2003). We calculated velocity (animal speed) using successive locations by dividing the horizontal distance moved by the elapsed time. We deleted velocity for any location if elapsed time to the previous location was <5 min or >240 min. Shorter elapsed times (less than 5 min) yielded velocities that were positively biased because of the random location error in the telemetry system. Velocities determined at longer elapsed times were negatively biased as a result of undetected movements between observations and home range effects (Ager *et al.* 2003). For habitat analysis, average sample size for elk during elk hunts was 254 observations per day on a total of 23 animals. Deer sample size during elk hunts was 171 observations per day on 15 animals. Sample sizes for velocity calculations were reduced approximately 15 percent as a result of the time filter placed on data.

Response Variables

We compared responses of elk and deer during elk and deer hunts to seven-day pre-hunt periods that started two weeks before the start of the hunting season. We calculated daily average velocity of elk and mule deer as dependent variables and used daily traffic counts and hunter density as independent variables in a regression analysis. We used the daily averages for the pre-hunt periods to set the intercept.

We calculated hourly velocities and habitats used for the pre-hunt and hunt periods and examined how normal diel patterns changed in relation to variation in hunter density. We pooled data across all animals and hunts to maximize the number of hunting days in the analysis. Although hunt-to-hunt variability was of interest, our goal was to obtain an overall estimate of animal response over a wide range of hunting conditions. Variation among hunts was high and a number of hunts had one or more of the following conditions: 1) limited data for pre-hunt conditions; 2) limited variability in the

hunter density and traffic counts; and 3) differences in the range of traffic and hunter density. Thus, using a single linear model containing a term for individual hunts would have reduced the possibility of obtaining useful information from several of the hunts, but the effects among the hunts would not have been comparable in many cases. We did not pool animals used in multiple years but rather considered them independent samples in each hunt because day was the sampling unit. We did not test for serial correlation in the data from successive days within a hunt after observing that elk and deer response to hunters at Starkey is dynamic and rapid in terms of changes in distribution and velocity.

Energetic Calculations

We estimated energy costs as a function of velocity from equations provided by Robbins *et al.* (1979:449) and Parker *et al.* (1984:478). Robbins *et al.* (1979) estimated the cost of locomotion in kcal/kg/hr where Parker *et al.* (1984) estimated cost of locomotion in kcal/kg/min. Robbins *et al.* (1979) estimated cost of location on slopes for uphill and downhill, but we did not factor energy costs for slope because we could not accurately estimate animal paths and their respective slopes. The differential energy expenditure for uphill versus downhill travel results in an underestimation of energy expenditure. Average slope at Starkey was 17 percent.

RESULTS

Daily density of hunters per square mile averaged 2.4 (0.91 hunters/km², range 0.03–1.66/km²) for elk hunts, 0.1 (0.04 hunters/km², 0–0.31/km²) for deer hunts, and 0.7 hunters per square mile (0.26 hunters/km², 0–0.67/km²) for archery hunts. Daily traffic counts averaged 78 (6–272, range) for elk hunts, 56 (10–158) for deer hunts, and 55 (17–133) for archery hunts. During the pre-hunt periods, vehicles per day averaged 46 (18–86) before archery, 45 (1–165) before elk rifle, and 27 (1–65) before deer hunts. All deer hunts were excluded from further

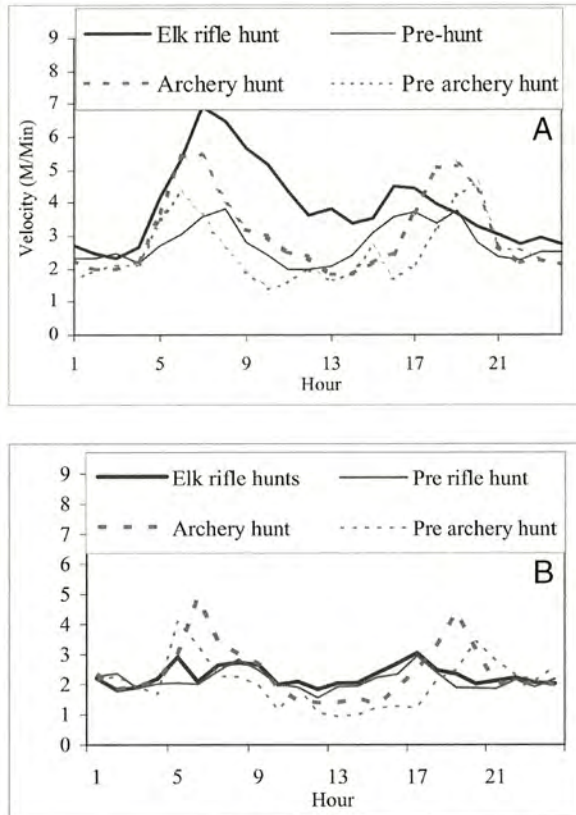


FIGURE 1. Mean hourly velocities of elk (A) and mule deer (B) during and before rifle and archery hunts at Starkey Experimental Forest and Range.

analysis because there was no measurable response of elk or mule deer during deer hunts, most likely because of the low hunter density and traffic rates.

Velocity

Velocity of elk movements increased during rifle and archery hunts (Figure 1A). During non-hunt periods, elk displayed daily patterns of velocity characterized by crepuscular peaks of about 11.5 feet per second (3.5 m/min) at 0600–0800 and 1700–1800 hours, and lower mid-day velocity of around 6.6 feet per second (2 m/min) during non-hunt periods. Elk velocity was greater in the early morning during rifle hunts than during archery hunts, but this pattern reversed during the afternoon (Figure 1A). Differences in timing of peaks during pre-hunt periods for archery and rifle hunts probably

reflects differences in sunrise and sunset times for September versus December hunts.

During elk rifle hunts, the daily patterns of velocity were strongly affected by hunter density (Figure 2). At the lower density values (<0.8 hunters per square mile, <0.3 hunters/km²) the crepuscular peaks were broader and increased by around 3.3 feet per minute (1 m/min), and the mid-day velocity returned to pre-hunt levels. At high hunter density, >3.2 hunters per square mile (>1.25 hunters/km²), the daily pattern consisted of large velocity increases throughout the day, with a peak at 0800 h that was about 20 feet per minute (6 m/min) above the pre-hunt velocities (Figure 2). Only between 0000 to 0400 h did the velocity at high hunter density return to values close to pre-hunt conditions.

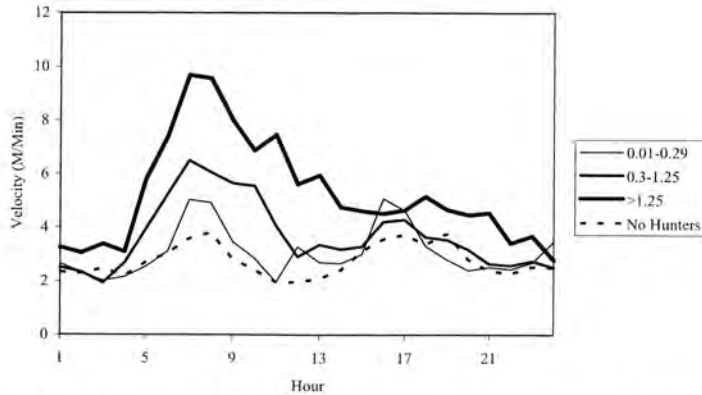


FIGURE 2. Hourly velocities of elk at four hunter densities (hunters/km²) for elk rifle hunts at Starkey Experimental Forest and Range.

Daily mean velocity of elk to rifle hunter density showed a linear relationship (Figure 3, $R^2 = 0.46$, $P < 0.001$), the velocity increasing 1.4 meters per min per hunter/km². The regression predicts that at the highest daily rifle hunter densities during the Starkey hunts, estimated mean velocity of elk would increase from 6.9 feet per minute (2.7 m/min) during the pre-hunt period to around 16.5 feet per minute (5 m/min). Effects of archery hunters on elk appeared to be greater than that of rifle hunters, as velocity increased 2.2 meters per minute per hunter/km² ($P < 0.001$) (Figure 4).

Mule deer showed little increase in hourly velocities during elk rifle hunting

seasons (Figure 1B) except for a small increase in velocity around 0500 h. However, there was no significant increase in mule deer velocity as rifle hunter density increased (Figure 3). Mule deer velocity increased as archery hunter density increased (Figure 4, $P < 0.001$), and the hourly velocities during archery season increased at sunrise and sunset (Figure 1B).

There was a positive relationship between traffic counts during elk rifle seasons and daily mean velocity of elk (Figure 5, $R^2 = 0.28$). However, this relationship was considerably weaker than that between hunter density and velocity. Also in contrast to rifle hunts, no relationship

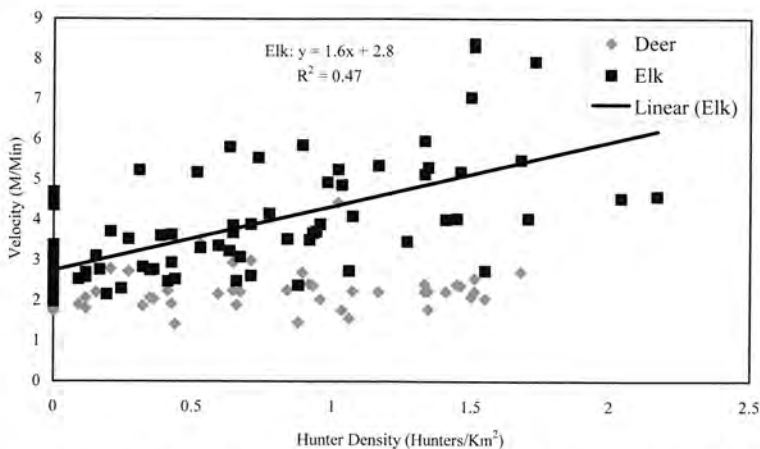


FIGURE 3. Daily mean elk and mule deer velocities versus hunter density for elk rifle hunts at Starkey Experimental Forest and Range.

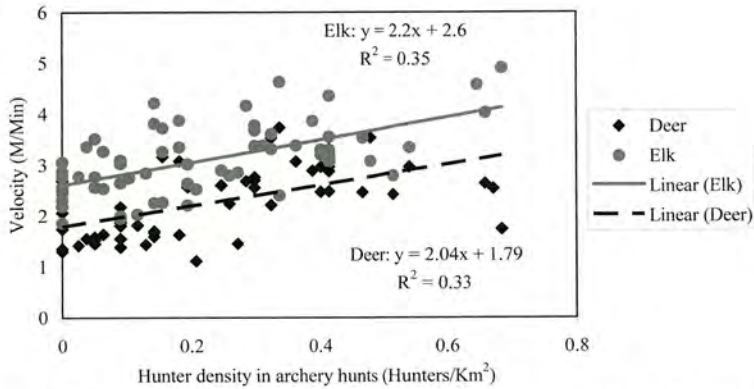


FIGURE 4. Daily mean elk and mule deer velocities versus hunter density for elk archery hunts at Starkey Experimental Forest and Range.

was observed between traffic counts and elk velocity during the archery hunts, likely due to the lower traffic levels. Deer showed a very low response to increased levels of traffic (Figure 5).

Habitat Variables

Distance of elk to open roads increased as both elk rifle hunter density ($y = 83x + 751$, $r^2 = 0.12$, where x = hunter/km²) and traffic counts increased ($y = 0.8x + 740$, $r^2 = 0.11$, where x = daily traffic count and y is distance in m). During archery seasons, as hunter density increased, elk use of canopy cover decreased ($y = -7.3x + 38.5$, $r^2 = 0.18$, where x = hunter/km² and y = percent canopy cover). There were no other sig-

nificant relations in traffic or hunter density during the archery seasons and any other habitat variables. Hourly habitat use at different levels of hunter density showed that pre-hunt daily patterns of habitat use for distance to open road (Figure 6) and all other habitat variables (not shown) were increasingly disrupted as hunter density increased. In addition to disruption, distance of elk to open roads increased especially in the nighttime hours, when elk did not move closer to roads when compared to pre hunt distributions.

Energetic Cost of Hunting for Elk

At the average hunter density observed in this study, 2.3 hunters per square mile

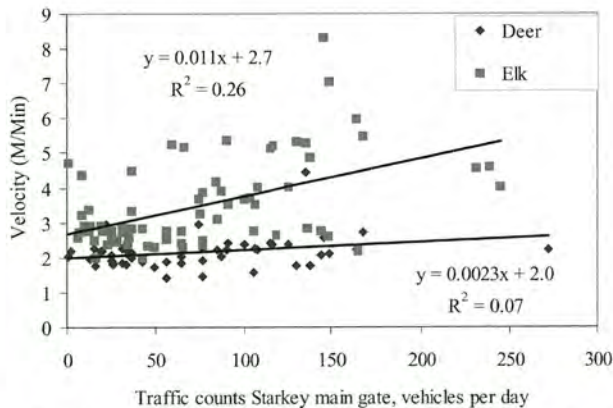


FIGURE 5. Elk and mule deer velocities versus traffic counts before and during elk rifle hunts at Starkey Experimental Forest and Range.

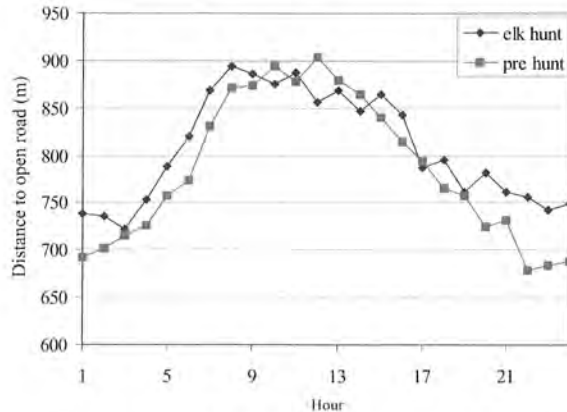


FIGURE 6. Hourly average distance of elk from an open road during rifle elk hunts at Starkey Experimental Forest and Range.

(0.91 hunters/km²), elk velocity increased 4.3 feet per minute (1.3 m/min) over the background velocity for the non-hunt periods. Based on the relationships provided by Robbins *et al.* (1979) and Parker *et al.* (1984), this velocity increase translates to a 4 percent (Parker *et al.* 1984) or 10 percent (Robbins *et al.* 1979) increase in the normal daily energy budget. This estimate was slightly conservative because it assumed travel was on level ground.

DISCUSSION

This study represents our first attempt to measure the effects of variation in hunting pressure on elk and deer over a wide range of hunter densities, hunting conditions, traffic rates, and rifle versus archery hunting. We found that elk responded by fleeing disturbance whereas deer appeared to elude hunters by hiding. Our data indicate that both traffic counts and hunter density have a positive linear relation with elk velocity. Moreover, hunter density appears to be a better indicator of animal disturbance than traffic counts, especially for archery hunts. We found differences between the archery and rifle hunts in terms of animal responses; however, the study only included two archery hunts. Archery hunts appeared to affect animal movements for a longer portion of the day, suggesting that archers are actively pursuing elk throughout the day and evening.

In contrast to other previous studies (Irwin and Peek 1979, Edge and Marcum 1985, Millspaugh *et al.* 2000), we did not find major shifts in habitat use by elk or mule deer during the elk rifle hunting seasons. However, the daily patterns of habitat use were disrupted. We also did not observe any effects on elk or deer from the deer rifle hunts, most likely due to the low hunter densities associated with these hunts.

The results of this study suggest that energetic costs to elk from hunting may be significant in the context of both hunter density and the number of days over which hunting occurs; however, the energetic costs to deer may not be as great. In northeast Oregon, many of the wildlife management units have 30 days of archery hunting followed by 12 days of mule deer rifle hunting, 14 days of rifle elk hunting, and up to 9 days of antlerless elk hunting, totaling 56 to 65 days of hunting. In 1999, Oregon Department of Fish and Wildlife (2000) estimated that there were 61,804 and 49,063 recreational days for elk and mule deer hunting in the Starkey and Ukiah Wildlife Management Units (WMU), respectively. There were 726 square miles (1,859 km²) and 568 square miles (1,453 km²) of deer and elk range in the Starkey and Ukiah WMUs, respectively (Oregon Department of Fish and Wildlife 1986) for a hunter density of 1.35 hunters per day per square mile (0.53 hunters/day/km²).

Based on our estimate of increased velocity associated with rifle hunter density, and the energetic relationships identified in Parker et al. (1984), this equated to an additional energy expenditure of 310 kcal/day for an adult cow elk assumed to weigh 510 pounds (232 kg). Assuming this additional energy comes from stored fat reserves and there are 9 kcal/g of fat, this results in 1.2 ounces (35 g) of fat consumed per day or 4.4 pounds (2 kg) for the entire 63 days of hunting due to disturbance from hunters. Assuming the ingesta-free body mass of a lactating cow elk is 440 pounds (200 kg) and has 10 percent body fat, these 4.4 pounds (2 kg) of body fat represent about a 10 percent reduction in body fat. Cook et al. (2004) suggest that elk reproduction may be affected when body fat falls below 9 percent and marginally affected at levels between 9–13 percent, conditions that occur in lactating cow elk in late autumn. Because most of the hunting disturbance occurs after the rut, the reduced fat levels may be more important during harsh winters and may carry over through the next year as cows rebuild tissues catabolized during winter.

Elk and mule deer at Starkey were closed populations; thus animals were unable to escape from human harassment by moving to private lands or other reserves. Without hunting, the movement rates we observed at Starkey were similar to those reported by Craighead et al. (1973) and Shoen (1977). In northeast Oregon, private lands, wilderness, and roadless or road management areas provide areas where hunter density is lower. Thus, our estimates of energy expenditure for elk in our example may be high for those animals that are able to move to secluded areas where hunter density is low. However, animals that respond to hunting pressure by moving long distances away from that pressure also would exert substantial energy that our study does not address.

Our energy calculations do not account for disruption of foraging cycles where foraging patterns are shortened or animals move to more secluded areas with poorer

forage resources. If those situations occur, then the effects of hunter density will be much more pronounced than we estimated. These potential effects deserve attention in future studies. Estimating absolute levels of energy loss will take more accurate measures of activity patterns, distributions, and forage quality of ungulates in relation to variation in hunting pressure. For our analysis we did not distinguish between flight movements and foraging, which require more precise monitoring of elk to quantify the disruption of foraging patterns.

Our results may have implications for design and management of access and hunting seasons for mule deer and elk. First, the energetic costs of eluding hunters may be substantial under the combination of high hunter densities and long hunting seasons. The added energetic costs may have the potential to increase mortality of animals beyond those harvested in areas with severe winter conditions. Second, the motorized access provided to hunters, in combination with hunter density and season length, may affect the degree to which non-harvested animals are negatively affected by hunting. For example, it may be possible to reduce or restrict human access, particularly motorized access, as part of hunting seasons, and still accommodate higher hunter density without negative energetic costs on non-harvested animals. Or, alternatively, if motorized access is relatively unrestricted and landscape conditions facilitate ease of human movement (e.g., flat terrain and open environments), then managers may consider modifications in hunter densities and season lengths to meet population objectives for elk and mule deer. Such trade-offs deserve careful consideration in the integrated planning of human access with design of hunting seasons for management of elk and mule deer.

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Movements and Habitat Use of Rocky Mountain Elk and Mule Deer

Alan A. Ager, Haiganoush K. Preisler, Bruce K. Johnson, and John G. Kie

INTRODUCTION

Understanding ungulate use of large landscapes to meet their daily needs for food, security and other resources is critical to wildlife management and conservation practices (Johnson et al. 2002). For ungulates like Rocky Mountain elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*), landscapes are a mosaic of different resources that are exploited in well defined seasonal and daily cycles to meet metabolic and security needs (Green and Bear 1990). Complex movement patterns emerge when the cyclical behaviors are realized on landscapes that are heterogeneous in space and time (Gross et al. 1995, Etzenhouser et al. 1998). Both the juxtaposition and grain of habitat patches within a home range are strong determinants of movement patterns and overall habitat suitability (Etzenhouser et al. 1998). The influence of patch arrangement on habitat quality was recognized in early elk habitat models (Leckenby 1984, Thomas et al. 1988). However, the linkage between movement patterns and habitat arrangements had not been explicitly studied.

In this paper we describe a progression of studies at Starkey that document Rocky Mountain elk and mule deer movements and habitat use. The work focused on inter-patch movements associated with crepuscular habitat transitions and did not consider finer-scale movements associated with foraging activities (Gross et al. 1995, Johnson et al. 2002). We first used the Starkey data to describe the linkage between ungulate movements and habitat selection at Starkey (Johnson et al. 2000, Rowland et al. 2000) and elsewhere (Mackie 1970, Craighead et al. 1973, Collins et al. 1978, Collins and Urness 1983, McCorquodale et al. 1986,

Beier and McCullough 1990, Green and Bear 1990, Unsworth et al. 1998). This work motivated a subsequent investigation about spatial patterns of movements on the Starkey landscape. We then explored ways to build a behavioral model of movement that encapsulated both habitat use and spatial organization of movements. The paper concludes with a discussion of the importance of understanding movement patterns at multiple scales in the management of elk and mule deer.

STUDY AREA AND DATA COLLECTION

Starkey Experimental Forest and Range (Starkey) covers 63 square miles (101 km²) on the Wallowa-Whitman National Forest, about 25 miles (40 km) southwest of La Grande, Oregon. Starkey is a mosaic of coniferous forest (ponderosa pine [*Pinus ponderosa*], Douglas-fir [*Pseudotsuga menziesii*], grand fir [*Abies grandis*]) and bunchgrass meadows (*Pseudorogneria* spp.) dissected by numerous small drainages (Figure 1), creating a complex array of topography and vegetation. The project area was enclosed with 8-foot (2.4 m) tall woven-wire fence and has been used for studies on Rocky Mountain elk, mule deer, and cattle since 1989 (Wisdom et al. 2004). An automated telemetry system was used to monitor locations of about 50 elk, 50 mule deer and 50 cows from April to December, obtaining locations every 1–2 hours on each animal. The work described here used 400,000 elk and mule deer locations collected over 6 years (1991–1996) within the 48 square mile (77.6 km²) Main Study Area. We used locations from a total of 144 elk and 58 mule deer. Habitat variables were selected based on their impor-

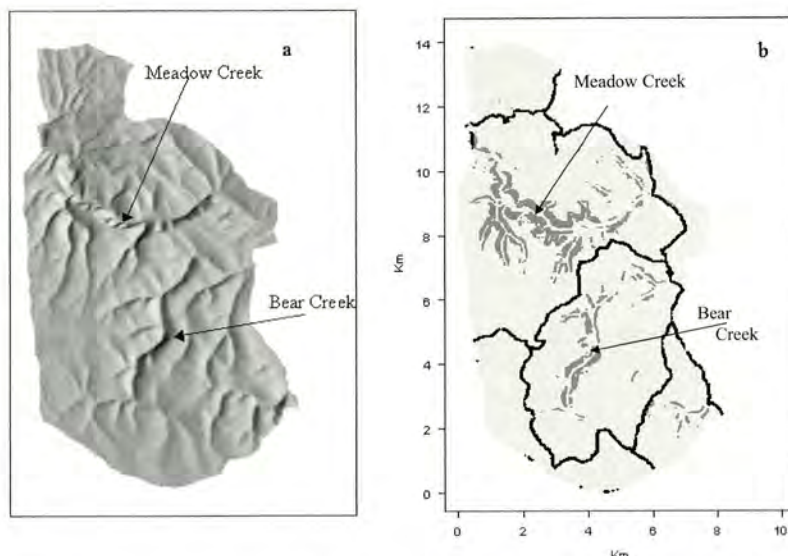


FIGURE 1. Map of Starkey showing topography and major drainages (a), and roads open to vehicular traffic (b). Shaded areas in Figure 1b are areas where slopes are greater than 40 percent.

tance in previous work at Starkey (Johnson et al. 2000).

CYCLES OF MOVEMENT AND HABITAT USE

We studied the daily cycles of elk and mule deer movements and seasonal changes in these cycles by fitting periodic functions to the 1991–1996 location data, and testing for differences among seasons at specific hourly intervals. The key findings of this work are briefly summarized as follows and are reported in detail by Ager et al. (2003). Elk showed pronounced 24-h cycles with crepuscular transitions for many habitat variables, including canopy cover, distance to hiding cover, cosine of aspect (Figures 2a–c), herbage, and distance to open roads (Figures 3a–b). Habitat transitions appeared to be closely linked to rapid changes in elk movements (Figures 4a–b) for most habitat variables, but not all (Figure 5a). Morning movements were uphill (Figure 4b), towards more convex topography (Figure 5b), and at increasing distance to streams (Figure 5c). Afternoon movements were directed towards easterly as-

pects (Figure 5a), steeper slopes (Figure 4c) in valley landforms (Figure 5b), and towards streams (Figure 5c). At dusk, movements were strongly upslope (Figure 4b), out of drainages, and towards areas that are characteristic of foraging areas (lower canopy cover, greater distance to hiding cover, increased herbage production, closer to roads, and more southerly and westerly aspects—Figures 2a–c, 3a–b, 5a). For mule deer, these cycles were largely absent from the data (cf. Figures 2a, 2d), and considerable variation was observed among the individual deer in terms of their habitat use patterns.

The daily patterns of habitat use and movements changed among monthly intervals for elk, and to a lesser extent mule deer. Canopy, distance to hiding cover (Figures 2a–b), and distance to open roads (Figure 3b) changed across monthly intervals in terms of daily amplitudes and average value. Seasonal differences were most evident between late spring (15 April–14 June) and early summer (15 June–14 August). The changes were best explained in terms of forage phenology at Starkey (Skovlin 1967). High daily amplitudes for velocity and habitat variables

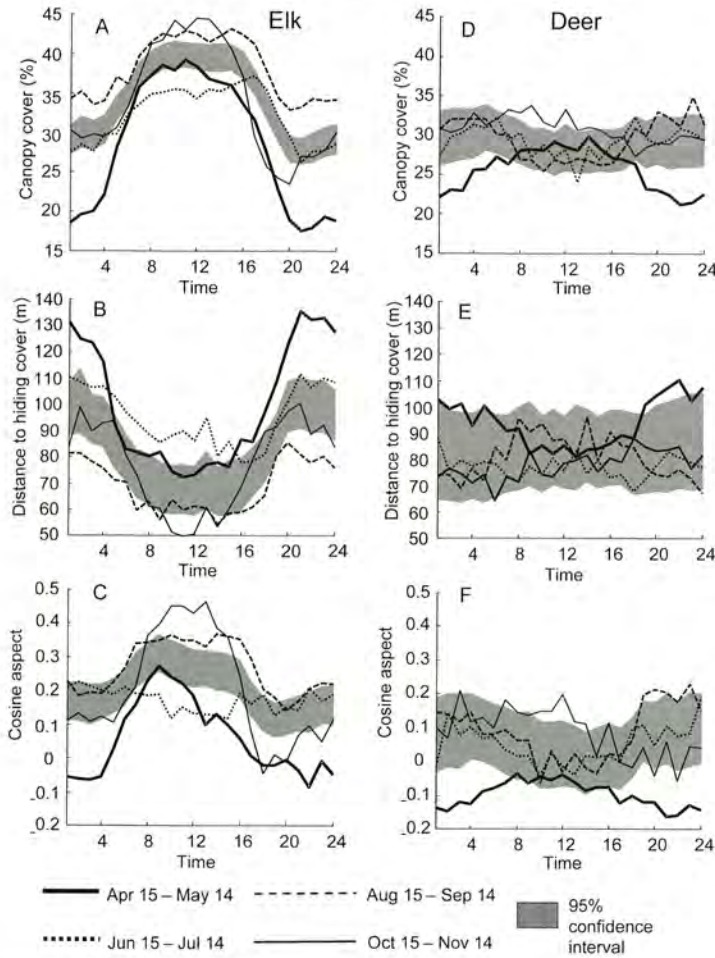


FIGURE 2. Means of habitat variables canopy cover, distance to cover, and cosine aspect by hour and monthly interval for elk (left column) and mule deer (right column). Values plotted are means across animals. For clarity, only 4 of the 7 1-month time intervals are shown (intervals 1, 3, 5, and 7). Shaded area is the grand mean bounded above and below by 2 pooled, within-interval SD. Pooled within-interval SDs represents the average SD within all 7 monthly intervals studied. Figure is from Ager *et al.* (2003).

in the spring (15 April–14 May) and autumn (15 October–14 November) reflected rapid movements to highly preferred meadows at Starkey that produce desired forage in early spring, and in autumn after the first substantial rains (Skovlin 1967). The lower velocity and dampened daily cycles during summer reflected a higher use of forested areas throughout the day and night, which are preferred due to their higher mid-summer forage production (Edgerton and Smith 1971, Holechek *et al.* 1982, Unsworth *et al.* 1998).

SPATIAL PATTERNS OF MOVEMENTS

The results from Ager *et al.* (2003) motivated a number of questions about how elk and mule deer movements are spatially organized on the Starkey landscape. For instance, are there movement corridors between the different habitats? What is the effect of edge on movements? Are movements organized after topography or other features in Starkey? Are there areas of high and low speed of animal move-

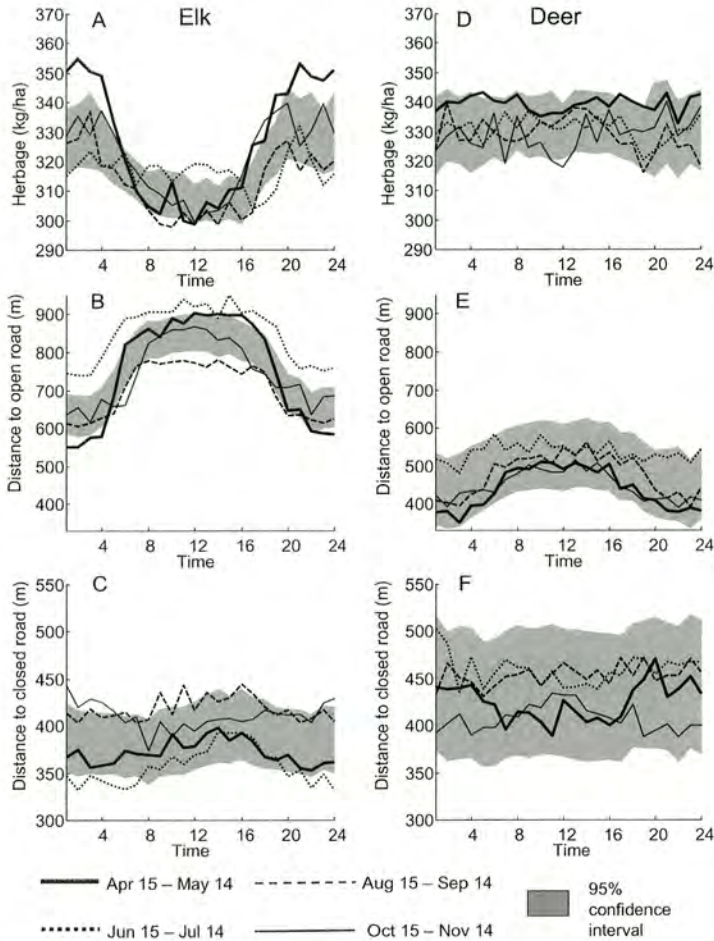


FIGURE 3. Means of habitat variables herbage production, distance to open road and distance to closed road by hour and monthly interval for elk (left column) and mule deer (right column). See Figure 2 for additional explanation. Figure is from Ager et al. (2003).

ments? Are there habitat features that impede movements? Are the dusk and dawn movements reciprocal? To address these questions we explored methods for visualizing spatial movement patterns and found that by smoothing movement vectors with nonparametric regression (Brillinger et al. 2002, 2004; Preisler et al. 2004) and plotting these on a rendered terrain of Starkey, we could address a number of questions related to the spatial component of movement. First, we observed that mule deer movement vectors appeared mostly random and thus had little or no spatial organization, perhaps due to the spatial resolution of the telemetry data and the sampling frequency (Ager et

al. 2003). Elk movement vectors for the mid-summer (15 July–15 August) season also appeared weak, reflecting the lower movement rates during this season (Ager et al. 2003). In contrast, elk movement vectors for spring (15 April–15 June) showed a strong directional component, especially for crepuscular periods (Figures 6a, b). The vector plots for the crepuscular periods showed interesting spatial patterns of movement and provided a number of insights relative to landscape movements. For instance, the vector fields revealed a dendritic pattern of movement (Forman 1995:270) in areas where there is significant topographic relief (Figure 1a). The consequence of the

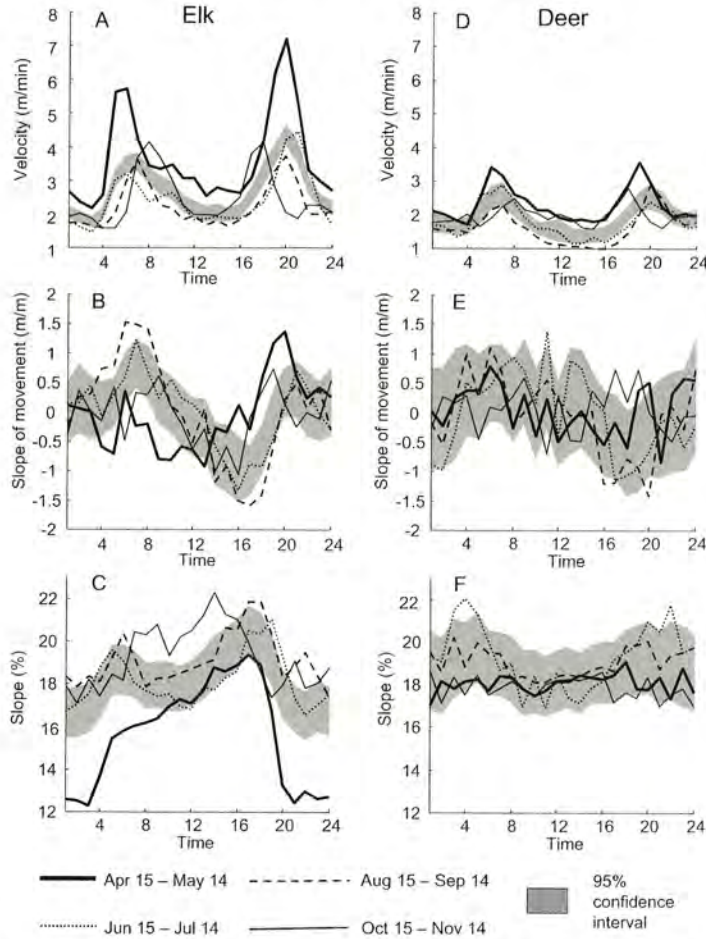


FIGURE 4. Means of habitat and movement variables velocity, slope of movement, and percentage slope by hour and monthly interval for elk (left column) and mule deer (right column). See Figure 2 for additional explanation. Figure is from Ager *et al.* (2003).

dendritic movement behavior appeared to split the elk into discrete movement cohorts in the project area. Subsequent analyses of movements relative to drainage directions showed a statistically significant association (Kie *et al.* in press). The effect of Meadow Creek Canyon (Figure 1b) on movement vectors is readily apparent, where movement vectors do not cross the canyon (Figures 6a, b). Bear Creek had similar effects. Movements also appeared to be reciprocal between dawn and dusk, i.e., the direction of arrows at dawn were opposite of those at dusk at most spatial locations. The dusk movements to grasslands (Figure 6b) appeared stronger and spatially focused as

compared to the dawn movements (Figure 6a). The seasonal changes in movement noted in Ager *et al.* (2003) were also apparent in the estimated vector fields (cf. Figures 6, 7). The plots for summer showed markedly diminished movement vectors, although there still is some evidence of the elk's avoidance of steep terrain.

LINKING SPATIAL MOVEMENT PATTERNS WITH HABITAT PREFERENCES

Movement vectors were related to habitat variables to explain the spatial cycles of movement on the basis of elk behavior.

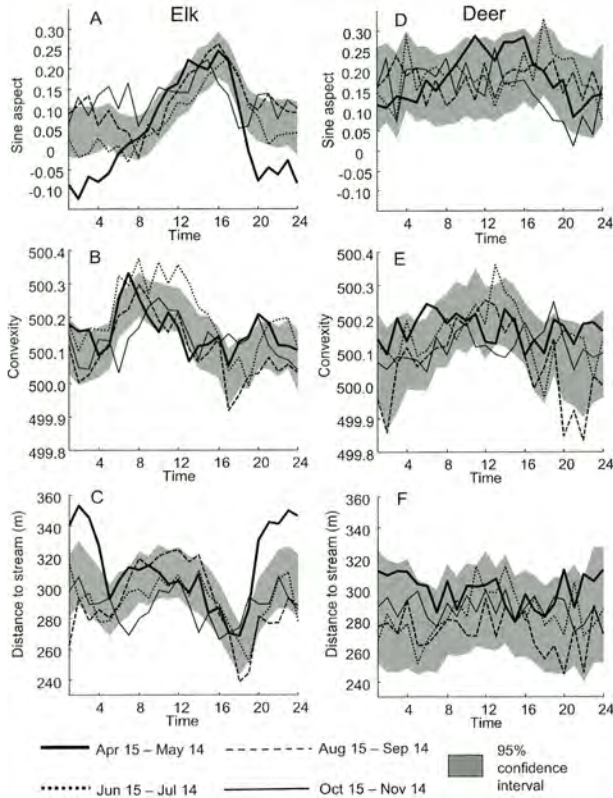


FIGURE 5. Means of habitat variables sine aspect, convexity, and distance to stream by hour and monthly interval for elk (left column) and mule deer (right column). See Figure 2 for additional explanation. Figure is from Ager et al. (2003).

This work was motivated by the concept of potential fields applied to animal movement (Brillinger et al. 2001a) and considers both the stochastic and correlated components of the animal movement behavior. A potential field may be visualized by imagining a ball rolling [the animal] around in the interior of bowl [potential surface], as the bowl is being shaken [random component]. In our case, the potential field is a complex surface representing attraction and repulsion to specific habitat features at different times of the day. The potential field is built from a set of additive potential functions for each habitat variable that affect movement. The individual potential functions describe movements [attraction/repulsion] as a function of distance to habitat features at specific times of day. Movements that are seemingly random, like foraging

paths in a meadow, or movements that cannot otherwise be explained with environmental covariates are included as stochastic terms in the model. The reader is referred to Brillinger et al. (2004) and Preisler et al. (2004) for details.

For an initial model we used the data from Ager et al. (2003) for elk in spring (15 April–15 May), and focused on the crepuscular movements between foraging and resting areas. We tested a number of habitat covariates and found four that had significant influence on movement vectors, these being distance to security areas, distance to foraging meadows, distance to steep slopes, and distance to streams (Preisler et al. 2004). A composite potential field was estimated for the crepuscular periods (Figures 8a, 9a) and, when plotted, showed areas of attraction corresponding to peak foraging and rest-

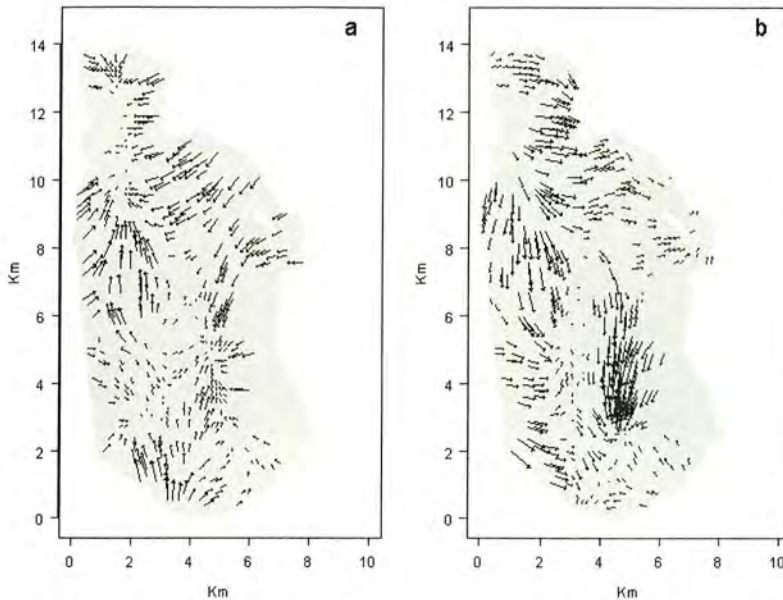


FIGURE 6. Gradient vector fields for 0500 (a) and 1900 (b) hours estimated for elk from the spring telemetry data. Arrows were plotted where at least one elk was observed. The unit vector corresponds to 0.8 km/hr. The plots illustrate the crepuscular transitions between areas used for resting and ruminating during the day, and foraging from dusk to dawn. Figure is from Preisler *et al.* (2004).

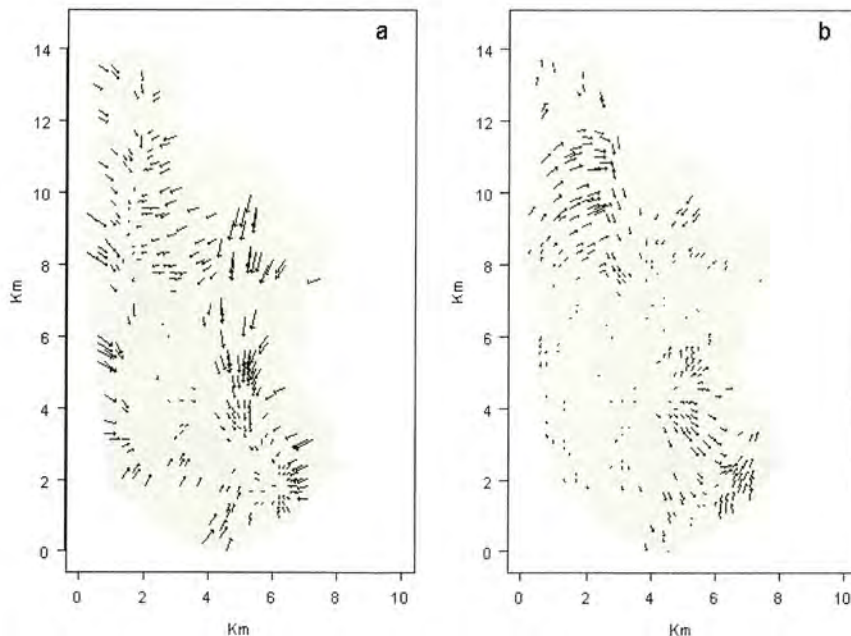


FIGURE 7. (a) Estimated potential surface of elk movements for 0500 hours during spring. (b) Kernel density estimate (elk/km²) for observed elk locations between the hours of 1000 and 1300. Most of the areas of low potential (attraction regions) at dawn correspond with regions of high elk density around noon. Figure is from Preisler *et al.* (2004).

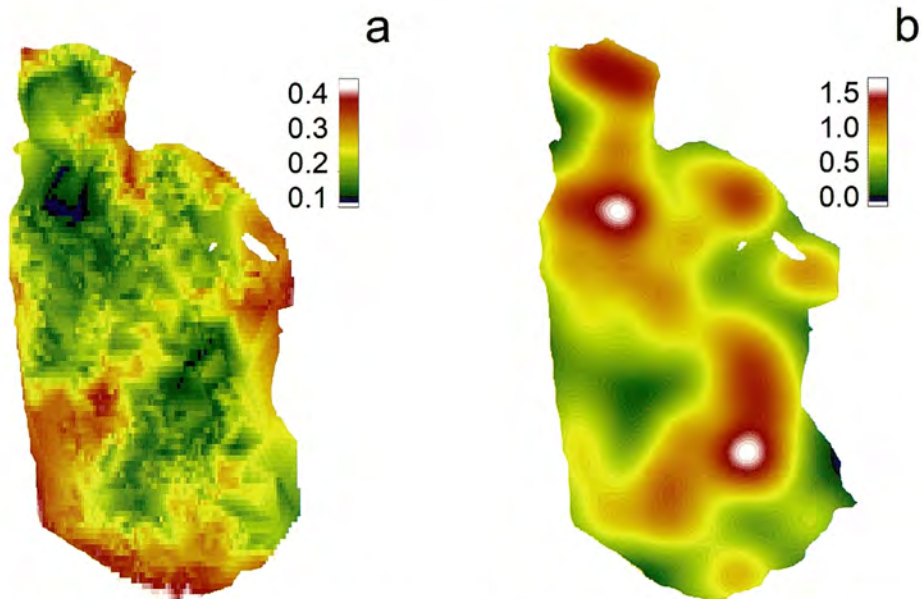


FIGURE 8. (a) Estimated potential surface of elk distribution for 1900 hours during spring. (b) Kernel density estimate (elk/km²) for observed elk locations between the hours of 2200 and 0100. Areas of low potential (attraction regions) at dusk correspond with regions of high elk density around midnight. Figure is from Preisler et al. (2004).

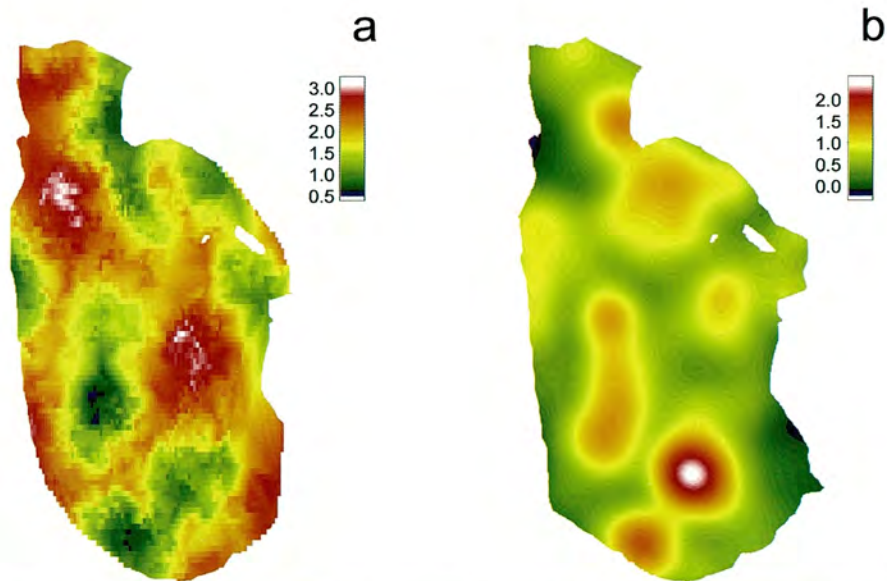


FIGURE 9. Smoothed estimates of the ratio of deterministic (drift) to random (standard deviation) terms for elk distribution. The ratios appear to be highest at dawn (0500 hours) and dusk (2000 hours). Figure is from Preisler et al. (2004).

ing areas. When compared to the elk distributions two hours later (Figures 8b, 9b), there is a general agreement between the potential field and elk densities. The potential functions for each habitat variable also showed specific relationships between the level of attraction/repulsion and distance (see Preisler *et al.* 2004). Thus a model showing habitat selection and habitat transitions was developed from movement vectors and habitat covariates. This work is a first step towards building an empirically-based stochastic movement model that accounts for both the spatial and temporal dynamics of movement and habitat preferences. Work is ongoing to incorporate finer-scale navigational cues that elk use during the crepuscular transitions that are relative to specific animal positions. This includes modeling the dendritic movement patterns (Forman 1995) that ungulates exhibit on steep terrain. Here, the potential function might change relative to the animal's position. Using potential fields to model fine-scale foraging movements like those among swards and adjacent feeding stations present further challenges.

MANAGEMENT IMPLICATIONS

Our description of daily and seasonal cycles of habitat use, spatial patterns of movement, and linkage between habitat use and movements adds to the interpretation of previous studies at Starkey (Johnson *et al.* 2000, Rowland *et al.* 2000, Coe *et al.* 2001). The daily and seasonal cycles of habitat use exhibited by elk and, to a lesser extent, mule deer show the dynamic nature of habitat use patterns and underscore the importance of movement studies. The movement analyses was limited to summer range conditions, and the consideration of movement on larger landscapes, including seasonal migrations offer additional challenges and insights into ungulate behaviors (Bergman *et al.* 2000, Johnson *et al.* 2002). Due to the sampling interval of the Starkey data [1–2 hours], telemetry location error, and perhaps the scale of the habitat data, we could not explain finer scale movements outside of the crepuscular periods. Mod-

eling movements during the foraging periods would require additional consideration of variables like forage intake rate, forage biomass, and other foraging behavior factors (Shipley and Spalinger 1995).

Current elk and mule deer habitat models do not consider inter-patch, landscape movements in their measurement of habitat quality. The influence of topographic pattern on crepuscular movements between preferred resting/ruminating and foraging habitats was manifested in movement patterns that were aligned with drainages. Thus it is likely the elk density in a given foraging habitat was dependent on their ability to connect to suitable security areas using movements that parallel the topographic pattern of drainages. We hypothesize that the fit of Starkey resource selection functions on other landscapes will be influenced by the spatial arrangement of habitats on the landscape and the presence of suitable movement corridors to link daytime and nighttime habitats. For instance, a canyon that lies between highly desirable foraging and security areas will degrade the resource value of these two habitats due to the lack of a suitable connection between them. Further work is needed to better understand how movement patterns might influence elk and mule deer densities in specific habitats, and whether these considerations are problematic in the extrapolation of resource selection functions.

The dynamic nature of habitat use and movements by elk and, to a lesser extent, mule deer has important implications for the development and application of habitat suitability models. Diel changes in habitat use needs to be considered when telemetry data are used to estimate resource selection functions.

The need for empirical methods to analyze movements will grow as the rapid advances in automated telemetry systems materialize, and large telemetry data sets are generated. New GPS telemetry with higher accuracy and sampling frequency will enable significant advances in our ability to build movement models that

represent a broad range of ungulate behavior and spatio-temporal scales.

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Spatial and Temporal Interactions of Elk, Mule Deer, and Cattle

Priscilla K. Coe, Bruce K. Johnson, Kelley M. Stewart, and John G. Kie

INTRODUCTION

Elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and cattle share millions of acres of public and private forests and rangelands across the western United States and Canada. These three species have important social, ecological, and economic values. Understanding their interspecific interactions may clarify two recurring issues in their management: competition for food and competition for space, both of which may result in decreased animal fitness. Animal unit equivalents (AUEs) among these three species have been based on equivalent body mass (Society for Range Management 1989), whereby 1 cow is equivalent to 2.5 elk or 6 mule deer. Hobbs and Carpenter (1986) argue that AUEs should be based on dietary overlap, and the argument can be extended to include spatial overlap. Consequently, the ecological impact of one species on the landscape may not be equivalent to another species. Furthermore, allocating forage becomes challenging if managers do not clearly understand the spatial and dietary overlap among these three species. Accurate predictions of ungulate distributions over time and space may help managers regulate densities and understand effects of specific ungulates on ecosystem processes.

Many factors may influence the seasonal distribution of domestic and native ungulates, including vegetation composition, topography, and distance to water (Mueggler 1965, Leckenby 1984, Peek and Krausman 1996, Wisdom and Thomas 1996). Ungulates also distribute themselves in response to disturbances such as traffic (Wisdom 1998, Rowland et al. 2000), hunting (Johnson et al. 2004), and logging (Pedersen et al. 1980). In addition,

there may be inter- and intraspecific influences on animal distribution. These interactions may produce different patterns of distribution at different scales of investigation (Bowyer et al. 1997). This paper summarizes studies of ungulate interactions at Starkey Experimental Forest and Range (Starkey) in terms of how interactions among ungulate species may affect animal distributions over space and time.

Past studies of interspecific interactions among elk, mule deer, and cattle have indicated potential competition (Skovlin et al. 1968, Mackie 1970, Dusek 1975, Knowles and Campbell 1982, Nelson 1982, Austin and Urness 1986, Wallace and Krausman 1987, Loft et al. 1991, Peek and Krausman 1996, Wisdom and Thomas 1996, Lindzey et al. 1997, Wisdom 1998), while others have inferred commensalism (Anderson and Scherzinger 1975, Frisina and Morin 1991, Peek and Krausman 1996). Competition occurs when individuals or species use similar resources that are also in short supply. Inadequate forage quality or quantity may decrease nutritional planes such that population performance of one or more species decreases (Birch 1957, Putnam 1996). In contrast, commensalism occurs when one species benefits from association with another species, while the other species is unaffected (Martin 1990).

Simple descriptive approaches to interactions among large herbivores result in inherent difficulties (Painter 1980). Overlapping distributions could be evidence for competition or dependence. Non-overlap could be an expression of active avoidance or ecological separation, which occurs when two species evolved together. Although sexual segregation, or spatial separation of sexes outside the mating

TABLE 1. Scales of species interaction analyses at Starkey Experimental Forest and Range, northeastern Oregon

Measure of scale	Elk and mule deer ^a	Elk, mule deer, and cattle ^b	Elk, mule deer, and cattle ^c
Spatial extent acre (ha)	19,012 (7,700)	19,012 (7,700) ^d , 5,926 (2,400) ^e , 5,926 (2400) ^f	3,457 (1,400)
Spatial grain acre (ha)	0.22 (0.09)	5,926 (2,400) ^d , 19 (7.7) ^e , 0.22 (0.09) ^f	5.55 (2.25)
Temporal extent (yrs)	4	2	3
Temporal grain (mean number of days)	56.5	27	7 ^g , 0.25 ^h

^a Spring (Johnson *et al.* 2000)^b Summer (Coe *et al.* 2001)^c Spring, summer, and fall (Stewart *et al.* 2002)^d Pasture level analysis^e Plant community level analysis^f Pixel level analysis (resource selection functions)^g 7-day model^h 6-hr model

season is nearly ubiquitous among polygamous ungulates (Bowyer 1984, McCullough *et al.* 1989, Scarbrough and Krausman 1998, Kie and Bowyer 1999) our paper concentrates on distribution of females. Comparisons of distribution with and without one ungulate species present during the same season and on the same ground should help to illuminate whether competition is occurring. Diet studies of ungulates during different seasons, both with and without prior grazing also should help to establish competitive interactions.

Studies of ungulate interactions began at Starkey in 1954 (Skovlin *et al.* 1968). Deer were summer-long residents while elk were spring (May–June) and fall migrants through the area. The investigators monitored use by deer and elk in two replicates of pasture systems supporting light [40 acres per animal unit (16 ha/animal unit)], moderate [30 acres per animal unit (12 ha/animal unit)], and heavy [20 acres per animal unit (8 ha/animal unit)] cattle grazing. Over a period of 11 years (1954–1964), elk and mule deer use was measured from pellet groups and plant utilization surveys. They found that both elk and mule deer used pastures not grazed by cattle more than any of the cattle-grazed pastures, with use declining as cattle stocking rate increased. They found

less of an effect by cattle on mule deer than on elk, indicating possible competition between elk and cattle.

METHODS

In 1989 an ungulate-proof fence was built around Starkey for long-term studies of elk, mule deer, and cattle (Rowland *et al.* 1997). Three studies of spatial interactions among elk, mule deer, and/or cattle took place in the enclosed areas. The largest-scale study was conducted in Main Study Area (19,026 acre [7,700 ha]) during spring, when only elk and mule deer were present (Johnson *et al.* 2000). In a smaller (5,930 acre [2,400 ha]) subpasture of Main Study Area, Smith-Bally, responses of elk and mule deer to cattle were investigated during early and late summer, and elk and mule deer distributions were analyzed with and without cattle present (Coe *et al.* 2001). Finally, in the 3,459 acre (1,400 ha) Northeast Study Area spatial and temporal competitive interactions among all three species were documented (Stewart *et al.* 2002). Scale of analysis was defined by spatial extent (the size of the study area), spatial grain (the smallest spatial unit used in analysis), temporal extent (the time span of the study), and temporal grain (the smallest unit of time used in analysis; Table 1).

In Main Study Area we investigated interactions of elk ($n = 88$) and mule deer ($n = 45$) during spring when cattle were not present (Johnson et al. 2000). Resource selection functions (RSF) were estimated for both species. A resource selection function is a value for a resource unit that is proportional to the probability of the unit being used by an animal (Manly et al. 1993). Resource units were represented as 98.4 by 98.4 feet (30 by 30 m) cells. A resource selection function may be mapped as a probability of use by the species across a landscape. To investigate interspecific interactions between mule deer and elk the probability of use for one species was used as a variable in estimating a resource selection function for the other species.

In Smith-Bally pasture we investigated responses of elk and mule deer to cattle at several spatial grains (Coe et al. 2001, Table 1). We analyzed counts of animal locations ($n = 25$ –55 elk, 12–36 mule deer, and 35–42 cattle) at the pasture and habitat level within the pasture. We estimated resource selection functions at the pixel level. To examine species use at the pasture level we used relative counts of elk and mule deer locations within the pasture versus in the rest of Main Study Area during years when cattle were present and the same days during years when cattle were absent. A temporally correlated Poisson regression accounted for autocorrelation among days and non-normally distributed count data. The same process was used to investigate whether elk and mule deer changed their use of four major habitat types within the Smith-Bally pasture when cattle were present compared to when they were absent. Finally, resource selection functions were estimated for both elk and mule deer at the pixel level when cattle were present and when they were absent in Smith-Bally pasture. Cattle resource selection functions were also estimated for the same time periods and at the same spatial grain.

In the Northeast Study Area, Stewart et al. (2002) investigated the relative influence of interference versus exploitive

competition among elk, mule deer and cattle, after accounting for niche partitioning. Stewart et al. (2002) used multivariate analysis of variance (MANOVA) to examine seasonal niche partitioning among these three species of large herbivores by examining the interactions of animal locations with random locations ($n = 465$) for independent variables associated with habitat selection (e.g. habitat type, distance to water, distance to roads, slope, and aspect). Habitat variables included in MANOVA models had been selected previously from species-specific logistic regression to determine which variables were important to that species (Stewart et al. 2002). Multiple regression was used to examine competition among the three species while accounting for niche partitioning, by including habitat variables that had been selected from logistic regression being held in the model, and the number of sympatric species and conspecifics within a 5.55 acre (2.25 ha) area surrounding a focal animal location. Stewart et al. (2002) used two temporal windows to examine the relative effects of interference and exploitive competition in those multiple-regression models: a 6-h temporal window to investigate interference competition, based on the number of sympatric animals that were present within the 5.55 acre (2.25 ha) window ± 3 hrs of a focal animal location; and a 7-day temporal window to examine effects of exploitive competition, based on the number of animals that were present 7 days prior to the focal animal location. Finally, Stewart et al. (2002) compared movements of mule deer and elk two weeks before and after cattle were introduced to the study area (early summer) and removed (autumn) to examine potential competitive displacement of mule deer and elk by cattle.

RESULTS

Elk and Mule Deer—Spring

In Main Study Area during spring elk were found on flatter and more westerly aspects than mule deer, and farther from roads with high (greater than 4 vehicles/

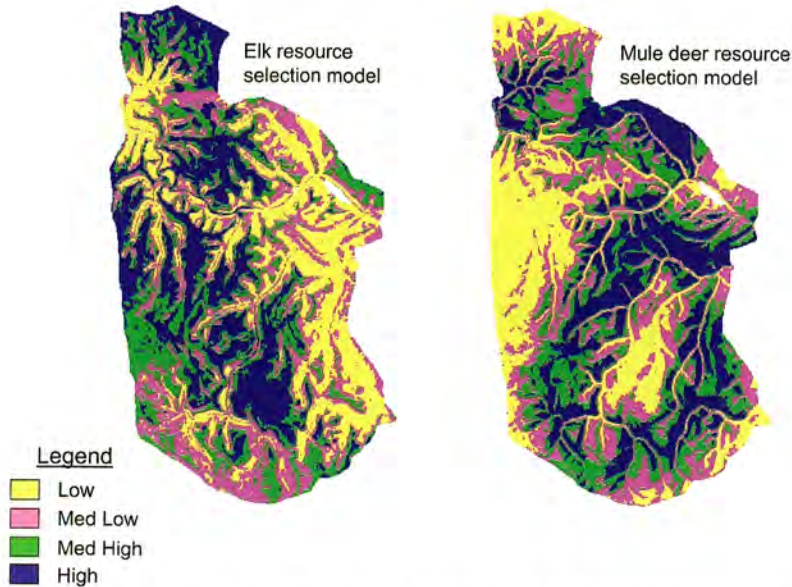


FIGURE 1. Resource selection function values for elk and mule deer during spring at Starkey Experimental Forest and Range (from Johnson et al. 2000).

day) and medium (1 to 4 vehicles/day) traffic (Figure 1). Several of the habitat attributes that mule deer selected were opposite from those elk selected: for example, mule deer selected steeper and northeast-facing aspects, and sites closer to high and medium traffic (Johnson et al. 2000). When the mule deer resource selection function was incorporated into the elk resource selection function, and vice versa, the resulting coefficients for the incorporated resource selection functions were negative and significant, indicating that each species selected resources that the other did not. The magnitude of the elk resource selection function in the mule deer model was greater, however, indicating that mule deer were more strongly affected by elk than elk were by mule deer. Further investigation revealed that mule deer use of five habitat types ranked according to elk RSF was inverse of elk selection. Elk habitat selection within the ranked mule deer resource selection function, however, displayed no pattern. This is further indication that mule deer may have been avoiding elk more than elk were avoiding mule deer.

Elk, Mule Deer, and Cattle—Summer

At the pasture level elk occurred less frequently in Smith-Bally pasture when cattle were introduced, both in early summer and late summer (Figure 2, top). The elk that stayed in the pasture when cattle were present shifted their use of the ponderosa pine/Douglas-fir type as a result of cattle (Figure 2, bottom). In early summer elk were displaced from the ponderosa pine/Douglas-fir habitat by cattle. In late summer, elk were displaced into the ponderosa pine/Douglas-fir habitat by cattle (Coe et al. 2001). Forage in this habitat was most palatable and nutritious in early summer, and consequently elk likely were negatively affected by this displacement. At the pixel level early summer resource selection functions for elk when cattle were present were significantly different from elk resource selection functions when cattle were absent. Conversely, late summer resource selection functions for elk when cattle were present were similar to elk resource selection functions when cattle were absent (Coe et al. 2001). In early summer elk selection for five habitat

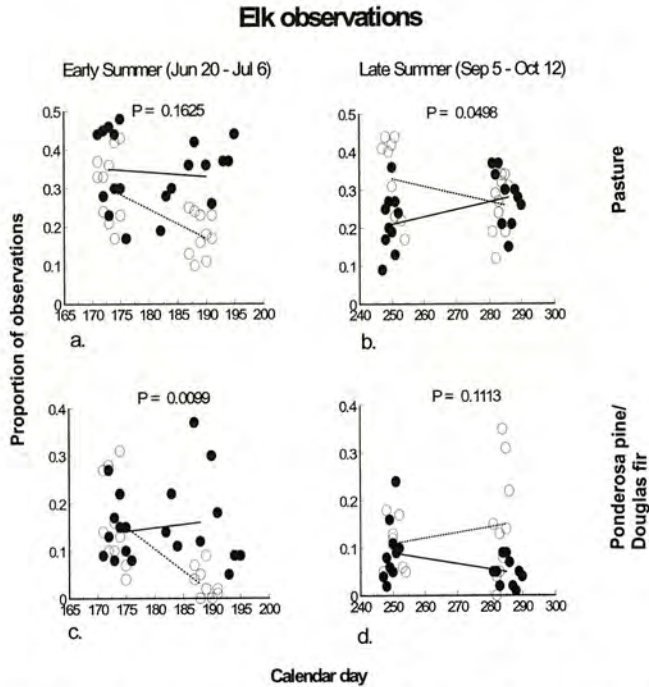


FIGURE 2. Comparison of the proportion of elk locations in Smith-Bally pasture and in the ponderosa pine/Douglas fir plant community within that pasture, when cattle were present (open circles, $n = 20$ days) versus when cattle were absent (closed circles, $n = 20$ days), Starkey Experimental Forest and Range, northeastern Oregon, 1993–1996 (from Coe et al. 2001).

variables differed if cattle were absent; they selected sites with gentler slopes, less convex topography, lower canopy, and sites closer to edge of forest stand, and further from roads with low traffic rates. In late summer, elk selected denser canopy when cattle were absent, but otherwise elk resource selection functions did not differ based on presence of cattle (Coe et al. 2001). When we included the cattle resource selection function in the elk models, we found that cattle could be used as a predictor of elk distribution in some conditions. With cattle absent elk selected some of the same resources that cattle select in early spring. When cattle were present, however, elk selected different resources and were spatially separate from cattle. Conversely, in late summer elk resource selection functions were similar to those of cattle, regardless of cattle presence.

Mule deer reduced use of the Smith-Bally pasture in late summer when cattle

were introduced but did not change use in early summer with regard to cattle presence. Mule deer use of the ponderosa pine/Douglas-fir habitat type was opposite that of elk; mule deer were probably responding to elk movements rather than cattle movements. We observed mule deer changes in habitat use to be opposite those of elk in three out of four season/year combinations. Mule deer resource selection functions were not affected by the presence of cattle.

Elk, Mule Deer, and Cattle—Spring, Summer, and Fall

In Northeast Study Area, habitat selection differed among seasons for elk, mule deer, and cattle. Wilks' lambda ($P = 0.015$) revealed an interaction of species (mule deer, elk, cattle) by location (used, random) that indicated differences in selection of some habitat variables among species (Stewart et al. 2002). Bivariate

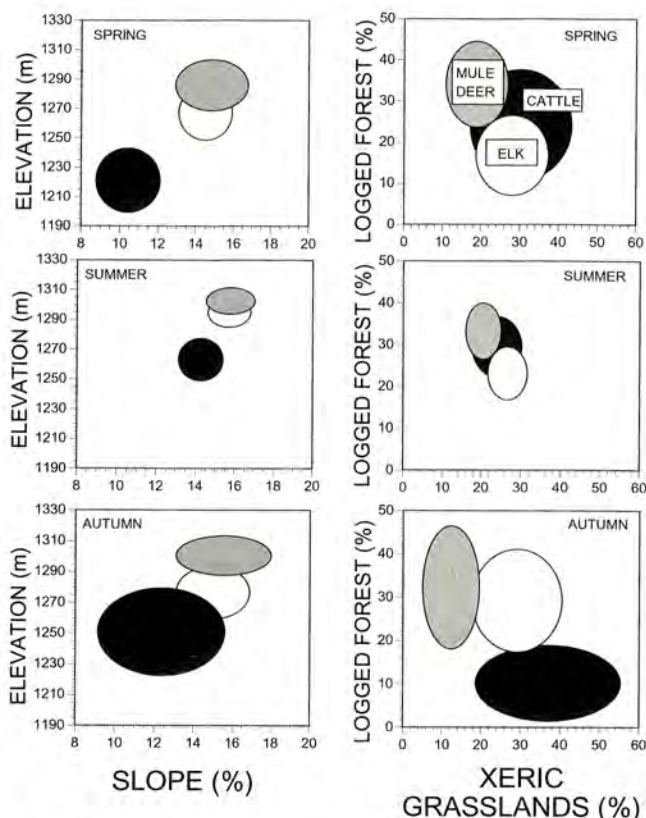


FIGURE 3. Bivariate plots of niche partitioning based on elevation and slope (left) and on logged forest and xeric grasslands (right). Ellipses are 95 percent confidence interval for cattle, elk, and mule deer across seasons on the Starkey Experimental Forest and Range, northeastern Oregon, 1993–1995 (from Stewart *et al.* 2002).

plots of 95 percent confidence intervals indicated that cattle differed from mule deer and elk by avoiding steeper slopes and high elevations, particularly during spring and summer; by contrast, mule deer and elk overlapped in use of slope and elevation, but partitioned use of vegetative communities (Stewart *et al.* 2002, Figure 3).

Spatial avoidance among mule deer, elk, and cattle was stronger for the 6-hr models than for the previous 7 days; coefficients of association from multiple regressions were strongly negative for the 6-hr models, indicating strong avoidance among the three species during all seasons (Stewart *et al.* 2002). Stewart *et al.* (2002) observed an interaction of season by species by treatment (Wilks' lambda, $P = 0.046$) and a species by treatment

interaction (Wilks' lambda, $P = 0.002$) for use of slope and elevation by elk and mule deer following introduction and removal of cattle during spring and autumn. Because those interactions were significant the authors analyzed species (elk and mule deer) and seasons separately. Elk moved to higher elevations following introduction of cattle during spring, returning to lower elevations following removal of cattle in autumn (Stewart *et al.* 2002). Conversely, mule deer moved to lower elevations following introduction of cattle during spring, possibly in response to displacement of elk following introduction of cattle (Stewart *et al.* 2002). The addition of cattle to Northeast Study Area did not affect the slope of habitats used by mule deer during spring, although deer moved to more level ground following re-

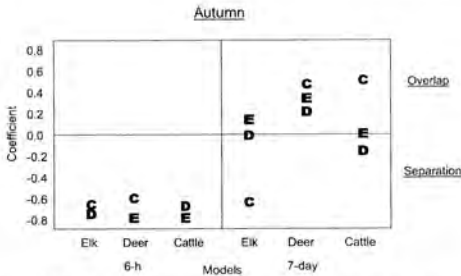


FIGURE 4. Standardized competition coefficients as determined from weighted multiple regressions for elk, mule deer, and cattle during autumn (September 15 to October 15) in Starkey Experimental Forest and Range, northeastern Oregon. Number of conspecifics (C = cattle, D = mule deer, and E = elk), plus the focal animal, was the dependent variable for 6-hr and 7-day models (from Stewart et al. 2002).

removal of cattle in autumn (Stewart et al. 2002).

Resource partitioning for the 6-hr models was interpreted as interference competition, while 7-day partitioning was interpreted as possible interference or exploitive competition. In autumn (Sep 15–Oct 15) coefficients were strongly positive, compared to spring and summer, in all of the 7-day models, indicating spatial overlap among all species occurred (Figure 4). The exception, during autumn, was the elk model, where elk continued to avoid cattle. Mule deer more strongly avoided elk than elk avoided mule deer as evidenced by non-significant mule deer variables in the elk models, but highly significant elk variables in the mule deer models. This occurred for all seasons except during the earliest period (15 June–30 June).

DISCUSSION

Three separate investigations yielded similar information about spatial relationships of elk, mule deer, and cattle within Starkey at three different scales. Spatial separation was noted for elk and mule deer and for elk and cattle at all scales analyzed during spring and early summer. At the largest scale, Main Study Area, remarkable spatial separation was seen for

elk and mule deer (no cattle present) in spring, so much so that maps of resource selection functions for each species were nearly mirror images. In Smith-Bally pasture spatial separation of elk and mule deer was evidenced in that mule deer response was opposite to that of elk in their use of plant communities. In Northeast Study Area spatial separation between elk and mule deer was maintained in the 5.55-acre (2.25-ha) neighborhood surrounding each focal animal in early summer for both temporal scales analyzed.

Elk and cattle spatial separation occurred in the two studies where cattle were present. Both studies concluded that elk avoid cattle during summer. Both studies also noted more overlap among all ungulates during late summer; spatial overlap of all species during late summer and fall occurred in the two studies that encompassed these seasons. This overlap is indicative of possible exploitive competition occurring both among and between the three species of ungulates as forage resources become depleted later in the grazing season, especially in light of other findings at Starkey. Other Starkey studies have found nutritional deficits of both elk and cattle in late summer (Cook et al. 2004, Holechek et al. 1982). Spatial overlap, indications of nutritional deficits, and diet overlap in grand fir (*Abies grandis*) habitats during August (Findholt et al. 2004), implicate competition for resources as a potential limiting factor in ungulate productivity during late summer and fall.

All of the analyses are consistent with the hypothesis of a cascading effect of larger ungulates displacing smaller ones. In both the Smith-Bally and the Northeast Study Area analyses, cattle displaced elk, and all three studies cited evidence of elk displacing mule deer. If this hypothesis is true (i.e., larger ungulates choose habitat first), elk could suffer nutritional deficits sooner than cattle, and deer sooner than elk in a foraging-limited situation.

POLICY IMPLICATIONS

- The cascading effects of larger herbivores choosing resources before small-

er herbivores imply that resource management decisions that change distribution of cattle will likely change distributions of elk and mule deer.

- Cattle are the most easily manipulated and largest herbivore in northeastern Oregon and thus can be a tool in managing spatial distributions of elk and mule deer.
- Careful management of ungulate density in late summer and fall (e.g., stocking reductions in areas of high ungulate overlap) could help achieve higher productivity of both wild and domestic ungulates as forage resources become limited.
- Resource selection functions, which account for interspecific interactions of elk, mule deer, and cattle, can be used to predict animal distributions over a landscape and as part of a larger model to predict forage removal and animal productivity.
- Estimating animal unit equivalents is dependent on two basic factors—distributional overlap and dietary overlap. Animal unit equivalents cannot be based strictly on body weight, as results from our studies indicate spatial separation occurs, effectively discounting the animal unit equivalencies for these three species.

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Diet Composition, Dry Matter Intake, and Diet Overlap of Mule Deer, Elk, and Cattle

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Mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and cattle share rangelands throughout much of interior western North America. Considerable debate exists about the degree to which facilitation or competition occurs for forage between these three species (Nelson 1982, Wisdom and Thomas 1996, Miller 2002).

Prior cattle grazing can have beneficial effects on elk nutrition. The removal of forage by cattle can improve forage quality by enhancing regrowth of forage or by changing ratios of live to dead plant material (Cook 2002), and forage quality on elk winter ranges in the interior Northwest can be improved by cattle grazing in the spring (Anderson and Scherzinger 1975, Clark 1996). To date, however, studies have not shown enhancement of forage quality in the summer following late spring or early summer grazing by elk or cattle.

Competition for forage between mule deer, elk, and cattle is probably greatest on winter and spring/autumn ranges (Nelson 1982, Wisdom and Thomas 1996), and minimal between wild ungulates and cattle during summer (Miller 2002). Most summer ranges for mule deer and elk are on large areas of public land containing a diversity of habitats and high potential for forage production (Miller 2002). On some summer ranges, however, competition for forage may exist in late summer and early fall because forage quality can be poor and not meet nutritional requirements of wild ungulates and cattle (Torbit 1985, Hanley et al. 1989, Cook 2002). This is especially evident in regions where summer drought is the normal part of the climatic regime (Vavra and Phillips 1980, Svejcar and Vavra 1985).

On the Starkey Experimental Forest and Range (Starkey), northeast Oregon,

competition for forage may occur in late summer among all three species, especially between elk and cattle (Coe et al. 2001, Stewart et al. 2002). Conditions at Starkey typify those on summer ranges shared by mule deer, elk, and cattle in forests of the interior western United States. Consequently, we conducted a manipulative experiment on Starkey summer range to evaluate the potential for competition or facilitation for forage among mule deer, elk, and cattle in grand fir (*Abies grandis*) forests. Our specific objectives were to determine diet composition, dry matter intake rates, and percent dietary overlap of all three species in response to prior grazing by elk and cattle. In this paper we focus on results obtained from the bite count data. A detailed analysis of the nutritional consequences of previous grazing by elk or cattle on subsequent diets of mule deer, elk, or cattle will be presented elsewhere (Damiran in prep.). Results from our study could improve range management for mule deer, elk and cattle on public land, especially with regard to allocating forage among these three species when ranges are shared in forested habitats (Ager et al. 2004).

STUDY AREA

Starkey is located on the Wallowa-Whitman National Forest, 22 miles (35 km) southwest of La Grande, Union County, northeast Oregon. Vegetation is a mosaic of coniferous forests and open areas containing shrublands and grasslands. Forest stands are dominated by ponderosa pine (*Pinus ponderosa*), with grand fir, and Douglas fir (*Pseudotsuga menziesii*) occurring on northern aspects. Elevation ranges from 3,675 to 4,922 feet (1,120 to 1,500 m).

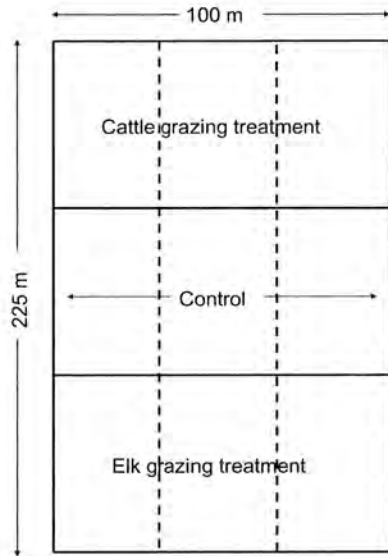


FIGURE 1. Layout of pastures used to determine diet composition, bite rates, dry matter intake, and diet overlap among cattle, elk, and mule deer in response to previous grazing by cattle or elk on the Starkey Experimental Forest and Range, northeast Oregon.

We conducted our research in four, 5.56-acre (2.25-ha) enclosures located in grand fir-forests logged 15–20 years ago. We chose the grand fir vegetation type because of its dominance on summer and fall ranges in the Blue Mountains and the interior western United States. Moreover, grand fir forests support a high level of forage production, particularly after logging or burning. In addition, other research at Starkey indicated that mule deer, elk, and cattle concentrated much of their foraging activity after mid-summer on early successional stages of logged grand fir vegetation types (Coe et al. 2001).

METHODS

Grazing Treatments

Each enclosure contained three, 1.85 acre (0.75 ha) pastures (Figure 1). In 1998 and 1999, during late June and again in mid to late July, one pasture of each enclosure was grazed by four to five steers and another pasture was grazed by four elk. The remaining pasture of each enclosure was not grazed (control pas-

ture). Our goal during grazing treatments was to have 40 percent of the current year's vegetation production utilized by elk and steers on each pasture. This is the standard used by the U.S. Department of Agriculture, Forest Service for cattle allotments on upland sites in good condition in northeast Oregon. Assignment of grazing treatments to pastures was done randomly, and remained the same in 1998 and 1999.

Feeding Trials

After completion of the grazing treatments each 1.85 acre (0.75 ha) pasture was subdivided into three, 0.62 acre (0.25 ha) pastures. In August 1998 and 1999 we used bite-counts to obtain information on diet composition of tractable mule deer, elk, and cattle from each pasture as described by Wickstrom et al. (1984). Each 0.62 acre (0.25 ha) pasture was grazed by 4 mule deer, 4 elk, or 4 steers. The elk and steers were the same animals used during grazing treatments. We conducted four feeding trials with each animal in each 0.62 acre (0.25 ha) pasture. This resulted in 16 feeding trials for each species in each treatment at the four enclosures, for a total of 192 feeding trials for each species each year.

During each 20 minute feeding trial we used a small hand-held tape recorder to record the number of bites of each plant species consumed. We randomly assigned animal species to pastures for the feeding trials at the start of each year.

Dry Matter Intake

After feeding trials were completed in each 0.62 acre (0.25 ha) pasture, we clipped at least 25 samples of the most common plant species (greater than 5 percent of the diet) to simulate plant parts and sizes of bites recorded during feeding trials. Samples were oven-dried at 122 degrees F (50 degrees C) to constant weight. We calculated mean weights of bites of each plant species found in the diet in each 0.62 acre (0.25 ha) pasture. Mean weights were multiplied by the

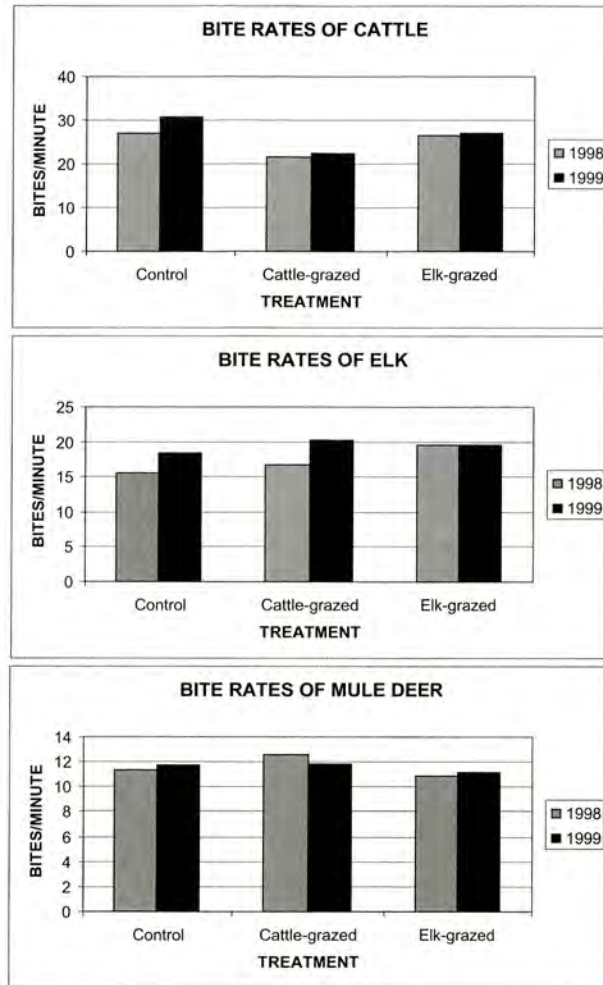


FIGURE 2. Bites/minute of cattle, elk, and mule deer in response to previous grazing by cattle or elk on the Starkey Experimental Forest and Range, northeast Oregon.

number of bites of each plant species to determine total dry matter intake.

Data Analysis

Data were analyzed as a split-plot design with the Proc Mixed procedure in SAS (Littell et al. 1996) to determine whether diets of mule deer, elk, and cattle differed among pastures previously grazed by cattle or elk and control (ungrazed) pastures. We used the least squares (LS) means procedure of SAS to determine if treatment means were different. Bite count data (bites/minute) were used to calculate percent overlap in diet.

Percent overlap of major forage classes composing the diets of mule deer, elk, and steers was determined with Horn's Index of Similarity (Horn 1966).

RESULTS

Diet Composition and Bite Rates

Cattle

Total bites/minute of steers was less in pastures previously grazed by cattle in 1998 and 1999 compared to ungrazed pastures and pastures previously grazed by elk ($P \leq 0.03$; Figure 2). Graminoids composed the bulk of the steer diets both

years (Figure 3). Steers consumed less graminoids and more shrubs/trees in pastures previously grazed by cattle however, compared to ungrazed pastures or pastures previously grazed by elk in 1998 and 1999 ($P \leq 0.04$). Also, steers consumed more forbs in pastures previously grazed by cattle in 1999 ($P \leq 0.02$) but not in 1998 ($P \geq 0.11$). Intake of major forage categories in steer diets did not change in response to prior elk grazing ($P > 0.10$).

Elk

Total bites/minute of elk was greater in pastures previously grazed by elk compared to ungrazed pastures in 1998 ($P = 0.02$), but not in 1999 ($P = 0.58$; Figure 2). Although elk consumed mostly forbs, graminoids, and shrubs/trees, lichens were also prevalent in their diets (Figure 3). Bites/minute of graminoids in elk diets was greater in pastures previously grazed by elk compared to pastures previously grazed by cattle during both years ($P \leq 0.01$). Elk diets also contained more graminoids in pastures previously grazed by elk compared to control pastures in 1998 ($P = 0.05$). Bites/minute of forbs was higher in pastures previously grazed by cattle compared to control pastures and pastures previously grazed by elk but less in pastures previously grazed by elk compared to control pastures ($P \leq 0.03$). In 1998 bites/minute of elk did not vary with treatment ($P \geq 0.43$). However, this same year elk consumed more shrubs/trees in pastures previously grazed by cattle compared to control pastures ($P = 0.02$). In 1998 and 1999 elk consumed less lichen in pastures previously grazed by elk ($P \leq 0.05$; Figure 3).

Mule deer

Total bites/minute of mule deer did not vary with treatment either year ($P > 0.10$; Figure 2). Mule deer consumed mostly forbs and shrubs/trees (Figure 3). Intake of graminoids, forbs, shrubs/trees, and other food did not differ in those pastures previously grazed by cattle or elk compared to control pastures (Figure 3).

Dry Matter Intake

In 1998 and 1999 total dry matter intake (grams/minute) of steers was less in pastures previously grazed by cattle compared to pastures previously grazed by elk or ungrazed pastures ($P \leq 0.03$; Figure 4). Total dry matter intake (grams/minute) did not vary among treatments either year for elk or mule deer ($P \geq 0.26$; Figure 4).

Percent Diet Overlap

Mean diet overlap of major forage classes in control pastures (ungrazed pastures) was 49 percent between cattle and elk, 59 percent between mule deer and elk, but only 19 percent between cattle and deer when data from 1998 and 1999 were combined (Figure 5). During both years, diet overlap between cattle and deer increased in pastures previously grazed by cattle ($P \leq 0.01$), but not in pastures previously grazed by elk ($P \geq 0.67$). Percent diet overlap between cattle and elk was higher in pastures previously grazed by elk compared to control pastures both years ($P \leq 0.006$) and also higher in pastures previously grazed by cattle in 1999 ($P \leq 0.001$). Percent diet overlap between mule deer and elk did not vary with treatment either year ($P \geq 0.17$).

DISCUSSION

Numerous studies have evaluated the food habits of mule deer, elk, and cattle (Kufeld 1973, Kufeld et al. 1973, Holechek 1979, Cook 2002). These studies show large variation by year of study, location, specific herbivore, and research technique. Thus, in this discussion we focus on the results of our study in relation to other studies in northeast Oregon where habitats are generally similar to those in our study area.

Forage intake estimated from clipping or handpicking simulated bites that represent bites ingested can be biased, especially with wild ungulates (Parker et al. 1993). In our study, results from bite counts (bites/minute) and dry matter in-

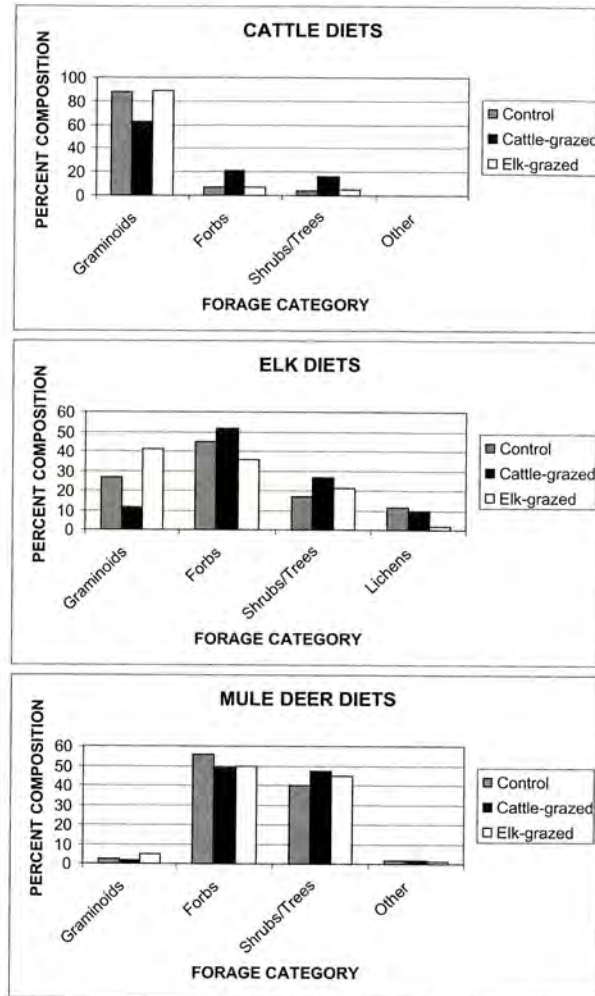


FIGURE 3. Diet composition of cattle, elk, and mule deer by major forage category on the Starkey Experimental Forest and Range, northeast Oregon. Diet composition was derived from bite count data.

take rates (grams/minute) showed similar effects of previous grazing by cattle or elk. This similarity suggests that both methods can be used to estimate diet composition and evaluate the potential for competition for forage among mule deer, elk, and cattle.

Holechek *et al.* (1982) found that cattle grazed mostly on grasses, but also consumed large quantities of forbs and shrubs in ponderosa pine or Douglas fir forest types at Starkey in late summer. In our study, cattle also consumed mostly grasses and sedges. In response to previous cattle grazing, however, cattle re-

duced their consumption of graminoids and increased their use of forbs and shrubs. The potential for competition for forage between cattle and elk and cattle and mule deer increased when cattle changed their diets as preferred cattle forage was consumed. Holechek *et al.* (1982) and Miller and Vavra (1981) also reported that cattle readily switch their diets from one forage type to another. Elk are an intermediate feeder compared to mule deer or cattle (Kufeld 1973, Hofmann 1988). Edgerton and Smith (1971) found that elk and mule deer diets consisted of 58 percent grasses and sedges,

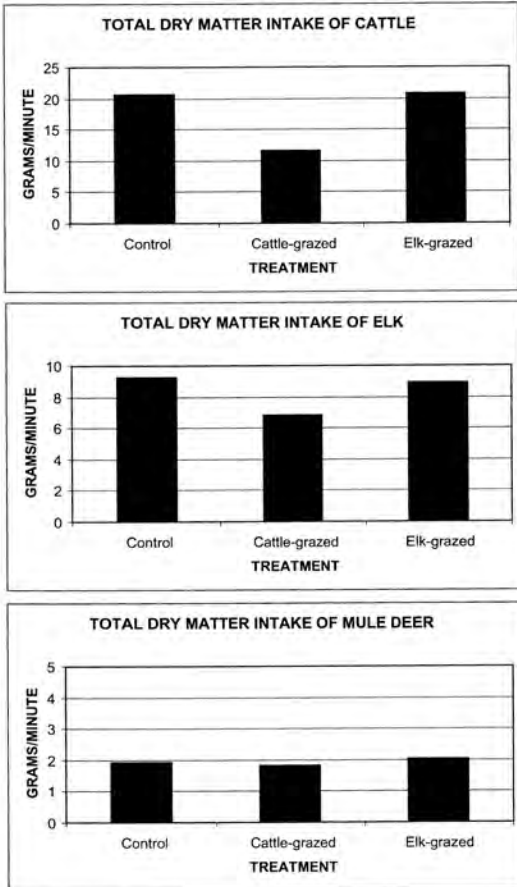


FIGURE 4. Total dry matter intake (grams/minute) of cattle, elk, and mule deer in response to previous grazing by cattle or elk on the Starkey Experimental Forest and Range, northeast Oregon.

27 percent forbs, and 15 percent shrubs during summer at Starkey. In their study it was not possible to separate elk from mule deer diets because forage production and utilization were estimated on summer range shared by the two species. Korfhage (1974) and Korfhage et al. (1980) found that elk diets in the Blue Mountains, northeast Oregon were evenly balanced among all major vegetative components but forbs and shrubs were more important dietary components than graminoids during late summer. In our study, elk diets consisted of a more even percentage of all major forage classes in contrast to the more concentrated diets of

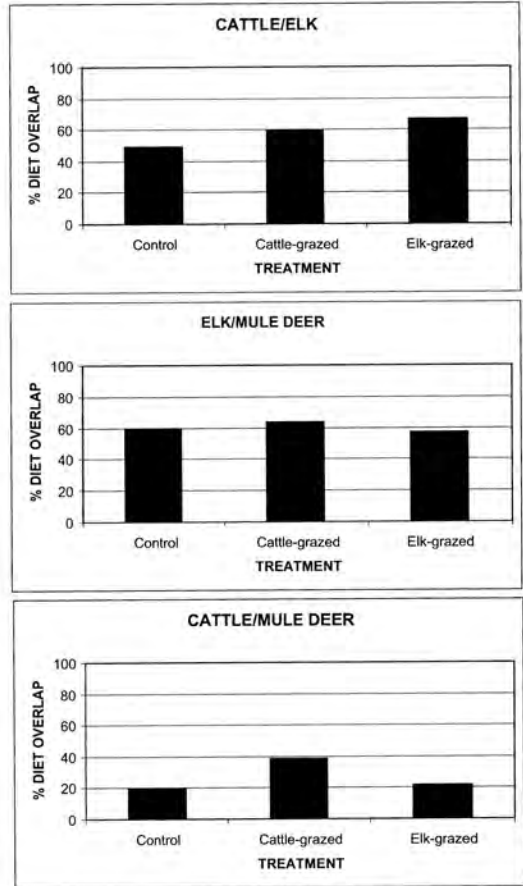


FIGURE 5. Percent diet overlap among mule deer, elk, and cattle by major forage category calculated with Horn's Index of Similarity at the Starkey Experimental Forest and Range, northeast Oregon. Bite count data were used to determine percent diet overlap.

mule deer and cattle. Interestingly, elk consumed a substantially higher percentage of lichens, with no consumption of this forage by cattle, and only a minor percentage consumed by mule deer. Like cattle, elk also switched their diets in response to previous grazing. The most dramatic change in elk diets was in pastures previously grazed by elk. Elk appeared to increase their consumption of graminoids in response to a decline of available lichens. This increased the potential for competition between cattle and elk.

Other research at Starkey suggests that competition may exist between cattle and

elk during late summer. In ponderosa pine-bunchgrass summer range at Starkey, Skovlin et al. (1968) found that elk use decreased as rate of cattle stocking increased. In a more recent study at Starkey, Coe et al. (2001) discovered that when cattle were present, elk use of the same pastures decreased and use of the ponderosa pine/Douglas fir plant community in the same pasture increased in late summer. In Colorado, however, Hobbs et al. (1996) found that at high densities, elk were in direct competition with cattle, but at low density, elk had a facilitative effect on cattle diets.

Because of their anatomical and digestive attributes, mule deer were expected to have a more selective diet and choose higher quality forages than elk or cattle (Hofmann 1988). Mule deer switched their diet the least of the three herbivores in response to previous grazing by cattle or elk. This lack of flexibility in their diet could result in increased competition with elk or cattle in areas that have high ungulate or cattle densities or low forage production. Kie et al. (1991) concluded that competition between cattle and mule deer was highest during years of below-average precipitation. Austin and Urness (1986), however, concluded that deer and cattle did not compete for forage in their study area as deer use increased.

In our study we determined the crude protein (CP), acid detergent fiber (ADF), neutral detergent fiber (NDF), and *in vitro* dry matter digestibility (IVDMD) of plant samples collected that represented those parts of species common in the diets of mule deer, elk, and cattle (Damiran et al. 2003). The most dramatic effect of prior grazing on subsequent diets of mule deer, elk, or cattle was the influence of previous cattle grazing on diets of steers. Grams/minute of CP and IVDMD consumed by cattle in pastures previously grazed by cattle was 32.4 and 43.0 percent less respectively, compared to control (ungrazed) pastures. This suggests that the potential for intraspecific competition among cattle in secondary succession grand fir vegetation types is high during late summer.

Our results support Holechek's et al. (1981) findings that, overall, the diets of cattle at Starkey did not meet the National Research Council (NRC) standard for nutrient (CP and digestible energy (DE)) requirements during late summer. By contrast, nutrient intake of mule deer and elk did not change in response to previous grazing by cattle or elk (Damiran et al. 2003).

One measure of the potential for competition between species is the amount of dietary overlap. Diet overlap or lack of diet overlap, however, does not necessarily equate to high or low levels of competition. One would expect that the distinct differences in ruminant physiology among mule deer, elk, and cattle would result in low dietary overlap, especially between mule deer and cattle (Hanley 1982, Baker and Hobbs 1987, Hofmann 1988). Willms et al. (1980) observed that mule deer diets in British Columbia changed in response to varying levels of forage utilization by cattle. When forages were abundant, cattle and deer diets were similar, but as forage utilization increased, diet overlap decreased, with deer preferring shrubs and cattle preferring grasses. In our study diet overlap was the lowest between cattle and mule deer in ungrazed pastures. The potential for competition between these two species, however, increased greatly in response to previous cattle grazing. Steers consumed less graminoids and more forbs and shrubs in response to prior cattle grazing. This switching of cattle diets from graminoids to forbs and shrubs nearly doubled the dietary overlap between cattle and deer. By contrast, Damiran et al. (2003) found that intake of CP and IVDMD for mule deer did not change in response to prior grazing by cattle or elk, suggesting that competition was not occurring at the grazing intensity in our study even though diet overlap increased.

The greatest potential for competition in ungrazed secondary succession grand fir was between mule deer and elk. Mule deer and elk consumed many of the same forbs and shrubs. Dietary overlap of mule deer with elk, however, did not change in

response to previous grazing by cattle or elk. Coe et al. (2001) found that mule deer use of pastures at Starkey declined when elk were present which suggests that interference competition may be occurring between these two species.

Dietary overlap was also high between cattle and elk, especially in pastures previously grazed by steers or elk. As others have suggested, the dietary choices of elk can overlap closely with dietary selection by cattle, making the two species potential competitors for available forage. Based on interactions between cattle and elk at Starkey Coe et al. (2001) concluded that dietary competition for forage could occur between elk and cattle in late summer. At the level of grazing in our study, CP and IVDMD in elk diets were not affected by previous grazing but these two nutrients declined in steer diets (Damiran et al. 2003). As mentioned previously, however, the decline in CP and IVDMD in cattle diets was a result of intraspecific competition for forage among cattle, not interspecific competition with elk.

In contrast to results from our study, Stewart et al. (2003) determined diet composition of free-ranging mule deer, elk, and cattle at Starkey using microhistological analyses of fecal samples and found little overlap in dietary niche among these three herbivores. This study was conducted later in the summer during July and August however, and on free-ranging animals with access to a variety of habitat types. Also, cattle feces were collected from the Main Study Area and feces from mule deer and elk were collected from the Northeast Study Area where cattle were not present. Finally, results from microhistological analyses of fecal samples are not comparable to bite count data because of inherent biases associated with fecal samples that cannot control for different rates of digestion of different forage classes (McInnis et al. 1983).

Our results suggest that inter- and intraspecific competition for forage may exist among all three species during summer in previously logged grand fir forests. However, realization of competition de-

pends on the densities of the various herbivores and annual net primary production, and on diet overlap resulting in negative nutritional consequences. The probability of competition would be increased during years of low forage production, heavy herbivore stocking, or both. Moreover, demonstration of true competition between two or more species requires a documented reduction in animal or population performance by one species as a result of sharing a limited resource with the other species (Wisdom and Thomas 1996).

POLICY IMPLICATIONS

1. Our results suggest that intra- and interspecific dietary competition may exist among mule deer, elk and cattle during the summer in secondary succession grand fir vegetation types. Consequently, it is important for managers to monitor the forage base in this habitat type and if necessary, reduce livestock use to maintain plant vigor and leave adequate forage for mule deer and elk. Or, alternatively, it may be necessary to reduce densities of mule deer and elk to maintain adequate nutrition for cattle. Which approach is taken (reduction of livestock or wild ungulate use) depends on the multi-species objectives set for the allotment, as evaluated from analyses of the trade-offs of varying stocking rates among the species (Wisdom and Thomas 1996). Although the fitness of mule deer and elk may not be affected during the summer, their ability to survive severe winters and reproduce may be negatively affected by poor summer nutrition (Cook et al. 2004).
2. We found no strong evidence that previous elk or cattle grazing improved forage quality of mule deer, elk or cattle that grazed the same pastures later that year. During the summer in secondary succession grand fir it appears that prior grazing by cattle or elk does not improve the forage quality for those herbivores that subsequently graze the same pastures. In our study, however, forage quality did not im-

prove subsequent to cattle and elk grazing because soil moisture may not have been adequate in late June and July for vegetation regrowth. The potential for prescribed cattle grazing, however, as a management tool to maintain or improve mule deer and elk forage during late summer needs more exploration.

3. High diet similarity among these three species and an increase in dietary overlap in response to previous grazing by cattle and elk indicate that cattle and elk readily shift their diets during late summer. This knowledge will help managers optimize use of grand fir vegetation types for grazing by wild ungulates and livestock.
4. Overall, based on our findings and research by others (Holechek et al. 1981), the diets of cattle may not meet the NRC standard for nutrient (CP and DE) requirements during summer in forested vegetation types at Starkey. This finding further suggests that competition for forage is more likely during summer, and deserves careful consideration in allotment management planning for areas with similar environmental conditions as Starkey.
5. Our project and other studies indicate a need for additional research on inter- and intraspecific competition for forage among mule deer, elk, and cattle. More questions remain on how the timing and intensity of grazing affects the nutritional condition and fitness of all three species. Likewise, it would be helpful to have more information on their habitat selection and distributional overlap. This will help contribute to the continuation of the multiple use concept mandated on public lands and guarantee proper management of the forage resource.

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Landscape Simulation of Foraging by Elk, Mule Deer, and Cattle on Summer Range

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INTRODUCTION

Cattle, mule deer (*Odocoileus hemionus*), and elk (*Cervus elaphus*) share more area of spring, summer, and fall range than any other combination of wild and domestic ungulates in western North America (Wisdom and Thomas 1996). Not surprisingly, conflicts over perceived competition for forage have a long history, yet knowledge about actual competition is limited (Van Dyne et al. 1984b, Hobbs et al. 1996, Johnson et al. 1996). One of the first studies of the Starkey Project (Rowland et al. 1997) was designed to address the issue of whether mule deer and elk compete with cattle for available forage on summer range. A component of this study was to build a forage allocation model that could be used to analyze forage allocation problems on summer range in the Blue Mountains. This model would use data on animal spatial distributions, resource selection patterns, behavioral interactions, and diet selection of cattle, elk, and mule deer collected as part of the Starkey Project at the Starkey Experimental Forest and Range (Johnson et al. 2000; Coe et al. 2001, 2004; Findholt et al. 2004).

Modeling the forage removal and animal performance for multiple species of ungulates across large landscapes is a complex problem (Weisberg et al. 2002). The high degree of temporal and spatial variability in ungulate distributions, forage production, and nutritional value of forage contribute to the problem (Wisdom and Thomas 1996). Several early forage allocation models built for western rangelands were never widely used, owing to insufficient data, model complexity, and institutional barriers (Van Dyne et al. 1984a, McInnis et al. 1990). A prototype forage allocation model built from Star-

key data (Johnson et al. 1996) suffered from similar problems, but did provide a framework for further discussions and model development (Vavra et al. 2004). This model used linear programming with a weighted objective function that contained terms for forage production, forage energy content, and resource selection coefficients. Animal foraging behavior could be optimized with respect to each of these three variables or some weighted combination. The Johnson et al. (1996) model generated reasonable predictions of species distributions and forage consumption patterns at monthly time steps. However, the linear programming framework was cumbersome and had limited capability to analyze the temporal dynamics of ungulate foraging behavior.

Using many of the parameters from the earlier work, we built a more detailed, spatially-explicit individual animal foraging model (heretofore Starkey Foraging Model, SFM). Initial testing of this model was described in Vavra et al. (2004). In this paper we describe additional developments and testing, and demonstrate the model's capability to predict forage removal and animal performance at Starkey. Ultimately, the model or subsequent outgrowths are intended for use in allotment management planning on summer ranges shared by cattle, mule deer, and elk.

METHODS

The Starkey Foraging Model uses empirical data on habitat preferences, forage production, forage quality, and energy dynamics of cattle, mule deer, and elk. These data are coupled with information on foraging behavior to simulate forage consumption by the three ungulates on the Starkey landscape. The SFM was de-

veloped in Object Pascal using the Delphi 6 (Borland Inc., Scotts Valley CA) integrated development environment. Data sources used for the SFM are described in detail by Vavra et al. (2004) and summarized here.

Habitat preferences for each species were incorporated using resource selection functions developed at Starkey (Johnson et al. 2000, Coe et al. 2001). These resource selection functions (RSFs) were estimated from Starkey telemetry data collected between 1993 and 1996, and were calculated for monthly time steps, from April through October (Tables 1, 2). The RSF's represent the probability of an animal visiting a particular pixel over the monthly interval, as described by Johnson et al. (1996, 2000).

Forage production was estimated using several empirical models built from Starkey data (clipped plots from 1993–2000) and other sources (Vavra et al. 2004). We built functions to predict herbage production as a function of calendar day for grasslands, ponderosa pine (*Pinus ponderosa*) and riparian ecotypes. The equations for these ecotypes were extrapolated to the seven plant association groups in the model (moist meadows, dry meadows, bunch grass and shrub lands, warm dry forests with grass understory, warm dry forests with shrub understory, cool moist forest with grass understory, cool moist forest with shrub understory). The forage production was partitioned into forbs, grass, and shrubs using scaling factors developed by Hall (1973) and Johnson and Hall (1990). The growth functions were also adjusted for canopy closure on a pixel basis using relationships developed at four grazing exclosures at Starkey and the data of Pyke and Zamora (1982). Forage growth was represented in the model on a daily time step, and we used the same growth functions for forage re-growth as those used for initial forage growth.

Forage quality, as measured by in-vitro digestible energy (IVDDM) of forage was obtained from the literature (Holechek et al. 1981, Svejcar and Vavra 1985, Sheehy 1987, Westenskow 1991) and data from

Starkey. Digestible energy (DE) was calculated from IVDDM using methods of McGinnis et al. (1990), with estimates made on a monthly time step.

The spatial dynamics of animal foraging were modeled as a multi-scale process that involved the selection of foraging patches and subsequent selection of forage within the patch. We used concepts and data from a variety of sources for the foraging component of the model (Spalinger and Hobbs 1992; Gross et al. 1993, 1995; Shipley and Spalinger 1995; Bailey 1996) as well as observations on elk and deer movements at Starkey (Ager et al. 2003). Foraging patches were defined at the same scale as the Starkey spatial database, that is, 30 by 30 m pixel. Selection of foraging patches was modeled by using a neighborhood search algorithm that searched a 10 by 10 pixel neighborhood, and that subsequently chose the pixel that maximized an index of preference according to:

$$\text{PREF}_p = (\text{RSF}_{\text{spm}} \times W_{\text{rst}}) + (\text{DE}_{\text{pm}} \times W_{\text{qual}}) + (\text{F}_{\text{pm}} \times W_{\text{mass}}) \quad (1)$$

where

PREF_p = pixel preference score for pixel p ;

RSF_{spm} = resource selection function score ($0 \leq \text{RSF} \leq 1$) for species s , pixel p , and month m ;

DE_{pm} = digestible energy in Mcal/kg forage for pixel p and month m ;

F_{pm} = forage (kg/ha) present on pixel p and month m .

Here, W_{rst} , W_{qual} , W_{mass} are weighting coefficients that control the relative importance of habitat selection, forage quality (DE) and standing forage biomass in the foraging process. The formulation recognized that both resource selection functions and forage characteristics need to be considered in the selection of foraging areas. Initially we used a product

TABLE 1. Coefficients of resource selection functions for mule deer and elk during six monthly time steps in Main Study Area 1993–1996, Starkey Experimental Forest, northeastern Oregon. Seasons 1–6 correspond to May 16–June 15, June 16–July 15, July 16–August 15, August 16–September 15, September 16–October 15, and October 16–November 15. Coefficients are standardized (top) and non-standardized (bottom). Coefficients for elk when cattle were not present were estimated in Smith-Bally pasture (seasons 2 and 5) and Bear pasture (seasons 3 and 4)

	Season	Intercept	Dist. edge of patch	Forage prod.	Shape of patch	Dist. traffic zero	Dist. traffic low	Dist. traffic med.
Deer	1	–3.4588						–0.4284
		–25.2478						–0.0005
	2	–3.8910						
		–15.4409						
	3	–4.4878						
		–12.1049						
	4	–3.7869						
		–12.3734						
	5	–3.9353						–0.3948
		–14.3405						–0.0003
	6	–3.9259						
		–17.8403						
Elk	1	–2.4546						0.1191
		–14.0412						0.0001
	2	–2.8329	–0.0378	–0.0568	–0.0455		–0.2775	0.0741
		–21.2643	–0.0008	–0.0003	–0.2897		–0.0004	0.0001
	No cattle	–2.9761			–0.1288		–0.2905	
		–26.8541			–0.7677		–0.0004	
	3	–3.6208	0.1038	0.0377	–0.0681			0.1237
		–20.3917	0.0022	0.0002	–0.4333			0.0002
	No cattle	–3.3056			–0.1649		0.3010	0.3256
		–32.3572			–0.9822		0.0004	0.0003
	4	–3.0575	0.0992			0.1182	0.0984	
		–20.4503	0.0021			0.0005	0.0002	
	No cattle	–2.6522		–0.1112				
		–19.5567		–0.0005				
	5	–3.1617	0.0463				0.0822	
		–19.0188	0.0010				0.0001	
	No cattle	–2.2976		–0.2736	–0.1136			
		–9.4488		–0.0012	–0.6781			
	6	–3.2960						
		–20.4223						

of RSF_{spm} , DE_{pm} , and F_{pm} to calculate the preference score and included the weighting coefficients W_{qual} , W_{rsf} , W_{mass} as exponents. This method created some scaling issues that led to the current formulation. Although the weighting coefficients could be species-specific, we used the same values for each species in the present simulations. Pixels were selected for foraging by randomly sampling the pixels and respective preference scores in each 10 by 10 pixel neighborhood 90

times (90 percent of the total number of pixels) to reflect the fact that animals have a less than perfect knowledge of the surrounding forage conditions. The pixel with the highest preference score was selected and foraging initiated. A range of values was used for the weighting coefficients in equation (1) as well as the spatial search parameters as part of the model building process. Values used in the simulations for equation (1) are described later. To prevent animals from foraging

TABLE 1. Extended

Dist. traffic high	Perc. slope	Aspect east west	Aspect north south	Topog convex	Soil depth	Dist. cover	Perc. can. cover	Dist. to cattle fence	Dist. to water
-0.3431	0.2505	0.2159		0.2346					
-0.0003	0.0200	0.2951		0.0449					
-0.5615	0.2326	0.1344		0.1250					
-0.0003	0.0186	0.1830		0.0239					
-0.5473	0.3817	0.1723	0.2151	0.0818					
-0.0006	0.0305	0.2353	0.3210	0.0156					
-0.4496	0.2767	0.1254		0.0936		-0.2073			
-0.0007	0.0221	0.1703		0.0179		-0.0016			
-0.5563	0.2355			0.1174					
-0.0006	0.0188			0.0224					
		0.0811		0.1466		-0.1514			
		0.1097		0.0280		-0.0012			
	-0.119			0.1181	0.1470		0.0552		
	-0.0089			0.0226	0.0121		0.0025		
	0.1075	-0.0442	0.1034	0.1944	0.1384				
	0.0086	-0.0607	0.1543	0.0371	0.0114				
	-0.2912	-0.1899		0.2856	0.1601	-0.2750	0.2510	0.2891	
	-0.0223	-0.2701		0.0477	0.0126	-0.0021	0.0015	0.0007	
0.2306	0.1190		0.2491	0.1617	0.1851	-0.1919	0.1776		
0.0002	0.0095		0.3722	0.0309	0.0153	-0.0015	0.0081		
0.5570	-0.1375	-0.1520	0.1803	0.3226	0.3783	-0.4220			0.1815
0.0008	-0.010	-0.2119	0.2587	0.0534	0.0300	-0.0032			0.0011
0.1946			0.1946	0.1706	0.1527	-0.1558	0.1709		
0.0003			0.2900	0.026	0.0126	-0.0012	0.0078		
			0.1301	0.1945	0.1697		0.2209		0.1823
			0.1867	0.0323	0.0134		0.0098		0.0011
			0.2379	0.1598	0.1212	-0.1813	0.1874		
			0.3556	0.0305	0.0100	-0.0014	0.0085		
			0.2324	0.0907		-0.3904			0.2638
			0.3325	0.0151		-0.0030			0.0016
	0.0978		0.1396	0.1757	0.0915	-0.1612	0.0580		
	0.0078		0.2073	0.0336	0.0075	-0.0012	0.0026		

on high RSF pixels with very low or non-existent forage biomass, we added a constraint that required a selected pixel to contain 80 percent of the forage biomass of the previously selected pixel. Although areas still could be selected based primarily on their RSFs, this constraint also had the effect of moderating the rate of forage depletion of the pixels with the highest RSF scores, and allowed the simulation of RSF-driven foraging without resulting in infinite pixel searches.

To allow for selection of foraging areas outside the animal's sensory detection range, we nested the neighborhood search within a low-frequency meta-neighborhood search that allowed simulated animals to move (i.e., Levy flight, Marell *et al.* 2002) to another neighborhood if larger values for equation (1) were found. We experimented with a range of values for the search neighborhood size, the meta-neighborhood size, the "jump" frequency and "jump" distance, and found that

TABLE 2. Coefficients of resource selection functions for cattle during four monthly time steps in cattle pastures 1993–1996 at Starkey Experimental Forest, northeastern Oregon. Seasons 2–5 correspond to June 16–July 15, July 16–August 15, August 16–September 15, September 16–October 15, and October 16–November 15. Coefficients are standardized (top) and non-standardized (bottom)

Sea- son	Intercept	Dist. edge of patch	Forage prod.	Dist. to road	Dist. to fence	Perc. slope	Aspect east west	Topog convex	Soil depth	Dist. cover	Perc. can. cover	Dist. to water
Cattle	2	-2.4895	-0.0613	-0.1756	0.3043	-0.4726	-0.1063	-0.0526		-0.2089	-0.2743	0.1252
		2.8039	-0.0014	0.0008	0.0008	-0.0365	-0.1489	-0.0088		-0.0016	-0.0123	0.0008
	3	-3.0240	-0.1597	-0.9849		-0.1370	-0.0917	-0.0660	0.0943		0.0563	-0.1300
		4.0840	-0.0033	-0.0007		-0.0120	-0.1217	-0.0139	0.0078		0.0028	-0.0007
	4	-2.8177	-0.1728	0.0747		0.0747	-0.0584					-0.7470
		-2.4244	-0.0036	0.0007		0.0007	-0.0754					-0.0009
	5	-2.7450	-0.2228	0.0864	0.1516			-0.4536	0.0711		-0.1650	
		0.9900	-0.1710	0.0004	0.0004			-0.0075	0.0056		-0.0013	

these variables would strongly influence animal movement measurements. In the current simulations we set values for the meta-neighborhood at 100 by 100 pixels, the “jump” frequency at 0.1, and the “jump” distance at 1,000 meters.

Once a foraging pixel was selected, consumption of forage (grass, forbs, and shrubs) was modeled with simulated individual bites. Bite size was estimated using data from foraging trials conducted at Starkey (Findholt et al. 2004) and elsewhere (J. Cook, personal communication), and equaled 1.1 g for cows, 0.20 g for mule deer, and 0.55 g for elk. It should be noted that we did not constrain intake rate by bite size (Gross et al. 1993) and hence the bite process served primarily as a mechanism to sample the three types of vegetation data in the pixel over successive bites. Bite selection in the pool of simulated forage at each pixel was modeled as a Monte Carlo process that simulated successive bites that removed forage types in proportion to the sum of total forage available multiplied by forage DE at the pixel, quantified as:

$$P_{ts} = [(F_{pdt} \times WB_{mass}) + (DE_{pmt} \times WB_{qual})] \div \left\{ \sum_1^t [(F_{pdt} \times WB_{mass}) + (DE_{pmt} \times WB_{qual})] \right\} \quad (2)$$

where

P_{ts} = probability of removing forage type t for species s ($0 \leq P_{ts} \leq 1$);

F_{pdt} = forage (kg/ha) of type t on pixel p at day d ;

DE_{pmt} = digestible energy (Mcal/kg) for forage type t , pixel p , and month m ;

WB_{mass} = weighting factor for forage biomass; and

WB_{qual} = weighting factor for forage quality.

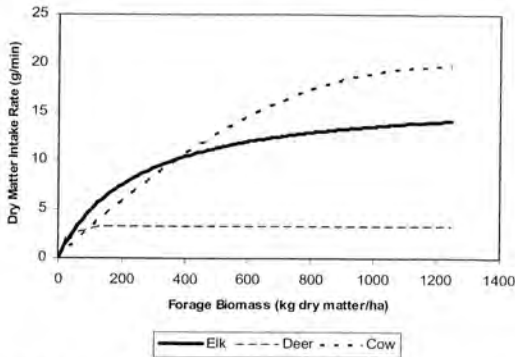


FIGURE 1. Relationship between standing forage biomass and dry matter intake rate for elk, mule deer and cattle. Functions for elk and deer were developed from data in Wickstrom *et al.* (1984). The elk relationship was developed from the Wickstrom *et al.* (1984) mixed forest type relationship. The function for cattle was developed from grazing trials on Starkey and the bison data in Spallinger and Hobbs (1992).

This foraging process simulated removal of vegetation in proportion to biomass and energy content, and/or some weighted combination, and recognized that while animals can focus their foraging on specific forage types, other non-preferred types are also depleted at some lesser rate. Initially we used WB_{mass} of 1.0 and $WB_{qual} = (\text{body weight})^{-0.75}$, with the idea that mule deer would select for high forage DE and cattle would select for forage bulk (Findholt *et al.* 2004). Elk, with their intermediate body weight, were simulated as having a foraging behavior intermediate to that of deer and cattle (Findholt *et al.* 2004). Initial simulations showed that stronger weighting of the energy component was needed to significantly influence the forage composition.

Using the foraging rules described above, simulated animals were allowed to forage until they consumed 135 g of forage dry weight per kg of metabolic body weight (Cook *et al.* 2004), or until the total foraging time per day exceeded 12 hours (Cook 2002), whichever condition came first. The foraging time was calculated using relationships between standing biomass and intake rate from Wickstrom *et al.* (1984:1291) for elk and deer,

TABLE 3. Daily energy demands of adult female mule deer, cow and elk (mcal per day) by month. Data from (Hudson and White 1985a,b; Sheehy 1987; Cook 2002)

Species	Month						
	Apr	May	Jun	Jul	Aug	Sep	Oct
Cattle	23	23	23	22	21	19	18
Elk	10.0	10.5	16.0	15.9	13.2	12.0	11.0
Deer	3.0	3.0	6.3	4.3	4.3	3.6	3.1

and from data from Starkey for cattle (Figure 1). For elk, we used the relationship for mixed forest conditions presented by Wickstrom *et al.* (1984), and combined the grass and mixed forest data to develop a relationship for deer. Intake rates could also have been predicted using relationships between bite size and plant size (Spallinger and Hobbs 1993), but the latter data were not available for conditions at Starkey.

Energy balance and weight change was updated daily using pro-rated monthly energy requirements (Table 3) obtained from a number of sources (Leege 1982; Hudson and White 1985a, b; Cook 2002). Daily energy generated by consumed forage was calculated using the energy conversion equation as:

$$Me = 1000 \frac{[F(0.038 \times \%DE + 0.18)]}{1.22} \quad (3)$$

Where,

DE = digestible energy (mcal/kg forage), and

F = forage biomass (dry matter kg/ha) consumed on a given day of forage.

Negative energy balances were translated into a weight loss by using a conversion of 6 Mcal/kg. Positive daily energy balances were translated into a weight gain by using the conversion 12 Mcal/kg.

Most simulations used herd sizes of 500 cows, 450 elk, and 250 mule deer under a summer deferred-rotation grazing system (April 15 to November 15, 210

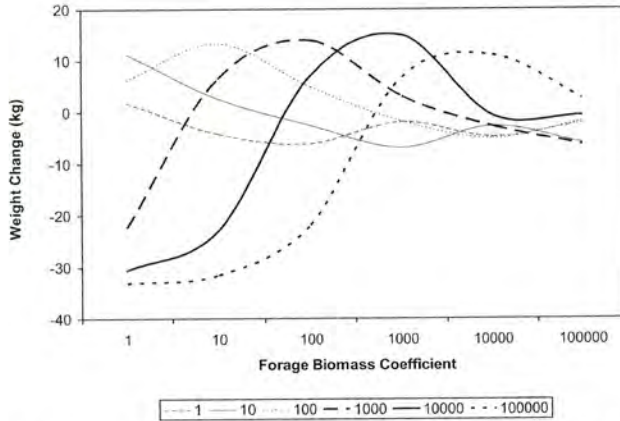


FIGURE 2. Simulated weight change in cattle for a range of values for W_{rsf} and W_{mass} in equation (1). X-axis contains values for the W_{mass} (forage biomass) weights for equation (1). Legend entries are the values for W_{rsf} in equation (1). Animal populations were 500 cows, 450 elk, and 250 mule deer.

days). These are the approximate stocking rates and summer range foraging season at Starkey. In other simulations, the stocking rates varied depending on the objective of the simulation. On each day, cattle foraging was simulated first, followed by elk and then mule deer, which gave cattle preference over elk and mule deer and elk preference over mule deer for the available forage (Coe et al. 2004). Initial weights were set at 992 pounds (450 kg), 507 pounds (230 kg), and 132 pounds (60 kg) per animal for cows, elk and mule deer, respectively, based on data from Starkey. Typical execution times for the model were about one minute. We first ran simulations to examine the effects of different weights in equation (1) on animal performance, foraging patterns and movements. This involved 125 simulations where each weight was varied by a factor of 10 between 1 and 100,000. We selected a set of weights where the model outputs appeared to be not overly influenced by the values, and roughly replicated observed animal performance at Starkey. The effects of different weights in equation (2) were then tested in a similar process in an additional 25 simulations and selected weights for equation (2). We then ran additional simulations to test how incremental changes in the number of cattle, mule deer and elk

(2–2,500), and forage production (10–100 percent of normal) affected animal performance. The latter simulations were intended to represent varying drought intensities. Reductions in forage quality from drought (Vavra and Phillips 1980, Weisberg et al. 2002) were not modeled due to limited data.

RESULTS

Simulations using a range of values (1–100,000) for the W_{rsf} , W_{mass} , and W_{qual} coefficients in equation (1) produced a range of plausible outputs in terms of predicted weight gains for cattle, elk, and mule deer (Figures 2–4). For instance, mule deer, which generally gain around 11–22 pounds (5–10 kg) per animal at Starkey, showed simulated weight gains of 15.4–19.8 pounds (7–9 kg) for the range of coefficients tested. Cattle and elk showed more pronounced changes in animal weights (Figures 2, 4), although a wide range of coefficients replicated the weight changes observed for cattle 0–22 pounds (0–10 kg) and elk 22–44 pounds (10–20 kg) at Starkey. For all species, increasing W_{rsf} relative to W_{mass} forced simulated animals to forage in areas of high RSF values (Figure 5) and generally resulted in decreased animal weights. The effect of increasing W_{rsf} on weight reduc-

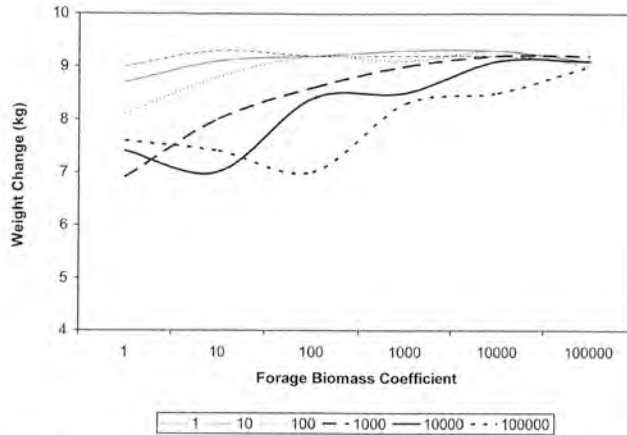


FIGURE 3. Simulated weight change in mule deer for a range of values for W_{rsf} and W_{mass} in equation (1). X-axis contains values for the W_{mass} . Legend entries are the values for the W_{rsf} . Animal populations were 500 cattle, 450 elk, and 250 mule deer.

tions was dampened as the forage biomass (F_{mass}) coefficient was increased to values above 1000.

Changes in average cattle weights ranged from -72.6 to 26.4 pounds (-33 to 12 kg) (Figure 2), the negative weight changes being associated with a high values of W_{rsf} and low values of W_{mass} . Cattle showed an intermediate optimal weight gain of 22 pounds (10 kg) when the W_{rsf} was increased by a factor of 10 over the W_{mass} . This trend was not found for elk or mule deer (Figures 3, 4). The most plausible explanation for this is that a higher forage quality is realized at this combi-

nation of W_{mass} and W_{rsf} , although this was not tested.

Results of simulations for elk showed weight changes between -44 pounds (-20 kg) and 77 pounds (35 kg), with weight gains over a wide range of W_{rsf} and W_{mass} . However, when the W_{rsf} became 1,000 times the W_{mass} , negative weight changes were observed. Unlike cattle, weight changes with different combinations of W_{rsf} and W_{mass} were asymptotic with the maximum values at about 77 pounds (35 kg). Compared to the W_{mass} and W_{rsf} coefficients, changing the forage quality (W_{qual}) coefficient had a very mi-

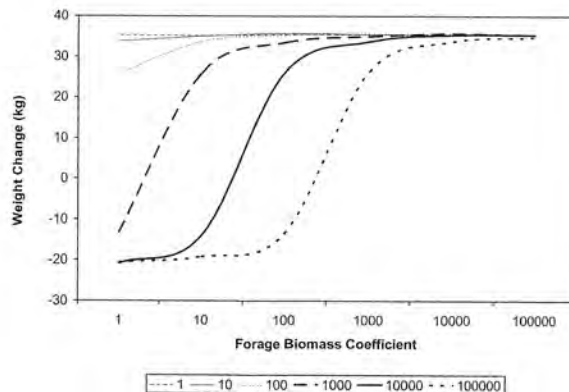


FIGURE 4. Simulated weight change in elk for a range of values for W_{rsf} and W_{mass} in equation (1). X-axis contains values for the W_{mass} weights for equation (1). Legend entries are the values for the W_{rsf} weights in equation (1). Animal populations were 500 cattle, 450 elk, and 250 mule deer.

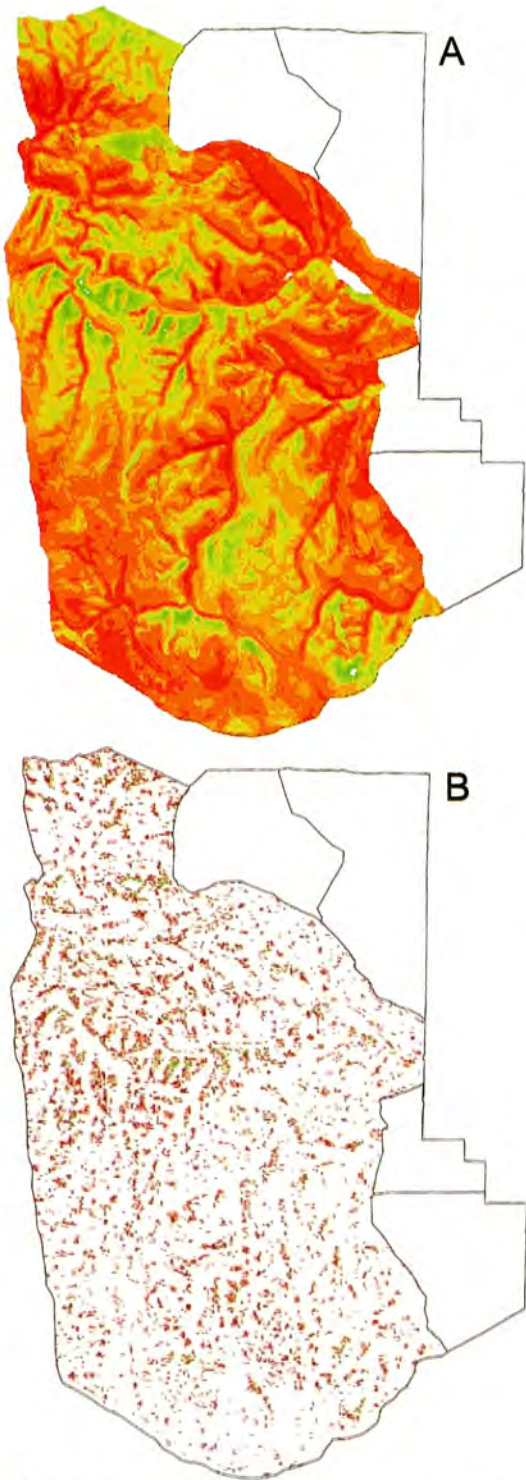


FIGURE 5. (A) Plot of resource selection functions for elk developed from Starkey data (Coe 2004). Values plotted were the sum of

nor effect, producing weight differences less than 2.2 pounds (1 kg) over the entire range (1–10,000) of values simulated.

Simulated animal distributions were compared with the maps of the RSF scores to examine how well the model replicated observed animal distributions at Starkey (Figure 5). For space reasons we limit the comparison to elk and note that the findings for elk are typical for the cattle and mule deer. The comparison is made difficult by the fact that the RSF maps represent a long-run probability of animal use during presumed periods of peak foraging based on six years of telemetry data, whereas the outputs from a simulation run represent animal use for one season, and represent only foraging activities. We did not perform statistical testing of the differences in simulated versus observed distributions, although this would have provided more definitive comparison. The maps show that simulations with high values of W_{rsf} generated animal distributions that were similar to the RSF maps (Figure 5). In contrast, simulations with a relatively high weighting for W_{mass} generated markedly different animal distributions that reflected high levels of foraging on productive grassland meadows (Figure 6a).

The effect of changing W_{rsf} and W_{mass} weights on the relative use of pixels with different RSF scores was examined by assigning the RSF probabilities to integer classes from 1 to 40 and then measuring the forage removal for each class. The integer classes were generated by re-scaling the RSF scores by $100\times$. Values above 0.4 were assigned the integer class 40. Simulations were run with W_{rsf} of 10,000 and W_{mass} of 1, and W_{rsf} and W_{mass} both

←
the monthly RSF scores as described in Coe (2004), and range from 0.15 (red) to 0.94 (green). (B) Results of simulation showing relative forage removal by elk within the Starkey area using W_{rsf} of 10,000 and W_{mass} of 1000. Low end of gradient (red) equals 1 to 5 kg/ha forage removal by elk. Maximum forage removal (green) equates to 220–225 kg/ha forage removal.



FIGURE 6. Results of simulation showing relative forage removal by elk within the Starkey area using weights of W_{rsf} of 1000 and

equal 1. The results (Figure 7) showed that a significant amount of forage was removed from higher RSF class pixels when W_{rsf} was weighted at 10,000 versus 1. The difference is somewhat magnified however by the overall higher total forage removal in the simulations where both the W_{rsf} and W_{mass} coefficients are set at one.

To choose a set of coefficients for further simulations we looked for values that resulted in weight changes that approximated those observed at Starkey using the highest possible values of W_{rsf} . In this way we could simulate the approximate animal performance at Starkey while replicating animal distributions to the extent possible. We also were interested in finding coefficients where the simulated weight gains did not change sharply with small changes in the coefficients. Using these criteria we selected a W_{mass} of 1,000 and W_{rsf} of 10,000, and W_{qual} of 1, and then simulated a range of values for the WB_{mass} and WB_{qual} coefficients in equation (2). These simulations examined how forage biomass versus energy affected animal performance. The results showed that a wide range of coefficients generated the same performance for all three species, except for the case when the WB_{qual} coefficient was reduced to less than 10. In the latter case, weights dropped by a maximum of 22 pounds (10 kg) for elk and lesser amounts for the other species. Accordingly, we set both WB_{qual} and WB_{mass} at 10 for the remaining simulations.

In a subsequent set of simulations, the forage production was varied from 10 to 100 percent of normal using the model coefficients selected above. These simulations examined the effect of disturbances like drought on animal performance. The results showed that, as forage production was decreased, weights for cattle

←

W_{mass} if 10,000. Low end of gradient (red) equals 1 to 5 kg/ha forage removal by elk. Maximum forage removal (green) equates to 35–40 kg/ha forage removal. (B) Same as (A) with forage production reduced to 10 percent of normal.

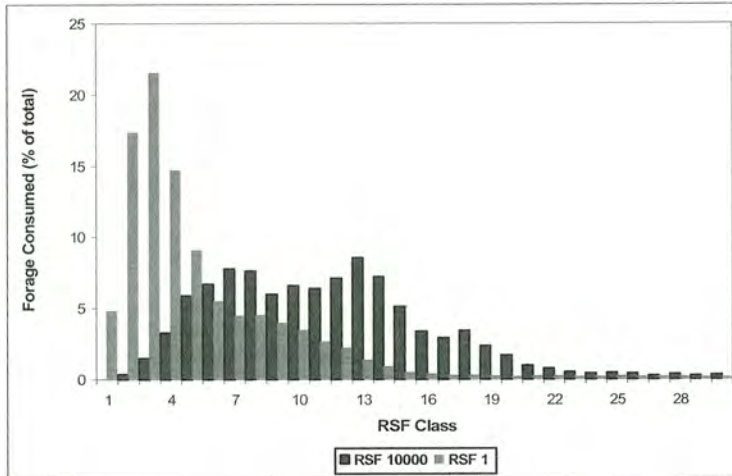


FIGURE 7. Forage consumption by two simulated elk using W_{rsf} weights of 1 and 10,000 and W_{mass} of 1. Data plotted are the percent of total forage consumed in each RSF class. RSF classes were calculated as $RSF \times 100$. The figure shows that increasing the RSF weight for selecting foraging pixels results in a larger percentage of forage removal from the higher RSF pixels.

and elk were markedly reduced, while mule deer were not affected (Figure 8). The effect of reduced forage production on weight change was nonlinear and started when forage production was about 60 percent of normal for cattle, and 50 percent for elk (Figure 8). For all species, the response resembled the intake rate functions incorporated into the model (Figure 1), and most likely the weight re-

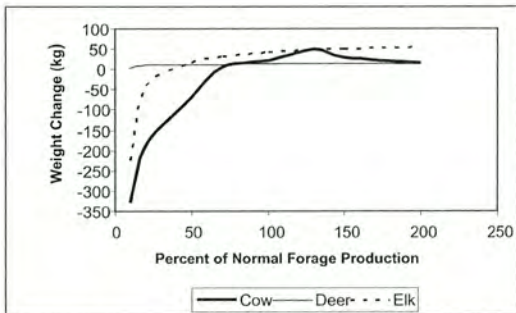


FIGURE 8. Results of simulations to examine the effect of reductions in forage production on average animal weight change for cattle, elk, and mule deer. Simulations used 500 cows, 60 mule deer and 450 elk. Forage production was reduced by a constant percentage of the normal growth rate throughout the growing season.

ductions resulted from lower intake rates associated with reduced standing forage biomass. Some slight differences were noted in the simulated animal distributions for between normal and 10 percent forage production, the latter showing more area foraged (Figure 6a, b).

Simulations to examine how animal performance varied under different population levels showed intraspecific effects for all three species. Simulations where the cattle herd was varied between 2 and 2,500 animals did not result in changes in elk or mule deer weights. However, average weight change per cow was reduced from 34.9 to 3.2 kg when the herd size was increased (Figure 9). Likewise, when the mule deer population was increased from 2 to 2500 animals, mule deer weights decreased from 17 to 4 pounds (7.8 to 1.7 kg) per animal. Elk population increases from 2 to 2500 animals resulted in elk weights decreasing from 74 to 15 pounds (33.7 to 6.8 kg) per animal. Interspecific effects on animal weights were negligible except in the case of the elk simulations where cattle weights declined from 44 to 35.9 pounds (20.0 to 16.3 kg) per animal when elk were increased from 2 to 2,500 animals. Elk weight decreased

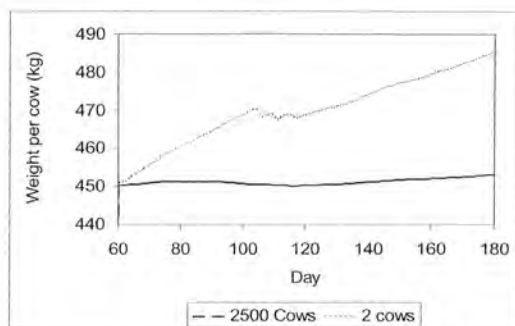


FIGURE 9. Changes in average animal weight for cattle over the grazing season for a cattle population of 2 and 2500.

by only a fraction 73.7 versus 73.3 pounds (33.5 versus 33.3 kg) per animal and mule deer weights were unchanged when the cattle population was increased from 2 to 2,500.

DISCUSSION

Foraging behavior by free ranging ungulates on large landscapes over time is a complex process that can only be approximated with models (Turner and Wu 1994, Moen *et al.* 1997, Weisberg *et al.* 2002). The current work illustrates the inherent complexity of the problem for summer range conditions in the Blue Mountains. While our model does not consider many of compensatory mechanisms in the foraging process, it can replicate animal weight dynamics observed at Starkey as well as provide reasonable predictions of animal distributions. The model demonstrated that both forage biomass and RSF scores need to be included in a simulation model to replicate observed animal distributions and weight changes, and that some balance between the two best summarizes actual foraging behavior at the landscape scale. We found that modeling forage site selection based on RSF scores resulted in significant weight loss for cattle and elk, and to a lesser extent, mule deer. Forage depletion on high RSF pixels probably reduced forage intake rates and led to the lower weight gains. In addition, RSF scores for elk and mule deer did not always reflect selection of the most productive foraging

areas, due to other habitat considerations like distance to open roads. When forage site selection was based primarily on standing biomass, the simulated animal distributions were not representative of Starkey telemetry data. Simulations showed that by weighting the RSF about 100 times less than forage biomass to calculate pixel preference scores, the model would produce reasonable animal weights and select high RSF pixels as well.

Comparing empirical animal distribution with those from the simulations were made difficult by the fact that the former were developed from six grazing seasons of data and show more diffuse spatial patterns of animal use compared to simulated distributions. Although the RSF values used for the model were estimated for peak foraging periods, they likely included observations when animals were not foraging as well. Thus without consideration of these other activities, there will always be some discrepancy between RSF values and simulated animal foraging patterns. The two data sources could be made more comparable if the animal distributions generated by the forage model were compared with the same number of animal locations simulated directly from the RSF probabilities.

When we measured forage removal with respect to RSF probabilities on the Starkey landscape and changed the RSF weights in the pixel preference equation, we found that the model did indeed lead simulated animals to spend more time foraging in areas with higher RSF scores. Using these methods, additional simulations could be performed to measure the loss of foraging opportunities as a result of selecting foraging pixels on the basis of distance to roads or other human influences. In this way the effect of human disturbance on animal performance could be examined.

We were also able to quantify changes in animal performance resulting from a reduction in forage production at the landscape scale. Reductions in forage production might result from drought or natural disturbance. Changes in animal weight with decreasing forage production

closely resembled the functional response of intake rate to decreasing forage biomass for the three species (Figure 1), and shows the importance of forage intake dynamics in the context of modeling animal performance (Gross et al. 1993). Simulating animal performance under a range of forage production values should also consider increased movements (Wickstrom et al. 1984), and, in the case of drought-limited forage production, a reduction in forage quality (Vavra and Phillips 1980, Weisberg et al. 2002). The latter relationship could easily be incorporated into the SFM, although there is little data from which to develop a quantitative relationship. Vavra and Phillips (1980) observed a 20–30 percent reduction in digestible dry matter during a drought year when precipitation was 39 percent of normal. Reductions in forage quality of this magnitude would have a significant impact on simulated animal weights.

We observed negligible interspecific effects on animal weight when population levels of each species were varied between 2 and 2,500 animals. However intraspecific effects were observed for all three species as manifested in reduced weight gain compared to simulations where population levels replicated those at Starkey. Weisberg et al. (2002) also found stronger intraspecific than interspecific competition for forage when they modeled cattle and elk on shared range. Hobbs et al. (1996) in their study of elk and cattle competition found significant reductions in calf weights while cow weights were not significantly changed. Competitive effects among the species might be better studied with our model by examining changes in forage intake rates over the season instead of animal weights. Adding calves to the model might also provide a means to study the competition question in more detail. In any event, additional model refinements and a battery of simulations are probably needed to carefully examine questions of competition among the three species.

The major challenge to refine the current model is to determine what mechanisms in the foraging process are the most

important determinants of landscape scale foraging behavior and animal performance. Factors such as environmental heterogeneity (Shipley and Spalinger 1995, Etzenhouser et al. 1998, Wallis-DeVries et al. 1999, Johnson et al. 2002), movement rules (Gross et al. 1995), and cognitive abilities (Bailey 1995), all influence the foraging behavior of ungulates on large landscapes. However, for the purpose of analyzing stocking on summer range in the Blue Mountains, some of the finer details of the foraging process may not be needed in the current model. One important gap in the model is the lack of local data on the functional response of intake rate for cattle, elk, and mule deer for conditions at Starkey. Development of these relationships should be a high priority since these functions are strong determinants of animal performance for scenarios where forage biomass is limited due to high stocking rates or low forage production. Modeling intake rate at the bite level rather than using standing biomass may provide different results than obtained here, since intake rate is poorly correlated with standing biomass for highly selective foragers like mule deer (Spalinger and Hobbs 1993).

Considerable detail could be added to the energetic component of our model by building on previous work (Wickstrom et al. 1984; Hudson and White 1985a,b). For instance, we did not change energy budgets to reflect increased daily movements at lower levels of standing forage biomass. We also did not consider the energy requirements as a function of animal age. Another important addition would be the growth and development of calves for all three species.

Our ultimate goal is to use the SFM to evaluate different grazing management strategies on summer range landscapes in areas like the forest types of the interior western United States, and test various hypotheses about the effects of alternative stocking rates for ungulates. In this regard, the objective might be to identify the existence of key stocking thresholds that correspond to changes in animal performance at the species level (Hobbs et

al. 1996). Such a tool is currently not available for use in allotment management planning on lands administered by the U.S. Department of Agriculture, Forest Service (FS) and U.S. Department of Interior, Bureau of Land Management (BLM), the two largest federal land managers in the United States. Moreover, the mechanistic structure of our model, based on individual foraging behavior, could help managers and public interests improve their understanding of how ungulates use the landscape to meet their foraging needs.

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Thermal Cover Needs of Large Ungulates: A Review of Hypothesis Tests

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INTRODUCTION

A great deal of big game research occurred in western North America during the 1960s through the 1980s, and many advances in our knowledge occurred as a result. Timber harvest increased during this period as well in many localities, and this trend was often perceived to threaten ungulate populations (Hieb 1976). Thus, it is not surprising that appreciable research in this era focused on relations between forestry and elk (*Cervus elaphus*). Logging's most apparent immediate effect is modification of the forest overstory, and a concept arose that was new at least in the West. This new concept assumed that dense forest cover moderates the effects of harsh weather sufficiently to confer survival and reproductive advantages in the winter, in particular, and during the summer. Forest stands that confer such advantages are referred to as thermal cover.

To some degree, support for the thermal cover concept arose from observations that forest cover can moderate weather. During winter, temperature can be several degrees warmer under forest canopies at night (Reifsnyder and Lull 1965, Parker and Gillingham 1990) due to long-wave radiation emitted from the forest canopy (Moen 1968, Beall 1974, Grace and Easterbee 1979). Long-wave radiation can be absorbed by animals, thereby potentially enhancing energy balance (Grace and Easterbee 1979). Forest canopies also reduce wind speed (Grace and Easterbee 1979) and thus theoretically reduce convective heat loss. During summer, shade from forest cover reduces diurnal, ambient temperature fluctuations and provides opportunity to avoid elevated heat loads that can result from direct solar radiation (Demarchi and Bunnell

1993). A number of habitat selection studies demonstrated that ungulates use dense forest stands disproportionately to their availability at certain times (e.g., Irwin and Peek 1983, Leckenby 1984). Selective use of dense forests under several circumstances was consistent with the prediction that thermal cover was operative, and thus, this was assumed to be in response to thermal protection provided by cover (Beall 1974, Armstrong et al. 1983, Leckenby 1984, Zahn 1985, Ockenfels and Brooks 1994). Such an interpretation can be supported by modeling using energy balance equations (e.g., Grace and Easterbee 1979, Parker and Gillingham 1990, Demarchi and Bunnell 1993).

Thus, over time a fairly broad base of literature was developed that supported the thermal cover hypothesis. However, arguments were made that the evidence was not sufficiently strong to demonstrate significant biological benefits. In particular, it was unclear if observed selection for forest cover, when it occurs, was related to thermal protection from harsh weather or due to some other reason (Peek et al. 1982). Evidence of support from habitat selection studies is only inferential (Riggs et al. 1993), and there is virtually no support for the thermal cover hypothesis from experimental research specifically designed to establish cause-and-effect relations. Using simulation models, Swift et al. (1980) and Hobbs (1989) concluded that thermal cover had negligible influences on ungulates during winter. Hobbs (1989) indicated that forage conditions, either during or prior to winter, exerted greater effects on winter survival of mule deer (*Odocoileus hemionus*) than did thermal cover. Later, doubts were raised that although thermal

cover benefits were certainly real in theory, their influences in the field may be too infrequent or inconsistent to be meaningful under many circumstances (Riggs et al. 1993).

Nevertheless, the preponderance of original research results seemed to support the concept of thermal cover. As these results became more widely accepted, they were incorporated into a variety of habitat-evaluation models. For elk, variables that provide measures of the abundance and, in some cases, quality of thermal cover, have been incorporated widely into habitat evaluation procedures (e.g., Wisdom et al. 1986, Thomas et al. 1988a, Christensen et al. 1993). These models were used extensively in development of national forest plans (Edge et al. 1990) and are often used to make site-specific decisions regarding timber harvest or other management activities across a variety of scales.

Over the last half-century, there have been four explicit experimental tests of thermal cover's influence on well-being of big game (Robinson 1960; Gilbert and Bateman 1983; Freddy 1984, 1985, 1986; Cook et al. 1998). Herein, we briefly review these studies and discuss their management implications in the context of new problems facing the game-management community in the 21st century.

OREGON ELK STUDY: COOK ET AL. (1998)

Of the studies attempting to directly evaluate the influence of thermal cover on animal performance, this study was the most intensive and long-term. Moreover, it is the only study, to our knowledge, that directly evaluated the effects of thermal cover on big game in summer.

Study Area and Methods

This elk study consisted of a series of controlled experiments conducted from 1991–1995 using tractable elk. The study area was located at 4,200 to 4,400 feet (1,300 to 1,350 m) in elevation on a northeast-facing slope in the grand fir (*Abies grandis*) forest zone in the Blue

Mountains of northeastern Oregon, lands typically used by elk as summer range in the area. As such, the site afforded colder and more mesic winter conditions than typically occur on elk winter ranges in the region, and provided weather conditions typically encountered by elk during summer.

The study area was created from a contiguous, mature, uneven-aged forest by prescriptive logging in nine 5-acre (2.3-ha) cover treatment units. By random selection, 3 units were clearcut, 3 were partially harvested to reduce density of overstory canopy (providing "marginal" cover as defined by Thomas et al. 1988a), and 3 were left unharvested (providing "satisfactory" cover as defined by Thomas et al. 1988a). This layout provided three replicates of four levels of cover for the experiment: (1) clear-cut habitat with no overstory cover, (2) partially cut habitat with an average of 30 percent overstory canopy cover, (3) uncut habitat with an average of 70 percent canopy cover, and (4) units set up to provide a combination of clear-cut and dense forest habitat to the elk. In the first three treatments, elk were sequestered at the center of the units in a 0.25-acre (0.1-ha) pen. In the combination treatment units, elk were held in a pen that extended 65 feet (20 m) into the clearcut and 165 feet (50 m) into the dense forest, providing elk with the ability to choose among cover types as they desired. All understory vegetation (potential forage) was removed from the pens. The 12 pens were designed to hold 3 elk each, providing a total capacity of 36 elk in the layout.

Experiments consisted of placing elk in the pens for four-month periods in winter (early December through mid-March) and summer (late May through late September), and documenting differences in body mass dynamics, nutritional condition, and activity. All elk received identical diets fed on a metabolic mass basis ($BM^{0.75}$); they received submaintenance rations in winter to induce loss of 5–10 percent of body mass, and received good quality diets in summer adequate for growth. Calves were used in the winter

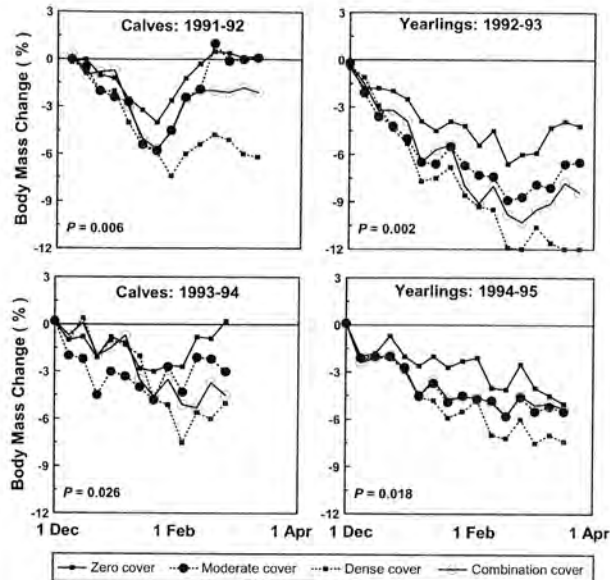


FIGURE 1. Body-mass dynamics of female elk calves and yearlings in four forest cover treatments during winter 1991–95 in northeastern Oregon (adapted from Cook et al. 1998). *P*-values indicate statistical significance level of the forest cover treatments on body mass change during each winter experiment.

experiment of 1991–1992, yearlings in summer of 1992, and yearlings in winter 1992–93. A new cohort of calves were raised in 1993 and used in the winter experiment of 1993–94, the summer experiment of 1994, and the winter experiment of 1994–95. Elk were randomly reassigned to new pens at the beginning of each seasonal experiment.

Elk were weighed twice weekly, body composition (percent fat, protein, water) was determined at the start and end of each experiment using dilution techniques with deuterium oxide, and activity was recorded automatically with leg-mounted activity sensors.

Findings

Micro-weather characteristics measured during the study demonstrated that forest canopy reduced wind speed, reduced solar radiation flux during the day, and increased net radiation flux at night. They indicated little to no effect of forest canopy on ambient temperature or relative humidity.

No positive effects of thermal cover on

elk were documented during any of the four winter experiments. But there were significant differences in body mass and body condition dynamics among cover treatments. Generally, elk in the dense forest stands lost the most mass and fat, elk in clearcuts lost least mass and fat, whereas mass and fat loss of elk in the moderate cover and combination cover units were intermediate (Figure 1). Each winter of the study, elk in clearcuts lost significantly less mass and body fat than did elk in the thermal cover treatment units. No relevant differences in activity patterns were documented among treatment units during any of the winters. These patterns were consistent across all winters despite substantial differences in winter weather conditions, ranging from abnormally cold (monthly minimum temperature averaging as low as -10° Fahrenheit (-15° C) and snowy in one winter, cool with substantial rain falling in another, and approximately normal temperature and precipitation in the other winters). During the winter (1993–94), substantial rain fell and nine elk calves either died or

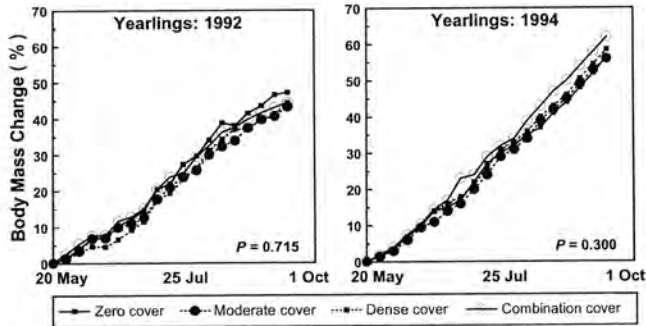


FIGURE 2. Body-mass dynamics of yearling elk cows in four forest cover treatments during summer 1992 and 1994 in northeastern Oregon (adapted from Cook et al. 1998). *P*-values indicate statistical significance level of the forest cover treatments on body mass change during each summer experiment.

were removed from the study to prevent death. Of these, 5 were in the dense cover treatment, 3 in the moderate cover treatment, and 1 in the zero cover treatment.

During the two summer experiments, no significant differences were found in body mass, fat gain, or activity patterns among the four cover treatments (Figure 2). Elk in clearcuts and moderate cover treatment units consumed more water than did elk in dense cover units, however. Both summers were warmer and drier than normal for this region of eastern Oregon.

COLORADO MULE DEER STUDY: FREDDY (1984, 1985, 1986)

This thermal cover research reported by Freddy (1984, 1985, and 1986) evaluated the effects of thermal cover on mule deer during winter from 1982–85, with the majority of data collected in winters of 1983–84 and 1984–85. It was unique in that thermal cover was provided by man-made structures designed to reduce the effects of heat loss on deer. Deer had free-choice among different cover structures that mitigated wind-chill heat loss, radiant heat loss at night, and conductive heat loss to snow-packed frozen soil while bedded. They had full access to solar radiation during the day.

Study Area and Methods

The study was conducted at the Colorado Division of Wildlife Junction Butte Research Center near Kremmling, an area located in the sagebrush (*Artemisia* spp) vegetative zone in a high mountain basin (7,300 feet [2,226 m]) of north-central Colorado. Twelve individual deer pens were constructed on the site with 6 equipped with artificial cover and the other 6 providing no cover. All vegetation was removed within and adjacent to pens and snow was packed to prevent deer from using snow as a source of cover. Pens were 33 by 33 feet (10 by 10 m) in size, constructed of large mesh woven wire, 7 feet (2.2 m) high, and were contained within a 5-acre (2.2-ha) fenced pasture that excluded neighboring wild deer.

Deer of various age classes (fawns to adults) were paired by body mass and randomly assigned to either the cover or no-cover treatments in experiments lasting from mid-December through mid-March. In 1983–84, deer were fed pelleted rations ad libitum. Response variables included changes in weight measured at 2.5-week intervals, amount of food consumed at 3-day intervals, and activity determined during 6 behavioral trials during the winter. During the winter of 1984–85, deer were fed a lower quality pellet offered in amounts equaling 60 percent of maintenance, adjusted to declining body

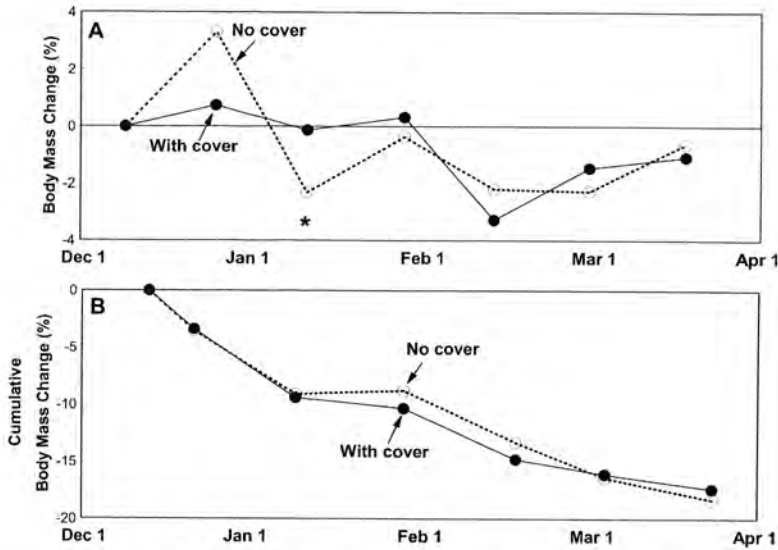


FIGURE 3. Body-mass dynamics of mixed-age mule deer with and without access to thermal cover barns during winter 1983–84 (A) and 1984–85 (B) in northcentral Colorado (adapted from Freddy 1984, 1985). In A, data values indicate percent change in body mass during each 2.5-week period of the winter; the asterisk denotes statistically different body-mass change during the 2.5-week period of late December–early January. In B, data values indicate cumulative body-mass change over the entire winter (no significant differences due to cover availability were detected).

mass every 2.5 weeks, such that the deer would be nutritionally stressed over the winter. During this second winter, cover was enhanced by incorporating a three-sided roofed wooden hut structure 4 feet (1.2 m) tall and improved wind-breaks, and more extensive darkened soil to enhance solar absorption and warming.

Findings

The winter of 1983–84 was unusually severe with periods of high winds and very cold ambient temperature to about -30° Fahrenheit (-35° C) (minimum temperature averaged below -5° Fahrenheit (-20° C) during much of the winter). Mortality in wild deer in the surrounding area represented 50–55 percent of the population (D. Freddy, personal communication 2004). Deer with cover lost on average 5.0 percent of their body mass over the entire winter (from 9 December through 17 March), whereas deer without cover lost 4.3 percent of their mass. There were no consistent patterns of mass loss within 2.5-week intervals of the winter

period (Figure 3A). Amount of food consumed and activity budgets did not differ between deer with and without cover across the entire winter period or within any 2.5-week interval.

Weather during the winter of 1984–85 was milder, although high winds and cold temperatures (less than -5° Fahrenheit, -20° C) again were common. The restricted feeding regime imposed this year of the study resulted in all deer consuming virtually identical amounts of food per pound of body mass^{0.75}. Between 13 December and 23 March, no significant differences in body mass loss were detected between treatment groups (Figure 3B). At least during the first half of winter, deer without cover spent 5–10 percent more of each day attempting to forage than did deer with cover (attempts at foraging were on aspen logs present in the pens only in 1984–85).

Overall, findings of the study indicated that thermal cover failed to significantly improve mule deer survival during winter. It was noted that cover in the form of

roofed huts with three covered sides along with additional wind breaks provided high quality thermal protection, probably at least as good as cover provided by natural forest conditions, and thus these experiments likely provided a "100 percent test" (Freddy 1985) of thermal cover's influence on deer in winter.

MAINE WHITE-TAILED DEER STUDY: GILBERT AND BATEMAN (1983)

Study Area and Methods

This study was conducted at the D. B. Demeritt Forest at Orono, Maine. The area received 76 inches (193 cm) of snowfall each winter and mean January temperature averaged 18.5° Fahrenheit (-7.5° C). Eleven pens, each 0.25 acres (0.10 ha) in size, were constructed to provide three to four replicates of three overstory conditions: (1) natural tree cover averaging 72 percent canopy cover, (2) "absolute" clear-cut averaging 6 percent cover, and (3) clear-cut, with vertical wall windbreaks, averaging 8 percent cover. Each pen contained a feeder in which pellets were provided ad libitum. Brush and tree limbs within reach of deer were removed; snow cover eliminated access to herbaceous vegetation. Eleven mixed-gender white-tailed deer (*Odocoileus virginianus*) fawns were used, with one deer per pen. This study was conducted over a single winter from December 1970 through March 1971.

Response variables included behavior, food intake, changes in body mass, and changes in fat levels. Behavior was estimated by direct observation. Food intake was measured at weekly intervals. Body mass was measured at the start and end of the experiment. At the end of the experiment, the deer were euthanized and kidney fat and femur fat indices were calculated.

Findings

Ambient temperatures were not clearly defined, but ranged as low as -30° Fahrenheit (-34°C) in this study. Deer in the

natural forest and absolute clear-cut pens consumed equal amounts of food, whereas deer in the clear-cut pens with windbreaks tended to consume less food. Similarly, body mass loss was virtually identical for deer in the natural forest pens (6.1 percent) and deer in the absolute clear-cut pens (6.2 percent), whereas deer in the clear-cuts with windbreaks lost 9.6 percent of their starting mass. Femur and kidney fat indices at the end of the experiment tended to be higher for deer in the natural forest pens than for deer in either of the clear-cut treatments. However, apparent differences in food intake, fat indices, and body mass changes failed to vary significantly among deer in any of the three cover treatments. Activity patterns were affected by changes in weather, but no differences were detected as a function of cover treatments.

Despite finding no effect of forest cover on deer, including no effect on food consumption, the authors held to a conservative conclusion that "if fawns have access to an adequate food supply, they can withstand severe winter weather even in the absence of shelter." But the authors also indicated that "increasing attention should be given to the quality of food available on winter range" (Gilbert and Bateman 1983:399), and then referenced the importance of physical condition of fawns in late autumn.

MAINE WHITE-TAILED DEER STUDY: ROBINSON (1960)

Study Area and Methods

This study was conducted at Orono, Maine, during the winters of 1957-58 and 1958-59. Forests in three 1.5-acre (0.6-ha) pens were modified to produce "sparse", "moderate", and "dense" coniferous cover. The sparse cover pen consisted of trees no larger than 5 inches (12.7 cm) diameter at breast height (d.b.h.) and supported canopy cover of 34 percent. The moderate pen contained an "all-aged" mixture of hardwood and conifers with coniferous canopy cover of about 55 percent. The dense cover pen was described as an "early-mature" stand

of several species of conifers with canopy cover of 73 percent. Natural browse within access of the deer was removed from the pens. Temperature during the study ranged as low as -22° Fahrenheit (-30°C) up to about 34° Fahrenheit (1°C), and snow accumulations "seldom" exceeded 2 feet (0.6 m).

During the first winter experiment, 1 male and 1 female fawn were placed in each pen; 3 males and 2 females were placed in each pen during the second winter experiment. Deer were fed a pelleted ration, the quantity of which was restricted to induce a submaintenance level of nutrition. At the start and end of the experiments, body mass, girth, and hind foot length were estimated and blood samples were collected. A condition factor was calculated based on body mass and hind foot length. A visual body condition score also was used to evaluate status of the deer. At the end of the experiment, deer were euthanized, and femurs were used to estimate femur fat levels. Meteorological measurements including nocturnal minimum temperatures, humidity, and wind speed were collected during the study.

Findings

Minimum temperature at night was lower and wind speed was greater in the sparse cover unit than in either of the other two treatment units. Nevertheless, decline in condition based on the "condition factor" was virtually identical among the three treatment areas in both winters of the study, and no differences were detected in condition based on their body condition score. Femur fat levels indicated no differences among treatments at the end of the first winter. Femur fat tended to be lower in deer in the sparse cover unit than in the moderate and dense cover units after the second winter experiment, but this was attributed to generally poorer condition of deer in the sparse unit at the start of this experiment.

Conclusions were conservative, in that the failure to find significant benefits of dense forest cover was attributed to flaws in the study. In particular, the sparse cov-

er pen contained a small patch of relatively dense forest cover. The author indicated this patch provided sufficiently moderate microclimatological conditions to preclude differences in animal response among the three treatment units.

DISCUSSION

Observations that dense forests can moderate harsh weather in summer and winter intuitively support the thermal cover hypothesis, and provided the bioenergetic basis of models that reported a significant benefit of thermal cover (e.g., Grace and Easterbee 1979, Demarchi and Bunnell 1993). But what has never really been clear was whether or not the magnitude of the thermal cover effect, relative to the anatomical and physiological adaptations of large mammals, was sufficient to induce a biologically relevant improvement in energy balance over sufficient time to improve survival and reproduction (Freddy 1984, Riggs *et al.* 1993). The preponderance of experimental evidence indicates that the weather-moderating effects of thermal cover indeed are probably insufficient to be of much biological value, at least under the conditions reflected in the experimental studies. Furthermore, findings that thermal cover could actually be detrimental (Cook *et al.* 1998) indicate that energetic benefits of greater solar radiation levels in the clearcuts can far outweigh whatever benefits may arise from thermal cover. Solar radiation effectively warms the animal (Parker and Robbins 1984, Parker and Gillingham 1990), thereby reducing the amount of food or endogenous energy required for thermal stasis. In the Colorado deer study, failure to show a positive effect of solar radiation would be expected because solar radiation was equally available in all pens. Reasons are unclear for failure to show a positive effect of solar radiation in the two Maine deer studies, but overcast skies typical of the northeastern U.S. would reduce the frequency of direct solar input.

Although forests can moderate harsh winter weather, substantially in the case of wind, Cook *et al.* (1998) showed that

the magnitude of the modification may be negligible, depending on short- and long-term weather patterns. For example, Cook et al. (1998) reported that elevated winds normally occurred during the day, when temperature was moderate, and thus the potentially deleterious effect of wind is reduced (see Blaxter et al. 1963, Chappel and Hudson 1978). However, wind was typically calm at night when cooler temperatures prevailed. Additionally, the contribution to energy balance of long-wave radiation from forest canopies is only relevant at night under clear skies because clouds also radiate long-wave radiation (Reifsnyder and Lull 1965). Clear skies at night are a relatively infrequent occurrence in maritime ecosystems of the Northwest (Cook et al. 1998). Similarly, because long-wave radiation accounts for temperature differences between forested and nonforested areas, it is only on clear nights when ambient temperature differences occur between forested and nonforested stands (Reifsnyder and Lull 1965). Even on clear nights, however, gentle breezes and cold airflows across uneven terrain mix air masses and reduce temperature differences (Cook et al. 1998).

The study by Cook et al. (1998) was the only study to directly test the effect of thermal cover in summer. In both summer experiments, the yearling elk were fed diets that were suboptimal, that is, adequate to support growth but at growth rates below which these animals are capable. Thus, this diet should have induced at least moderate energetic stress and would be expected to heighten sensitivity of these elk to their energetic environment. In both summers, maximum ambient temperatures were greater than or equal to 77° Fahrenheit (25°C) during at least 30 percent of the days. Parker and Robbins (1984) reported that upper critical temperature (the point at which metabolic rate increases to dissipate heat) of yearling elk while standing was 77–86° Fahrenheit (25–30°C) (operative temperature, which integrates effects of wind and solar and long-wave radiation). Thus, elk in this study, particularly those in the no-

cover treatments, should have been heat-stressed because operative temperature ranges markedly higher than ambient temperature during sunny days (Demarchi and Bunnell 1993).

Studies with livestock indicate severe heat stress can affect performance, particularly of high producing breeds (e.g., milk cows) (National Research Council 1984, Young 1988). This occurs because high ambient temperature may reduce feed intake (Young 1988) and may induce panting and elevate respiration, thus increasing maintenance requirements (National Research Council 1984). Heat-stress effects are greatest when temperature and humidity are both high, and nocturnal cooling is minimal, such as in the southeastern U.S. (National Research Council 1984, Young 1988). Despite observations that large ungulates often use shade in summer (Zahn 1985, Demarchi and Bunnell 1995, but see Merrill 1991), results of the Oregon experiments show that regimes of ambient temperature, humidity, and solar radiation occurring on western montane summer ranges in forest zones fail to exert sufficient heat stress to affect performance of elk, even if shade is completely unavailable.

Parker and Robbins (1984) showed that elk in summer pelage are well-adapted to high operative temperature, even that in excess of their upper critical temperature, mostly due to a relatively great concentration of cutaneous sweat glands. Merrill (1991) calculated that heat loss of elk standing in openings during hot summer days was sufficient to compensate for solar radiation flux and high ambient temperature in the Cascades of western Washington. McCorquodale and Eberhardt (1993) concluded that elk colonizing the Arid Lands Ecology Reserve, a low-elevation, hot, shrub-steppe area in Washington, did so with no appreciable detriment to their fitness (e.g., population growth rate was among highest ever reported for elk) despite the lack of any forest cover.

The reductionist approach used in all four studies directly testing the thermal cover hypothesis certainly is open to

some criticism, because these studies cannot possibly account for all of the complex interactions among habitat, weather, animal behavior, and animal performance inherent to free-ranging settings. Nevertheless, the value of such manipulative studies is that they can indeed tease out possible cause-and-effect relations and test their veracity. In contrast, most empirical support for the thermal cover hypothesis arose from observations of habitat selection. Linking animal survival and reproduction to availability of thermal cover, based on observations of animal choice for dense forests, was first questioned over two decades ago (Peek *et al.* 1982). Since then, recognition has increased that habitat selection studies as typically conducted must infer explanations for observed selection patterns, because they generally are ineffective for identifying cause-and-effect mechanisms, particularly mechanisms that link habitat characteristics to animal performance and carrying capacity (Hobbs and Hanley 1990, Parker *et al.* 1999, Morrison 2001). Thus, the practice of attributing effect (*i.e.*, in this case observed habitat use) to cause (*i.e.*, in this case enhancing energy balance) amounts to hypothesis generation, not hypothesis testing.

MANAGEMENT IMPLICATIONS

The experimental studies outlined above evaluated the weather-moderating influences of forest cover (*i.e.*, influences on wind speed, ambient temperature, and long- and short-wave radiation fluxes). They did not evaluate other potentially beneficial aspects of forest cover, which under some circumstances could certainly include enhanced security, reduced snow depth, and perhaps under some conditions, a better foraging environment. Thus, results of these experimental studies obviously cannot be used to categorically reject all potentially important benefits of forest cover to elk. Together, however, what they do indicate is that a thermal cover benefit attributed to dense forest cover is probably not operative across a considerable range of climate, including those in boreal ecosystems of the

northeastern U.S., maritime ecosystems of the inland Pacific Northwest, and cold, dry ecosystems of the central Rocky Mountains. At least in these ecological settings, we see little justification for retaining thermal cover as a primary component of habitat evaluation models for elk.

Wildlife management's focus on thermal cover has had an important influence on the profession's thinking, in that it implicitly directed attention on the importance of energy balance to reproductive success and survival. Regardless of the thermal cover hypothesis' lack of veracity, the central theme it was intended to address remains credible. Among habitat attributes that can be managed, two remain fundamentally influential to energy balance: (1) forage quality and quantity, due to their effect on energy intake and (2) structural attributes of habitat that mediate energy expenditures associated with travel and harassment (*e.g.*, snow intercept, security cover).

Reducing human disturbance via minimizing unrestricted road traffic and attendant harassment and providing security cover have hardly been controversial among biologists. Along with providing thermal cover, these goals came to form the primary emphasis and focus of current management paradigms embodied in habitat planning models and procedures used on behalf of elk (Christensen *et al.* 1993). Meanwhile, attention to nutrition was low, and in some cases was de-emphasized in practice (Edge *et al.* 1990, Cook *et al.* 1998). This occurred despite an ever-growing body of science demonstrating nutrition's importance to animal performance (*e.g.*, National Research Council 1984, Verme and Ullrey 1984, Cook 2002).

Continued attention to cover management may be warranted in many circumstances where security is low and/or where snow accumulations are factors limiting animal performance. However, it may be time to shift our attention toward relationships between herd productivity and nutrition-based attributes of habitat. The inverse relation between overstory

canopy density and forage abundance (McConnell and Smith 1970, Klinka et al. 1996) indicates an important tradeoff between providing dense forest cover and providing forage resources that affect carrying capacity (e.g., Hett et al. 1978). While research has certainly demonstrated the importance of energy balance to animal performance, the last 30 years of research has paid little attention to developing coarse-scale, management-level habitat models and planning procedures that address nutritional issues, and it has paid little attention to the effects of specific silvicultural systems that have potential to influence the nutritional value of large landscapes to large herbivores. Defining overstory-understory relationships and their relation to animal nutritional status, particularly in the context of specific silvicultural systems, remains a substantial hurdle to modeling elk-production relations in western forest landscapes.

The biopolitical setting has changed considerably over the last two decades, creating new challenges to elk managers and researchers. First, gone are the days of comparatively high timber harvests on federal lands, and with them the urgency of the concerns that emerged 30 years ago (Hieb 1976). The declines in timber harvest in turn may warrant increasing concern about reductions in the benefits from timber harvest, namely, increased forage abundance. Where forestry practices have intensified on private lands, more articulate understanding of how intensive forestry practices influence elk forage values would certainly be useful.

Second, in many areas particularly in the northwestern U.S., elk herds are declining (Irwin et al. 1994, Gratson and Zager 1999, Ferry et al. 2001), like mule deer herds across much of the West (Carpenter 1998). Thus, to a greater degree than in the past, if habitat models are to be relevant, they must effectively integrate those aspects of habitat that in fact significantly influence productivity and demographics of elk herds. Most extant elk-habitat models "predict only effectiveness of the habitat to facilitate elk use.

They are neither designed nor expected to predict elk numbers or productivity" (Thomas et al. 1988b:6). Yet, numbers and productivity are indeed the variables ultimately of interest to elk managers and the public. Thus, it seems to us that we should refocus our attention on these variables and their relationship to forestry to a greater extent in the 21st century than we have in the past.

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Cattle and Elk Responses to Intensive Timber Harvest

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INTRODUCTION

Forested habitats for cattle and elk (*Cervus elaphus*) in the western United States have changed substantially in response to intensive timber management during the latter half of the 20th century. Consequently, the subject of how elk and other ungulates respond to timber management is a high-profile, long-standing issue that continues to be studied and debated (Lyon and Christensen 2002). The need for additional knowledge about effects of timber management on cattle and elk remains high, given the fact that timber management continues to affect nearly all cattle and elk ranges on National Forests in the western United States (Wisdom and Thomas 1996, Lyon and Christensen 2002).

Accordingly, we conducted a landscape experiment regarding cattle and elk responses to timber harvest and associated human activities at the Starkey Experimental Forest and Range (Starkey) (Figure 1) in northeast Oregon. Our specific objectives were to (1) summarize knowledge regarding cattle and elk responses to timber harvest; (2) document changes in spatial distributions and weight gains by these ungulates, and changes in elk vulnerability to hunting, as measured before, during, and after timber harvest at Starkey; and (3) describe management implications of our findings related to timber harvest planning.

MEASURING EFFECTS OF TIMBER MANAGEMENT ON UNGULATES

We define timber harvest as “logging” activities that extract merchantable wood from forest stands; that is, tree felling and

bucking and the subsequent yarding, decking, and hauling of logs for subsequent manufacture of wood products. By contrast, we define timber management as timber harvest and all other activities implemented in direct support of sustainable production of merchantable wood. Timber management therefore includes field layout of harvest units (cut units), such as marking trees and harvest boundaries; site preparation after timber harvest, such as prescribed burning, windrowing, and mechanical removal of fine fuels; seeding or planting of commercially-desirable tree seedlings after site preparation; and subsequent mechanical thinning of trees and other silvicultural treatments designed to enhance wood production.

Past research indicates that cattle and elk responses to timber harvest can change substantially in relation to four factors: (1) the types of response variables measured; (2) the spatial scales of measurement; (3) the time period following timber harvest, over which the response variables are measured (temporal scale); and (4) the confounding effects of other human activities associated with timber harvest, such as increased human activities from increased road access. Types of response variables can include estimates of change in ungulate behavior (Ward 1976), resource selection (Lyon 1976), or population performance (Leege 1976). Changes in habitat condition brought about by timber harvest, such as modification of biomass and quality of forage in relation to each ungulate’s requirements, also have been studied extensively (e.g., Hershey and Leege 1976, Lyon 1976, Miller and Krueger 1976, Svejcar and Vavra 1985). Such differences in response variables in relation to tim-

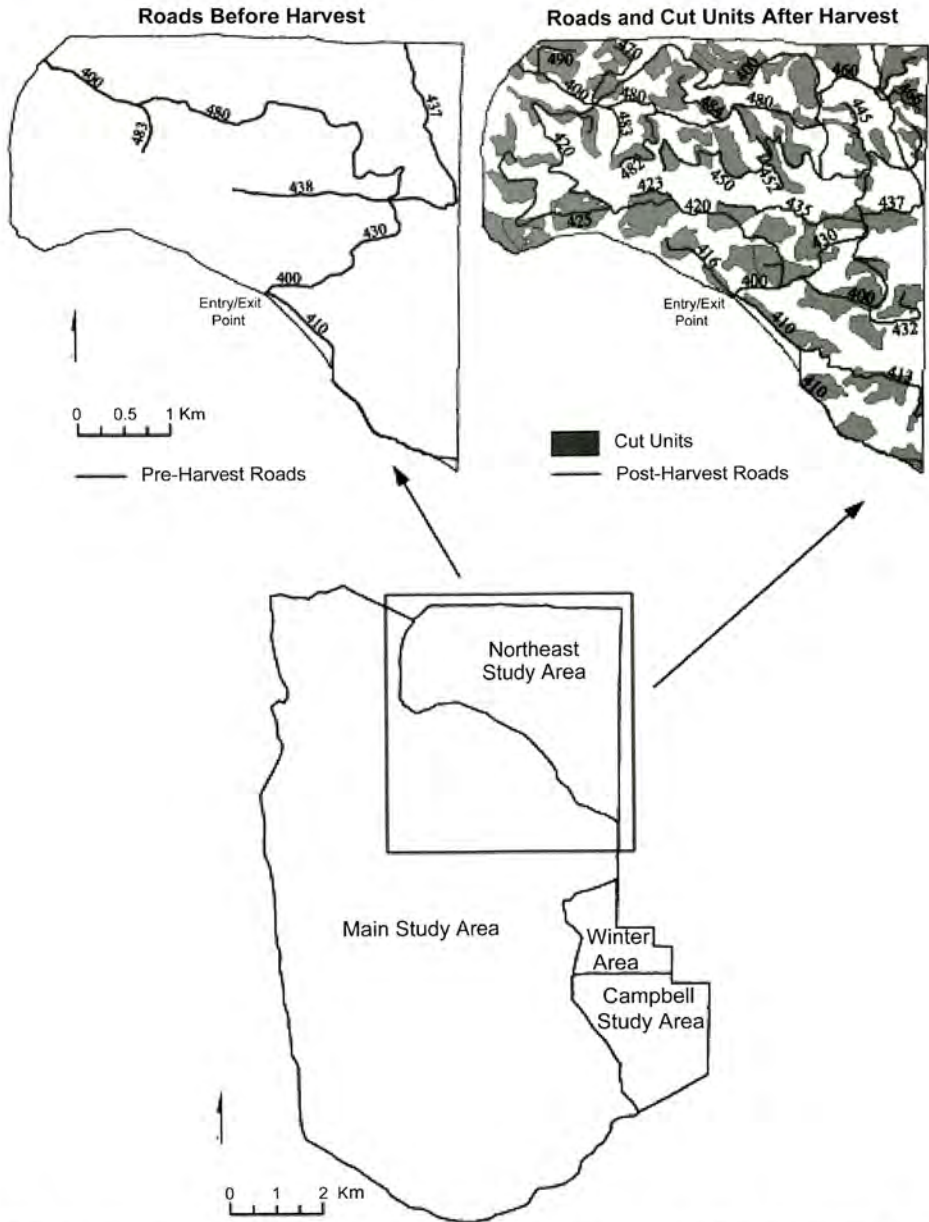


FIGURE 1. Northeast Study Area of Starkey, a 3,590-acre ungulate-proof enclosure, with roads before timber harvest (top left) versus roads and cut units after timber harvest (top right). The main haul routes used by log trucks during timber harvest (1992) included the 400, 420, 430, 437, 440, 460, and 480 roads that formed a set of interconnected loops spanning the inner portions of the study area (top right), and that led to the entry/exit point of the enclosure on its southwest boundary.

ber harvest have contributed to differences in results and conclusions among various studies, leading to confusion about potential effects on ungulates. For exam-

ple, documenting a change in ungulate habitat condition or habitat use in response to timber harvest says nothing about the effect on ungulate populations

or their nutritional status (see discussion by Garton et al. 2001).

Similarly, the spatial scales at which ungulate responses are measured directly affect the interpretation of results (Boyce et al. 2002, Parker 2002). Spatial scale refers to the extent (boundaries and size of an area evaluated) over which an evaluation is conducted, and the mapping resolution (accuracy of each mapping unit, such as a pixel or polygon) at which a response is measured at a given extent (Turner et al. 2001, Gutzwiller 2002). For example, ungulate responses can be measured within a given stand that is subjected to timber harvest, or measured among a mosaic of stands that surround the area of harvest. Measurements of ungulate responses at the stand-level, versus a mosaic of stands encompassing the area of timber harvest, yield different but complementary insights (Boyce et al. 2002, Parker 2002).

One of the most important factors affecting ungulate responses to timber harvest is the temporal scale at which effects are measured. We define near-term effects as ungulate responses measured 1–10 years after timber harvest. We consider long-term effects as ungulate responses measured >10 years after harvest. Confounding the long-term responses of ungulates to timber harvest is the frequency of subsequent harvest activities. For example, if timber harvest occurs every 10 years in a given watershed, it may not be possible to measure a long-term response to any one set of harvest units beyond that of individual stands.

Perhaps the most challenging aspect to studies of timber harvest is the confounding effect of other human activities associated with harvest, such as road construction and the subsequent changes in human access. Increased human access can lead to increased hunting pressure on elk, owing to the larger network of roads established as part of timber management (Christensen et al. 1991, Unsworth et al. 1993). Although these factors can be mitigated, such as with road obliterations or closures, the effects of such management activities are difficult to evaluate sepa-

rately from the effects of other harvest activities, such as tree felling and bucking, during the time of harvest. By contrast, changes in human access resulting from timber harvest can be studied as a separate effect after harvest is completed.

OVERVIEW OF CURRENT KNOWLEDGE

Elk and other ungulates typically thrive in early-seral forests, owing to the high biomass of palatable forage produced under these open-canopy sites (see review by Wisdom and Cook 2000). Consequently, the increased forage produced by timber harvest could be perceived as a positive event to ungulates. Several factors however, provide confounding influences, both short- and long-term, complicating this perception.

Short-term disturbances by the act of timber harvest (Ward 1976, Edge and Marcum 1985), concomitant road building, and resultant traffic (Hershey and Legee 1976, Legee 1976, Perry and Overly 1976, Ward 1976) affect elk behavior. From a review of several studies, Lyon and Christensen (2002) found that elk are sometimes displaced from harvest areas by as much as 5 miles (8 km). Most often, however, the distance elk moved appeared to be the minimum required to avoid contact with people and equipment. Continual logging within an individual watershed (5 consecutive years) may impose learned behavior that delays return to previously used habitats (Lyon 1979). Edge et al. (1985) reported that home ranges of individual animals were not altered when areas of extensive cover remained available within their home range. The authors speculated that where cover is limited, harvest activities increase home-range size and reduce home-range fidelity.

Many studies support the concept that timber harvest is beneficial to forage production for elk and other wild ungulates (Hershey and Legee 1976, Legee 1976, Lyon 1976, Schroer et al. 1993, Unsworth et al. 1998). In the Coast Range of western Oregon, Crouch (1974) found that clearcutting and slash burning were the

most practical means of maintaining black-tailed deer (*Odocoileus hemionus columbianus*) habitat, at no cost to wildlife managers. Continued harvest was required as forage production declined rapidly post-harvest because of the rapid regeneration rate of coniferous trees in the Coast Range.

Size of harvest units, however, has a substantial influence on subsequent forage use by ungulates. Scott et al. (1982) reported that small areas of disturbance are used more heavily than large ones. In that light, optimum size and arrangement of timber harvest units have been identified to maximize ungulate use of resulting forage areas. Lyon (1976) reported that harvest units of 10 to 40 acres (4 to 16 ha) were optimum. Reynolds (1966) found elk use was heavy on clearcuts <20 acres (<8 ha) in size, but use declined as opening size increased. Lyon and Jensen (1980) suggested that elk are more prone to use large harvest units in regions where large natural openings occur. Edge and Marcum (1991) suggested that both topography and forest cover should be considered in the development of logging operations and road placement. Wisdom et al. (1986) and Thomas et al. (1988) summarized knowledge of elk use in relation to edges between forage and cover areas, showing that highest use occurs within 100 yards (91 m) of such edges, decreasing with distance from the edges. These summaries supported the earlier guidelines established by Black et al. (1976) and Thomas et al. (1979), which identified a ratio of 40% cover to 60% forage areas as an optimal mix of habitats for elk.

If timber harvest changes human access within and near the harvest units, elk distributions can be expected to shift, with elk avoiding areas with increased access, and selecting areas with little or no access (Wisdom and Cook 2000). Specifically, high road densities negatively influence elk distribution, in that elk avoid habitats near roads open to traffic (Rowland et al. 2000, Wisdom et al. 2004). The influence of open roads is not uniform, however, in that elk show increasing

avoidance of areas near roads with increasing rates of motorized traffic (Wisdom et al. 2004). Cole et al. (1997) found that road management areas where access was restricted to administrative uses reduced home-range size and increased the survival of Roosevelt elk. Additionally, Lyon (1976) found that elk used habitats with greater canopy closure in areas of higher road density.

Timber harvest also affects the vulnerability of elk to hunting. Lyon and Christensen (1992:3) defined elk vulnerability as a "measure of elk susceptibility to being killed during the hunting season." Elk vulnerability to hunting can be affected by two aspects of timber harvest (Christensen et al. 1991). First, the removal of timber opens up the landscape, making elk more visible and therefore more vulnerable to harvest by hunters. And second, the increased number and extent of roads established to facilitate removal of logs greatly enhances the opportunity for more hunters to access the landscape, increasing the likelihood of hunter contact with elk. These effects were documented by Leptich and Zager (1991), Unsworth et al. (1993), and Hayes et al. (2002), and discussed at length in the compilation of papers by Christensen et al. (1991).

In contrast to elk, no major changes in cattle distribution during timber harvest are likely because domesticated animals typically are confined to pastures and generally tolerate human activities. Following timber harvest and the concomitant decrease in overstory canopy, however, a release of understory vegetation occurs that alters forage biomass, quality, and phenology, often leading to changes in cattle distribution. Forage biomass can increase from 2 to 8 times that of pre-harvest forage production (Svejcar and Vavra 1985) depending on intensity of the cut, site potential, and soil disturbance (Hedrick et al. 1968). Miller and Krueger (1976) reported that 60% of the forage consumed in a given pasture by cattle was from areas logged and reseeded. Road construction to facilitate harvest also provides improved distribution for cattle (Hedrick et al. 1968). Consequently, tim-

ber harvest generally provides new grazing areas for cattle.

Harris (1954) also reported that cattle seldom use dense overstory canopies except during conditions of extreme heat or intense insect harassment. Hedrick et al. (1968) found it more difficult to obtain moderate or heavy forage use by cattle under dense overstory canopies than under open canopies. Consequently, cattle distribution and use of new forage areas can be expected to increase substantially after timber harvest, until such time that overstory canopies again become dense.

Depending on season of use, livestock production may or may not be improved by timber harvest. Svejcar and Vavra (1985) found that forage quality on timber-harvested sites declined more rapidly than on unharvested sites. Consequently, weight gain per individual animal could actually decline in late summer on harvested sites. However, weight gain per acre could improve dramatically if stocking rates were increased to match the improvement in forage production in early and mid summer (Svejcar and Vavra 1985).

TIMBER HARVEST EXPERIMENT AT STARKEY

Methods of Implementing the Timber Harvest Activities

We studied cattle and elk responses to timber harvest in the 3,590-acre (1,454 ha) Northeast Study Area of Starkey (Figure 1) from 1989–1996, encompassing periods before, during, and after harvest. The area is enclosed with an ungulate-proof fence, thus allowing direct measurements of ungulate responses to controlled, landscape experiments such as timber harvest, traffic, hunting, and other public land uses (Rowland et al. 1997, Wisdom et al. 2004). To study cattle and elk responses to our timber harvest experiment, a mosaic of units was harvested across the study area over a short time period, and no other human activities beyond those associated with timber management and hunting were allowed.

Timber sale planning and layout of har-

vest units occurred from 1989–1991, timber harvest and log hauling occurred during 1992, and conifer regeneration activities (site preparation, planting of tree seedlings, and stocking surveys) occurred from 1993–1996. Throughout our analyses and paper, we refer to the period of timber sale planning and layout as “before” harvest, the period of timber harvest and log hauling as “during” harvest, and the period of conifer regeneration activities as “after” harvest. Details about each period were described by Rowland et al. (1997).

Timber harvest during 1992 consisted of approximately 7 million board feet of commercial tree species that were logged from 1,207 acres (488 ha) of the study area from November 1991 through 1992 (referred to here as 1992 or “during” harvest period). Timber harvest encompassed 50% of forested lands in the Northeast Study Area (Figure 1). Harvest was a salvage sale that focused on removal of grand fir (*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) that had been killed by the combined effects of western spruce budworm (*Choristoneura occidentalis*), Douglas-fir tussock moth (*Orgyia pseudotsugata*), and drought during 1988–1990.

Most timber harvest took the form of shelterwood and seed tree regeneration cuts, with some commercial thinning and individual tree selections. The 63 harvest units ranged in size from 3 to 55 acres (1.2 to 22 ha). Harvest units were dispersed throughout the study area, denying ungulates the opportunity to find large areas of escape cover (Figure 1). Moreover, management guidelines for elk cover, such as maintenance of dense cover for presumed hiding and thermoregulatory benefits (Thomas et al. 1979, 1988), were intentionally ignored as part of the experimental design. Finally, the relatively small size of the study area (3,590 acres (1,454 ha)), smaller than many summer ranges used by elk (Leckenby 1984, Edge et al. 1985), combined with the ungulate fence, did not allow animals the option of avoiding the experiment by leaving the area or moving to locations far from har-

vest activities. Instead, the experiment was intentionally designed to measure cattle and elk responses to changes in the environment brought about by timber harvest, in the absence of options for ungulates to avoid the experimental area.

Extensive road construction also took place to facilitate log removal (Figure 1). Approximately 24 miles (39 km) of new roads were constructed. Another 4 of the 10 miles (6.5 of the 16 km) of roads present before timber harvest were renovated. The study area, however, was closed to public access, with the exception of hunting seasons each fall, when hunters were allowed entry for hunting purposes only (Rowland et al. 1997).

Despite no public entry, the study area received substantial road traffic in relation to timber sale planning and layout, timber harvest and log hauling, and conifer regeneration activities. Motorized traffic entering the study area during timber sale planning and layout (1989–1991) averaged 10 vehicles per day and was composed mostly of Forest Service vehicles and some vehicles associated with reconnaissance work by logging crews. During timber harvest and log hauling (1992), traffic entering the study area increased to an average of 29 vehicles per day; this traffic was composed almost entirely of log trucks, hauling logs from the harvest units, and minor traffic from logging crews and Forest Service contract administrators.

When harvest was completed (1993–1996), traffic entering the study area declined substantially to an average of 3 vehicles per day, composed mostly of Forest Service vehicles and some contractor's vehicles associated with conifer regeneration activities. An even lower rate of traffic (<1 vehicle per day) occurred during the hunting seasons each fall, from 1989–1995, when hunters were allowed vehicle entry only to retrieve game brought to roads. Traffic rate increased to >10 vehicles per day during hunting seasons in 1996, when vehicle access by hunters was allowed on established roads.

For all periods of study, estimates of traffic rate were based on automated traf-

fic counters installed and monitored at or near the entry/exit point to the study area (Figure 1), using methods described by Rowland et al. (1997) and Wisdom et al. (2004). An automated, 16-millimeter camera also was installed and monitored at the entry/exit point (Rowland et al. 1997), which verified that traffic was dominated by Forest Service vehicles before harvest, by log trucks during harvest, and again by Forest Service vehicles after harvest.

Methods of Measuring Cattle and Elk Responses to Timber Harvest

We assessed the short-term effects of timber harvest on cattle and elk by evaluating their spatial distributions before (1989–1991), during (1992), and after (1993–1996) harvest. We also evaluated annual weight gains of each species before, during, and after harvest across those same years. Finally, we estimated the vulnerability of elk to hunting before, during, and after timber harvest. The experiment ended in 1996, and thus we did not measure long-term (>10 years post-harvest) responses of ungulates to timber harvest.

We maintained approximately 50 cow elk, their calves, and 12 adult bull elk in our study area each year, from spring through fall, throughout all periods of study. Elk entered the study area during early to mid-April of each year from an adjacent Winter Area (Rowland et al. 1997). By late fall (early to mid-December), elk typically were trapped and moved or baited from the study area back to the adjacent Winter Area (see Rowland et al. 1997). Winter 1991–1992 was extremely mild and we were unable to remove or entice many of the elk from the study area that winter, which reduced sample sizes of animals during 1991–1992 that were used to estimate spatial distributions with radio-telemetry (Table 1) and to estimate weight gains. We stocked 50 cow/calf pairs of cattle in the study area from mid-June through mid-October of each year as part of a season-long summer grazing system described by Rowland et al. (1997).

TABLE 1. Number of radio-collared elk and cattle for each year before (1989–1991), during (1992), and after (1993–1996) timber harvest in the Northeast Study Area of Starkey Experimental Forest and Range, northeast Oregon

Year	No. elk	No. cattle
1989	10	9
1990	18	15
1991	11	13
1992	4	12
1993	12	11
1994	20	13
1995	13	9
1996	13	10

Estimating changes in cattle and elk distributions

To estimate changes in spatial distributions of cattle and elk, we monitored the movements of radio-collared adult females of each species (Table 1) with an automated telemetry system described by Findholt et al. (1996, 2002), Rowland et al. (1997), and Kie et al. (2004). We used random samples consisting of 1,000 locations selected from the radio-collared animals that were monitored during each of the three periods (before, during, and after harvest, Table 1). Samples of locations therefore were a representative (random) composite taken from all radio-collared animals that were monitored in a given period.

We used the animal locations to estimate the distribution of each species during each period under a fixed-kernel analysis (Worton 1989). We used a bandwidth set at 0.5 of the reference bandwidth and plotted volume contours at increments of 0.05 from 0.05 to 0.95. Kernel methods provide a “probability density estimate of a distribution based on a sample of points” (Seaman et al. 1998:95). The kernel method of estimating and mapping distributions has been used extensively in wildlife research because it is a non-parametric estimator that requires few assumptions in contrast to parametric methods (Kernohan et al. 2001; Marzluff et al. 2001, 2004). Moreover, the kernel method is an unbiased estimator of the under-

lying, true animal distribution when a sufficient number (>300 locations) of unbiased animal locations are used (Garton et al. 2001).

We initially mapped the kernel distributions of animal locations, by the 0.05-contour intervals, for each species and time period in the study area. These maps provided an overall picture of spatial use by each species for each time period. For all subsequent analyses, we used the portion of each species’ distribution occurring within the upper 50% of kernel volume, or 50% contour, for each time period. The upper 50% of kernel volume highlights areas of concentrated use by elk or cattle. Such areas often are referred to as “core areas” in analyses of spatial use (Kernohan et al. 2001). Throughout our paper, we refer to these areas as the “upper 50% of kernel volume”, “50% core area”, or “core area”. These areas also are referred to as centers of a “utilization distribution,” as described by Millsaugh et al. (2000) and Marzluff et al. (2001).

Because core areas or centers of utilization distributions are based on a substantially higher number of animal locations than the outer contours of such distributions, the core areas typically provide a more robust estimate in contrast to estimates made at the periphery of the kernel volume (Seaman et al. 1998, 1999; Marzluff et al. 2001). Moreover, our interest was in monitoring changes in concentrated areas of use (the most frequently used areas) across time periods, as could be done with analysis of the core areas.

We used maps of the upper 50% of kernel volume to estimate the change in spatial use by cattle and elk in four ways. First, we calculated the percent area within the upper 50% of kernel volume for each species and time period that occurred in each of four regions, or quadrants, in our study area. For this analysis, we subdivided the study area into northwest, northeast, southwest, and southeast quadrants, each of equal size. We then expressed the percent area of the upper 50% of kernel volume occurring within each

of the quadrants as a percentage, for each species and time period. This analysis allowed us to further quantify the shift in species' distributions across periods. Millspaugh et al. (2000) employed similar concepts in their application of utilization distributions for assessing hunter-elk interactions.

Second, we calculated the percent overlap of the cut units (top right, Figure 1) within the upper 50% of kernel volume, by species and time period. This analysis was intended to portray the degree to which cattle or elk distributions may have shifted away from or toward the harvest units during or after harvest. For example, if percent overlap of the harvest units with the upper 50% of kernel volume was 70% before timber harvest but 35% during harvest, this would suggest the species was avoiding the units during harvest activities.

Third, we calculated the percent area within the 50% core area for each species and time period across the entire study area. Under this analysis, if a higher percentage of the study area occurred under the core area, this would indicate that distributions of cattle or elk were more diffuse, or spread out, across a larger area. A lower percentage would indicate that distributions were more concentrated in smaller portions of the study area. The degree to which distributions are more diffuse or concentrated has been used as an index of habitat quality in home-range analyses. Larger core areas or home ranges suggest lower habitat quality, whereas smaller areas indicate higher habitat quality, owing to like differences in the area over which animals must meet their needs (e.g., see Carey et al. 1992, Zabel et al. 1995, Cole et al. 1997).

And fourth, we assessed the degree to which cattle and elk selected or avoided the mainline roads, which received highest frequency of motorized traffic (N. Cimon, unpublished data, 2004) that entered the study area (see traffic rates stated earlier). Mainline roads were identified as the 400, 430, and 480 roads before harvest (top left, Figure 1), and the 400, 420, 430, 437, 440, 460, and 480 roads during

and after harvest (top right, Figure 1). For this analysis, we calculated the mean distance of 30- × 30-meter pixels to the closest mainline road, for those pixels within each species' core area during each period; this constituted our estimate of the area used by each species in relation to distance from the mainline roads. We then divided this number by the mean distance of the entire study area's 30- × 30-meter pixels ($n = 16,133$) to the closest mainline road, which constituted our estimate of the area available to each species in relation to distance from the mainline roads. A ratio of 1.0 of used versus available pixels suggests neither selection nor avoidance of roads. A ratio >1.0 indicates avoidance; a ratio <1.0 suggests selection toward roads.

We also calculated the mean percent slope and mean percent overhead canopy closure of all 30- × 30-meter pixels within the species' 50% core for each time period, and compared these estimates across time and with overall estimates for the study area. We did this to gain further insight as to whether ungulates might have been seeking areas of greater security (Christensen et al. 1991) in proximity to roads or cut units during and after harvest. These variables were available from spatial layers estimated and used in prior ungulate research at Starkey (Johnson et al. 2000, Rowland et al. 2000).

A minor effect on our distribution analyses resulted from our not restricting the kernel estimation to the specific boundaries of the study area. That is, elk and cattle movements were restricted to the enclosure boundaries that formed our study area (Figure 1), but kernel estimation was not. This resulted in a small portion of kernel volume being mapped along or just outside the study area boundaries. Consequently, the core areas used in our analyses would have changed slightly if we had constrained the kernel estimation to the specific enclosure boundaries.

Estimating changes in weight gains of cattle and elk

To evaluate potential effects of changes in nutritional status of ungulates follow-

ing timber harvest, we estimated annual weight gains of each species, and compared these annual changes over time. To account for annual variation in ungulate weight gains due to annual differences in weather and associated forage conditions, we also calculated weight gains for cattle and elk in the Main Study Area of Starkey (Figure 1) as a background reference for conditions of no timber harvest. The Main Study Area is immediately adjacent to the Northeast Study Area, is subject to the same weather conditions, and was not subjected to timber harvest activities during the period of our study (1989 through 1996) (See Rowland et al. 1997 for details). Thus, we used the weight gains from the Main Study Area as a control, against which changes in ungulate weight gains in the Northeast Study Area could be compared.

To estimate annual weight gain, we weighed adult cow elk (>2 yrs old) during late winter or early spring (late February to early April) before animals entered each study area, and during late fall or early winter (late November to early January) after these same animals left that study area. We weighed calf elk after they left the study areas in early winter. Similarly, we weighed adult cattle (>2 yrs old) and calves as they entered the study areas in mid-June and as they left the study areas in mid-October of each year.

Annual weight gains were expressed as an average daily gain for elk cows and for beef cows and calves. Specifically, we computed the difference between each animal's weight before it entered the study area and the weight after it left. We divided that difference by the number of days over which the difference was computed. We then calculated a mean daily gain and 95% confidence interval about the mean for each species and age class for each year.

Standardizing each animal's weight gain by the number of days over which the gain was measured accounted for the fact that some animals were weighed earlier or later than other animals before entering or after leaving the study areas. Only elk cows and beef cows and calves with weights mea-

sured both before entering the study areas, and after leaving the study areas, were included in our analysis of a given year's weight gains. Thus, we used a repeated measures approach in calculating weight gains, in that gains were computed for each animal, based on its weight before entering and after leaving the study area, which increased the precision of our estimates.

For elk calves, all of which were born in the study areas, we calculated the weight gain in absolute amount for each animal, based on their fall weights after they left the study area. We calculated a mean weight of elk calves, and 95% confidence interval about the mean, for each year and study area.

Under our analysis, if timber harvest did not affect weight gains, we would expect that variation in gains observed in our study area would remain consistent with gains calculated for these species and age classes each year in the Main Study Area, and that annual variation in gains in both study areas was due to variation in weather or other factors. By contrast, if timber harvest caused an increase or decline in weight gains, we would expect gains in our study area to increase or decrease in relation to such gains observed for the same species and age class in the Main Study Area.

Monitoring changes in elk vulnerability to hunting

We evaluated the vulnerability of elk to being killed by hunters before, during, and after timber harvest with data from hunts of branch-antlered bulls that occurred in the study area from 1989 through 1996 (Rowland et al. 1997). For each year, we calculated hunter success rates and the number of days required for hunters to harvest an animal, using information from Starkey's hunter check station (Rowland et al. 1997). From 1990 through 1995, the branch-antlered bull hunt was foot-access only, with permission to use vehicles to retrieve dead animals. In 1996, vehicle access during the hunting season was allowed. Under this analysis, if hunter success increased or

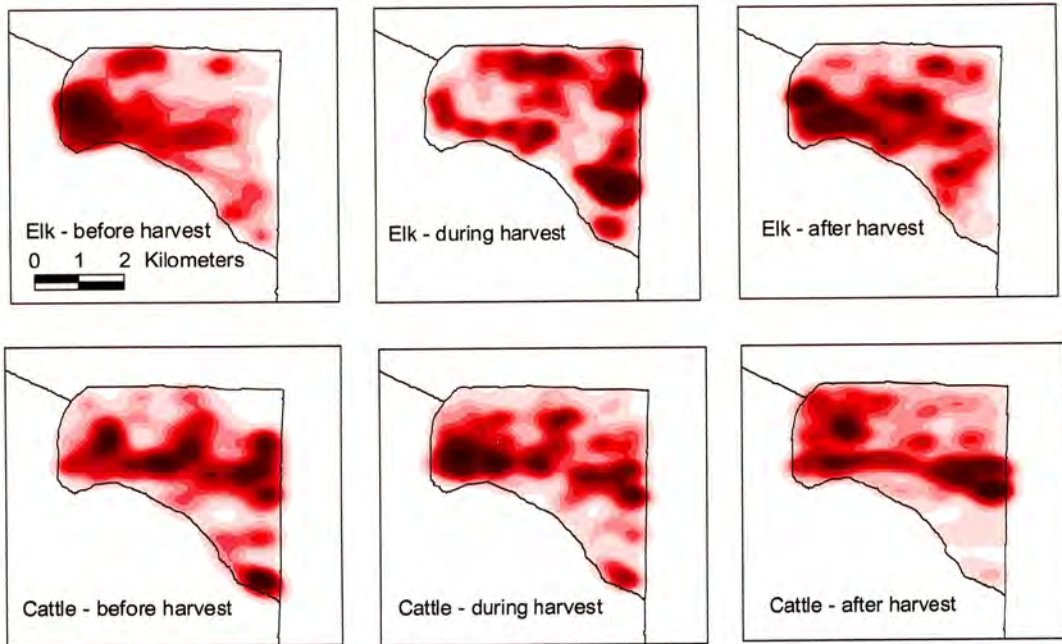


FIGURE 2. Spatial distributions of elk and cattle before (1989–1991), during, (1992), and after (1993–1996) timber harvest, using fixed-kernel analysis of animal locations for each time period in the Northeast Study Area of Starkey Experimental Forest and Range, northeast Oregon. Darkest shades of red represent the highest species' use. Lightest shades represent lowest use.

the number of days required to kill an elk decreased during or after timber harvest, this would suggest that the increased openness and road access resulting from timber harvest caused elk to be more vulnerable to hunting.

CHANGES IN CATTLE AND ELK DISTRIBUTIONS

Before timber harvest (1989–1991), elk were concentrated in the western portion of the Northeast Study Area (Figure 2), particularly in the southwest quadrant (Figure 3). Elk distribution shifted substantially during timber harvest (1992), however, with use concentrated along portions of the study area's outer boundaries (Figure 2). Elk distribution shifted most to the southeast and northeast quadrants during harvest, which had received little use beforehand (top right, Figure 3). Elk distributions also became more diffuse during timber harvest. Nearly twice as much of the study area was within the

upper 50% of kernel volume compared to the period before harvest (bottom right, Figure 3).

Distribution shifts by elk during harvest were not related to elk avoidance of the cut units, as areas where timber cutting occurred overlapped more with the 50% core area for elk during harvest than before harvest (bottom left, Figure 3). Distribution shifts by elk during timber harvest also were not related to elk avoidance of the mainline roads used most frequently by log trucks (400, 420, 430, 437, 440, 460, and 480 roads, Figure 1)—the 50% core area for elk during harvest was closer to these roads than overall habitat available to elk. Specifically, the mean distance of all pixels in the 50% core area for elk was 655 yards (599 m) from these roads, but the overall area available to animals had a mean distance of 916 yards (838 m) to the same roads, for a selection ratio of 0.72 during harvest. Elk selection toward roads, however, was even stronger before harvest, when the selection ratio

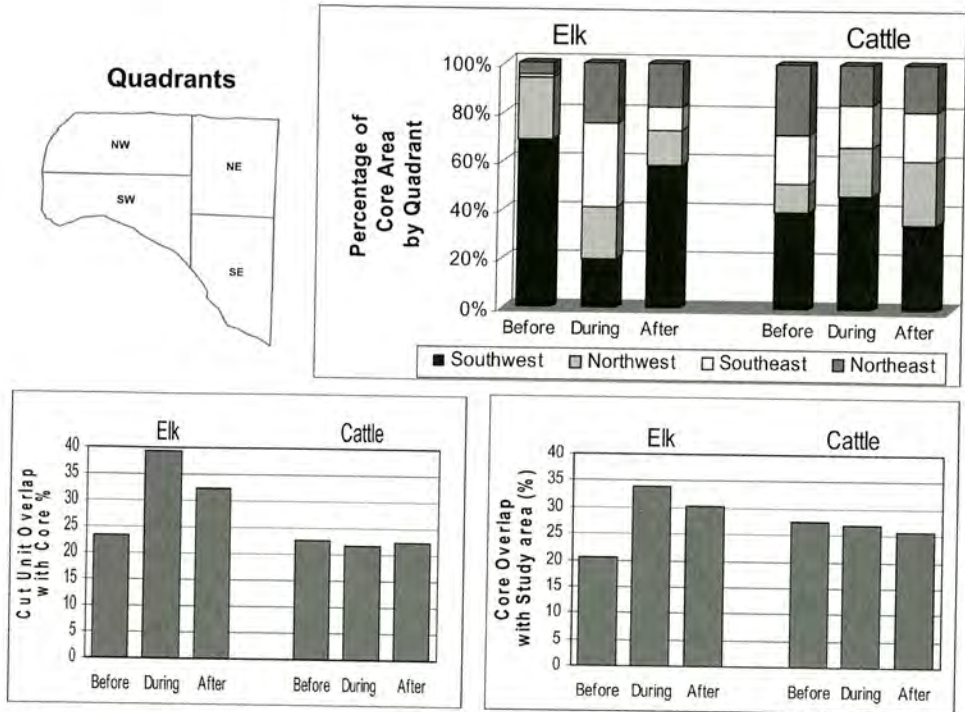


FIGURE 3. Percentage of the upper 50% of kernel volume, or 50% core area, of cattle and elk distributions occurring in each of four quadrants (top map) by time period (top right bar charts), the spatial overlap of timber harvest units, or cut units, within the 50% core area for each species (bottom left bar charts), and the percent area of the entire Northeast Study Area within the upper 50% of kernel volume, by time period and species (bottom right bar charts).

was 0.42, indicating that elk decreased their use near roads during harvest when traffic rate increased substantially (per traffic rates stated in methods).

In addition, the 50% core area for elk had a steeper average slope (21%) during harvest compared to the average slope (17%), suggesting that elk selected areas of greater security while close to roads. By contrast, the core area for elk had an average slope of 16% before harvest, similar to the average slope of 17% available to animals. Contrary to the pattern of elk seeking steeper slopes during timber harvest, the core area for elk had a mean overhead canopy closure (33%) similar to its availability (32%). This also was the pattern before harvest, when the core area for elk had a mean overhead canopy closure of 40% compared to available canopy closure of 41%.

In 1993–1996, after timber harvest was completed, elk again concentrated in the

western half of the study area, as well as in the interior portions of the study area that were largely unused during timber harvest (Figure 2). As with the period before harvest, elk use was concentrated in the southwest quadrant (top right, Figure 3). Elk use of the southeast quadrant also diminished substantially, as occurred during harvest. Elk distribution also was more diffuse after timber harvest as compared to before harvest, but not as diffuse as during harvest (bottom right, Figure 3).

After timber harvest, elk also continued to select areas closer to the mainline roads than the area available for use. The mean distance of pixels in the 50% core area for elk was 332 yards (304 m) from these roads, but overall habitat available to animals had a mean distance of 916 yards (838 m) to the same roads, for a selection ratio of 0.36 after harvest. This selection ratio was twice as strong as that observed during harvest (0.72), further

suggesting that elk moved closer to roads after log hauling was completed and traffic subsided (per traffic rates stated in methods). The average slope of pixels within the 50% core area for elk after harvest (17%) also was similar to that before harvest (16%), indicating that elk moved back to more gentle slopes once timber harvest had ended.

In contrast to elk, cattle showed little change in distribution during all periods of study (Figures 2, 3). The areas of highest concentration were generally consistent before, during, and after timber harvest, with little change in the percentage of the upper 50% of kernel volume by quadrant across time (top right, Figure 3) or across the study area (bottom right, Figure 3). Harvest unit overlap with the 50% core area of cattle remained consistently between 20%–25% across all three periods (bottom left, Figure 3). The focal point of cattle distribution was along the Syrup Creek drainage (the east-west continuum of uncut area running east-west through the middle of the study area between the 420 and 480 roads, top right, Figure 1), coinciding with darkest areas of cattle use during all three periods in Figure 2. Interestingly, overlap of the cut units with the 50% core area for cattle was less than that for elk, both during and after timber harvest (bottom left, Figure 3), as was the percent area under the 50% core for cattle versus elk during these two periods (bottom right, Figure 3).

Cattle distributions, like those of elk, were consistently closer to the mainline roads than available habitat. The mean distance of pixels in the 50% core area for cattle was 1052 yards (962 m) from these roads, but overall habitat available to animals had a mean distance of 1206 yards (1103 m) to the same roads, for a selection ratio of 0.87 before harvest. The 50% core area for cattle was progressively closer to the mainline roads during and after harvest, with road selection ratios of 0.69 and 0.35, respectively.

Unlike elk, cattle showed no evidence of selection of areas with characteristics of greater security from humans. Average slopes under the core area used by cattle did not appear to change across time pe-

riods (before—17%; during—18%; after—16%) and was the same or similar to the average slope of 17% in the study area. Moreover, average overhead canopy closure of pixels in the core areas of cattle was highest before harvest (43%) but declined during and after harvest (34% for both periods), a pattern that corresponded to the change in average overhead canopy closure for the study area (42% before harvest, 32% during and after harvest).

CHANGES IN WEIGHT GAINS OF ELK AND CATTLE

Annual weights gains of adult female elk and calf elk in the Northeast Study Area were not different from gains for these same age classes in the Main Study Area, based on overlapping 95% confidence intervals between mean gains within each year and age class (Figure 4). Moreover, no trend in weight gains in either study area was evident (Figure 4). Instead, weight gains of elk cows and calves were highly variable across years in the Northeast Study Area, but consistent with the variability in weight gains observed across years in the Main Study Area, where timber harvest did not occur (Figure 4). That is, the direction and degree of variability in annual weight gains was generally consistent between the two study areas, suggesting that weight gains in elk were largely affected by annual variability in weather patterns that affect annual changes in forage biomass and quality (see Management Implications).

In contrast to elk, mean weight gains for beef cows and calves in the Northeast Study Area were mostly higher (non-overlapping 95% confidence intervals) than those documented in the Main Study Area within each year and age class (Figure 5). In 1992 and 1993, however, the 95% confidence intervals overlapped between mean weight gains of beef cows in the two study areas; and in 1995, mean weight gain of beef cows was higher in the Main Study Area (Figure 5). The pattern of higher weight gains in Northeast Study Area versus those in Main Study Area was more consistent for beef calves, except for one year (1992) where confidence intervals overlapped.

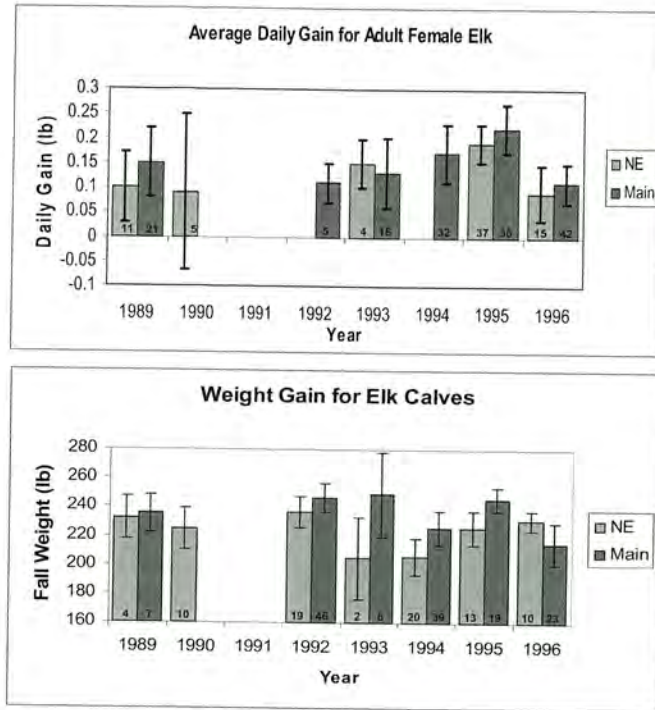


FIGURE 4. Mean weight gain by adult female elk and calf elk before (1989–1991), during (1992), and after (1993–1996) timber harvest in the Northeast Study Area as compared to mean weight gain for the same years and age classes in the Main Study Area, Starkey Experimental Forest and Range, northeast Oregon. Error bars are the 95% percent confidence intervals about each mean. No weight data were available for cows or calves during 1991 in either study area, and for cows in Northeast Study Area during 1994. Data on the insufficient sample size of one cow elk weighed during 1992 in Northeast Study Area also was not included. Sample size (number of animals weighed) is shown at the bottom of each bar.

As with elk, no trend in weight gains in either study area was evident for either age class of cattle (Figure 5). Also similar to elk was the high annual variability in weight gain observed for beef cows and calves, and the strong consistency in the degree and direction of this variability between Main and Northeast Study Areas across years (Figure 5). In contrast to elk, however, cattle weight gains were more precise for each year, and the annual variability appeared to be more similar between the two study areas (compare Figure 4 with Figure 5).

CHANGES IN ELK VULNERABILITY TO HUNTER HARVEST

Compared to the period before timber harvest, hunter success improved and the

number of hunter days per harvested animal declined during and after timber harvest (Table 2). The highest hunter success and the lowest number of hunting days required to take an animal occurred in 1996, when post-harvest, open conditions existed together with unlimited vehicle access (Table 2).

For the years before timber harvest (1989–1991), hunter success averaged 22%, requiring an average of approximately 19 days to achieve this level of success. During timber harvest (1992), hunter success increased to 35%, with hunters spending an average of approximately 9 days to achieve this success (number of days required to harvest an animal). For the years after timber harvest (1993–1996), hunter success remained higher and similar to success during the

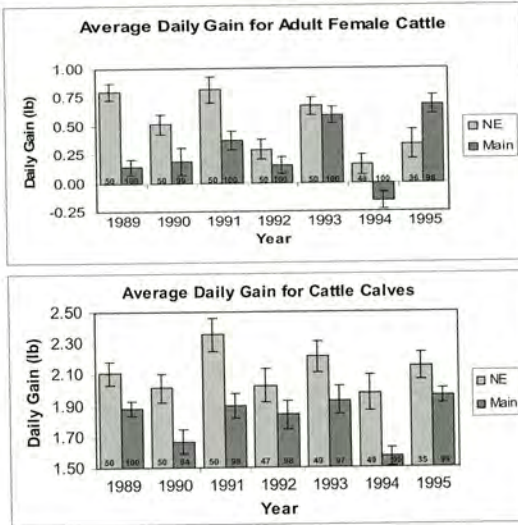


FIGURE 5. Mean weight gain by cattle, for adult cows and calves, before (1989–1991), during (1992), and after (1993–1995) timber harvest in the Northeast Study Area as compared to mean weight gain for the same years and age classes in the Main Study Area, Starkey Experimental Forest and Range, northeast Oregon. Error bars are the 95% percent confidence intervals about each mean. Weight data for 1996 were not available. Sample size (number of animals weighed) is shown at the bottom of each bar.

year of timber harvest, with an average success of 32%. Moreover, an average of 14 days were required for hunters to take an animal post-harvest.

MANAGEMENT IMPLICATIONS

Elk responded to the period of timber harvest by making a substantial shift in distribution, while cattle did not. Interestingly, the shift in distribution by elk, and the lack of change in distribution by cattle, did not appear to change animal performance for either species. Our study is one of the few cases in which a measure of animal or nutritional performance (weight gain) was evaluated in combination with distributional responses of animals under a landscape experiment. Garton et al. (2001) strongly emphasized the need to evaluate the population or nutritional consequences of landscape choices made by wildlife under studies of resource selection, habitat use, and spatial distribution. Garton et al. (2001) also highlighted the few studies where the demographic or nutritional consequences of landscape choices made by a wildlife species were documented, and particularly noted that changes in animal selection or distribution do not always result in changes in population or animal performance.

In our study, the nutritional consequences of each species' spatial response to timber harvest suggest that each species' was able to maintain animal performance during and after harvest. And yet, one species (elk) substantially changed distribution during the experiment, while

TABLE 2. Success rates and number of days hunted by elk hunters during branch-antlered bull hunts that occurred before (1989–1991), during (1992), and after (1993–1996) timber harvest in Northeast Study Area, Starkey Experimental Forest and Range. Data on number of days hunted and number of days hunted per animal harvested were not available (na) for 1989

Year	No. hunters	No. elk harvest	No. days hunted	Hunter success (percent)	No. days hunted per animal harvested	No. animals available for harvest	Type of hunter access allowed
1989	10	3	Na	30	na	6	foot only
1990	23	5	127	22	25.4	10	foot only
1991	14	2	63	14	31.5	8	foot only
1992	26	9	78	35	8.7	13	foot only
1993	15	3	66	20	22.0	10	foot only
1994	27	5	95	19	19.0	12	foot only
1995	23	8	81	35	10.1	12	foot only
1996	24	13	69	54	5.3	14	vehicle access

the other species (cattle) did not. These results serve as a demonstration that studies of animal behavior and distribution in relation to human disturbances may not provide strong inference about demographic or nutritional effects.

Our results must be viewed with caution, however, as the relatively small sample sizes on which weight gains were estimated suggests that we had low statistical power and a higher likelihood of committing Type II errors; that is, of falsely concluding that weight gains did not change in relation to timber harvest when in fact such changes did occur, but were not detected. Moreover, we did not evaluate the long-term (>10 years post-harvest) effects of timber harvest on weight gains, which could be substantially different than short-term weight gains.

The substantial increase in percent area under the upper 50% of kernel volume for elk during and after timber harvest also serves as a cautionary note. This finding indicates that the elk population became more dispersed during and after timber harvest, suggesting longer movements over larger areas by elk to meet their needs. Larger areas used by a species indicate lower habitat quality and reduced population performance when these patterns exist over extended periods (e.g., see Carey et al. 1992, Zabel et al. 1995).

We also did not assess other response variables related to animal and nutritional performance of ungulates, such as those studied and discussed by Cook (2002) and Cook et al. (2004). Examples include estimates of pregnancy rates and body fat, which provide complementary insights on ungulate performance beyond measures of weight gain. Moreover, we did not evaluate changes in forage biomass, quality, and phenology that could have provided additional insights about changes in potential carrying capacity. We also did not assess diet selection or diet quality of ungulates, which provide direct estimates of the nutritional plane of animals (Cook 2002, Cook et al. 2004). Density of both species in the study area may have been low enough that weight gains for both were high before timber harvest, and

therefore did not change substantially following the presumed change in forage conditions after harvest.

Results from our analysis of cattle and elk distributions complement an earlier analysis of ungulates in our study area by Stewart et al. (2002), who found that cattle and elk were spatially separated during summer. Our results demonstrated a substantial shift in elk distributions during timber harvest, while cattle distributions were nearly unchanged. Our results therefore indicate that elk were responding more strongly to timber harvest activities than to cattle distributions.

Our results also are surprising in that we found no evidence that elk avoided the cut units or the mainline roads during and after timber harvest. The mainline roads received a high frequency of log-truck traffic throughout the harvest period of 1992, and it is possible that elk became habituated to this form of predictable, consistent traffic. This contrasts with the less predictable and diverse forms of motorized traffic that occur when roads are open to the public, which presumably contribute to elk avoidance of these open roads (e.g., Rowland et al. 2004, Wisdom et al. 2004). Importantly, our study area was not open to public access and motorized traffic, with the exception of highly restricted public traffic that was allowed as part of timber harvest and elk hunting. Model predictions of elk avoidance of roads open to traffic (e.g., Thomas et al. 1979; Rowland et al. 2000, 2004) do not account for specialized, restricted forms of high-frequency traffic such as that associated with timber harvest in areas that otherwise are closed to public access. This aspect of elk response to motorized traffic deserves more attention in future research.

Our results on weight gain for elk also complement an earlier analysis by Rinehart (2001), who found no difference in early winter weights of elk before versus after timber harvest in our study area. Rinehart (2001) also found no difference between annual weights of elk in our study and those in the adjacent, Main Study Area where timber harvest did not

occur. Finally, Rinehart (2001) also noted that changes in resource selection and home-range size after timber harvest did not equate to a reduction in animal performance of elk, as indicated by the lack of a trend in early winter weights before versus after harvest.

The high variability in weight gains across years for both ungulate species and all age classes strongly suggests that annual gains were largely affected by annual variability in weather patterns that affect annual changes in forage biomass and quality. This suggestion is supported by work of Vavra and Phillips (1979, 1980), who found that variation in summer precipitation directly affected the diet quality and subsequent weight gains of cattle on northeast Oregon summer ranges having similar weather and forage conditions as those in our study area. During a drought year (1977), diet quality of cattle was substantially lower than years of higher summer moisture (1975 and 1976), resulting in substantially lower weight gains during the drought year.

These patterns of high variability in weight gains of domestic ungulates in response to year-to-year variation in weather, precipitation, and subsequent forage conditions were summarized by Holechek et al. (1989, 1998); these authors concluded that growing season variability in precipitation exerted a strong effect on ungulate performance on rangelands across the western United States, particularly during drought years. Similar inferences were made by Cook et al. (2002) regarding annual variation in elk performance, as affected by annual variation in summer weather that appears to have a strong influence on summer nutrition of animals.

Although animal performance of elk did not appear to change in response to timber harvest, the post-harvest landscape in our study area clearly increased hunter success and reduced the number of hunting days required to harvest an animal. These results suggest that increased visibility and access associated with timber harvest increased the vulnerability of elk to being killed by hunters. These results

further suggest that timber harvest may have the strongest and most enduring effects on elk vulnerability to hunting, in contrast to other effects we measured such as changes in distribution and potential avoidance of human disturbances. Consequently, our results suggest that the potential for intensive timber harvest to substantially increase elk vulnerability to hunting is a key issue that deserves careful attention as part of timber harvest planning.

Those points as context, consideration of our results, combined with results from previous studies (see "Overview of Current Knowledge"), could focus on timber sale designs that minimize elk vulnerability to hunting and that provide a relatively even and continuous stream of forage availability over space and time. Example considerations at the watershed scale could include the following:

- Manage for and retain security areas for elk in watersheds when planning the layout of harvest units in time and space. Security areas serve primarily to mitigate any increase in elk vulnerability to hunting when timber harvest activities result in increased visibility and human access in a watershed. A security area for elk was defined by Hillis et al. (1991:38) as a nonlinear block of hiding cover at least 250 acres (101 ha) in size and at least one-half mile (0.8 km) from roads open to motorized traffic. Hiding cover was defined by Thomas et al. (1979:109) as vegetation capable of hiding 90% of a standing adult deer or elk from the view of a human at a distance equal to or less than 200 feet (61 m). In particular, Hillis et al. suggested that security areas are most effective in minimizing elk vulnerability to hunting when such areas compose at least 30% of a watershed. However, other management options, such as minimizing road access, accounting for elk security provided by steep slopes and convex topography, and changes in hunting season regulations, also can be considered in tandem with management of security areas. These additional management options

were outlined and discussed by Thomas (1991).

- Restrict motorized and mechanized forms of hunter access in watersheds after timber harvest, to prevent an increase in elk vulnerability to harvest by hunters. Maintain such restrictions on motorized and mechanized forms of hunter access until such time that vegetative growth in timber harvest units provides sufficient hiding cover to help reduce vulnerability. In watersheds with flat terrain and large areas subjected to timber harvest over a short time period, restrictions on human access will be especially effective in minimizing an increase in elk vulnerability to hunting. In watersheds with steep terrain and large areas of hiding cover, restrictions on hunter access after timber harvest may be neither necessary nor effective, in that elk may have ample areas in which to hide or find security from hunters. In particular, plan the layout of harvest units to retain security areas (particularly areas with steeper slopes and greater convexity) near the cut units to facilitate animal escapement from these focal points of hunter access (per discussion by Hillis et al. 1991).
- Plan timber harvest activities in time and space such that a mosaic of seral stages are maintained to provide a variety of foraging conditions for cattle and elk. Timber harvest is likely to cause an immediate but short-term (1–3 year) decline in forage availability in the harvest units, followed by a large increase in forage that may last 10 years or longer. The biomass and phenology of forage plants is likely to be more diverse and stable with the implementation of a mosaic of timber harvest activities in time and space. Security areas for elk can also be sustained consistently under a strategy of timber harvest that produces a mosaic of seral stages in time and space.

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Management Implications of Ungulate Herbivory in Northwest Forest Ecosystems

Robert A. Riggs, John G. Cook, and Larry L. Irwin

INTRODUCTION

Understanding is now emerging that wild and domestic ungulates are not merely products that compete for resources, but are among the agents controlling ecosystem processes and properties (McNaughton 1984, 1992; Pastor and Naiman 1992; Molvar et al. 1993; Hobbs 1996; Pastor and Cohen 1997). With this understanding has come recognition that greater attention should be given to understanding how these ungulates function together in forests of the Northwest (Irwin et al. 1994, Schreiner et al. 1996, Riggs et al. 2000).

In the Interior Northwest, forest zones receive greater precipitation, have deeper soil profiles, and/or higher soil moisture-holding capacity than most adjacent non-forested uplands, and thus can contribute substantially to landscape potential for production of ungulate herbivores. In coastal and in many interior forests, infrequent but intense natural disturbances (e.g., fire) and episodic management activities (e.g., logging) set in motion potentially food-rich secondary successions, and are thereby often the primary determinants of herbivore carrying capacity (e.g., Hett et al. 1978). Seasonal concentration of ungulates on some forest sites can have profound influences on forest vegetation and even site characteristics, a keystone influence (Paine 1969, McShea and Rappole 1992, Molvar et al. 1993, Waller and Alverson 1997). Better knowledge of such relationships may help ungulate managers in the Northwest to define consequences of alternative ungulate-management strategies, and to define a more integrated vision for forestry-ungulate management systems.

Forestry and game management have been viewed traditionally as separate if albeit potentially complementary endeavors.

Attempts have been made to integrate game management objectives with forestry through regulation of forest practices. However, these attempts have not sought integration of the keystone influences of herbivory with those of silviculture. If integration is to ever be achieved on that basis, models will have to be used to organize the integration.

BRIEF SUMMARY OF HERBIVORY EFFECTS

Scientists know precious little about how ungulate herbivores influence northwestern forests. Most of what is “known” is actually based on studies in boreal and eastern deciduous forests. Nevertheless, results of work in these ecosystems have been more or less borne out in northwestern studies to the extent experimental designs have allowed comparison. Consequently, this literature can help us draw a generalized picture of how herbivores function in forests of this region.

We know that foraging habits are strongly linked to the chemistry and structure of plant tissues (Hobbs 1996) and to morphological adaptations of herbivores (Hofmann 1973, Shipley 1999). Palatable plant tissues tend to contain lower amounts of secondary metabolites that suppress palatability and digestibility, and contain lower amounts of indigestible components, than do unpalatable plant tissues. Thus palatable tissues are more easily biodegraded, assimilated, and recycled. Palatable plants also tend to have less formidable structural defenses, and are more easily cropped. Where choices are available, large herbivores tend to select those plants and tissues that are most efficiently cropped and biodegraded.

Selective foraging can have a host of direct and indirect influences on forest

communities. These include changing understory and overstory plant composition and structure (Alverson and Waller 1997, McShea 1997, Waller and Alverson 1997), acceleration of conifer growth (Bryant et al. 1983, DeToit et al. 1991, Pastor et al. 1993, Pastor and Cohen 1997), modification of forest structure (e.g., Stromayer and Warren 1997), modification of associated fauna (DeCalesta 1994, McShea 1997) and development of alternate stable states (Starfield and Chapin 1996, Stromayer and Warren 1997, Augustine et al. 1998). In the short term, selective herbivory by ungulates may enhance forest productivity, simply because of the accelerated flow of nutrients that herbivores facilitate via their consumption, degradation, and cycling of plant-bound nutrients (Pastor et al. 1993, Hobbs 1996, Pastor and Cohen 1997). Over the long term, however, the suppression of palatable plants conveys a competitive advantage to unpalatable plants, particularly to conifers. This advantage facilitates an acceleration of the rate at which conifers become dominant, and as forest nutrients become progressively cycled and bound in the less palatable and less degradable conifer tissues, forest productivity ultimately declines. There has been some suggestion that moose (*Alces alces*) may be able to facilitate elevated stable states of plant production in sub-arctic forests (Molvar et al. 1993), but it remains unclear whether such facilitated equilibria are either frequent or persistent in other ecosystems.

Western temperate forests are characterized by substantial variation in climate, and nutrient and water relations that ultimately limit production potential on any given forest site. These forests are also characterized by extreme variation in the frequency, intensity and extent of episodic disturbances (e.g., fire, silviculture) that arrest and reinitiate successions while simultaneously re-partitioning nutrients. Thus, even in the absence of herbivores these forests have tremendous potential for spatially explicit dynamism in vegetation. Adding multiple species of herbivore only complicates the picture.

Although northwestern forests are dotted with grazing exclosures, knowledge of how ungulate herbivores interact with other disturbance agents to influence these forests is neither extensive nor highly detailed. Long-term data sets describing grazing history and succession have been collected at relatively few sites. Where long-term data sets do exist, differences in succession are readily apparent and in a few cases the stable end-point of succession evidently has been affected (e.g., Peek et al. 1978, Schreiner et al. 1996, Riggs et al. 2000, Alldredge et al. 2001). Selective herbivory during the growing season can suppress plant taxa that are palatable at that time of year (Figure 1, Riggs et al. 2000), but dormant-season browsing can enhance some plant taxa (Peek et al. 1978). In grand fir (*Abies grandis*) and Douglas fir (*Pseudotsuga menziesii*), accumulation of understory biomass, and accumulation of understory and forest-floor nutrients (N, P, S, Ca, Mg, and K) is greater where ruminant herbivores are excluded than where they are allowed to graze (Table 1, Riggs et al. 2000). Selective herbivory probably enhances conifer production in the short-term (Monfore 1993, Weigand et al. 1993), but may reduce conifer production over the long term (Weigand et al. 1993, Riggs et al. 2000). The capacity of seral vegetation to support herbivores can be reduced by selective suppression of palatable plants early in succession (Irwin et al. 1994, Riggs et al. 2000, Alldredge et al. 2001).

Different species or combinations of herbivores can have dramatically different influences on the composition of forest understory provided that foraging selectivity is accommodated. In Douglas fir and grand fir forests of the interior, early-season grazing by cattle suppresses herbaceous plants, while season-long grazing by big game suppresses shrubs (Erickson 1974, Krueger and Winward 1974, Hedrick et al. 1968, Edgerton 1987, Riggs et al. 2000, but see Peek et al. 1978).

To a large extent herbivores operate in sequence with episodic disturbances. Fire, logging, herbicides, and fertilizer appli-

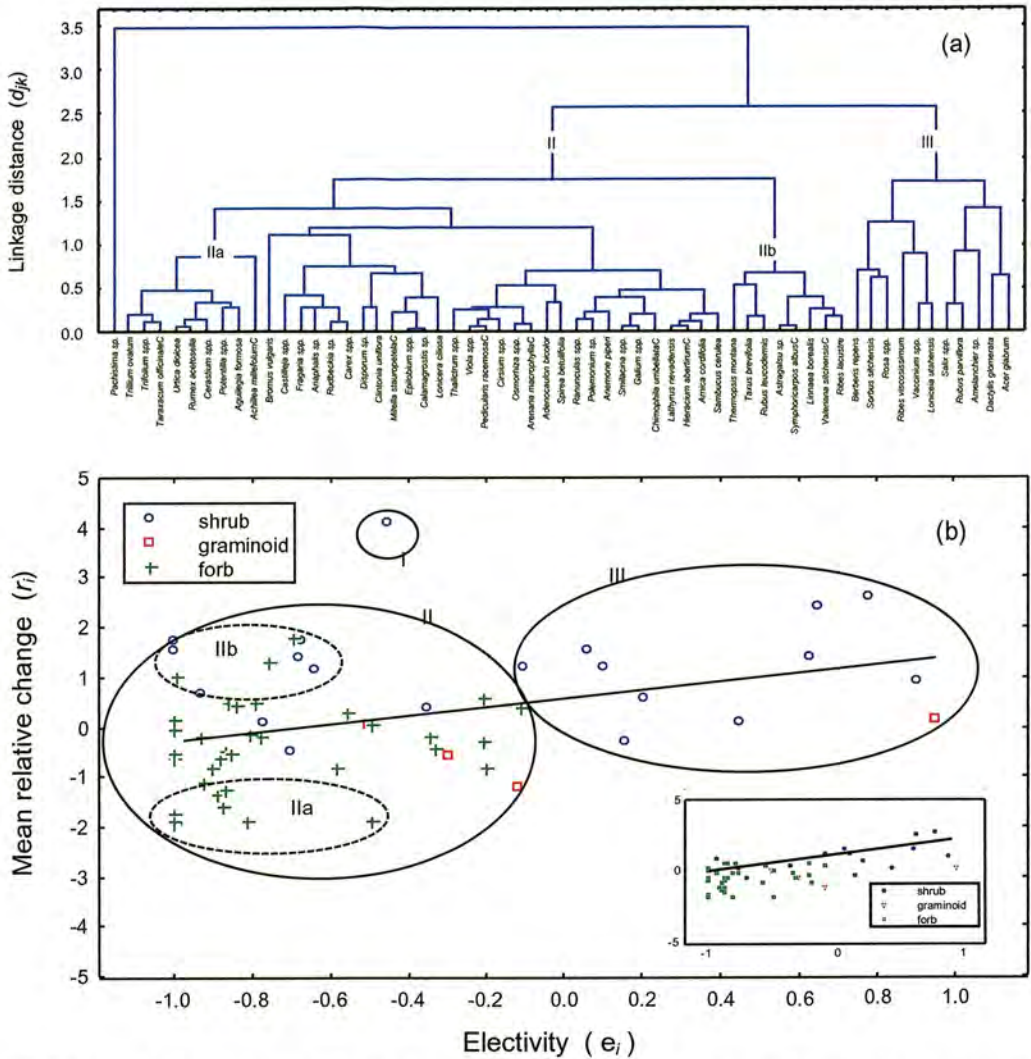


FIGURE 1. Joining tree (a) and scatter plot (b) for cluster analysis of secondary succession in grazed and ungrazed areas. In (b), e_i represents elk dietary electivity (after Ivlev 1961), and r_i represents relative change of plant taxa (inside relative to that outside of exclosures) over 27 years of secondary succession. Positive values of r_i indicate greater development inside exclosures than outside; for example, the shrub in group I (*Pachystima myrsinites*) developed four times more canopy inside exclosures than it did outside exclosures over the 27-yr period. Elk dietary preferences explained from 15 percent (large graph, $n = 59$ taxa) to 37 percent (inset graph, $n = 51$ taxa) of the difference in succession. Nearly all species exhibiting positive dietary electivity are shrubs, and all but one of these developed to a greater extent on sites protected from ungulates. Figure adapted from Riggs et al. (2000).

cations each catalyze changes in plant composition and nutrient pools, and herbivores then modify the subsequent secondary succession by altering plant composition and nutrient dynamics. Influences of herbivory on a given forest site are

regulated by foraging selectivity, nutrient and dry-matter demand, and by productivity and grazing resistance of plants in secondary succession (Riggs et al. 2000). Prescribed fire may initially produce shrub-dominated seres, but repeated fire

TABLE 1. Mean biomass and nutrient accumulation in understory vegetation and forest floor, outside and inside seven ungulate exclosures on forest sites in northeastern Oregon. Differences in nutrient accumulations are largely attributable to reduced accumulation of shrub biomass, which in turn can be attributed largely to selective foraging by wild herbivores. Time lapsed to produce these effects ranged from 27 to 30 years (see Riggs et al. 2000 for details)

Component	Outside	Inside	P
Understory vegetation:	Pounds per acre (kg/ha)		
Graminoids	210 (187)	149 (133)	NS ^a
Forbs	458 (409)	477 (426)	NS
Shrubs	1,168 (1,042)	3,203 (2,858)	0.05
Total, understory	1,836 (1638)	3,829 (3,147)	0.05
Forest Floor	9,971 (8,896)	15,394 (13,735)	0.05
Nutrients:			
Nitrogen	213 (190)	351 (313)	0.01
Phosphorus	36 (32)	50 (45)	0.01
Sulfur	11 (10)	16 (14)	NS
Calcium	306 (273)	500 (446)	0.01
Magnesium	31 (28)	56 (50)	0.01
Potassium	59 (53)	91 (81)	0.05
Total, nutrients	656 (586)	1,064 (949)	0.01

^a NS = not significant; difference between outside and inside the exclosure was not significant ($P > 0.10$).

coupled with chronic browsing by big game produces alternate seres in which the dominant plants are herbs (Peek 1989). Aspen (*Populus tremuloides*) regeneration can be suppressed by chronic post-fire herbivory (Bartos et al. 1994). Nutrient dynamics and attendant site productivity may be modified when large herbivores selectively suppress nitrogen-fixing plants in post-fire successions as well (Riggs et al. 2000). Such interactions, involving herbivores and episodic disturbance, can influence the effectiveness of habitat management based on episodic disturbance (Riggs et al. 1996).

THE CONCEPT OF "REGIME"

The term "regime" has been used by fire ecologists to place fire behavior and effect in common context (e.g., Heinselman 1981, Kilgore 1981, Woodmansee and Wallach 1981, Agee 1993). In efforts to understand effects of livestock grazing on ecosystems, range scientists have similarly characterized livestock grazing regimes in terms of the type of livestock, livestock density, seasonal timing, intensity, and frequency of grazing, and in "systems" that integrate these factors

(e.g., Valentine 1990). Other vegetation controlling agents such as forest site, forestry practices, and herbivory by big game can be characterized in similar terms. Each vegetation-controlling agent can be characterized by a multi-factor regime (Figure 2). Regimes for individual agents may be independent of one another, or inter-dependent in the disturbance sequence (Figure 3). Spatial context can be key to understanding interactions as well, as interspersed plant communities influences seed dispersal and animal use patterns.

Many different combinations of disturbance agents can be hypothesized. Only some constitute practical management strategies, and among these even fewer are functionally different from one another. The salient point is that understanding the role of herbivory in controlling forest vegetation necessarily involves understanding how herbivory functions in an interactive sequence with other disturbance agents (Riggs et al. 2000).

SOME CONCEPTUAL MODELS TO CONSIDER

Management disciplines necessarily employ models that describe how man-

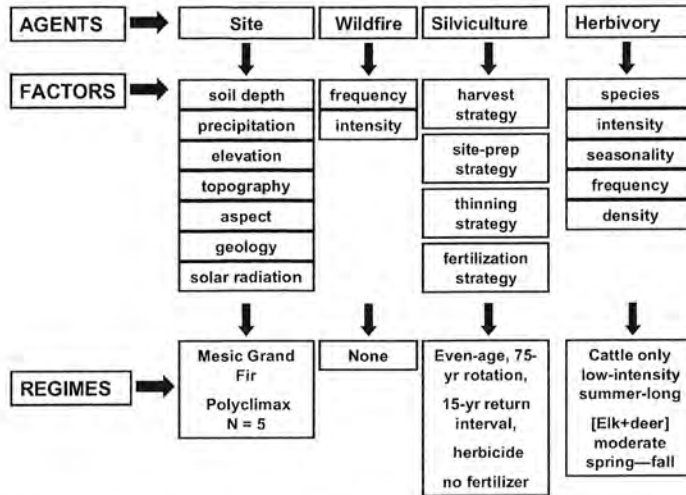


FIGURE 2. Schematic of selected factor regimes for vegetation-controlling agents in north-western forests. The more likely combinations can be represented with rather simple descriptions as shown in boxes at bottom.

agement systems are organized and function (Westoby et al. 1989), a number of which might integrate herbivory's influences in forests. There is no wide consensus on the "best" model for integrat-

ing herbivory into forestry, and comparison of alternatives can be useful.

The Range Succession Model

Most research concerning ungulate herbivory has been conducted in rangeland and pasture settings. The dominant model in range management has been the "range succession model" as described by Westoby et al. (1989). This model describes vegetation in terms of a linear succession to a single persistent state in the absence of grazing (a "monoclimax", after Clements 1916). All possible states of vegetation occur along the continuum, and changes all occur continuously and are reversible. Under the range succession model, managers seek herbivore stocking that establishes an equilibrium between the grazing pressure and the successional tendency of a given plant community, thereby stabilizing it in succession.

The range succession model has been criticized for lacking realism in several situations, chiefly where succession (i.e., trend) has not responded continuously to grazing modifications. The most extreme of such situations is represented by alternate, stable communities of apparently low seral status that persist despite mod-

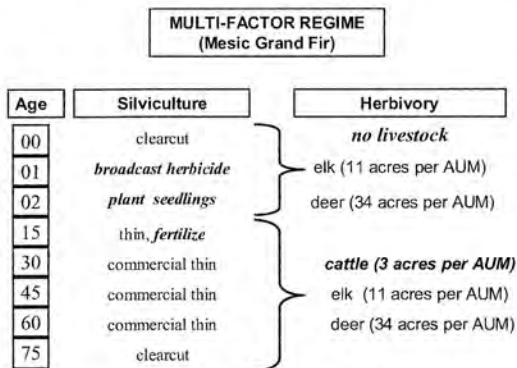


FIGURE 3. Seventy-five-year disturbance chronology for a mesic grand fir site in the Blue Mountains of northeastern Oregon. In this scenario, timber harvest and planting strategies are fixed, fire is categorically precluded, and italics indicate those disturbance agents over which the manager has discretion (herbicides, fertilization, and livestock). Herbivory operates in a sequence with episodic agents. Grazing regimes illustrated here are derived from historical estimates for sites studied by Riggs et al. (2000).

ifications of grazing regime, these communities having been commonly referred to as alternate "states" (Westoby et al. 1989, Laycock 1991) or domains (Friedel 1991). Transitions to such states are often not linear, continuous, or easily reversible, and often their inducement requires more than modification of the grazing regime. Forest succession is often dominated by overstory dynamics rather than by understory dynamics (where grazing is operative), and thus forest succession is problematic to this model, as is the introduction of exotic species (Smith 1978).

State-and-Transition Model

The "state-and-transition" model described by Westoby et al. (1989) and Laycock (1991) is an alternative to the range succession model. This model does not require that vegetation succeed to monoclimate and it does not require that vegetation responses to grazing modification be continuous. Instead, the state-and-transition model simply describes vegetation in terms of a catalogue of alternative states and a catalogue of transitions between states. States are considered stable within reasonable bounds, and are typically identified based on management significance rather than on theoretical significance. In state-and-transition modeling it is not necessary to recognize climax vegetations as such, although climax communities may indeed be approximated by one or more alternate stable states in a particular model. Transition between two stable states is induced by episodic events (e.g., drought, fire, chaining of juniper stands), by changes in herbivory regime, or by combinations of episodic events and herbivory regime.

The most obvious benefit of the state-and-transition model to managers is its ability to categorize multiple states of stable vegetation and to conceptually link them via transitions that integrate episodic and chronic disturbance agents. However, where the occurrence and severity of episodic conditions necessary for transition cannot be predicted with certainty (e.g., precipitation, wildfire), implementation of the state-and-transition model in

management may be difficult to plan, and in some settings this constraint may render it less practical in reality than it may seem in concept. Also, because the model is constructed to conceptualize "switching" (inducing transitions) from one relatively stable state of vegetation to another, and because states are stable, it is relatively insensitive to continuous changes in vegetation that occur within stable states.

Range Succession versus States and Transitions in Northwestern Forests

The range succession model and the state-and-transition model of Westoby et al. (1989) are each derived largely from the labors of ecologists concerned with the management of arid rangelands. Because our focus is forests, comparing these models in forest settings might provide insight to their management utility there.

The range succession model has been widely applied in forests, principally by the U.S. Forest Service. This application probably derives from both an adoption of early monoclimate ecological theory by range managers (see Westoby et al. 1989) and from a perceived need for operational consistency between forestry and range management programs. The logic of the state-and-transition model is recent but not new to northwestern forestry (Kessel 1979). State-and-transition logic has been employed explicitly to conceptualize forest overstory dynamics (Hemstrom et al. 2001), illustrated implicitly in diversity matrices for forest ecosystems (e.g., Haufler and Irwin 1993, Haufler et al. 1996), and used to model understory succession and herbivore carrying capacity (Jenkins and Starkey 1996). In none of these applications, however, has there been explicit consideration of quantitative herbivory, by either wild ungulates or livestock, as a transition-inducing agent.

The root criticism of the range succession model is its basis in the early Clementsian notion of a monoclimate preceded by linear succession in which grazing simply induces retrogression or retards succession. Later monoclimate theory,

however, did indeed approach recognizing alternate states of vegetation such as "subclimax", "proclimax", "disclimax", and "neoclimax" (Clements 1916, 1934; Weaver and Clements 1938; Oosting 1956), albeit lacking explicit recognition of the factors responsible for each alternative (see Tansley 1935).

The monoclimax theory's rudimentary treatment of alternate stable states, and its simplified application in the range succession model, might be mitigated to a substantial extent by integrating concepts of the polyclimax (Tansley 1935). Tansley (1935) drew attention to Godwin (1929) who insisted that subclimaxes might exist as stable, equilibrium communities because a factor could arrest or deflect a sere. The term "plagiosere" was applied to "bent" or "twisted" seres in which vegetation was not in equilibrium with the arresting factor, while the term "plagioclimax" was suggested for referring to vegetations that had actually "... come into equilibrium with the deflecting factor ..." (Tansley 1935:292). Tansley (1935) ultimately recognized three climax vegetations that he considered in equilibrium with primary factors (i.e., climatic climax, edaphic climax, and physiographic climax) and three others that could be derived from primary climaxes through equilibrium with disturbance agents (i.e., fire climax, biotic climax, mowing climax), among which the biotic climax was considered to develop where the "... incidence and maintenance of a decisive biotic factor such as continuous grazing determines the species that persist." In the Northwest, these forms of "disturbance climax" are often referred to as "disclimax" vegetations, after Daubenmire (1968) who specifically applied the term to equilibrium vegetations that required chronic disturbance for maintenance (Nevertheless the term "disclimax" actually originated much earlier, as noted above).

Two salient points can be drawn from this review thus far. First, "climax theory" is not limited to the monoclimax construction, but also includes the polyclimax alternative. The monoclimax and po-

lyclimax are distinguished from one another largely by the latter's somewhat more overt accommodation of alternate climaxes (i.e., alternate equilibrium states), and by the latter's explicit recognition of the agents (some of which are disturbance agents) that produce alternate climaxes. Second, the notion of herbivore-induced, stable states and transitions was conceptually formed in classical ecology by 1935 at the latest, albeit in terms of climax communities and successions, rather than in terms of states and transitions.

As the monoclimax and polyclimax theories evolved through refinement of terminology, the distinction between the two theories eventually came to be as much semantic as substantive (see Oosting 1956). Nevertheless it is important to understand the distinction to fully understand the application of climax theory in northwestern forest ecology. As applied in range management, the early monoclimax (after Clements 1916) is an equilibrium state of vegetation in which herbivory is not operative (herbivory is operative in the development of lower seral states only; Westoby et al. 1989). This application in range management, however, is not consistent with application of later climax theory in northwestern forestry ecology. As applied in forest ecology, the climax is a polyclimax in which some forms are in equilibrium with herbivory (i.e., herbivory is operative in the climax vegetation). Northwestern forest classifications, as exemplified by Daubenmire and Daubenmire (1968), Hall (1973), Pfister et al. (1977), Steele et al. (1981), Johnson and Simon 1987, and Johnson and Clausnitzer 1992 (all adapted after Daubenmire 1952) are all polyclimax classifications. Indeed, the regionally universal practice of "habitat typing" northwestern forests based on the composition of plant associations amounts to taxonomic classification of forest sites (not vegetations) based on potential natural vegetation, after Tansley's (1935) polyclimax (see Daubenmire 1952, Pfister and Arno 1980). "Habitat types" (Daubenmire 1952), "potential natural vegeta-

tions" (Küchler 1964) and "potential natural communities" (Hall 1998) each reflect polyclimax logic. In the Blue Mountains ecological province, only 7 of 31 climax forest associations have been successfully predicted based on their site characteristics alone (Kelly et al. In press). Documentation of these regimes, in context with those for seral vegetations (see Hall 1998) would clarify herbivory's role in determining stable states of forest vegetation in the region.

Nevertheless, the state-and-transition model is an attractive alternative to both the monoclimax and polyclimax models. It might be attractive to some because it does not require explicit distinction between climax and lower seral states as such. More importantly, however, the state-and-transition model clearly requires explicit definition of conditions that induce transitions (see Westoby et al. 1989), not merely identification of the agents that are involved in producing alternate stable states (see Tansley 1935), or knowledge that alternate stable states can exist (see Clements 1916, 1934; Weaver and Clements 1938). Thus, greatest management utility of state-and-transition modeling lies in the fact that it does not accommodate ambiguity to the extent of either the monoclimax or polyclimax model.

Application of the state-and-transition model nonetheless can be challenging in the forestry context. Foremost is the basic problem of defining a stable state. Commercial foresters might classify forest stands based on apparent commercial value or position in a sequence of explicit management events (e.g., seedling, sapling, pole, small saw-log, etc.). Whereas those not so concerned with commodity production might be attracted to classifications more reflective of gradual succession (e.g., stand initiation, stem exclusion, understory reinitiation, old growth; after Oliver and Larson 1990). In either case, the classification of stands amounts to a sequence of seral stages (some management-induced) that are explicitly linked by some combination of disturbance (i.e., management, herbivores) and succession.

These stands also vary to substantial extent in their composition while at the same time often sharing in common the majority of plant taxa. The initial and intermediate "stages" in these artificial sequences are virtually never stable, but rather are dynamic, often highly and purposefully so. Switching can be induced between seral stages by invoking defined conditions, such as clear-cut logging to transform a saw-log stand into an herbaceous or shrub stage, or controlled cattle grazing to facilitate development of a shrub understory. However, stability in the ecological sense is not achieved short of an equilibrium state in which the vegetation can be expected to persist indefinitely (i.e., some form of polyclimax). Thus, an explicit reconciliation of state-and-transition modeling with polyclimax theory seems unavoidable in northwestern forests.

Stromayer and Warren (1997) recognized that transition-inducing mechanisms in forests probably involve multiple disturbance agents such as fire, logging, and chronic herbivory, but they added that confirmation of new stable states might require monitoring over centuries. Kienast et al. (1999) concluded that rather extreme browsing by large herbivores would not dramatically alter successional pathways or long-term woody biomass dynamics. Such observations beg a critical question. *How dramatic and persistent must an herbivore-induced change in forest vegetation be in order to represent a change in "stable state"?* It is clear that disturbance-induced, seral forest vegetations do not typically represent "stable states" in the same sense as do stable, low-seral-state, rangeland communities (as described by Westoby et al. 1989). In absence of clear evidence to the contrary, seral forest stages should probably be modeled explicitly as "transient" rather than as "stable" states, because these seral vegetations typically "... (do not) persist indefinitely but rather (change) into one or other persisting states, depending on events while ... in the transient state." (see Westoby et al. 1989:268).

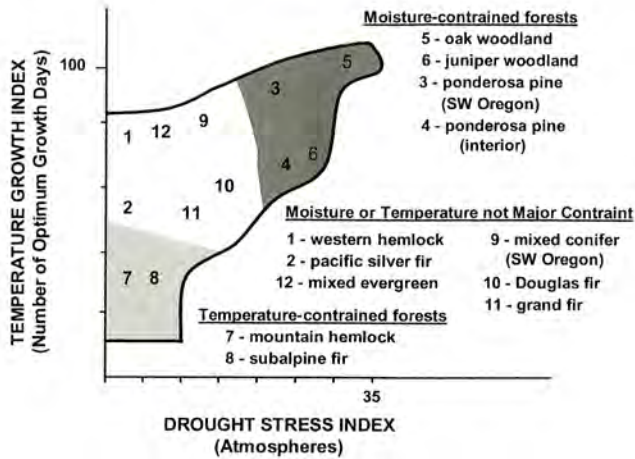


FIGURE 4. Forest zones in the northwest are distributed along a 2-dimensional gradient defined by drought stress and temperature. Oak woodlands, ponderosa pine, Douglas fir, and the drier mixed conifer types are those most likely to suffer frequent drought stress and periodic fire. Transition-inducing interactions that involve herbivores, drought, and fire are probably more frequent there than in coastal and more mesic mixed-conifer forests, but the frequency of such transitions can be increased through anthropogenic disturbances such as logging, prescribed fire, and persistently high herbivory regimes. Climate warming should increase the frequency of transition-inducing interactions along the warm-dry margin of each zone but would perhaps be most apparent in the temperature- and moisture-constrained forests. This figure is simplified from that of Franklin and Dyrness (1973:50).

Productivity of arid lands is usually constrained by moisture, and thus precipitation has played a pivotal role in state-and-transition models for rangeland applications (Westoby *et al.* 1989, Laycock 1991). Northwestern conifer forests, however, are strongly zonal in this respect (Daubenmire 1969, Franklin and Dyrness 1973), occurring along a two-dimensional gradient defined by drought stress and number of optimum growing days. Five zones are arrayed typically (oak-juniper woodlands, ponderosa pine, mixed conifer, coastal temperate, and subalpine/boreal). The woodlands, ponderosa pine and dry mixed-conifer forests are usually considered to be moisture-constrained and in this sense are similar to steppe and shrub-steppe vegetations. Subalpine and boreal forests often are considered to be temperature-constrained (Franklin and Dyrness 1973:50). In between these two extremes, most mixed-conifer and coastal-temperate forests are less likely to be constrained by moisture or temperature (Figure 4).

The nature and extent of herbivory's involvement in facilitating transitions be-

tween stable states should vary across these zones. In the dry, moisture-constrained forests, coupling of some herbivory regimes with relatively frequent drought, resultant moisture limitation, and in some cases frequent, low-intensity fire should produce frequent opportunities for herbivory to induce transitions. In wetter forests, drought-induced moisture limitation is less frequent, as is the fire frequency, but fire intensity increases with the fire-return interval (Agee 1993). Thus opportunities for herbivores to interact with fire regimes to induce transitions between alternate stable states probably occur relatively infrequently in wetter, more productive forests, albeit more dramatically under normal fire-return intervals.

Anthropogenic disturbance regimes (e.g., logging, herbicides, fertilization, and/or prescribed fire), however, should increase the frequency of such opportunities. For example, the typical fire-return interval on a cool-moist grand fir site might be 100–300 years (Agee 1993). Under intensive silvicultural management, however, the same site might have

a disturbance-return interval (i.e., logging, herbicides, fertilization, fire) of only 10–15 years (Figure 3), thus increasing the potential frequency of interaction between episodic agents and herbivores. Where episodic disturbances markedly alter nutrient pools in these forests, and where subsequent herbivory alters nutrient accumulation such as through selective suppression of nitrogen-fixing plants, alternate states of forest productivity may be inducible (Riggs et al. 2000).

The zonal distribution of northwestern forests might influence the effective magnitude of such interactions as well, because the influences of herbivores depend on the rate of forest succession relative to the rate of herbivore population increase (Crawley 1983). In mesic coastal forests, wild ungulate populations may not be able to increase at sufficient rates to have much of an effect on the long-term stability of successions (i.e., from one forest rotation to the next), because sites in these forests are so rapidly colonized by plants and ultimately dominated by forest canopy. In drier forests of the Interior, however, secondary succession proceeds more slowly, thereby providing a longer “window of opportunity” for wild ungulate populations to grow and effectively exert influences on secondary successions.

Growth and Yield Models

We have discussed that northwestern forests can be characterized by complicated inter-agent disturbance regimes. Many of these regimes involve “intensive forestry” practices such as pre-programmed thinning, herbicide and fertilizer applications. In these settings, forest growth simulators play a crucial role in building deterministic projections of timber growth and yield based on model strategies that dictate both type and sequence of management intervention. The dominant simulator in the Northwest is probably the Forest Vegetation Simulator (FVS; after Wykoff 1986, Wykoff et al. 1982), of which many regional variants exist in public and private domains (see <http://www.fs.fed.us/fmsc/fvs/variants/>

[index.php](http://www.fs.fed.us/fmsc/fvs/index.php)). These simulators project conifer growth and yield based on input for site productivity, conifer in-growth, mortality, and applied silviculture. Output is in the form of periodic projections (e.g., 3-, 5-, 10-, or 20-yr periods) of stand attributes (e.g., trees per acre, diameter distribution, volume, etc.) that can be interpreted to classes or stages of forest vegetation. In some of these regional variants, tree growth is calibrated according to polyclimax associations, and “post-processor” programs are also available for linking understory dynamics with overstory dynamics (after Moeur 1985; see <http://www.fs.fed.us/fmsc/fvs/description/model.php>).

The FVS and its post-processors can be calibrated to herbivory regimes as well, thereby providing integration of herbivory and silviculture in an operational context. However, none of the regional variants have been calibrated to integrate herbivory effects explicitly. Growth simulators nevertheless are the primary tools used by foresters to simulate forest dynamics in forest management, and if properly calibrated can provide powerful projections of wildlife habitat quality under varying silviculture regimes (e.g., Roloff et al. 1999, McGrath et al. 2003). They are thus a logical contact point for integrating herbivores into the context of operational forestry.

Landscape Models

Ecosystem management implies a landscape focus and a planning horizon measured in tens to hundreds of years (Tester et al. 1997). The range succession model, state-and-transition model (as described by Westoby et al. 1989), and vegetation simulators represented by the FVS are focused on vegetation trajectories, or on states and transitions within a patch of vegetation over relatively short time periods (e.g., a few decades). It has been argued that these models can not mechanistically model either the processes or responses involved in the ecosystem (Starfield et al. 1993, Tester et al. 1997), and can not be asked how the ecosystem will respond to specific changes in the

driving variables or sporadic environmental events (Starfield *et al.* 1993). In these models, herbivores modify successions or induce transitions in the patch, but the range of possibilities is defined by expectations considered realistic for the site based on historical ranges of variation at similar sites. Events or trends outside of that range, as might be expected due to climate change for example, cannot be explicitly considered. Also, because these models focus on sites or patches, they are not well suited to consider how events or conditions in nearby patches may influence events or processes in the focal patch (e.g., seed production and dispersal, fire intensity and spread, herbivore density and the predictable spatial pattern of grazing intensity). Thus, neither the range-succession or state-and-transition models are well suited to modeling herbivory effects across landscapes or in context with transient climate. There are better alternatives.

“Frame-based” models are a type of “top-down”, state-and-transition model emerging from landscape ecology (Starfield *et al.* 1993, Tester *et al.* 1997). In their simplest form, each frame represents an ecosystem (e.g., grassland, deciduous forest, conifer forest, etc.). Each ecosystem frame runs as an independent subroutine, only one at a time, and transitions occur from one ecosystem frame to another when the conditions necessary for maintenance of a frame are no longer met (Figure 5). Frame-based models have been used to explore how herbivores could interact with disturbance to alter vegetation in a variety of ecosystems (Starfield *et al.* 1993, Starfield and Chapin 1996, Tester *et al.* 1997). Using a frame-based model, Starfield and Chapin (1996) concluded that management policies related to logging and moose populations could affect vegetation stability as much or more than could climate change. Like the other models we have considered, frame-based modeling was initially patch-focused but it now incorporates spatially explicit relationships in landscape contexts (see Rupp *et al.* 2000a, b).

Like the more traditional state-and-

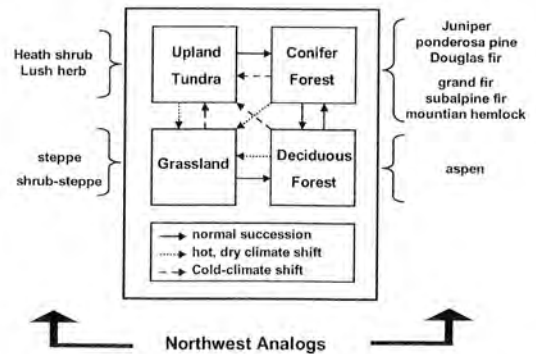


FIGURE 5. Frame-based model structure (large box, after Starfield and Chapin 1996) shows normal succession among arctic and boreal ecosystem types (frames) and transitions under transient climatic conditions. In this model, herbivory interacts with fire and logging to influence the probability of each transition occurring (see Starfield and Chapin 1996:856). Bracketed vegetations (outside the large box) represent Northwest analogs to the more northern vegetations.

transition models used in rangelands, frame-based models are relatively insensitive to linear trajectories of vegetation within their frames. Frame-based models are probably best used to explore relatively long-term and large-scale vegetation dynamics. Frame-based models should be explored in northwestern forests given the apparent likelihood of global warming, the region's zonal limitations to forest growth and distribution, and the likelihood that transition-inducing interactions occur between climate, fire, forest management and herbivory. Calibration of frame-based models to northwestern forests will probably be challenging because of zonal factors, complicated inter-agent disturbance regimes, and the complexity of herbivore assemblages.

Multi-herbivore systems often present the challenge of evaluating influences of modifying one or another herbivore regime. An obvious example of this is comparing the influence of modifying livestock numbers to that of modifying wild herbivore populations (Weisberg *et al.* 2002). This problem involves interacting submodels for weather, carbon, nitrogen, water, light, fire, predators, vegetation

production and herbivore population dynamics; simulating vegetation dynamics in terms of plant composition and production responses to climate, fire, and herbivory; simulating animal responses in terms of distribution, production, and population growth (Coughenour 1993).

SUMMARY AND CONCLUSIONS

Influences of large herbivores on northwestern forests may range from benign to profound, and wild herbivores are just as capable of affecting forest ecosystem properties and processes as are domestic livestock. Wild ungulates and livestock are agents of chronic disturbance that interact with episodic agents in sequence, modifying transient states that are catalyzed by episodic disturbance. Enlightened management of herbivory effects in northwestern forest ecosystems must be based on knowledge of how herbivores interact sequentially with episodic disturbance agents. We offer the following suggestions for integrating herbivory science in the regional forestry model.

First, continuing management with only the range succession model would be problematic for forest managers as indeed it has been for range managers. The range succession model remains useful for managing short-term responses of vegetation where herbivory is indeed the primary agent responsible for change. However, as utilized historically it does not reconcile easily with the polyclimax theory of forest succession, with regional classifications of stable forest vegetations, or with disturbance-agent interactions.

Second, in seeking alternatives to the range succession model, we should seek models that can distinguish herbivory regimes that merely alter successions in the short-term from those that are likely to produce alternate stable states over the long term. Long-term changes in vegetation states will probably result from interactions involving herbivores and other controlling agents, and will probably be more likely in forests that are characterized by high-frequency disturbances, and frequent water and/or nutrient stress. The state-and-transition model represents an

attractive alternative for conceptualizing patch-level disturbance regimes and their consequences. However, state-and-transition models are not necessarily sensitive to gradual changes in vegetation, require unambiguous articulation and calibration, and as proposed in range management thus far are not capable of addressing landscape-level dynamics.

Third, the selection of a model to integrate herbivory into forest management should also depend on the nature and the scale of the manager's information need. Growth simulators like the FVS provide a convenient tool for integrating herbivory influences into the operational context with overstory management, and their calibration for herbivory-induced effects could provide unambiguous management utility. State-and-transition models provide a convenient tool for organizing herbivory's influences in context with those of episodic disturbances, provided that stable-states (i.e., polyclimaxes) and their transitions are not confused with transient-state dynamics (i.e., of seral stages). Landscape models offer ecosystem frameworks in which managers can consider spatially-explicit interactions between herbivores and other disturbance agents, and their long-term effects on forest ecosystem stability. Still, these models remain to be calibrated in the Northwest. Forest managers interested in integrating herbivory into their management programs are more constrained by inadequate data for calibration than by availability of models, and applied research should focus on calibration.

Fourth, some experimental research will be required to understand how herbivores interact with other disturbance agents to influence forest vegetation. Ultimately, the management utility of these experiments will depend upon their blending of ungulate biology, range science, forestry science, landscape ecology, and even climatology to an extent not often seen before. Agency and university administrators would do well to force that integration into their research programs as rapidly as possible. Because the nature and magnitude of herbivore effects can be

expected to vary across the region's environmental gradient, long-term funding for interdisciplinary research should be undertaken at several experiment stations.

Finally, integrating large herbivores into the organizational model for northwestern forestry will not be a mere exercise in modeling effects. Ultimately, it must involve managing herbivore populations in context with specific landscape disturbance regimes. Managing herbivore populations will be as important to that integration as managing the pattern of forestry practices. Thus, to the extent that landscape management defines herbivore carrying capacity, game departments and their constituents have a vested interest in understanding the biological processes and forest dynamics involved.

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The Role of Ungulate Herbivory and Management on Ecosystem Patterns and Processes: Future Direction of the Starkey Project

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INTRODUCTION

In the National Forests of the Blue Mountains, a high percentage of commercial tree species, such as Douglas-fir (*Pseudotsuga menziesii*) and true firs (*Abies* spp.), have died as a result of overcrowding on drier sites, drought, and insects (Johnson et al. 1995, Quigley and Arbelbide 1997). These conditions are typical of forested lands throughout the West (Covington and Moore 1994, Quigley and Arbelbide 1997). Traditional forest management practices (fire exclusion, harvest practices) (Johnson et al. 1995) and livestock grazing (Belsky and Blumenthal 1997) have contributed substantially to the current situation (Hann et al. 1997). Additionally, because of these influences, trees in many stands exist at higher basal areas and higher densities (live and dead) than occurred historically, creating ladder fuels that have dramatically increased the risk of catastrophic wildfires covering very large acreages. In the coming years it can be expected that fires will continue in forests where excessive fuel build-ups have occurred, and that extensive fuels reduction projects will be initiated to prevent them (Healthy Forest Restoration Act 2003).

Secondary succession of both understory and conifer components is initiated following either large fires or fuel reduction treatments. These areas often become focal points of ungulate herbivory for two reasons: 1) vegetation developing after disturbance is often more palatable to ungulates relative to that available on undisturbed sites (Asherin 1976), and 2) forage production in recently disturbed areas is often greater than in surrounding forest communities with dense

canopies (McConnell and Smith 1970, Klinka et al. 1996). Large herbivores are attracted to areas that are characterized by relatively high biomass of palatable food resources, and thus can be expected to focus foraging activity in recently disturbed areas.

Only rudimentary data exists (Riggs et al. 2000) but strongly implicate ungulate herbivory as a significant agent in altering successional trajectories following disturbance (fire, logging, fuels reduction) in the Blue Mountains. Raedeke (1988) stated that selective feeding by forest animals can result in complete changes in the structure, composition, and productivity of the forest. In general, plant communities within grazing exclosures are more diverse than the surrounding forest community subjected to continual herbivory (Raedeke 1988). Recent literature reviews (Hobbs 1996, Augustine and McNaughton 1998) clearly indicate the important role of ungulate herbivory not only in modifying the composition of plant communities, but of ecosystems.

In the Blue Mountains, herbivory has long been recognized to be a competitive factor in ungulate relationships (Cliff 1939, Pickford and Reid 1943) and in suppressing the understory shrub component (Mitchell 1951). The role of ungulate herbivory as a major disturbance agent is not well recognized in the predominant management paradigms, however, both in the Blue Mountains and in all forest ecosystems of the western U.S. Moreover, knowledge of herbivory effects is more anecdotal than predictive (Riggs et al. 2000).

In this paper, we briefly describe current knowledge regarding the effects of ungulate herbivory on ecosystem patterns

and processes in forests of western North America. We then describe new research underway at the Starkey Experimental Forest and Range (Starkey) to understand ungulate herbivory effects. Finally, we identify some of the key policy implications associated with management of ungulate herbivory on National Forests in the western United States.

WHY STUDY AND MANAGE UNGULATE HERBIVORY?

In the western United States, state and federal land management plans outside of national parks have not recognized the ecological effects of foraging by wild ungulates as evidenced by the lack of its mention in land management plans. Aber et al. (2000) made no reference to ungulate herbivory, either wild or domestic, in their publication "Applying ecological principles to management of the U. S. National Forests". In Europe, the effects of ungulate herbivory are better recognized, but primarily for impacts on regeneration of conifers (Kräuchi et al. 2000). At the same time, livestock grazing has long been identified as a potent agent of change in the composition, structure and production of plant communities (Fleischer 1994), and management and research have attempted to address the potentially deleterious effects of this agent. Historically, however, native herbivores such as deer and elk usually were perceived as benign constituents of the environment. In this context, native herbivores are considered a product of management rather than a disturbance factor that might influence other resources and ecological processes. More recently, empirical evidence increasingly indicates that ungulate herbivory, wild or domestic, can have dramatic effects on ecosystem structure and function (Hobbs 1996, Augustine and McNaughton 1998).

In the Blue Mountains, recent findings indicate that wild ungulates dramatically alter the successional pathways of forest understories following disturbance (Riggs et al. 2000) and impact grasslands (Johnson and Vavra 2001, but see Coughenour 1991a, Singer 1995). This evidence large-

ly refutes the notion that successional pathways can be predicted without regard to the herbivory regimes, and thus underscores the need to understand how interactions between herbivores and episodic disturbance function, in the context of both wild and domestic herbivory. We define ungulate herbivory as including both wild and domestic herbivores. Identifying how ungulate herbivory influences composition and structure of forest understories following disturbance is critical to the success of forest planning over the next several years for several reasons.

Forest conditions in the western United States are such that major changes in management are likely during the next several years. Years of fire suppression, resulting forest ingrowth and tree mortality caused by insect and disease outbreaks have contributed to the development of forests that exceed the natural range of variability and are susceptible to conflagrations (Quigley and Arbelbide 1997). For example, 17 percent of the Wallowa-Whitman National Forest has burned in the last 10 years. As a result, management actions are being planned (National Fire Plan 2003 and Healthy Forest Restoration Act 2003) to reduce tree density and fuels, and increase prescribed burning. Nevertheless, vast areas will probably remain untreated well into the future and so the risk of conflagrations will remain high in many areas. Management to restore more natural conditions and continuing wildfire conflagrations both set in motion secondary plant successions that will then be influenced by ungulate herbivory. The nature and extent of these herbivory effects are currently unknown, but sufficient evidence indicates the effects may be relevant and perhaps deleterious to other wildlife species, biodiversity, and ecosystems processes in general. Additionally, herbivory-induced changes in understory may affect productivity of native ungulate herds via negative feedbacks (Irwin et al. 1994) and may increase the degree of interspecific competition among ungulates (Vavra and Riggs 2004).

NEW RESEARCH AT STARKEY: EFFECTS OF UNGULATES ON THE FOREST ECOSYSTEM

Past research at Starkey focused on deer and elk responses to management (Wisdom et al. 2004). New research, however, also will focus on the effects of deer, elk, and cattle as disturbance agents in the ecosystem. This new research will specifically measure effects of ungulate herbivory on plant succession and associated changes in nutrient cycling and biodiversity. Results are expected to provide insights to how herbivore regimes can be sustainably integrated with other disturbances in conifer-dominated ecosystems in the Blue Mountains.

The new herbivory research at Starkey specifically is designed to evaluate the effects of ungulate grazing, interacting with episodic disturbances, on vegetation development and a variety of other resources in grand fir (*Abies grandis*) and Douglas-fir forests predominate across much of the interior western United States. Within this context, we will assess effects of herbivory by elk and by cattle, the two dominant ungulate species in these ecosystems, using a variety of response variables including (a) understory forest development, (b) elk and cattle forage selection and digestibility, (c) nitrogen availability and other key nutrients that affect forest productivity, (d) insect herbivory and biodiversity, and (e) small mammal herbivory and biodiversity.

The research is designed to answer the following questions:

1. How does herbivory by elk and by cattle affect alien plant invasions and the composition, life forms, species richness, cover, and structure of forest understories of grand fir and Douglas-fir forests?
2. How do effects of herbivory by elk and by cattle on vegetation development vary with low, moderate, and high densities of each ungulate, in contrast to no herbivory by either ungulate?
3. How does nitrogen availability and that of other key nutrients change in relation to low, moderate, and high densities of elk and cattle, and how might this affect vegetation development?
4. How does diet selection by elk and cattle interact with herbivory effects on vegetation development under low, moderate, and high ungulate densities?
5. How does diet selection by elk and cattle, and resultant digestibility of forage consumed, change over time in relation to low, moderate, and high ungulate densities, as changes in forage biomass and quality occur?
6. What are the implications of question 5 on the long-term performance of elk and cattle populations?
7. How do herbivory effects by elk and by cattle change in relation to episodic disturbances of intensive timber harvest and prescribed fire, in contrast to effects with no harvest or fire?
8. How does herbivory by insects and small mammals affect vegetation development, as such forms of herbivory interact with ungulate herbivory?
9. Does biodiversity of insects and small mammals change in relation to ungulate herbivory?
10. How might conceptual models of ungulate herbivory-episodic disturbance interactions be refined and parameterized for stand-level management of grand fir and Douglas-fir forests of the Interior Northwest?

These questions are being addressed with the use of 8 ungulate exclosures, each 17 acre (7 ha) in size that have been constructed at Starkey. Exclosure sites were selected within the strata of timber harvest and fire versus no timber harvest or fire. Each exclosure has been subdivided into 7 enclosed paddocks, each 2.5 acre (1 ha) in size, for stocking density manipulation of ungulates (Figure 1).

Each of the 7 individual paddocks that compose a 17-acre (7-ha) exclosure (Figure 1) are randomly assigned 1 of 7 different treatment levels: 3 levels of grazing by tame elk (low, moderate, or high density), 3 levels of grazing by cattle, (low,

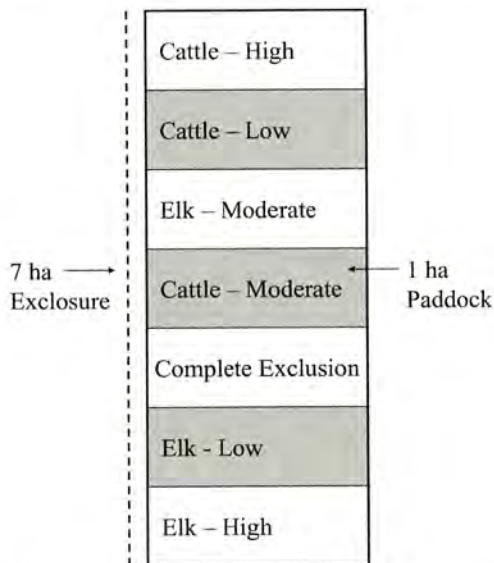


FIGURE 1. Schematic of one of eight 17-acre (7-ha) enclosures at Starkey Experimental Forest and Range. Each enclosure contains 7 paddocks, each 1 ha in size, within which the grazing trials for cattle and elk will be conducted. Each of 7 treatment levels will be randomly assigned to a given 1-ha paddock. Stocking densities of both elk and cattle will be low, moderate, or high. An additional treatment level consists of mixed stocking of both species, with elk using the 2.5-acre (1-ha) paddock early in the summer grazing season, followed by cattle using the paddock late in the summer grazing season, both at low stocking densities.

moderate, or high density), and 1 level of total ungulate exclusion (for a total of 7 paddocks per enclosure).

Construction of the eight enclosures began in summer of 2002 and will continue through 2004. Summer grazing trials will take place each July, using tame elk and cattle at each stocking level in the paddocks. Over 40 response variables related to effects on plants, nutrients, ungulate diets, ungulate nutrition, and insect and small mammal diversity will be measured over the life of the study, which is intended to last at least 10 years.

This new herbivory study will address effects of multiple densities of ungulates, of wild versus domestic ungulates, and the interactions of herbivory with episodic disturbances of reduction in wood fuels

and prescribed fire. These treatment effects have rarely been evaluated in past herbivory research, which more typically compared complete exclusion versus extant herbivore use, with little or no measurement of stocking levels, identification of herbivore species, and little consideration of interactions with other disturbances (Riggs et al. 2000, Wisdom et al. in press).

To complement this research, models will be developed to predict effects of varying densities of ungulates on plant succession and fire risk (Wisdom et al. in press). The new research at Starkey will be used to parameterize the models for integrated management of ungulate herbivory with episodic disturbances of timber harvest, fuels reduction, and fire.

NEW RESEARCH AT STARKEY: UNGULATE RESPONSE TO FOREST MANAGEMENT PRACTICES

As a result of the recently passed Healthy Forests Restoration Act of 2003 (HR 1904), efforts to reduce fuel loadings throughout eastern Oregon, eastern Washington, and western Idaho will be intensified. These efforts will likely include mechanical treatments, prescribed burning, and other techniques used in the past. One such project was recently completed at Starkey. In 1996 the Pacific Northwest Research Station and the Wallowa-Whitman National Forest began planning an Adaptive Resource Management (ARM) fuel reduction program. ARM projects offer unique opportunities for collaboration between research and management. Rarely do research stations have the funds, personnel, and expertise to conduct land management activities at such a broad scale. Conversely, national forests lack personnel trained in experimental design and the infrastructure to conduct sound, scientific experiments. By combining the talents and resources of both Research and the National Forest System in a collaborative ARM project, benefits accrue that would be impossible for either branch operating independently. Many

professional scientific organizations have identified the value of such adaptive, collaborative resource management efforts (Lancia et al. 1996).

The fuel reduction treatments began in spring 2001 and were completed in fall 2003. A total of 46 stands of true fir and Douglas-fir that had suffered substantial mortality during the spruce budworm outbreak in the late 1980s were chosen for treatment. A similar number of stands were left untreated as experimental controls. The treated stands totaled 1,999 acres (809 ha) in size (mean = 34.6 acres (14 ha), range = 2.8–114.0 acres (1.1–46 ha)). In many of those stands, fuel loadings exceeded 60 tons per acre. The objective of the treatments was to reduce fuel loadings to no more than about 15–20 tons per acre. All stands were mechanically thinned using a feller-buncher. About 75 percent of the treated stands were then either broadcast burned or piled and burned to achieve final fuel objectives.

At Starkey, we are using an automated radio telemetry system to track elk, mule deer, and cattle and determine how ungulates respond to fuel reduction treatments at the landscape level. Some specific hypotheses we are testing include: 1) animals will be attracted to the treatment areas because of increased production of preferred forages, 2) elk and deer use of treatment areas will be influenced by the presence of roads and traffic levels, 3) spatial memory (remembering where the treatments areas are located and the amount of forage in each) and exploratory trips (to find newly treated patches) will influence the process by which animals use fuel treatment areas, and 4) the shape, size, and spacing of treatment patches will affect their use by elk, mule deer, and cattle. The automated telemetry system is critical to successfully testing these hypotheses.

This study will yield critically needed information about how overstory and understory vegetation responds once the fuel reduction treatments have been completed. The success of future fuel treatments, and even the ability to complete

such treatments, will be greatly enhanced if we understand the vegetation response to treatments. In addition, identification of cattle, deer, and elk responses will be useful for future environmental assessments and planning efforts.

Similar future research is in the planning stages that will incorporate prescribed fire and, if needed, prior fuel reduction treatments in ponderosa pine (*Pinus ponderosa*) communities. The design of the experiment will be similar to that just described in that experimental protocols will be used but the size of the treatments applied will be on a management scale.

POLICY IMPLICATIONS

Herbivory exists as an unrecognized disturbance on landscapes in western North America. Extant plant communities may be influenced by herbivory and termed grazing disclimaxes (Riggs et al. 2000). However, the influence of herbivory in altering successional trajectories may be most critical following disturbance such as fire or fuels reduction treatments. After disturbance, plants often re-establish either from rootstocks or seeds and are more susceptible to foraging by herbivores. Research results from the Starkey Experimental Forest and Range and elsewhere in eastern Oregon relating herbivory and disturbance are critically important as the new Healthy Forest Initiative is implemented.

Important management and policy implications relevant to herbivory are:

- Ungulates act as keystone species that control ecosystem function and properties. These effects have substantial ecological, economic, and social consequences that deserve increased focus in forest research and management. Improved understanding of the effects of wild and domestic ungulates, under varying population densities, is a critical need for improved management of ungulate herbivory.
- Structure and composition of vegetation can change dramatically in relation to the intensity of ungulate herbivory,

and can have significant impacts on biodiversity. Biodiversity responses to varying levels of ungulate herbivory are not well documented and deserve high priority in research.

- Marked changes in structure and composition of vegetation due to herbivory may increase error associated with identification of vegetative communities (Riggs et al. 2000) in the context of potential natural vegetation, reducing the accuracy and the value of the predominant vegetative/land classification systems currently used by federal management agencies throughout the Northwest (e.g., see Henderson et al. 1992).
- Ungulate herbivory can negatively affect ungulate productivity through negative feedback mechanisms mediated through suppression of food resources. Declining biomass of forage is likely to increase the intensity of ungulate herbivory. In turn, the increased herbivory may not allow preferred forage plants to establish, recover and persist unless disturbances such as fire or timber harvest occur across spatial extents sufficient to providing a forage biomass far in excess of what can be utilized by ungulates. On the other hand, where disturbance is not sufficient, ungulate populations will have to be reduced to avoid degradation. In any event, managers and policy makers might consider how the balance between landscape disturbance and herbivore population management influence long term carrying capacity and ecosystem stability. These relations deserve attention in future ungulate-landscape research.
- Ungulate herbivory may contribute to conifer ingrowth in forest understories, particularly when high levels of herbivory are combined with fire suppression, resulting in substantially higher risk of stand-replacement fires than existed historically.
- When considering forest management practices such as timber harvest, fuels reduction, and prescribed burning, the size and number of treated areas will

affect the recovery of those areas, with smaller treatments likely to attract intensive herbivory and associated changes in vegetation development and other ecosystem processes.

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Has The Starkey Project Delivered On Its Commitments?

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INTRODUCTION

The Starkey Project was conceived from intense debate about how best to manage habitats and populations of mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) in western North America (Rowland et al. 1997). Founders of the research effort promised to provide definitive knowledge about effects of the dominant public land uses on mule deer and elk, and to transfer that knowledge in relevant and synthesized forms for ease of management application.

In our paper, we review the commitments of the Starkey Project and summarize its major achievements. We also identify key research opportunities that, in our view, are optimally addressed by the Project's unique research facility and compelling partnerships. Our review is focused on the historical performance of the Project in generating knowledge of high management utility, and the efficient transfer of that knowledge to land and wildlife managers in western North America.

COMMITMENTS AND ACCOMPLISHMENTS

The Starkey Project was designed to address the most contentious of resource uses on public lands, and to provide cause-effect responses of mule deer and elk to those uses. When the Project was first proposed in the early 1980s (Wisdom et al. 2004a), four resource issues were the focus of debate in relation to deer and elk: (1) road management; (2) intensive timber production and thermal cover; (3) competition with cattle; and (4) breeding efficiency of male elk. These four issues became the foundation of the Starkey Project's original studies that began in 1989 and ended during the mid- to late

1990s at the Starkey Experimental Forest and Range (Starkey) and Kamela research sites in northeast Oregon (Rowland et al. 1997, Cook et al. 1998, Wisdom et al. 2004a).

Road Management

Project scientists undertook new research to estimate the long-term spatial relations of mule deer and elk to the type of road management (open, closed, and administrative use) and to the rate of motorized traffic (number of vehicle trips per unit time) on the roads. Scientists designed the research to estimate these relations accurately, with sufficient sample sizes to clearly portray spatial patterns, and at landscape scales commensurate with ungulate use and management decisions.

Investigators met this commitment by generating the largest data set ever amassed on locations of deer and elk in relation to distance from roads of different types and rates of traffic; scientists characterized these relations with spatially explicit models that could be directly applied in management (Rowland et al. 2000, 2004; Wisdom 1998; Wisdom et al. 2004b). Results are now used by state wildlife agencies and federal land management agencies throughout western North America. Findings constituted part of the foundation for the national roads policy established by the U.S. Department of Agriculture, Forest Service (FS), thus affecting road management on all National Forests.

Intensive Timber Production and Thermal Cover

Thermal cover is defined as "cover used by deer or elk to assist in maintaining homiothermy" and as "... any stand

of coniferous forest trees 40 feet (12 m) or more tall with an average canopy closure exceeding 70 percent" (Thomas et al. 1979:113–114). Whether thermal cover was a requirement of elk (that is, whether animal performance suffered without thermal cover) constituted a major question that the Starkey Project promised to examine. A corollary question that the Project pledged to answer was whether intensive timber harvest had any measurable effects on habitats and populations of mule deer and elk. Prior investigations had shown that elk avoided or substantially reduced their use of areas subject to timber harvest and associated road use. But, what if the entire landscape was so treated and deer and elk had to react to the resultant conditions?

The question of whether elk require or benefit from thermal cover was addressed in an experimental study at Kamela (Cook et al. 1998). Here, the nutritional condition of tractable elk maintained in pens was monitored in relation to varying amounts of thermal cover and no cover. Results, which detected no positive physiological benefits to elk from the presence of thermal cover, have changed managers' thinking about elk-cover relations (Cook et al. 2004a). As a result, many land managers have modified their thermal cover direction for elk. (Elk use of dense forest stands, such as for hiding cover and escapement, remain important considerations in management [Lyon and Christensen 2002]). Notably, contentious litigation related to meeting thermal cover standards on National Forests was resolved, saving millions of dollars to the FS planning process.

Effects of timber management (harvest and roading) were addressed by conducting a landscape experiment to evaluate cattle and elk responses to intensive harvest and associated human activities at Starkey from 1989–1996 (Rinehart 2001, Wisdom et al. 2004c). Thousands of ungulate locations were collected before, during, and after completion of a timber sale that substantially reduced canopy closure on over half the forested study site, and more than doubled the road den-

sity. Measures of animal response provided little evidence of lasting negative effects with the major exception of the substantial increase in elk vulnerability to harvest by hunters (Wisdom et al. 2004c). Results (Rinehart 2001, Wisdom et al. 2004c) are now available for timber sale planning on National Forests.

Competition with Cattle

The degree to which mule deer, elk, and cattle compete for food and space was another key research problem. By evaluating the spatial distributions, resource selection patterns, and behavioral interactions of the three ungulates as cattle were rotated through the livestock pastures each summer during the 1990s (Coe et al. 2001, 2004), scientists estimated a realistic forage allocation among cattle, deer, and elk by month and season (Johnson et al. 1996). Combined with a subsequent study of diet overlap among the three species (Findholt et al. 2004), scientists used the results to build new models capable of assessing the trade-offs and benefits of different grazing management scenarios on summer ranges shared by cattle, mule deer, and elk (Ager et al. 2004).

These models of forage allocation (Johnson et al. 1996) and grazing management (Ager et al. 2004) allow rangeland managers to evaluate trade-offs of changing stocking rates among the three ungulates under different assumptions that reflect ecological differences in ungulate use of summer ranges. Application of these tools is expected to facilitate timely completion of new allotment plans now under development in National Forests in the western U.S.

Breeding Efficiency of Bull Elk

Determining the degree to which elk productivity is affected by age of breeding males was a major objective of the Starkey Project in the 1990s (Noyes et al. 2004). During two separate, five-year studies, conception dates in female elk were shown to occur earlier and be more synchronous with increasing breeding age

of male elk (Noyes et al. 1996, 2002). That is, breeding by older bulls resulted in calves being born earlier and over a shorter time period each spring, conferring a number of survival benefits (Noyes et al. 2004).

As a result, states and provinces throughout western North America modified their hunting regulations to protect older male elk from being taken by hunters. Protection of older males from hunting is now recognized and implemented as an important management strategy, owing to the benefits of older males as breeders, in combination with the recognized social and aesthetic benefits of viewing these animals (Bunnell et al. 2002).

ADDITIONAL ACCOMPLISHMENTS

As Project investigators completed their initial studies during the 1990s, several new resource issues in public land management emerged that could be addressed with the use of the Project's novel research technologies (Wisdom et al. 2004a). Those issues became the focus of subsequent ungulate research at Starkey. New research completed or underway includes:

- Effects of woody fuels reduction on distributions and forage conditions for mule deer, elk, and cattle (Vavra et al. 2004);
- Deer and elk responses to off-road recreation, including travel by all-terrain vehicles, horseback, mountain bike, and foot (Wisdom et al. 2004d);
- Development and testing of new road models for elk management (Rowland et al. 2004);
- Synthesis and modeling of factors that affect elk vulnerability to harvest by hunters (Vales 1996, Johnson et al. 2004);
- Energetic costs to deer and elk exposed to, but not harvested, under varying levels of hunting pressure and season designs (Johnson et al. 2004);
- Hourly, daily, and seasonal changes in movements and habitat use by mule deer and elk, measured at fine resolution with one of the largest data sets on ungulate locations ever amassed (Ager et al. 2003);
- Effects of sampling design on resource selection and home range estimators for wildlife research (Garton et al. 2001, Leban et al. 2001);
- Exploration and use of diffusion theory to model animal movements (Brillinger et al. 2004);
- Consideration of nutrition demands and animal condition to enhance elk productivity (Cook et al. 2003, 2004b);
- Effects of ungulate herbivory on vegetation development and ecosystem processes (Riggs et al. 2004, Vavra et al. 2004);
- Validation of resource selection patterns for elk to strengthen and expand inference space for management (Coe 2003).

Results from these follow-on studies have yielded compelling benefits to managers. For example, defensible options for managing off-road vehicles and other off-road recreation on public lands are now being developed. Findings are expected to provide information about effects of off-road recreation, particularly motorized recreation, the most-rapidly growing use of public lands in the United States (Havlick 2002).

Another example is the current research on management of deer, elk, and other wildlife in relation to fuels treatments to reduce fire risk (Vavra et al. 2004). The Starkey Experimental Forest and Range has been identified by the FS as a national research site to evaluate success of fuels treatments to reduce fire risk in National Forests, and to assess effects on wildlife.

Two other studies of keen interest and utility to managers are (1) energetic and movement responses of deer and elk to hunting, specifically when animals are exposed to hunting activities but not harvested (Johnson et al. 2004), and (2) effects of nutrition on elk productivity (Cook et al. 2003, 2004b). State, federal, private, and provincial resource managers are using findings from this new research

to meet increasing demands for hunting and viewing of elk, which generate hundreds of millions of dollars annually to local and regional economies in western North America (Bunnell et al. 2002).

EFFECTIVE TRANSFER OF KNOWLEDGE TO MANAGEMENT

The Starkey Project has been one of the few research programs in the FS with a full-time focus on the science of technology transfer (Rowland et al. 1997). The transfer program has served as an effective liaison between management and research. As a result, the Project has shared research technologies and results directly with more than 200,000 recipients encompassing local, regional, national, and international organizations, groups, and agencies. These communication mediums beyond scientific publications included field tours, presentations, workshops, symposia, news releases, newspaper features, magazine articles, radio interviews, and television coverage. Over 600 field tours and presentations have been given, and scientists have organized over 15 field tours and more than 20 presentations per year during the past decade.

The technology transfer program helped garner widespread public acceptance and support of Project research and results (Rowland et al. 1997). Transfer efforts have been viewed as one of the primary reasons that many land and wildlife managers have readily adopted Starkey research findings.

STARKEY'S FUTURE: BEST USES OF A UNIQUE FACILITY

The unique research facility at Starkey, described in detail elsewhere (Rowland et al. 1997, 1998; Wisdom et al. 2004a), is an optimal environment in which to conduct manipulative experiments and elucidate cause-effect responses of ungulates at landscape scales. We know of no other research facility that has the combination of experimental controls and animal tracking technologies needed to conduct

such cause-effect research at landscape scales. There are emerging, significant research questions ideally suited for study within the Project's unique research facility.

Effects of Elk Removal on Mule Deer

Scientists have noted the anecdotal evidence suggesting that as elk invade mule deer ranges and become plentiful, mule deer numbers decline (e.g., see Wallmo 1981, Wisdom and Thomas 1996). In support of this hypothesis, one of the more interesting findings from research at Starkey has been the consistently strong avoidance shown by mule deer for elk (Johnson et al. 2000; Coe et al. 2001, 2004; Stewart et al. 2002; Wisdom et al. 2004b). Interference competition may be operating, causing mule deer avoidance of elk and reducing population performance of deer.

The only definitive manner in which to document whether mule deer avoidance of elk results in reduced population performance of deer is to conduct a manipulative experiment, where elk are removed from an area and the population response of deer is measured. Then, elk could be reintroduced to the study area, first at low density, and mule deer population response measured. Finally, elk could be allowed to reach high density, and mule deer response again measured. The cycle could be repeated to validate the initial set of mule deer responses to elk removal and reintroduction.

The Starkey facility is one of the few sites in which such removal experiments could be done in a definitive manner to document whether interference competition is operating between mule deer and elk. Given that mule deer populations are declining throughout much of western North America (Kie and Czech 2000), this research should be viewed as one of the highest priorities of the Starkey Project.

Effects of Hunting Season Designs on Mule Deer and Elk

Research at Starkey has documented substantial energetic costs to mule deer

and elk under different types and lengths of hunting seasons (Johnson et al. 2004). What remains to be evaluated, however, are the effects of a full spectrum of different hunt types, season lengths, hunter densities, and associated options for road and off-road access on deer and elk. In particular, how all-terrain vehicles (ATVs), with full access to the hunting landscape, affect harvest rates of targeted animals, and energetic costs of non-targeted animals, has not been studied. This issue is a major concern of state wildlife agencies. Starkey, with its capability to design and administer a variety of hunts as part of landscape experiments, and accurately measure the population responses of ungulates, is well-suited for such research.

Off-road Vehicle Effects on Wildlife and other Resources

Use of ATVs during non-hunting periods can substantially increase movement rates of elk, and consequently, is likely to increase the daily energetic expenditures of animals (Wisdom et al. 2004d). What remains unclear, however, is the effect of ATVs on elk during hunting seasons. Moreover, the effects of ATVs and other forms of off-road recreation on additional species of wildlife, on exotic plant invasions, and other resources such as soil productivity and water quality, have not been studied experimentally.

These topics are well suited for new research at Starkey, to complement and validate current research on effects of off-road recreation (Wisdom et al. 2004d). ATV riding is the most rapidly-growing recreational use on public lands (Havlick 2002), and other forms of off-road recreation such as mountain biking, horseback riding, and hiking also are increasing. New research on the comparative effects of these different forms of off-road recreation is urgently needed. Starkey is ideally suited for conducting such research with appropriate experimental controls to elucidate cause-effect relations.

Effects of Ungulate Herbivory on Forest Development and Productivity

Ungulate herbivory has profound effects on vegetation development and productivity in forest ecosystems (Hobbs 1996; Riggs et al. 2000, 2004). Livestock grazing has long been recognized as an agent of change in composition, structure, and development of plant communities (Fleischner 1994), but herbivory by wild ungulates has not always been recognized as an ecological force in western North America (Augustine and McNaughton 1998).

New research is currently being planned at Starkey that would evaluate effects of varying levels of grazing by cattle and elk on plant succession, soil nutrients, animal biodiversity, and ungulate nutrition, as measured over long (10 or more years) time periods (Vavra et al. 2004). This research will use a series of large, 18-acre (7.3-ha), exclosures each subdivided into 7 pastures with different levels of elk and cattle grazing during summer. The research, however, requires substantial funding (at least \$500,000 per year) that currently is unavailable. Moreover, herbivory by cattle versus elk is a highly contentious issue, fraught with uncertainty, and clouded by strong political interests. For example, stringent utilization standards are often imposed on cattle grazing in riparian habitats to meet objectives for management of salmonids. And yet, effects of herbivory by wild ungulates may also affect habitat conditions, and in ways neither acknowledged nor understood. The new herbivory research at Starkey is needed to understand the effects of wild versus domestic ungulates in relation to management goals for wildlife, vegetation, silviculture, nutrient availability, and other measures of forest productivity (Vavra et al. 2004).

Habitat Management Relations with Ungulate Nutrition

The individual, stand-level effects of timber management, fuels reduction, prescribed burning, wildfires, insect defolia-

tion, and other episodic disturbances on the nutritional condition of ungulates is understood at a coarse level. However, the nutritional effects of the combination of these disturbance events in time and space on the landscape are complex and poorly documented. For example, episodic disturbances create open-canopy forests, resulting in substantial increases in forage biomass for ungulates (Peek et al. 2001). And yet the degree to which these episodic disturbances, and the mosaic of such disturbances in time and space, adequately meet the nutritional demands of wild and domestic ungulates is neither well understood nor well studied (Cook et al. 2003).

New studies of ungulate foraging dynamics and nutritional intake are needed with the use of tame elk, deer, and cattle. The Starkey Project and its many partners maintain tractable mule deer, elk, and cattle for such grazing studies (Cook et al. 2003). These animals, and scientists experienced in their use, could be quickly put to work at Starkey to discern the nutritional benefits of fuels reduction treatments, timber harvest, and other habitat manipulations at the stand level, and for the mosaic of stands across the landscape.

Moreover, Project scientists have developed a compelling set of maps depicting the probabilities of habitat use by elk, mule deer, and cattle across the landscape, estimated by month and season from years of research at Starkey (Ager et al. 2004). These probabilities could be linked to the underlying nutritional conditions of each habitat type, using the tractable cattle, deer, and elk available at Starkey. Such research would provide insight about the nutritional consequences of ungulate habitat choices. Given current concerns about declining productivity in elk and mule deer populations (Kie and Czech 2000, Johnson et al. 2004), a basic management question still needs to be addressed. That is, how well are current habitat conditions, and those planned under future landscapes, providing for the nutritional needs of wild and domestic ungulates? New studies on ungulate nutrition in relation to habitat conditions at

Starkey could fill this increasingly important gap in current knowledge.

CONCLUSIONS

The Starkey Project has delivered on its promises. In fact, the Project has paid off far in excess of those promises. To drive home that point, consider the following: over 140 publications completed or in press; over 40 partners actively involved in the research; over 50 studies completed or underway; more than 600 tours and presentations to local, regional, national, and international audiences; and common and increasing use of results by state, federal, tribal, and private land and wildlife managers across western North America. Keys to the Project's remarkable success have been many: (1) unique technologies that have facilitated the completion of needed studies previously considered difficult or impossible to conduct under appropriately controlled conditions; (2) long-term commitments by diverse federal, state, private, and tribal interests; (3) continued focus on ungulate issues of highest relevance to management; and (4) constant and open dialogue and sharing of the research with all interests and resource users (for details, see Kie et al. 2004, Quigley and Wisdom 2004 and Wisdom et al. 2004a).

Perhaps most impressive is the economic return from the research, which is conservatively estimated to far exceed the 20 million dollars invested by partners during the Project's 22-year history. This economic return will increase in the future, as use of resulting information by land and wildlife managers continues to expand. This unique and long-lasting research program is a shining example of applied research conducted under controlled and rigorous conditions, and made available to users and interested parties through publications, tours, presentations, and media outlets. We urge partners in the Starkey Project to continue supporting this long-term research for the mutual benefit of land and wildlife managers and those who benefit from and care about forests, rangelands, and the wildlife these habitats support.

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