COLORADO
Department of
Natural Resources

Executive Director's Office
1313 Sherman Street, Room 718
Denver, CO 80203

October 1, 2019

Objection Reviewing Officer
United States Department of Agriculture
United States Forest Service
Rocky Mountain Region
1617 Cole Boulevard, Building 17
Lakewood, CO 80401

RE: Objection to the Revision of the Land Management Plan for the Rio Grande National Forest

To whom it may concern:

Please accept this Objection to the United State Forest Service (USFS) Rio Grande National Forest Land Management Plan (LMP) and Final Environmental Impact Statement (FEIS), submitted by the State of Colorado acting through its Department of Natural Resources (Colorado DNR – Lead Objector). Colorado DNR participated in the planning process as a formal cooperating agency including participation from our Division of Parks and Wildlife (CPW), Division of Water Resources (DWR) and Colorado Water Conservation Board (CWCB). We appreciate the attention to the comments provided by DWR and CWCB. Our objection reflects outstanding issues raised by CPW to maintain and enhance wildlife habitat that we seek to resolve.

CPW provided input on multiple occasions throughout the planning process, and submitted written comments on the Assessment Reports and the Need for Change Document (2016), Proposed Action (2016), and Draft LMP (2017). We appreciate several changes that were made between the Draft and Final, including the incorporation of Standard VEG 7. CPW staff were part of numerous discussions, meetings, and field trips that led directly from CPW research to VEG S7. This standard was developed to provide direction on timber salvage in beetle killed forests with respect to lynx habitat and use. We also appreciate that Rocky Mountain Bighorn Sheep were classified as a Species of Conservation Concern in the Final LMP per our recommendation in 2017.

On August 21, 2019, Governor Polis signed Executive Order (EO) D-2019-011, Conserving Colorado's Big Game Winter Range and Migration Corridors. This EO recognizes the contribution that big game species make to the economy and quality of life for every Coloradan, and empowers CPW to identify important migration corridors and seasonal habitats for big game. As CPW collects new information and identifies important seasonal habitats and migration corridors, it is important to have specific plan components associated with these habitats incorporated into the Final LMP to support continued sustainable wildlife populations and connectivity within the Rio Grande National Forest.

**Objection of issues in the LMP**

1. Changes and removal of Standards and Guidelines between the Draft and Final LMP
2. Removal of Management Area 5.41 and Lack of Protection for Winter Ranges, Production Areas, and Migration Corridors Necessary for CPW to Sustain Big Game Population Objectives

**Standards and Guidelines**

Throughout the planning process and in CPW's 2016 and 2017 comments on the Draft LMP, CPW recommended specific Desired Conditions, Objectives, Standards and Guidelines to maintain and enhance wildlife habitat including big game winter ranges, production areas, and migration corridors. As outlined in the comments on the Draft LMP in 2017, we identified our concerns with the lack of Standards and Guidelines to achieve the Desired Conditions and Objectives specified in the Draft LMP, and we recommended the addition of specific Standards and Guidelines to meet the Desired Conditions and Objectives for wildlife. Despite our concerns and recommendations, the Final LMP contains even fewer Standards and Guidelines than the Draft LMP. The USFS FSH 1909.12-2015-1 outlines the plan components necessary in each LMP. Standards and Guidelines are required to be incorporated into the LMP to help achieve or maintain the Desired Conditions, and to avoid or mitigate undesirable effects. The use of Management Approaches is discretionary. There is a disproportionate use and reliance upon unenforceable Management Approaches (as opposed to enforceable Standards and Guidelines) to achieve Desired Conditions in the Final LMP.

As discussed in our comments on the Draft LMP, crucial winter habitats are known to be a limiting factor on big game populations in western Colorado and other high mountain areas of the western United States (Bergman et al. 2015, Bishop et al. 2009, Bartman et al. 1992, Hobbs 1989). To maintain habitat effectiveness of big game winter range, CPW recommended that the Final LMP incorporate a Standard requiring seasonal closures of routes within big game winter range. This Standard is necessary to manage activities and uses on the forest that conflict or reduce winter range capacity and use by big game species. These Standards were in the Draft LMP as **S-WLDF-3** and **S-WLDF -12** (forest wide). To resolve our Objection:

- Incorporate Standards **S-WLDF-3** and **S-WLDF-12** back into the Final LMP with the corrected dates of December 1–April 15.

Additionally, in our 2017 comments on the Draft LMP, CPW recommended that USFS adopt a Standard that limits road and trail densities in winter ranges, production areas, and migration corridors in order to maintain habitat effectiveness, to meet CPW's big game population objectives outlined in Data Analysis Unit (DAU) plans, and to maintain and enhance recreational hunting opportunities. Specifically, we "recommended a road and motorized trail density of 1 mile/square mile or less in production areas, winter concentration areas, and severe and critical winter range for big game." We recommended converting **DC-WLDF-9** into a Standard rather than a Desired Condition, and requiring compensatory mitigation to offset proposed developments on the Forest when the densities exceed 1 mile/square mile to maintain habitat effectiveness (forest wide). This recommendation is based on a body of research documenting displacement of big game from roads and trails and a decline in habitat effectiveness for big game as road and trail densities increase (Wisdom et al. 2018, Preisler et al. 2013, Sawyer et al., 2013, WAFWA 2013, Rogala et al. 2011, Wilber et al. 2008, Rowland et al. 2005, Rowland et al. 2000, Phillips and Alldredge 2000)[1].

Route density limitations are integrally tied to other resource uses (such as oil and gas development and well pad densities, recreation management, travel management, etc.), and should be considered as a package during the land allocation decisions adopted during the LMP revision process. The LMP currently includes land allocation decisions that overlap with important winter ranges, production areas, and migration corridors identified by CPW without consideration of how the functionality and connectivity of these important habitats will be maintained. To resolve our Objection:

- Change the Draft LMP DC-WLDF-9 to a Standard that states road and trail density will be 1 mile/square mile or less in production areas, migration corridors, and winter ranges for big game, and that compensatory mitigation will be required if this standard is exceeded, and incorporate it in the Final LMP

**Removal of Management Area 5.41-Big Game Winter Range and Lack of Protection for Winter Range, Production Areas, and Migration Corridors Necessary for CPW to Sustain Big Game Population Objectives**

The Draft LMP included Management Area 5.41-Big Game Winter Range, and we were encouraged that the USFS recognized the importance of these habitat types. This Management Area (MA) incorporated and relied on CPW expertise, data, and published maps on big game species seasonal distribution, migration, and use on the Forest. Additionally, this MA had a Desired Condition to limit route density and a Standard (**5.41-S-1**) to prohibit travel during the winter to maintain habitat effectiveness for big game. However, this MA was removed from the Final LMP. We are concerned that the loss of this MA will affect CPW's wildlife management objectives. To resolve our Objection with the removal of MA 5.41 from the Final LMP, we request that the USFS:

- Incorporate the Standards we articulated above for production areas, migration corridors, and winter ranges, and;

- Commit to incorporating the most up to date CPW mapped habitats for big game species including: production areas, migration corridors, and winter ranges, during project level implementation.

**The Cooperating Agencies' Role**

In addition to these issues, Colorado wishes to express its concern that the cooperating agencies were not given an opportunity to review and comment on the Final LMP – specifically, the final version of Modified Alternative B. In the years that passed between the time that the cooperators commented on the Draft

---

[1] Per the Objection regulations all of the referenced studies are provided in Attachment 2

Preferred Alternative B, in 2017, and its final rollout in August 2019, substantial changes were made to Agency preferred Alternative B, including the elimination of Management Area 5.41 Big Game Winter Range and the deletion of Standards and Guidelines.

This process is not consistent with the MOUs signed between the cooperators and the USFS, which require the RGNF to provide the cooperating agency with meaningful opportunities for participation. Moreover, it is inconsistent with the purpose of the cooperating agency relationship, which is intended to result in better decisions by fostering trust and cooperation between various federal, state, and local governments. We hope that future LMP planning processes in Colorado respect the input and needs of the cooperating agencies.

Thank you for your attention to our concerns. We look forward to working with you during the implementation of the LMP by applying the standards and guidelines in the Final LMP to the habitats mapped by CPW. We greatly appreciate USFS's partnership with Colorado in managing lands and wildlife for multiple uses while conserving species and habitat.

Sincerely,

Dan Gibbs
Executive Director
Department of Natural Resources

cc: Doug Vilsack, DNR Assistant Director Parks, Wildlife, and Lands
Amy Moyer, DNR Assistant Director for Water
Dan Prenzlow, Director Colorado Parks and Wildlife
Cory Chick, CPW Southwest Region Manger
Reid DeWalt, CPW Assistant Director Wildlife and Natural Resources
Rick Basagoitia, CPW Area Wildlife Manager
Brian Mage, CPW SW Region Land Use Coordinator
Jon Holst, CPW SW Energy Liaison

# Reference Materials

---

Compensatory Mortality in a Colorado Mule Deer Population
Author(s): Richard M. Bartmann, Gary C. White and Len H. Carpenter
Reviewed work(s):
Source: *Wildlife Monographs*, No. 121, Compensatory Mortality in a Colorado Mule Deer Population (Jan., 1992), pp. 3-39
Published by: Allen Press
Stable URL: http://www.jstor.org/stable/3830602
Accessed: 01/10/2012 12:54

---

# WILDLIFE MONOGRAPHS

(ISSN:0084-0173)

*A Publication of The Wildlife Society*

# COMPENSATORY MORTALITY IN A COLORADO MULE DEER POPULATION

by

RICHARD M. BARTMANN, GARY C. WHITE,
AND LEN H. CARPENTER

**NO. 121** **JANUARY 1992**

**FRONTISPIECE.** Starved mule deer fawn on pinyon-juniper winter range in Piceance Basin, Colorado (photo by Robert A. Garrott).

# COMPENSATORY MORTALITY IN A COLORADO MULE DEER POPULATION

**RICHARD M. BARTMANN**

Research Section, Colorado Division of Wildlife, 317 West Prospect Road, Fort Collins, CO 80526

**GARY C. WHITE**

Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523

**LEN H. CARPENTER**

Research Section, Colorado Division of Wildlife, 317 West Prospect Road, Fort Collins, CO 80526

*Abstract:* A thorough test of the hypothesis of compensatory mortality is a fundamental requirement for a better understanding of the population dynamics of wildlife species. This knowledge is vital, whether populations are managed for recreational hunting or other purposes. Our research on a pinyon pine (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) winter range in Piceance Basin, northwest Colorado, from 1981 to 1988 tested for compensatory mortality in the fawn portion of a mule deer (*Odocoileus hemionus hemionus*) population.

Three experimental manipulations were used employing radio-collared deer. In a field study, removing 16–22% of the population from the treatment unit each winter for 2 years had no measurable effect on fawn survival rates as compared to rates on the control unit ($P = 0.566$). We attributed this mostly to not removing enough deer to immediately affect fawn survival under existing range conditions. In a controlled study, deer removed from the treatment unit were used to stock 3 large pastures at densities of 44, 89, and 133 deer/km$^2$ to simulate hunting removals of 67, 33, and 0%, respectively. Fawn survival rates varied inversely with density ($P < 0.001$). Starvation was the leading cause of fawn mortality in all pastures indicating a nutritional limitation at all densities. We believe the density-dependent survival response in the pastures demonstrated that a strong compensatory mortality process operated in this mule deer population. In another field study, 49–77% of fawns were killed by predators during 4 winters. We then reduced the coyote (*Canis latrans*) population for 3 winters while we continued to monitor fawn mortality. Predation rates decreased ($P = 0.004$) and starvation rates increased ($P = 0.042$) between pre- and posttreatment periods, but no change in fawn survival was detected ($P = 0.842$). These results support those from the pastures even though the primary mortality causes differed.

Mean fawn weights varied among years, study areas, and trap sites ($P < 0.001$). Male fawns averaged 2.4 and 3.0 kg heavier than females ($P < 0.001$) on the 2 field-study areas. Larger fawns had higher survival ($P < 0.001$), but size was not a significant predictor of whether or not a fawn starved ($P = 0.237$). In both field-study areas, female fawns had higher survival than males ($P < 0.001$) when weight was a covariate, but not when weight was excluded ($P = 0.697$). Adult females had higher survival rates than fawns ($P < 0.001$) even though adult rates were calculated over 5.5 more months.

Vegetation biomass differed among pastures ($P < 0.001$), but differences were unrelated to fawn survival rates. Biomass estimates indicated adequate forage was available in all pastures. Tame deer in the low density pasture took more bites per 15-minute trial ($P < 0.001$), had shorter mean times between consecutive bites of Utah serviceberry (*Amelanchier utahensis*) and true mountainmahogany (*Cercocarpus montanus*) ($P \leq 0.002$), and traveled less distance during afternoon trials ($P = 0.015$) than tame deer in the high density pasture. These differences were assumed to reflect lower forage quality in the high density pasture.

For the Piceance Basin mule deer population, mortality rather than reproduction seemed the major process driving the density-dependent mechanism because the former fluctuated over a much broader range. High survival of adult females, even during severe winters, tended to temper population fluctuations that can occur in harsher environments and allowed density-dependent processes in the fawn segment to continue operating. With density-dependent population regulation, the common management strategy of decreasing harvest when fawn survival is low and increasing harvest when survival is high is counterproductive.

***WILDL. MONOGR. 121, 1–39***

## CONTENTS

---

## INTRODUCTION

The interaction of mortality causes in a population is a fundamental ecological question. An increase in 1 cause of mortality, or the introduction of a new cause, in a natural population may or may not increase the overall mortality rate depending on whether there is additivity or compensation of mortality causes. With additivity, any additional risk of death does not result in declines in other forms of mortality but, rather, adds to the overall mortality rate. With compensation, an additional risk of death results in decreased mortality due to other causes and the overall mortality rate changes either not at all or at least less than it would with additivity. For example, recreational hunting is predicated on the notion of a harvestable surplus (Connolly 1981*a*), and surplus animals not removed by hunters will die from other causes within some time-constrained period.

A rudimentary example clarifies these important concepts. Consider a hypothetical population of 90 deer on 1 October. Also assume the population is at ecological carrying capacity (ECC), which is the equilibrium between plants and animals that is attained unaided, i.e., in the absence of hunting (Caughley 1979:5). Without a hunting season, 50% of these animals succumb to natural mortality from causes such as malnutrition and predation. Thus, by the following 30 September, 45 deer would remain alive. Now consider the same population, but with a hunting season during which 33% of the population is harvested on 1 October (no natural mortality occurs during this 1-day season). Under the additive mortality hypothesis, the 60 deer remaining after the hunting season would still undergo a natural mortality rate of 50% (unchanged from the no hunting scenario), and only 30 deer would remain alive on the following 30 September. In contrast, under the compensatory mortality process, a density-dependent response (compensation) in the natural mortality rate would occur because of the decreased density due to hunting. Thus, 25% of the remaining 60 deer would die of other causes so that 45 deer would still be alive on the following 30 September. In this case, complete compensation results, but less than complete compensation could result for natural mortality rates in the interval >25–50%. However, if the mortality rate due to hunting increases beyond a threshold value (50% in this example), all mortality above the threshold must be additive because the natural mortality rate cannot decline to <0 to compensate for hunting.

The compensatory mortality hypothesis has been stated mathematically by Nichols et al. (1984) in terms of the harvest rate. The primary mechanism explaining compensatory mortality is density-dependent population regulation. Increased harvest results in lowered postharvest population size, which results in decreased natural mortality rates. Thus, compensatory mortality implies density-dependent population regulation, but the converse is not necessarily true. Density-dependent population regulation may be implemented through the reproductive process so that the death process is not affected by population density. Further, it is possible that the relationship between density and survival may be positive so that increased density results in increased survival. Such a relationship would most likely occur at low densities, as reported for moose (*Alces alces*) in Finland (Nygren 1990) and is clearly not compensatory mortality. The opposite relationship of increasing survival with decreasing density is compensatory mortality, and demonstration of this relationship in a population indicates compensatory mortality is operating in the population over the range of densities studied. Additive mortality in a population implies a density-independent mortality process is operating over the range of densities observed, but does not imply a lack of density-dependent population regulation, because higher densities may result in compensatory mortality and/or reproduction.

Compensatory mortality is most likely to occur in populations near ECC where densities and mortality rates are high. It is least likely to occur in populations far below ECC where densities and mortality rates are lower and there is less room for compensation. Environmental variation further complicates the detection of compensatory mortality, because the effect of such variation is to alter the carrying capacity of habitats. To illustrate this concept, consider the previous hypothetical example. Natural mortality was assumed to be 50% with no harvest. However, a particularly mild winter might decrease the natural mortality rate, and could conceivably lower the threshold at which hunting mortality becomes additive. For example, with no hunting, a natural mortality rate during a mild winter might be 25% instead of the 50% that would occur during a more typical winter. This means that if more than 25% of the population is harvested during a mild winter, the additional mortality has to be additive.

Errington (1945) was one of the first to propose that risks of mortality might compensate for one another when he suggested the "winter threshold effect." Basically, he studied northern bobwhite quail (*Colinus virginianus*) and muskrats (*Ondatra zibethicus*) in environments with carrying capacities delimited primarily during winter. When the fall population was thought to exceed winter carrying capacity, many animals died from predation, disease, etc., because they all could not have access to high-quality habitats. He suggested that hunting during fall merely removed animals that would die from other causes. Errington (1945) termed these animals the "doomed surplus." Hunting mortality in this conceptual model is compensated by a decline in natural mortality.

Anderson and Burnham (1976) extensively reviewed compensatory mortality in their analysis of the North American mallard (*Anas platyrhynchos*) population. Their results failed to reject the hypothesis that hunting mortality is largely compensated by decreased natural mortality when hunting mortality is below some threshold point. Nichols and Hines (1983) also failed to reject this hypothesis with an analysis of mallard band-return data that involved randomly partitioning the data into 2 independent sets. A third analysis of the degree of compensatory mortality in mallard populations was presented by Burnham et al. (1984). Here, the conclusion was that most waterfowl hunting mortality is compensated by a decrease in natural mortality. A review of compensatory mortality in waterfowl populations was given by Nichols et al. (1984).

The density-dependent nature of mortality has been reported for Himalayan thar (*Hemitragus jemlahicus*) (Caughley 1970); Soay sheep (*Ovis aries*) (Grubb 1974); African buffalo (*Syncerus caffer*) (Sinclair 1977); red deer (*Cervus elaphus*) (Staines 1978, Filinov 1983, Clutton-Brock et al. 1987); and sika deer (*C. nippon*), roe deer (*Capreolus capreolus*), and European elk (*Alces alces*) (Filonov 1983). But due to our limited understanding of the dynamics of natural populations, we have yet to segregate the impacts of man's activities from natural variability.

In his work on population dynamics of white-tailed deer (*Odocoileus virginianus*) at the George Reserve, McCullough (1979) demonstrated the existence of compensatory processes and density dependence. However, he did not attempt to separate the mortality process from the birth process because his study design only allowed measuring recruitment at 6 months of age. In addition, McCullough (1979) did not consider that changes in survival of animals >6 months of age were part of the density-dependent population regulation mechanism. His model of the George Reserve herd only included changes in the recruitment rate as a function of population density. Because much of the mortality of the George Reserve herd was due to hunting, these data cannot be used to detect compensatory mortality in the population.

Clutton-Brock et al. (1987) demonstrated a density-dependent response of decreasing calf survival with increasing hind population size in red deer (*Cervus elaphus elaphus*). His data were taken over multiple winters during a period of red deer population increase. Earlier, Staines (1978) reported density-dependent natural mortality among 10 red deer populations throughout Scotland. Filonov (1983) studied compensatory mortality functions of red deer, sika deer, roe deer, and elk on reserves in the European U.S.S.R. He concluded that when certain natural mortality factors (primarily predation) declined, others (primarily disease and starvation) replaced them. In addition, artificial regulation of ungulate populations (primarily trapping and hunting) was not functionally equivalent to natural mortality; natural mortality did not decline after artificial regulation was increased.

Other authors have concluded that human exploitation of wildlife populations may be compensated by a decline in natural mortality (*see* Anderson and Burnham 1976 and Fowler 1987 for reviews of this literature). However, only a study by Clark (1987) was based on manipulation under field conditions. Waterfowl researchers have difficulty manipulating the exploitation rate or the population density of mallards while maintaining appropriate controls so that they might observe changes in natural mortality rates. Most evidence for compensatory mortality is correlative, and cause–effect experiments to demonstrate compensatory mortality are lacking for large mammalian species. This absence of convincing experimental evidence may be the reason most managers ignore compensatory mortality when setting harvest levels for mule deer (*Odocoileus hemionus*).

Here we report on 2 field perturbations in conjunction with a controlled pasture experiment to test for compensatory mortality in the juvenile segment of a mule deer population. Our objective in each of the 3 experiments was to manipulate or stimulate manipulation of a mortality cause and measure the resulting changes in mortality rates of fawn mule deer (*O. h. hemionus*).

*Acknowledgments*.—We thank T. A. Abbott, A. W. Alldredge, J. D. Depperschmidt, D. A. Garrott, R. A. Garrott, B. T. Helmich, D. G. Saltz, and D. L. Weybright for assistance in numerous aspects of the study. B. L. Dupire, J. H. Ellenberger, R. B. Gill, V. K. Graham, J. P. Gray,

J. E. Morris, and many other Colorado Division of Wildlife (CDOW) personnel provided field assistance and logistical and administrative support. T. H. Pysto of Cathedral Bluffs Shale Oil Company facilitated access to the Federal Prototype Shale Oil Tract Cb (CB) and helped trap deer. A. H. Foster, G. P. Papez, R. L. Raley, and G. J. Rowley of the Animal and Plant Health Inspection Service, U.S. Department of Agriculture, removed coyotes (*Canis latrans*) from the CB study area. The Bureau of Land Management (BLM) facilitated road improvements and establishment of some trap sites. Shell Minerals Corporation and local ranchers allowed access to their property and establishment of several trap sites. T. E. Hakonson and K. V. Bostick provided administrative and logistical support to initiate the project. R. E. Franklin and D. H. Hamilton (deceased) steered the project through numerous bureaucratic tangles. Numerous individuals from the BLM, CDOW, Colorado State University, and Los Alamos National Laboratory helped trap deer. D. R. Anderson, D. L. Baker, T. D. I. Beck, and J. K. Ringelman reviewed early drafts of the manuscript. The in-depth reviews and constructive comments by R. G. Anthony, M. J. Conroy, and R. L. Kirkpatrick greatly improved the final product.

## STUDY AREAS

Piceance Basin in northwestern Colorado included extensive pinyon pine (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) winter range for a large migratory population of mule deer present from October through April. Climate was semiarid with warm summers and cold winters. Mean maximum temperature was 32.2 C in July and mean minimum temperature −15.6 C in January. Annual precipitation averaged 33 cm, about half occurring as snow. Snow depths of 45 cm were common on ridges and northern exposures, but there was considerable local variation due to tree cover and aspect.

Pinyon and juniper were dominant overstory species. Major shrubs included big sagebrush (*Artemisia tridentata*), Utah serviceberry (*Amelanchier utahensis*), true mountainmahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), mountain snowberry (*Symphoricarpos oreophilus*), Douglas and rubber rabbitbrushes (*Chrysothamnus viscidiflorus*, *C. nauseosus*), and Gambel oak (*Quercus gambelii*). Additional shrubs plus a variety of forbs and grasses were described by Bartmann (1983*a*).

Two study areas were located in the northern part of the basin and 1 in the southern part (Fig. 1). The Ridge and the Federal Prototype Shale Oil Tract Cb (CB) areas were previously used for studies of mule deer movements (Garrott et al. 1987) and survival (White et al. 1987); thus, pretreatment data crucial for this study were available.

### Ridge

The Ridge study area was 48 km$^2$ and included much of the north side and part of the south side of a southeast–northwest oriented ridge between the White River and Dry Fork Creek. Boundaries were based on winter movements of radio-collared does (Garrott et al. 1987) and fawns (R. M. Bartmann, Colo. Div. Wildl., unpubl. data) and were delineated only for concentration of deer trapping effort and winter census work. Land ownership was about 54% Colorado Division of Wildlife (CDOW), 39% Bureau of Land Management (BLM), and 7% private.

Elevations ranged from 1,770 to 2,170 m. Topography was steep with elevational changes of ≥350 m within 2 km typical. The drainage pattern provided aspect diversity that allowed deer to find favorable sites even during harsh winters. The study area was included within a BLM grazing allotment due to lack of fencing. Cattle were usually present during May and June and sporadically present during October and November. However, grazing was not uniform over the area because of steep terrain.

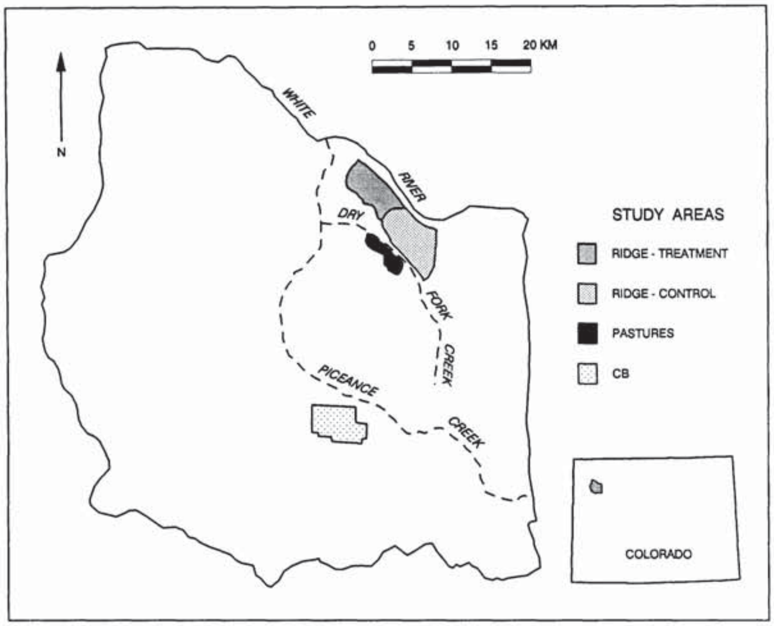


Fig. 1. Location of study areas within Piceance Basin, Colorado.

## Pastures

The Pasture study area, immediately south of the Ridge study area, included 336 ha along the south side of Dry Fork Creek (Fig. 2). Nine pastures were originally constructed during 1948–54 of 2.1-m-high fencing and ranged in size from 31 to 83 ha. They were used until 1968 for a deer and livestock competition study (McKean and Bartmann 1971). Some pastures had single species use (deer, cattle, or sheep) and others had combined use (deer and cattle or deer and sheep). From 1968 to 1977, they were vacant except for a few deer that occasionally gained entry due to lack of regular fence maintenance. From 1977 to 1980 and from 1983 to 1985, various pastures were stocked with deer at rates considered low to moderate and sometimes for only part of a winter (Bartmann and Carpenter 1982; Bartmann et al. 1982, 1986; Bartmann 1983*a*). Vegetation in all pastures was considered to be in relatively good condition at the start of this study in 1985. Like the Ridge, the pastures had a predominantly northern aspect, but terrain was less steep. Elevations ranged from 1,890 to 2,050 m.

## CB

The study area on and in proximity to the Federal Prototype Shale Oil Tract Cb (CB) was 20 km south of the Ridge and Pasture areas. Deer trapping was concentrated within a 50-km$^2$ area and coyote population reductions within a 140-km$^2$ area. Otherwise, no specific study area boundaries were defined. Elevations on the CB area ranged from 1,900 to 2,200 m. Unlike the other 2 areas, terrain was only moderately broken with gently sloping ridges. Maximum relief from gully bottoms to ridgetops was 75 m. Large blocks of pinyon–juniper woodland had been chained in the late 1960's to improve forage for livestock.

## APPROACH

We tested the hypothesis of compensatory mortality in the fawn segment of a mule deer population in 3 separate experiments. Compensatory changes in adult females were not studied (although we did estimate annual survival rates) because their mortality was not concentrated during any 1 period, causes of mortality were more varied than with fawns, and adult mortality rates were relatively low (White et al. 1987). Data were gathered on survival rates of 2 subpopulations of the Piceance deer herd from 1981 to 1988. The earlier work, 1981–85, was reported by White et al. (1987). The later work, 1985–88, involved changing, or simulating change of, 1 mortality cause in these subpopulations through experimental manipulations and evaluating the nature and degree of compensatory relations among causes of mortality.

We were not concerned in these studies with the birth process, i.e., density-dependent reproduction. Rather, our interest in all 3 experiments was understanding the degree, if any, of compensatory mortality operating within the Piceance Basin mule deer population.

A limitation of all our experiments was the lack of spatial replication. Years also cannot be considered as replications because of differences in winter severity. Instead, the strength of our experiments was in the manipulation, or simulated manipulation, of the type and extent of mortality causes and of deer densities. Nevertheless, we encourage spatial replication in experiments of this magnitude whenever possible as it broadens the scope of conclusions.

## Experimental Manipulation of Harvest

We used 2 procedures, a field experiment and a pasture experiment under controlled conditions, to test the null hypothesis that an increase in mule deer mortality by simulated hunting does not change the survival rate of the remaining fawn population. For the field experiment, hunting mortality was simulated by live trapping and removing part of the population on half of the Ridge study area (treatment unit) in November and December. Radiotelemetry was then used to estimate mortality rates of fawns on treatment and control units until the following 15 June.

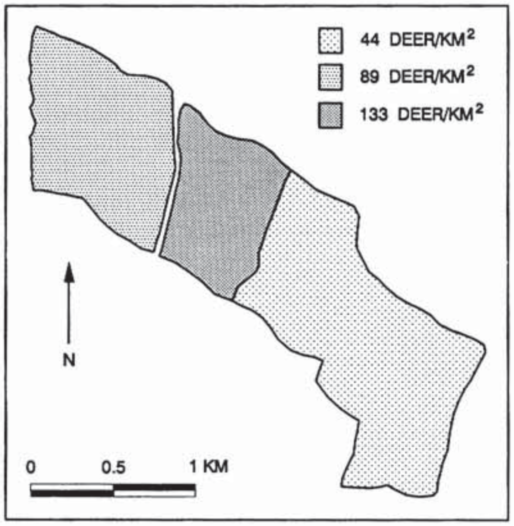


Fig. 2. Configuration of pasture treatments at the Little Hills Wildlife Area, Colorado.

The pasture experiment provided another approach with more rigid controls to test the same null hypothesis as for the Ridge area. We stocked 3 pastures in November and December at densities of 44, 89, and 133 deer/km² and estimated overwinter fawn mortality rates at each density. This situation is analogous to one where all 3 pastures were stocked to the same high density (133 deer/km²) and then a different harvest level (67, 33, and 0%) was imposed in each pasture to achieve low, medium, and high densities. If compensatory mortality operates in the population, the highest survival should occur in the low density pasture and the lowest survival should occur in the high density pasture.

## Experimental Manipulation of Predation

In another field experiment, we tested for compensatory mortality among natural mortality forces. Here, the null hypothesis was that a decreased predation rate on mule deer fawns does not affect their overall survival rate. About 57% of fawns on the CB study area during the 1981–82 through 1984–85 winters died from predation (White et al. 1987). Of these, 76% were killed by coyotes and coyotes were suspected in another 16%. We reduced predation on fawns over the next 3 years by reducing coyote numbers on and around the study area. During those same years, we monitored radio-collared fawns for changes in survival and source-specific mortality through winter and spring.

## METHODS

### Ridge

The Ridge study area was divided into 2 units along a north–south road near its midpoint. A coin flip was used to assign the east end (26.4 km$^2$) as the control unit and the west end (21.6 km$^2$) as the treatment unit. Movement data indicated little interchange between units by does (Garrott et al. 1987) or fawns (R. M. Bartmann, Colo. Div. Wildl., unpubl. data). A line transect survey was established in 1985 to estimate deer densities on both units so we could estimate deer removal rates. Twenty-five transects, systematically spaced 400-m apart from east to west across the area, were flown by 2 observers in a helicopter in December or January each winter using procedures described by White et al. (1989). One observer navigated and monitored the centerline for deer while the other monitored the area from the centerline to the right of the helicopter and estimated distances to each deer group seen.

From mid-November to mid-December 1985 and 1986, we simulated a harvest on the treatment unit by removing approximately 20% of the estimated population. Deer were captured with modified Clover traps (Clover 1956, Roper et al. 1971) without regard to sex or age. They were placed in pastures either for use in the controlled phase of the study or to hold them until spring migration when they were released. In 1987, there was no simulated harvest removal on the treatment unit, but 180 deer were removed from the entire Ridge study area to stock the pastures. We continued to monitor fawn and adult survival as reference for the other 2 studies.

Deer were captured with drop nets (Ramsey 1968, Schmidt et al. 1978) from mid-November to mid-December, 1982–87. Six to 15 trap sites/unit were used each year and were prebaited for 1–2 weeks with alfalfa hay and fermented apple pomace. Twenty-six to 34 fawns/unit were instrumented each year except 1985 and 1986 when 57–61 fawns/unit were radio collared. Male fawns were fitted with breakaway collars that dropped off after 8–12 months except in 1982 when some ear-tag transmitters were used (Garrott et al. 1985). Female fawns were fitted with expandable collars in 1982 and 1983 so they could be monitored later as adults (Garrott et al. 1987) and with breakaway collars the last 4 years. Transmitters contained a motion sensor set with a 3–4-hour delay to enable detecting mortalities. Fawns were weighed prior to release.

Radio-collared fawns were monitored from the ground for mortality 5–7 days per week beginning soon after trapping until they migrated in late April and May. Once migration started, aerial monitoring was done every 2–4 weeks until 15 June when fawns were approximately 1 year old and were considered adults. Until spring migration, two-thirds of the fawn mortalities were checked within 1–2 days of death. Time intervals were slightly longer once aerial monitoring began, but <3% of the mortalities occurred then. Cause of death was determined from the location and position of the carcass, field necropsy, and observation of tracks and other signs in the vicinity (White et al. 1987).

Survival of adult females was monitored on the Ridge to detect any large changes that might reflect conditions not associated with the removal treatment. We radio collared 21, 32, and 13 adult females in 1982, 1985, and 1986, respectively, and monitored them every year until they died or their radios quit. In 1983 and 1984, the population of radio-collared adults was supplemented with 8 and 1 female fawns, respectively, that carried expanding collars and lived to become adults at 1 year of age. After 1986, no more adults were radio collared, but survivors from previous years were monitored through the end of the study. Monitoring of adults varied from once every 1–2 weeks to once every 2–3 months. Therefore, cause of death was unknown more often than with fawns.

Weather data were collected at the Little Hills National Weather Service reporting station for the winters of 1981–82 through 1987–88. Monthly (Nov–Mar) mean snow depth (cm) on the ground and mean temperature (C) were selected for analysis because they were believed to have major influence on mortality and were available from most weather stations.

### Pastures

Division fences between some original pastures were removed to form 3 pastures of 1.69, 1.01, and 0.66 km² (Fig. 2). This enabled stocking similar numbers of deer in each pasture to achieve target densities of 44, 89, and 133/km², but precluded the random assignment of densities among pastures.

Pastures were stocked from 10 November to 6 December in 1985 and 1987 and from 10 November to 22 December in 1986. Each year, 50–51 radio-collared fawns were placed in each pasture along with 26–44 adults. In mid-December 1985, 8 fawns breached the fence from the low to the high density pasture. Pastures were stocked on a rotating basis to maintain the desired relationships among densities and to reduce possible bias due to changing deer condition over the stocking period. Resultant ratios of fawns:100 does were 1.5 to 2.5 times greater than on surrounding winter range—a necessary trade-off to implement the study. Another difference from free-ranging deer was that fawn–mother groups were often disrupted due to trapping methods and stocking patterns. This may have influenced fawn survival, but we assumed the effect was similar across pastures. In 1985, all stocked deer were from the treatment unit on the Ridge. The next 2 years, trapping conditions were poorer, and we captured some fawns in areas closer to the pastures. We weighed all fawns prior to release in the pastures and monitored them for mortality on the same schedule as fawns on the Ridge.

In 1985, we weighed adult females and marked them with numbered vinyl neckbands prior to release in the pastures. On 1 April 1986, we began trapping deer out of the pastures. We removed radio collars and neckbands and weighed animals to enable calculating weight losses of fawns and adults over the winter. By 28 April, trapping success dwindled, and pasture gates were opened to allow remaining deer to leave at will. Twelve, 6, and 1 fawns from the low, medium, and high density pastures, respectively, were still radio collared and were monitored for survival until 15 June. The next 2 years we considered it more critical to monitor fawn survival through the spring and did not trap deer out of the pastures. Instead, we opened pasture gates in mid-April when deer usually began migrating and continued monitoring fawn survival until 15 June. Gates were left open through the summer because essentially all deer migrated in the spring. They were closed again in late summer before the fall migration.

### CB

Procedures for trapping, radio collaring, and monitoring 58–66 fawns/year on the CB study area from 1981 to 1988 were similar to those described for the Ridge. An exception was the use of ear-tag transmitters on some male fawns in 1981, 1982, and 1983 (Garrott et al. 1985).

Personnel from the Animal and Plant Health Inspection Service (APHIS) were contracted to remove coyotes from 140 km² on and around the CB area for 3 years beginning in the fall of 1985. Intensity of removal efforts was similar each year with a month of trapping during September and about 20 hours of gunning from a helicopter after fresh snowfalls during November–January. A few coyotes also were shot from the ground and from a fixed-wing aircraft. We had no data on coyote densities and considered them irrelevant to the study objective. Our only concern was to remove enough coyotes to reduce predation rates on fawns.

## Vegetation Biomass Estimates

We estimated production of vegetation biomass in the pastures and on the Ridge after the third year of stocking. We were primarily interested in documenting if vegetation production was sufficient to support the densities of deer stocked. The high cost and relatively low precision of these vegetation surveys constrained us to 1 effort. The posttreatment period was chosen because we assumed that was when vegetation production, affected by heavy deer use, would be poorest.

In August 1988, the current year's growth was sampled on 500 31.1 × 62.2-cm plots/pasture. Twenty transects of 25 plots each were systematically spaced from east to west across each pasture. Plot spacing was adjusted for different transect lengths and measured by pacing. Three categories of vegetation (shrub, forb, and grass) were clipped and sacked separately. Pinyon and juniper trees were not sampled. Only current year's vegetation within the vertical plot boundaries to a height of 1.52 m was collected. Vegetation samples were oven-dried at 100 C for 24 hours and then weighed to the nearest 0.1 g.

Vegetation biomass also was estimated on the 2 Ridge units in August 1988 with a 2-stage cluster sampling technique (Scheaffer et al. 1986). The Ridge study area was gridded into 0.65-km$^2$ quadrats or clusters. Fourteen clusters were randomly selected from the 37 available on the control unit and 9 from the 28 available on the treatment unit. Five transects of 25 plots each were systematically spaced across each cluster. Otherwise, vegetation was collected and handled the same as for the pastures.

## Tame Deer Foraging Behavior

Tame deer were used to evaluate the cumulative effects of differential stocking on forage that might be reflected in deer behavior. We conducted foraging trials in the low and high density pastures in January 1989. The medium density pasture was not used because we believed it was more productive to concentrate our efforts at the 2 extreme densities where the chance of detecting differences was greatest. In mid-November 1988, the low and high density pastures were stocked with 55 and 66 wild deer, respectively, (three-fourths the original densities) to maintain browsing pressure. At the same time, 5 tame deer, 2.5 years of age, were radio collared and placed in each pasture. They had been in the pastures the previous 2 winters as part of a companion study on stress (Saltz 1988) and were familiar with the area. They each received 0.5 kg of supplemental feed during weekly visits to check their condition.

Grazing trials were conducted 3–7 January by 2 observers alternating daily between pastures. Deer in the low density pasture usually were located via radiotelemetry and observed where they were found. Deer in the high density pasture often heard us arrive and met us at the gate. Therefore, we either drove to different gates or led the deer to different starting points in the pasture. Each deer was observed for 15 minutes during early morning and again during late afternoon for 5 days. The tame deer usually fed as a group for 1.5–2 hours at a time, and the 15-minute interval improved chances that all 5 deer would feed to provide 75 minutes of observations during each daily sampling period. An assistant unrolled a tape along the deer's path during each 15-minute trial to obtain total meters traveled while the observer recorded bites of each species on a Tandy Model 102 portable computer. Each bite was entered by tapping the appropriate key, which also recorded time of each bite to the nearest second for comparison of mean bite times.

## Statistical Methods

Density of deer groups on the 2 Ridge study units was estimated from line transect data using Program TRANSECT

(Laake et al. 1979) as modified by White et al. (1989). The exponential polynomial estimator was used with observations treated as perpendicular grouped distances as recommended by White et al. (1989). Estimated density of individuals ($\hat{D}$) was calculated from the density estimate of clusters ($\hat{D}_c$) and mean cluster size ($\bar{c}$), as $\hat{D}_c \times \bar{c}$. Because observations were taken on only 1 side of the helicopter, density estimates and standard errors from program TRANSECT were multiplied by 2 to obtain appropriate values. The estimated variance ($\widehat{\text{var}}$) of density of individuals is calculated as $\bar{c}^2 \times \widehat{\text{var}}(\hat{D}_c) + \hat{D}_c^2 \times \widehat{\text{var}}(\bar{c}) - \widehat{\text{var}}(\hat{D}_c) \times \widehat{\text{var}}(\bar{c})$, where the product of variances is subtracted because estimates of variances are being used (Goodman 1960). Population size was estimated as $\hat{D} \times$ (area size), and variance was estimated as $\widehat{\text{var}}(\hat{D}) \times$ (area size)$^2$.

Survival rates of mule deer fawns were estimated for the 7-month-interval 15 November–15 June with the staggered-entry Kaplan-Meier estimator (Kaplan and Meier 1958, Pollock et al. 1989). The Kaplan-Meier estimator allows use of censored animals (those with failing radios or with collars that dropped off prematurely) to produce survival rate estimates. However, the multifactor analyses used for hypothesis testing require that fawn survival data be treated as a binomial process. Simple binomial estimates of survival (number that lived divided by number alive at the start of the interval), on the other hand, require that censored animals be eliminated from the analysis. For data with no censored observations, Kaplan-Meier (Kaplan and Meier 1958) and binomial estimators produce identical estimates.

Annual survival rates of adult female mule deer were estimated for the combined treatment and control units for the 1-year-interval 1 December–30 November. They were computed with staggered-entry Kaplan-Meier estimates (Kaplan and Meier 1958, Pollock et al. 1989) because censoring was common.

Some fawn survival and mortality data and adult survival data presented in this study differ slightly from those reported by White et al. (1987) due to re-evaluation of censoring procedures and to use of the Kaplan-Meier estimator (Kaplan and Meier 1958). Also, the fate of several animals was updated based on information received subsequent to publication of White et al. (1987). None of these changes, however, affect conclusions in the earlier report.

The staggered-entry Kaplan-Meier estimator (Kaplan and Meier 1958, Pollock et al. 1989) also was used to generate survival functions for fawns in the pasture study. Pair-wise comparisons of survival functions were made with the log-rank tests described by Pollock et al. (1989).

Fawn survival rates were tested with categorical data analysis methods (Grizzle et al. 1969, Cox 1970) using PROC CATMOD (SAS Institute, Inc. 1987) using data from uncensored animals. This procedure is equivalent to conducting Chi-square tests of independence with 2 or more factors. Thus, we predicted survival as a function of 1 or more independent factors such as control and treatment units on the Ridge, pasture density, and/or year. In PROC CATMOD (SAS Institute, Inc. 1987), survival estimates from categorical data were transformed using the logistic transformation $\log_e[\hat{S}/(1 - \hat{S})]$, so results were equivalent to logistic regression. Tests of individual survival rates against the average survival rate were conducted with the CONTRAST statement.

Fawn survival was predicted with a logistic regression equation that included fawn weight at trapping as a continuous variable, and gender, year, and area (CB and Ridge) as categorical variables, plus all 2- and 3-way interactions of gender, year, and area using PROC CATMOD (SAS Institute, Inc. 1987). The maximum likelihood estimates were used to test significance of each of these terms. The same procedure was used with the pasture data with pastures substituted for area.

Fate of fawns in pastures also was tested with PROC CATMOD (SAS Institute, Inc. 1987). The Chi-square statistic was partitioned into lived versus died, starvation versus all other mortality causes, and predation versus remaining mortality causes.

Fate of fawns as a function of coyote removal on the CB study area was tested with a logistic model using Program SURVIV (White 1983). Mean responses for the 3 years prior to coyote removals (1982–84) were tested against the 3 years during removals (1985–88) with data from the Ridge study area included to improve estimates of the year effect. The 1981 data were not used because there was no comparable data for the Ridge. They were used, however, in a confirmatory analysis using only CB data to compare mean responses for the 4 years prior to coyote removals and those for the 3 years during removals.

We used stepwise logistic regression (SAS Institute, Inc. 1990) to predict fawn survival for the CB (7 yrs of data) and Ridge (6 yrs of data) study areas from 10 weather variables (monthly mean snow depths [cm] and mean temperatures [C] for Nov–Mar) along with a dummy variable for study area. The value for entry and removal of variables from the model was $P = 0.05$. As emphasized by Bartmann and Bowden (1984), spurious correlations are possible with only 6 or 7 years of data and 11 independent variables, and our results should be thought of as describing characteristics of this data set only.

Fawn weights for each year, area (CB and Ridge), and gender combination were standardized by subtracting the mean weight and dividing by the standard deviation. The standardized fawn weights from the 7 years, 2 areas, and 2 sexes were combined and tested for goodness of fit to a normal distribution with the Shapiro-Wilk statistic (Shapiro and Wilk 1965) of PROC UNIVARIATE (SAS Institute, Inc. 1985). Fawn weights were compared between the CB and Ridge study areas, gender, and years with a fixed-effects ANOVA model using the Type III sums of squares of PROC GLM (SAS Institute, Inc. 1987). Multiple range tests to determine which years differed were performed with the Waller-Duncan *K*-ratio *T* test (Waller and Duncan 1969).

Fawn weights from the Ridge study area and from a similar area that included the Ridge during the 1950's were compared with an ANOVA model that included the factors for gender, decade, and year within decade. Years were treated as nested effects within decade using PROC GLM (SAS Institute, Inc. 1987). Because of the unbalanced design, the Satterthwaite approximation (Satterthwaite 1946) was used with the RANDOM statement of PROC GLM to perform the test of equal means between decades. Only weight data for Clover-trapped fawns were used as this method most closely approximated that with the box traps used in the 1950's.

Weights of fawns and adults placed in the pastures, weights of fawns and adults released from the pastures at the end of the 1985–86 winter, and weights of dead fawns in the pastures were tested with linear models using PROC GLM (SAS Institute, Inc. 1987). Independent variables included in these tests were gender, weight at the start of winter, pasture, and year.

We used fawn survival on the CB and Ridge study areas in lieu of weather data as an index of winter severity to test for a carry-over effect on fawn weight the following fall. Fawn survival was used as a covariate with gender as a main effect to predict next year's fawn weight. This analysis used the Type III sums of squares from PROC GLM (SAS Institute, Inc. 1987).

Vegetation biomass estimates for each pasture were computed from the mean and variance of the 500 31.1 × 62.2-cm plots clipped in each pasture. A multivariate ANOVA (dependent variables of shrub, forb, and grass biomass) was used to test the differences among pastures, with the mean square error (MSE) of plots within pastures used as the denominator of the *F* test. For the 2 Ridge study units, a stratified cluster sample estimator (Scheaffer et al. 1986:236) was used to compute means and variances. A multivariate nested ANOVA (dependent variables of shrub, forb, and grass biomass) was used to test for differences among the 3 pastures and between the 2 Ridge units. Independent variables were area, clusters within areas, and plots within clusters. The denominator of the *F* test was the MSE of clusters within areas. An equivalent univariate ANOVA was used to test for differences in total biomass among the 3 pastures and 2 Ridge

Table 1. Mule deer densities on the control (26.4 $km^2$) and treatment (21.6 $km^2$) units of the Ridge study area estimated from aerial line transects, and deer removals from the treatment unit in Piceance Basin, Colorado, 1985–87.

| Month and year flown | Control unit | | Treatment unit | | | |
|---|---|---|---|---|---|---|
| | Density estimate (deer/$km^2$) | SE | Density estimate (deer/$km^2$) | SE | Deer removed No. | Deer removed %[a] |
| Dec 1985 | 78.4 | 9.4 | 60.6 | 17.8 | 361 | 22 |
| Jan 1987 | 67.7 | 23.1 | 79.7 | 12.2 | 323 | 16 |
| Dec 1987 | 72.0 | 19.2 | 62.8 | 22.5 | [b] | |

[a] Percent of deer removed is based on the population estimate plus the number removed because removals occurred before line transect surveys.

[b] In 1987, 80 and 100 deer were removed from the control and treatment units, respectively, for stocking the pastures.

units. These tests were performed with PROC GLM (SAS Institute, Inc. 1987). All 3 pastures and the 2 units of the Ridge study area were compared with a multivariate nested ANOVA similar to that used to test for differences between the 2 units of the Ridge study area. Each pasture was treated as a single cluster with 500 plots. Again, the denominator of the *F* test was the MSE of clusters within areas. Whenever significant differences were found, Tukey's studentized range test was used to identify which areas differed.

Species composition of tame deer diets was estimated as the mean of percent compositions of the 15-minute trials. Differences in species composition of diets between high and low density pastures were tested with a general linear model using PROC GLM (SAS Institute, Inc. 1987). Variables included to predict bite composition were pasture, deer within pastures, date, and time of day. A mixed-effects model was used, with the pasture effect tested by the deer within pastures sums of squares.

Mean times between consecutive bites of a species were tested with a nested ANOVA model that included the independent variables pasture (high or low), period (morning or afternoon), and deer within pastures. The 2-way interactions also were included in the analysis performed with PROC GLM (SAS Institute, Inc. 1987). Only times <60 seconds were used in the analysis to exclude larger intervals of interrupted feeding or moving to new plants. A $\log_e$ transformation was used to stabilize the variance and reduce skewness of the data.

Mean number of bites per trial and mean distance traveled per trial by each deer were tested with a fixed-effects ANOVA that included the independent variables pasture (high or low), date (days 1 to 5), and period (morning or afternoon), plus all 2-way and 3-way interactions. A $\log_e$ transformation was applied to distances traveled to stabilize the variance and reduce skewness of the data.

## RESULTS

### Deer Density Estimates—Ridge

Estimated deer densities on the Ridge study area from 1985 to 1987 were fairly uniform indicating the population was stable during the study (Table 1). The 3-year-average density on the control unit (72.7 deer/$km^2$) was 5.0 deer/$km^2$ higher than on the treatment unit. Based on density estimates, 22 and 16% of the deer on the

Table 2. Survival rate estimates ($\hat{S}$) for radio-collared mule deer fawns on control and treatment units of the Ridge study area before and during deer removals from the treatment unit in Piceance Basin, Colorado, from time of collaring in November and December until the following 15 June 1982–83 through 1987–88.

| Winter | Deer removed (%) | Control unit | | | Treatment unit | | |
|---|---|---|---|---|---|---|---|
| | | $n$ | $\hat{S}$ | SE($\hat{S}$) | $n$ | $\hat{S}$ | SE($\hat{S}$) |
| 1982–83 | | 29 | 0.321 | 0.088 | 31 | 0.387 | 0.087 |
| 1983–84 | | 28 | 0.071 | 0.049 | 32 | 0.033 | 0.033 |
| 1984–85 | | 34 | 0.196 | 0.078 | 26 | 0.431 | 0.105 |
| 1985–86 | 22 | 59 | 0.537 | 0.070 | 58 | 0.439 | 0.070 |
| 1986–87 | 16 | 60 | 0.431 | 0.064 | 58 | 0.471 | 0.067 |
| 1987–88 | | 32 | 0.241 | 0.077 | 28 | 0.107 | 0.058 |

Table 3. Cause of mortality for radio-collared mule deer fawns on control and treatment units of the Ridge study area in Piceance Basin, Colorado, from time of collaring in November and December until the following 15 June 1982–83 through 1987–88. Percentages are of total uncensored[a] fawns.

| | | | | Mortality cause | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Starvation | | Predation | | Other | |
| Unit | Winter | No. of radio-collared fawns | Censored | No. | % | No. | % | No. | % |
| Control | 1982–83 | 28 | 1 | 15 | 56 | 4 | 15 | | |
| | 1983–84 | 28 | | 22 | 79 | 4 | 14 | | |
| | 1984–85 | 34 | 7 | 16 | 59 | 5 | 19 | 1 | 4 |
| | 1985–86 | 59 | 11 | 10 | 21 | 7 | 15 | 7 | 15 |
| | 1986–87 | 60 | 6 | 14 | 26 | 17 | 31 | 3 | 6 |
| | 1987–88 | 32 | 2 | 22 | 73 | | | 2 | 7 |
| Treatment | 1982–83 | 31 | 1 | 15 | 50 | 2 | 7 | 2 | 7 |
| | 1983–84 | 32 | 1 | 27 | 87 | 3 | 10 | | |
| | 1984–85 | 26 | 4 | 8 | 36 | 2 | 9 | 3 | 14 |
| | 1985–86 | 58 | 9 | 17 | 35 | 11 | 22 | 1 | 2 |
| | 1986–87 | 58 | 5 | 16 | 30 | 13 | 25 | 1 | 2 |
| | 1987–88 | 28 | | 19 | 68 | 1 | 4 | 5 | 18 |

[a] Uncensored fawns are those with nonfailing radios or with collars that did not drop off prematurely.

treatment unit of the Ridge study area were removed by trapping in 1985 and 1986, respectively. The lower percentage the second year resulted primarily from a 31% increase in the estimated population on the treatment unit. This may be a sampling artifact as suggested by similarity of estimates for that unit in 1985 and 1987, and by the smaller fluctuation in estimates on the control unit over the 3 years.

## Survival Rate Estimates

*Ridge.*—We did not detect a difference in fawn survival between the treatment and control units for the 3 pretreatment years on the Ridge study area ($P = 0.696$) (Table 2). Removing 22 and 16% of the deer from the treatment unit in 1985 and 1986, respectively, produced no detectable change in fawn survival compared to the control unit ($P = 0.566$). Our inability to detect the expected increase in survival under the compensatory mortality hypothesis prompted cessation of deer removals for this study in 1987 because we logistically could not reduce the population much below the level of the 2 previous years. Also, even if a change in survival was found the third year, the effect over all 3 years would still have been nonsignificant.

Table 4. Annual (1 Dec–30 Nov) survival rate estimates ($\hat{S}$) of radio-collared adult female mule deer on the Ridge study area in Piceance Basin, Colorado, 1982–83 through 1987–88.

| Winter | No. radio-collared adults | $\hat{S}$ | SE($\hat{S}$) |
|---|---|---|---|
| 1982–83 | 21 | 0.848 | 0.071 |
| 1983–84 | 30 | 0.856 | 0.067 |
| 1984–85 | 19 | 1.000 | |
| 1985–86 | 46 | 0.909 | 0.043 |
| 1986–87 | 45 | 0.760 | 0.067 |
| 1987–88 | 24 | 0.875 | 0.083 |

Based on combined data for the 2 study units, annual differences in fawn survival ($P < 0.001$) tended to reflect winter conditions. Survival was lower than average during the severe winter of 1983–84 ($P < 0.001$) and higher than average during the milder 1985–86 and 1986–87 winters ($P \leq 0.001$). But fawn survival was poor even during milder winters. The highest survival rate for both units based on a weighted average was only 0.488 (SE = 0.049) in 1985–86. The highest rate for an individual unit was 0.537 on the control that same winter (Table 2).

Causes of fawn mortality did not differ between control and treatment units among years ($P = 0.405$). High levels of starvation and low levels of predation occurred on both units except in 1985–86 and 1986–87 when rates for the 2 causes were

Table 5. Number of mule deer stocked in 3 pastures in Piceance Basin, Colorado, during winters 1985–86 through 1987–88.

| Target density (deer/km$^2$) | Pasture area (km$^2$) | 1985–86 | | | 1986–87 | | | 1987–88 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Fawn | Adult | True[a] density | Fawn | Adult | True density | Fawn | Adult | True[a] density |
| 44 | 1.69 | 43 | 26 | 44 | 46 | 27 | 43 | 51 | 29 | 49 |
| 89 | 1.01 | 50 | 40 | 91 | 49 | 42 | 90 | 51 | 44 | 96 |
| 133 | 0.66 | 59 | 37 | 147 | 51 | 40 | 138 | 50 | 41 | 139 |

[a] True density in 1985–86 and 1987–88 includes 1–6 deer already in some pastures when stocking began.

more comparable (Table 3). Causes of mortality on both units also displayed annual variation ($P < 0.001$) mainly because starvation increased dramatically relative to predation during harsher winters.

In contrast to fawns, adult female survival on the Ridge study area varied relatively little among years ($P = 0.396$) with a range from 0.760 to 1.0 (Table 4). Even during the severe winter of 1983–84, when fawn survival dropped to 0.051 (SE = 0.029), adult female survival was near the 6-year weighted average of 0.862 (SE = 0.025).

*Pastures.*—From 1985 through 1987, the 3 pastures were stocked to within 1–11% of target densities (Table 5). Significant differences in fawn survival were found among densities ($P < 0.001$) and years ($P = 0.005$), but not for the density times year interaction ($P = 0.922$) (Table 6). However, this model included density as a linear, continuous variable and fit the data poorly ($P = 0.023$). Therefore, a fully-specified model with levels of density treated as discrete factors that fit the data was used. This model explained survival as a significant effect of density ($P < 0.001$), year ($P < 0.001$), and their interaction ($P = 0.046$).

Fawn survival was inversely related to density all 3 winters (Fig. 3). The relationship was slightly weaker in 1987–88 ($P = 0.014$) compared to the previous 2 winters ($P < 0.001$). We believe adverse snow conditions that winter accelerated the onset of zero survival in the high density pasture and forced mortality to nearly identical high rates in the other 2 pastures.

Starvation increased in all pastures each year ($P < 0.001$) and was largely responsible for the average 0.255 and 0.228 decreases in survival rates between the first and second and the second and third winters, respectively (Table 7). Differences in starvation across pastures within any 1 year, however, were smaller ($P = 0.133$) (Fig. 3). Starvation was the major cause of fawn mortality in the high density pasture the first year, whereas predation by bobcats (*Felis rufus*) took a higher toll in the low and medium density pastures (Fig. 3). The same levels of predation again occurred in all pastures in 1986–87, but total mortality rates increased due to higher starvation losses. There was only 1 predator kill in 1987–88 and starvation losses in all pastures continued to rise. Consequently, predation differed among years ($P < 0.001$), but was independent of density ($P = 0.367$).

Daily fawn survival rates, plotted as survival functions, were higher through most of the winter and spring in the low density pasture than in the medium and high density pastures (Fig. 4). In 1985–86, fawn survival was comparable in all pastures during the first 3.5 months after stocking.

Table 6. Survival rate estimates ($\hat{S}$) for radio-collared mule deer fawns stocked at 3 densities in pastures in Piceance Basin, Colorado, from the time of collaring in November and December until the following 15 June 1985–86 through 1987–88.

| Target density (deer/km$^2$) | Winter | No. radio-collared fawns | $\hat{S}$ | SE($\hat{S}$) |
|---|---|---|---|---|
| 44 | 1985–86 | 43 | 0.814 | 0.059 |
| | 1986–87 | 46 | 0.455 | 0.073 |
| | 1987–88 | 51 | 0.102 | 0.043 |
| 89 | 1985–86 | 50 | 0.480 | 0.071 |
| | 1986–87 | 49 | 0.353 | 0.070 |
| | 1987–88 | 51 | 0.108 | 0.045 |
| 133 | 1985–86 | 59 | 0.424 | 0.064 |
| | 1986–87 | 51 | 0.104 | 0.044 |
| | 1987–88 | 50 | 0.000 | |

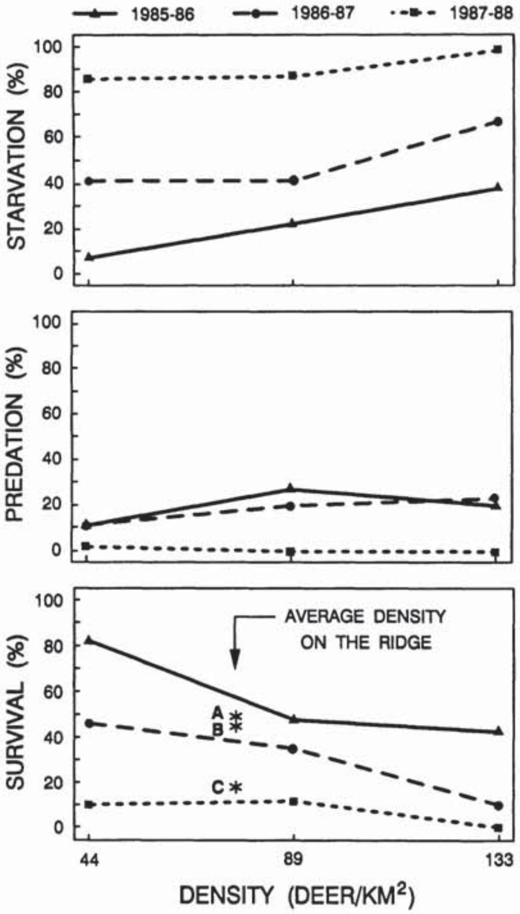


Fig. 3. Relationship of mule deer density to survival, predation, and starvation rates of radio-collared mule deer fawns stocked in pastures during winters 1985–86 through 1987–88. Survival demonstrates a compensatory (density-dependent) effect, starvation a weak compensatory effect, and predation a noncompensatory (density-independent) effect. Average fawn survival rates on the Ridge study area for 1985–86 (A), 1986–87 (B), and 1987–88 (C) are shown for comparison.

Afterwards, no fawns from the low density pasture died whereas survival continued to decline in the other 2 pastures. As a result, the survival function for the low density pasture was significantly higher than those for the medium and high density pastures ($P \leq 0.002$), but functions did not differ between the medium and high density pastures ($P = 0.730$). In 1986–87 and 1987–88, survival functions in the high density pasture were lower than those in the low and medium density pastures ($P \leq 0.004$), but functions were not different between the low and medium density pastures ($P \geq 0.142$). In 1986–87, survival functions began to diverge after approximately 50 days when mortality accelerated in the high density pasture. In 1987–88, the harsher winter caused closer alignment of all functions.

Trends in fawn survival rates would suggest that total deer use of vegetation, based on deer-days per km$^2$, should have decreased in all pastures over the 3-year period (we assumed zero adult mortality). The largest reduction should have occurred in the high density pasture where fawns died at higher rates. If true, then by the end of the study, the effects on vegetation would have been considerably less than indicated by the differences in stocking densities. Such, however, was not the case. Total deer-days per km$^2$ did decrease 26% in the high density pasture between the first and second winters, but use was similar the last 2 winters (Fig. 5). In the other 2 pastures, there were only token decreases in deer-days use between the first and third winters. We suspect that differences in timing of pasture stocking each year were sufficient to offset most reductions in deer-days use due to increased mortality.

*CB*.—We removed 93, 78, and 47 coyotes from 140 km$^2$ on and around the CB study area in 1985–86, 1986–87, and 1987–88, respectively. The number of trap nights per coyote captured changed from 54 to 116 to 96 and the number of helicopter flight hours per coyote killed increased from 0.5 to 0.6 to 0.9 over the same respective years. Therefore, we assumed the local coyote population was decreasing. During trapping in September, the juvenile : adult ratio of coyotes that were aged ($n = 93$) was 1.8:1. With aerial gunning in winter, this ratio was reversed, 0.5:1, in favor of adults ($n = 50$). Cost of coyote removal increased each year from $49 to $116 to $139/coyote.

Coyote removals significantly changed the fate of radio-collared fawns on the CB study area ($P = 0.008$). Predation rates on radio-collared fawns declined from an average 0.596 in the 3 years before coyote

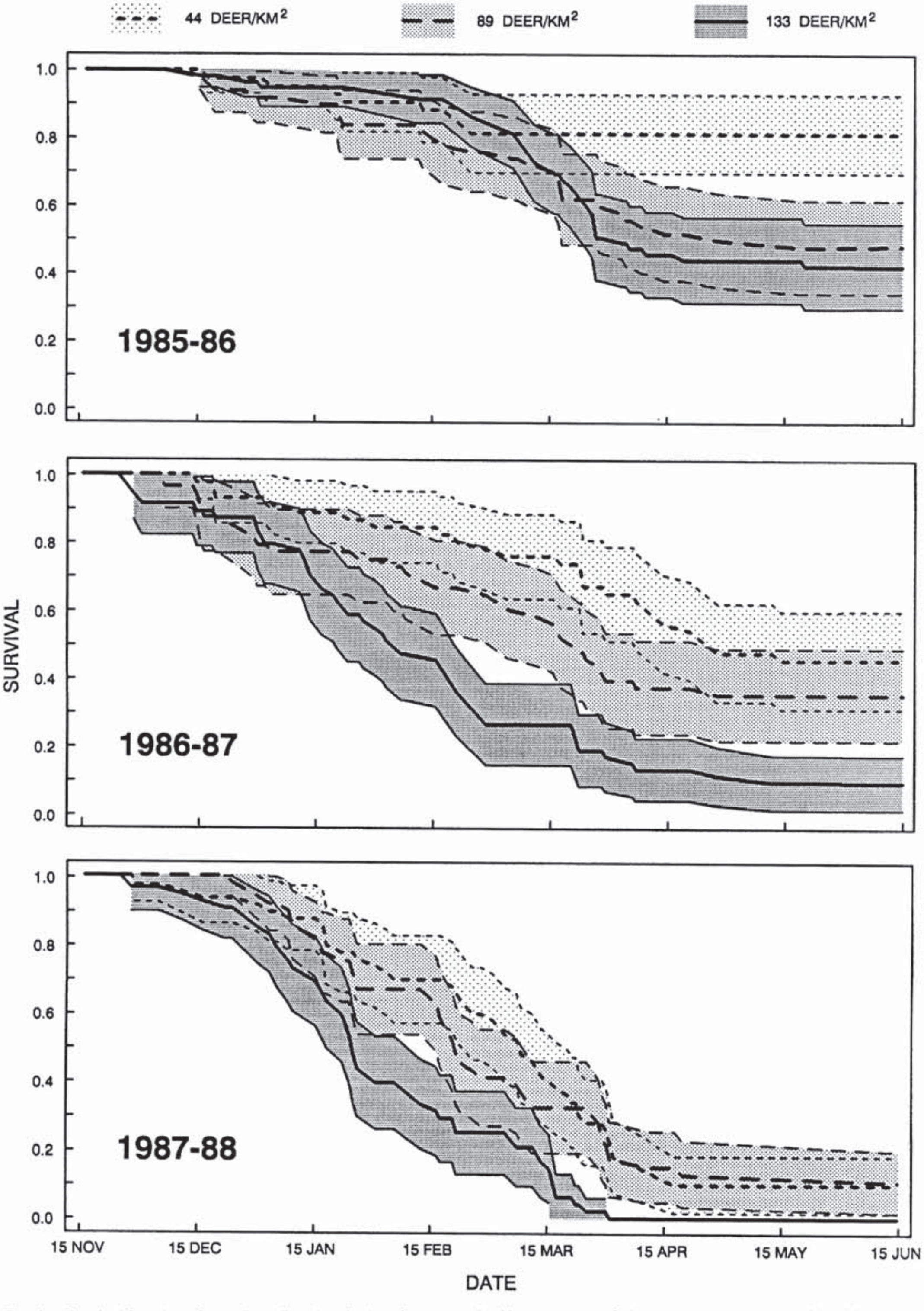


Fig. 4. Survival functions for radio-collared mule deer fawns stocked in pastures at 3 densities during winters 1985–86 through 1987–88. Shaded areas about each function are 95% confidence intervals.

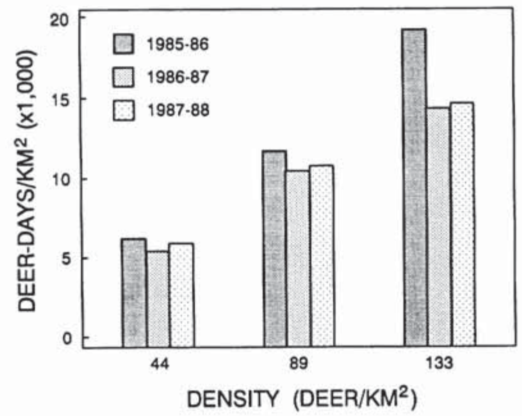


Fig. 5. Total deer-days per km² in 3 pastures stocked with mule deer at different densities during winters 1985–86 through 1987–88.

removals to 0.424 in the 3 years during removals ($P = 0.004$) (Table 8). During the same respective periods, the average starvation rate increased from 0.187 to 0.232 ($P = 0.042$), while the increase in the average fawn survival from 0.173 to 0.246 was not significant ($P = 0.842$) (Table 9). Without the Ridge data included to improve estimates of year effects, the predation rate decreased by 0.159 ($P = 0.002$), whereas we could detect no significant change in starvation ($P = 0.432$) or survival rates ($P = 0.134$).

Many deer moved off the CB area during midwinter (Garrott et al. 1987). Terrain was mostly north aspect and, when snow became deeper and crusted, deer moved up to 15 km to more favorable sites. During the first 3 years, nearly all predation occurred while deer were on the CB area during fall and early winter and when they returned again in spring (Table 10). Once off the area, fawns appeared relatively safe. However, in 1984–85, predation on the CB area was about the same as for previous years, but additional predation off the area contributed another 25% to the annual mortality rate and inflated the 4-year mean rate 6 percentage points. However, if we consider only the CB area, fawn mortality from predation still declined each of the 3 years during removals, and annual predation rates were the lowest for the 7 years of study.

## Differential Mortality by Sex and Age

Female fawns had higher survival rates than males on the CB and Ridge areas ($P < 0.001$) when area, year, and fawn weight were included in the model. Much of the effect came from 1 year (1982), although the sex effect was still significant with that year deleted ($P = 0.022$). With the same model, we did not detect a greater probability of males that died succumbing to starvation ($P = 0.301$) or predation ($P = 0.975$). When fawn weight was excluded, survival rates did not significantly differ between sexes ($P = 0.697$).

In the pastures, neither the probability of survival ($P = 0.974$), starvation ($P = 0.974$), nor predation ($P = 0.975$) differed

Table 7. Cause of mortality for radio-collared mule deer fawns stocked at 3 densities in pastures in Piceance Basin, Colorado, from the time of collaring in November and December until the following 15 June 1985–86 through 1987–88. Percentages are of total uncensored[a] fawns.

| Target density (deer/km²) | Winter | No. of radio-collared fawns | Censored | Mortality cause | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Starvation | | Predation | | Other | |
| | | | | No. | % | No. | % | No. | % |
| 44 | 1985–86 | 43 | 1 | 3 | 7 | 5 | 12 | | |
| | 1986–87 | 46 | | 19 | 41 | 5 | 11 | 1 | 2 |
| | 1987–88 | 51 | 1 | 43 | 86 | 1 | 2 | 1 | 2 |
| 89 | 1985–86 | 50 | | 11 | 22 | 13 | 26 | 2 | 4 |
| | 1986–87 | 49 | 3 | 19 | 41 | 9 | 20 | 2 | 4 |
| | 1987–88 | 51 | 4 | 41 | 87 | | | 1 | 2 |
| 133 | 1985–86 | 59 | | 23 | 39 | 11 | 19 | | |
| | 1986–87 | 51 | | 34 | 67 | 11 | 22 | 1 | 2 |
| | 1987–88 | 50 | 1 | 48 | 98 | | | 1 | 2 |

[a] Uncensored fawns are those with nonfailing radios or with collars that did not drop off prematurely.

Table 8. Cause of mortality for radio-collared mule deer fawns on the CB study area in Piceance Basin, Colorado, from the time of collaring in November and December until the following 15 June 1981–82 through 1987–88. Percentages are of total uncensored[a] fawns.

| Winter | No. of radio-collared fawns | Censored | Mortality cause: Starvation No. | Starvation % | Predation No. | Predation % | Other No. | Other % |
|---|---|---|---|---|---|---|---|---|
| 1981–82 | 66 | 20 | 1 | 2 | 25 | 54 | 5 | 11 |
| 1982–83 | 61 | 4 | 4 | 7 | 28 | 49 | 6 | 11 |
| 1983–84 | 60 | 3 | 23 | 40 | 30 | 53 | 2 | 4 |
| 1984–85 | 60 | 3 | 5 | 9 | 44 | 77 | 3 | 5 |
| 1985–86 | 60 | 2 | 11 | 19 | 29 | 50 | 3 | 5 |
| 1986–87 | 58 | 4 | 5 | 9 | 23 | 43 | 8 | 15 |
| 1987–88 | 61 | 3 | 24 | 41 | 20 | 34 | 8 | 14 |

[a] Uncensored fawns are those with nonfailing radios or with collars that did not drop off prematurely.

between sexes. Results were similar with weight included in the model and with data excluded for 1987 when mortality at all 3 densities was ≥89%.

Adult females had consistently higher survival rates ($P < 0.001$) than fawns. The highest overwinter fawn survival on any area excluding the pastures (0.537) was only two-thirds of the lowest annual adult survival (0.760). Adult survival rates would be even higher if computed over the same 7-month period as for fawns as only three-fourths of adult mortalities occurred then.

## Predicting Fawn Survival from Weather Data

All but 1 of the weather variables (Nov snow, $P = 0.399$) were significant predictors of fawn survival ($P < 0.001$) on the Ridge and CB study areas. When data were excluded for the 1981–82 and 1982–83 winters because of missing November and December temperatures (resulting in a total of 10 observations for the 2 areas), the model selected with stepwise regression included February snow ($P < 0.001$), area ($P = 0.001$), and November temperature ($P = 0.001$). None of the remaining variables was significant ($P \geq 0.356$). When November and December temperature variables were excluded to allow using all 13 observations, the model selected with stepwise regression included February snow ($P < 0.001$), area ($P = 0.005$), and January temperature ($P = 0.044$). None of the remaining variables was significant ($P \geq 0.295$).

## Deer Weights

*Ridge and CB.*—Fawns on the CB study area were heavier than those on the Ridge ($P < 0.001$) with males and females av-

Table 9. Survival rate estimates ($\hat{S}$) for radio-collared mule deer fawns before and during coyote removals on the CB study area in Piceance Basin, Colorado, from time of collaring in November until the following 15 June 1981–82 through 1987–88.

| Winter | Coyotes removed | No. of radio-collared fawns | $\hat{S}$ | SE($\hat{S}$) |
|---|---|---|---|---|
| 1981–82 | No | 66 | 0.484 | 0.067 |
| 1982–83 | No | 61 | 0.368 | 0.063 |
| 1983–84 | No | 60 | 0.055 | 0.031 |
| 1984–85 | No | 60 | 0.092 | 0.039 |
| 1985–86 | Yes | 60 | 0.271 | 0.058 |
| 1986–87 | Yes | 58 | 0.355 | 0.065 |
| 1987–88 | Yes | 61 | 0.119 | 0.042 |

Table 10. Percent of radio-collared mule deer fawns dying from predation, before and during coyote removals, on and off the CB study area in Piceance Basin, Colorado, during winters 1981–82 through 1987–88.

| Year | No. of coyotes removed | No. of radio-collared fawns | Predation (%): On CB area | Off CB area |
|---|---|---|---|---|
| 1981–82 |  | 46 | 52 | 2 |
| 1982–83 |  | 57 | 44 | 5 |
| 1983–84 |  | 57 | 44 | 9 |
| 1984–85 |  | 57 | 53 | 25 |
| 1985–86 | 93 | 58 | 40 | 10 |
| 1986–87 | 78 | 54 | 35 | 7 |
| 1987–88 | 47 | 58 | 24 | 10 |

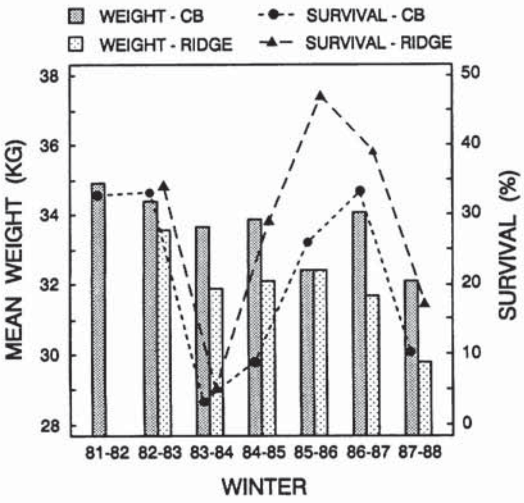


Fig. 6. Mean weight loss and survival of radio-collared mule deer fawns on the Ridge and CB study areas during winters 1981–82 through 1987–88.

eraging 1.8 and 1.3 kg more, respectively, than their counterparts ($P < 0.001$) (Table 11). Also, males were heavier than females ($P < 0.001$) by 3.0 and 2.4 kg on the CB and Ridge, respectively. Mean fawn weights also differed among years on the Ridge and CB areas ($P < 0.001$) supporting the general downward trend displayed over time (Fig. 6). None of the 2- or 3-way interactions of the variables area, gender, or year was significant ($P \geq 0.111$).

Fawn weights showed significant spatial variation among trap sites on the Ridge ($P = 0.019$) and CB ($P = 0.045$) study areas with year and gender included in the model. This indicates significant spatial heterogeneity of weights within the population, although examination of the data revealed no logical spatial pattern. In 1 instance, a significant difference occurred between 2 trap sites 1.2 km apart, and, in several other cases, some of the larger weight differences occurred between nearest-neighbor trap sites.

Hobbs (1989:16) assumed energy reserves of individuals in a population are normally distributed, suggesting weights also might be normally distributed. This assumption is critical to predicting survival in his model. We could not reject the hypothesis that fawn weights were normally distributed ($P = 0.429$).

*Pastures.*—We detected no differences in the weights of fawns stocked in different pastures within years ($P = 0.817$). This was expected because fawns were assigned to pastures on a predetermined rotating schedule. Significant differences in fawn weights between years ($P = 0.003$) and sexes ($P < 0.001$) generally are consistent with results from the Ridge study area. However, fawns stocked in pastures in 1985 averaged 2 kg less than fawns released on the Ridge ($P = 0.003$) even though all were captured on the same area. That year fawns stocked in pastures were caught with Clover traps and fawns released on the Ridge were caught with drop nets. During the next 2 years when fawns stocked in pastures also were captured in other areas, Clover-trapped fawns still averaged about 2 kg less than drop-netted fawns ($P < 0.001$).

Spring weights of fawns that survived the 1985–86 winter were not significantly

Table 11. Mean weights (kg) of mule deer fawns trapped on the Ridge and CB study areas in Piceance Basin, Colorado, during November–December 1981–87.

| | Ridge | | | | | | CB | | | | | | Combined |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Males | | | Females | | | Males | | | Females | | | |
| Year | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $\bar{x}$ |
| 1981 | | | | | | | 35 | 36.6 | 0.62 | 31 | 33.0 | 0.58 | 34.9A[a] |
| 1982 | 36 | 34.3 | 0.70 | 23 | 32.7 | 0.61 | 26 | 37.8 | 0.95 | 35 | 32.0 | 0.60 | 34.0A |
| 1983 | 34 | 32.9 | 0.59 | 26 | 30.9 | 0.76 | 30 | 34.9 | 0.58 | 30 | 32.4 | 0.76 | 32.8B |
| 1984 | 27 | 33.6 | 0.97 | 33 | 31.2 | 0.76 | 30 | 35.2 | 0.64 | 30 | 32.5 | 0.52 | 33.0B |
| 1985 | 66 | 33.5 | 0.51 | 54 | 31.2 | 0.58 | 34 | 33.2 | 0.78 | 26 | 31.6 | 0.49 | 32.5B |
| 1986 | 55 | 33.2 | 0.55 | 66 | 30.6 | 0.45 | 28 | 35.2 | 0.55 | 32 | 33.1 | 0.69 | 32.6B |
| 1987 | 34 | 31.5 | 0.70 | 27 | 28.2 | 0.81 | 34 | 33.2 | 0.73 | 27 | 30.9 | 0.74 | 31.1C |

[a] $\bar{x}$'s for combined sexes followed by the same letter do not differ significantly ($P > 0.05$) by Waller-Duncan $K$-ratio $T$ test.

different among pastures ($P = 0.366$) even with weight at time of stocking included as a significant covariate ($P < 0.001$). The 2-way interaction between initial weight and pasture also was not significant ($P = 0.601$).

The average weight loss of all fawns that survived the 1985–86 winter was 16% (SE = 0.88) (Fig. 7). In contrast, fawns that starved lost an average 27% (SE = 1.53), 28% (SE = 0.91), and 29% (SE = 0.69) of their initial stocking weight in 1985–86, 1986–87, and 1987–88, respectively. Consequently, weights of dead fawns were not different among pastures ($P = 0.450$) and years ($P = 0.533$). Weight at time of stocking was a significant covariate ($P < 0.001$), but none of the 2- or 3-way interactions was significant ($P \geq 0.113$).

Weights of adult deer at time of stocking in 1985 were not significantly different among pastures ($P = 0.248$) and neither were weights the following spring of adults that survived ($P = 0.584$). Mean weights across all pastures at time of stocking were as follows: males, 75.7 kg (SE = 16.6, $n = 2$); females, 62.5 kg (SE = 0.796, $n = 96$). Weight at stocking was a significant covariate in predicting spring weight ($P < 0.001$), but the 2-way interaction of stocking weight times pasture was not significant ($P = 0.366$). Average weight loss of surviving adults across all pastures was 19% (SE = 0.97) (Fig. 7). A weight-loss differential between the low and high density pastures was recorded during the 1987–88 winter with tame yearling deer. Six deer in the low density pasture lost significantly ($P = 0.003$) less weight (25%) than 7 deer in the high density pasture (31%) (Saltz 1988).

*Relation of Fawn Weights to Survival.*—Weight of fawns at time of collaring was a significant predictor of their fate ($P < 0.001$) on the Ridge and CB areas. The variables area, year, and gender, and their 2- and 3-way interactions were all included in the model. When this test was partitioned, survived versus not survived was the main contributor ($P < 0.001$) with larger fawns having higher survival. For fawns that died, starved versus not starved was not significant ($P = 0.237$).

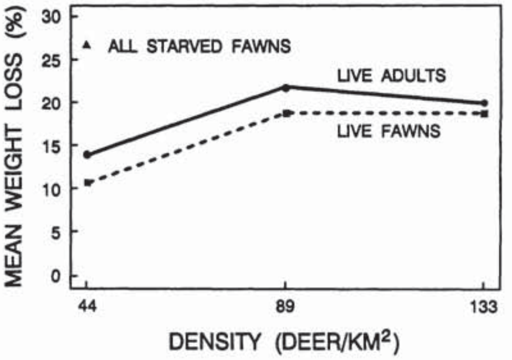


Fig. 7. Overwinter weight losses of adult female and fawn mule deer stocked in 3 pastures at different densities during winter 1985–86.

Deer were caught with box traps on the Ridge and adjacent areas during the 1950's and many were weighed (Gilbert et al. 1955; Shepherd and Gilbert 1956; Smith 1957, 1958, 1959, 1960). We reasoned that if fawns were larger in the 1950's, their survival also may have been higher, which could reflect better range conditions. However, such speculation was unfounded as fawns in the 1950's ($n = 104$) (Table 12) averaged only 1.3 kg heavier ($P = 0.239$) than Clover-trapped fawns ($n = 316$) in this study.

Weight of fawns at time of stocking in the pastures showed the same pattern as on the Ridge and CB areas; weight was a significant predictor of fate ($P < 0.001$) and larger fawns had higher survival ($P < 0.001$). The variables pasture, year, and gender were included in the analysis and, with partitioning, we still could not show weight as a significant predictor ($P = 0.578$) of whether or not a fawn starved, given that it died.

*Relation of Previous Year's Fawn Survival to Mean Weight.*—Sex-specific fawn survival was used as an index of winter severity to test for a possible effect on development of fawns produced the following summer. We could not show a relationship between previous year's fawn survival and the next year's (Nov–Dec) fawn weight ($P = 0.125$). However, the data for CB males in 1981 appeared to be an outlier (Fig. 8). There were a large number of censored males that year, so we removed all 1981 data and repeated the

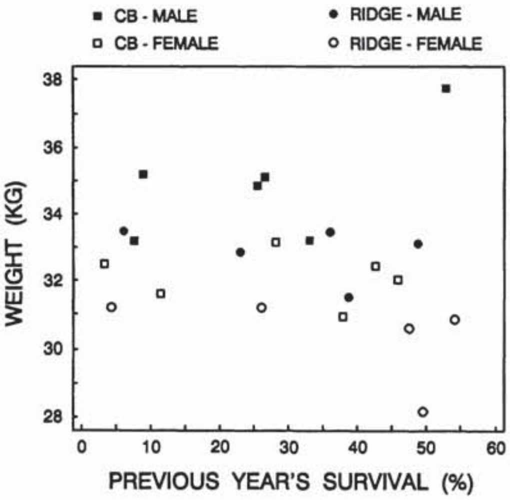


Fig. 8. Relationship of previous year's survival of radio-collared mule deer fawns to mean fawn weight (Nov–Dec) on the Ridge and CB study areas, 1981–88.

analysis. Previous year's fawn survival ($P = 0.002$) and gender ($P = 0.001$) were then significant, but the relationship was still weak ($r = -0.298$) and the 2-way interaction was not significant ($P = 0.819$).

## Vegetation Biomass Estimates

Total vegetation biomass was greater in the low and high density pastures than in the medium density pasture ($P < 0.001$) (Table 13). Shrub production, which composed 57–61% of the total vegetation, almost differed significantly among pastures ($P \geq 0.066$). Forb and grass production were different ($P \leq 0.008$) with less of both in the medium density pasture than in the high density pasture. On the Ridge, there was more total vegetation ($P = 0.045$) and more grass ($P = 0.011$) on the control unit, but we found no difference between units for shrubs and forbs ($P \geq 0.126$).

When the 3 pastures and 2 Ridge units were analyzed together, no differences in biomass were detected ($P = 0.409$). The apparent discrepancy with the above results is explained by the increased within-cluster variability when pastures were combined with Ridge clusters because differences among the 5 areas were tested by the MSE of clusters within areas, not the MSE of plots within areas.

## Tame Deer Foraging Behavior

Shrubs and trees dominated tame deer diets in the low and high density pastures with forbs and grass each contributing only 2% (Table 14). Species composition of diets differed with more Utah serviceberry and Utah juniper eaten in the high density pasture ($P \leq 0.036$) and more antelope bitterbrush eaten in the low density pasture ($P < 0.001$). All 3 species are common winter foods (Bartmann 1983*a*) and, when taken together, their percentages in both diets were nearly the same.

Tame deer in the low density pasture took 70% more bites/15-minute trial ($\bar{x} = 247$) than deer in the high density pasture ($\bar{x} = 145$) ($P < 0.001$). This difference was largely a result of the shorter mean times between consecutive bites of Utah serviceberry ($P = 0.002$) and true mountain-mahogany ($P = 0.001$) in the former pasture (Table 15). There also were differences in the mean number of bites per trial between days ($P < 0.001$), the 2-way inter-

Table 12. Mean weights (kg) of mule deer fawns trapped on and in proximity to the Ridge study area in Piceance Basin, Colorado, during November and December 1954–59.[a]

| | Males | | | Females | | | Combined | | |
|---|---|---|---|---|---|---|---|---|---|
| Year | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE | $n$ | $\bar{x}$ | SE |
| 1954 | 7 | 36.1 | 1.50 | 14 | 31.5 | 0.99 | 21 | 33.0 | 0.94 |
| 1955 | 12 | 33.0 | 1.64 | 10 | 29.6 | 0.81 | 22 | 31.5 | 1.02 |
| 1956 | 25 | 31.3 | 1.30 | 11 | 24.9 | 1.09 | 36 | 29.4 | 1.08 |
| 1957 | 3 | 24.8 | 4.11 | 1 | 29.0 | | 4 | 25.9 | 3.09 |
| 1958 | 9 | 35.8 | 0.96 | 6 | 32.0 | 1.98 | 15 | 34.3 | 1.06 |
| 1959 | 6 | 31.8 | 1.67 | | | | 6 | 31.8 | 1.67 |

[a] Data from Gilbert et al. 1955, Shepherd and Gilbert 1956, and Smith 1957, 1958, 1959, and 1960.

Table 13. Mean biomass (kg/ha) of shrubs, forbs, and grasses estimated on 31.1 × 62.2-cm plots in 3 pastures and on 2 Ridge study units in Piceance Basin, Colorado, August 1988.

| Area | No. of plots | Shrubs | | Forbs | | Grasses | | Total | |
|---|---|---|---|---|---|---|---|---|---|
| | | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE |
| Pasture | | | | | | | | | |
| Low density | 500 | 322A[a] | 24.0 | 53A | 5.5 | 192A | 14.3 | 567A | 28.6 |
| Medium density | 500 | 249A | 23.3 | 29B | 3.3 | 131B | 10.4 | 408B | 26.5 |
| High density | 500 | 314A | 25.4 | 40AB | 7.1 | 157AB | 13.1 | 511A | 29.3 |
| Ridge | | | | | | | | | |
| Control unit | 1,750 | 337A | 92.3 | 52A | 21.8 | 189A | 66.5 | 578A | 123.7 |
| Treatment unit | 1,125 | 253A | 119.8 | 43A | 14.6 | 107A | 34.1 | 404B | 132.8 |

[a] $\bar{x}$'s within each forage category followed by the same letter do not differ significantly ($P > 0.05$) by Tukey's studentized range test.

action between date and time of day ($P = 0.002$), and the 3-way interaction between date, time of day, and pasture ($P = 0.041$).

Mean distances traveled by tame deer during 15-minute feeding trials were not different between pastures, day of trial, and time of day ($P \geq 0.273$). However, deer in the low density pasture traveled less distance than their counterparts in the high density pasture during afternoon trials ($P = 0.015$).

## DISCUSSION

The strongest evidence of a compensatory mortality response in mule deer fawns was from the pasture experiment where simulated posthunt (late fall) deer densities were set by stocking. Overall mortality rates and survival functions reflected the density-dependent nature of the mortality process. The environmental noise attributed to differences between winters was not confounded with the density-dependent response, which, without spatial and temporal controls, is often obscured by year-to-year variation in winters.

The estimated deer density on the Ridge study area was fairly constant among years, varying only 6% between 1985 and 1987, and was close to that in the medium density pasture (Fig. 3). Annual fawn survival rates on the Ridge and in the medium density pasture also were similar with the largest difference, 0.098, occurring the second year. Thus, declining survival rates in all pastures seemed more a function of winter conditions than forage depletion and could partly explain our failure to detect many

Table 14. Percentages of forage species in diets of 5 tame mule deer in the low (12,347 bites) and high density (7,271 bites) pastures in Piceance Basin, Colorado, during January 1989.

| Species | Low density | | High density | | P[a] |
|---|---|---|---|---|---|
| | $\bar{x}$ | SE | $\bar{x}$ | SE | |
| Shrubs and trees | | | | | |
| Utah serviceberry (*Amelanchier utahensis*) | 16.2 | 2.76 | 41.3 | 4.33 | 0.003 |
| Big sagebrush (*Artemisia tridentata*) | 14.4 | 3.75 | 9.1 | 2.73 | 0.215 |
| True mountainmahogany (*Cercocarpus montanus*) | 17.2 | 4.32 | 18.3 | 5.46 | 0.789 |
| Rubber rabbitbrush (*Chrysothamnus nauseosus*) | 5.9 | 2.26 | 3.6 | 1.91 | 0.248 |
| Utah juniper (*Juniperus osteosperma*) | 0.1 | 0.14 | 5.4 | 2.51 | 0.036 |
| Pinyon pine (*Pinus edulis*) | 6.5 | 2.60 | 9.8 | 3.65 | 0.539 |
| Antelope bitterbrush (*Purshia tridentata*) | 32.4 | 5.06 | 4.6 | 2.32 | <0.001 |
| Mountain snowberry (*Symphoricarpos oreophilus*) | 2.2 | 2.00 | 3.8 | 2.63 | 0.490 |
| All shrubs and trees | 96.5 | 1.73 | 96.2 | 1.71 | 0.918 |
| Forbs | 1.7 | 0.87 | 0.3 | 2.27 | 0.170 |
| Grasses | 1.8 | 0.96 | 3.5 | 2.08 | 0.478 |

[a] Probability that $\bar{x}$ proportions were similar between densities.

Table 15. Mean times (sec) between consecutive bites of browse species that averaged ≥5% of diets of 5 tame mule deer in low and high density pastures in Piceance Basin, Colorado, during January 1989.

| | High density | | | Low density | | | |
|---|---|---|---|---|---|---|---|
| Species | No. of bites | $\bar{x}$ time between bites | SE | No. of bites | $\bar{x}$ time between bites | SE | $P$[a] |
| Utah serviceberry (*Amelanchier utahensis*) | 2,693 | 4.74 | 0.102 | 1,748 | 3.07 | 0.085 | 0.002 |
| True mountainmahogany (*Cercocarpus montanus*) | 1,199 | 5.31 | 0.164 | 2,161 | 2.96 | 0.076 | 0.001 |
| Pinyon pine (*Pinus edulis*) | 513 | 8.52 | 0.392 | 505 | 4.09 | 0.235 | 0.455 |
| Big sagebrush (*Artemisia tridentata*) | 1,028 | 2.11 | 0.115 | 1,586 | 2.13 | 0.082 | 0.955 |
| Antelope bitterbrush (*Purshia tridentata*) | 456 | 2.52 | 0.128 | 5,110 | 2.05 | 0.037 | 0.721 |

[a] Probability that $\bar{x}$ times between bites were similar between densities.

meaningful differences in vegetation and tame deer responses.

We attributed our lack of success in demonstrating compensatory mortality in a free-ranging population on the Ridge to not being able to remove enough animals. Another contributing factor may have been our concern with total numbers removed rather than age composition. Presumably, there were still too many adults and they successfully competed with fawns for food, particularly food of nutritionally higher quality.

The compensatory response among mortality factors found on the CB study area corroborates the pasture results even though primary mortality causes differed. Predation was the main mortality cause on CB and was a significant part of the compensatory process with starvation being a minor component. This situation was reverse of that in the pastures where starvation was most important. However, the contribution of predation to the overall compensatory process in the pastures is supported by the stronger relationship between mortality and density when predation was included with starvation.

## Survival Estimates from Telemetry Compared to Banding

White and Bartmann (1983) estimated the survival rates of mule deer for the White River population in Colorado, a superset of the population studied here. In that study, animals were neckbanded over the entire winter, and survival intervals are not entirely comparable to those presented here. Still, White and Bartmann (1983) estimated a mean fawn survival rate for the period 1972–76 of 0.29 (SE = 0.02), which is comparable to the weighted means of estimates for the Ridge (0.309, SE = 0.022) and CB (0.207, SE = 0.021) study areas in Tables 2 and 9. Their mean survival estimate for adult does was 0.67 (SE = 0.09). Although considerably below the weighted average of annual survival rates (0.862, SE = 0.025) for the Ridge in Table 4, confidence intervals overlapped. White et al. (1987) indicated 2 of the 4 winters reported by White and Bartmann (1983) were considered severe compared to only 1 in their study. However, adult survival during that 1 winter was near average suggesting weather was of minor consequence. A greater influence on survival may have been liberal doe harvests during 2 of the 4 years in the 1970's study compared to the token harvests during the 1980's study. Also, precision of annual survival estimates obtained from banding data was lower than for radiotelemetry because recovery rates were <20%.

## Survival Versus Density Functions—Pastures

The logistic functions for fawn survival ($\hat{S}$) in the pastures were calculated as a function of density for each year along with the average across years (Fig. 9). Equations ($a + bx$) describing these curves are

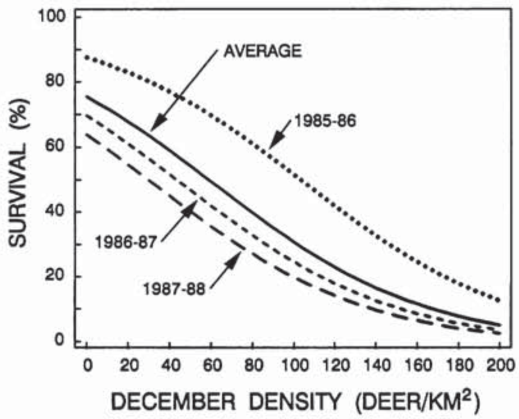


Fig. 9. Mule deer fawn survival predicted with a logistic regression fitted to observed survival of radio-collared fawns from the pasture experiment.

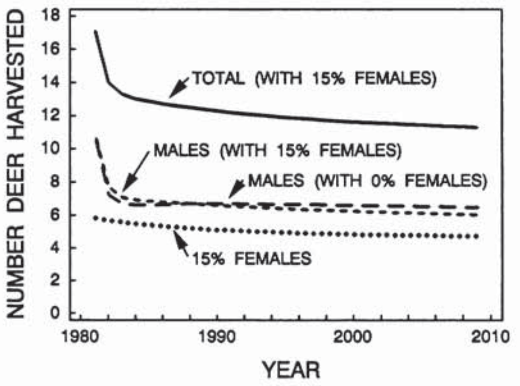


Fig. 10. Predicted adult male and total harvest for a mule deer population with unrestricted adult male harvest and with 0 and 15% of adult females harvested annually.

$$\log_e[\hat{S}/(1-\hat{S})] = \begin{cases} 2.0591 - 0.0195\ (\text{Dec density}) \\ \quad \text{for 1985–86,} \\ 0.8900 - 0.0195\ (\text{Dec density}) \\ \quad \text{for 1986–87,} \\ 0.6226 - 0.0195\ (\text{Dec density}) \\ \quad \text{for 1987–88, and} \\ 1.1906 - 0.0195\ (\text{Dec density}) \\ \quad \text{for the 3-year } \bar{x}. \end{cases}$$

These functions relate the overwinter survival of fawns to deer density and clearly demonstrate the compensation in survival ($P < 0.001$) that takes place with decreasing density or, implicitly, increased harvest. A horizontal line would be expected in Figure 9 under additive mortality.

The relationships shown in Figure 9 are the strongest evidence published to date to demonstrate compensatory mortality in an ungulate population. They are based on a manipulative experiment and, thus, a cause-and-effect relationship is documented. Clutton-Brock et al. (1987) also presented a logistic regression analysis of overwinter survival of red deer calves with a significant negative relationship of survival to population size. However, their results were based on correlative data and, hence, do not carry as strong an inference as the relationship shown in Figure 9.

The average function in Figure 9 was used in a simple population model constructed with Lotus 1-2-3® (available from G. C. White) to demonstrate the effect of compensatory mortality in fawns as a function of adult female harvest (Fig. 10). At first, there was no adult female harvest, and annual survival was set to 0.86, the weighted average survival from Table 4. Annual nonhunting survival of adult males was set at 0.95 because we assumed 80% of this age–sex class was harvested annually. The preharvest fawn : doe ratio was set at 70:100 with a fawn sex ratio of 50:50.

For comparison, we assumed a 15% harvest of adult females and little natural mortality, i.e., natural nonhunting survival was increased to 0.95. This survival rate assumes compensation in the natural mortality rate in response to the 15% harvest. In addition, we assumed 1 fawn was harvested for every 9 adult females harvested. Although the total population declined from an approximate equilibrium size of 83 to 51, nearly the same number of adult males was harvested when adult females also were harvested. Total harvest also was much higher indicating more thorough utilization of the resource.

These results are conservative because only overwinter fawn survival and adult female survival were increased. Other factors that also may improve with decreasing density (e.g., fecundity rates and fawn survival immediately postpartum) were not incorporated in the simulation. Hence, the true response in production of males should be higher than predicted, and we would expect a higher male harvest than shown in Figure 10.

An important result of this study, incorporated into the above model, is that decreasing fawn survival suggests increasing deer density and, hence, density-dependent population regulation. High fawn survival, therefore, is indicative of a population far below ECC, whereas low fawn survival is an indication of a population closer to ECC. Deer managers commonly recommend reduced harvests when survival of young is considered poor and increased harvests when survival of young is considered good (cf. Connolly 1981*b*:335). An appropriate harvest recommendation for a particular deer population, of course, will depend on the management objective and the population size relative to that objective. However, if density-dependent processes are operating, the former strategy will result in a population closer to ECC and the latter a population farther below ECC.

## Compensatory Effects of Predation

The role of predation in regulating ungulate populations is not clear. Connolly (1978:384–388) cited 45 references that tended to support the hypothesis of population regulation by predators (i.e., mortality from predation was additive) and another 27 that suggested no regulation (i.e., mortality from predation was compensatory). However, he also conceded that documentation varied substantially among reports.

Indications from the literature are that predation can run nearly the full gamut from additive to compensatory depending on the species of predator and prey and their densities, habitat conditions, and other factors such as man's influence. In general, compensatory effects are most likely to occur when prey populations are near ECC because higher mortality rates allow more latitude for compensation. In our study on CB Tract, we had no data on deer population size or habitat conditions. Rather, we assumed the population had reached winter range carrying capacity based on population estimate data for the past 15 years in Piceance Basin (Bartmann 1983*b*) and the conservative (antlered only) harvests that prevailed for much of the same period. Given this, and that mean survival rates were <50% even during milder winters, we would conclude there was a high level of compensation among mortality factors. Intuitively, however, we should not dismiss the effects of weather. Relatively deep snow in 1987–88, during the period of coyote removals, enhanced the difference between predation and starvation rates. But a much more severe winter occurred in 1983–84 during the preremoval period. If we exclude both years, mean fawn survival rates for the 2 periods increase slightly, but the difference is nearly the same as before and, thus, still supports the above conclusion.

Predation played a compensatory role in the mortality of mule deer fawns on the CB study area, but we cannot extrapolate much beyond that conclusion. Along with the lack of deer census data for that specific area, we also had no information on coyote densities, although APHIS field personnel believed they were high. Thus, what the results might have been with different combinations of deer and coyote densities remains unknown as does the response of predation had we, instead, manipulated other mortality causes.

## Compensatory Mortality Versus Density-dependent Reproduction

Density-dependent population regulation is divided between the reproductive and mortality processes. Reproduction is frequently considered the more important component of density dependence and, consequently, is often the only aspect measured. For example, density dependence in the George Reserve white-tailed deer population (McCullough 1979) was mostly attributed to the reproductive process. White-tailed deer show more variability in reproduction than mule deer, because fawns are capable of having fawns and adults are more prone to have triplets when forage conditions are good. Therefore, McCullough's (1979) analysis may be appropriate for that herd.

The rate of population growth is equally sensitive to reproduction and to survival of young of the year. For example, if the reproductive rate is reduced by half, the rate of population growth also is reduced by half. The same is true for survival of young of the year. Therefore, the relative effect of each of these processes on population growth is governed by the magnitude of variation in each of them. On this basis, mortality appears to be the dominant process of density dependence operating in the Piceance Basin mule deer herd. We propose this hypothesis based on comparisons of annual variation in fawn survival and reproductive rates.

Annual estimates of survival reflect 2 sources of variance: sampling variation and year-to-year variation. In our study, sampling variation is determined by the number of radio-collared deer used to produce the survival estimate. Year-to-year variation is the variation in the true annual survival rate among years. Years with harsh winters cause low fawn survival whereas mild winters allow higher survival. Likewise, reproductive rates also exhibit sampling and year-to-year variation. To evaluate relative variation of the 2 processes, we must remove sampling variation and only compare the year-to-year variation.

We computed the annual variance in overwinter fawn survival from the combined data for the CB and Ridge study areas using the procedures described by Burnham et al. (1987:260–266). These procedures remove sampling variation from the sample variance computed from 7 annual estimates of survival. The weighted average of survival across all years, using the estimator of Burnham et al. (1987), was 0.248 with the variance component due to year-to-year variation in survival estimated as 0.017 (95% CI 0.006–0.087). These values give a coefficient of variation (CV) for year-to-year variation of 53%.

There were no reproductive data for the same time interval as survival data. Such data were available for an earlier period and support the hypothesis that reproduction in the Piceance herd does not vary as much as overwinter fawn mortality. Fetus : doe ratios were obtained during 1971–74 and 1978 from road kills and trapping mortalities in the Piceance Basin (R. M. Bartmann, unpubl. data). Mean numbers of fetuses per doe for these years were 1.47, 1.38, 1.50, 1.50, and 1.51 for samples of size 19, 21, 64, 6, and 45, respectively. The year-to-year variation was estimated as zero (upper 95% confidence bound 0.004) giving a CV of 0%. To corroborate this variation, we used fetus : doe ratios sampled in Middle Park, approximately 160 km east of Piceance Basin, during the period 1969–72 (R. B. Gill, Colo. Div. Wildl., unpubl. data). Deer were collected at random. Mean numbers of fetuses per doe were 1.97, 1.62, 1.70, and 1.94 for samples of size 32, 34, 33, and 31, respectively. The year-to-year variation was estimated as 0.020 (95% CI 0.001–0.408) with a CV for year-to-year variation of 7.7%—only 15% of the year-to-year variation in overwinter fawn survival.

Another indication of lower variation in reproduction comes from December age ratios. Estimated ratios of fawns:100 does were 77.7, 75.5, 78.8, 70.2, 72.5, and 63.5 for 1981–86 based on ≥726 deer/year ($\bar{x}$ = 1,066) classified from a helicopter on randomly selected quadrats (Colo. Div. Wildl., unpubl. data). The ratio estimates were converted to the proportion of fawns to fawns plus does to provide estimates on the same scale as survival estimates (range 0–1). The weighted mean was 0.421, with the variance component for year-to-year variation of 0.0001 (95% CI 0–0.002). The CV was 2.7%, suggesting relatively small annual variation compared to the 53% CV estimated for overwinter survival rate of fawns. Conservatively, the CV of the year-to-year variation in mortality was >15 times that of year-to-year variation in December recruitment.

It can be argued that age ratios also contain June–November mortality rates that we did not measure. However, the low variability in fetus:doe ratios and fawn: doe ratios indicates little variation in mortality of fawns to 1 December when our survival rate estimates start.

These results support our hypothesis that the Piceance Basin mule deer population exhibits less year-to-year variation in reproductive rates than in fawn mortality rates. Consequently, we contend that the Piceance population is regulated more by density-dependent mortality than density-dependent reproduction. Other deer populations may perform similarly, but this result is not commonly demonstrated because of difficulties in measuring mortality rates. We would expect reproduction and first-year mortality rates to be correlated in most deer populations so that paradigms such as McCullough's (1979) model of reproductive rates as a function of density, based on only 1 side of the density-dependent mechanism, would correlate to observed densities as well as when mortality also is included in the analysis.

## Differential Mortality by Sex and Age

An unbalanced sex ratio favoring females in adult mule and black-tailed deer is expected in hunted populations, but also was reported for an unhunted one (Hines 1975). The disparity in sex ratios is caused by differential mortality sometime between birth and adulthood (Connolly 1981*b*:306), but the timing is not easily identified and can vary among areas and years. Available information for the Piceance mule deer population indicates most of this divergence probably does not occur until after deer reach 1 year of age on approximately 15 June.

A sample of 236 fetuses, collected mainly from road-killed does during 5 years in the 1970's, implied an even sex ratio at birth (49.6% males, $P = 0.896$) (R. M. Bartmann, unpubl. data). The lack of sex-differential mortality from birth to 5–6 months of age is indicated by the even sex ratios of trapped fawns. Although trapping data can yield biased ratios (Garrott and White 1982), we believe the effect was minimal in our study. Fawns captured with drop nets were usually part of a family group, i.e., accompanied by a doe. With Clover trapping, intensity of effort was great and fawns were removed from the area, which allowed subdominant ones to ultimately be captured. Consequently, sex ratios produced by the 2 methods were not different ($P = 0.840$) and did not differ from unity (drop nets—$n = 1{,}421$, 51.6% males, $P = 0.233$; Clover traps—$n = 314$, 50.6% males, $P = 0.821$). Sex ratios of fawns also did not differ between the Ridge and CB areas ($P = 0.357$) or among years ($P = 0.573$), and we contend, therefore, that fawn sex ratios were even going into winter.

The lack of strong sex-differential mortality from 15 November to 15 June is supported by the small difference in overwinter mortality rates for males (0.773) and females (0.707) ($P = 0.036$). In the multifactor analysis, sex-differential mortality was significant when weight was included ($P < 0.001$) along with year and area, but was not significant when weight was removed ($P = 0.697$) but with year and area still included. Thus, we are hesitant to draw conclusions from our results because of the variation contributed by year and area effects. In addition, the sex ratio of 191 fawn carcasses, found during mortality surveys conducted during spring 1973–79 in Piceance Basin (Bartmann 1984), did not differ from unity (47.6% males, $P = 0.515$).

Trainer et al. (1981) used radiotelemetry to monitor mule deer fawn mortality from shortly after birth through the first winter of life. Male and female mortality was similar from June through December (males 60%; females 58%). From January through March, higher male mortality was recorded (46 vs. 32%), but the difference was nonsignificant.

There was a substantial difference in mortality rates between fawn and adult females. This is consistent with the review by Ralls et al. (1980) of mammalian mortality patterns, the discussion by Clutton-Brock et al. (1982:278–279), and the discussion of Connolly (1981*b*:302–306). However, we could not demonstrate a

U-shaped female mortality curve mainly because we were unable to accurately age captured females ≥2 years old. Also, we could not monitor animals marked at 0–1 year of age beyond 9 years of age, when an increase in mortality may occur at the right side of the U-shaped curve.

Connolly (1981*b*:305–306) reviewed sex-differential mortality in mule and black-tailed deer populations and found that the few studies addressing the question supported differential mortality in the first or second year of life. Our results, as well as Trainer et al. (1981), suggest only a small difference in male and female mortality during the first year of life.

## Survival and Weather

Bartmann and Bowden (1984) found snow depth during early winter (Nov–Dec) was most associated with deer winter mortality, with no particular period of mean temperature as good a predictor. Our data revealed that February snow depth was the best predictor of survival. This seeming contradiction, however, is confounded by methodological differences between the 2 studies. Bartmann and Bowden (1984) used estimates of population size and winter mortality from quadrat surveys to calculate percent winter mortality for combined deer age and sex classes. In this study, we used radiotelemetry to directly estimate fawn survival rates. We excluded data for adult females because their survival rates were relatively high and displayed little response to different winter conditions. Without corroborating data, it is difficult to rationalize the seeming contradiction in the above results. More likely, this dilemma serves to highlight the futility of trying to explain highly complex and variable relationships with relatively few observations—years in this case.

## Survival and Weight

We found differences in fawn weights in many comparisons: CB versus Ridge areas, males versus females, among trap sites within areas, among years, and between fawns stocked in the pastures and those released on the Ridge even though trapped in the same area. This latter difference suggests a trap bias with Clover traps selecting for smaller fawns than drop nets, but treatment of animals also must be considered. Clover traps usually were checked only once daily, so fawns could have been in traps for up to 24 hours with limited food and water (the small amount of bait and snow in traps was usually churned by the animal's movements). They also were subjected to additional stress by being placed in a carrying crate and hauled in a pick-up truck for up to several hours before being weighed. Drop-netted fawns, on the other hand, usually had been feeding on abundant bait and often were weighed within 5–10 minutes of capture.

Differences in fawn weights usually coincided poorly with observed differences in survival. CB fawns were heavier than Ridge fawns but had, on average, lower survival ($P < 0.001$). Males were heavier than females, but they also showed overall lower survival ($P < 0.001$). In contrast, logistic regressions demonstrated weight was positively correlated with survival, and White et al. (1987) demonstrated a significant positive relationship between time survived and fawn weight. In this study, fawn survival fluctuated much more than weight on both areas and, as a result, positive correlations between them were weak (Ridge—$r = 0.473$, $P = 0.343$; CB—$r = 0.442$, $P = 0.321$). Presumably, the effects of winter severity and other factors were strong enough to mask potential relationships.

We suspect fawn weights were influenced by variables we did not measure and that localized selection pressures further obscured this picture. Shields (1982) argued genetic heterozygosity is maintained at an intermediate level via opposing processes. Local selection pressure tends to minimize heterozygosity, whereas environmental changes through time tend to select for heterozygosity. The mechanisms suggested by Shields (1982) also would apply to phenotypic variation such as fawn weights. Differences among trap sites argue for local selection pressure, whereas wide variation in annual survival argues for temporal changes in the selection process.

Feldhamer et al. (1989) found that the previous fall's acorn crop was related to the current fall weight of fawn and yearling white-tailed deer in Tennessee. Verme (1962) reported the main effect of winter and spring nutrition levels on Michigan whitetails was on fawn survival immediately postpartum. Birth weights also were affected, but these disparities were nearly erased after 1 month (Verme 1963). Hence, the subtle relationship between early-winter fawn weights and the previous year's survival in our study may reflect a tempering effect of summer range conditions. Alternatively, searching for correlatives among variables not directly manipulated in a study can lead to spurious and unexplainable relationships.

## Vegetation and Tame Deer Foraging Behavior

We assume that differences in vegetation biomass among pastures were pre-existing rather than a consequence of deer use in this study. For example, it seems unreasonable that deer use directly affected forb and grass production. Both forages were senescent and covered by snow during much of the winter, and new growth was available only for a brief period during spring before the deer migrated. Furthermore, estimated biomass of all forage classes on the Ridge, where there was spring–fall cattle grazing in addition to deer use, was not significantly different from that in the pastures.

From a quantitative aspect, biomass estimates indicate there was 2.4 times the amount of forage required by deer in the high density pasture had they all survived for 150 days. This approximation is based on daily dry matter intakes of 1.0 and 1.2 kg for fawns and adults, respectively (Alldredge et al. 1974). It does not take into account unpalatable and unavailable forage, but neither does it consider pinyon and juniper forage that was not estimated but composed 15% of tame deer diets in that pasture in early January, nor the use of new growth in the spring. Therefore, we assume there was adequate forage produced in all pastures.

We contend that fawn mortality was more responsive to forage quality limitations. Hobbs and Swift (1985) found forage quantity and quality to be integrated when estimating carrying capacity, with tradeoffs between animal numbers and condition. For example, there is only a limited amount of high quality forage that will maintain a certain number of animals in good condition. As more animals share this limited forage, their condition decreases until a point is reached where mortality begins to occur. Fawns succumb first because they enter the winter with lower energy reserves (Torbit et al. 1988) and deplete them faster than adults (Parker and Robbins 1984).

Other data serve to underscore a major role for forage quality in fawn mortality. Nutritional-based estimates of carrying capacity were made in 1979 on 26 km$^2$ of winter range immediately southwest of the pastures (Carpenter et al. 1980). Deer distribution (Bartmann and Steinert 1981) and pellet-group surveys (Freddy 1978, 1979) indicated this area, like the Ridge, supported a high winter density of deer. Vegetation sampling was with clipped plots as described in this study. Separate estimates of carrying capacity were based on supplies of metabolizable energy and nitrogen. The energy-based estimate (27 deer/km$^2$), about half that of the nitrogen-based estimate (51 deer/km$^2$), was most limiting and considered the best estimate of the true carrying capacity. The pasture data align better with the lower estimate because, even at the lowest density (44 deer/km$^2$), fawn mortality increased each year, although (as we suggested earlier) winter severity also may have been a factor.

In a companion study to ours, Saltz and White (1991) measured urinary cortisol levels of tame mule deer fawns in the low and high density pastures in 1986–87 and again the next winter when the tame deer were yearlings. Higher cortisol : creatinine ratios for deer in the high density pasture both winters indicated higher stress levels. Saltz and White (1991), without the benefit of vegetation biomass data, concluded that reduced forage availability and quality, rather than deer density, were the underlying causes. Our subsequent data indicating adequate forage production would tend to shift the emphasis towards the quality aspect.

The foraging behavior of tame deer in the pastures provided a link between forage conditions and fawn mortality. Although differences in diet compositions provided no insight to this situation, deer in the high density pasture did take fewer bites per 15-minute interval, had longer mean times between bites of some species, and traveled farther while feeding in the afternoon. This suggests that, compared to deer in the low density pasture, they were unable to find as much food, or as much high quality food, resulting in a lower nutrition plane that could decrease their survival. The difference in food quantity could have been partially offset by longer foraging time, a variable we did not measure. However, this would be counterproductive if the nutritional gain from the additional food did not offset the extra energy expended in its procurement.

With his model of energy balance in mule deer, Hobbs (1989) was able to show that predicted mule deer fawn mortality during winter was most responsive to body fat reserves and quality of forage consumed. We assume fawn fat reserves were comparable among pastures at the time of stocking (Nov–Dec) because of stocking procedures. Differences in forage quality among pastures, on the other hand, were suggested indirectly through behavior of the tame deer.

## Detection of Density Dependence

Our results suggest a strong density-dependent mortality process operated in the fawn segment of this mule deer herd. We were able to detect this process through a controlled, manipulative experiment conducted in a pasture complex with temporal and spatial controls, but without spatial replication. Other research demonstrating density dependence in cervids has lacked temporal and spatial controls and, hence, does not provide the cause–effect relationship we were able to show here. McCullough's (1979) research demonstrated density dependence, but no spatial control was available to compare to his manipulation of the George Reserve herd. Clutton-Brock et al. (1987), Albon et al. (1983), and Guinness et al. (1978) demonstrated density-dependent responses within individual red deer populations, but they also lacked spatial controls. The George Reserve and Isle of Rhum represent controlled situations—a fenced population for the former and, for the latter, an island with a fairly constant maritime environment substantially different from the more variable continental climates for McCullough's (1979) and our research.

We suspect the reason density dependence is not often recognized in mule deer populations is because of highly variable environments. Hamlin and Mackie (1989) suggested density-independent factors, mainly weather, regulate the mule deer population of the Missouri River Breaks in Montana. This population is exposed to enormous annual differences in both summer and winter conditions. Unless accounted for in some manner, such large irregularities can mask the effects of density dependence and considerably reduce the power of any test to detect it. Carefully controlled experiments would be required to demonstrate the phenomena in such cases. Thus, it is not surprising Hamlin and Mackie (1989) could not find density dependence operating in their populations and concluded there was no density-dependent feedback loop. We further suggest Clutton-Brock et al. (1987) might not have demonstrated a relationship between calf survival and population density had there been sizable fluctuations in annual weather conditions. The increased noise in the data could have masked any relationships, given the sample size and magnitude of the effect they reported, and resulted in low statistical power to detect a difference and reject the null hypothesis of density independence.

Besides reducing the researcher's ability to detect density dependence, highly variable winter conditions also may affect the density-dependent processes themselves. If there is high overwinter mortality among adults, the effect is to reduce the population to a point so far below ECC under "normal" winter conditions that additional mortality imposed on the rebounding population may well be additive. In contrast, the mule deer populations we studied were subjected to, but apparently not influenced by, severe winters to the extent of populations in other habitats and at higher elevations in Colorado. During the severe 1983–84 winter in our study, the 14% adult mortality was near average whereas fawn mortality increased to 95%. During the same winter, a mule deer population not supplementally fed in Middle Park, Colorado, had estimated adult female and fawn mortality of 38 and 74%, respectively (Carpenter et al. 1985). Thus, the Piceance population dipped only slightly below the overwinter carrying capacity for a "normal" winter, and density-dependent processes in the fawn segment of the population continued to operate.

## CONCLUSIONS

Wintering mule deer populations must be viewed as consisting of 2 segments—adults that can survive when forage quantity and/or quality are limited because of advantages in bodily energy reserves and body size, and fawns that have lower bodily energy reserves and a smaller stature that hinders their access to forage. The main cause of fawn deaths on the Ridge study area was starvation, an indication the fall population was too large for the available food supply. Presumably, a 20% reduction of the population was insufficient to overcome this imbalance. In contrast, fawn survival in the pastures was negatively correlated with density. That starvation was the main cause of death in the pastures further suggested a forage deficiency; one that we contend was more quality oriented. Therefore, we believe results of the pasture experiment provide evidence for the existence of a compensatory mortality process.

We reason that compensatory mortality was readily demonstrated in the pastures at densities encompassing those observed on the Ridge because the pastures did not have the prolonged high densities estimated in the field and more high quality forage was initially available. The decline in fawn survival among years observed in all pastures suggests such forage was being eliminated at all 3 stocking levels, but this is confounded by other evidence suggesting a strong influence of weather conditions.

Compensation also was detected on the CB study area when predation rates were lowered by removing coyotes. The basic question there was the same as for the other 2 experiments; only the mortality cause we manipulated (predation) was different. In this case, predation played a role in population dynamics, but only to the extent that it replaced other mortality causes.

Our results are pertinent to managing those mule deer populations where abiotic factors do not overshadow biotic ones involved in density-dependent regulation. In many established populations, low overwinter fawn survival should be interpreted as a symptom of density-dependent population regulation. Incremental reduction of the population, as suggested by McCullough (1984), would then be appropriate to increase fawn survival as well as the ratio of bucks to does. Earlier, Keith (1973) advocated studies of population dynamics within the framework of perturbation experiments to understand relationships between various causes of mortality in wildlife populations. Management by experiment (Macnab 1983) is still needed and may be the most practical approach to further explore the phenomena of density dependence in mule deer populations.

## LITERATURE CITED

ALBON, S. D., B. MITCHELL, AND B. W. STAINES. 1983. Fertility and body weight in female red deer: a density-dependent relationship. J. Anim. Ecol. 52:969–980.

Alldredge, A. W., J. F. Lipscomb, and F. W. Whicker. 1974. Forage intake rates of mule deer estimated with fallout cesium-137. J. Wildl. Manage. 38:508–516.

Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the mallard VI. The effect of exploitation on survival. U.S. Fish and Wildl. Serv. Resour. Publ. 128. 66pp.

Bartmann, R. M. 1983*a*. Composition and quality of mule deer diets on pinyon–juniper winter range, Colorado. J. Range Manage. 36:534–541.

———. 1983*b*. Appraisal of a quadrat census for mule deer in pinyon–juniper vegetation. Colo. Div. Wildl., Game Inf. Leafl. 109. 4pp.

———. 1984. Estimating mule deer winter mortality in Colorado. J. Wildl. Manage. 48:262–267.

———, A. W. Alldredge, and P. H. Neil. 1982. Evaluation of winter food choices by tame mule deer. J. Wildl. Manage. 46:807–812.

———, and D. C. Bowden. 1984. Predicting mule deer mortality from weather data in Colorado. Wildl. Soc. Bull. 12:246–248.

———, and L. H. Carpenter. 1982. Effects of foraging experience on food selectivity of tame mule deer. J. Wildl. Manage. 46:813–818.

———, ———, R. A. Garrott, and D. C. Bowden. 1986. Accuracy of helicopter counts of mule deer in pinyon–juniper woodland. Wildl. Soc. Bull. 14:356–363.

———, and S. F. Steinert. 1981. Distribution and movements of mule deer in the White River drainage. Colo. Div. Wildl. Spec. Rep. 51. 12pp.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. Am. Fish. Soc. Monogr. 5. 437pp.

———, G. C. White, and D. R. Anderson. 1984. Estimating the effect of hunting on annual survival rates of adult mallards. J. Wildl. Manage. 48:350–361.

Carpenter, L. H., D. L. Baker, and R. B. Gill. 1980. Tests of a nutritionally based big game habitat evaluation system. Colo. Div. Wildl., Denver. 95pp.

———, R. B. Gill, D. L. Baker, and N. T. Hobbs. 1985. Colorado's big game supplemental winter feeding program, 1983–84. Colo. Div. Wildl., Denver. 92pp.

Caughley, G. 1970. Eruption of ungulate populations with emphasis on Himalayan thar in New Zealand. Ecology 51:53–72.

———. 1979. What is this thing called carrying capacity? Pages 2–8 *in* M. S. Boyce and L. D. Hayden-Wing, eds. North American elk: ecology, behavior and management. Univ. Wyo., Laramie.

Clark, W. R. 1987. Effects of harvest on annual survival of muskrats. J. Wildl. Manage. 51:265–272.

Clover, M. R. 1956. Single-gate deer trap. Calif. Fish and Game 42:199–201.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. J. Anim. Ecol. 56:857–871.

———, F. E. Guinness, and S. D. Albon. 1982. Red deer behavior and ecology of two sexes. Univ. Chicago Press, Chicago, Ill. 378pp.

Connolly, G. E. 1978. Predation and predator control. Pages 369–394 *in* J. L. Schmidt and D. L. Gilbert, eds. Big game of North America: ecology and management. Stackpole Books, Harrisburg, Pa.

———. 1981*a*. Limiting factors and population regulation. Pages 245–285 *in* O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

———. 1981*b*. Assessing populations. Pages 287–345 *in* O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

Cox, D. R. 1970. Analysis of binary data. Methuen & Co., London, U.K. 142pp.

Errington, P. L. 1945. Some contributions of a fifteen-year study of the northern bobwhite to a knowledge of population phenomena. Ecol. Monogr. 15:1–34.

Feldhamer, G. A., T. P. Kilbane, and D. W. Sharp. 1989. Cumulative effect of winter on acorn yield and deer body weight. J. Wildl. Manage. 53:292–295.

Filonov, K. P. 1983. Variability of mortality factors in wild ungulate populations. Soviet J. Ecol. 14:116–122.

Fowler, C. W. 1987. A review of density dependence in populations of large mammals. Pages 401–441 *in* H. H. Genoways, ed. Current mammology. Vol. 1. Plenum Press, New York, N.Y.

Freddy, D. J. 1978. Experimental deer inventory—Piceance Basin—Northwest Region. Colo. Div. Wildl., Fed. Aid in Wildl. Restor. Job Prog. Rep., Proj. W-38-R-33. July:245–263.

———. 1979. Experimental deer inventory—Piceance Basin—Northwest Region. Colo. Div. Wildl., Fed. Aid in Wildl. Restor. Job Prog. Rep., Proj. W-38-R-34. July:209–215.

Garrott, R. A., R. M. Bartmann, and G. C. White. 1985. Comparison of radio-transmitter packages relative to deer fawn mortality. J. Wildl. Manage. 49:758–759.

———, and G. C. White. 1982. Age and sex selectivity in trapping mule deer. J. Wildl. Manage. 46:1083–1086.

———, G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. J. Wildl. Manage. 51:634–643.

Gilbert, P. F., B. Baker, R. Campbell, and H. Shepherd. 1955. Migration between summer and winter ranges. Colo. Dep. Game and Fish, Fed. Aid in Wildl. Restor. Job Completion Rep., Proj. W-38-R-8. July:199–211.

Goodman, L. A. 1960. On the exact variance of products. J. Am. Stat. Assoc. 55:708–713.

GRIZZLE, J. E., C. F. STARMER, AND G. G. KOCH. 1969. Analysis of categorical data by linear models. Biometrics 25:489–504.

GRUBB, P. 1974. Population dynamics of the Soay sheep. Pages 242–272 *in* P. A. Jewell, C. Milner, and J. M. Boyd, eds. Island survivors: the ecology of the Soay sheep of St. Kilda. Athlone Press, London, U.K.

GUINNESS, F. E., T. H. CLUTTON-BROCK, AND S. D. ALBON. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). J. Anim. Ecol. 47: 817–832.

HAMLIN, K. L., AND R. J. MACKIE. 1989. Mule deer in the Missouri River Breaks, Montana: a study of population dynamics in a fluctuating environment. Montana Dep. Fish, Wildl., and Parks, Fed. Aid in Wildl. Restor. Final Rep., Proj. W-120-R-7-18. 401pp.

HINES, W. W. 1975. Black-tailed deer behavior and population dynamics in the Tillamook Burn, Oregon. Oreg. Wildl. Comm., Wildl. Res. Rep. 5. 31pp.

HOBBS, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildl. Monogr. 101. 39pp.

———, AND D. M. SWIFT. 1985. Estimates of carrying capacity incorporating explicit nutritional constraints. J. Wildl. Manage. 49:814–822.

KAPLAN, E. L., AND P. MEIER. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53:457–481.

KEITH, L. B. 1973. Some features of population dynamics in mammals. Trans. Int. Congr. Game Biol. 11:17–58.

LAAKE, J. L., K. P. BURNHAM, AND D. R. ANDERSON. 1979. User's manual for program TRANSECT. Utah State Univ. Press, Logan. 26pp.

MACNAB, J. 1983. Wildlife management as scientific experimentation. Wildl. Soc. Bull. 11:397–401.

MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. Univ. Michigan Press, Ann Arbor. 271pp.

———. 1984. Lessons from the George Reserve, Michigan. Pages 211–242 *in* L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

MCKEAN, W. T., AND R. M. BARTMANN. 1971. Deer–livestock relations on a pinon–juniper range in northwestern Colorado. Colo. Div. Game, Fish and Parks, Fed. Aid in Wildl. Restor. Final Rep., Proj. W-101-R-13. 132pp.

NICHOLS, J. D., M. J. CONROY, D. R. ANDERSON, AND K. P. BURNHAM. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Trans. North Am. Wildl. Nat. Resour. Conf. 49:535–554.

———, AND J. E. HINES. 1983. The relationship between harvest and survival rates of mallards: a straightforward approach with partitioned data sets. J. Wildl. Manage. 43:334–348.

NYGREN, T. 1990. The relationship between reproduction rate and age structure, sex ratio and density in the Finnish moose population. Proc. Congr. Int. Union Game Biol. 14:30–42.

PARKER, K. L., AND C. T. ROBBINS. 1984. Thermoregulation in mule deer and elk. Can. J. Zool. 62:1409–1422.

POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, AND P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. 53:7–15.

RALLS, K., R. L. BROWNELL, JR., AND J. BALLOU. 1980. Differential mortality by sex and age in mammals, with specific reference to the sperm whale. Int. Whaling Comm. Rep., Spec. Issue 2: 233–243.

RAMSEY, C. W. 1968. A drop-net deer trap. J. Wildl. Manage. 32:187–190.

ROPER, L. A., R. L. SCHMIDT, AND R. B. GILL. 1971. Techniques of trapping and handling mule deer in northern Colorado with notes on using automatic data processing for data analysis. Proc. West. Assoc. State Game and Fish Comm. 51: 471–477.

SALTZ, D. G. 1988. Urinary cortisol and urea nitrogen responses to winter stress in mule deer (*Odocoileus hemionus*). Ph.D. Diss., Colorado State Univ., Ft. Collins. 65pp.

———, AND G. C. WHITE. 1991. Urinary cortisol and urea nitrogen responses to winter stress in mule deer. J. Wildl. Manage. 55:1–16.

SAS INSTITUTE, INC. 1985. SAS procedures guide for personal computers, version 6 ed. SAS Inst., Inc., Cary, N.C. 373pp.

———. 1987. SAS/STAT guide for personal computers, version 6 ed. SAS Inst., Inc., Cary, N.C. 1028pp.

———. 1990. SAS technical report P-200, SAS/STAT software: CALIS and LOGISTIC procedures, release 6.04. SAS Inst., Inc., Cary, N.C. 236pp.

SATTERTHWAITE, F. E. 1946. An approximate distribution of estimates of variance components. Biom. Bull. 2:110–114.

SCHEAFFER, R. L., W. MENDENHALL, AND L. OTT. 1986. Elementary survey sampling. Third ed. Duxbury, Boston, Mass. 324pp.

SCHMIDT, R. L., W. H. RUTHERFORD, AND F. M. BODENHAM. 1978. Colorado bighorn sheep-trapping techniques. Wildl. Soc. Bull. 6:159–163.

SHAPIRO, S. S., AND M. B. WILK. 1965. An analysis of variance test for normality (complete samples). Biometrika 52:591–611.

SHEPHERD, H. R., AND P. F. GILBERT. 1956. Migration between summer and winter ranges. Colo. Dep. Game and Fish, Fed. Aid in Wildl. Restor. Job Completion Rep., Proj. W-38-R-9. October: 1–16.

SHIELDS, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. State Univ. New York Press, Albany. 245pp.

SINCLAIR, A. R. E. 1977. The African buffalo: a study of resource limitation of populations. Univ. Chicago Press, Chicago, Ill. 355pp.

SMITH, D. G. 1957. Migration between summer and winter ranges. Colo. Dep. Game and Fish, Fed.

Aid in Wildl. Restor. Job Completion Rep., Proj. W-38-R-10. July:121–142.

———. 1958. Dentition and age-weight correlation. Colo. Dep. Game and Fish, Fed. Aid in Wildl. Restor. Job Completion Rep., Proj. W-38-R-11. October:161.

———. 1959. Dentition and age-weight correlation. Colo. Dep. Game and Fish, Fed. Aid in Wildl. Restor. Job Completion Rep., Proj. W-38-R-12. July:43–52.

———. 1960. Dentition and age-weight correlation. Colo. Dep. Game and Fish, Fed. Aid in Wildl. Restor. Job Completion Rep., Proj. W-38-R-13. July:51–58.

STAINES, B. W. 1978. The dynamics and performance of a declining population of red deer (*Cervus elaphus*). J. Zool., Lond. 184:403–419.

TORBIT, S. C., L. H. CARPENTER, R. M. BARTMANN, A. W. ALLDREDGE, AND G. C. WHITE. 1988. Calibration of carcass fat indices in wintering mule deer. J. Wildl. Manage. 52:582–588.

TRAINER, C. E., J. C. LEMOS, T. P. KISTNER, W. C. LIGHTFOOT, AND D. E. TOWEILL. 1981. Mortality of mule deer fawns in southeastern Oregon, 1968–1979. Oreg. Dep. Fish and Wildl., Wildl. Res. Rep. 10. 113pp.

VERME, L. J. 1962. Mortality of white-tailed deer fawns in relation to nutrition. Proc. Natl. Deer Dis. Symp. 1:15–28, 37–38.

———. 1963. Reproduction studies on penned white-tailed deer. J. Wildl. Manage. 29:74–79.

WALLER, R. A., AND D. B. DUNCAN. 1969. A Bayes rule for the symmetric multiple commparison problems. J. Am. Stat. Assoc. 64:1484–1499.

WHITE, G. C. 1983. Numerical estimation of survival rates from band recovery and biotelemetry data. J. Wildl. Manage. 47:716–728.

———, AND R. M. BARTMANN. 1983. Estimation of survival rates from band recoveries of mule deer in Colorado. J. Wildl. Manage. 47:506–511.

———, ———, L. H. CARPENTER, AND R. A. GARROTT. 1989. Evaluation of aerial line transects for estimating mule deer densities. J. Wildl. Manage. 53:625–635.

———, R. A. GARROTT, R. M. BARTMANN, L. H. CARPENTER, AND A. W. ALLDREDGE. 1987. Survival of mule deer in northwest Colorado. J. Wildl. Manage. 51:852–859.

*Received 14 November 1990.*
*Accepted 24 September 1991.*

# Density dependence in mule deer: a review of evidence

Author(s): Eric J. Bergman, Paul F. Doherty, Jr., Gary C. White and A. Andrew Holland

Source: Wildlife Biology, 21(1):18-29. 2015.
Published By: Nordic Board for Wildlife Research
DOI: http://dx.doi.org/10.2981/wlb.00012
URL: http://www.bioone.org/doi/full/10.2981/wlb.00012

**Wildlife Biology 21: 18–29, 2015**
doi: 10.2981/wlb.00012

Subject Editor: Anne Loison. Editor-in-Chief: Ilse Storch. Accepted 3 October 2014

# Density dependence in mule deer: a review of evidence

**Eric J. Bergman, Paul F. Doherty, Jr., Gary C. White and A. Andrew Holland**

*E. J. Bergman (eric.bergman@state.co.us) and A. A. Holland, Colorado Parks and Wildlife, 317 West Prospect Avenue, Fort Collins, CO, 80526, USA. – P. F. Doherty, Jr. and G. C. White, Dept of Fish, Wildlife and Conservation Biology, Colorado State Univ., Fort Collins, CO, 80523, USA*

Wildlife managers often need tangible evidence of density dependence in populations to support decision making. Field experimentation to identify density dependent effects is often cost and time prohibitive. Thus, assimilation of existing knowledge into a balance of probabilities can serve as a surrogate for experimental research. A case study of such a process is found in the mule deer *Odocoileus hemionus* herds of Colorado. Wildlife managers and hunters expressed concern over a recent decline in western Colorado mule deer herds, yet the underlying cause of this decline is yet to be determined. In response to this management concern, we conducted a review of scientific evidence on Colorado's mule deer population dynamics. This review was done in the context of a conceptual model that portrays population growth as a function of population size, per capita growth rate and population carrying capacity. Similar declines that occurred during the 1960s and early 1990s resulted in similar reviews that identified research and management topics that would benefit mule deer. These topics included: harvest, predation, intraspecific competition, disease, interspecific competition, and habitat loss and degradation. Between the late 1990s and present time, many of these topics were addressed by research. The conventional working hypothesis in Colorado is that mule deer herds are limited by winter range habitat. We identify new gaps in knowledge and suggest potential, future research topics, as well as potential management strategies. We suggest a focus on integrated studies of multiple herbivores with density reduction experiments to address intra- and inter- specific competition. In addition, we suggest focused experiments that address the roles of mountain lion predation, black bear predation, and disease in mule deer population dynamics.

Density dependence in populations can be summarized as a series of biological feedback mechanisms that lead to high population growth rates when density is low and low population growth rates when density is high. The scientific literature is replete with explanations of how density dependence can be manifest in populations (Tanner 1966, Sinclair 1989, Hixon et al. 2002). Examples of density dependence in free-ranging herbivore populations also exist (Sæther 1997, Gaillard et al. 1998, Brown 2011). However, wildlife managers often need direct, tangible evidence to support decision making at local scales. Yet experimental inquiry of density dependence is typically cost and time prohibitive. Thus, scientific reviews that generate a preponderance of evidence provide an important alternative to direct inquiry. These reviews serve a role in decision making processes, but also for identifying gaps in knowledge. As a case study, we consider the population dynamics of mule deer in Colorado.

Colorado's mule deer population has demonstrated several dramatic shifts in abundance during the past six to seven decades. Typically these fluctuations have mirrored regional mule deer population dynamics (Workman and Low 1976, Gill 2001). However, biologists, managers, and hunters have expressed concern over a recent decline in some western Colorado mule deer herds (Fig. 1). Preliminary evidence suggests that this recent decline in Colorado is again part of a broad, regional pattern (Walker 2011). Within Colorado, this recent decline has primarily been observed in the herds that are located in the western most third of the state (Fig. 2). However, these areas have also historically comprised the most abundant herds and this trend has thus driven broad perceptions about all of Colorado's mule deer herds. Despite this pattern, model based abundance estimates for the smaller herds located in the higher central mountains have appeared to increase during the last decade (Fig. 2).

Historical declines in mule deer populations have resulted in similar reviews (Workman and Low 1976, Gill 2001). In particular, a decline in mule deer populations during the late 1960s and early 1970s resulted in a regional symposium that was focused specifically on identifying potential causes of that decline (Workman and Low 1976). After a period of population increase during the late 1970s and 1980s, mule deer populations declined again during the early and middle portions of the 1990s. While this second decline was also observed at the regional scale, it was the impetus for a Colorado-centric symposium in 1999, resulting in a report to Colorado's legislature that called for a renewed focus on mule deer research and increased population monitoring activities (Gill 2001). A product of both symposia was the

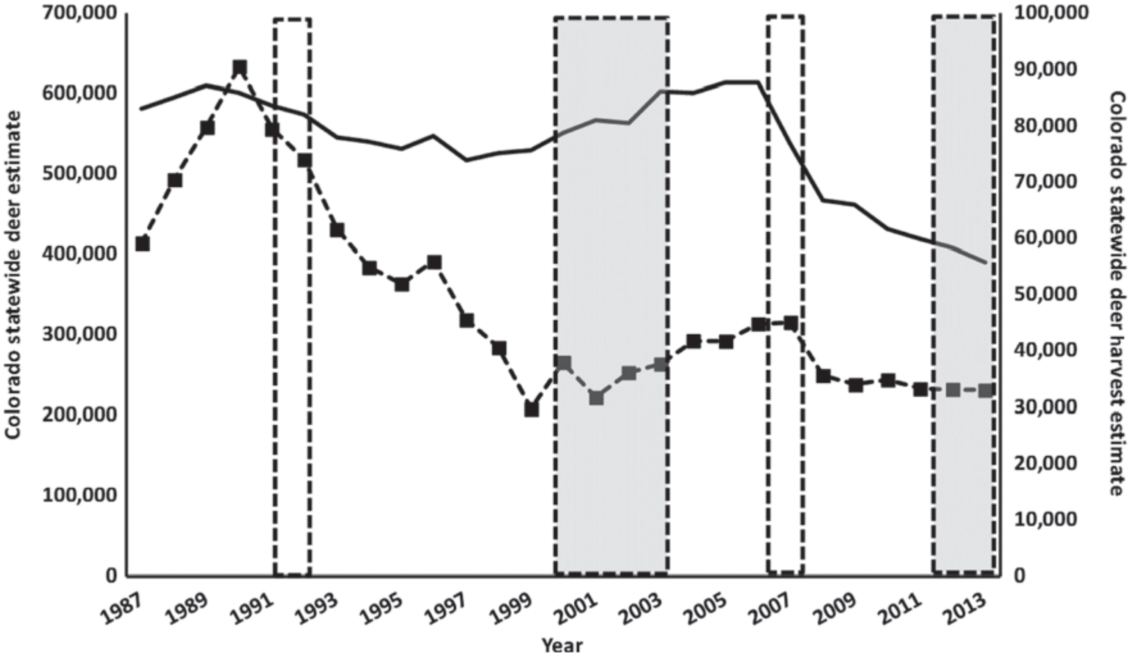


Figure 1. Historical statewide estimates of modeled total deer abundance (solid black line) and statewide deer harvest (dashed line) from Colorado. Harsh winter events during 1992 and 2007 are denoted by white boxes with dashed perimeters. Drought conditions from 2000–2003 and 2012–2013 are represented by gray boxes with dashed perimeters. The perceived population decline beginning in 2007 and driven by several large mule deer herds in the western third of Colorado served as the impetus for this review.

identification of several recurring potential causes for mule deer population decline: habitat loss, habitat degradation, predation, disease, interspecific competition (i.e. with elk *Cervus elaphus* and livestock) and intraspecific competition (i.e. increased density or overabundance of mule deer relative to available habitat). For these causes, the definition of habitat was primarily concentrated on browse availability and browse condition, and to a lesser extent escape and thermal cover provided by vegetation. In particular to Colorado, the review by Gill (2001) identified shortcomings in the

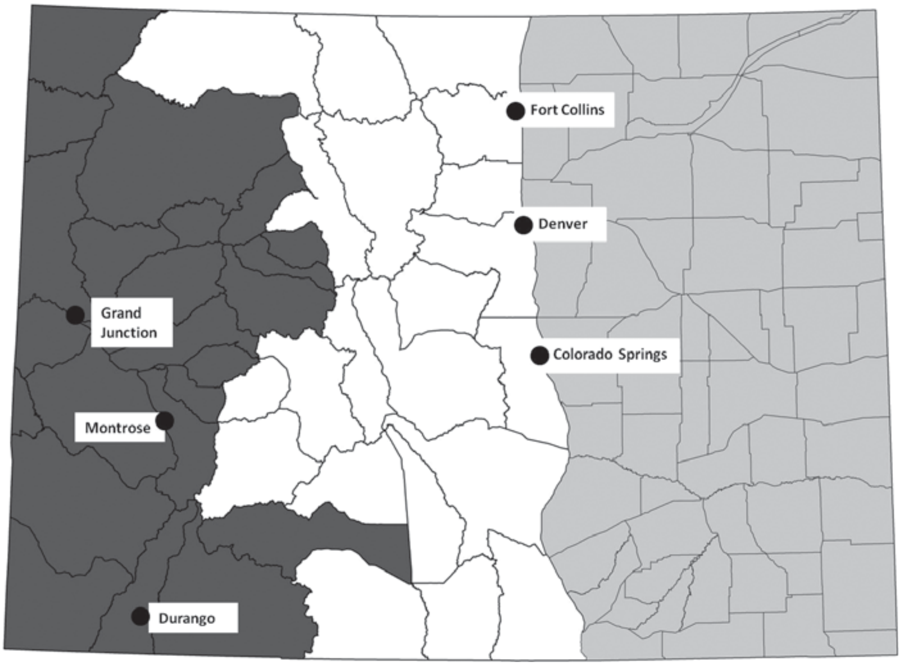


Figure 2. Map of Colorado reflecting mule deer herd management unit boundaries. Herd units that are shaded dark gray in the western third of the state reflect mule deer herds that have historically represented the largest herds, but also herds that have experienced perceived declines since 2007. White herd units in the central third of the state primarily occupy the higher, central mountains, and have been perceived as stable during the same time period. Herd units that are shaded light gray in the eastern third of the state are comprised of grassland and prairie ecosystems with extensive private land agriculture. These herds have been perceived as stable during the period of interest.

collective knowledge base, and thereby indirectly provided a recipe for research, management experiments, and population monitoring that would benefit deer management. Many of these studies have been completed, yet a collective review of research results has not occurred.

## Terminology and assumptions

In order to provide a review of scientific evidence and to assess key characteristics of a population, terminology must be clearly defined. A key component of many vertebrate population models is that populations are limited (i.e. unlimited population growth is not feasible). Under this constraint, the number of deaths eventually equals the number of births, resulting in no population growth. While the factors setting this upper limit to populations are debated and commonly researched, the notion that an upper limit exists (i.e. carrying capacity – *K*) is fundamental to other population attributes. For example, the terms 'regulation' and 'limitation' can easily be confused. For the purposes of this paper, and following the distinctions drawn by Messier (1991) and Boutin (1992), we define a regulating factor as any factor that has the ability to bring a population back into equilibrium after perturbation. The strength of a regulating factor is dependent on overall deer density and population size relative to *K*. Stronger regulating effects occur at higher deer densities when populations are near *K*. Regulatory effects are weaker when populations and deer densities are lower. Alternatively, a limiting factor is defined as the single factor that prevents populations from increasing beyond a threshold. Removal or adjustment of the limiting factor would result in a population that is capable of reaching a new, presumably higher, threshold. The rate at which a population achieves this new threshold is dictated by regulating factors.

Population regulation and population limitation can also be expressed as part of theoretical population growth models. In a generic form, population growth can be written as

$$\frac{dN}{dt} = f(N, r, K)$$

in which the change in population size (*dN*) occurs during a discrete time interval (*dt*). This rate of population growth is a function (*f*) of the current population size (*N*), the intrinsic rate of increase (*r*), and carrying capacity for the population (*K*). The value *dN*/*dt* is a population's growth rate. The function relating population size, population growth rate and carrying capacity can take many forms (e.g. logistic growth, theta-logistic growth) and can be expanded to include harvest (Williams et al. 2001). Such derivations have been extensively explored (Ricker 1954, Hassell 1975, Hassell et al. 1976, Williams et al. 2001, Gotelli 2008). While the major differences between different theoretical population growth models are often manifest when populations are below carrying capacity, with each model having a different set of ecological circumstances under which it is most useful, any single mathematical function is of nominal consequence to this review.

Expanding our theoretical model to accommodate the per capita rate of change (*R*)

$$R = \frac{\left(\frac{dN}{dt}\right)}{N}$$

reveals a value that can be easily confused with the intrinsic rate of increase (*r*). As noted above, whereas *r* is a constant value, *R* changes depending on population size (*N*). In keeping with the definitions of population regulation and population limitation, the strength of regulating factors manifested in *R* are dependent on current population size (*N*). Limiting factors are those that influence carrying capacity for the population (*K*).

Regardless of how population models are conceptualized, several noteworthy assumptions and simplifications are commonly made. First, the perspective that populations have a single limiting factor is a common oversimplification. This simplification facilitates both communication and study design. In reality, populations may be limited by an interaction of factors, such as habitat condition and weather severity: interactions that are partially driven by random processes that complicate scientific and management endeavors. Another common oversimplification for many conceptual models is that *K* is assumed to be known and fixed. In applied settings, neither of these assumptions is valid. A simple demonstration of how *K* can change over short time intervals can be found by considering the influence of weather on browse availability. During harsh winters during which the snowpack greatly exceeds normal depths and temperatures are lower than those traditionally experienced, winter browse for deer can be buried under thickly crusted snow layers, rendering it unavailable for immediate use. Under these extreme conditions, the quantity of available food is reduced. If deer are food limited on the winter range that is experiencing these conditions, *K* is reduced. Alternatively, during mild winters in which snow depths are below average and temperatures are higher than traditionally expected, access to plant resources on winter range is unrestricted and *K* is increased. Similarly, extended periods of drought or abundant moisture can change the long term trajectory of available browse, and subsequently *K*. Due to the dynamic nature of browse availability, managers rarely know how many deer can be supported by current conditions. A similar assumption that is commonly made for simplification purposes is that all mule deer browse is of equal quality. As demonstrated by Hobbs and Swift (1985), forage quality is often inversely related to forage quantity. Thus, traditional range food supply/animal food requirements models require a simplification that fails to accommodate the interaction between *K* and the nutritional status of animals. One final oversimplification that is commonly made when considering *K* is that all animals have an equal competitive advantage, a similar nutritional response, and an equal likelihood of facing mortality when *K* is reached. However, an extensive body of literature has demonstrated that adult mule deer are more robust in terms of survival than fawns (Unsworth et al. 1999, Lukacs et al. 2009, Bishop et al. 2009). In particular, studies that have assimilated mule deer survival data over broad spatial and temporal scales have demonstrated that the variation in fawn survival exceeds that of adult survival (Unsworth et al. 1999, Lukacs et al. 2009). Similarly, other studies have provided evidence that adults have a competitive advantage over fawns

(Garrott and White 1982, Bishop et al. 2005, Bergman et al. 2011). Ultimately, this can be viewed as evidence that *K* is different for adults and fawns.

Much of the research on mule deer population dynamics has also investigated the principals of additive and compensatory mortality (Bartmann et al. 1992, Bishop et al. 2009). Compensatory mortality is a phenomenon that is dependent on a population being above *K*, implying that by the end of an annual cycle the number of individuals exceeding that threshold will have necessarily died. The portion of the population that will have necessarily died has been referred to as the 'doomed surplus' (Errington 1934, Kokko and Lindström 1998, Boyce et al. 1999). For simplicity in communication, all of the doomed individuals will die from causes related to the limiting factors for the population. However, this scenario is not necessarily the case and is unlikely. A hypothetical example can be found in a nondescript deer population that is limited by winter habitat, but is also exposed to hunter harvest. In this example, the available habitat is capable of supporting no more than 500 individuals during the winter months and annual hunter harvest is 25 individuals. During some years far more than 500 animals arrive on winter range, such as 600, but harvest may remain static at 25 individuals. Under this scenario, 100 individuals are expected to die, presumably of malnutrition (i.e. the doomed surplus is 100 individuals). If 25 individuals die due to hunter harvest and 75 still die of malnutrition, harvest-caused mortality is completely compensatory with malnourishment-caused mortality. During years in which fewer than 500 animals arrive on winter range, yet 25 animals are harvested, those 25 deaths can be considered completely additive as resources were available to support those animals had they not been harvested. These two scenarios represent opposite ends of a mortality spectrum, thereby also creating a false dichotomy in the illusion that mortality is either always additive or always compensatory. A final derivation of this example can be found during years in which slightly more than the carrying capacity of deer arrive on winter range, such as 510, with harvest remaining static at 25 deer. During these years, partially additive mortality is expected as the loss of 10 deer can be considered compensation between harvest and starvation, yet the loss of 15 extra deer is additive. While these scenarios are for a hypothetical example, they reflect the driving principals of harvest management programs in which harvest objectives are based on the desire for hunter harvest to be compensatory, and to accommodate the relationships between density dependence, mortality and timing of harvest (Kokko and Lindström 1998, Boyce et al. 1999).

The biological feedback mechanisms experienced by populations as they reach *K* have been a topic of interest to ecologists and managers for several decades (Eberhardt 1977). In particular, among many taxa, predictions of the sequence and role of density-dependent feedback mechanisms are surprisingly consistent – density-dependent effects are predicted to impact populations sequentially in the order of reduced juvenile survival, increased age of first reproduction, declines in the reproductive rates of adult females, and reduced survival of the adult age class (Eberhardt 1977, Gaillard et al. 1998, 2000). The perspective that populations demonstrate shifts in life history characteristics as overall abundance nears carrying capacity is a logical extension of the objectives of Hobbs and Swift (1985). Hobbs and Swift (1985) demonstrated that when the interaction of forage quality and forage quantity was considered in carrying capacity models, they could predict the maximum number of animals that could maintain a diet of a specified quality, or they could predict the maximum quality of diet for a specified number of animals. However, despite the foundational premise of density dependence and the repetition of predictions, the effect of density on the dynamics of free-ranging ungulate populations is difficult to demonstrate.

## A review of evidence – potential limiting factors

Due to the uncertainty surrounding the geographic extent of this most recent decline, but also to the certainty that it has occurred in Colorado, we focused this review on research and analyses that are particular to mule deer herds in Colorado. However, research and collaboration among Colorado and other western states is common, and we expanded this review to include pertinent literature from outside Colorado, and from other North American ungulates, to gain insight on ecological processes that have not been the focus of research in Colorado. In particular, this review is focused on harvest, predation, intraspecific competition, disease, interspecific competition, and habitat loss and degradation.

### Harvest

Many harvest management systems are based on the premise that a doomed surplus, or harvestable surplus, of animals exist in populations. As described above, this surplus occurs when populations are at or near *K*. The most publicized of these systems pertains to harvest of waterfowl in North America (Burnham and Anderson 1984, Nichols et al. 1995, 2007). However, similar examples can found in the ungulate literature (Wallmo 1981, Swenson 1985). Alternative harvest management strategies also exist. A well-known example of one of these alternatives, which was embraced by marine fishery managers during the 1950s, is based on the desired outcome of maximizing a sustained yield (Hilborn et al. 1995). The principal of maximum sustained yield is that populations can be held below *K* in order to maximize production and recruitment of new individuals into the population (Williams et al. 2001). From a numerical perspective, the same number of individuals recruited into the population can be harvested with no change in overall abundance (Williams et al. 2001). These two harvest management philosophies represent opposite ends of a continuum – the harvestable surplus strategy assumes harvest is completely compensatory while the maximum sustained yield strategy assumes harvest is completely additive – yet both philosophies are based on the premise of density dependence. The fundamental difference between the two strategies is that they exploit different aspects of *R*, a population's per capita rate of change. These two strategies also create a false dichotomy as managers rarely know how many animals are in a population, what *K* is for a system, or if *K* is changing. This is particularly evident for mule deer when considering that harvest recommendations are set and harvest occurs prior to winter. Winter is commonly the period in which *K* can be stochastically suppressed by deep snow depths and low temperatures. In the face of this uncertainty, the potential for harvest to drift between being completely additive, partially additive and completely compensatory is high. The most complete documentation of this harvest management dilemma for large ungulate systems stems from moose *Alces alces* management in Alaska, where multiple harvest objectives were placed on a system that was subjected to periodic and harsh environmental fluctuations, as well as a rich predator assemblage (Gasaway et al. 1983, 1992, Boertje et al. 2009, Young and Boertje 2011).

This diversity in harvest management strategies can also be found in Colorado's deer herd management plans (Colorado Parks and Wildlife unpubl.). For example, some of Colorado's deer herds are managed such that *N* (abundance) is maximized. While the total number of animals that can be supported in these herds remains unknown, this approach to herd management reflects the principals of a doomed surplus – herd abundance is maximized after each winter and is thus capped by winter habitat (*K*). Specifically, summer and fall abundance of these herds are believed to exceed winter range *K*. Thus, harvest is intended to capture this doomed surplus, making it a compensatory source of mortality. Alternatively, other herds that experience harsh winter events at more frequent intervals are managed such that *N* is preferentially kept at *K* set by those extreme winter conditions and thus below *K* that is set by mild winter conditions. During mild winters when range capacity is less restricted, this approach to herd management reflects sustained yield principles. The last example stemming from Colorado's deer herd management pertains to an entirely separate objective that is geared towards providing individual hunters with a high quality hunting experience. High quality hunting experiences are typified by: 1) herds that have high adult male:adult female ratios, 2) opportunities for hunters to encounter male deer that have reached older age classes and thus have more developed antler structure, and 3) lower encounter rates between hunters.

Two evaluations of Colorado's harvest management decisions have occurred (Bishop et al. 2005, Bergman et al. 2011). Each of these was an evaluation of restrictions to deer hunting, and primarily within this, restrictions on the hunting of adult male deer. In each case, as harvest was restricted, an increase in adult male:adult female ratios was observed. In particular, ratios increased by as many as 4.52 adult males per 100 adult females in one study (Bishop et al. 2005) and by as many as 21.86 adult males per 100 adult females in the other study (Bergman et al. 2011). However, simultaneous declines in fawn:adult female ratios were observed as part of each study. Declines were as high as 6.96 fawns per 100 adult females (Bergman et al. 2011) and 7.51 fawns per 100 adult females (Bishop et al. 2005). While neither study was a direct experimental evaluation of intraspecific competition or density dependence, both studies provide circumstantial evidence that increasing the proportion of adult male deer in the population came at the expense of population productivity. Interaction between the male, female, and young components of populations, similar to that presented by Bishop et al. (2005) and Bergman et al. (2011), can result in second order feedback effects that are non-trivial (Mysterud et al. 2002). If lowered fawn:adult female ratios can be interpreted as an indicator of suppressed population growth, the studies of Bishop et al. (2005) and Bergman et al. (2011) may provide evidence that harvest decisions that change the sex and age structure of deer herds to favor mature animals may have a regulating effect – thereby slowing the rate of population growth (*dN*/*dt*) by reducing the per capita rate of change (*R*) in our conceptual model. Moreover, at a given population size (*N*), a herd with a higher proportion of males has a lower reproductive potential because it has a lower proportion of females. In the event of stochastic reductions in *K* due to harsh winters, die-offs in herds with a higher proportion of males may experience delayed rebounding (i.e. sex ratio may have a regulating effect on population growth). Colorado's current statewide ratio of total males to adult females, when weighted by herd size, is 33.4 adult males per 100 adult females (Colorado Parks and Wildlife unpubl.). However, it is unknown if sex ratios at this level have a regulating effect.

The effect of hunting on wildlife species extends beyond population management. In particular, the indirect effect of hunters on ungulates, specifically movement patterns and animal behavior, has received recent attention (Conner et al. 2001, Vieira et al. 2003, Ciuti et al. 2012). Similarly, the effect of trophy-focused hunting pressure on large ungulates, and the subsequent effect on trends in antler size, has also been the focus of recent research (Allendorf and Hard 2009, Monteith et al. 2013).

## Predation

The role of predation in shaping ungulate population dynamics is a common research topic with many different conclusions being possible, depending on individual circumstances. In the Rocky Mountain West, the motivation to study coyote *Canis latrans* predation on mule deer is several-fold. First, encounter rates between coyotes and hunters (i.e. observation of coyotes and coyote tracks, hearing coyote howls, and finding coyote kill sites) are likely higher than those for any other predator of deer. Stemming from this, an intuitive reaction by hunters is often that coyote predation has a stronger effect on deer population dynamics than other sources of predation. Thus, pressure from the public for a more complete understanding of the impact of coyote predation on deer populations has frequently been articulated (Willoughby 2012). Secondly, investigations into the causes of mortality of mule deer have consistently identified coyote predation as a common source of mortality (Bartmann et al. 1992, Whittaker and Lindzey 1999, Pojar and Bowden 2004, Bishop et al. 2009). Stemming from this demand and from these patterns, the effect of coyote predation on mule deer has been more thoroughly investigated than other sources of predation. Experimental manipulation of coyote density as a treatment effect on deer population dynamics has occurred as part of two studies. Research conducted by Bartmann et al. (1992) in northwest Colorado evaluated the effectiveness of coyote control as a management strategy to increase productivity within a deer herd. While the annual removal of 47–93 coyotes from the 140 km$^2$ winter range study area reduced coyote predation, a simultaneous increase in malnourishment deaths occurred and no overall increase in survival rates was detected. This switch between mortality causes, with no increase in survival, was viewed as strong evidence that coyote predation was compensatory with starvation. Specifically, if this were a top–down system in which coyotes were limiting (i.e. predation determined *K*), removal of coyotes should have increased *K*, translating to an increase in *R* as the deer population responded. No change in *R* was observed.

More recently, research conducted by Hurley et al. (2011) in southeast Idaho also tested the effectiveness of coyote removal from mule deer winter range as a management strategy to improve mule deer population performance. Hurley et al. (2011) removed an average of 53.3 coyotes/1000 km$^2$ per year during a six-year period. Coyote removal did result in increased neonate survival during years in which lagomorph populations were low; however, the increase in survival was temporary. Subsequent December fawn:adult female ratios showed no population level increase stemming from coyote control efforts. No effect of coyote removal was observed during years of normal lagomorph abundance. As was the case with Bartmann et al. (1992), no change in *R* was observed.

In addition to these large scale predator manipulation studies, several other studies have quantified coyote predation on mule deer in Colorado. In particular, work by Bishop et al. (2009) reported coyote-caused mortality rates for two groups and age classes of deer. In the first group, comprised of animals that had received a nutrition enhancement, fawns had a coyote-caused overwinter mortality rate of 0.04 (SE = 0.01) and adults had an annual coyote-caused mortality rate of 0.01 (SE = 0.01). Alternatively, fawns that had not received the nutrition enhancement experienced an overwinter coyote-caused mortality rate of 0.12 (SE = 0.03) and adults experienced an annual coyote-caused mortality rate of 0.02 (SE = 0.01).

Other, non-experimental, research has also been conducted in Colorado. Work conducted by Whittaker and Lindzey (1999) assessed the frequency of coyote predation on mule deer neonates (≤ 30 days old) on Colorado's Front Range. Whittaker and Lindzey (1999) reported a 30-day survival rate of 0.66 for mule deer neonates during a two-year study, with coyotes accounting for 79% of the mortality. When compared to other neonatal survival data during the first 30 days of life (Pojar and Bowden 2004), the survival rates reported by Whittaker and Lindzey (1999) appeared to be slightly lower, with coyotes accounting for a higher proportion of the mortality. In each study, coyote predation diminished after the first 30 days of life, highlighting the role of prey vulnerability in the predation process. While this example links vulnerability to age and immaturity, vulnerability can also be associated with malnourishment (Bartmann et al. 1992) or landscape features (Bergman et al. 2006). Because neither the study conducted by Whittaker and Lindzey (1999), nor the study conducted by Pojar and Bowden (2004) measured survival to the stage of recruitment into the adult age class, determining if the predation they documented was additive or compensatory is not possible. However, if the deer herds studied by Whittaker and Lindzey (1999) and Pojar and Bowden (2004) were above *K*, predator caused neonate mortality during the first one to three months of life would be compensatory with winter fawn mortality that would be linked to malnutrition.

Other research in Colorado assessed the secondary impact of coyote removal, for livestock protection purposes, on mule deer (Harrington and Conover 2007). Based on sex ratio data, Harrington and Conover (2007) found that coyote control efforts had no effect on deer herd productivity. An extensive literature review conducted by Ballard et al. (2001) resulted in several general conclusions about predation. First, as noted by studies from Colorado, coyote predation can be a significant mortality factor for mule deer. However, Ballard et al. (2001) also noted that discerning the role of coyote predation on deer population dynamics was often confounded by other factors such as weather and habitat condition. This confounding between mortality factors highlights the necessity of discerning between proximate and ultimate mortality causes.

While the role of coyote predation has been the focus of deliberate research, in Colorado there have been no studies that have directly assessed the effect of increased mountain lion *Puma concolor* harvest, or mountain lion removal, on mule deer population dynamics. However, the research conducted by Hurley et al. (2011) in Idaho provides experimental evidence on this topic. Hurley et al. (2011) found that overwinter mortality of adult mule deer decreased and fawn:adult female ratios increased in areas of intense mountain lion removal, indicating that mountain lion predation was partially additive. Despite these patterns, no significant change in population trend was documented. This result was partially attributed to the conclusion that winter severity was the most significant factor limiting mule deer population growth (Hurley et al. 2011). Thus, the process variation in *K* stemming from weather had a stronger influence on deer population dynamics than predation. In Colorado, Pojar and Bowden (2004) reported a 3.2% mountain lion caused mortality rate for mule deer ≤ 6 months old. Also in Colorado, Bishop et al. (2009) reported a mountain lion caused mortality rate of 0.5% for adult female deer that had received a nutrition enhancement and 3.2% for adult females that had not received the enhancement. While Bishop et al. (2009) found that felid predation comprised nearly 15% of all mortality for deer ≥ 6 months old, predation on deer that had received a nutrition enhancement was greatly reduced. This was interpreted as evidence that mountain lions selected for animals in poorer condition, which can also be interpreted as that mountain lion predation was at least partially compensatory with starvation.

The role of black bear *Ursus americanus* predation on mule deer population dynamics has not received focused attention in Colorado or elsewhere in the Rocky Mountain West. While bear predation on neonates has been reported in numerous studies (Pojar and Bowden 2004, Bishop et al. 2009), this predation appears to be highly synchronous with birth pulses. Specifically, predation by bears peaks shortly after the peak in parturition before quickly waning during the subsequent three to five week period. This pattern has largely lent itself to the perspective that bear predation is not likely a limiting factor in mule deer population dynamics. Literature reviews conducted by Ballard (1992) and Zager and Beecham (2006) identified conditions under which the pulse in bear predation following parturition was most likely additive. In particular, bear predation appeared to be additive when bear densities, particularly black bear densities, were high and ungulate densities were low. However, this evidence was largely specific to brown bear *Ursus arctos* and black bear predation on moose in Alaska and Canada (Stewart et al. 1985). More recent evidence provided by Barber-Meyer et al. (2008) has extended this perspective to elk populations as well. Pojar and Bowden (2004) reported a bear-caused mortality rate of 4.0% for mule deer fawns $\leq 6$ months old, although the bulk of this mortality occurred between early June and the middle of August. Bishop et al. (2009) reported low bear-caused mortality rates for adult female deer (0.0%–0.8%), with bear predation probabilities that quickly decayed from a maximum of 0.20 during the first 100 days of life for newborn fawns. Thus, while black bear predation likely does not affect *K*, it could affect *R*. However, if herds are winter habitat limited, black bear predation during this period would be compensatory with overwinter malnutrition related deaths.

### Intraspecific competition

The research projects that have addressed intraspecific competition on mule deer in Colorado can be broken into three broad categories: stocking experiments, density reduction experiments, and habitat manipulation studies. Of note, with the exception of general management studies, all of these research projects were focused on winter range. Bartmann et al. (1992) used deer-proof fenced pastures, stocked with different densities of deer, to test the effect of intraspecific competition on overwinter fawn survival. Three pastures, ranging from 0.66–1.69 km$^2$ were stocked with mule deer during three separate winters. Deer densities in the pastures were 44, 89 and 133 deer km$^{-2}$. Bartmann et al. (1992) found that overwinter survival of fawns was inversely related to density during all years of the study, although malnourishment was the primary cause of mortality in all three pastures. The fact that malnourishment related mortality occurred in even the lowest density pasture was considered to be evidence that food limitation was occurring on this winter range. No coyote predation was reported.

The effect of deer density and intraspecific competition was tested under free-ranging conditions as part of two different studies. Each of these studies relied on a reduction in deer density as a treatment effect. The first of these utilized deer removal from a non-fenced, winter range study area in order to conduct the previously described stocking experiment (Bartmann et al. 1992). During a two-year study period, overwinter mule deer density on a treatment study unit was reduced by 22% and 16%, whereas density was left unaltered on control units. Despite these reductions in density, no difference in overwinter survival of fawns was observed between the treatment and control study units. Bartmann et al. (1992) concluded that density reductions were not high enough to induce a treatment effect on overwinter survival of fawns. No differences in mortality causes were observed between treatment and control study units, although as winter severity increased, the percent of fawns that died due to malnourishment increased. Following this initial project, a second density reduction experiment was conducted in which hunter harvest was increased in a treatment study unit, whereas no increased harvest occurred in a control study unit (White and Bartmann 1998). Building on the results of Bartmann et al. (1992) in which reductions in density of 22% and 16% resulted in no detectable treatment effect, desired reduction in density for this second study was $>50\%$ (White and Bartmann 1998). Conducted over a four-year period, the increased harvest resulted in a 76% reduction in density. The reduction in density resulted in increased fawn survival from 0.31 to 0.77 during the treatment period, an increase of 0.46, whereas an increase of 0.29 was observed in the control unit. Despite the fact that an increase in survival occurred in both the treatment and control study units, the higher survival that occurred in the treatment area – the area with lower deer density – was evidence that population regulating effects were occurring.

As an alternative to reducing the density of deer, recent research has focused on habitat alteration as a mechanism to increase the finite supply of food. The first of these studies was an experimental manipulation of winter resource availability delivered via pelleted food (Bishop et al. 2009). Using a cross-over study design, Bishop et al. (2009) delivered ad libitum food to mule deer on two winter range experimental study units. Average overwinter survival of fawns on the treatment study unit was 0.905, whereas it was 0.684 on control units. Bishop et al. (2009) found that nutritional enhancement did not affect pregnancy or fetal rates, but enhancements did increase neonatal survival in treated animals. Ultimately, this nutritional enhancement led to a projected population rate of change of 1.17 on treatment study units, versus 1.03 on control study units. The increases in survival rates and productivity were viewed as evidence that *K* for mule deer was set by nutritional limitation. Bergman (2013) extended the results of Bishop et al. (2009) by replacing pelleted food with mechanical habitat treatments on mule deer winter range. While the treatment effect on the overwinter survival of fawns was smaller, Bergman (2013) documented a 1.15 times magnitude increase in survival in study units that had received mechanical disturbance treatments, reseeding, and chemical control of weeds over study units that hadn't received any treatments. Changes to vital rates impacting long-term population performance (i.e. pregnancy rates, twinning rates, neonatal survival, and adult body mass) were not documented. However, the increase in fawn survival translated to an increase in the projected finite population growth rate from 1.10 in untreated study units to 1.15 in treated study units (E. Bergman, Colorado Parks and Wildlife, unpubl.). As part of concurrent research, Bergman (2013) failed to conclusively demonstrate an effect when determining if habitat treatments extended to overall abundance. This lack of effect, in regards to abundance, was attributed to insensitivity of the abundance estimation procedures, annual variation in weather patterns that periodically forced additional animals on to study units, and to a lag effect between increased survival of fawns and an attending increase in abundance.

### Disease

Research on disease within Colorado's mule deer population, especially during the past 15 years, has primarily focused on Chronic wasting disease (CWD). However, the focus of much of this research has been on the spatial ecology of the disease (Conner and Miller 2004, Farnsworth et al. 2006) and mechanisms for reducing the prevalence of the disease in deer herds (Wolfe et al. 2004, Conner et al. 2007).

Extension of CWD research to deer population dynamics has largely been based on simulation. Results from these simulation efforts have been variable, although Gross and Miller (2001) demonstrated that population growth and productivity could be strongly influenced by low infection rates, implying a potentially regulating influence. Extension of simulation results to field assessment demonstrated weaker effects. In particular, Dulberger et al. (2010) concluded that while effects were present, the influence of CWD on recruitment was weak and could be ignored when considering the effects of the disease on population growth rates. Part of the difficulty in making conclusions about the population level impact of CWD on mule deer is imbedded in the evidence that infected deer are more vulnerable to predation (Miller et al. 2008, Krumm et al. 2009). Mountain lions have demonstrated the ability to select for CWD positive deer, demonstrating that compensation between predation and disease-related mortality occurs.

Other diseases, particularly bluetongue and Epizootic hemorrhagic disease (EHD), also occur in Colorado, but outbreaks of these diseases tend to be spatially localized and unpredictable. Thus, the frequency and magnitude of outbreaks has remained undocumented. However, Thorne et al. (1988) estimated that 1000 mule deer died during a bluetongue outbreak in Wyoming, providing evidence that disease impacts may not be trivial. In such cases, disease outbreaks would likely impact *N*, but not *K* or *R*.

### Interspecific competition

Competition between mule deer and other species has received attention since the 1950s (McKean and Bartmann 1971). The majority of competition research, when focused on other wild ungulates, has focused on elk (Beck and Peek 2005, Torstenson et al. 2006). In consideration of domestic livestock, the majority of research has focused on competition between mule deer and cattle (Beck and Peek 2005, Torstenson et al. 2006). A common trend among all of these research projects has been the quantification of dietary and spatial overlap between different species. Studies have consistently concluded that in regards to dietary overlap between mule deer, elk, and cattle, mule deer demonstrate a high degree of diet partitioning as compared to the other two species (Beck and Peek 2005, Torstenson et al. 2006). Although not in Colorado, Beck and Peek (2005) found evidence of moderate (45%–59%) diet overlap between mule deer and elk during summer months. Torstenson et al. (2006) reported similar overlap (45%) between these two species during spring, although mule deer showed preference for forbs and shrubs, whereas elk showed preference for graminoids. In Colorado, research focused on range response to different stocking rates of mule deer, sheep, and cattle was conducted during the 1950s and 1960s (McKean and Bartmann 1971). This research demonstrated variable preference for different species of plants by all three species. However, McKean and Bartmann (1971) concluded that only under higher density stocking rates of multiple species did deterioration of range conditions occur. Unfortunately, research focused on competition between mule deer and other species has not been extended to population-level effects. Specifically, a robust estimation of how many mule deer may be replaced by other species in locations of range overlap has not occurred. While the need for such research has been identified (Lindzey et al. 1997), the financial and logistic constraints to accomplish such work are high. While the research results noted above demonstrate that the direct effects of competition between mule deer and other species are likely low, the indirect effects such as displacement of deer from optimal foraging locations or periods, and the subsequent cascade effect on body condition and productivity can only be speculated.

### Habitat loss and degradation

Loss of habitat for wildlife species is incremental, with likely effects eventually stemming from the accumulation of those incremental losses. Thus, unlike many other factors that have a negative impact on mule deer, the impact of habitat loss is subtle and effects may only be realized after many years of compounding. Evaluation of the impacts of habitat loss on wildlife populations thus becomes a long process in which repeated quantification of both impacts and populations is necessary. For example, Nellemann et al. (2003) studied the impacts of hydroelectric reservoir infrastructure development on reindeer *Rangifer tarandus* during a 10-year period. This effort required monthly surveys of reindeer, but subsequently documented an overall reduction to 8% of pre-development densities in areas within 4 km of developed sites. Similar results for mule deer facing habitat loss due to energy development in Wyoming were reported by Sawyer and Nielson (2011). In the case of Sawyer and Nielson (2011), a 43% decline in mule deer abundance was observed in herds facing energy extraction and development, whereas a congruent decline of 23% was observed in nearby control areas. In each of these cases, habitat loss was slow (i.e. spread out over multiple years), but quick enough to be documented during a 10-year period. Habitat loss or habitat deterioration due to other causes, such as exurban and rural residential development, or vegetative succession to less desirable species, may occur over a time period spanning multiple decades. Documenting effects over such long time periods is increasingly difficult. Extension of historical trends into forecasts or predictions of future conditions is subsequently a difficult challenge to overcome. For example, Schwartz et al. (2012) linked projections of road density models with brown bear demographic criteria to estimate the loss of source habitat through 2020, and thus predicted that future exurban development would result in conversion of suitable habitat into sink habitat for brown bears. Similar efforts were made for mule deer in Oregon, although predictions about future habitat conditions were not extended to mule deer abundance (Kline et al. 2010). While recognized as a management dilemma in Colorado, no assessment of mule deer habitat loss or habitat conversion has occurred. Modeling efforts initiated by Johnson et al. (2012) will be the first effort to quantify this habitat conversion by land type as well as by landowner (e.g. private lands, state owned lands and federally owned lands). Thus, while the effects of habitat and nutritional limitation on deer herd productivity are well documented, the effects of habitat loss and conversion on population size have not been quantified. However, the modeling work by Johnson et al. (2012) may ultimately provide a data-based link between $dN/dt$ and reductions in *K*.

In addition to direct habitat loss, vegetational conversion within mule deer habitat to new, less desirable or less palatable species can also occur. While not quantified, a subtle example of such a conversion that has likely impacted mule deer in Colorado has been the conversion of mixed agricultural fields that included a higher non-native alfalfa *Medicago sativa* component to predominantly grass fields. More widely identified problems that result in lower quality and less palatable species include drought, expansion of exotic species such as cheatgrass *Bromus tectorum*, and overgrazing (Watkins et al. 2007).

## Discussion

Based on published evidence from Colorado and elsewhere, the working hypothesis continues to be that many of Colorado's mule deer herds are limited by habitat, and more specifically, quality of winter range habitat. Refining this hypothesis leads to the conclusion that herds are limited by overwinter fawn survival, which in turn is a function of *K* for that winter. The preponderance of evidence, particularly the evaluations of winter nutrition and habitat management, but also evidence of compensation between predation and starvation support this position. Under the habitat limitation assumption, which assumes that a population is at or above *K*, the cause of mortality for deer is largely irrelevant as it pertains to the doomed surplus in a population; removal of one source of mortality would result in an increase in other mortality causes. Due to the partial dependence of *K* on weather and other stochastic events, even populations that are thought to be slightly below *K* may be subject to a doomed surplus if harsh or extreme conditions occur. Several of the key mule deer research projects discussed in this review demonstrate the phenomena of additive and compensatory mortality. This was particularly evident when coyotes were removed as part of the work conducted by Bartmann et al. (1992). A clear exception to this generalization, but an exception that provides support for the working hypothesis, is the lack of compensation that occurred when Bishop et al. (2009) reduced the opportunity for malnutrition by providing pelleted food. In this case, survival rates increased. Bishop et al. (2009) also demonstrated a consistent pattern of higher predation occurring, in the absence of enhanced nutrition, regardless of treatment location. In the case of harvest management studies (Bishop et al. 2005 and Bergman et al. 2011), reductions in fawn:adult female ratios were observed following increases in the male component of different herds. While not direct evidence of a cause-and-effect relationship, these results were potentially indicative that resource limitation was occurring and competitive interactions between different sexes and age classes of deer resulted in shifts in population ratios. A review by Mysterud et al. (2002) also emphasizes the asymmetric and non-trivial effects that males can inject into population dynamics.

In line with the hypothesis that mule deer are limited by winter range habitat, the role of coyote predation on mule deer does not appear to be limiting. The experimental evaluation of coyote removal on deer population dynamics has been robust. However, whether the effects of mountain lion predation on adult female deer in Colorado are additive or compensatory remains unclear. It is likely the impact of this predation is variable, depending on other environmental factors such as deer density, alternate prey species, winter severity, or disease incidence. Based on the abundance of mountain lion habitat in Colorado, as well as conservative mountain lion harvest management strategies, assuming that mountain lion predation on Colorado's mule deer is weakly additive may be reasonable. The population-level effect of bear predation on mule deer neonates (≤ 2 months old) also remains unclear. Evidence from other predator–prey systems that are comprised of a more complex predator assemblage (e.g. brown bears, black bears, wolves *Canis lupus* and mountain lions) indicates that bear predation during this period is additive. In the absence of robust experimentation on the roles of mountain lion and bear predation, their impact on mule deer population dynamics will remain elusive.

Despite the existing research and knowledge, other key factors that may influence Colorado's mule deer population dynamics remain untested. For example, despite a large increase in Colorado's elk population between the 1960s and present time, interspecific competition between mule deer and elk has not been evaluated. An additional factor that limits the inference of this review is the fact that the research pertaining to density-dependence and winter range limitation on Colorado's mule deer herds has occurred at small spatial scales. To extend the existing body of knowledge to field management levels, we recommend a large scale integrative study that would address interactions between multiple predator and prey species, and multiple sources of mortality. In particular, experimental manipulations of the density of multiple herbivores at the herd level would allow investigation of interspecific competition, while also providing further insights into intraspecific competition. When put in the context of harvest management and herd management plans, managers and biologists would benefit from a quantitative assessment of deer and elk population interactions. A specific example might include the experimental reduction in herd size of one species, with the desired outcome being a positive response in population parameters (e.g. young:adult ratios, or survival rates) for both species, or an increase in overall abundance for the other species. Such an integrated study would also allow for an evaluation of the interactive effects of multiple mortality sources on populations. While winter browse availability and quality appears to set the upper limit for deer herds in Colorado (i.e. habitat is population limiting), a suite of other factors may regulate how quickly a deer herd reaches that limit. A hypothetical example can be constructed for Colorado's Front Range where CWD prevalence is high. Krumm et al. (2009) and Miller et al. (2008) found that mountain lions are capable of selecting for CWD infected deer. However, mountain lion diets are diverse and also included non-infected deer. Similarly, due to private land ownership and limited hunter access, hunter harvest of mountain lions is typically low in this region, potentially leading to high densities of mountain lions. The interaction of disease and predation, coupled with high predator/prey ratios could conceivably have a strong regulatory effect on deer population growth.

An integrated density experiment could also evalauate the regulating effects of coyote predation on deer. Evidence from a white-tailed deer *Odocoileus virginianus* and coyote predator–prey system demonstrated that coyote predation may have greater impact on deer populations, and thereby become additive in nature, when deer populations are at lower densities, although this result was confounded by the fact that predation rates on deer were also linked to densities of alternative prey, snowshoe hares *Lepus americanus* (Patterson and Messier 2000). To date, there are insufficient data to make similar conclusions about the impacts of coyotes on low density mule deer herds in Colorado. Specifically, if coyote predation becomes additive at low deer densities, determining the density at which that switch begins to occur is currently impossible. An ideal study would assess the inflection points at which the effects of predation switch from being additive – likely at low prey densities – to compensatory – likely at high prey densities.

Finally, research focused on the roles of weather, climate and summer range has not been conducted. A growing body of evidence has shown that plant phenology during spring, summer, and fall plays an important role on large ungulate demography. In particular, the role of forage abundance and quality outside of winter months has been shown to drive body mass for several North American ungulates (Cook et al. 2004, Giroux et al. 2014, Hurley et al. 2014). Declining body condition and body mass of adult females can impact age of first reproduction, neonatal rates, and also annual pregnancy rates, all of which are components of lagged density dependence. However, mule deer research in Colorado has been narrowly focused on winter habitat. Similarly, the relationship between climate phenomena and Colorado's mule deer population performance remains unexplored. While addressed more frequently for European and arctic ungulates, and North Atlantic weather patterns (Post and Forchhammer 2002, Stien et al. 2012), the relationship between weather, climate and mule deer remains largely uninvestigated (but see Marshal and Bleich 2011). Particularly as they relate to shifts in abundance in Colorado, linking the contribution of El Niño and La Niña weather events to large declines in mule deer may prove to temper concerns over herd health.

In conclusion, understanding of mule deer population ecology and management remain constrained by several gaps in knowledge. While research can be expected to continue, other useful sources of data can be exploited in the interim. For example, age, mass and reproductive data from hunter harvested deer are not currently collected. If these data can be collected in an unbiased manner, they will lend insight to important population attributes such as population age structure, cohort effects, and overall productivity. Likewise, in the absence of further information, herd management strategies can be re-evaluated. Based on the premise that $K$ is variable, and largely dependent on stochastic weather patterns, setting abundance ($N$) objectives to align with $K$ during extreme conditions may be prudent. By maintaining $N$ at or below the perceived $K$ for harsh winters, the per capita rate of change ($R$) will increase, thus minimizing the negative impacts of stochastic weather events, and also allowing quick population growth if forage quality or quantity improve.

*Acknowledgements* – Financial and logistic support for this research was provided by Colorado Parks and Wildlife and Colorado State University. The ideas presented in this manuscript stem from conversations with many people. In particular, we are indebted to C. Anderson, C. Bishop, J. Broderick, M. Hurley and P. Lukacs, as well as many of the terrestrial biologists and wildlife researchers that work for Colorado Parks and Wildlife. Comments on earlier versions of this manuscript were provided by C. Anderson, C. Bishop, R. Conrey, K. Logan and Paul Doherty's lab group at Colorado State University. The critical comments provided by A. Loison also improved the quality of this paper.

## References

Allendorf, F. W. and Hard, J. J. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. – Proc. Natl Acad. Sci. USA 106(Suppl. 1): 9987–9994.

Ballard, W. B. 1992. Bear predation on moose: a review of recent North American studies and their management implications. – Alces 28 (Suppl. 1): 162–176.

Ballard, W. B. et al. 2001. Deer–predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. – Wildl. Soc. Bull. 29: 99–115.

Barber-Meyer, S. M. et al. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. – Wildl. Monogr. 169: 1–30.

Bartmann, R. M. et al. 1992. Compensatory mortality in a Colorado mule deer population. – Wildl. Monogr. 121: 3–39.

Beck, J. L. and Peek, J. M. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. – Rangeland Ecol. Manage. 58: 135–147.

Bergman, E. J. 2013. Evaluation of winter range habitat treatments on overwinter survival, density, and body condition of mule deer. – PhD thesis, Colorado State Univ., Fort Collins, CO.

Bergman, E. J. et al. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. – Ecol. Appl. 16: 273–284.

Bergman, E. J. et al. 2011. Biological and socio-economic effects of statewide limitation of deer licenses in Colorado. – J. Wildl. Manage. 75:1443–1452.

Bishop, C. J. et al. 2005. Effect of limited antlered harvest on mule deer sex and age ratios. – Wildl. Soc. Bull. 33: 662–668.

Bishop, C. J. et al. 2009. Effect of enhanced nutrition on mule deer population rate of change. – Wildl. Monogr. 172: 1–28.

Boertje, R. D. et al. 2009. Managing for elevated yield of moose in interior Alaska. – J. Wildl. Manage. 73: 314–327.

Boutin, S. 1992. Predation and moose population dynamics: a critique. – J. Wildl. Manage. 56: 116–127.

Boyce, M. S. et al. 1999. Seasonal compensation of predation and harvesting. – Oikos 87: 419–426.

Brown, G. S. 2011. Patterns and causes of demographic variation in a harvested moose population: evidence for the effects of climate and density-dependent drivers. – J. Anim. Ecol. 80: 1288–1298.

Burnham, K. P. and Anderson, D. R. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. – Ecology 65: 105–112.

Ciuti, S. et al. 2012. Human selection of elk behavior in a landscape of fear. – Proc. R. Soc. B 279: 4407–4416.

Conner, M. M. and Miller, M. W. 2004. Movement patterns and spatial epidemiology of a prion disease in mule deer populations. – Ecol. Appl. 14: 1870–1881.

Conner, M. M. et al. 2001. Elk movement in response to early-season hunting in northwest Colorado. – J. Wildl. Manage. 65: 926–940.

Conner, M. M. et al. 2007. A meta-BACI approach for evaluating management intervention on chronic wasting disease in mule deer. – Ecol. Appl. 17: 140–153.

Cook, J. G. et al. 2004. Effects of summer–autumn nutrition and parturition date on reproduction and survival of elk. – Wildl. Monogr. 155: 1–61.

Dulberger, J. et al. 2010. Estimating chronic wasting disease effects on mule deer recruitment and population growth. – J. Wildl. Dis. 46: 1086–1095.

Farnsworth, M. L. et al. 2006. Linking chronic wasting disease to mule deer movement scale: a hierarchical Bayesian approach. – Ecol. Appl. 16: 1026–1036.

Eberhardt, L. L. 1977. "Optimal" management policies for marine mammals. – Wildl. Soc. Bull. 5: 162–169.

Errington, P. L. 1934. Vulnerability of bobwhite populations to predation. – Ecology 15: 110–127.

Gaillard, J. M. et al. 1998. Population dynamics of large herbivores: variable recruitment with constant survival. – Trends Ecol. Evol. 13: 58–63.

Gaillard, J. M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – Annu. Rev. Ecol. Syst. 31: 367–393.

Garrott, R. A. and White, G. C. 1982. Age and sex selectivity in trapping mule deer. – J. Wildl. Manage. 46: 1083–1086.

Gasaway, W. C. et al. 1983. Interrelationships of wolves, prey, and man in interior Alaska. – Wildl. Monogr. 84.

Gasaway, W. C. et al. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. – Wildl. Monogr. 120: 1–59.

Gill, R. B. 2001. Declining mule deer populations in Colorado: reasons and responses. – Colorado Div. of Wildlife, Spec. Rep. No. 77, Fort Collins, CO, USA.

Giroux, M. A. et al. 2014. Forage-mediated density and climate effects on body mass in a temperate herbivore: a mechanistic approach. – Ecology 95: 1332–1340.

Gotelli, N. J. 2008. A primer of ecology, 4th edn. – Sinauer.

Gross, J. E. and Miller, M. W. 2001: Chronic wasting disease in mule deer: disease dynamics and control. – J. Wildl. Manage. 65: 205–215.

Harrington, J. L. and Conover, M. R. 2007. Does removing coyotes for livestock protection benefit free-ranging ungulates? – J. Wildl. Manage. 71: 1555–1560.

Hassell, M. P. 1975. Density-dependence in single-species populations. – J. Anim. Ecol. 44: 283–295.

Hassell, M. P. et al. 1976. Patterns of dynamical behavior in single species populations. – J. Anim. Ecol. 45: 471–486.

Hilborn, R. et al. 1995. Sustainable exploitation of renewable resources. – Annu. Rev. Ecol. Syst. 26: 45–67.

Hixon, M. A. et al. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. – Ecology 83: 1490–1508.

Hobbs, N. T. and Swift, D. M. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. – J. Wildl. Manage. 49: 814–822.

Hurley, M. A. et al. 2014. Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. – Phil. Trans. R. Soc. B 369: 20130196.

Hurley, M. A. et al. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. – Wildl. Monogr. 178: 1–33.

Johnson, H. et al. 2012. Quantifying loss and degradation of mule deer habitat across western Colorado. – Res. Project Proposal, Colorado Parks and Wildlife, Durango, CO, USA.

Kline, J. D. et al. 2010. Anticipating forest and range land development in central Oregon (USA) for landscape analysis, with an example application involving mule deer. – Environ. Manage. 45: 974–984.

Kokko, H. and Lindström, J. 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. – Ecol. Modell. 110: 293–304.

Krumm, C. E. et al. 2009. Mountain lions prey selectively on prion-infected mule deer. – Biol. Lett. 6: 209–211.

Lindzey, F. G. et al. 1997. Potential for competitive interactions between mule deer and elk in the western United States and Canada: a review. – Wyoming Cooperative Fish. Wildl. Res. Unit, Laramie, WY, USA.

Lukacs, P. M. et al. 2009. Separating components of variation in survival of mule deer in Colorado. – J. Wildl. Manage. 73: 817–480.

Marshal, J. P. and Bleich, V. C. 2011. Evidence of relationships between El Niño Southern Oscillation and mule deer harvest in California. – Calif. Fish Game 97: 84–97.

McKean, W. T. and Bartmann, R. W. 1971. Deer–livestock relations on a pinyon–juniper range in northwestern Colorado. – Wildl. Res. Rep., Colorado Game, Fish and Parks, Fort Collins, CO, USA.

Messier, F. 1991 The significance of limiting and regulating factors on the demography of moose and white-tailed deer. – J. Anim. Ecol. 60: 377–393.

Miller, M. W. et al. 2008. Lion and prions and deer demise. – PloS ONE 3(12): e4019.

Monteith, K .L. et al. 2013. Effects of harvest, culture, and climate on trends in size of horn-like structures in trophy ungulates. – Wildl. Monogr. 183: 1–28.

Mysterud, A. et al. 2002. The role of males in the dynamics of ungulate populations. – J. Anim. Ecol. 71: 907–915.

Nellemann, C. et al. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. – Biol. Conserv. 113: 307–317.

Nichols, J. D. et al. 1995. Managing North American waterfowl in the face of uncertainty. – Annu. Rev. Ecol. Syst. 26: 177–199.

Nichols, J. D. et al. 2007. Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. – J. Ornithol. 149 (Suppl. 2): 343–349.

Patterson, B. R. and Messier, F. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. – J. Wildl. Manage. 64: 721–732.

Pojar, T. M. and Bowden, D. C. 2004. Neonate mule deer fawn survival in west-central Colorado. – J. Wildl. Manage. 68: 550–560.

Post, E. and Forchhammer, M. C. 2002. Synchronization of animal population dynamics by large-scale climate. – Nature 420: 168–177.

Ricker, W. E. 1954. Stock and recruitment. – J. Fish. Res. Board Can. 11: 624–651.

Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. – Trends Ecol. Evol. 12: 143–149.

Sawyer, H. and Nielson, R. 2011. Mule deer monitoring in the Pinedale Anticline Project Area. – 2011 Annu. Rep., Western EcoSystems Tech., Laramie, WY, USA.

Schwartz, C. C. et al. 2012. Impacts of rural development on Yellowstone wildlife: linking grizzly bear *Ursus arctos* demographics with projected residential growth. – Wildl. Biol. 18: 246–257.

Sinclair, A. R. E. 1989. Population regulation in animals. – In: Cherrett, J. M. (ed.), Ecological concepts: the contribution of ecology to an understanding of the natural world. Proc. Brit. Ecol. Soc. Symp., Blackwell.

Stewart, R. R. et al. 1985. The impact of black bear removal on moose calf survival in east-central Saskatchewan. – Alces 21: 403–418.

Stien, A. et al. 2012. Congruent responses to weather variability in high arctic herbivores. – Biol. Lett. 8: 1002–1005.

Swenson, J. E. 1985. Compensatory reproduction in an introduced mountain goat population in the Absaroka Mountains, Montana. – J. Wildl. Manage. 49: 837–843.

Tanner, J. T. 1966. Effects of population density on growth rates of animal populations. – Ecology 47: 733–745.

Thorne, E.T. et al. 1988. Bluetongue in free-ranging pronghorn antelope (*Antilocapra americanus*) in Wyoming: 1976 and 1984. – J. Wildl. Dis. 24: 113–119.

Torstenson, W. L. F. et al. 2006. Elk, mule deer, and cattle foraging relationships on foothill and mountain rangeland. – Rangeland Ecol. Manage. 59: 80–87.

Unsworth, J. W. et al. 1999. Mule deer survival in Colorado, Idaho and Montana. – J. Wildl. Manage. 63: 315–326.

Vieira, M. E. P. et al. 2003. Effects of archery hunter numbers and opening dates on elk movement. – J. Wildl. Manage. 67: 717–728.

Walker, R. 2011. State status reports. – Western States and Provinces Deer and Elk Workshop Proc. 9: 46–64.

Wallmo, O. C. 1981. Mule and black-tailed deer of North America. – Univ. of Nebraska Press.

Watkins, B. E. et al. 2007. Habitat guidelines for mule deer: Colorado Plateau shrubland and forest ecoregion. –Mule Deer Working Group, Western Ass. of Fish and Wildlife Agencies, Cheyenne, WY, USA.

White, G. C. and Bartmann, R. M. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. – J. Wildl. Manage. 62: 214–225.

Whittaker, D. G. and Lindzey, F. G. 1999. Effect of coyote predation on early fawn survival in sympatric deer species. – Wildl. Soc. Bull. 27: 256–262.

Willoughby, S. 2012. Colorado among states struggling to stop decline of mule deer herds. – Denver Post. Published 16 May 2012, accessed 14 January 2013 (<www.denverpost.com/outdoors/ci_20630849/colorado-among-states-struggling-stop-decline-mule-deer>).

Williams, B. K. et al. 2001. Analysis and management of animal populations. – Academic Press.

Wolfe, L. L. et al. 2004. Feasibility of “test-and-cull” for managing chronic wasting disease in urban mule deer. – Wildl. Soc. Bull. 32: 500–505.

Workman, G. W. and Low, J. B. (eds) 1976. Mule deer decline in the West: a symposium. – Utah State Univ. and Utah Agric. Exp. Stn, Logan, UT, USA.

Young, D. D. and Boertje, R. D. 2011. Prudent and imprudent use of antlerless moose harvests in Alaska. – Alces 47: 91–100.

Zager, P. and Beecham, J. 2006. The role of American black bears and brown bears as predators on ungulates in North America. – Ursus 17: 95–108.

# Effect of Enhanced Nutrition on Mule Deer Population Rate of Change

**CHAD J. BISHOP,**[1] *Colorado Division of Wildlife, 317 W Prospect Road, Fort Collins, CO 80526, USA*
**GARY C. WHITE,** *Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA*
**DAVID J. FREDDY,** *Colorado Division of Wildlife, 317 W Prospect Road, Fort Collins, CO 80526, USA*
**BRUCE E. WATKINS,** *Colorado Division of Wildlife, 2300 S Townsend Avenue, Montrose, CO 81401, USA*
**THOMAS R. STEPHENSON,** *California Department of Fish and Game, 407 W Line Street, Bishop, CA 93514, USA*

**ABSTRACT** Concerns over declining mule deer (*Odocoileus hemionus*) populations during the 1990s prompted research efforts to identify and understand key limiting factors of deer. Similar to past deer declines, a top priority of state wildlife agencies was to evaluate the relative importance of habitat and predation. We therefore evaluated the effect of enhanced nutrition of deer during winter and spring on fecundity and survival rates using a life table response experiment involving free-ranging mule deer on the Uncompahgre Plateau in southwest Colorado, USA. The treatment represented an instantaneous increase in nutritional carrying capacity of a pinyon (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) winter range and was intended to simulate optimum habitat quality. Prior studies on the Uncompahgre Plateau indicated predation and disease were the most common proximate causes of deer mortality. By manipulating nutrition and leaving natural predation unaltered, we determined whether habitat quality was ultimately a critical factor limiting the deer population. We measured annual survival and fecundity of adult females and survival of fawns, then estimated population rate of change as a function of enhanced nutrition. Pregnancy and fetal rates of adult females were high and did not vary in response to treatment. Fetal and neonatal survival rates increased in response to treatment, although the treatment effect on neonatal survival was marginal. Overwinter rates of fawn survival increased for treatment deer by 0.16–0.31 depending on year and fawn sex, and none of the 95% confidence intervals associated with the effects overlapped zero. Overwinter rates of fawn survival averaged 0.905 (SE = 0.026) for treatment deer and 0.684 (SE = 0.044) for control deer. Nutritional enhancement increased survival rates of fetuses to the yearling age class by 0.14–0.20 depending on year and fawn sex; 95% confidence intervals slightly overlapped zero. When averaging estimates across sexes and years, treatment caused fetal to yearling survival to increase by 0.177 (SE = 0.082, 95% CI: 0.016–0.337). Annual survival of adult females receiving treatment ($\hat{S} = 0.879$, SE = 0.021) was higher than survival of control adult females ($\hat{S} = 0.833$, SE = 0.025). Our estimate of the population rate of change ($\hat{\lambda}$) was 1.165 (SE = 0.036) for treatment deer and 1.033 (SE = 0.038) for control deer. Increased production and survival of young (i.e., fetal, neonatal, and overwinter fawn survival) accounted for 64% of the overall increase in $\hat{\lambda}$, whereas adult female survival accounted for 36% of the increase in $\hat{\lambda}$. The effect of nutrition treatment on overwinter fawn survival alone accounted for 33% of the overall increase in $\hat{\lambda}$.

We documented food limitation in the Uncompahgre deer population because survival of fawns and adult females increased considerably in response to enhanced nutrition. We found strong evidence that enhanced nutrition of deer reduced coyote (*Canis latrans*) and mountain lion (*Puma concolor*) predation rates of ≥6-month-old fawns and adult females. Our results demonstrate that observed coyote predation, by itself, is not useful for evaluating whether coyotes are negatively impacting a deer population. Our results also indicate that mountain lions may select for deer in poorer condition under some circumstances, suggesting that mountain lion predation may not always be an additive source of mortality. Disease mortality rates of adult females did not decline in response to enhanced nutrition. Winter-range habitat quality was a limiting factor of the Uncompahgre Plateau mule deer population. Therefore, we recommend evaluating habitat treatments for deer that are designed to set-back succession and increase productivity of late-seral pinyon–juniper habitats that presently dominate the winter range. (WILDLIFE MONOGRAPHS 172:1–28)

DOI: 10.2193/2008-107

**KEY WORDS** Colorado, compensatory mortality, fecundity, food limitation, habitat quality, lambda, life table response experiment, mule deer, nutrition, *Odocoileus hemionus*, predation, survival.

# El Efecto de la Nutrición Aumentada en la Tasa de Cambio Poblacional de Venados Bura (*Odocoileus hemionus*)

**RESUMEN** Preocupaciones sobre disminuciones poblacionales de venados bura (*Odocoileus hemionus*) durante los años noventa han incitado esfuerzos de investigación para identificar y entender los factores claves limitantes de los venados. Semejante a disminuciones pasadas de los venados, la prioridad alta de las autoridades estatales era evaluar la importancia relativa del hábitat y la depredación. Por lo tanto, evaluamos el efecto de la nutrición aumentada de venados durante invierno y primavera en las tasas de fecundidad y supervivencia utilizando un experimento de respuesta de tabla de vida involucrando venados bura silvestres de la Meseta de Uncompahgre en el sudoeste de Colorado. El tratamiento representó un aumento instantáneo en la capacidad nutricional en una área invernal dominado por piñon (*Pinus edulis*) y enebro de Utah (*Juniperus osteosperma*), y fue pretendido simular la calidad óptima del hábitat. Estudios previos en la Meseta de Uncompahgre indicaron que la depredación y la enfermedad fueron las causas más comunes de la mortalidad de venados. Determinamos si la calidad del hábitat fue últimamente un factor limitante crítico de la población de venados por manipular la nutrición y dejar la depredación como fue. Medimos fecundidad y la supervivencia anual de hembras adultas y la supervivencia de los cervatos, entonces estimado la tasa de cambio poblacional en función de nutrición aumentada. El embarazo y las tasas fetales de hembras adultas eran altos y no variaron en respuesta al tratamiento. Las tasas de supervivencia fetales y neonatales aumentaron en respuesta al tratamiento, aunque el efecto del tratamiento sobre supervivencia neonatal fuera marginal. La supervivencia de ciervos por invierno fue considerablemente más alto entre venados del tratamiento que venados de control. La supervivencia de invierno incrementó por 0.16–0.31, dependiendo del año y sexo de cervato, y ninguno de los intervalos de confianza de 95% asociado con el efecto incluyó 0. La supervivencia de cervatos por invierno promediado 0.905 (EE = 0.026) para venados de tratamiento y 0.684 (EE = 0.044) para venados de control. El tratamiento de nutrición aumentada incrementó la supervivencia de fetos a la edad añal por 0.14–0.20 dependiendo de año y sexo de cervato, aunque los intervalos de confianza de 95% asociado con el efecto apenas incluyó 0. Al promediar las estimaciones a través de sexos y años, el tratamiento causó supervivencia de fetos a la edad añal incrementar por 0.177 (EE = 0.082, IC 95%: 0.016, 0.337). Supervivencia de venados hembras recibiendo el tratamiento ($\hat{S} = 0.879$, EE = 0.021) fue más alto que la

---

[1] *E-mail: chad.bishop@state.co.us*

supervivencia de venados controles ($\hat{S} = 0.833$, EE = 0.025). Nuestra estimación de la tasa de cambio poblacional, $\hat{\lambda}$, fue 1.165 (EE = 0.036) para venados tratados y 1.033 (EE = 0.038) para venados controles. La supervivencia por invierno de crías (i.e, supervivencia fetal-neonatal-ciervos pro invierno) explicó 64% del aumento global en $\hat{\lambda}$, mientras que la supervivencia de los venados hembras adultas explicó 36% del aumento en $\hat{\lambda}$. El efecto del tratamiento de nutrición en la supervivencia de ciervos por invierno solo explicó 33% del aumento global en $\hat{\lambda}$.

Documentamos limitación de alimento en la población de venados de la Uncompaghre porque la supervivencia de los ciervos y las venados hembras incrementó considerablemente en respuesta a la nutrición aumentada. Encontramos evidencia fuerte que nutrición aumentada de venados redujó depredación por coyotes (*Canis latrans*) y pumas (*Puma concolor*) en ciervos ≥6 meses de edad y en venados hembras. Nuestros resultados demuestran que depredación por coyotes observada, sola, no es útil para evaluar si los coyotes impactan negativamente a una población de venados. Nuestros resultados indican también que las pumas pueden seleccionar venados en peor condición bajo algunas circunstancias, sugeriendo que depredación por pumas no siempre puede ser una fuente aditiva de la mortalidad. Las tasas de mortalidad por enfermedad de venados hembras no disminuyeron en respuesta a la nutrición aumentada. Calidad del hábitat en el área invernal fue un factor limitante de la población de venados bura de la Meseta Uncompahgre. Por lo tanto, recomendamos evaluar tratamientos del hábitat para venados que son diseñados para retrasar la sucesión y incrementar la productividad de los habitats del piñon-enebro en etapas avanzadas de sucesión los cuales actualmente dominan la área invernal.

# Effet d'un Complément d'Alimentation sur le Taux de Croissance d'une Population de Cerfs Mulet

**RÉSUMÉ** L'inquiétude concernant le déclin des populations de cerf mulet (*Odocoileus hemionus*) durant les années 1990 a orienté les efforts de recherche vers l'identification et la compréhension des facteurs limitant ces populations. Lors des précédents déclins, l'une des priorités des agences d'état en charge de la faune sauvage a porté sur l'évaluation de l'importance relative de l'habitat et de la prédation. C'est pourquoi nous avons évalué l'impact d'un complément d'alimentation en hiver et au printemps sur les taux de fécondité et de survie, grâce à une analyse démographique impliquant des cerfs mulets en liberté sur le Plateau Uncompahgre, dans le sud-ouest du Colorado. Le complément de nutrition peut être considéré comme un accroissement immédiat de la capacité d'accueil de l'aire d'extension hivernale dont l'habitat est composé de pins du Colorado (*Pinus edulis*) et de genévriers (*Juniperus osteosperma*). Ce traitement visait à simuler un habitat de qualité optimale. Des études préliminaires sur le Plateau de Uncompahgre ont montré que la prédation et les maladies sont les principales causes immédiates de mortalité du cerf mulet. En manipulant la nutrition et en laissant la prédation inchangée, nous avons déterminé si la qualité de l'habitat constituait un facteur limitant la performance de la population. Nous avons mesuré la fécondité et la survie annuelle des femelles adultes et la survie des faons. Nous avons ensuite utilisé ces paramètres pour estimer le taux de croissance de la population en présence ou non de complément alimentaire. Les taux de gestation et le nombre moyen de foetus des femelles adultes étaient élevés et ne variaient pas dans la réponse au traitement. Le taux de survie foetale et néonatale a augmenté en réponse au traitement, bien que l'effet du traitement sur la survie néonatale ait été marginal. Le taux de survie hivernale des faons était nettement plus élevé pour les cerfs ayant reçu l'apport nutritionel que pour les cerfs ayant servi de témoin. La survie hivernale des faons a augmenté de 0.16–0.31, suivant l'année et le sexe du faon, et aucun des intervalles de confiance à 95% associés à l'effet n'incluait 0. La survie hivernale des faons était en moyenne 0.905 (SE = 0.026) pour les cerfs de traitement et 0.684 (SE = 0.044) pour les cerfs de contrôle. L'amélioration nutritionnelle a augmenté le taux de survie des foetus âgés de 1 an de 0.14?0.20, suivant l'année et le sexe, bien que l'intervalle de confiance à 95% incluait 0. En faisant une moyenne des estimations sur les sexes et les années, le traitement d'apport nutritionel a permis une augmentation de la survie depuis le stade foetal jusqu'à deux ans de 0.177 (SE = 0.082, 95% CI: 0.016, 0.337). Le complément alimentaire a également eu un effet positif sur la survie des femelles adultes. La survie des femelles ayant reçu le traitement ($\hat{S} = 0.879$, SE = 0.021) était supérieure à la survie des individus témoins ($\hat{S} = 0.833$, SE = 0.025). Notre estimation du taux de multiplication de la population $\hat{\lambda}$ est égale à 1.165 (SE = 0.036) pour les cerfs ayant reçu le traitement et 1.033 (SE = 0.038) pour les cerfs témoins. L'augmentation de survie des jeunes (i.e., survie fétale, néonatale et survie hivernale des faons) expliquait 64% de l'augmentation totale de $\hat{\lambda}$, contre 36% pour l'augmentation de survie des femelles adultes. L'effet du traitement nutritionnel sur la survie hivernale des faons représentait à elle seule 33% de l'augmentation totale de $\hat{\lambda}$.

L'augmentation de $\hat{\lambda}$ en réponse à un supplément alimentaire nous a permis de mettre en évidence que la croissance de la population de cerfs de l'Uncompahgre est limitée par la ressource en nourriture. Nous avons montré que l'amélioration de la nutrition réduit les taux de prédation par le coyote (*Canis latrans*) et le puma (*Puma concolor*) sur les femelles adultes et les faons de plus de 6 mois. Nos résultats montrent que l'observation de prédation les coyotes n'est pas en soi utile pour déterminer si cette prédation a ou non un impact négatif sur une population de cerfs. Nos résultats indiquent également que, sous certaines circonstances, les pumas pourraient sélectionner les cerfs en mauvaise condition, ce qui suggère que la prédation par les pumas n'est probablement pas toujours une source de mortalité additive. Le taux de mortalité par maladie des femelles adultes n'a pas diminué en réponse à l'amélioration de la nutrition. La qualité de l'habitat dans l'aire de répartition hivernale est un facteur limitant la population de cerfs mulets du Plateau de Uncompahgre. Par conséquent, nous recommandons l'évaluation de traitements visant au retour des successions végétales et à l'accroissement de la productivité des habitats non-climaciques de pins/genévriers, lesquels dominent actuellement la répartition hivernale du cerf-mulet.

## Contents

## INTRODUCTION

Mule deer (*Odocoileus hemionus*) populations apparently declined during the 1990s across much of the western United States and present numbers are well below peak population levels documented during the 1940s–1960s (Unsworth et al. 1999, Gill et al. 2001, Heffelfinger and Messmer 2003). An understanding of limiting factors is necessary to understand why populations may have declined and to guide management efforts aimed at increasing deer numbers (Gill et al. 2001, de Vos et al. 2003). Factors limiting growth of mule deer populations are difficult to understand because they are numerous, interacting, and subject to variability. Climatic variation can cause wide population fluctuations and may be the primary reason for observed changes, yet managers are concerned with factors that can be manipulated through management actions. Predation and habitat have typically received the most attention from wildlife agency administrators, biologists, and sportsmen. Predation is routinely identified as the most common proximate cause of deer mortality. Habitat quality is believed to have declined across much of the western United States because of altered fire regimes and associated plant successional changes, invasion of noxious weeds, overgrazing, energy development, and habitat loss caused by urban development (Lutz et al. 2003, Watkins et al. 2007).

Identification of principal limiting factor(s) is necessary to make informed management decisions. Some mule deer populations may be driven by extreme environmental variation that is primarily density independent, in which case the preferred management strategy may be to monitor populations, or perhaps climate variables, and make responsive harvest decisions (Mackie et al. 1998). However, in less-variable environments, determining whether habitat or predation is most limiting has substantial management implications because the 2 factors represent divergent limitation scenarios.

The relationship between habitat quality and deer population size is heavily rooted in density-dependence theory. As populations approach or exceed nutritional carrying capacity (NCC) of a given environment, fecundity and survival are expected to decline. Nutritional carrying capacity refers to the number of animals that can be supported on a specified landscape given animal nutrient requirements relative to nutrient availability (McLeod 1997). Density-dependent effects have been demonstrated in body condition (Gaillard et al. 1996, Stewart et al. 2005, Kjellander et al. 2006), fecundity (Clutton-Brock et al. 1987, Stewart et al. 2005), and survival (Clutton-Brock et al. 1987, Bartmann et al. 1992, Singer et al. 1997, White and Bartmann 1998) of ungulates. Gaillard et al. (2000) provided a detailed review of density-dependent effects in fecundity and survival of ungulates. If a population is limited by NCC and demonstrating density-dependent feedback, wildlife managers have 2 main options for improving fawn production and survival. One option is to increase adult female harvest to reduce adult female density and increase fawn production and survival. Under this option, the management goal is to optimize age and sex ratios to increase the number of adult males available for harvest (McCullough 1979, 2001). A second option is to improve habitat quality for deer to increase total deer numbers.

When deer populations are below NCC, predation will more likely be a source of additive mortality and biological concern (Ballard et al. 2001). If a population is limited by predation, wildlife managers should pursue management options different than those mentioned above. First, adult female harvest should be minimized, or at least conservatively managed, to maximize production and survival of young. Second, predator control or liberalized harvest of predator species may be considered to lessen mortality and increase deer numbers. Habitat treatments and predator control can be costly in terms of both economic and social capital. Neither option should be pursued without adequate justification.

To determine the importance of different limiting factors, a specific effect must be isolated, often in the context of considerable background variation (i.e., process variance). The relative importance of habitat quality versus predation can be ascertained by manipulating one factor and leaving the other unaltered in a field experiment. If habitat quality is ultimately limiting the deer population, such that further population growth is restricted by NCC, then we would expect observed predation to have minimal effect on population growth (Bartmann et al. 1992, Ballard et al. 2001). In contrast, if the population is below NCC and predation is a common proximate mortality cause, we might expect some threshold of predator removal to cause an increase in the deer population. Ideally, 2 field experiments should be conducted: one that manipulates predation and one that manipulates habitat. Hurley and Zager (2006) conducted an intensive predator control study in southeast Idaho, USA, measuring deer population parameters in response to reductions in coyote (*Canis latrans*) and mountain lion (*Puma concolor*) numbers. Coyote reductions caused an increase in neonatal deer survival during some years, although coyote predation on neonates was found to be partially compensatory. Coyote reductions had no measurable effect on 6-month-old fawn survival, adult female survival, or population size. Mountain lion reductions caused an increase in deer survival that resulted in a small increase in population size. We complemented Hurley and Zager's (2006) study by manipulating deer nutrition and not manipulating coyote and mountain lion predation.

We studied a deer population in southwest Colorado, USA, that declined during the decade preceding our research (B. E. Watkins, Colorado Division of Wildlife [CDOW], unpublished data); the decline was in part caused by a concurrent decline in December fawn recruitment (White et al. 2001). Anecdotal evidence indicated that quality of winter-range habitat in the area declined during recent decades in response to fire suppression, long-term grazing practices, and a surge in urban and exurban development on winter range. Winter-range habitat predominantly comprised late-seral pinyon (*Pinus edulis*)–Utah juniper (*Juniperus osteosperma*) woodlands with minimal understory vegetation and limited species diversity. In contrast, anecdotal evidence indicated summer range, which comprised mosaics of aspen (*Populus tremuloides*), mountain shrub, mountain big sagebrush (*Artemisia tridentata*), and Gambel oak (*Quercus gambelii*) with vigorous understory, was highly productive for deer. We hypothesized that poor habitat quality on winter range contributed to the observed decline of the deer population. Predation by coyotes and mountain lions was presented as a competing hypothesis as to why the population declined.

We implemented an instantaneous increase in NCC of winter range habitat and measured deer population responses. We did not manipulate predator numbers or any other potential limiting factor, and we conducted the entire study with free-ranging mule deer. Our research objective was to evaluate the effect of enhanced nutrition on a mule deer population in the context of a life table response experiment (Caswell 2001). Specifically, we evaluated the effect of enhanced nutrition on pregnancy rates and numbers of fetuses produced; fetal, neonatal, and overwinter fawn survival; and annual survival of adult females. We then used these estimates to quantify the effect of enhanced nutrition on population rate of change. Our ultimate goal was to determine whether habitat was limiting a deer population in which predation was the most common proximate mortality factor.

# STUDY AREA

We conducted our research in southwest Colorado on the southern half of the Uncompahgre Plateau and in the adjacent San Juan Mountains (Fig. 1). Our winter range study area comprised 2 sites, or experimental units (EUs; Fig. 2): the Colona EU (38°21′N, 107°49′W) and the Shavano EU (38°27′N, 108°01′W). Winter-range EUs ranged in elevation from 1,830 m to 2,290 m and comprised pinyon–Utah juniper woodlands with interspersed big sagebrush adjacent to irrigated agricultural fields. During our study, annual precipitation averaged 22.3 cm and minimum temperature in January averaged −8.2° C in Montrose, Colorado, which is 60 m below the lowest winter range elevation in either EU (Western Regional Climate Center [WRCC] 2005). Deer occupied winter range EUs from November through April each year. Estimated deer densities varied between 31 deer/km$^2$ and 59 deer/km$^2$ in each EU during the study, with densities periodically reaching 85 deer/km$^2$ in portions of an EU when receiving nutritional enhancement treatment. We estimated deer densities in each EU using mark–resight surveys from helicopter on 4 occasions and from the ground on one occasion (C. J. Bishop, CDOW, unpublished data).

Summer range fell between 37°49′N and 38°28′N latitude and 107°26′W and 108°17′W longitude (Fig. 1). Elevations ranged from 1,830 m to 3,500 m, with most deer summering between 2,600 m and 3,000 m. Radiocollared deer from the 2 winter-range EUs were intermixed throughout most of the summer range,

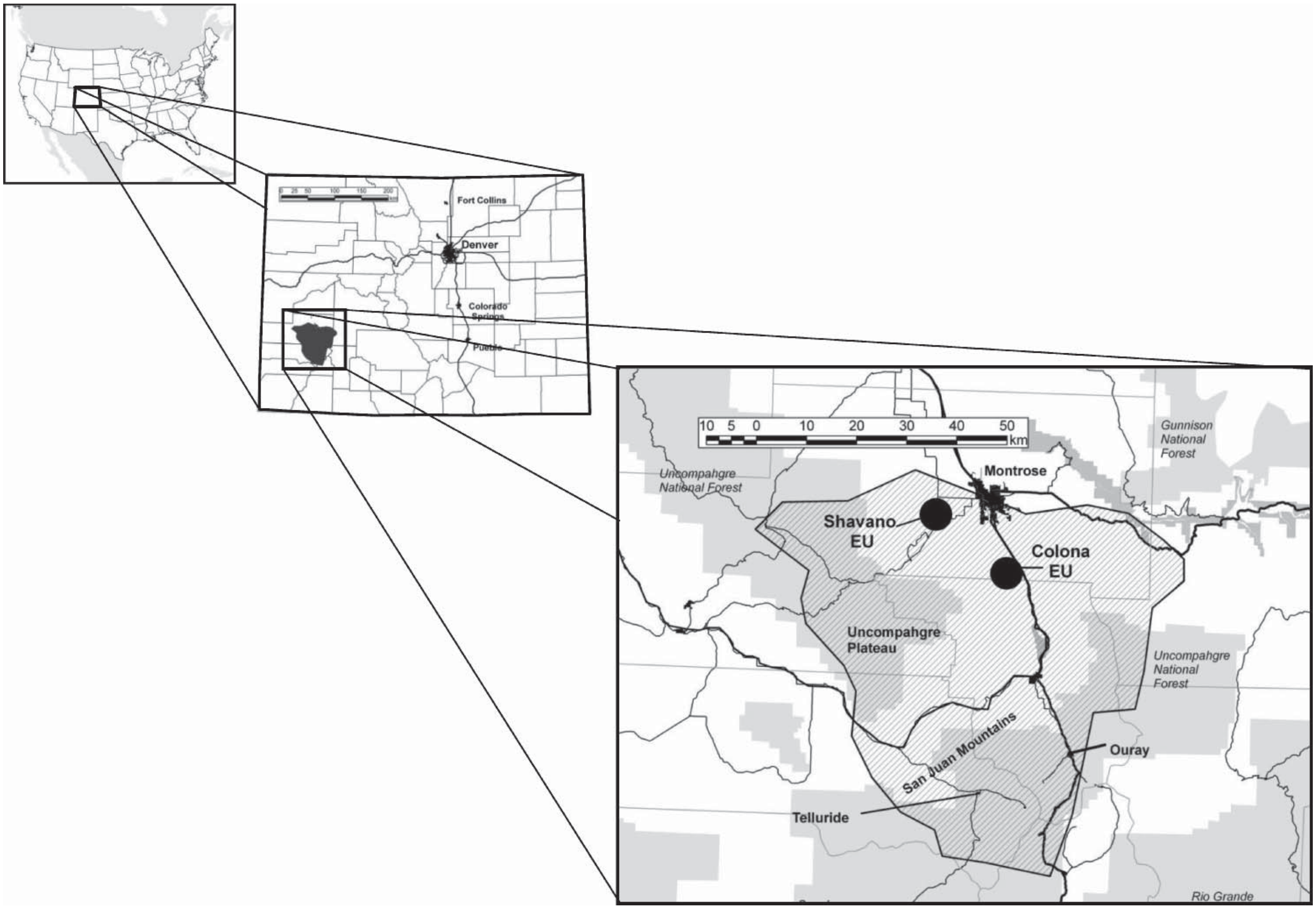


**Figure 1.** Location of winter-range experimental units (EU; ●) and summer-range study area (diagonal lines) on the Uncompahgre Plateau and adjacent San Juan Mountains in southwest Colorado, USA, where we studied effects of enhanced nutrition on mule deer population performance, 2000–2004.

lessening potential confounding of summer-range habitat use on the effect of the winter-range nutrition treatment (Fig. 2). The notable exception was an area located 12 km directly southwest of the Shavano EU, which was used exclusively by deer from the Shavano EU.

Dominant habitat types on the summer range, from lower to higher elevations, were pinyon–juniper, Gambel oak, ponderosa pine (*Pinus ponderosa*), big sagebrush, aspen, and mixed forests of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Diverse habitat mosaics occurred at interfaces of each of the major habitat types. Snowberry (*Symphoricarpos* spp.) was a common understory shrub in Gambel oak, ponderosa pine, and aspen habitats and occasionally in sagebrush habitats. Annual precipitation averaged 57.4 cm and maximum temperature in July averaged 26.7° C at the Ouray weather station situated at 2,376 m elevation in the summer range (WRCC 2005).

Deer hunting was limited throughout our study area and hunting pressure was nearly constant during 2000–2004. Our study area comprised substantial portions of CDOW Game Management Units (GMUs) 61, 62, and 65. These 3 GMUs encompassed 7,700 $km^2$ with an estimated population of approximately 40,000 deer (B. E. Watkins, unpublished data).

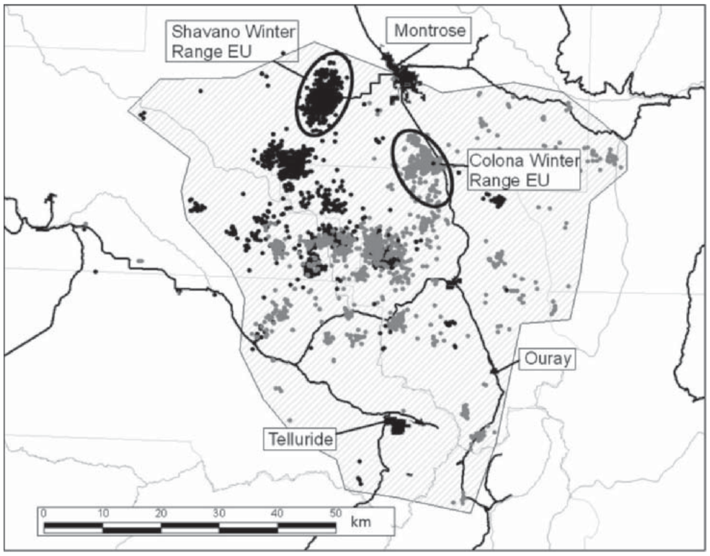


**Figure 2.** Annual locations of radiocollared mule deer on the Uncompahgre Plateau and adjacent San Juan Mountains in southwest Colorado, USA, 2000–2004. Locations of deer captured in the Shavano experimental unit (EU) are shown in black; locations of deer captured in the Colona EU are shown in gray.

The population estimate was based on a 20-year population model that incorporated periodic estimates of population size from sample-based aerial surveys, annual harvest estimates, and annual measurements of age and sex ratios. Beginning in 1997, the model included annual measurements of overwinter fawn survival and annual survival of adult females. The CDOW issued 2,435–2,760 licenses for adult male deer annually across the 3 GMUs during our study. Hunters harvested 1,200–1,600 adult male deer/year, or roughly 3–4% of the population. There were no hunting seasons for adult female or fawn deer, although ≤135 adult females were harvested annually to alleviate game damage across the 3 GMUs. Each winter-range EU comprised mostly public land and received roughly equal hunting pressure on adult male deer during late October and early November.

# METHODS

## Site Selection

We selected our winter range EUs (Fig. 2) based on several criteria. First, we selected EUs that were separated by ≥15 linear km to prevent individual deer from occupying >1 EU. Second, we selected EUs with high deer densities (i.e., >30 deer/km$^2$) so that we could capture adequate samples of deer without making EUs large. We restricted the size of EUs to roughly 15 km$^2$ to lessen logistical constraints associated with daily delivery of the nutrition enhancement treatment. We believed 15 km$^2$ would be adequate to meet sample-size objectives of deer, given deer densities. Deer densities were estimated across the Uncompahgre Plateau using sample-based helicopter surveys with 0.65-km$^2$ sample units (Kufeld et al. 1980; B. E. Watkins, unpublished data). Deer densities generally increased from northwest (<2 deer/km$^2$) to southeast (>30 deer/km$^2$) across the Uncompahgre Plateau; therefore we located our study area on the southern half of the plateau. Finally, we selected EUs that comprised similar habitats with low numbers of wintering elk (i.e., <50 elk in a normal winter). We defined summer range based on migratory movements of radiocollared deer captured in the winter-range EUs.

We studied free-ranging deer and therefore EU size was not static. We defined the core of each EU as the area that received the nutrition treatment and contained roughly 90% of the radiocollared deer captured in that unit. The core of the Colona EU was 7 km$^2$ when it received the treatment during 2000–2002. However, during 2002–2004, to achieve sample-size objectives we expanded the core area to 12 km$^2$ in response to shifts in deer distribution. The core of the Shavano EU was 22 km$^2$ throughout the study. Each EU encompassed approximately 40 km$^2$ when considering movements of all radiocollared deer (Fig. 2). Summer range for 95% of the radiocollared deer covered 2,500 km$^2$, whereas the total summer range encompassed approximately 4,000 km$^2$.

## Treatment

We increased NCC by enhancing deer nutrition using a supplemental diet, which was intended to simulate optimum habitat quality from a nutritional standpoint. We opted not to use mechanical treatments or prescribed fire because the treatments could have failed to effectively increase NCC, making it impossible to determine the relative importance of habitat quality and predation. Additionally, we did not want to study the effectiveness of habitat-treatment strategies until after we determined whether habitat was indeed limiting.

The Colona EU received a nutrition enhancement treatment during winters 2000–2001 and 2001–2002 and the Shavano EU served as a control. We then reversed the treatment–control designations during winters 2002–2003 and 2003–2004 (i.e., crossover experimental design). We only enhanced nutrition of deer on winter range. Multiple studies have found habitat quality on summer range to be a key limiting factor of ungulate body condition, fecundity, and survival (Julander et al. 1961, Gaillard et al. 2000, Cook et al. 2004). In our study area, however, anecdotal evidence strongly suggested that quality of summer-range habitat was high relative to other summer ranges across the western United States, whereas quality of winter-range habitat was poor relative to other winter ranges.

We enhanced nutrition of deer in the treatment EU from early-mid December through April each year by providing a pelleted supplemental feed. The supplement was developed through testing with both captive and wild deer and has been safely used in applied research and management (Baker and Hobbs 1985, Baker et al. 1998). The pelleted ration was commercially produced in the form of 2 × 1 × 0.5 cm wafers (Baker and Hobbs 1985) by Ranch-Way Feed Mills (Fort Collins, CO). The supplement provided 63% in vivo dry matter digestibility and 22% crude protein (Baker et al. 1998). Average-sized fawns and adult females in the treatment EU should have met maintenance energy requirements during winter (Thompson et al. 1973, Baker et al. 1979, Holter et al. 1979*b*) by consuming 0.7–0.9 kg and 1.1–1.4 kg of the supplement per day, respectively (Swift 1983, Baker et al. 1998). Based on estimated deer and elk densities in treatment EUs (C. J. Bishop, unpublished data), expected elk consumption rates (i.e., 4.5 kg/elk/day), and daily quantities of the supplement provided, we estimated that consumption was roughly 1.4–2.0 kg/deer/day. Deer consuming the supplement should have exceeded maintenance protein requirements (Ullrey et al. 1967, Smith et al. 1975, Holter et al. 1979*a*).

We distributed pellets daily from 22.7-kg bags using pickup trucks, all-terrain vehicles, and snowmobiles on primitive roads throughout the EU. We distributed each bag of pellets in approximately 20–25 piles in a linear fashion. We spread pellets throughout the entire EU to minimize animal concentrations and to prevent dominant animals from restricting fawn access to the feed. We supplied pellets ad libitum such that residual pellets remained throughout the EU when we provided the next day's ration, except during winters 2001–2002 and 2003–2004, when elk often consumed residual pellets. This protocol required distribution of 800–2,000 kg of feed per day, depending on number of elk present, weather, and availability of natural forage. Our approach typically allowed all ages and sexes of deer unlimited access to the supplement. We documented deer use of feed using visual observations and daily monitoring of radiocollared deer. We recorded 1,957 visual observations of radiocollared deer consuming the supplement.

We designed our study such that diet quality of treatment deer should have exceeded diet quality potential of deer on native winter range, even under optimum habitat conditions. Our intent was not to determine the exact level of nutritional enhancement necessary to effect a change in fecundity or survival, but rather to determine if nutrition was a significant factor limiting fawn recruitment in a declining population where predation and disease were common proximate mortality factors.

### Response Variables

Enhanced nutrition of wintering deer could positively impact populations by increasing productivity of adult females and by increasing survival of ≥6-month-old fawns and adult females. We therefore evaluated the effect of treatment on fawn production, neonatal survival, overwinter fawn survival, and annual survival of adult females. We initially planned to use December fawn:adult female ratios as a response variable to reflect fecundity and neonatal survival. However, we struggled to measure fawn:adult female ratios with desired precision and without bias (Bishop et al. 2005*b*). High deer densities and heavy cover in combination with small EUs contributed to the problem of measuring age ratios adequately. Others have demonstrated that young:adult female ratios can be poor measures of recruitment in ungulates and that pregnancy rates, fetal numbers, and juvenile survival rates should be estimated directly from marked animals (Bonenfant et al. 2005). We therefore measured fecundity and survival rates directly beginning in year 2 of the study. Specifically, we measured pregnancy and fetal rates of adult females (Feb), fetal survival (Feb–Jun), neonatal survival (Jun–Dec), and overwinter survival of fawns (Dec–Jun). We defined pregnancy rate as the proportion of adult females having ≥1 fetus in utero during late February, and we defined fetal rate as mean number of fetuses per pregnant adult female during late February. We defined fetal survival as the survival rate of fetuses in utero from February to birth, which we treated as a fecundity parameter. We evaluated the effect of treatment on fawn production and survival exclusively using direct measures of fecundity and survival rates. We also measured annual survival of adult females each year. We then used fecundity parameters (i.e., pregnancy and fetal rates and fetal survival) and survival parameters (i.e., neonatal, overwinter fawn, and adult female survival) in a matrix population model to quantify the population rate of change (λ; Caswell 2001).

### Sample Size Objectives

All fetuses and neonates we used were offspring of radiocollared adult females occupying one of the winter-range EUs. This condition was necessary to appropriately assign treatment status to neonates captured on summer range. Given our dependence on marked adult females to achieve target samples of neonates, we increased our adult female sample throughout the study rather than maintain a specified sample size. We placed vaginal implant transmitters (VITs) in some adult females to facilitate capture of neonates. During 2002, we based sample size of adult females receiving VITs on an evaluation of VIT effectiveness for capturing neonates (Bishop et al. 2002, 2007; Bishop 2007). During 2003–2004, we based sample sizes on number of adult females needed to achieve a target sample of neonates.

We desired to have adequate power to detect a difference in neonatal survival rates of 0.15 between experimental groups (EGs) because this difference reflected the approximate reduction in December fawn:adult female ratios that occurred during the 2 decades in which the Uncompahgre deer population declined (White et al. 2001; B. E. Watkins, unpublished data). Experimental group refers to deer that directly (ad F and ≥6-month-old fawns) or indirectly (fetuses and neonates) received treatment (treatment EG) or did not receive treatment (control EG). For example, treatment EG included neonatal fawns born from radiocollared adult females that occupied the treatment EU the previous winter. A sample size of 40 neonates per EG per year provided power of 0.81 to detect a difference of 0.15 in survival between treatment and control fawns, assuming survival of control fawns was 0.40. We assumed a control survival rate of 0.40 based on previous neonatal survival rates measured on the Uncompahgre Plateau and December fawn:adult female ratios measured during the late 1980s and 1990s, when the Uncompahgre population declined (White et al. 2001, Pojar and Bowden 2004). We determined that 60 radiocollared adult females (30 treatment and 30 control) equipped with VITs would facilitate capture of ≥80 newborn fawns (Bishop et al. 2002, 2007; Bishop 2007). We also assumed that we would capture some fawns from treatment and control adult females that were wearing radiocollars but lacking VITs.

Our target sample size for estimating overwinter survival of fawns was 40 fawns/EG/year. White and Bartmann (1998) measured a 0.15 change in overwinter fawn survival in response to reduced deer density in northwest Colorado. We expected enhanced nutrition to cause a similar effect, and therefore, desired to detect a 0.15 difference for purposes of determining sample size. We assumed a control survival rate of 0.40 based on long-term data from Colorado, Idaho, and Montana, USA (Unsworth et al. 1999). However, data from 4 deer populations across western Colorado indicated that overwinter fawn survival averaged 0.72 during our study (Lukacs et al. 2009).

### Capture, Handling, and Radiomarked Samples

We captured and radiomarked 139 adult females during 20 November–14 December 2000–2003, and 241 6-month-old fawns during 20 November–19 December 2001–2003 using baited drop nets (Ramsey 1968) and helicopter net-gunning (Barrett et al. 1982, van Reenen 1982). We captured 165 adult females (including 19 recaptures) during 26 February–2 March 2002–2004, using helicopter net-gunning, and we radiomarked those that were pregnant (2002, $n = 36$; 2003, $n = 58$; 2004, $n = 60$). We hobbled and blindfolded all deer before handling. During drop-net captures, we used stretchers to carry deer away from nets before release. During net-gun captures, we ferried deer ≤3.5 km by helicopter to a central handling location.

We fitted deer with vinyl-belted radiocollars equipped with mortality sensors (Lotek, Inc., Newmarket, ON, Canada; Advanced Telemetry Systems, Inc., Isanti, MN), that activated after remaining motionless for 4 hours. We permanently attached radiocollars on all adult females; thus, many adult females were present in samples from multiple years. We temporarily attached radiocollars on 6-month-old fawns by cutting the collar belting in half and reattaching the 2 ends using rubber surgical tubing. Fawns shed collars ≥6 months postcapture. We stitched neckband material (Ritchey Mfg. Co., Brighton, CO) to the left side of each radiocollar, which we engraved with a unique marking for visually identifying deer. We measured mass (kg), hind foot length (cm), and chest girth (cm) of each deer and estimated deer age using tooth replacement and wear (Severinghaus 1949, Robinette et al. 1957, Hamlin et al. 2000).

We measured maximum subcutaneous fat thickness on the rump (cm) and thickness of the longissimus dorsi muscle (cm) of each adult female during captures in February–March using a SonoVet 2000 portable ultrasound unit (Universal Medical Systems, Bedford Hills, NY) with a 5-MHz linear transducer (Stephenson et al. 1998, 2002; Cook et al. 2001). We plucked an area of hair at each measurement point and used lubricant to enhance contact between the transducer and skin. We determined a body condition score for each deer by palpating the rump (Cook et al. 2001, 2007). We combined ultrasound measurements with the body condition score to estimate body fat of each deer (Cook et al. 2007).

We also established pregnancy status and measured fetal rates of each adult female during captures in February–March by performing transabdominal ultrasonography using an Aloka 210 portable ultrasound unit (Aloka, Inc., Wallinford, CT) with a 3-MHz linear transducer (Stephenson et al. 1995). We shaved the left caudal abdomen from the last rib and applied lubricant to facilitate transabdominal scanning. We were unable to obtain accurate fetal counts for 9 adult females, which we excluded from the fetal sample. We also excluded fetuses from 5 adult females that died before giving birth and from 2 adult females that we could not locate following spring migration. Our resulting fetal sample comprised 255 fetuses from 138 adult females in our radiocollared sample (29 ad F with 1 fetus, 101 ad F with 2 fetuses, 8 ad F with 3 fetuses). Nine adult females were present in 2 different years' samples; thus, the 255 fetuses were from 129 unique adult females. Of the 9 adult females 6 had twins each year, 2 females had a singleton one year and twins the other year, and one female had twins and triplets in successive years.

We fitted each pregnant deer with a VIT (Advanced Telemetry Systems, Inc.) and released nonpregnant adult females without a radiocollar or VIT. We performed the ultrasound and VIT-insertion procedures in a 4.3 × 4.9-m wall-frame tent to minimize disturbance from helicopter rotor wash and adverse weather conditions and to create a dim environment to facilitate ultrasonography. Our VITs had temperature-sensitive switches that caused pulse rates to increase from 40 pulses to 80 pulses per minute when the temperature dropped below 32° C. A temperature drop below 32° C was indicative of the VIT being expelled from the deer. We used VITs as an aid to determine timing and location of birth the following June. Bishop et al. (2007) provided a detailed description of VITs and VIT insertion procedures we used.

We located each adult female with a VIT using aerial telemetry every 2–3 weeks during March–May and every morning during June. When we detected a VIT with a fast (i.e., postpartum) pulse rate, we used very high frequency receivers and directional antennae from the ground to simultaneously locate the VIT and radiocollared adult female, which were typically in close proximity. We attempted to account for each adult female's fetus or fetuses as live or stillborn fawns to quantify in utero fetal survival from February to birth. We assumed that no fetuses were resorbed, which is a reasonable assumption for mule deer (Robinette et al. 1955, Medin 1976, Carpenter et al. 1984). We classified each fawn found dead at a birth site as stillborn unless evidence suggested the fawn was born alive. In most cases, we confirmed that the fawn had died before birth via laboratory necropsy. We located most radiocollared adult females that did not receive VITs approximately every other day from the ground during June, relying on adult female behavior and searches in the vicinity of the adult female to locate neonates. We did the same for any adult female with a VIT that failed because of premature expulsion or battery failure. We usually terminated unsuccessful neonate searches 30–45 minutes following initial location of the radiocollared adult female, although search times occasionally lasted an hour in heavy cover.

We captured and radiocollared 276 neonates born from radiocollared adult females during 4 June–8 July 2002–2004 (2002, $n = 54$; 2003, $n = 103$; 2004, $n = 119$). We removed 6 fawns from the sample because of possible capture-related abandonment or injury, resulting in a sample of 270 radiocollared neonates from 178 adult females in our radiocollared sample (88 ad F with 1 marked fawn, 88 ad F with 2 marked fawns, 2 ad F with 3 marked fawns). We captured neonate(s) from the same adult female as in a previous year on 32 occasions, and we captured the same female's fawns for a third consecutive year on 5 occasions. Thus, we captured 270 neonates from 136 unique adult females. We captured and monitored an average of 2.0 (SE = 0.085), and maximum of 5, neonates per unique adult female during the study.

We wore surgical gloves when securing and handling neonates to minimize transfer of human scent. We captured 75% of neonates in our sample within 2 days of birth. We secured and handled neonates with little or no effort because they rarely attempted to run or resist handling. A short chase was occasionally required to capture older neonates, which often struggled during handling. We placed a drop-off radiocollar with a 2-hour mortality sensor (Advanced Telemetry Systems, Inc.) on each captured neonate. Radiocollars were constructed with elastic neckband material to allow expansion. Hole-punched, vinyl-belting tabs extended from the end of the elastic and from the transmitter for attachment purposes. We made collars temporary by cutting the vinyl tab extending from the elastic and reattaching the belting with latex tubing, which generally caused the collars to shed from the animal >6 months postcapture. We right-censored 46 neonates that snagged and shed their collars on fences during fall migration, typically 4–5 months postcapture.

We recorded mass (kg), hind foot length (cm), age (days), and sex of each captured neonate. We placed neonates in a cloth bag to measure mass. We estimated neonate age primarily based on radiomonitoring of the adult females and secondarily based on hoof characteristics, condition of the umbilical cord, pelage, and behavior (Haugen and Speake 1958, Robinette et al. 1973, Sams et al. 1996, Pojar and Bowden 2004). Daily monitoring of adult females with functioning VITs allowed us to determine specific dates of birth, and monitoring of other radiocollared adult females often allowed us to identify dates of birth within a 1–2 day period. Handling times approximated 5 minutes per fawn. All deer capture and handling procedures, including VIT techniques, were approved by the CDOW's Animal Care and Use Committee (project protocols 11-2000 and 1-2002).

## Monitoring and Cause-Specific Mortality

We radiomonitored deer daily from the ground and approximately biweekly from the air throughout the study to determine fates and mortality causes. We detected signals daily from all radiocollared neonates during the summer and fall and from most radiocollared deer during winter, which typically allowed us to retrieve mortalities within 24 hours of the mortality event. During summer and migration periods, we could not ground-monitor approximately 15–25% of adult and yearling deer on a routine basis. We therefore failed to detect some deer mortalities for several days, or on occasion, for $\geq$1 week.

When we located a dead deer in the field, we conducted a thorough site inspection to record tracks, scat, drag trails, blood, hair, and any other signs that could help determine cause of death. We then collected the carcass or performed a field necropsy on site. We collected and submitted all fresh, intact neonate carcasses to the CDOW's Wildlife Health Laboratory (Fort Collins, CO) or the Colorado State University Diagnostic Laboratory (Fort Collins, CO) for necropsy. We also submitted fresh, intact adult and 6-month-old fawn carcasses to the laboratory for necropsy when logistically feasible. During laboratory necropsies, various tissue samples were extracted for bacteriology, virology, polymerase chain reaction, and virus isolation. We performed field necropsies on all other deer mortalities when at least some portion of the carcass was present. When feasible, we collected and submitted heart, lung, liver, kidney, and spleen samples to the laboratory for analysis. We submitted one fresh sample and one formalin-fixed sample of each tissue. Myers (2001) provided a detailed explanation of necropsy protocols and laboratory diagnostic techniques.

We identified coyote and domestic dog predation based on canine puncture wounds and associated hemorrhaging, torn tissue on the hind legs, tracks, signs indicating a chase or struggle, blood on the ground or vegetation, and buried carcasses (neonates only). Carcasses of deer killed by coyotes were sometimes dismembered and spread across the site, although we did not rely on this observation alone to confirm coyote predation. We identified mountain lion and bobcat (*Lynx rufus*) predation based on cached carcasses, canine puncture wounds and associated hemorrhaging, and tracks. We identified black bear (*Ursus americanus*) predation based on canine punctures and associated hemorrhaging, bruising, peeled hide, and bear sign. We identified malnutrition as a cause of death based on an intact carcass with minimal or no femur marrow fat and the lack of any sign indicating disease, predation, or hemorrhaging. We evaluated femur marrow fat based on appearance and texture (Riney 1955), which was sufficient for identifying deer that had mostly or entirely depleted their fat reserves.

We classified fawn mortalities as canid predation, black bear predation, felid predation, unknown predation (i.e., unidentified predator), disease, starvation or malnutrition, injury or accident, and unknown. Canid predation was caused by coyotes, and to a much lesser extent, domestic dogs. Felid predation was caused by mountain lions and bobcats. Disease mortalities included deaths caused by or associated with hemorrhagic disease, severe diarrhea, pneumonia, infections, and congenital deformities. Injuries and accidents included fence injuries, blunt trauma, drowning, entanglement in debris, and collisions with vehicles.

We classified adult female mortalities as mountain lion predation, coyote predation, black bear predation, unknown predation, disease, suspected disease, malnutrition, injury, parturition death, and unknown. We did not include harvest as a mortality factor because there were no hunting seasons for adult females during our study. Disease mortalities included deaths caused by hemorrhagic disease, pneumonia, and malignant catarrhal fever (MCF; Schultheiss et al. 2007). Suspected disease mortalities comprised deaths we could not specifically diagnose yet were consistent with disease. We suspected disease because carcasses were intact and field necropsies indicated the deer did not die of predation, malnutrition, or trauma. Injuries primarily included collisions with vehicles, and parturition deaths included any death associated with giving birth.

## Statistical Methods

We separately modeled body fat of adult females, pregnancy rates, fetal rates, fetal survival, neonatal survival, overwinter survival of fawns, and annual survival of adult females as a function of the nutrition treatment and other relevant variables. We also modeled cause-specific mortality separately for neonates, wintering fawns, and adult females. For each analysis, we developed a priori model sets based on our expectations of important variable relationships with the ultimate goal of quantifying the effect of nutrition enhancement treatment. We used Akaike's Information Criterion adjusted for sample size ($AIC_c$) to select among candidate models and we corrected for overdispersion when appropriate using quasi-likelihood ($QAIC_c$). We used model-averaging to reflect model selection uncertainty in estimates of parameters (Burnham and Anderson 2002). In a few instances, however, we based parameter estimates on the model with the lowest $AIC_c$, generally because that model received all of the Akaike weight.

*Body fat and reproductive rates.*—We modeled estimated body fat of adult females as a function of treatment and year using PROC MIXED in SAS (SAS Institute, Cary, NC). We modeled pregnancy rates of adult females as a function of treatment and year using PROC LOGISTIC in SAS, and we modeled fetal rates of pregnant adult females as a function of treatment, year, and age class (yearling or $\geq$2-yr-old F) using PROC MIXED. We did not obtain any data on yearling fetal rates during 2002, and we obtained fetal counts from only 9 yearlings during 2003 and 2004. Thus, we only had power to detect large differences in fetal rates between yearlings and older females.

*Fetal survival.*—We were unable to determine fate of 96 of the 255 fetuses documented in utero because some VITs were ineffective and newborn fawns were difficult to detect. We therefore developed a joint likelihood that included several nuisance detection parameters to estimate fetal survival in the absence of known fates (Bishop 2007, Bishop et al. 2008). We numerically maximized the natural logarithm of the likelihood function using a quasi-Newton optimization algorithm in PROC NLMIXED in SAS to obtain parameter estimates and the variance–covariance matrix. We modeled fetal survival as a function of treatment and year. There was a potential for overdispersion because our fetus sample comprised a high proportion of siblings. Sibling fetuses may have lacked independent fates because they shared the same maternal resources. However, we did not find evidence of overdispersion in our fetal data (Bishop et al. 2008).

*Neonatal survival.*—We analyzed neonatal survival using the Known Fates option in Program MARK (White and Burnham 1999), which accommodated staggered entry and exit times of marked fawns during the analysis period (Kaplan and Meier 1958, Pollock et al. 1989). We modeled survival as a function of fawn age (i.e., days survived since birth), Julian date of birth, treatment, year, fawn sex, estimated fawn mass at birth (kg), and estimated fawn hind foot length at birth (cm). We incorporated fawn age into our models first by evaluating whether survival varied weekly or biweekly as fawns aged and second by fitting linear and nonlinear trend models. Trend models required fewer parameters and evaluated whether daily survival probabilities of neonates changed as fawns aged. We expressed Julian date of birth as the number of days following the earliest detected birth in a given year. We used 182 daily intervals to construct encounter histories of survival from birth to 6 months of age. We included fawns that were $\leq$1 day old at capture in the first interval, fawns that were $>$1 and $\leq$2 days old at capture in the second interval, and so forth. A majority of neonates in our sample (0.748) were $\leq$2 days old at capture and most (0.904) were $\leq$4 days old at capture. We measured fawn mass and hind foot length at capture rather than at birth, so measurements were confounded with fawn age. To make measurements comparable, we estimated fawn mass and hind foot length at birth by regressing capture mass and foot length as a function of age using PROC REG in SAS (Bishop 2007, Bishop et al. 2008).

Similar to fetal survival, our neonatal survival data were potentially overdispersed because our sample included 88 sets of twins and 2 sets of triplets. Sibling neonates shared maternal resources and used the environment similarly in time and space, which could have caused dependence among neonate fates. Bishop et al. (2008) found evidence of modest overdispersion in these data and recommended setting the overdispersion parameter ($c$) equal to 1.25 in a quasi-likelihood analysis. We therefore used QAIC$_c$ to select among neonatal survival models with $\hat{c} = 1.25$.

*Overwinter survival of fawns.*—We analyzed overwinter survival of fawns using the Nest Survival option in Program MARK (White and Burnham 1999) because it allowed data with irregular radiomonitoring of collared animals (i.e., ragged telemetry data; Rotella et al. 2004). On winter range, we monitored signals of most radiocollared fawns daily, whereas we monitored a few fawns weekly or biweekly. Once deer left winter range, our monitoring of all fawns became more sporadic because of field logistics. We typically determined exact dates of fawn mortalities, although in some cases, we could only determine an approximate date. The ragged telemetry analysis allowed us to incorporate all available information from these different monitoring scenarios.

We modeled overwinter survival of fawns as a function of time, treatment, year, fawn sex, early winter mass (kg), chest girth (cm), and hind foot length (cm). We estimated survival from 17 December to 16 June, which resulted in 182 daily intervals. We selected 17 December as the start date because 16 December was the mean 6-month birthday of fawns captured as neonates. We estimated survival over a 6-month period (i.e., through 16 Jun), which is when fawns reached 1 year of age. We constrained time 4 ways in our models: weekly, monthly, seasonally (i.e., winter or spring), and as a trend. We included all fawns captured and radiocollared in the treatment EU in survival analyses with a treatment designation regardless of whether they accessed the pelleted supplement.

*Annual survival of adult females.*—We analyzed annual survival of adult females using the Nest Survival option in Program MARK (White and Burnham 1999) because our radiomonitoring was irregular among individuals and throughout the year. We modeled annual survival of adult females as a function of time, treatment, year, age, timing of capture, early winter mass (kg), chest girth (cm), and hind foot length (cm). We estimated annual survival from 15 December to 14 December, which resulted in 365 daily intervals. We constrained time 3 ways in our models: biweekly, monthly, and seasonally (i.e., winter–spring or summer–fall). Many adult females were included in multiple years' samples, although we only measured individual covariates when adult females were initially captured and radiocollared. We used these individual covariate values in multiple years' samples because they reflected overall differences in deer body size. We included timing of capture (i.e., Nov–Dec or Feb–Mar) as a variable to evaluate whether individual covariates of adult females varied depending on what time of year we measured them. Similar to 6-month-old fawns, we included all adult females captured and radiocollared in the treatment EU in survival analyses with a treatment designation regardless of whether they accessed the pelleted supplement.

Deer–vehicle collisions (DVCs) were a common cause of mortality of adult females captured in the Colona EU but not the Shavano EU. Deer from the Colona EU were commonly in close proximity to highways during spring and fall whereas most Shavano deer were not. We analyzed survival of adult females in the context of a balanced crossover experimental design, which should have minimized confounding of DVCs with the nutrition treatment. However, to evaluate the potential for confounding, we performed 2 analyses of annual survival of adult females. We included all observed DVCs in the first analysis, whereas we right-censored DVCs in the second analysis.

*Cause-specific mortality.*—We modeled cause-specific mortality of neonates, wintering fawns, and adult females using a generalized logits model (i.e., multinomial logistic regression) in PROC LOGISTIC in SAS. We modeled mortality causes of neonates during summer and fall as a function of fawn age (i.e., days survived since birth), Julian date of birth, treatment, year, sex, and estimated fawn mass at birth (kg). We modeled mortality causes of fawns during winter and spring as a function of year, treatment, sex, time, and early winter mass (kg). We modeled annual mortality causes of adult females as a function of year, treatment, season, age (yr), and mass (kg). We evaluated 2 season variables; the first comprised 4 levels (winter, spring, summer, and fall), whereas the second had 2 levels (winter–spring and summer–fall). In these analyses we only included mortalities rather than the entire sample of radiocollared deer. Our objective was to evaluate variability in relative contributions of different mortality factors to the total observed mortality.

We performed 2 analyses based on 2 resolutions of the proximate categories of mortality for each deer age group (i.e., neonates, winter fawns, ad F). In the first analysis, the dependent variable comprised a separate level for each individual mortality category except the unknown category. We excluded unknown mortalities because they did not represent a unique mortality cause(s), but rather a combination of the other mortality categories. Thus, unknown mortalities provided no information on the distribution of cause-specific mortality in our study. Unknown mortalities comprised 11% of all neonatal and wintering fawn mortalities and 18% of all adult female mortalities. In the second analysis, we reduced the number of mortality categories to 3: predation, disease–malnutrition–starvation, and injury–accident. The latter analysis considered widely differing mortality factors that were easily discernible from one another.

We computed cause-specific rates of mortality for neonates, winter fawns, and adult females by combining the results of our cause-specific mortality and survival analyses. Specifically, for each EG, we multiplied the estimated probabilities of each mortality cause by the overall mortality rate. We obtained the overall mortality rate simply as $1 - \hat{S}$, where $\hat{S}$ is our estimated survival rate. We used the delta method to estimate variances of cause-specific rates of mortality for each EG and deer age group (Seber 1982).

*Continuous survival rates.*—We estimated fawn survival from the fetal stage to 6 months old as the product of fetal and neonatal survival rates. Similarly, we estimated fawn survival from the fetal stage to 1 year old as the product of fetal, neonatal, and overwinter fawn survival rates. We estimated a treatment effect as the difference in survival between treatment and control EGs. We estimated variances using the delta method (Seber 1982).

Our estimate of survival from fetus to 1 year of age was structured to represent the treatment effect rather than any specific cohort of deer. This structure was necessary because any given winter's treatment applied to 2 cohorts of fawns. We measured overwinter fawn survival as a function of treatment using the current year's cohort of 6-month-old fawns whereas we measured fetal and neonatal survival using the upcoming year's cohort of fawns. Additionally, the crossover point of the experimental design occurred in December, meaning that the fawn cohort associated with the Colona EU switched from a treatment designation to a control designation in December 2002 and vice versa for the fawn cohort associated with the Shavano EU. In this case, estimating survival from the fetal stage to the yearling age class for a specific cohort of fawns would mix treatment and control assignments. Thus, for each year of the study, we estimated survival from the fetal stage to the yearling age class as a function of treatment by taking the product of fetal and neonatal survival rates measured immediately posttreatment and the overwinter survival rate of fawns measured during administration of treatment. For example, during 2001–2002, we estimated survival of fetuses to the yearling age class as the product of 2002 fetal survival, 2002 neonatal survival, and 2001–2002 overwinter fawn survival.

*Population rate of change.*—We used our fecundity and survival parameter estimates to construct a matrix population model (Leslie 1945, Caswell 2001) for each combination of treatment (treatment, control) and year (2001–2002, 2002–2003, 2003–2004) in our study. We estimated the finite rate of population change ($\lambda$) by applying the same fecundity and survival rate estimates over time to an artificial population until fawn:adult female ratios reached a steady state. This approach provided a theoretical estimate of $\lambda$ that was representative of the set of input parameters. We used $\lambda$ estimates as a means to quantify the effect of nutrition enhancement treatment on mule deer population performance. When estimating year-specific $\lambda$, we structured population models to represent the treatment effect rather than any specific cohort of fawns, as explained above. We imputed an expected value of yearling fetal rate in 2002 based on our fetal rate models because we lacked data to directly estimate the rate.

Each population model included estimates of pregnancy rates of adult females ($PR$), fetal rates of yearling females ($FR_{Yr}$), fetal rates of $\geq$2-yr-old females ($FR_{Ad}$), survival rates of fetuses ($S_{Fet}$), survival rates of male and female neonates ($S_{MNeo}$ and $S_{FNeo}$, respectively), overwinter survival rates of female fawns ($S_{FWntFwn}$), and survival rates of adult females during summer–fall ($S_{ASum}$), winter–spring ($S_{AWnt}$), and annually ($S_A$). Our models included 5 population segments: newborn fawns ($Neo$), 6-month-old female fawns ($FwnF$), 6-month-old male fawns ($FwnM$), yearling females ($YrF$), and $\geq$2-yr-old females ($AdF$). Our models did not include adult males because we needed only adult females to estimate $\lambda$. We used the following equations to project a population of deer from December of year $t$ to December of year $t+1$ for each combination of treatment and year:

$$\begin{aligned} N_{Neo}(t+1) = {} & N_{YrF}(t) PR\ FR_{Yr} S_{AWnt} S_{Fet} \\ & + N_{AdF}(t) PR\ FR_{Ad} S_{AWnt} S_{Fet} \end{aligned}$$

$$N_{FwnF}(t+1) = (0.5) N_{Neo}(t+1) S_{FNeo}$$

$$N_{FwnM}(t+1) = (0.5) N_{Neo}(t+1) S_{MNeo}$$

$$N_{YrF}(t+1) = N_{FwnF}(t) S_{FWntFwn} S_{ASum}$$

$$N_{AdF}(t+1) = N_{YrF}(t) S_A + N_{AdF}(t) S_A$$

Population size ($N_T$) of young and adult female deer in December in year $t$ is thus

$$N_T(t) = N_{FwnF}(t) + N_{FwnM}(t) + N_{YrF}(t) + N_{AdF}(t)$$

and the fawn:adult female ratio ($R_{FwnAd}$) in December in year $t$ is

$$R_{FwnAd}(t) = [N_{FwnF}(t) + N_{FwnM}(t)] / [N_{YrF}(t) + N_{AdF}(t)]$$

We estimated the variance–covariance matrix of our $\lambda$ estimates ($\hat{\Sigma}_\lambda$) as follows:

$$\hat{\Sigma}_\lambda = \left( \frac{\partial \hat{\lambda}_j}{\partial \hat{\theta}_i} \right) \hat{\Sigma}_\theta \left( \frac{\partial \hat{\lambda}_j}{\partial \hat{\theta}_i} \right)^T$$

where $\hat{\lambda}_j$ are $\lambda$ estimates for each combination of treatment and year, for averages across years (e.g., $\hat{\bar{\lambda}}_{Treatment}$), and for treatment effect sizes (e.g., $\hat{\bar{\lambda}}_{Treatment} - \hat{\bar{\lambda}}_{Control}$); $\hat{\theta}_i$ are the various fecundity and survival estimates; and $\hat{\Sigma}_\theta$ is the variance-covariance matrix of fecundity and survival estimates. The partial derivatives of $\hat{\lambda}_j$ with respect to $\hat{\theta}_i$ are sensitivities (Caswell 2001). Thus, we evaluated the sensitivity of $\hat{\lambda}$ to changes in estimated fecundity and survival rates. We also decomposed the treatment effect on $\hat{\lambda}$ into individual contributions from each fecundity and survival rate by taking the product of vital rate differences between treatment and control deer and vital rate sensitivities (Caswell 2001).

# RESULTS

## Adult Female Body Fat and Fecundity

The model of estimated body fat of adult females with the lowest AIC$_c$ included a treatment × year interaction (no. parameters = 6, AIC$_c$ wt = 1.000). The model with the next lowest AIC$_c$, which lacked the treatment × year interaction, had a $\Delta$AIC$_c$ of 27. Estimated percent body fat of treatment adult females was higher than that of control adult females each year, although magnitude of the effect varied annually (Table 1). We found no evidence of variation in pregnancy rates between treatment and control adult females or among years because the intercept model received the most support (no. parameters = 1, AIC$_c$ wt = 0.631). The pregnancy rate model containing the treatment effect had one additional parameter and a $\Delta$AIC$_c$ of 1.97 (no. parameters = 2, AIC$_c$ wt = 0.235), which indicated treatment had minimal effect on pregnancy. Pregnancy rate of all adult female deer during the study was 0.935 (SE = 0.019). Models explaining variation in fetal rates of adult female deer with the lowest AIC$_c$ included year and female age class in interactive (yr × age class, no. parameters = 6, $\Delta$AIC$_c$ = 0.00, AIC$_c$ wt = 0.428) and additive (yr + age class, no. parameters = 4, $\Delta$AIC$_c$ = 0.47, AIC$_c$ wt = 0.338) models. We found minimal evidence of a treatment effect (yr + age class + treatment, no. parameters = 5, $\Delta$AIC$_c$ = 2.10, AIC$_c$ wt = 0.150). Thus, fetal rates of adult females varied among years and between age classes but did not vary as a function of the treatment (Table 2).

The fetal survival model with the lowest AIC$_c$ included a treatment × year interaction (no. parameters = 20, $\Delta$AIC$_c$ = 0.00, AIC$_c$ wt = 0.293; Appendix A). The same model, but without the treatment effect on fetal survival (i.e., year only), received essentially no support (no. parameters = 17, $\Delta$AIC$_c$ = 5.99, AIC$_c$ wt = 0.015). Fetal survival was higher overall in the treatment EG than in the control EG, although we observed considerable annual variation in the magnitude of the effect. We observed virtually no difference in fetal survival between treatment and control EGs in 2003, whereas we observed a large difference between EGs in 2004 (Table 3).

## Neonatal Survival

The 4 most parsimonious models of neonatal survival had similar QAIC$_c$ weights (Appendix B). The first of these models included neonatal sex, a third-order polynomial trend in fawn age, Julian date of birth, and estimated birth mass (no. parameters = 7, $\Delta$QAIC$_c$ = 0.00, QAIC$_c$ wt = 0.129). The second model included the same variables as the first model and a year × birth mass interaction (no. parameters = 11, $\Delta$QAIC$_c$ = 0.03, QAIC$_c$ wt = 0.127). Addition of the treatment effect resulted in a slight increase in QAIC$_c$ (no. parameters = 12, $\Delta$QAIC$_c$ = 0.21, QAIC$_c$ wt = 0.116). The fourth model included only the trend in fawn age, date of birth, and birth mass (no. parameters = 6, $\Delta$QAIC$_c$ = 0.43, QAIC$_c$ wt = 0.104). We found modest evidence of treatment ($\hat{\beta}_{trt}$ = 0.276, 95% CI: −0.123 to 0.675), sex ($\hat{\beta}_{sex}$ = 0.322, 95% CI: −0.083 to 0.728), and year ($\hat{\beta}_{year02}$ = 0.705, 95% CI: −0.014 to 1.424; $\hat{\beta}_{year03}$ = 0.380, 95% CI: −0.078 to 0.839) effects because addition of these parameters to models caused little change in QAIC$_c$ and confidence intervals on beta estimates slightly overlapped zero. Survival of treatment neonates averaged 0.528 (SE = 0.055) and survival of control neonates averaged 0.482 (SE = 0.057). Survival of female neonates averaged 0.533 (SE = 0.058) and survival of male neonates averaged 0.478 (SE = 0.059). The year effect indicated neonatal survival declined during the study (2002: $\hat{S}$ = 0.562, SE = 0.104; 2003: $\hat{S}$ = 0.520, SE = 0.059; 2004: $\hat{S}$ = 0.435, SE = 0.062).

**Table 1.** Estimated body fat (%) of adult female mule deer occupying a pinyon–juniper winter range during late February–early March in southwest Colorado, USA, 2002–2004. Adult females in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation.

| Yr | Experimental group | *n* | Body fat | SE |
|---|---|---|---|---|
| 2002 | Treatment | 18 | 10.21 | 0.597 |
| | Control | 18 | 7.60 | 0.597 |
| 2003 | Treatment | 30 | 13.90 | 0.463 |
| | Control | 28 | 6.64 | 0.479 |
| 2004 | Treatment | 30 | 10.63 | 0.463 |
| | Control | 30 | 7.28 | 0.463 |

The polynomial trend in fawn age indicated that daily survival probability of fawns was lowest shortly after birth, increased steadily during the first month postpartum, and then remained high and constant except for a slight decrease during fall migration ($\hat{\beta}_{A}$ = 0.101, 95% CI: 0.068 to 0.134; $\hat{\beta}_{A^2}$ = −0.0011, 95% CI: −0.0016 to −0.0006; $\hat{\beta}_{A^3} = 3.6 \times 10^{-6}$, 95% CI: $1.5 \times 10^{-6}$ to $5.7 \times 10^{-6}$). Neonatal survival probability decreased the later fawns were born ($\hat{\beta}_{bdate}$ = −0.223, 95% CI: −0.409 to −0.037; Fig. 3) and survival probability increased with greater birth mass ($\hat{\beta}_{bmass}$ = 0.260, 95% CI: 0.054 to 0.465; Fig. 4). Birth mass had a greater effect on survival probability during 2002 than either 2003 or 2004 ($\hat{\beta}_{year02 \times bmass}$ = 0.667, 95% CI: 0.024 to 1.310; $\hat{\beta}_{year03 \times bmass}$ = 0.104, 95% CI: −0.345 to 0.554). The effect of birth mass and birth date on survival was partially related to treatment. Fawns in the treatment EG averaged 3.64 kg (SE = 0.058) at birth whereas fawns in the control EG averaged 3.49 kg (SE = 0.057). Mean birth date, expressed as number of days following the first fawn birth, was earlier for fawns in the treatment EG (13.95, SE = 0.509) than fawns in the control EG (15.76, SE = 0.498).

**Table 2.** Fetal rates of adult female mule deer during late February–early March in southwest Colorado, USA, 2002–2004.

| Yr | Age class | *n* | Fetal rate[a] | SE |
|---|---|---|---|---|
| 2002 | ≥2 yr old | 36 | 1.79 | 0.075 |
| | Yearling | 0 | | |
| 2003 | ≥2 yr old | 45 | 1.82 | 0.066 |
| | Yearling | 5 | 1.07 | 0.190 |
| 2004 | ≥2 yr old | 56 | 2.01 | 0.061 |
| | Yearling | 4 | 1.41 | 0.206 |

[a] We used model-averaging to estimate fetal rates (Burnham and Anderson 2002).

**Table 3.** Estimated in utero survival ($\hat{S}$) of mule deer fetuses from February until birth on a pinyon–juniper winter range in southwest Colorado, USA, 2002–2004. Adult females in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation.

| Yr | Experimental group | *n* | $\hat{S}^{a}$ | SE($\hat{S}$) |
|---|---|---|---|---|
| 2002 | Treatment | 24 | 0.857 | 0.113 |
| | Control | 33 | 0.779 | 0.158 |
| 2003 | Treatment | 38 | 0.966 | 0.033 |
| | Control | 44 | 0.935 | 0.059 |
| 2004 | Treatment | 57 | 0.983 | 0.028 |
| | Control | 59 | 0.747 | 0.090 |

[a] We averaged across all models in our model set to estimate survival (Burnham and Anderson 2002).

Distribution of cause-specific mortality of neonates varied as a function of age. The model including an intercept and fawn age received all of the Akaike weight (no. parameters = 12, AIC$_c$ wt = 1.000). Causes of fawn mortality changed as fawns aged and as the summer–fall season progressed (Fig. 5). Disease-related deaths were most commonly associated with hemorrhagic disease or severe diarrhea. Also, we isolated bovine viral diarrhea virus (BVDV) from a neonate, but we could not determine whether BVDV contributed to or interacted with fetal or neonatal mortality. When we pooled mortalities into 3 categories, the intercept-only model (no. parameters = 2, AIC$_c$ wt = 0.205) received slightly more Akaike weight than any other model. Proportions of total mortality comprised of predation (0.667, SE = 0.044), starvation and disease (0.243, SE = 0.040), and injuries and accidents (0.090, SE = 0.027) were similar throughout the study and among EGs. Therefore, predation mortality rates were 0.315 (SE = 0.042) for treatment neonates and 0.345 (SE = 0.044) for control neonates. Starvation and disease mortality rates were 0.115 (SE = 0.023) for treatment neonates and 0.126 (SE = 0.025) for control neonates. Injury and accident mortality rates were 0.043 (SE = 0.014) for treatment neonates and 0.047 (SE = 0.015) for control neonates.

### Overwinter Fawn Survival

Overwinter fawn survival varied as a function of nutrition enhancement treatment, year, sex, time (monthly), and early winter mass and chest girth (Appendix C). The model with the lowest AIC$_c$ included treatment, year, sex, time, and mass (no. parameters = 11, $\Delta$AIC$_c$ = 0.00, AIC$_c$ wt = 0.435). The same model without the treatment effect received no support (no. parameters = 10, $\Delta$AIC$_c$ = 19.12, AIC$_c$ wt = 0.000). We found strong evidence of a treatment effect ($\hat{\beta}_{trt} = 1.350$, 95% CI: 0.723 to 1.978; Table 4). Survival of fawns receiving treatment averaged 0.905 (SE = 0.026) whereas survival of control fawns averaged 0.684 (SE = 0.044). The year effect ($\hat{\beta}_{year0102} = -0.523$, 95% CI: $-1.187$ to 0.142; $\hat{\beta}_{year0203} = -0.104$, 95% CI: $-0.826$ to 0.617) indicated overwinter fawn survival increased during the study (Table 4). Similar to neonates, we found some evidence that female fawns had higher survival than male fawns ($\hat{\beta}_{sex} = 0.362$, 95% CI: $-0.200$ to 0.925; Table 4). Lowest monthly survival occurred between mid-January and mid-February ($\hat{\beta}_{month2} = -1.552$, 95% CI: $-2.520$ to $-0.584$), whereas highest monthly survival occurred between mid-March and mid-April ($\hat{\beta}_{month4} = 0.291$, 95% CI: $-1.139$ to 1.720). Probability of fawn survival increased as early winter mass and chest girth increased, although the effect of mass was much greater than that of chest girth ($\hat{\beta}_{mass} = 0.145$, 95% CI: 0.087 to 0.202; $\hat{\beta}_{chest} = 0.043$, 95% CI: $-0.032$ to 0.117; Fig. 6).

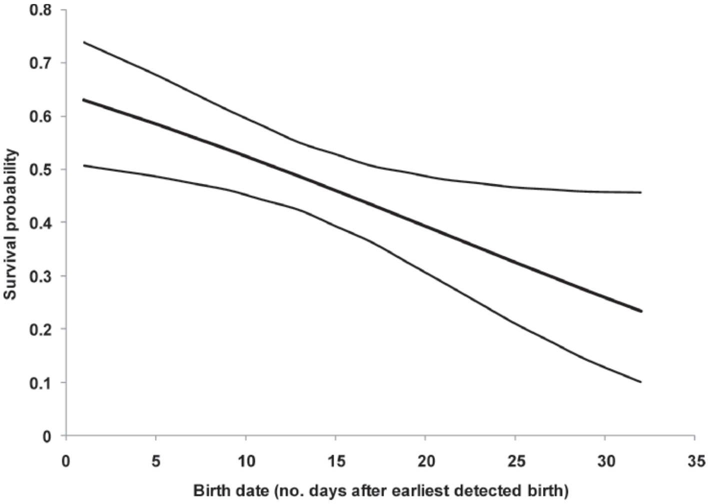


**Figure 3.** Survival probability (with 95% CI) of mule deer neonates as a function of Julian date of birth of neonates in southwest Colorado, USA, 2002–2004. We expressed Julian date of birth as number of days following the earliest detected birth in a given year.

Distribution of cause-specific mortality of wintering fawns did not vary over time, among years, or between treatment and control deer. The intercept-only model received virtually all of the Akaike weight (no. parameters = 5, AIC$_c$ wt = 0.911). Coyote predation was the most common proximate cause of overwinter fawn mortality throughout the study (Fig. 7). When we combined mortalities into 3 categories, models with year (no. parameters = 6, $\Delta$AIC$_c$ = 0.00, AIC$_c$ wt = 0.269) and year + sex (no. parameters = 8, $\Delta$AIC$_c$ = 0.45, AIC$_c$ wt = 0.215) received the most support. However, the intercept-only model also received some support (no. parameters = 2, $\Delta$AIC$_c$ = 1.31, AIC$_c$ wt = 0.140), indicating only marginal evidence of annual and sex-specific variation. The

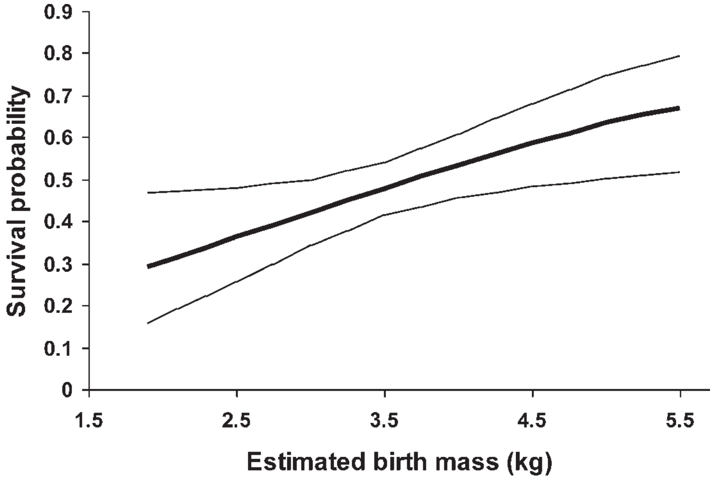


**Figure 4.** Survival probability (with 95% CI) of mule deer neonates as a function of estimated birth mass of neonates in southwest Colorado, USA, 2002–2004.

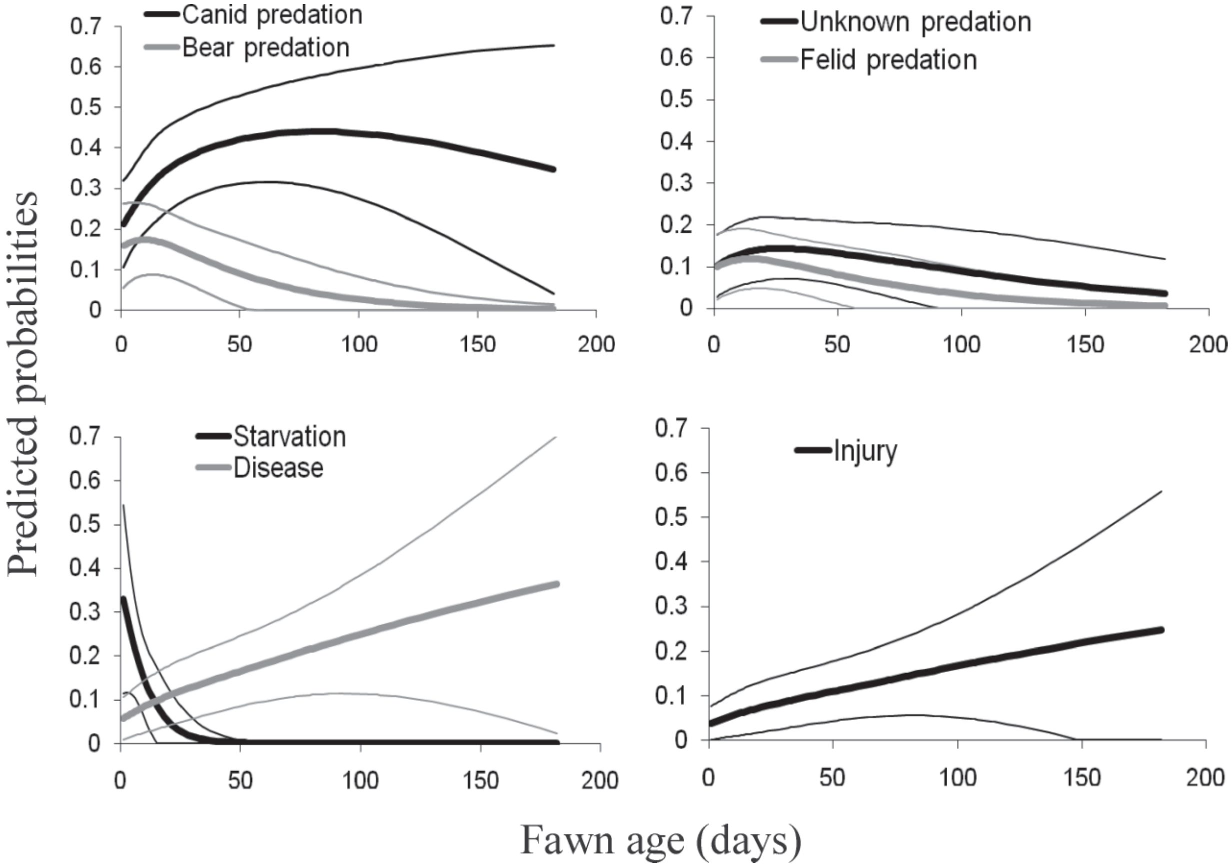


**Figure 5.** Predicted probabilities (with 95% CIs) of mortality causes of mule deer neonates as a function of fawn age in southwest Colorado, USA, 2002–2004. Cause-specific mortality probabilities are based on total mortality (i.e., $\sum$ probabilities = 1), and therefore represent a deer's relative likelihood of dying from a particular cause given that the deer dies.

year effect indicated that the proportion of total mortality attributed to malnutrition or disease declined through the study whereas the proportion of injury and accident mortalities increased (Fig. 8). We lacked evidence to suggest mortality causes varied between EGs, in part because few treatment fawns died during the study ($n = 13$). Increased survival of treatment fawns was therefore explained by roughly a 70% reduction in all cause-specific mortality rates (Table 5).

Predation and malnutrition together accounted for 83% of total fawn mortality (Fig. 7), and most fawns dying from these causes were malnourished. All but 2 fawns killed by coyotes had limited or no femur marrow fat remaining. Four of 6 fawns killed by mountain lions, and both fawns killed by bobcats, were malnourished based on depleted femur marrow fat, and in several cases, evident emaciation. The other 2 fawns killed by mountain lions were in poor condition but had some femur marrow fat remaining.

## Annual Survival of Adult Females

Annual survival of adult females varied as a function of treatment, season, age, and hind foot length (Appendix D), regardless of whether DVCs were included in the analysis. For the analysis including DVCs, the model with the lowest AIC$_c$ included a treatment × season interaction, age, and age$^2$ (no. parameters = 6, $\Delta$AIC$_c$ = 0.00, AIC$_c$ wt = 0.130). The same model without the treatment effect received less support (no. parameters = 4, $\Delta$AIC$_c$ = 1.59, AIC$_c$ wt = 0.055). Including DVCs, model-averaged annual survival estimates were 0.879 (SE = 0.021) for treatment adult females and 0.833 (SE = 0.025) for control adult females. Excluding DVCs, model-averaged annual survival estimates were 0.898 (SE = 0.019) for treatment adult females and 0.867 (SE = 0.023) for control adult females. Also, there was a treatment × season interaction regardless of whether DVCs were included in

**Table 4.** Estimated overwinter survival ($\hat{S}$) of mule deer fawns occupying a pinyon–juniper winter range in southwest Colorado, USA, 2001–2004. Fawns in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation.

| Yr | Experimental group | Sex | *n* | $\hat{S}^{a}$ | SE($\hat{S}$) |
|---|---|---|---|---|---|
| 2001–2002 | Treatment | F | 18 | 0.894 | 0.038 |
| | Treatment | M | 21 | 0.853 | 0.047 |
| | Control | F | 15 | 0.648 | 0.081 |
| | Control | M | 24 | 0.542 | 0.087 |
| 2002–2003 | Treatment | F | 18 | 0.932 | 0.027 |
| | Treatment | M | 22 | 0.902 | 0.035 |
| | Control | F | 17 | 0.763 | 0.069 |
| | Control | M | 21 | 0.671 | 0.082 |
| 2003–2004 | Treatment | F | 19 | 0.938 | 0.025 |
| | Treatment | M | 19 | 0.912 | 0.034 |
| | Control | F | 25 | 0.780 | 0.064 |
| | Control | M | 16 | 0.702 | 0.082 |

[a] We used model-averaging to estimate survival (Burnham and Anderson 2002).

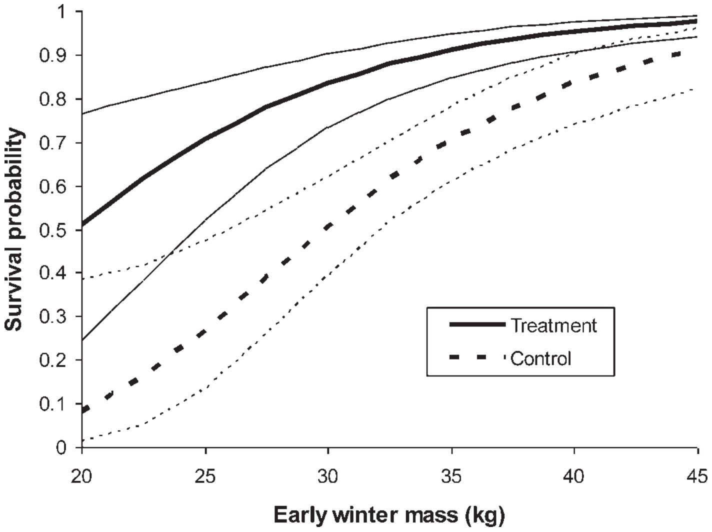


**Figure 6.** Predicted survival probabilities (with 95% CIs) of mule deer fawns during winter (Dec–Jun) as a function of early winter mass in southwest Colorado, USA, 2001–2004. We present survival probabilities separately for fawns that received enhanced nutrition (treatment) during winter-spring and fawns that did not receive supplementation (control).

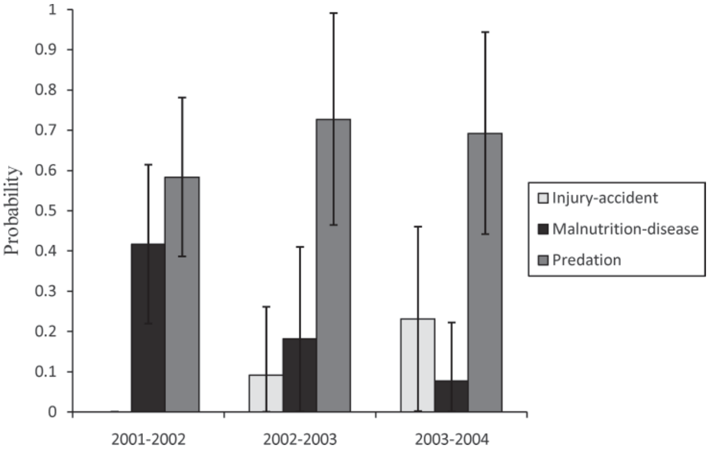


**Figure 8.** Estimated probabilities (with 95% CIs) of mortality causes of ≥6-month-old mule deer fawns as a function of year in southwest Colorado, USA, 2001–2004. Cause-specific mortality probabilities are based on total mortality (i.e., Σ probabilities = 1), and therefore represent a deer's relative likelihood of dying from a particular cause given that the deer dies. We lumped mortality causes into 1 of the 3 categories shown.

the analysis. Treatment deer experienced higher survival during winter–spring than summer–fall, whereas control deer did not (Table 6). Probability of adult female survival increased as hind foot length increased; the effect was most pronounced in the analysis that excluded DVCs ($\hat{\beta}_{foot} = 0.116$, 95% CI: $-0.032$ to 0.263). Models that evaluated a linear relationship between survival probability of adult females and age of adult females had similar weight to models that tested a quadratic relationship between survival and age. The quadratic effect received most support in the analysis that included DVCs, which indicated that survival probability increased slightly until females were 5 years old, after which survival probability declined with age ($\hat{\beta}_{age} = 0.188$, 95% CI: $-0.134$ to 0.509; $\hat{\beta}_{age^2} = -0.018$, 95% CI: $-0.039$ to 0.004; Fig. 9).

Distribution of cause-specific mortality of adult females varied in response to female age. The model with an intercept and female age received most of the Akaike weight (no. parameters = 16, $AIC_c$ wt = 0.834). Adult females ≤8 years old died principally from collisions with vehicles, disease, and mountain lion predation. Older females died principally from malnutrition and coyote predation (Fig. 10). All but 2 adult females killed by coyotes had minimal or no femur marrow fat remaining, indicating they were malnourished. When we pooled mortalities into 3 categories, 2 models received most of the Akaike weight: 1) intercept + season (no. parameters = 8, $AIC_c$ wt = 0.521) and 2)

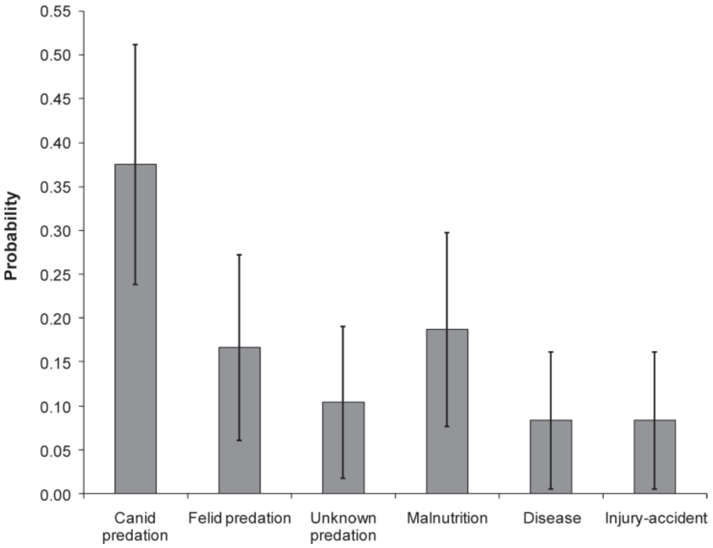


**Figure 7.** Estimated probabilities (with 95% CIs) of mortality causes of ≥6-month-old mule deer fawns in southwest Colorado, USA, 2001–2004. Cause-specific mortality probabilities are based on total mortality (i.e., Σ probabilities = 1), and therefore represent a deer's relative likelihood of dying from a particular cause given that the deer dies.

**Table 5.** Estimates of cause-specific mortality rates of mule deer fawns during winter on a pinyon–juniper winter range in southwest Colorado, USA, 2001–2004. Fawns in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation. The sum of cause-specific mortality rates across each experimental group equals the overall mortality rates of treatment (0.095) and control (0.316) fawns in our study.

| Mortality cause | Experimental group | Mortality rate | SE |
|---|---|---|---|
| Canid predation[a] | Treatment | 0.036 | 0.012 |
| | Control | 0.119 | 0.027 |
| Felid predation | Treatment | 0.016 | 0.007 |
| | Control | 0.053 | 0.018 |
| Unknown predation | Treatment | 0.010 | 0.005 |
| | Control | 0.033 | 0.014 |
| Malnutrition | Treatment | 0.018 | 0.007 |
| | Control | 0.059 | 0.019 |
| Disease | Treatment | 0.008 | 0.004 |
| | Control | 0.026 | 0.013 |
| Injury-accident | Treatment | 0.008 | 0.004 |
| | Control | 0.026 | 0.013 |

[a] Canid predation mostly represents coyote predation. Of 18 canid predation events on wintering fawns, 15 were caused by coyotes, 1 was caused by domestic dog, and 2 others were caused by either coyotes or domestic dogs.

**Table 6.** Estimated annual survival ($\hat{S}$) of adult female mule deer ($n = 274$) in southwest Colorado, USA, 2000–2004. Adult females in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation. We present estimates from 2 analyses. We included mortalities resulting from deer–vehicle collisions (DVCs) in the first analysis, whereas we right–censored DVCs in the second analysis.

| Analysis | Experimental group | Season | $\hat{S}^{a}$ | SE($\hat{S}$) |
|---|---|---|---|---|
| DVCs included | Treatment | Winter–spring | 0.952 | 0.016 |
| | Treatment | Summer–fall | 0.924 | 0.017 |
| | Control | Winter–spring | 0.911 | 0.018 |
| | Control | Summer–fall | 0.915 | 0.019 |
| DVCs censored | Treatment | Winter–spring | 0.964 | 0.014 |
| | Treatment | Summer–fall | 0.932 | 0.016 |
| | Control | Winter–spring | 0.922 | 0.018 |
| | Control | Summer–fall | 0.941 | 0.016 |

[a] We used model-averaging to estimate survival (Burnham and Anderson 2002).

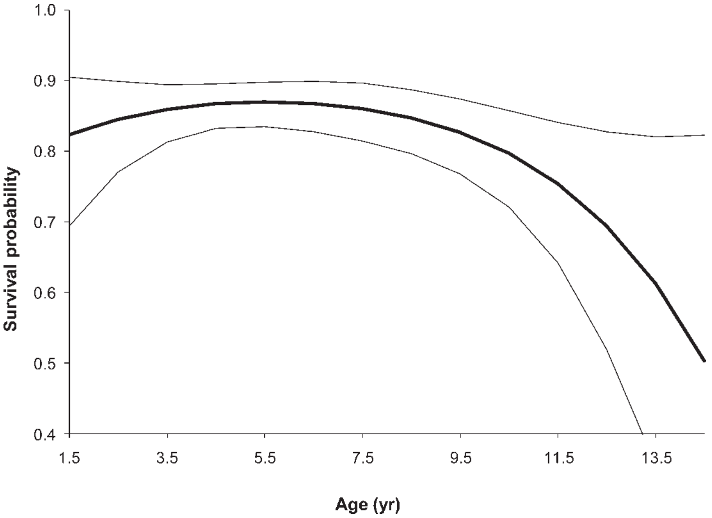


**Figure 9.** Predicted probability (with 95% CI) of annual survival of adult female mule deer as a function of age, southwest Colorado, USA, 2000–2004.

intercept + season + age (no. parameters = 10, AIC$_c$ wt = 0.412). During winter and summer, mortalities caused by disease or malnutrition were most common and there were few DVCs. The opposite was true during spring and fall (Fig. 11). Predation was relatively constant throughout all seasons.

We observed modest evidence that cause-specific mortality of adult females varied between experimental groups. The model with an intercept and treatment effect received the third-most Akaike weight (no. parameters = 16, AIC$_c$ wt = 0.034) after age and season models. Survival of adult females receiving treatment was higher than control adult females primarily because malnutrition was eliminated and mountain lion predation declined by 86% (SE = 15) in response to treatment (Table 7). We also observed a 32% (SE = 48) reduction in coyote predation, although the confidence interval on the effect was large and overlapped zero. Rates of mortality caused by DVCs were nearly identical for treatment and control deer, although most DVCs were associated with the Colona EU, which indicates the crossover experimental design minimized any potential confounding between the nutrition enhancement treatment and DVCs (Table 7). Combined rates of disease and suspected disease were similar among treatment and control deer. We found no evidence of novel diseases or chronic wasting disease, the latter of which has not been documented in southwest Colorado. We observed several cases each of hemorrhagic disease, MCF (Schultheiss et al. 2007), and pneumonia, and we failed to identify the exact cause of death in a number of other disease-related cases. During 2000–2002, >50% of adult females were seropositive (i.e, titers ≥1:32) for BVDV, although seroprevalence unexpectedly dropped to <25% in 2002–2003. We are uncertain if or how BVDV interacted with fecundity or mortality.

### Recruitment and Population Rate of Change

We estimated fawn survival from the fetal stage to 6 months of age separately for each treatment, year, and sex combination, consistent with model selection results from our fetal and neonatal survival analyses (Table 8). We likewise estimated fawn survival from the fetal stage to 1 year of age separately for each treatment, year, and sex combination (Table 9). Fetal to yearling survival rates increased by 0.14–0.20 in response to the treatment, although 95% confidence intervals slightly overlapped zero (Table 10). Across years, survival from the fetal stage to the yearling age class averaged 0.478 (SE = 0.061) for treatment females and 0.417 (SE = 0.062) for treatment males, and survival averaged 0.306 (SE = 0.053) for control females and 0.238 (SE = 0.046) for control males. Across sexes and years, survival of treatment fetuses to the yearling age class averaged 0.447 (SE = 0.052), whereas survival of control fetuses to the yearling age class averaged 0.271 (SE = 0.042). Thus, treatment caused the rate of fetal to yearling survival to increase by 0.177 (SE = 0.082, 95% CI: 0.016 to 0.337).

We used survival estimates of adult females that included DVCs when estimating population rate of change ($\lambda$) because we did not find evidence that DVCs were confounded with the nutrition treatment. Our estimates of $\lambda$ were 1.15–1.17 for treatment deer and 1.02–1.06 for control deer, with some overlap in 95% confidence intervals (Fig. 12). Average $\hat{\lambda}$ was 1.165 (SE = 0.036) for treatment deer and 1.033 (SE = 0.038) for control deer. Treatment caused $\hat{\lambda}$ to increase by 0.139 (95% CI: 0.020 to 0.259) during 2001–2002, 0.113 (95% CI: 0.023 to 0.204) during 2002 to 2003, and 0.145 (95% CI: 0.048 to 0.242) during 2003–2004. When averaged across years, treatment caused $\hat{\lambda}$ to increase by 0.133 (95% CI: 0.049–0.217). Population rate of change was more sensitive to changes in annual survival of adult females than to changes in any other demographic rate (Table 11). However, treatment effects on overwinter fawn survival and adult female survival caused similar increases in $\hat{\lambda}$ (Table 11). The treatment effect on production and survival of young (i.e., fetal, neonatal, and overwinter fawn survival) caused $\hat{\lambda}$ to increase by 0.084 whereas the treatment effect on adult female survival caused $\hat{\lambda}$ to increase by 0.048.

## DISCUSSION

### Diet Quality

Deer receiving the supplemental pellet were in better condition than deer consuming natural vegetation only (Table 1). We provided a supplemental pellet that would allow deer to meet or exceed maintenance nutrient requirements. Maintenance energy requirements reported for wintering deer include estimates

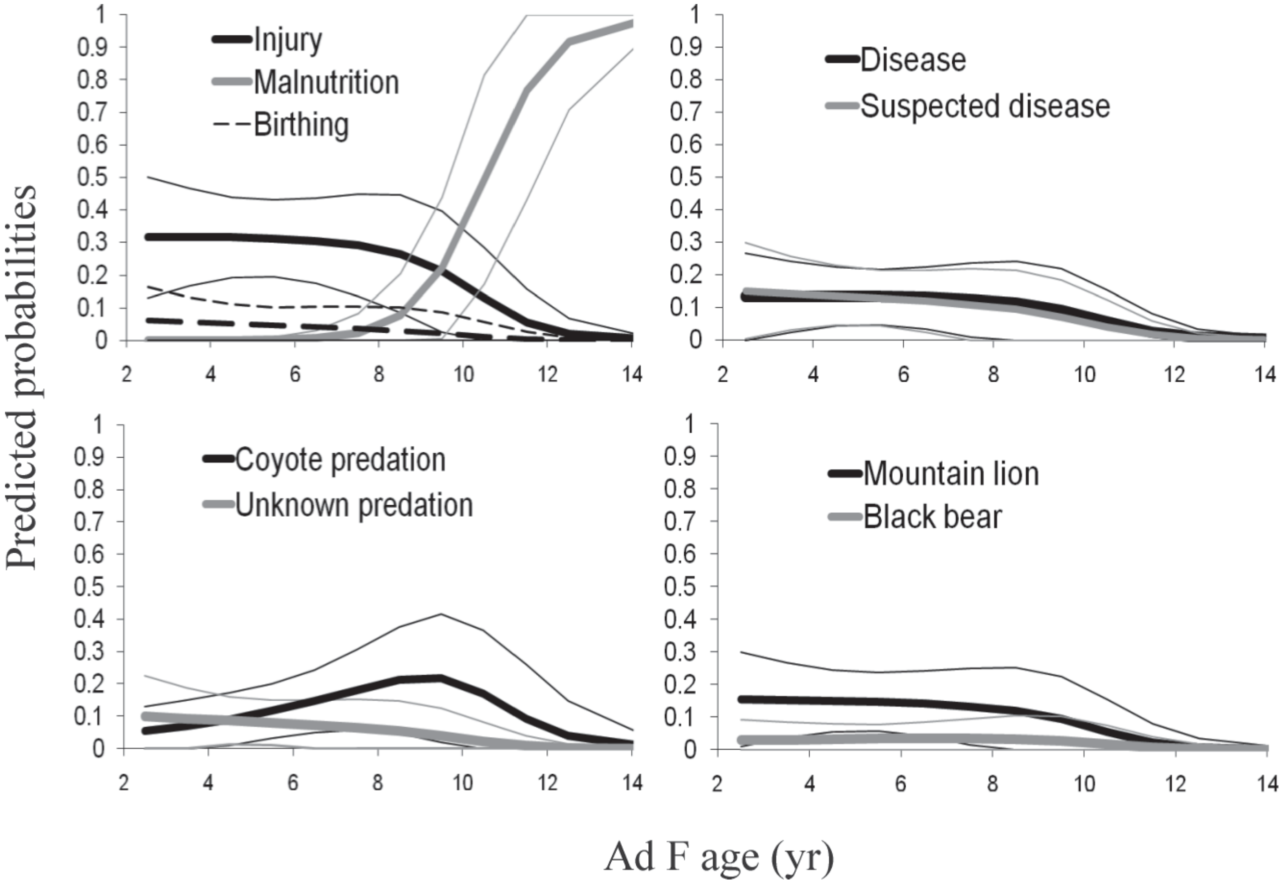


**Figure 10.** Predicted probabilities (with 95% CIs) of mortality causes of adult female mule deer as a function of female age in southwest Colorado, USA, 2000–2004. Cause-specific mortality probabilities are based on total mortality (i.e., $\sum$ probabilities = 1), and therefore represent a deer's relative likelihood of dying from a particular cause given that the deer dies.

ranging from 109 to 158 kilocalories (kcal) of metabolizable energy (ME) per kilogram body weight$^{0.75}$ ($W_{kg}^{0.75}$) per day (Thompson et al. 1973, Baker et al. 1979, Holter et al. 1979*b*). Assuming a requirement of 135 kcal ME/$W_{kg}^{0.75}$/day, a 36-kg fawn consuming 900 g dry matter/day, or a 65-kg adult female consuming 1,400 g dry matter/day, would require a diet having approximately 60% digestible energy (DE) to achieve maintenance (Swift 1983). Ammann et al. (1973) found that deer must consume diets containing ≥50% DE to adjust intake to meet maintenance energy requirements. Deer must consume diets containing roughly 6–7% crude protein (CP) to meet maintenance nitrogen requirements (Dietz 1965, Holter et al. 1979*a*). As described in the Methods, deer consuming the supplement should have exceeded maintenance protein and energy requirements.

In contrast, deer consuming only natural forage likely failed to meet maintenance nutrient requirements from dietary intake during much of the winter. Principal forage species of deer on the winter range EUs were Utah juniper, big sagebrush, black sagebrush (*Artemisia nova*), cheatgrass (*Bromus tectorum*), crested wheatgrass (*Agropyron cristatum*), and alfalfa (*Medicago* spp.) residual. Sagebrush and juniper were the main forage species available from late December through early March. Winter estimates of in vitro dry matter digestibility (IVDMD) are 40–48% for Utah juniper (Bunderson et al. 1986, Welch 1989), 45–65% for big sagebrush (Ward 1971, Kufeld et al. 1981, Welch and Pederson 1981, Welch 1989), and 53% for black sagebrush (Welch et al. 1983, Welch 1989). Winter estimates of CP range from 6–12% for these same species (Welch 1989, Wambolt 2004). Diet quality of wintering deer in the control EU may have been

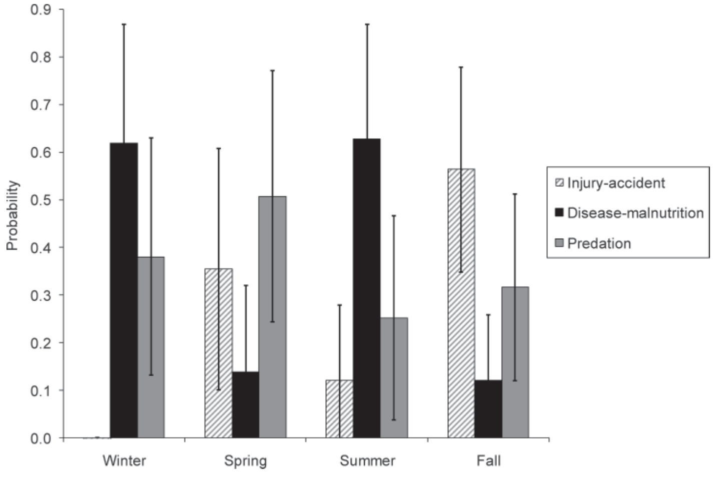


**Figure 11.** Estimated probabilities (with 95% CIs) of mortality causes of adult female mule deer as a function of season in southwest Colorado, USA, 2000–2004. Cause-specific mortality probabilities are based on total mortality (i.e., $\sum$ probabilities = 1), and therefore represent a deer's relative likelihood of dying from a particular cause given that the deer dies. We lumped mortality causes into 1 of the 3 categories shown.

**Table 7.** Annual estimates of cause-specific mortality rates of adult female mule deer in southwest Colorado, USA, 2001–2004. Adult females in the treatment group received enhanced nutrition via supplementation whereas those in the control group received no supplementation. The sum of cause-specific mortality rates across each experimental group equals the overall mortality rates of treatment (0.121) and control (0.167) adult females in our study.

| Mortality cause | Experimental group | Mortality rate | SE |
|---|---|---|---|
| Vehicle collision-injury | Treatment | 0.040 | 0.013 |
| | Control | 0.040 | 0.012 |
| Mountain lion predation | Treatment | 0.005 | 0.004 |
| | Control | 0.032 | 0.011 |
| Coyote predation | Treatment | 0.013 | 0.008 |
| | Control | 0.020 | 0.009 |
| Unknown predation | Treatment | 0.013 | 0.008 |
| | Control | 0.008 | 0.006 |
| Bear predation | Treatment | 0.000 | 0.000 |
| | Control | 0.008 | 0.006 |
| Malnutrition | Treatment | 0.000 | 0.000 |
| | Control | 0.028 | 0.010 |
| Disease | Treatment | 0.027 | 0.011 |
| | Control | 0.008 | 0.006 |
| Suspected disease | Treatment | 0.009 | 0.006 |
| | Control | 0.024 | 0.010 |
| Birthing | Treatment | 0.013 | 0.008 |
| | Control | 0.000 | 0.000 |

lower than the above values indicate because sagebrush and juniper species contain terpenoids, which may inhibit microbial digestion (Nagy et al. 1964, Carpenter et al. 1979, Schwartz et al. 1980). On a similar pinyon–juniper–sagebrush winter range in northwest Colorado, deer diets during January–March ranged from 24% to 38% IVDMD and 5% to 7% crude protein (Bartmann 1983). Spring IVDMD and CP estimates of immature, green cheatgrass (IVDMD, 65–72%; CP, 17–21%) and crested wheatgrass (IVDMD, 71–73%; CP, 27–28%) are high (Austin et al. 1994, Bishop et al. 2001), although these species offer minimal forage value during winter. In vitro dry matter digestibility of alfalfa generally ranges from 50% to 70% (Weir et al. 1960, Robles et al. 1981, Lenssen et al. 1988, Belyea et al. 1989) and CP of alfalfa is roughly 17–25% (Weir et al. 1960, Lenssen et al. 1988). Alfalfa was clearly a valuable forage item for deer, but it was limited in quantity and only available through mid-December.

**Table 8.** Estimated survival ($\hat{S}$) of mule deer fawns from the fetal stage to 6 months old as a function of a nutrition enhancement treatment, year, and fawn sex in southwest Colorado, USA, 2001–2004.

| Yr | Experimental group | Sex | $\hat{S}$ | SE($\hat{S}$) |
|---|---|---|---|---|
| 2001–2002 | Treatment | F | 0.527 | 0.122 |
| | Treatment | M | 0.485 | 0.124 |
| | Control | F | 0.436 | 0.129 |
| | Control | M | 0.395 | 0.122 |
| 2002–2003 | Treatment | F | 0.553 | 0.076 |
| | Treatment | M | 0.501 | 0.087 |
| | Control | F | 0.488 | 0.079 |
| | Control | M | 0.435 | 0.081 |
| 2003–2004 | Treatment | F | 0.470 | 0.083 |
| | Treatment | M | 0.413 | 0.078 |
| | Control | F | 0.336 | 0.075 |
| | Control | M | 0.292 | 0.075 |

**Table 9.** Estimated survival ($\hat{S}$) of mule deer fawns from the fetal stage to 1 year old as a function of a nutrition enhancement treatment, year of treatment delivery, and fawn sex in southwest Colorado, USA, 2001–2004.

| Treatment yr | Experimental group | Sex | $\hat{S}$ | SE($\hat{S}$) |
|---|---|---|---|---|
| 2001–2002 | Treatment | F | 0.471 | 0.111 |
| | Treatment | M | 0.414 | 0.109 |
| | Control | F | 0.282 | 0.091 |
| | Control | M | 0.214 | 0.075 |
| 2002–2003 | Treatment | F | 0.516 | 0.072 |
| | Treatment | M | 0.452 | 0.080 |
| | Control | F | 0.372 | 0.069 |
| | Control | M | 0.292 | 0.065 |
| 2003–2004 | Treatment | F | 0.441 | 0.079 |
| | Treatment | M | 0.377 | 0.073 |
| | Control | F | 0.262 | 0.062 |
| | Control | M | 0.205 | 0.058 |

### Fecundity and Survival

We found no differences in pregnancy and fetal rates between EGs. Any treatment effects likely would have been carried over from the previous year's treatment because most adult females were bred before the start of treatment delivery each year. Both pregnancy and fetal rates were high for each EG, equaling or exceeding previous estimates measured on the Uncompahgre Plateau and elsewhere across Colorado (Andelt et al. 2004). Pregnancy and fetal rates were not a limiting factor to the mule deer population during our study.

We observed strong support for a treatment effect in fetal survival, primarily because the effect was large during 2004. We found marginal evidence of a treatment effect in neonatal survival. Our sample sizes were insufficient to detect small to moderate effects (i.e., survival increase of 0.05–0.10) with desired power, especially during 2002. Overdispersion in our neonatal survival data further reduced power to detect a treatment effect (Bishop 2007, Bishop et al. 2008). Principal drivers of neonatal survival included birth mass and birth date, which were only partly related to the treatment. Survival increased with earlier birth dates and increased birth mass, which has been observed previously in mule deer (Lomas and Bender 2007) and other ungulates (Singer et al. 1997, Keech et al. 2000, Cook et al. 2004).

We found strong evidence of a treatment effect on overwinter fawn survival, even when survival of control fawns was high. Overwinter survival of treatment fawns ($\hat{\hat{S}} = 0.905$, SE = 0.026) was exceptionally high when compared to overwinter fawn survival across Colorado during 1997–2008 ($\hat{\hat{S}} = 0.721$, SD = 0.024;

**Table 10.** Estimated effect of a nutrition enhancement treatment, delivered during winter and spring, on survival of mule deer fawns from the fetal stage to 1 year old in southwest Colorado, USA, 2001–2004. The treatment effect represents the increase in survival attributable to the treatment.

| Treatment yr | Sex | Effect | 95% lower CL | 95% upper CL |
|---|---|---|---|---|
| 2001–2002 | F | 0.189 | −0.108 | 0.486 |
| | M | 0.199 | −0.082 | 0.478 |
| 2002–2003 | F | 0.144 | −0.020 | 0.308 |
| | M | 0.160 | −0.004 | 0.323 |
| 2003–2004 | F | 0.179 | −0.009 | 0.367 |
| | M | 0.172 | −0.012 | 0.356 |

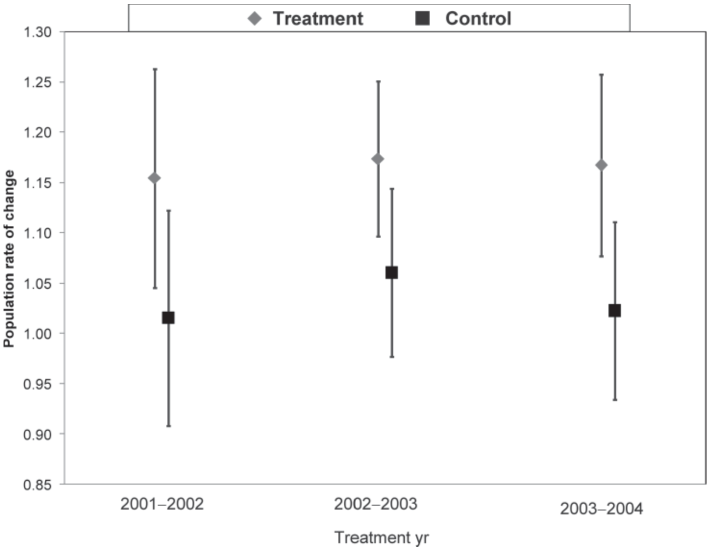


**Figure 12.** Estimates and 95% confidence intervals of the population rate of change, λ, for mule deer that received enhanced nutrition via supplementation during winter and early spring (treatment) and mule deer that received no supplementation (control) in southwest Colorado, USA, 2001–2004.

**Table 11.** Sensitivity of estimated population rate of change ($\hat{\lambda}$) to changes in estimated fecundity and survival rates of mule deer; contributions of each vital rate parameter to the overall effect of enhanced nutrition (treatment) of deer on $\hat{\lambda}$; and percent of the treatment effect on $\hat{\lambda}$ accounted for by each parameter; in southwest Colorado, USA, 2001–2004.

| | | Treatment effect on $\hat{\lambda}$[b] | |
|---|---|---|---|
| Parameter | Sensitivity of $\hat{\lambda}$[a] | $\Delta\hat{\lambda}$ | % |
| Pregnancy rate | 0.201 | 0.000 | 0.0 |
| Ad fetal rate | 0.085 | 0.000 | 0.0 |
| Yearling fetal rate | 0.025 | 0.000 | 0.0 |
| Fetal survival | 0.213 | 0.025 | 18.7 |
| Neonatal survival | 0.354 | 0.016 | 11.8 |
| Overwinter fawn survival | 0.227 | 0.044 | 33.1 |
| Ad F survival | 1.049 | 0.048 | 36.4 |

[a] We averaged sensitivities of each parameter across treatment classes and yr.

[b] We averaged contributions of each vital rate parameter to the treatment effect on $\hat{\lambda}$ across yr.

Lukacs et al. 2009) and overwinter fawn survival in Colorado, Idaho, and Montana during 1981–1996 ($\hat{\bar{S}} = 0.444$, SE $= 0.033$; Unsworth et al. 1999). Early winter mass explained additional variation in the data. Probability of survival increased as early winter mass increased, which has been documented previously (White et al. 1987, Unsworth et al. 1999, Bishop et al. 2005*a*, Taillon et al. 2006). Effects of nutrition treatment and early winter mass on survival probability provide strong evidence that fawn body condition dictated overwinter survival.

We observed higher survival of female fawns than male fawns during both the neonatal and overwinter survival periods. Higher survival of female neonates has been documented in deer previously (Jackson et al. 1972), but most studies have found little or no evidence for sex differences in neonatal survival (Gaillard et al. 1997, Ricca et al. 2002, Pojar and Bowden 2004, Lomas and Bender 2007). Sex differences in overwinter fawn survival have been documented more commonly, with females having higher survival (Bartmann et al. 1992, White and Bartmann 1998, Unsworth et al. 1999, Bishop et al. 2005*a*). Higher survival of female fawns, and hence higher recruitment of female yearlings, creates a reduced adult male:adult female ratio prior to any harvest effects.

The nutrition treatment had a positive effect on adult female survival during winter and spring, when deer received treatment. During summer and fall, however, survival was similar among treatment and control adult females and lower than expected. A priori, we expected survival of control adult females to be lower during winter and spring than summer and fall because of harsher weather and limited nutrient availability, which is consistent with past research (Bartmann et al. 1992, Ricca et al. 2002, Bender et al. 2007). However, survival of control adult females was similar during winter–spring and summer–fall periods. Natural survival rates of adult females (i.e., hunting mortality excluded) across the whole Uncompahgre Plateau during the past 10 years were lower during summer and fall than winter and spring (Lukacs et al. 2009). Most summer mortalities of adult females appeared to be disease related and were apparently independent of nutrition. Adult female mortality during summer–fall equaled or exceeded winter–spring mortality in 3 other deer populations in western Colorado as well (Lukacs et al. 2009). Thus, although summer mortality was higher than expected, our results are consistent with other recent findings in Colorado.

## Dependence Among Fecundity and Survival Rates

Fetal rates and fetal, neonatal, and overwinter fawn survival varied annually, as did the magnitude of treatment effects, but not in synchrony. The highest measured fetal rates occurred during 2004, when fetal and neonatal survival rates (i.e., survival from fetus to 6 months old) were lowest. The largest treatment effect in fetal survival occurred during 2004, when treatment had the least effect on neonatal survival. Neonatal survival rates declined during the study, whereas overwinter survival rates increased each year of the study. We observed annual variation in each fecundity and survival parameter, yet recruitment of yearlings as a function of treatment was relatively constant. Likewise, we observed minimal temporal variability in the estimated population rate of change ($\hat{\lambda}$) for each EG, particularly treatment deer (Fig. 12). These results suggest a compensatory relationship among stage or season-specific survival rates, and therefore, emphasize the need to consider overall yearling recruitment when assessing population dynamics. For example, many state wildlife agencies measure December fawn recruitment annually to evaluate population status and to help determine numbers of deer licenses to issue to hunters. December fawn recruitment alone, without accompanying data on overwinter fawn survival, could be misleading.

A possible explanation for this compensatory relationship is the timing of death of lightweight or otherwise unthrifty fawns, which have a lower probability of surviving to the yearling age class. In some years, conditions may facilitate high survival of these fawns to winter, at which point their survival probability declines significantly. In other years, these fawns may have low survival probabilities during summer and fall, which reduces December fawn recruitment but increases overwinter fawn survival because the poorest condition fawns have already been removed from the population. The same relationship could apply to fetuses and neonates, as we saw among control deer in 2004. Stillborn fetuses in 2004 were mostly small, lightweight, and seemingly undernourished. If these fetuses had been born alive, they likely would have suffered high mortality rates as neonates. The effect would have been to increase fetal survival and decrease neonatal survival. Population monitoring programs should evaluate overall recruitment of young to the yearling age class.

### Proximate Mortality Factors

We found minimal evidence of differences in mortality causes of fawns between EGs. Increased survival rates of fawns associated with the treatment effect were explained by the reductions in rates of all mortality causes rather than any specific mortality cause. Incidence of predation, malnutrition, starvation, disease, and injuries and accidents all declined as a result of enhanced nutrition. The magnitude of the decline was far more pronounced for ≥6-month-old fawns because that cohort is where we observed the greatest treatment effect. We found some evidence of differences in mortality causes of adult females between experimental groups. Increased survival rates of adult females associated with the treatment were explained by reductions in malnutrition and predation rates.

We expected rates of malnutrition and starvation to decline in response to treatment because enhanced nutrition should directly counteract these factors. Malnutrition was substantially reduced among wintering fawns and eliminated among adult females as a result of the treatment. However, we observed only a small reduction in starvation rates of neonates in response to the treatment, which could have several explanations. First, neonates received the treatment indirectly through their dams, whereas wintering fawns and adult females consumed treatment directly. Second, treatment allowed adult females in poor condition to survive winter and reproduce; these adult females may have been poorly prepared to meet lactation demands. In contrast, control adult females in the poorest condition died overwinter, prior to fawning. Third, adult females occupying the periphery of the treatment EU likely did not receive ad libitum portions of treatment throughout winter. Partial utilization of treatment may have improved survival of these adult females without improving their reproductive performance. We did not censor individuals on the periphery of EUs because we lacked detailed location data to make objective determinations and we wanted to avoid biased detection of a treatment effect.

The effect of the treatment on factors other than malnutrition and starvation is less straightforward. Several explanations exist to explain why predation on neonates might decline in response to enhanced nutrition of adult females. First, adult females may better detect predators and defend their fawns. Second, enhanced nutrition might reduce rates of diarrhea that increase fawn scent, making fawns less vulnerable to detection by predators. Third, as fawns become older, those in better condition may be better able to escape predators. We observed only modest evidence that enhanced nutrition of adult females lowered rates of predation on neonates. Our results are consistent with past research suggesting that some amount of predation on newborn fawns is expected independent of adult female or fawn nutrition (Hamlin et al. 1984, Ballard et al. 2001).

Predation rates of older fawns and adults would be expected to decline in response to enhanced nutrition if improved body condition enhanced the ability of deer to escape or avoid predators. We found strong evidence that enhanced nutrition of deer reduced coyote predation of ≥6-month-old fawns. Studies have found that coyotes primarily killed malnourished fawns during winter (Bartmann et al. 1992, Bishop et al. 2005*a*). We found that most fawns killed by coyotes in the control EU were malnourished based on degree of emaciation and visual inspection of femur marrow fat. Our results suggest that coyote predation of ≥6-month-old fawns was compensatory with respect to nutrition. That is, coyotes selected fawns in poor condition, which would be expected to have the lowest survival probabilities regardless of proximate mortality cause. Our results are consistent with other field experiments that directly demonstrated compensatory mortality by manipulating coyote numbers instead of deer nutrition (Bartmann et al. 1992, Hurley and Zager 2006). Our results further support the notion that observed coyote predation of wintering fawns in the intermountain West, albeit common, should not be viewed as sufficient evidence that coyotes are having a negative impact on deer populations. Our results also suggest that coyote predation on adult females was largely compensatory with respect to nutrition because coyotes selected for older females in poor condition, which is consistent with Hurley and Zager (2006).

Felid predation accounted for roughly 15% of total mortality of ≥6-month-old fawns and adult females, most of which was caused by mountain lions. We expected mountain lion predation to account for a greater proportion of total mortality of treatment deer, because mountain lions are capable of killing healthy animals and of potentially having a negative impact on ungulate populations (Bleich and Taylor 1998, Ballard et al. 2001, Robinson et al. 2002, Festa-Bianchet et al. 2006). Instead, mountain lion predation was substantially reduced among adult females and ≥6-month-old fawns as a result of treatment, indicating that mountain lions selected for animals in poorer condition. Our winter-range EUs were characterized by pinyon–juniper–sagebrush mosaics with high deer densities and limited canyon habitat. Perhaps predation strategies of mountain lions in our EUs favored selection of deer in poorer condition, whereas under different circumstances, predation strategies may be weakly related, or even unrelated, to prey body condition. We encourage cautious interpretation of our finding because EUs were small relative to home range sizes of mountain lions, indicating a few mountain lions may have accounted for most of the predation we observed. Therefore, our results may reflect individual behavior of only a few lions, which may or may not typify the species in this type of environment. Similar to our findings, in a recent study in north-central Colorado near Boulder, chronic wasting disease infection increased predation rates of mountain lions on mule deer nearly 4-fold, suggesting lions selected deer that were in a compromised state of health (Miller et al. 2008).

Our daily activity in the treatment EU (i.e., delivering pellets) could have deterred predation; however, we spent similar time in each EU each winter monitoring radiocollared deer and collecting fawn:adult female ratio data from the ground. Treatment was delivered by ≤3 individuals during morning hours, when deer were typically bedded. Our largest winter field crew comprised 4 individuals, who divided tasks among treatment and control EUs.

Additionally, our winter-range EUs were situated in a rapidly developing area where human activity was common. Presence of our field crew likely had little influence on predator activities.

The large effect of enhanced nutrition on $\hat{\lambda}$ in the presence of ongoing predation suggests habitat was ultimately the critical limiting factor of the Uncompahgre deer population. Predation should have minimal impact on populations that are at or near NCC (Ballard et al. 2001). Hurley and Zager (2006) observed no increase in $\hat{\lambda}$ in response to coyote reductions and only a slight increase in $\hat{\lambda}$ in response to mountain lion reductions. Our findings regarding relative effects of habitat versus predation should not be extrapolated to more complex predator-prey systems that include additional predator species such as wolves (*Canis lupus*).

Disease was a common mortality factor among neonatal fawns and adult females, but not $\geq$6 month old fawns. We found no evidence that enhanced nutrition reduced rates of disease in adult females. Deer intermixed with domestic sheep and cattle on summer range and were occasionally in close proximity to livestock on winter range, which likely explains the prevalence of BVDV and MCF. Bovine viral diarrhea has been linked to stillbirths and neonatal mortality in livestock (Sprecher et al. 1991, Baker 1995, Grooms 2004); however, we lacked means to evaluate any possible link between BVDV and deer fetal or neonatal mortality. The degree to which disease may be negatively impacting the deer population remains unclear; however, our findings indicate disease would not restrict population growth if deer obtained adequate nutrition.

### Population Rate of Change

Our estimates of $\lambda$ were most sensitive to changes in adult female survival, which was expected based on past research (Gaillard et al. 1998, 2000). Pfister (1998) found that sensitivities of demographic parameters were inversely related to process variance for a host of diverse plant and animal species. This pattern is also found in ungulates, in which process variance is low for adult females and comparatively high for juveniles (Gaillard et al. 1998, 2000; Unsworth et al. 1999). Parameter sensitivity and parameter variability are each important considerations when evaluating ungulate population dynamics. Although $\hat{\lambda}$ was most sensitive to changes in adult female survival, overwinter fawn survival was as important as adult survival in explaining the effect of treatment on $\hat{\lambda}$. Furthermore, the treatment effect on production and survival of young (i.e., fetal, neonatal, and overwinter fawn survival) accounted for nearly twice the increase in $\hat{\lambda}$ as did adult female survival.

Treatment caused $\lambda$ to increase by an average of 0.133 (SE = 0.043) during our study. The 95% confidence intervals on our estimates of the treatment effect on $\lambda$ did not overlap zero, providing strong evidence for the effect. The mean estimate of $\lambda$ for the treatment EG (1.165) would cause a population to double in size in approximately 5 years. For perspective, the Uncompahgre Plateau deer population is currently estimated at roughly 31,000 deer based on a 20-year population model that incorporated periodic estimates of population size from sample-based aerial surveys, annual harvest estimates, annual measurements of age and sex ratios, and beginning in 1997, annual measurements of overwinter fawn survival and annual survival of adult females (Kufeld et al. 1980; B. E. Watkins and B. A. Banulis, CDOW, unpublished data). Treatment conditions in our study would cause the Uncompahgre Plateau population to increase by >6,000 deer per year. This level of response supports the hypothesis that the deer population was food limited, and therefore, limited by NCC. Our results demonstrate that deer nutrition, and therefore forage quality and quantity, is ultimately a critical limiting factor of the population. Our finding is particularly noteworthy considering predation and disease were overall the most common proximate causes of deer mortality prior to and during our study (Gill et al. 2001, Pojar and Bowden 2004). Furthermore, our study took place during 4 mild to average winters, when nutrition might be expected to have a lesser impact on population growth than during more severe winters.

Our research provides additional insights into the role of nutrition in ungulate population limitation. Our results are consistent with research linking nutrition to fecundity and survival in mule and white-tailed deer (Verme 1969, Robinette et al. 1973, Ozoga and Verme 1982, Baker and Hobbs 1985, Mech et al. 1991) and other ungulates (Thorne et al. 1976, Cameron et al. 1993, Keech et al. 2000, Cook et al. 2004). These studies directly link fecundity and survival to 1) body condition of adult females throughout the year, 2) rates of growth and fat accretion in young animals during late summer and fall, and 3) rates at which fat and protein are depleted during winter.

Our results are also consistent with studies that documented density-dependent effects on fecundity or survival of ungulates by manipulating density (Clutton-Brock et al. 1987, Bartmann et al. 1992, White and Bartmann 1998, Stewart et al. 2005). If a population is food limited (i.e., limited by NCC), density reductions should reduce animal competition for the limited supply of higher quality forage and improve fecundity or survival. In our study, enhanced nutrition increased the supply of high-quality forage (i.e., pellets) available for the given number of animals occupying the EUs. Whether reducing density or enhancing nutrition, the amount of higher quality forage items available per animal increases, which should result in increased fecundity or survival if a population is limited by NCC. We emphasize higher quality forage because much of the plant material available to ungulates is of insufficient quality for meeting nutrient needs, particularly during winter. Therefore, ungulate access to forage items that exceed some quality threshold (i.e., higher quality forage) is critical when considering NCC and population limitation (Hobbs and Swift 1985).

## MANAGEMENT IMPLICATIONS

The ultimate question is whether habitat treatments can improve deer population performance, or conversely, minimize population declines as other habitat is lost. Our findings provide a scientific basis for pursuing and evaluating vegetative manipulation techniques in late-seral pinyon–juniper winter range as a means to set back succession and increase habitat productivity. However, our measured rates of population increase, in response to artificial nutrition enhancement, would likely not be feasible or sustainable in response to habitat improvements via vegetative manipulations. The objective of such habitat management might be to achieve smaller, yet sustainable, deer population increases over time. Availability of quality habitat is likely to become even more limiting because productive winter- and summer-range habitats on the Uncompahgre Plateau and adjacent San Juan Mountains are being lost to human development. A coordinated effort to manage habitat at a landscape scale is underway on the Uncompahgre Plateau, referred to as the Uncompahgre Plateau Project (UPP 2007). To evaluate effectiveness of the Project from a deer perspective, an ongoing study is quantifying effects of habitat treatments in pinyon–juniper on deer population parameters (Bergman et al. 2007).

Habitat treatments in the pinyon–juniper woodlands could improve habitat productivity by increasing the quantity and diversity of higher quality forage. Treatments would likely cause the greatest increase in diet quality during winter, although late fall and spring diets might also improve because of increased forage availability. During the past decade, roller-chop and hydro-axe treatments have been performed in pinyon–juniper woodlands on the Uncompahgre Plateau and reseeded with mostly native species, with the intent to increase the quantity and diversity of forbs, grasses, and certain browse species (UPP 2007).

We specifically chose the Uncompahgre Plateau as a study site because the deer population had declined and there were competing hypotheses with respect to habitat versus predation as limiting factors. Our results should not be extrapolated beyond the Uncompahgre Plateau for these reasons. However, given resource limitations that prevent similar studies from being conducted across numerous mule deer populations, it seems warranted to make cautious inference to other pinyon–juniper winter ranges across the Colorado Plateau, which are uniquely dominated by pinyon and Utah juniper (West 1999). The current late-seral status of pinyon–juniper on the Uncompahgre Plateau, which was the basis for our hypothesis of why deer declined, is not unique. Many pinyon–juniper communities are considered degraded primarily because of altered fire patterns and excessive grazing, and therefore, warrant proactive management (Gruell 1999, West 1999). Proposed strategies to restore pinyon–juniper communities could likewise improve deer habitat productivity, and therefore, may be advisable anywhere in the Colorado Plateau ecoregion where deer populations have declined (Watkins et al. 2007). However, there is a need to evaluate the effectiveness of various habitat treatments for mule deer (Bergman et al. 2007).

We caution against the use of our findings to justify winter feeding as a management tool because our objective was to simulate optimum habitat conditions for deer. We provided pellets ad libitum and distributed pellets widely to avoid creation of feed grounds. We expended, on average, \$40,000 and roughly 1,000 person hours per winter to purchase and deliver the supplemental feed to $<$1,000 deer and $\leq$300 elk across 7–22 km$^2$. As a rough extrapolation, $>$40,000 person hours and approximately \$1.75 million in feed costs would be required to provide supplement in this manner to most of the Uncompahgre deer population for a winter. Others have evaluated the utility of winter feeding as a management strategy to mitigate deer mortality (Baker and Hobbs 1985, Peterson and Messmer 2007).

## SUMMARY

- We enhanced nutrition of free-ranging mule deer during winter and spring to simulate an instantaneous increase in nutritional quality of winter range habitat on the Uncompahgre Plateau in southwest Colorado.
- We evaluated the effect of enhanced nutrition on deer fecundity and survival rates using a life table response experiment.
- Pregnancy rates (i.e., proportion of ad F with $\geq$1 fetus) and fetal rates (i.e., mean no. of fetuses/pregnant ad F) were high among all deer and did not vary in response to the nutrition treatment.
- We observed an overall increase in survival of fetuses from February to birth in response to the treatment, although the magnitude of the effect varied annually.
- We observed marginal evidence of increased neonatal survival in response to the nutrition treatment.
- We observed a large treatment effect in overwinter fawn survival. Overwinter survival of fawns receiving the treatment averaged 0.905 (SE = 0.026) whereas overwinter survival of control fawns averaged 0.684 (SE = 0.044).
- Nutrition treatment had a positive effect on yearling recruitment, expressed as the product of fetal, neonatal, and overwinter survival rates. Survival of treatment fetuses to the yearling age class was 0.447 (SE = 0.052), whereas survival of control fetuses to the yearling age class was 0.271 (SE = 0.042).
- Nutrition treatment had a positive effect on annual survival of adult females (treatment: $\hat{S} = 0.879$, SE = 0.021; control: $\hat{S} = 0.833$, SE = 0.025).
- Combining all fecundity and survival rates into a matrix population model, we observed an increase in $\hat{\lambda}$ in response to enhanced nutrition. Average $\hat{\lambda}$ was 1.165 (SE = 0.036) for treatment deer and 1.033 (SE = 0.038) for control deer. Treatment caused $\hat{\lambda}$ to increase by 0.139 (95% CI: 0.020–0.259) during 2001–2002, 0.113 (95% CI: 0.023–0.204) during 2002–2003, and 0.145 (95% CI: 0.048–0.242) during 2003–2004. Averaged across years, treatment caused $\hat{\lambda}$ to increase by 0.133 (95% CI: 0.049–0.217).
- Increased production and survival of young (i.e., fetal, neonatal, and overwinter survival) accounted for 0.084 of the overall increase in $\hat{\lambda}$ and increased survival of adult females accounted for the remaining 0.048 increase in $\hat{\lambda}$. The treatment effect on overwinter fawn survival alone accounted for 0.044 of the increase in $\hat{\lambda}$.
- Enhanced deer nutrition caused a reduction in coyote and mountain lion predation of $\geq$6-month-old fawns and adult females.
- The large increase in $\hat{\lambda}$ in response to enhanced nutrition indicates the deer population was food limited, and therefore, limited by habitat in terms of forage quality.
- Our study provides support for evaluating effectiveness of habitat treatments for deer in pinyon–juniper winter range. Specifically, future research is needed to determine whether habitat improvements, as opposed to artificial nutritional supplementation, are capable of causing an increase in $\hat{\lambda}$.

## ACKNOWLEDGMENTS

We thank J. L. Grigg, C. A. Schroeder, and J. A. Padia for contributing thousands of field hours and helping oversee field crews. We thank E. J. Bergman, K. C. Crane, M. L. Del Tonto, H. J. Halbritter, J. W. McMillan, W. J. Padia, R. M. Powers, J. E. Risher, C. M. Solohub, J. A. Thayer, M. A. Thonhoff, C. E.

Tucker, T. M. Banulis, S. K. Carroll, M. J. Catanese, D. L. Coven, C. L. Harty, M. D. Johnston, J. D. Nicholson, M. H. Swan, R. M. Wertsbaugh, M. Sirochman, and T. Sirochman for field assistance. L. L. Wolfe provided assistance with deer captures. We thank R. C. Cook for assistance with body condition measurements and body fat estimation, and L. A. Baeten for performing necropsies and coordinating tissue analyses. K. Griffin transported carcasses and handled tissue samples. Various other CDOW personnel provided project support and assistance with winter deer captures. Colorado Division of Wildlife volunteers supported drop-net deer captures throughout the study. Volunteers J. Beck, W. Hawley, and D. Manhart contributed countless hours to various aspects of winter research. Fixed-wing pilots L. D. Felix, L. L. Gepfert, J. H. Olterman (deceased), G. L. Lust, C. Schork, and L. Coulter provided many hours in the air. G. Brennan and J. Olson (deceased) and their crews captured necessary samples of deer using helicopter net guns. P. M. Lukacs assisted with data analyses. We thank R. B. Gill and L. H. Carpenter for critical insights during study design, and we thank G. C. Miller for overall project support. E. J. Bergman, P. F. Doherty, J.-M. Gaillard, D. M. Swift, D. P. Walsh, K. R. Wilson, and one anonymous reviewer improved the manuscript through constructive reviews. O. Devineau, K. P. Huyvaert, and N. Komar translated the abstract into French and Spanish. We thank E. C. Hellgren for improving the quality of the manuscript for publication.

## LITERATURE CITED

Ammann, A. P., R. L. Cowan, C. L. Mothershead, and B. R. Baumgardt. 1973. Dry matter and energy intake in relation to digestibility in white-tailed deer. Journal of Wildlife Management 37:195–201.

Andelt, W. F., T. M. Pojar, and L. W. Johnson. 2004. Long-term trends in mule deer pregnancy and fetal rates in Colorado. Journal of Wildlife Management 68: 542–549.

Austin, D. D., R. Stevens, K. R. Jorgensen, and P. J. Urness. 1994. Preferences of mule deer for 16 grasses found on intermountain winter ranges. Journal of Range Management 47:308–311.

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

Baker, D. L., D. E. Johnson, L. H. Carpenter, O. C. Wallmo, and R. B. Gill. 1979. Energy requirements of mule deer fawns in winter. Journal of Wildlife Management 43:162–169.

Baker, D. L., G. W. Stout, and M. W. Miller. 1998. A diet supplement for captive wild ruminants. Journal of Zoo and Wildlife Medicine 29:150–156.

Baker, J. C. 1995. The clinical manifestations of bovine viral diarrhea infection. Veterinary Clinics of North America Food Animal Practice 11:425–446.

Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos, Jr. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99–115.

Barrett, M. W., J. W. Nolan, and L. D. Roy. 1982. Evaluation of a hand-held net-gun to capture large mammals. Wildlife Society Bulletin 10:108–114.

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

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

Belyea, R. L., F. A. Martz, and G. A. Mbagaya. 1989. Effect of particle size of alfalfa hay on intake, digestibility, milk yield, and ruminal cell wall of dairy cattle. Journal of Dairy Science 72:958–963.

Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118–1124.

Bergman, E. J., C. J. Bishop, D. J. Freddy, and G. C. White. 2007. Evaluation of winter range habitat treatments on over-winter survival and body condition of mule deer. Wildlife Research Report, July:73–96. Colorado Division of Wildlife, Fort Collins, USA.

Bishop, C. J. 2007. Effect of enhanced nutrition during winter on the Uncompahgre Plateau mule deer population. Dissertation, Colorado State University, Fort Collins, USA.

Bishop, C. J., D. J. Freddy, and G. C. White. 2002. Effect of enhanced winter nutrition of adult female mule deer on fetal and neonatal survival rates: a pilot study to address feasibility. Wildlife Research Report, July:81–92. Colorado Division of Wildlife, Fort Collins, USA.

Bishop, C. J., D. J. Freddy, G. C. White, B. E. Watkins, T. R. Stephenson, and L. L. Wolfe. 2007. Using vaginal implant transmitters to aid in capture of mule deer neonates. Journal of Wildlife Management 71:945–954.

Bishop, C. J., E. O. Garton, and J. W. Unsworth. 2001. Bitterbrush and cheatgrass quality on 3 southwest Idaho winter ranges. Journal of Range Management 54: 595–602.

Bishop, C. J., J. W. Unsworth, and E. O. Garton. 2005*a*. Mule deer survival among adjacent populations in southwest Idaho. Journal of Wildlife Management 69: 311–321.

Bishop, C. J., G. C. White, D. J. Freddy, and B. E. Watkins. 2005*b*. Effect of nutrition and habitat enhancements on mule deer recruitment and survival rates. Wildlife Research Report, July:37–65. Colorado Division of Wildlife, Fort Collins, USA.

Bishop, C. J., G. C. White, and P. M. Lukacs. 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. Journal of Wildlife Management 72:1085–1093.

Bleich, V. C., and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. Great Basin Naturalist 58:265–272.

Bonenfant, C., J.-M. Gaillard, F. Klein, and J.-L. Hamann. 2005. Can we use the young:female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. Journal of Applied Ecology 42: 361–370.

Bunderson, E. D., B. L. Welch, and D. J. Weber. 1986. In vitro digestibility of *Juniperus osteosperma* (Torr.) Little from 17 Utah sites. Forest Science 32:834–840.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71:480–486.

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

Carpenter, L. H., O. C. Wallmo, and R. B. Gill. 1979. Forage diversity and dietary selection by wintering mule deer. Journal of Range Management 32:226–229.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1987. Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. Journal of Animal Ecology 56:857–871.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain Elk. Journal of Wildlife Management 65:973–987.

Cook, R. C., T. R. Stephenson, W. L. Myers, J. G. Cook, and L. A. Shipley. 2007. Validating predictive models of nutritional condition for mule deer. Journal of Wildlife Management 71:1934–1943.

de Vos, J. C., Jr., M. R. Conover, and N. E. Headrick, editors. 2003. Mule deer conservation: issues and management strategies. Berryman Institute Press, Utah State University, Logan, USA.

Dietz, D. R. 1965. Deer nutrition research in range management. Transactions of the North American Wildlife and Natural Resources Conference 30:274–285.

Festa-Bianchet, M., T. Coulson, J.-M. Gaillard, J. T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. Proceedings of The Royal Society B 273:1537–1543.

Gaillard, J.-M., J.-M. Boutin, D. Delorme, G. Van Laere, P. Duncan, and J.-D. Lebreton. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia 112:502–513.

Gaillard, J.-M., D. Delorme, J.-M. Boutin, G. Van Laere, and B. Boisaubert.

1996. Body mass of roe deer fawns during winter in 2 contrasting populations. Journal of Wildlife Management 60:29–36.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gill, R. B., T. D. I. Beck, C. J. Bishop, D. J. Freddy, N. T. Hobbs, R. H. Kahn, M. W. Miller, T. M. Pojar, and G. C. White. 2001. Declining mule deer populations in Colorado: reasons and responses. Special Report Number 77, Colorado Division of Wildlife, Fort Collins, USA.

Grooms, D. L. 2004. Reproductive consequences of infection with bovine viral diarrhea virus. Veterinary Clinics of North America Food Animal Practice 20:5–19.

Gruell, G. E. 1999. Historical and modern roles of fire in pinyon-juniper. Pages 24–28 *in* S. B. Monsen and R. Stevens, editors. Proceedings: ecology and management of pinyon-juniper communities within the Interior West. Proceedings RMRS-P-9, United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. Journal of Wildlife Management 64:441–449.

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

Haugen, A. O., and D. W. Speake. 1958. Determining age of young fawn white-tailed deer. Journal of Wildlife Management 22:319–321.

Heffelfinger, J. R., and T. A. Messmer. 2003. Introduction. Pages 1–11 *in* J. C. de Vos, Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Berryman Institute Press, Utah State University, Logan, USA.

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

Holter, J. B., H. H. Hayes, and S. H. Smith. 1979*a*. Protein requirement of yearling white-tailed deer. Journal of Wildlife Management 43:872–879.

Holter, J. B., W. E. Urban, Jr., and H. H. Hayes. 1979*b*. Predicting energy and nitrogen retention in young white-tailed deer. Journal of Wildlife Management 43:880–888.

Hurley, M. A., and P. E. Zager. 2006. Influence of predators on mule deer populations. Idaho Department of Fish and Game, Federal Aid in Wildlife Restoration, Project W-160-R-33, Completion Report, Boise, USA.

Jackson, R. M., M. White, and F. F. Knowlton. 1972. Activity patterns of young white-tailed deer fawns in south Texas. Ecology 53:262–270.

Julander, O., W. L. Robinette, and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. Journal of Wildlife Management 25: 54–60.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457–481.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

Kjellander, P., J.-M. Gaillard, and A. J. M. Hewison. 2006. Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. Oecologia 146:521–530.

Kufeld, R. C., J. H. Olterman, and D. C. Bowden. 1980. A helicopter quadrat census for mule deer on Uncompahgre Plateau, Colorado. Journal of Wildlife Management 44:632–639.

Kufeld, R. C., M. Stevens, and D. C. Bowden. 1981. Winter variation in nutrient and fiber content and in vitro digestibility of gambel oak [*Quercus gambellii*] and big sagebrush [*Artemisia tridentata*] from diversified sites in Colorado. Journal of Range Management 34:149–151.

Lenssen, A. W., E. L. Sorensen, G. L. Posler, and L. H. Harbers. 1988. In vitro dry matter disappearance, crude protein concentration, and leaf percentage of erect glandular-haired *Medicago* populations. Journal of Dairy Science 71:954–963.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.

Lomas, L. A., and L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. Journal of Wildlife Management 71:884–894.

Lukacs, P. M., G. C. White, B. E. Watkins, R. H. Kahn, B. A. Banulis, D. J. Finley, A. A. Holland, J. A. Martens, and J. Vayhinger. 2009. Separating components of variation in survival of mule deer in Colorado. Journal of Wildlife Management 73:in press.

Lutz, D. W., M. Cox, B. F. Wakeling, D. McWhirter, L. H. Carpenter, S. Rosenstock, D. Stroud, L. C. Bender, and A. F. Reeve. 2003. Impacts and changes to mule deer habitat. Pages 13–61 *in* J. C. de Vos, Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Berryman Institute Press, Utah State University, Logan, USA.

Mackie, R. J., D. F. Pac, K. L. Hamlin, and G. L. Dusek. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Montana Fish, Wildlife, and Parks, Helena, USA.

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

McCullough, D. R. 2001. Male harvest in relation to female removals in a black-tailed deer population. Journal of Wildlife Management 65:46–58.

McLeod, S. R. 1997. Is the concept of carrying capacity useful in variable environments? Oikos 79:529–542.

Mech, L. D., M. E. Nelson, and R. E. McRoberts. 1991. Effects of maternal and grandmaternal nutrition on deer mass and vulnerability to wolf predation. Journal of Mammalogy 72:146–151.

Medin, D. E. 1976. Modeling the dynamics of a Colorado mule deer population. Dissertation, Colorado State University, Fort Collins, USA.

Miller, M. W., H. M. Swanson, L. L. Wolfe, F. G. Quartarone, S. L. Huwer, C. H. Southwick, and P. M. Lukacs. 2008. Lions and prions and deer demise. PLoS ONE 3:e4019.

Myers, E. P. 2001. Assessing the role of select infectious disease agents in neonatal mule deer fawn mortality on the Uncompahgre Plateau of western Colorado. Thesis, Colorado State University, Fort Collins, USA.

Nagy, J. G., H. W. Steinhoff, and G. M. Ward. 1964. Effects of essential oils of sagebrush on deer rumen microbial function. Journal of Wildlife Management 28:785–790.

Ozoga, J. J., and L. J. Verme. 1982. Physical and reproductive characteristics of a supplementally-fed white-tailed deer herd. Journal of Wildlife Management 46: 281–301.

Peterson, C., and T. A. Messmer. 2007. Effects of winter-feeding on mule deer in northern Utah. Journal of Wildlife Management 71:1440–1445.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213–218.

Pojar, T. M., and D. C. Bowden. 2004. Neonatal mule deer fawn survival in west-central Colorado. Journal of Wildlife Management 68:550–560.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered-entry design. Journal of Wildlife Management 53:7–15.

Ramsey, C. W. 1968. A drop-net deer trap. Journal of Wildlife Management 32: 187–190.

Ricca, M. A., R. G. Anthony, D. H. Jackson, and S. A. Wolfe. 2002. Survival of Columbian white-tailed deer in western Oregon. Journal of Wildlife Management 66:1255–1266.

Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. New Zealand Journal of Science and Technology 36:429–463.

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

Robinette, W. L., J. S. Gashwiler, D. A. Jones, and H. S. Crane. 1955. Fertility of mule deer in Utah. Journal of Wildlife Management 19:115–136.

Robinette, W. L., D. A. Jones, G. Rogers, and J. S. Gashwiler. 1957. Notes on tooth development and wear for Rocky Mountain mule deer. Journal of Wildlife Management 21:134–153.

Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Canadian Journal of Zoology 80:556–568.

Robles, A. Y., R. L. Belyea, and F. A. Martz. 1981. Intake, digestibility, ruminal characteristics and rate of passage of alfalfa diets fed to sheep. Journal of Animal Science 53:774–779.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–205.

Sams, M. G., R. L. Lochmiller, E. C. Hellgren, W. D. Warde, and L. W. Varner. 1996. Morphometric predictors of neonatal age for white-tailed deer. Wildlife Society Bulletin 24:53–57.

Schultheiss, P. C., H. Van Campen, T. R. Spraker, C. J. Bishop, L. L. Wolfe, and

B. Podell. 2007. Malignant catarrhal fever associated with ovine herpesvirus-2 in free-ranging mule deer in Colorado. Journal of Wildlife Diseases 43:533–537.

Schwartz, C. C., J. G. Nagy, and W. L. Regelin. 1980. Juniper oil yield, terpenoid concentration, and antimicrobial effects on deer. Journal of Wildlife Management 44:107–113.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Macmillan, New York, New York, USA.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12–25.

Smith, S. H., J. B. Holter, H. H. Hayes, and H. Silver. 1975. Protein requirement of white-tailed deer fawns. Journal of Wildlife Management 39:582–589.

Sprecher, D. J., J. C. Baker, R. E. Holland, and B. Yamini. 1991. An outbreak of fetal and neonatal losses associated with the diagnosis of bovine viral diarrhea virus in a dairy herd. Theriogenology 36:597–606.

Stephenson, T. R., V. C. Bleich, B. M. Pierce, and G. P. Mulcahy. 2002. Validation of mule deer body composition using *in vivo* and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557–564.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717–722.

Stephenson, T. R., J. W. Testa, G. P. Adams, R. G. Sasser, C. C. Schwartz, and K. J. Hundertmark. 1995. Diagnosis of pregnancy and twinning in moose by ultrasonography and serum assay. Alces 31:167–172.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85–93.

Swift, D. M. 1983. A simulation model of energy and nitrogen balance for free-ranging ruminants. Journal of Wildlife Management 47:620–645.

Taillon, J., D. G. Sauvé, and S. D. Côté. 2006. The effects of decreasing winter diet quality on foraging behavior and life-history traits of white-tailed deer fawns. Journal of Wildlife Management 70:1445–1454.

Thompson, C. B., J. B. Holter, H. H. Hayes, H. Silver, and W. E. Urban, Jr. 1973. Nutrition of white-tailed deer. I. Energy requirements of fawns. Journal of Wildlife Management 37:301–311.

Thorne, E. T., R. E. Dean, and W. G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. Journal of Wildlife Management 40:330–335.

Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, and B. L. Bradley. 1967. Protein requirement of white-tailed deer fawns. Journal of Wildlife Management 31:679–685.

Uncompahgre Plateau Project [UPP]. 2007. UPP home page. <http://www.upproject.org>. Accessed 30 Aug 2007.

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

van Reenen, G. 1982. Field experience in the capture of red deer by helicopter in New Zealand with reference to post-capture sequela and management. Pages 408–421 *in* L. Nielsen, J. C. Haigh, and M. E. Fowler, editors. Chemical immobilization of North American wildlife. Wisconsin Humane Society, Milwaukee, USA.

Verme, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. Journal of Wildlife Management 33:881–887.

Wambolt, C. L. 2004. Browsing and plant age relationships to winter protein and fiber of big sagebrush subspecies. Journal of Range Management 57:620–623.

Ward, A. L. 1971. In vitro digestibility of elk winter forage in southern Wyoming. Journal of Wildlife Management 35:681–688.

Watkins, B. E., C. J. Bishop, E. J. Bergman, A. Bronson, B. Hale, B. F. Wakeling, L. H. Carpenter, and D. W. Lutz. 2007. Habitat guidelines for mule deer: Colorado Plateau shrubland and forest ecoregion. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies.

Weir, W. C., L. G. Jones, and J. H. Meyer. 1960. Effect of cutting interval and stage of maturity on the digestibility and yield of alfalfa. Journal of Animal Science 19:5–19.

Welch, B. L. 1989. Nutritive value of shrubs. Pages 405–424 *in* C. M. McKell, editor. The biology and utilization of shrubs. Academic Press, San Diego, California, USA.

Welch, B. L., and J. C. Pederson. 1981. In vitro digestibility among accessions of big sagebrush by wild mule deer and its relationship to monoterpenoid content. Journal of Range Management 34:497–500.

Welch, B. L., J. C. Pederson, and W. P. Clary. 1983. Ability of different rumen inocula to digest range forages. Journal of Wildlife Management 47:873–877.

West, N. E. 1999. Distribution, composition, and classification of current juniper-pinyon woodlands and savannas across western North America. Pages 20–23 *in* S. B. Monsen and R. Stevens, editors. Proceedings: ecology and management of pinyon-juniper communities within the Interior West. Proceedings RMRS-P-9, United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA.

Western Regional Climate Center [WRCC]. 2005. WRCC home page. <http://www.wrcc.dri.edu>. Accessed 27 Apr 2005.

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

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–139.

White, G. C., D. J. Freddy, R. B. Gill, and J. H. Ellenberger. 2001. Effect of adult sex ratio on mule deer and elk productivity in Colorado. Journal of Wildlife Management 65:543–551.

White, G. C., R. A. Garrott, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Survival of mule deer in northwest Colorado. Journal of Wildlife Management 51:852–859.

*Received: 21 February 2008.*
*Accepted: 25 December 2008.*

**Appendix A.** Model selection results, based on Akaike's Information Criterion with small sample size correction (AIC$_c$), from an analysis of mule deer fetal survival as a function of year and a nutritional enhancement treatment (trt) in southwest Colorado, USA, 2002–2004.

| Model[a] | No. parameters | AIC$_c$ | ΔAIC$_c$ | Akaike wt |
|---|---|---|---|---|
| $S_1$(trt × yr) $S_2$(.) $p_1$(yr) $p_2$(yr) $r$(.) $a$(yr) $b$(yr) | 20 | 1,137.79 | 0.00 | 0.293 |
| $S_1$(trt × yr) $S_2$(trt) $p_1$(yr) $p_2$(yr) $r$(.) $a$(yr) $b$(yr) | 21 | 1,138.27 | 0.48 | 0.231 |
| $S_1$(trt + yr) $S_2$(.) $p_1$(yr) $p_2$(yr) $r$(.) $a$(yr) $b$(yr) | 18 | 1,139.20 | 1.41 | 0.145 |
| $S_1$(trt) $S_2$(.) $p_1$(yr) $p_2$(yr) $r$(.) $a$(yr) $b$(yr) | 16 | 1,139.39 | 1.60 | 0.132 |
| $S_1$(trt × yr) $S_2$(.) $p_1$(.) $p_2$(yr) $r$(.) $a$(yr) $b$(yr) | 18 | 1,140.30 | 2.51 | 0.084 |
| $S_1$(trt × yr) $S_2$(yr) $p_1$(yr) $p_2$(yr) $r$(.) $a$(yr) $b$(yr) | 22 | 1,141.06 | 3.27 | 0.057 |
| $S_1$(trt × yr) $S_2$(.) $p_1$(yr) $p_2$(yr) $r$(.) $a$(trt × yr) $b$(trt × yr) | 26 | 1,142.06 | 4.27 | 0.035 |
| $S_1$(yr) $S_2$(.) $p_1$(yr) $p_2$(yr) $r$(.) $a$(yr) $b$(yr) | 17 | 1,143.78 | 5.99 | 0.015 |
| $S_1$(trt × yr) $S_2$(.) $p_1$(yr) $p_2$(.) $r$(.) $a$(yr) $b$(yr) | 18 | 1,146.00 | 8.21 | 0.005 |
| $S_1$(trt × yr) $S_2$(.) $p_1$(yr) $p_2$(trt × yr) $r$(.) $a$(trt × yr) $b$(trt × yr) | 29 | 1,146.93 | 9.14 | 0.003 |
| $S_1$(trt × yr) $S_2$(.) $p_1$(trt × yr) $p_2$(trt × yr) $r$(.) $a$(trt × yr) $b$(trt × yr) | 32 | 1,153.51 | 15.72 | 0.000 |
| $S_1$(trt × yr) $S_2$(trt) $p_1$(trt × yr) $p_2$(trt × yr) $r$(.) $a$(trt × yr) $b$(trt × yr) | 33 | 1,155.15 | 17.36 | 0.000 |
| $S_1$(trt × yr) $S_2$(trt × yr) $p_1$(trt × yr) $p_2$(trt × yr) $r$(.) $a$(trt × yr) $b$(trt × yr) | 37 | 1,163.96 | 26.17 | 0.000 |
| $S_1$(trt × yr) $S_2$(.) $p_1$(.) $p_2$(.) $r$(.) $a$(.) $b$(.) | 12 | 1,167.19 | 29.40 | 0.000 |
| $S_1$(.) $S_2$(.) $p_1$(.) $p_2$(.) $r$(.) $a$(.) $b$(.) | 7 | 1,174.95 | 37.16 | 0.000 |

[a] Fetal survival probability is represented by parameter $S_1$. All other model parameters are nuisance parameters: $S_2 =$ neonatal survival probability from birth to 5 days old, $p_1 =$ probability of detecting a neonatal fawn $\leq 1$ day old given that we conducted a search $\leq 1$ day postpartum, $p_2 =$ probability of detecting a neonatal fawn $>1$ day old given that we conducted a search $>1$ day postpartum, $r =$ probability of detecting a stillborn fetus when a vaginal implant transmitter (VIT) was not shed at a birth site, $a =$ probability of radiolocating an ad F and searching for her fawn(s) $\leq 1$ day postpartum, and $b =$ probability a VIT was shed at a birth site.

**Appendix B.** Model selection results, based on quasi-likelihood using Akaike's Information Criterion with small sample size correction (QAIC$_c$), from an analysis of mule deer neonatal survival as a function of sex, year, a nutritional enhancement treatment (trt), fawn age trend (A), Julian date of birth (bdate), estimated birth mass (bmass, kg), and estimated birth hind foot length (bhft, cm), in southwest Colorado, USA, 2002–2004.

| Model[a] | No. parameters | QAIC$_c$[b] | ΔQAIC$_c$ | QAIC$_c$ wt |
|---|---|---|---|---|
| Sex, bmass, A, A$^2$, A$^3$, bdate | 7 | 1,212.49 | 0.00 | 0.129 |
| Sex, bmass × yr, A, A$^2$, A$^3$, bdate | 11 | 1,212.52 | 0.03 | 0.127 |
| Sex, trt, bmass × yr, A, A$^2$, A$^3$, bdate | 12 | 1,212.70 | 0.21 | 0.116 |
| Bmass, A, A$^2$, A$^3$, bdate | 6 | 1,212.92 | 0.43 | 0.104 |
| Sex, trt, bmass, A, A$^2$, A$^3$, bdate | 8 | 1,213.33 | 0.84 | 0.085 |
| Bmass × yr, A, A$^2$, A$^3$, bdate | 10 | 1,213.53 | 1.04 | 0.077 |
| Trt, bmass, A, A$^2$, A$^3$, bdate | 7 | 1,214.07 | 1.58 | 0.059 |
| Trt, bmass × yr, A, A$^2$, A$^3$, bdate | 11 | 1,214.14 | 1.66 | 0.056 |
| Trt, bmass, yr, A, A$^2$, A$^3$, bdate | 9 | 1,214.70 | 2.21 | 0.043 |
| Trt, bmass, yr, A, A$^2$, A$^3$ | 8 | 1,215.18 | 2.69 | 0.034 |
| Trt × yr, bmass × yr, A, A$^2$, A$^3$, bdate | 13 | 1,215.60 | 3.11 | 0.027 |
| Trt, bmass × yr, A, A$^2$, A$^3$, bdate, bhft | 12 | 1,215.61 | 3.12 | 0.027 |
| Trt × yr, A, A$^2$, A$^3$, bdate × bmass | 12 | 1,216.39 | 3.90 | 0.018 |
| Trt × yr, bmass × yr, A, A$^2$, A$^3$, bdate × bmass | 14 | 1,216.50 | 4.01 | 0.017 |
| Trt × yr, bmass × yr, A, A$^2$, A$^3$, bdate, bhft | 14 | 1,216.82 | 4.33 | 0.015 |
| Trt × yr, bmass, A, A$^2$, A$^3$, bdate | 11 | 1,217.02 | 4.53 | 0.013 |
| Trt × yr, bmass, A, A$^2$, A$^3$ | 10 | 1,217.48 | 4.99 | 0.011 |
| Trt × yr, bmass, A, A$^2$, A$^3$, bdate, bhft | 12 | 1,217.63 | 5.14 | 0.010 |

[a] We considered 40 models. We listed in the table only those models that received $\geq 0.01$ QAIC$_c$ wt. All models that included daily, weekly, or biweekly variation in fawn age received 0 QAIC$_c$ wt.

[b] Model selection results were based on $\hat{c} = 1.25$ (Bishop 2007, Bishop et al. 2008).

**Appendix C.** Model selection results, based on Akaike's Information Criterion with small sample size correction ($AIC_c$), from an analysis of overwinter survival of mule deer fawns as a function of a nutritional enhancement treatment (trt), year, sex, time (t), early winter mass (mass, kg), early winter chest girth (chest, cm), and hind foot length (cm), in southwest Colorado, USA, 2001–2004. We constrained time 4 ways: weekly, monthly, seasonally (i.e., winter, spring), and as a trend (T).

| Model[a] | No. parameters | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ wt |
|---|---|---|---|---|
| Trt, yr, sex, t(month), mass | 11 | 650.42 | 0.00 | 0.435 |
| Trt, yr, sex, t(month), mass, chest | 12 | 651.12 | 0.70 | 0.307 |
| Trt × t(month), yr, sex, mass | 16 | 653.03 | 2.61 | 0.118 |
| Trt, yr × sex, t(month), mass | 13 | 653.76 | 3.34 | 0.082 |
| Trt, yr, sex, t(T), mass | 7 | 655.71 | 5.29 | 0.031 |
| Trt, yr × t(month), sex, mass | 21 | 657.82 | 7.40 | 0.011 |
| Trt, yr, sex, t(season), mass | 7 | 658.52 | 8.11 | 0.008 |
| Trt, yr, sex, t(week), mass | 31 | 660.52 | 10.10 | 0.003 |
| Trt, sex, mass | 4 | 661.99 | 11.57 | 0.001 |
| Trt, mass | 3 | 662.04 | 11.62 | 0.001 |
| Trt, yr, mass | 5 | 662.08 | 11.66 | 0.001 |
| Trt, yr, sex, mass | 6 | 662.25 | 11.83 | 0.001 |

[a] We considered 23 models. We listed in the table only those models that received ≥0.001 $AIC_c$ wt.

**Appendix D.** Model selection results, based on Akaike's Information Criterion with small sample size correction ($AIC_c$), from an analysis of annual survival of adult female mule deer as a function of a nutritional enhancement treatment (trt), year, time (t), age, mass (mass, kg), chest girth (chest, cm), and hind foot length (foot, cm), in southwest Colorado, USA, 2000–2004. We constrained time 3 ways: biweekly, monthly, and seasonally (i.e., winter–spring, summer–fall).

| Model[a] | No. parameters | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ wt |
|---|---|---|---|---|
| Trt × t(season), age, $age^2$ | 6 | 1,275.18 | 0.00 | 0.130 |
| Trt × t(season), age | 5 | 1,275.58 | 0.40 | 0.106 |
| Trt × t(season), age, $age^2$, foot | 7 | 1,275.77 | 0.59 | 0.096 |
| Trt × t(season) | 4 | 1,276.06 | 0.89 | 0.083 |
| Trt, age | 3 | 1,276.16 | 0.98 | 0.079 |
| Trt | 2 | 1,276.62 | 1.44 | 0.063 |
| Trt, age, foot | 4 | 1,276.62 | 1.45 | 0.063 |
| t(season), age, $age^2$ | 4 | 1,276.77 | 1.59 | 0.055 |
| Trt × t(season), age, $age^2$, $age^3$ | 7 | 1,276.79 | 1.61 | 0.055 |
| Trt × t(season), foot | 5 | 1,276.91 | 1.74 | 0.051 |
| Trt, t(season), age | 4 | 1,277.14 | 1.96 | 0.046 |
| Trt × t(season), age × foot | 7 | 1,277.69 | 2.51 | 0.035 |
| Trt, t(season) | 3 | 1,277.73 | 2.55 | 0.034 |
| Trt × t(month) | 24 | 1,277.84 | 2.66 | 0.032 |
| Trt, t(season), foot | 4 | 1,278.60 | 3.43 | 0.022 |
| Trt, t(biweekly) | 27 | 1,279.40 | 4.22 | 0.015 |
| Trt, t(season), chest | 4 | 1,279.66 | 4.49 | 0.013 |
| Trt, t(season), mass | 4 | 1,279.69 | 4.51 | 0.013 |

[a] We considered 32 models. We listed in the table only those models that received ≥0.01 $AIC_c$ wt.

Twin mule deer (*Odocoileus hemionus*) fawns newly born of a radiocollared adult female deer on the southern end of the Uncompahgre Plateau, Colorado, USA. Photo by Michael L. Del Tonto.

Mule deer (*Odocoileus hemionus*) fawn recently captured and radiocollared on the southern end of the Uncompahgre Plateau, Colorado, USA. Photo by Chad J. Bishop.

Adult female and fawn mule deer (*Odocoileus hemionus*) consuming apple pulp and alfalfa hay under a dropnet on the Uncompahgre Plateau, Colorado, USA. Photo by Chad J. Bishop.

WILEY

---

Linking Energy Balance to Survival in Mule Deer: Development and Test of a Simulation Model
Author(s): N. Thompson Hobbs
Source: *Wildlife Monographs*, No. 101, Linking Energy Balance to Survival in Mule Deer: Development and Test of a Simulation Model (Apr., 1989), pp. 3-39
Published by: Wiley on behalf of the Wildlife Society
Stable URL: https://www.jstor.org/stable/3830599
Accessed: 20-09-2019 18:25 UTC

WILDLIFE MONOGRAPHS
(ISSN:0084-0173)

*A Publication of The Wildlife Society*

# LINKING ENERGY BALANCE TO SURVIVAL IN MULE DEER: DEVELOPMENT AND TEST OF A SIMULATION MODEL

by

N. THOMPSON HOBBS

**NO. 101** **APRIL 1989**

**FRONTISPIECE.** Mule deer fawns in Middle Park, Colorado. (Photo by R. Bruce Gill)

# LINKING ENERGY BALANCE TO SURVIVAL IN MULE DEER: DEVELOPMENT AND TEST OF A SIMULATION MODEL

**N. THOMPSON HOBBS**
Colorado Division of Wildlife, Research Center, 317 W. Prospect, Fort Collins, CO 80526

*Abstract:* I developed a model of energy balance in mule deer (*Odocoileus hemionus*) that predicts changes in body size and fatness of the average doe and fawn and predicts rates of mortality due to starvation in populations of does and fawns. Model predictions respond to input on the amount, quality, and structure of forage, the density of deer, and daily weather conditions (max. and min. temp. and snow depth). Application of the model is restricted to shrub–steppe and shrub–woodland ranges. Energy expenditure is simulated as the sum of hourly costs of activity (posture, locomotion, eating), resting (lying, ruminating), and thermoregulation. Daily snow depth and characteristics of forage influence energy intake. Differences between energy intake and expenditure are related to a normal distribution of energy reserves that is used to predict mortality rate. Model predictions of overwinter mortality in does and fawns closely resembled trends in field measurements of mortality during 14 different years in 2 different habitats. Model predictions of fat reserves did not differ from measured values during early and midwinter, but diverged from measurements at winter's end. Weather during a severe winter increased simulated energy expenditure by 4% (10,019 vs. 9,621 kcal/kg$^{0.75}$/winter) in does and 2% (10,879 vs. 10,632 kcal/kg$^{0.75}$/winter) in fawns relative to their expenditures during a mild winter, and reduced intake of metabolizable energy by 17% in both does (133,183 vs. 161,292 kcal/winter) and fawns (94,663 vs. 114,643 kcal/winter). Predictions of mortality were more responsive to changes in snow depth than to changes in temperature. Simulated mortality declined sharply in response to increases in parameter values for digestibility of winter forage, forage intake rate, supplemental feed offered, and fatness of animals during autumn. Reducing deer density and increasing forage amount influenced mortality only when prewinter forage was scarce ($<150$ kg/ha) or when there was a high variance in the quality or availability of food. Enhancing thermal cover had negligible effects on simulated mortality. By organizing results of nutritional research in a form that is accessible and interactive, the model can facilitate decisions on managing mule deer populations and their habitats.

***WILDL. MONOGR. 101, 1–39***

## CONTENTS

## INTRODUCTION

Recent advances in understanding processes controlling energy intake, assimilation, storage, and expenditure in mule deer offer a basis for predicting their energy balance at a higher level of realism than has been possible before (Parker and Robbins 1984; Parker et al. 1984; Wickstrom et al. 1984; Torbit et al. 1985*a*,*b*, 1988; Spalinger et al. 1986; Baker and Hobbs 1987). Such predictions depend on constructing a model simulating the influence of the environment on the animal's energy gains and losses.

A simulation model of energy balance in mule deer assembles knowledge in a form particularly useful to wildlife managers and researchers. Although studies of animal energetics can enhance decisions on managing mule deer populations and their habitats (e.g., Parker and Robbins 1984:486), much of this information remains inaccessible to decision makers. This is the case because the focused studies that are essential to understanding singular aspects of deer energetics cannot be expected to predict the multiple responses of the whole animal or the implications of those responses for deer populations. However, wildlife managers must choose among actions affecting populations rather than those affecting a single deer. Consequently, models linking processes in individual animals with processes in animal populations are urgently needed. Assembled in a validated model, studies of deer energetics can collectively influence management decisions in ways they have not achieved individually.

A model also is needed by researchers. Rapid progress in understanding physiological processes in mule deer threatens to surpass our understanding of the ecological significance of those processes. Collecting the results of reductionist studies in a model that responds to environmental variables will place findings on deer physiology in their proper ecological context. Moreover, planning effective research depends on identifying influential but poorly understood elements of past findings. By assessing the relative importance of variables and processes, a model can illuminate worthwhile objectives for future investigation. Finally, there are many questions in deer ecology, particularly questions operating at the ecosystem level, that are not amenable to traditional, designed experiments (Romesburg 1981, Hurlbert 1984). Such experiments demand environmental manipulation on a scale that is simply too costly to impose. For example, it is plausible that the effect of deer density on population mortality rates depends on the biomass of forage available to those populations. However, the nature of this interaction remains undescribed, and a replicated, factorial experiment simultaneously varying population density and food supply is probably not soon forthcoming. Developing adequately predictive models may offer the only feasible way to address such otherwise intractable problems.

Here, I describe a model of energy balance in mule deer during winter. The model was built to predict changes in body condition of the average mule deer doe and fawn and to predict the relationship of those changes to rates of mortality in populations of does and fawns. In so doing, I wanted the model to illuminate the relative importance of processes of energy loss and gain in mule deer. I also developed the model to provide a gaming tool for addressing ecosystem-level questions on interactions between mule deer populations and the habitats they use. I used this tool to evaluate the ability of prevalent management practices to reduce starvation in mule deer populations during winter.

*Acknowledgments.*—Helpful comments on early drafts were graciously given by D. L. Baker, R. M. Bartmann, K. M. Giesen, T. A. Hanley, R. J. Hudson, D. M. Swift, and G. C. White. D. J. Freddy and G. C. White provided unpublished data for model validation. R. B. Gill and L. H. Carpenter offered motivating leadership and enlightened administrative support.

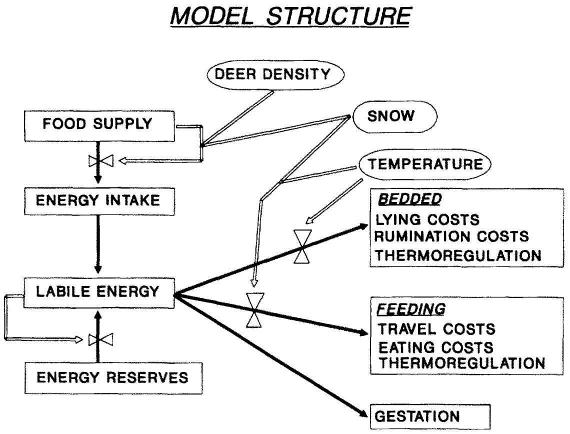


Fig. 1. Simplified schematic of model structure. Variables in boxes are calculated within the model. Variables in ellipses are input by the user. Solid lines show transfer of energy. Clear lines illustrate control of processes.

# METHODS

## Model Boundaries

The model operates within distinct spatial and temporal boundaries. Spatially, the model simulates mule deer on shrub–steppe and shrub–woodland ranges of the central Rocky Mountains. Its predictions are limited to areas where starvation is the major cause of winter mortality or is compensatory with other causes. In a strict sense, the model operates within the confines of an "average" doe or fawn and extrapolates from its behavior to the behavior of a normally distributed population of does or fawns. The model is bounded in time by the beginning and end of plant senescence, and applies only to months of the year when plants are predominantly dormant.

## Model Structure and Implementation

The structure of the model follows the conceptual approach of Wunder (1978). The model simulates energy flow from forage resources to the animal and the allocation of that energy to individual expenditures by the animal (Fig. 1). When the sum of energy expenditures exceeds energy gains, the animal's endogenous reserves of energy are reduced to offset those deficits. State variables include the calories of metabolizable energy in the forage stand-

Table 1. Glossary of principal parameters in simulation model of energy balance in mule deer.

| Name | Type[a] | Definition | Units | Initial value[b] | Reference |
|---|---|---|---|---|---|
| AMIN | var | Time spent active | min | 0.0 | |
| ATR | var | Cost of thermoregulation in active state | kcal/min | 0.0 | |
| BAL | var | Daily energy balance | kcal | 0.0 | |
| BMIN | var | Time spent bedded | min | 0.0 | |
| BH | cons | Doe brisket height | cm | 57.1 | Parker et al. 1984 |
| BH | cons | Fawn brisket height | cm | 48.4 | |
| BW | var | Doe daily body mass | kg | 60.0, 65.0 | Torbit et al. 1988 |
| BW | var | Fawn daily body mass | kg | 25.0, 30.0 | Torbit et al. 1988 |
| $BW_{in}$ | cons | Doe prewinter body mass | kg | 60.0, 65.0 | Torbit et al. 1988 |
| $BW_{in}$ | cons | Fawn prewinter body mass | kg | 25,0, 30.0 | Torbit et al. 1988 |
| CHEWMAX | cons | Maximum instantaneous rate of intake | g/min | 37.6 | Wickstrom et al. 1984 |
| DMI | var | Instantaneous rate of dry matter intake | g/min | 0.0 | |
| DMICO | cons | Maximum rate of daily intake for does | % of $BW_{in}$ | 1.7 | Baker and Hobbs 1987 |
| DMICO | cons | Maximum rate of daily intake for fawns | % of $BW_{in}$ | 2.9 | Alldredge et al. 1974 |
| DIG | var | Digestibility of gross energy in grass–browse diet | unitless | 0.38 | Baker and Hobbs 1987 |
| DKM | var | Distance traveled | km | 0.0 | |
| EA | var | Cost of active state | kcal | 0.0 | |
| EBAL | var | Size of energy reserves needed to survive winter | kcal | 0.0 | |
| EEAT | var | Net cost of eating | kcal | 0.0 | |
| EI | var | Metabolizable energy intake | kcal | 0.0 | |
| EL | var | Costs of bedded state | kcal | 0.0 | |
| ES | var | Costs of posture in the active state | kcal | 0.0 | |
| ET | var | Net cost of travel | kcal | 0.0 | |
| ELTR | var | Thermoregulation cost of lying animal | kcal/min | 0.0 | |
| FATPER | cons | % of body mass as fat in does, prewinter | unitless | 0.11, 0.13 | Torbit et al. 1988 |
| FATPER | cons | % of body mass as fat in fawns, prewinter | unitless | 0.05, 0.08 | Torbit et al. 1988 |
| GEST | var | Costs of gestation | kcal | | |
| HERB | var | Proportion of herbs (grasses + forbs) in diet | unitless | 0.80 | Carpenter et al. 1979 |
| HRBDIG | cons | Digestibility of herbs | unitless | 0.40 | Milchunas et al. 1978<br>Hobbs et al. 1983<br>Hobbs and Spowart 1984 |
| HRBMASS | var | Biomass of herbs | kg/ha | 200.0 | Carpenter et al. 1980 |
| HRBHT | cons | Height of the herb layer | cm | 30.0 | |
| HERBIN | cons | Initial conditions for herbs in diet | unitless | 0.80 | Carpenter et al. 1979 |
| $LCT_a$ | var | Lower critical temperature of active animal | C | 0.0 | |
| LCT | cons | Lower critical temperature of bedded animal | C | −22.0 | Parker and Robbins 1984 |
| LYCOST | cons | Energy cost of lying in thermoneutrality | kcal/min | 0.0 | |
| ME | cons | Metabolizability of digestible energy | unitless | 0.82 | Robbins 1983: Table 13.8 |
| OBJ | cons | Hourly objective for dry matter intake | g | 0.0 | |
| PERGEST | var | Elapsed proportion of gestation period | unitless | 0.0 | |

Table 1. Continued.

| Name | Type[a] | Definition | Units | Initial value[b] | Reference |
|---|---|---|---|---|---|
| RATEIN | cons | Rate constant for functional response | unitless | 33.5 | Wickstrom et al. 1984 |
| RES | cons | Labile energy reserve | kcal | 0.0 | |
| RESCV | | Coefficient of variation on % body fat in does | unitless | 0.21 | Torbit et al. 1988 |
| RCV | cons | Coefficient of variation on body fat in fawns | unitless | 0.45 | Torbit et al. 1988 |
| RMUL | cons | Proportion of active time spent traveling in untracked snow for does | unitless | 0.50 | |
| RMUL | cons | Proportion of active time spent traveling in untracked snow for fawns | unitless | 0.25 | |
| RSD | var | Relative sinking depth | unitless | 0.0 | |
| RUM | var | Cost of rumination in does | kcal/min | 0.085 | Fancy and White 1985*a* |
| RUM | var | Cost of rumination in fawns | kcal/min | 0.012 | Fancy and White 1985*a* |
| RUMTIME | var | Hourly rumination time[c] | min | 26.7 | |
| SD | var | Snow depth | cm | input | |
| SHRUB | var | Proportion of shrubs (stems + evergreen leaves) in diet | unitless | 0.20 | Carpenter et al. 1979 |
| SHRBDIG | cons | Digestibility of shrubs | unitless | 0.30 | Milchunas et al. 1978<br>Hobbs et al 1983<br>Hobbs and Spowart 1984 |
| SHBMASS | var | Biomasss of shrubs | kg/ha | 500.0 | Carpenter et al. 1980 |
| SHBHT | cons | Height of shrubs | cm | 100.0, 80.0 | |
| SNO | var | Relative increase in net cost of travel due to snow | unitless | 0.0 | |
| STANDCO | cons | Energy cost of standing in thermoneutrality for does | kcal/kg$^{0.75}$/min | 0.0627 | Parker and Robbins 1984 |
| STANDCO | cons | Energy cost of standing in thermoneutrality for fawns | kcal/kg$^{0.75}$/min | 0.0750 | Parker and Robbins 1984 |
| T | var | Hourly temperature | C | 0.0 | |
| TMAX | var | Daily maximum temperature | C | input | |
| TMIN | var | Daily minimum temperature | C | input | |
| $TC_a$ | cons | Thermal conductance of standing animal | kcal/kg$^{0.75}$/min/C | 0.004 | Parker and Robbins 1984 |
| $TC_l$[d] | cons | Thermal conductance of lying animal | kcal/kg$^{0.75}$/min/C | 0.0027 | Parker and Robbins 1984 |
| TOTIN | var | Daily intake of metabolizable energy | kcal | 0.0 | |
| TOTOUT | var | Daily expenditure of energy | kcal | 0.0 | |
| WTBAL | var | Daily change in weight | g | 0.0 | |
| ZBAL | var | Standard normal variate for energy reserves | unitless | 0.0 | |
| ZINTAKE | var | Realized hourly intake of dry matter | g | 0.0 | |

[a] var = variable, cons = constant.

[b] Values of variables with initial conditions = 0.0 are calculated internally during the first hour of the simulation. When 2 values are given, the first value (leftmost) is for Piceance simulations; the second is for Middle Park simulations.

[c] During 18 hours of day when feeding is not at peak. Rumtime = 0.0 during peak feeding.

[d] Assuming that $TC_l = TC_a \cdot 0.67$.

ing crop, the labile energy pool in the animal, and the animal's endogenous energy reserves. Rates of flow from these variables respond to changes in operative temperature, snow depth, and animal density.

The model is structured as a series of difference equations and operates at an hourly time step. It is programmed in FORTRAN 77 (Microsoft version 4.01) for execution on IBM-compatible microcomputers. Many of the initial conditions and constants in the model can be easily modified by the user. I constructed the model to make it accessible to persons with minimal experience with computer simulations. (*See* Appendix for a user's guide and instructions on obtaining the program.)

## Model Formulation

*Energy Intake and Activity Budget.*—The model is formulated such that energy intake is closely coupled with the animal's activity budget. (*See* Table 1 for a glossary of model variables.) Voluntary intake of dry matter is controlled on 2 temporal scales. I presume that gut fill limits daily intake of dry matter (Ammann et al. 1973, Spalinger et al. 1986, Baker and Hobbs 1987) and that forage availability regulates instantaneous intake in a threshold fashion (Wickstrom et al. 1984, Hudson and Watkins 1986, Renecker and Hudson 1986, but also *see* Spalinger et al. 1988). It follows from this premise that feeding time increases when availability of food is sufficiently reduced to cause instantaneous intake rate to decline, but that daily intake will remain unchanged until feeding time becomes constrained. Thus, the animal compensates for declining food availability by spending more time feeding in an attempt to obtain its maximum possible daily intake, which is determined by gut fill. The extent to which the animal can achieve that compensation is limited by rumination time and by the energy costs of activity.

Specifically, maximum daily intake is set at 1.7% of the initial body mass ($BW_{in}$, in kg) of adult does (Alldredge et al. 1974, Baker and Hobbs 1987) and at 2.9% of the body mass of fawns (Alldredge et al. 1974). I assume that total daily intake is not influenced by diet composition (Baker and Hobbs 1987:fig. 1C). This represents a departure from previous models (Swift 1983, Hudson and White 1985*a*) where intake was controlled by dietary characteristics. However, Baker and Hobbs (1987:fig. 1G) found that deer could expand gut fill to compensate for slowly excreted forages, thereby maintaining relatively constant dry matter intake in the face of marked changes in their diets. Moreover, rumen turnover, and hence intake, is relatively insensitive to differences in physical characteristics of diets when dietary cell-wall levels exceed about 40% of dry matter, or when lignin exceeds 5% of dry matter (Spalinger et al. 1986:figs. 4, 6). This is frequently the case for winter forages, particularly for mature grasses and woody browse (Milchunas et al. 1978:table 4). Thus, the assumption of a constant limit on intake will be reasonable when deer diets are dominated by senescent grass and stems of shrubs (e.g., Carpenter et al. 1979), but may underestimate potential daily intake when diets contain a substantial portion of forbs or shrub leaves with thin cell walls (Spalinger et al. 1986).

Potential daily intake is represented as a function of initial body weight. Realized food intake is calculated as the sum of hourly intake as it is modified by feeding behavior. Hourly intake is determined by eating rate and feeding time. Eating rate is estimated as a function of biomass of selected food using the equations of Wickstrom et al. (1984:fig. 1). Because these equations did not extend to low levels of biomass for mixed shrub–herb communities, I developed a relationship between biomass and intake as follows. Maximum eating rate was set at 3.76 g/minute (Wickstrom et al. 1984). I assumed that eating rate declines when available food biomass falls below 50 kg/ha (as it does in grasslands, Wickstrom et al. 1984:fig. 1). I changed the denominator in a Mechalis-Menton equation to achieve an asymptote at about 50 kg/ha. This produced a rate constant where the instantaneous rate of intake was half its maximum value at food biomass equal to 33.5 kg/ha:

$$\mathrm{DMI} = [\mathrm{CHEWMAX} \cdot (\mathrm{HRBMASS} + \mathrm{SHBMASS})] \div (\mathrm{RATEIN} + \mathrm{HRBMASS} + \mathrm{SHBMASS})$$

where

DMI = instantaneous rate of dry matter intake (g/min),
CHEWMAX = maximum instantaneous intake rate (=3.76 g/min),
HRBMASS = biomass of selected herbs (kg/ha),
SHBMASS = biomass of selected shrubs (kg/ha), and
RATEIN = rate constant (=33.5).

Thus, instantaneous eating rate by the animal is controlled by the available biomass of herbs and shrubs in the plant community being modeled.

Food biomass is determined by the initial supply of herbs and shrubs and is modified by snow depth and daily forage removal by the deer population. The user enters data on the biomass (kg/ha) of herbs and shrubs present at the beginning of winter, as well as information on the structure of their standing crops. Required structural information includes an approximation of the average height of the herb and shrub layers in the plant community. This information is input by the user for the plant community being modeled.

Increasing snow depth causes linear reductions in food supply. I assume that the availability of herbs (HRBAV in kg/ha) is proportional to snow depth; herb biomass begins to decrease in availability when snow depth is > 0 and diminishes until herbs become completely unavailable when snow depth exceeds the height of the herb layer:

$$\mathrm{HRBAV} = \mathrm{HRBMASS} - [\mathrm{SD} \cdot (\mathrm{HRBMASS} \div \mathrm{HRBHT})]$$

where

HRBMASS = biomass of herbs,
SD = snow depth (cm), and
HRBHT = average height of the herb layer (cm).

Availability of shrubs is modeled similarly. This is a simplification of reality and does not incorporate effects of changes in characteristics of the snow surface (crusting, slabbing) or behavioral response of deer (pawing). Although the influence of snow accumulation on availability of forage to deer remains poorly described, there is evidence (Gilbert et al. 1970, Carpenter et al. 1979, Sweeney and Sweeney 1984, Adamczewski et al. 1988) that the above formulation, although simple, represents this influence in a reasonable way.

The animal's "objective" for hourly intake is controlled by the maximum intake allowable each day. This hourly objective, in turn, is used to calculate feeding time. During each hour the animal divides its time between 2 states—feeding (AMIN, in min) and bedded (BMIN, in min):

$$\mathrm{AMIN} + \mathrm{BMIN} = 60.0$$

Feeding time expands to allow the animal to approach or meet its objective for dry matter intake during each hour ($\mathrm{OBJ}_{ihr}$, in g). That goal is calculated from the potential daily intake. I assume that feeding time is spaced continuously throughout the day and night with peaks occurring during early morning and evening (Miller 1970, Carpenter 1976, Eberhardt et al. 1984). Thus, deer feeding behavior is represented such that 30% of daily intake occurs during 0600–0800 hours, 30% during 1800–2000 hours, and the remaining 40% during the rest of the day and night. For example, assuming that daily intake of the average doe can be estimated as 1.7% of her initial body weight ($\mathrm{BW}_{in}$, in kg) (Alldredge et al. 1974, Baker and Hobbs 1987), her "goal" for hourly intake during 0700 hour is

$$\mathrm{OBJ}_{0700} = [(\mathrm{BW}_{in} \cdot 0.017) \cdot 0.30] \div 3.0.$$

The animal feeds long enough each hour to obtain its intake goal ($\mathrm{OBJ}_{ihr}$),

$$\mathrm{AMIN} = \mathrm{OBJ}_{ihr} \div \mathrm{DMI},$$

and is bedded (BMIN) for the remainder of the hour,

$$\mathrm{BMIN} = 60.0 - \mathrm{AMIN}.$$

However, the duration of feeding each hour is limited by rumination time (RUMTIME, in min) required for the food eaten. I assume that the animal ruminates for 8 hours a day and that rumination occurs while the animal is bedded during hours other than those of peak feeding. When feeding is not at its peak, bedded time (BMIN) cannot fall below RUMTIME, and hourly feeding time (AMIN) cannot exceed it. Given these constraints on AMIN, the realized hourly dry matter intake (ZINTAKE, in g) is

$$\text{ZINTAKE} = \text{DMI} \cdot \text{AMIN}$$

where

$$\text{AMIN} \leq (60.0 - \text{RUMTIME}).$$

Hourly intake of metabolizable energy (EI, in kcal) is calculated as the product of the realized dry matter intake and forage gross energy (4.2 kcal/g, Golley 1961, Milchunas et al. 1978) multiplied by appropriate coefficients as follows:

$$\text{EI} = \text{ZINTAKE} \cdot 4.2 \cdot \text{ME} \cdot \text{DIG}$$

where

ME = 0.82 kcal metabolized/kcal digested (Robbins 1983:table 13.8) and
DIG = kcal digested/kcal gross (calculated below).

I do not include a coefficient of net energy in this calculation because energy requirements are formulated to include heat increment (i.e., measurements were made on fed animals, Parker and Robbins 1984). Thus, because the summed energy requirements of the animals implicitly include the cost of heat increment, the summed energy intake should include energy that can be used to offset that cost. If requirements were based on fasted animals, then those requirements would not reflect calories expended in work of digestion, rumen fermentation, etc. Such calories should be excluded from energy intake (using a net energy coefficient) only when they cannot meaningfully offset a component of the animal's summed energy requirements. My approach resembles that of Fancy (1986), except that I do not explicitly account for dietary influences on heat increment.

The digestibility of dietary energy is influenced by the composition of the dietary dry matter, which is determined by the availability of herbs and shrubs as it is modified by snow depth. I assume that the composition of deer diets is not influenced by snow depth (SD, in cm) until accumulated snow exceeds 10 cm. Above that point, the proportion of herbs in the diet dry matter (HERB, a decimal fraction) decreases in proportion to increasing snow depth (Carpenter et al. 1979:fig. 3) until the diet is composed entirely of shrubs when snow depth exceeds the height of the herb layer. Thus,

$$\text{HERB} = \text{HERBIN} - \{(\text{SD} - 10.0) \cdot [\text{HERBIN} \div (\text{HRBHT} - 10.0)]\},$$

but if SD > HRBHT, then HERB = 0

where

HERBIN = initial condition for % herbs in diet,
SD = snow depth, and
HRBHT = average height of the herb layer.

The digestibility of the diet (DIG, in kcal digested energy/kcal gross energy) is then calculated as the average of the digestibilities of herbs (HRBDIG) and shrubs (SHRBDIG) weighted by their calculated percentage in the diet as follows:

$$\text{DIG} = (\text{HERB} \cdot \text{HRBDIG}) + (\text{SHRUB} \cdot \text{SHRBDIG}).$$

If the animal's energy costs of feeding during any hour exceed the energy it could gain by feeding during that hour, then I assume the animal beds rather than feeds (AMIN = 0, BMIN = 60); I set dry matter intake to 0, and I add the dry matter the animal would have obtained during that hour to the intake goal for the remaining hours of the day. There is no carryover in the intake goal between days.

At the end of each day, I reduce the supply of herbs and shrubs by the amount consumed by the animal multiplied by the density of deer in the habitat weighted by the sex and age composition of the population. Thus, although the model simulates a doe or fawn, forage removal reflects the collective effects of a population of does, bucks, and fawns. It follows that changes in forage biomass and deer density have parallel effects on forage availability; each influences the amount of forage available per animal in the population.

*Energy Expenditure.*—Energy costs incurred by the animal are influenced by daily snow depth and hourly temperature. The user enters values for daily snow depth and maximum and minimum air temperatures. Hourly temperatures are estimated from daily maximum and minimum temperatures following the algorithm of Parton and Logan (1981). Energy costs are summed over the time the animal spends in the 2 possible behavioral states—active and bedded. Bedded energy costs are formulated as the sum of costs of lying, rumination, and thermoregulation.

The cost of lying in a thermoneutral environment (LYCOST, in kcal/min) is calculated as a function of the standing cost:

$$\text{LYCOST} = (\text{STANDCO} \div 1.33) \cdot \text{BW}^{0.75}$$

where STANDCO = 0.0627 kcal/min/kg$^{0.75}$ for does and 0.075 kcal/min/kg$^{0.75}$ for fawns. (The value for fawns represents a weighted average for the winter to account for changes in STANDCO as the animal matures.) This formulation is based on the data of Parker and Robbins (1984: fig. 12) on standing costs, assuming that energy expenditure is 33% higher for standing than for lying (mean of 9 studies of wild ruminants: Maloiy 1968, Wesley et al. 1973, Renecker and Hudson 1978, White and Yousef 1978, Chappel and Hudson 1979, Gates and Hudson 1979, Mautz and Fair 1980, Parker and Robbins 1984, Fancy 1986). I assume that the animal ruminates when it is bedded and that rumination costs (RUM, in kcal/min) are 2% of lying costs (Fancy and White 1985*a*: 146). Therefore,

$$\text{RUM} = \text{LYCOST} \cdot 0.02.$$

Calculating the costs of thermoregulation of the lying animal is problematic because the best measurements of energy costs of thermoregulation in mule deer were obtained from standing animals (Parker and Robbins 1984). I used the following approach to deal with this problem. I assumed that the thermal conductance of a lying animal ($\text{TC}_l$) is 67% (Gates and Hudson 1979:fig. 2) of that of a standing animal ($\text{TC}_s = 0.004$, Parker and Robbins 1984:fig. 12) and that heat production can be estimated as a linear function of temperature below the animal's lower critical temperature (Parker and Robbins 1984:fig. 12, but also *see* fig. 14). However, if thermal conductance and heat production change when the animal lies down relative to their value when the animal stands (Gates and Hudson 1979), then lower critical temperature also will change. Following the reasoning of Kleiber (1975:169), I calculated a lower critical temperature for the lying state as

$$\text{LCT}_l = \text{XIN} - (\text{LYCOST} \div \text{TC}_l)$$

where

$\text{LCT}_l$ = lower critical temperature of bedded animal (C),
XIN = $X$-intercept of extrapolated line describing heat production below lower critical temperature (C),
LYCOST = heat production of bedded animal in thermoneutrality (kcal/min), and
$\text{TC}_l$ = thermal conductance of bedded animal (kcal/kg$^{0.75}$/min/C).

Theoretically, XIN should equal the animal's core body temperature assuming that thermal conductance can be described by Newton's Law of Cooling (Kleiber 1975). In fact, the animal's core temperature exceeds XIN in several North American ungulates (Parker and Robbins 1985). However, I assume that the consistently linear relationship between heat production and operant temperature below the animal's lower critical temperature allow me to treat thermal conductance and XIN as constants (Parker and Robbins 1984:fig. 12).

Thermoregulation costs associated with the lying state (ELTR, in kcal/min) are set at 0.0 until the hourly temperature drops below $LCT_l$ when they are calculated as

$$ELTR = [TC_l \cdot (LCT - T)] \cdot BW^{0.75}$$

where

$ELTR$ = bedded costs of thermoregulation (kcal/min),
$T$ = hourly temperature (C),
$LCT_l$ = lower critical temperature of bedded animal (C), and
$TC_l$ = thermal conductance of bedded animal (kcal/kg$^{0.75}$/min/C).

Total bedded costs (EL, in kcal) for the hour are then calculated as the sum of costs of thermoregulation, lying, and ruminating:

$$EL = [(ELTR + LYCOST) \cdot BMIN] + (RUM \cdot RUMTIME).$$

Energy costs of activity are formulated as the sum of the costs of maintaining posture (i.e., the "standing" component of travel), the net cost of locomotion as it is influenced by snow, and the net cost of eating. Posture costs (ES, in kcal) are calculated (Parker and Robbins 1984) as

$$ES = STANDCO \cdot BW^{0.75} \cdot AMIN.$$

The net cost of locomotion (ET, in kcal) is estimated as the energy needed to move a specific distance assuming the travel velocity while feeding equals 1.5 m/minute (Wickstrom et al. 1984). The distance traveled (DKM, in km) is thus

$$DKM = AMIN \cdot 1.5 \div 1{,}000$$

and locomotion costs (ET, in kcal) can be calculated as follows (Parker and Robbins 1984):

$$ET = 2.97 \cdot BW^{-0.34} \cdot DKM \cdot BW.$$

Following the formulation of Parker et al. (1984), the net cost of locomotion is elevated by a scalar (SNO, unitless) that represents the relative increase in energy expended to travel in snow:

$$ET = ET + (ET \cdot SNO).$$

This scalar is a function of relative sinking depth (RSD), which is calculated from snow depth (SD, in cm) and the animal's brisket height (BH, in cm):

$$RSD = (SD \div BH) \cdot 100.$$

Brisket height is calculated from the formula of Parker et al. (1984) as

$$BH = 21.0 \cdot [\ln(BW_{in} + 1.0)^{0.707}],$$

and SNO can then be calculated as

$$SNO = [0.71 \cdot RSD \cdot e^{(0.19 \cdot RSD)}] \div 100.$$

However, because mule deer are gregarious, 1 animal often follows in another's footsteps. Consequently, I reduce the effect of snow by the proportion of the animal's hourly feeding time it spends traveling in untracked snow (RMUL, unitless):

$$SNO = SNO \cdot RMUL.$$

There were no data available to estimate RMUL, so I approximated a value of 0.50 for does and 0.25 for fawns.

The energy cost of eating over standing and travel (EEAT, in kcal) is estimated from values derived from studies of elk (Wickstrom et al. 1984) as

$$EEAT = 0.0053 \cdot BW \cdot AMIN,$$

and the total cost of activity in thermoneutrality (EA, in kcal) is calculated by summing the costs of posture, travel, and eating as

$$EA = ET + ES + EEAT.$$

Thermoregulation costs of the active state (ATR, in kcal/min) are added to EA whenever the hourly operative temperature drops below the animal's lower critical temperature during activity ($LTC_a$, in C):

$$ATR = [0.004 \cdot (LCT_a - T)] \cdot BW^{0.75}$$
$$EA = EA + (ATR \cdot AMIN).$$

I assume that the thermal conductance for a slowly moving animal (1.5 m/min, Wickstrom et al. 1984) does not differ substantially from that for a standing animal. There is evidence that thermal conductance increases during activity (Gates and Hudson 1979). However, these data are difficult to interpret because the level of activity (and hence heat production) is virtually impossible to control. Consequently, differences in activity costs are confounded with differences in thermoregulation costs.

Based on the same reasoning I described above for $LTC_l$, I calculate a lower critical temperature for the active state as a function of heat production (EA, in kcal) and thermal conductance for a standing animal ($TC_a$, in kcal/kg$^{0.75}$/min/C). Thus,

$$LCT_a = [XIN - (EA \div AMIN)] \div (BW^{0.75} \div TC_a),$$

where

$LCT_a$ = lower critical temperature of active animal (C),
XIN = $X$-intercept of the extrapolated line describing heat production below lower critical temperature (C),
EA = heat production of active animal in thermoneutrality (kcal), and
$TC_a$ = thermal conductance of active animal (kcal/kg$^{0.75}$/min/C).

Energy costs of gestation (GEST, in kcal) are added daily to the sum of the hourly costs of lying and activity. Gestation costs are calculated from initial body weight and the elapsed percentage of the gestation period (PERGEST, in %) following the formulation of Robbins (1983):

$$GEST = (70 \cdot BW_{in}{}^{0.75}) \cdot [.000024 \cdot (PERGEST^{3.13}) \div 100].$$

I assume a 200-day gestation period and conception on 1 December.

*Energy Balance, Weight Change, and Mortality.*—At the end of each day, I sum the hourly values for energy intake (TOTIN, in kcal) and expenditure (TOTOUT, in kcal) and use their difference (BAL = TOTOUT − TOTIN, in kcal) to predict weight change (WTBAL, in g). Thus,

$$WTBAL = [0.70 \cdot (BAL \div 9.5)] + [0.30 \cdot 4.0 \cdot (BAL \div 4.8)]$$

where

0.70 = proportion of total calories catabolized from fat (Torbit et al. 1985*b*),
9.5 = kcal/g fat catabolized (Kleiber 1975:table 7.3),
0.30 = proportion of calories catabolized from protein (Torbit et al. 1985*b*),
4.0 = g $H_2O$/g protein catabolized (Torbit et al. 1985*a*), and
4.8 = kcal/g protein catabolized (Kleiber 1975:table 7.3).

Whenever WTBAL is > 0.0, I subtract it from the animal's body weight. This formulation requires 2 major assumptions. I assume that the ratio of calories catabolized from fat relative to those catabolized from protein is not influenced by the magnitude of energy deficits (Torbit et al. 1985*b*, but also *see* Owen et al. 1969). Moreover, I assume that deer will not "grow" during winter; when energy balance is ≥ 0.0, body weight does not increase. Although this is probably the case for adults, it may oversimplify the situation for fawns (Wood et al. 1962, Nordan et al. 1968, McEwan 1975, Bahnak et al. 1981). However, I felt this simplification was justified to eliminate the need to represent processes of anabolism. At the end of the winter, I sum the daily values for energy deficits to estimate the size of energy reserves needed by an animal to survive winter (EBAL, in kcal):

$$EBAL = \sum (TOTIN - TOTOUT)$$

where

TOTIN = daily metabolizable energy intake (kcal), and
TOTOUT = daily energy expenditure (kcal).

To survive, animals must be able to mobilize reserves of energy ≥ EBAL. Thus, the proportion of the population that starves to death can be estimated as the proportion of the population that began the winter with energy reserves smaller than EBAL.

I approximate this proportion as follows. I create a standard normal variate (ZBAL) by subtracting the mean energy reserves in the population (RES) from EBAL and dividing that difference by the population standard deviation,

$$\text{ZBAL} = (\text{EBAL} - \text{RES}) \div (\text{RES} \cdot \text{RESCV}),$$

where RESCV is the coefficient of variation on energy reserves. Assuming that energy reserves in the population are normally distributed, the area under the standard normal curve to the left of ZBAL provides an estimate of the proportion of the population with prewinter energy reserves < EBAL. This area represents the model's estimate of percent mortality due to starvation.

Parameters for estimating ZBAL values are derived from field measurements of endogenous reserves (Table 1). I assume that the animal can catabolize 67% of its fat before death (Torbit et al. 1985*b*), that each gram of fat yields 9.5 kcal (Kleiber 1975:table 7.3), and that 70% of total calories catabolized are derived from fat and 30% from lean body (Torbit et al. 1985*b*). For example, I calculate the average energy reserves for does as

$$\text{RES} = (\text{FATPER} \cdot 0.67 \cdot \text{BW}_{in} \cdot 9.5 \cdot 1{,}000) \div 0.70$$

where

FATPER = proportion of body mass that is fat (g/g),
0.67 = proportion of fat that can be catabolized before death (g/g),
$\text{BW}_{in}$ = initial body mass (kg),
9.5 = kcal/g fat catabolized,
1,000 = g/kg, and
0.70 = proportion of total calories catabolized from fat.

## Model Validation

*Study Area.*—I tested predictions of the model against field measurements of fatness of the average mule deer doe and fawn and mortality in populations of does and fawns in the Piceance Basin and Middle Park, Colorado. The Piceance Basin in northwestern Colorado is a shrub–woodland dominated by pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*). Deer winter range usually extends from 2,000 m in elevation along Piceance Creek to 2,500 m on the surrounding mesas. In north-central Colorado, Middle Park forms the headwater basin of the Colorado River. Vegetation is predominantly shrub–steppe; big sagebrush (*Artemisia tridentata*) provides a relatively uniform canopy over cool season grasses and forbs. Deer spend the winter between 2,200 and 4,500 m in elevation. Climate in both areas is semiarid. Wallmo et al. (1977) and Bartmann (1983) described these areas in detail.

*Input Data.*—Weather input was obtained from Green Mountain Dam for simulations of Middle Park deer (National Oceanic and Atmospheric Administration 1967–85) and from the Little Hills Game Research Station for Piceance simulations (National Oceanic and Atmospheric Administration 1972–85). In the strictest sense, the model requires operant temperatures as input. However, because real-time data on daily operant temperatures for the average mule deer are virtually impossible to obtain, approximations are needed. To approximate operant temperatures during validation runs and model experiments, I used hourly estimates of ambient temperatures derived from daily maximum and minimum temperatures following the algorithm of Parton and Logan (1981). I justify this simplification because the model must provide reasonable predictions with readily accessible data if it is to be broadly useful.

Initial conditions for validation runs were set as described (Table 1) for does and fawns in the Piceance Basin. With a single exception, model parameters were derived from values reported in the literature and were not tuned in response to model output. Tuning was required to estimate fat reserves for Middle Park deer because no data were available to set initial conditions for that area. The model consistently overestimated mortality of does and fawns in Middle Park when initial conditions for body composition were based on data for Piceance Basin deer. Several ecologists with experience in both areas believed that frequent doe harvest and higher quality range in Middle Park has produced larger, fatter deer relative to those in the Piceance Basin (R. M. Bartmann, L. H. Carpenter, D. J. Freddy, Colo. Div. of Wildl.; G. C. White, Colo. State Univ., pers. commun.). Therefore, I increased initial body weight and fatness of simulated Middle Park does and fawns relative to the body weight and fatness of animals from Piceance (Table 1).

*Validation Data.*—I compared model predictions to field estimates of total mortality based on ground surveys (R. B. Gill and D. J. Freddy, Colo. Div. Wildl., unpubl. data; Gill 1971; Bartmann 1984; Bartmann and Bowden 1984; Baker and Hobbs 1985) and telemetry studies (White et al. 1987; G. C. White, Colo. State Univ., unpubl. data). I did not use mortality estimates based on band recovery data (White and Bartmann 1983) because winter mortality could not be differentiated from mortality during other seasons. Estimates of dead deer/km$^2$ from ground surveys were converted to percent mortality of does and fawns using postharvest estimates of the sex and age composition of the population and population size (J. Gray, Colo. Div. Wildl., unpubl. data). Confidence intervals on ground surveys were based on standard errors of dead deer/km$^2$ and an assumed error of $\pm 15\%$ in estimates of prewinter population size. In cases where estimates of standard errors on numbers of dead deer were not available (e.g., Middle Park, 1971–75), I assumed that the number of dead deer was estimated within $\pm 50\%$ of the mean (Gill 1971:fig. 8). Confidence intervals on mortality rates derived from telemetry data were calculated using binomial standard errors and a normal approximation to the binomial distribution (Simpson et al. 1960: 157).

Although comparing predicted with observed mortality at the end of winter provides a test of the outcomes of the model, it does not validate the mechanisms that produced those results. A more revealing test of the mechanisms represented in the model is provided by comparisons of its output with a time series of measurements throughout the winter. I used observed and predicted daily mortality and body fat levels to achieve this type of validation. I tested the model's cumulative daily predictions of mortality rate during 1982–85 against cumulative daily measurements derived from the telemetry studies of White et al. (1987). Model estimates of percent fat were derived from simulations using weather data for 1 December through 15 April 1982–84 from the Little Hills station, Colorado (National Oceanic and Atmospheric Administration 1982–84) as input. These estimates were compared with field measurements for does ($n = 6$/month, 1982–83) and fawns ($n = 8$/month, 1983–84) collected during December, February, and April from the Piceance Basin (Torbit et al. 1988). Initial conditions for percent fat were set using measured values for fatness in October (Torbit et al. 1988). Percentage fat of each animal collected was determined by ether extraction of samples taken from its homogenized carcass (Torbit et al. 1988).

Simulations of overwinter mortality were run from December through March unless $>10$ cm of snow remained on 31 March, in which case simulations were extended to 31 April. I omitted 1973–74 from the Piceance Basin simulations because 22 days of weather data were missing.

## Model Experiments

Meeting model objectives for enhancing understanding of the winter ecology of mule deer depends on performing model experiments. I use experiment here in the sense of planned manipulations of model variables—manipulations used to illuminate the processes being modeled and the relative importance of their component variables.

Sensitivity analysis of models frequently emphasizes changing model parameters by equal amounts and comparing the effect of those changes on model output (e.g.,

Table 2. Characteristics of mild (1976–77) and severe (1978–79) winters in the Piceance Basin, northwestern Colorado. Daily temperatures and snow depths from these winters were used as input in model experiments.

| Characteristic | Mild | Severe |
|---|---|---|
| Avg max. temp (C) | 6.7 | 2.1 |
| Avg min. temp (C) | −13.2 | −14.1 |
| Avg snow depth (cm) | 1.4 | 33.2 |
| No. days with min. temp <−20 C | 9 | 29 |
| No. days with snow depth >10 cm | 8 | 108 |

Weins and Innis 1974, Steinhorst et al. 1978, Clark and Innis 1982, Hobbs et al. 1982, Fancy 1986, Frederick et al. 1987). This approach implicitly assumes that perturbing model parameters individually or in small groups will provide model outputs that are comparable among perturbations and will thereby reveal which parameters and processes are most influential in determining model behavior. I avoided this approach in model experiments for several reasons. First, different variables offer different ranges of variation. For example, the standing metabolic rate of mule deer is probably estimated within ±5% of the value in the population, whereas measures of body fatness may vary by as much as ±20%. It follows that a 10% increase in these 2 parameters would overestimate the potential importance of standing metabolic rate and underestimate the potential importance of fatness. This problem is exacerbated by the fact that many processes represented in the model are nonlinear and operate in a threshold fashion. Thus, the importance of changing a single variable will depend fundamentally on the value of other variables. This is the case because the outcome of proportional changes in parameters (changes that are inherently linear) will depend on whether those changes occur in the vicinity of thresholds. Consequently, I believe that traditional approaches to sensitivity analysis frequently fail to yield commensurate changes in model predictions.

As an alternative, I chose individual manipulations of initial conditions of variables within ranges that were plausible for those variables and constructed specific experiments to examine interactions. The disadvantage of my approach is that it does not provide direct comparisons of model sensitivity among variables. The advantage is that it does not provide misleading comparisons.

I ran model experiments with parameters (Table 1) set to represent does and fawns in the Piceance Basin using weather data from a severe and a mild winter as input (Table 2). Model manipulations were planned to provide inferences useful in decisions on managing mule deer populations and the habitats they occupy. In particular, I evaluated the efficacy of several prevalent tactics for improving the condition of deer and reducing starvation during winter. These are described in the following sections.

*Change Food Quantity and Animal Density.*—Managing mule deer to enhance population performance often emphasizes reducing deer population size (reviewed by Short 1979, Connolly 1981) or increasing the standing crops of deer food (reviewed by Wallmo et al. 1981). Each of these tactics is believed to improve the nutritional status of individual animals by making more food available to each deer. To examine the effect of increased food supply and reduced density on starvation, I varied deer density (DENS) from 4 to 60 deer/km$^2$ over 5 levels in a factorial arrangement with 5 levels of initial forage biomass (100–1,200 kg/ha).

*Improve the Nutritional Quality of Forage.*—The chemical composition and physical structure of forages may be more important to the welfare of small ruminants like mule deer than the absolute amount of food available to them (reviewed by Hanley 1982). To examine the role of forage quality in determining mortality in deer, I varied the digestibility of herbs (HRBDIG) from 35 to 45% over 5 levels in a factorial arrangement with 5 levels of shrub digestibility (SHRBDIG = 25–35%). Although the effects of forage cell-wall characteristics on intake are not explicitly represented in the model, these influences were simulated implicitly by changing parameters controlling intake. Under the assumption that dry matter intake is influenced by forage physical structure (Spalinger et al. 1986, Baker and Hobbs 1987, Spalinger et al. 1988), I varied total daily intake of dry matter (DMICO = 1.5–2.3% of body mass) together with instantaneous intake rate (CHEWMAX = 1.5–5.5 g/min).

*Alter Snow Distribution and Accumulation.*—Altering snow distribution and accumulation to increase access to forage and reduce energy costs of travel can be achieved directly by physical intervention (Regelin and Wallmo 1975, Regelin et al. 1977) and indirectly by favoring seral stages of vegetation that maximize snow interception (Hanley 1984, Hanley et al. 1984). The effect of snow on energy costs and energy intake were investigated by varying input data on daily snow depth at 7 levels (−50%, −20%, −10%, 0%, +10%, +20%, +50%). Effects of snow on energy intake were isolated from its effects on expenditure by separately varying snow depth input to model subroutines that calculated energy costs and gains. I also examined the effects of temperature by leaving temperature data from a mild winter unaltered, while changing the snow regime to the severe case. I then compared model output of these simulations with baseline simulations for a mild winter.

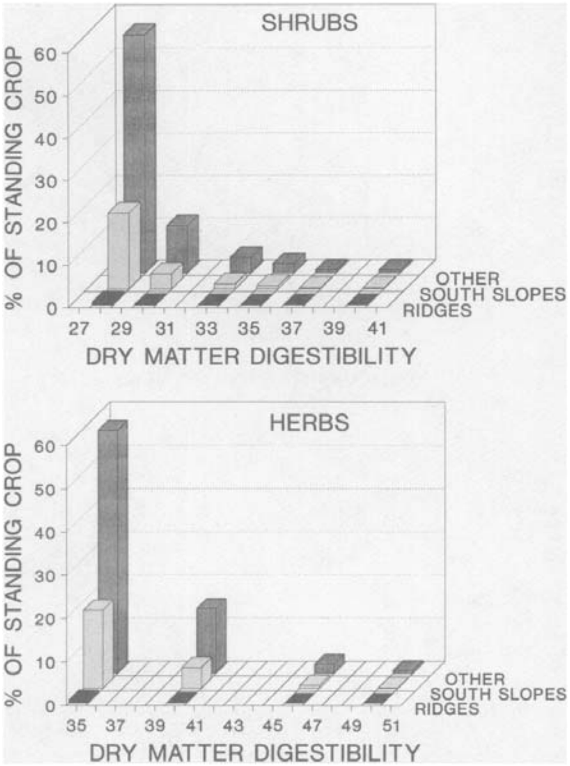


Fig. 2. Hypothetical distribution of digestible energy within forage standing crops on mule deer winter range. I assume that 1% of each energy category occurs on windswept ridges and remains available regardless of snow depth, that 20% occurs on south-facing slopes where snow depth is 20% below the average depth, and that 79% is found in areas where snow depth equals input values.

*Interactions of Animal Density with Quantity, Quality, and Availability of Forage.*—Although the above experiments were constructed to isolate the effects of individual perturbations of the model, the management interventions they were designed to mimic realistically cause multiple rather than singular changes in relationships between mule deer populations and their habitats. It follows that interactions among outcomes of management practices may alter their individual, isolated effects. To reveal the importance of interactions of biomass, digestibility, and availability of forage with the density of mule deer populations, I changed the model's formulation representing food supply. In this experiment, food supply was reformulated as a joint distribution of quality and availability following the approach of Sibbald et al. (1979). I also varied the density of deer using that food supply. In so doing, I assumed (Fig. 2) that forage standing crops were dominated by tissue with low digestibility, but contained small amounts of relatively highly digestible forage (Hobbs and Swift 1985). I also assumed that 1% of the total standing crop occurred on topography where it remained accessible regardless of snowfall (e.g., windswept ridges) and that an additional 20% of forage was found on south-facing slopes where assumed snow accumulation was 20% less than elsewhere. For the purposes of this experiment, I assumed that on each day in the simulation, mule deer consumed the food that yielded the highest energy gain.

*Enhance Thermal Cover.*—Topography and vegetation that mitigate thermal stress are believed to be important features of habitat for mule deer (Loveless 1967, Black et al. 1975). I tested this belief by varying input for ambient temperatures

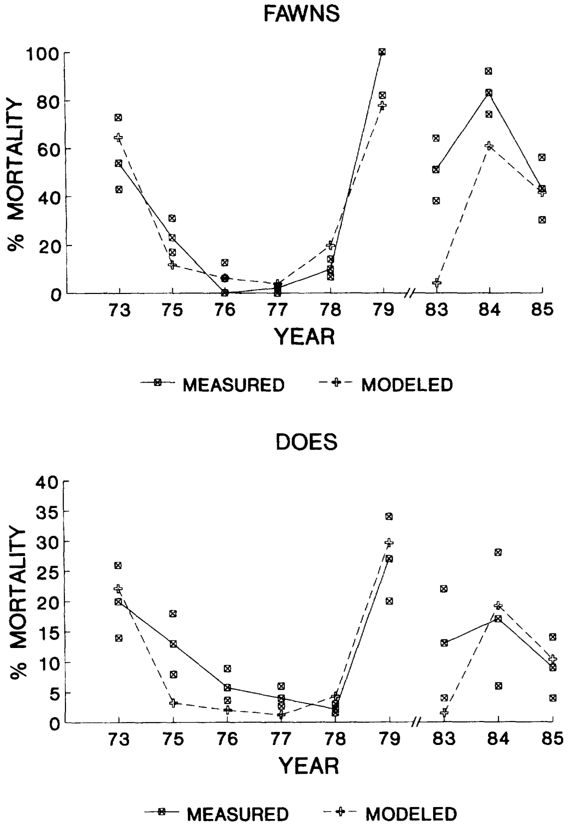


Fig. 3. Validation of model estimates of mortality in mule deer does and fawns in Piceance Basin in northwestern Colorado. Field measurements of mortality during 1972–79 include deaths from all causes based on Bartmann (1984) and Bartmann and Bowden (1984). Field measurements for does during 1983–85 are means from the Colorado Federal Shale Oil Tract (CB) and Little Hills (LH) study areas (all sources of death included for winter months only; G. C. White, Colo. State Univ., unpubl. data). Field measurements for fawns during 1983–85 are based on starvation losses from the LH study area during winter (White et al. 1987). The CB study area was excluded because of high levels of predation observed there. Upper and lower squares represent 95% confidence limits on field estimates.

by −50%, −20%, −10%, 0%, +10%, +20%, and +50% during mild and severe winters. I also examined the effects of temperature by changing the temperature regime of a mild winter to the severe case while leaving the snow regime of the mild winter unaltered. I then compared model output of these simulations with baseline simulations for a mild winter.

*Improve Condition of Animals in Autumn.*—It has been argued that habitat improvements aimed at summer and transition habitats, improvements that enhance the energy reserves of animals arriving on winter ranges, may achieve greater benefits than actions directed at winter ranges themselves (Mautz 1978: 342). To evaluate the efficacy of improving prewinter condition on reducing overwinter mortality, I varied fatness over 5 levels (9–13% for does, 2–8% for fawns) in a factorial arrangement with 4 levels of body size (50–70 kg for does, 20–35 kg for fawns). Moreover, although condition of the average animal is frequently believed to offer a sufficient indicator of the relative condition of the prewinter population, individual variation in condition may be equally important in determining rate of starvation. To investigate this interaction, I varied fat reserves over 5 levels (*see* above) in a factorial arrangement with the coefficient of variation for fatness (15%, 20%, 25%).

*Reduce Disturbance.*—Although it is clear that disturbance by people can increase the energy costs of mule deer, the significance of that increase for animal survival remains poorly understood (Freddy et al. 1986). I compared 3 regimes of disturbance with the undisturbed state. I assumed disturbance occurred 1, 7, or 14 times weekly and that each disturbance caused the average deer to travel 50, 100, 250, or 500 m that it would not have moved in the absence of disturbance. I assumed that deer fled through untracked snow (RMUL = 1.0) at a speed of 100 m/minute.

*Provide Supplemental Feed.*—Development of concentrate rations that can be fed to starving mule deer without causing digestive disorders has provided an efficacious, if expensive, management alternative for reducing mortality of mule deer during winter (Baker and Hobbs 1985). To simulate alternative feeding regimes, I increased metabolizable energy intake by 100–1,000 kcal/day over 10 levels in a factorial arrangement with starting date for supplementation (1 Jan, 1 Feb, 1 Mar).

## RESULTS

### Model Validation

Trends in model predictions of mortality in mule deer resembled trends in mea-

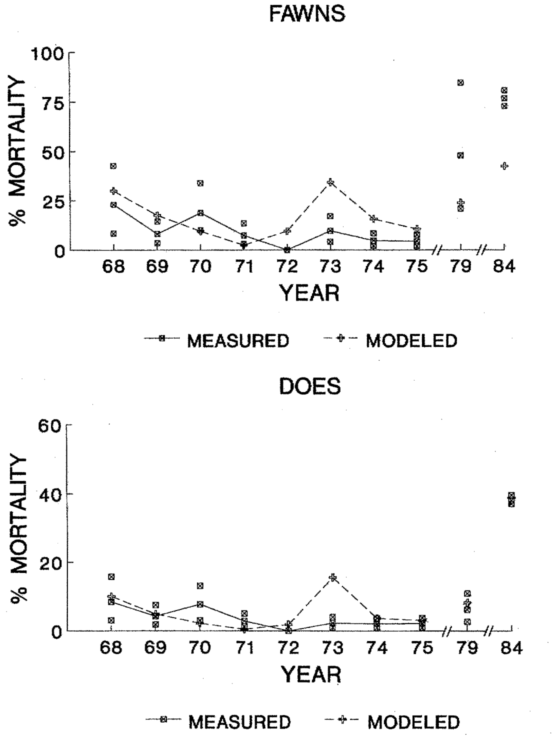


Fig. 4. Validation of model estimates of mortality in mule deer does and fawns in Middle Park in west-central Colorado. Field data include all causes of mortality (R. B. Gill and D. J. Freddy, Colo. Div. Wildl., unpubl. data; Gill 1971; Baker and Hobbs 1985). Upper and lower squares represent 95% confidence limits on field estimates.

sured values during most years. Simulated mortality fell within 95% confidence limits on measured values of doe mortality during 13 of 19 years and agreed with measured fawn mortality during 9 of 19 years (Figs. 3, 4). Overall, model predictions accounted for 71% of the variation in measurements of mortality (Fig. 5). The slope of the regression of model predictions vs. measured values did not differ from 1 ($P = 0.67$) and the intercept did not differ from zero ($P = 0.30$), indicating there was no consistent tendency for the model to over- or underestimate measured mortality. However, examination of the time series data (Figs. 3, 4) showed that the model frequently underestimated fawn mortality during years immediately following severe winters. Temporal patterns in predictions of daily mortality resembled observed patterns except during 1982–83 (Fig. 6).

Model estimates of the percentage of body fat in does and fawns closely tracked measured values during early and midwinter, but exceeded measured values at winter's end (Fig. 7). Model predictions accounted for 72% of the variation in measured fat levels (Fig. 8). The slope of the regression of model predictions vs. measured values did not differ from unity ($P = 0.54$), nor did the intercept differ from zero ($P = 0.25$).

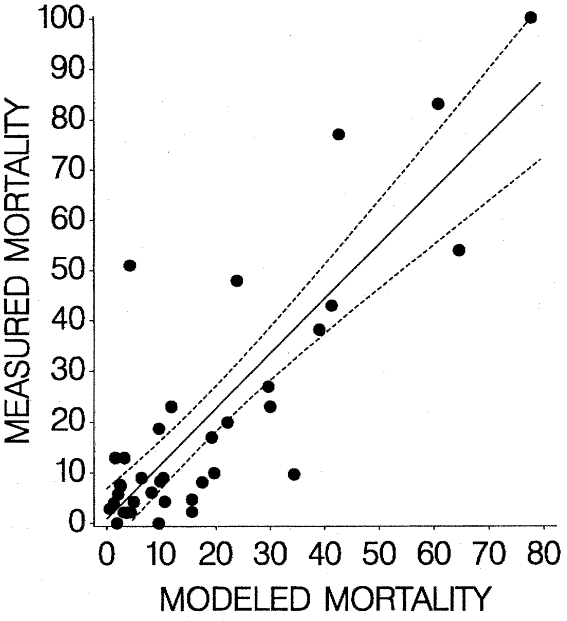


Fig. 5. Measured values for mortality for does and fawns from all study areas and years regressed against model predictions of mortality. Equation is given by $Y = 0.88 + 1.08X$ ($r^2 = 0.71$, $P = 0.0001$). Dashed lines show 95% confidence intervals on the mean prediction of measured mortality.

## Simulations of Energy Budgets

Model predictions of total energy expenditure during a mild winter exceeded predicted expenditure during a severe one, despite increases in costs of thermoregulation and activity in response to severe weather (Table 3). This seeming paradox occurred because energy intake was greater during a mild winter, and, hence, weight loss was substantially less. Thus, because deer were heavier and because energy expenditure is strongly influenced by body mass, total energy costs were greater during mild winters than severe ones. Mass specific energy costs reflected the effect of winter weather on energy expenditure

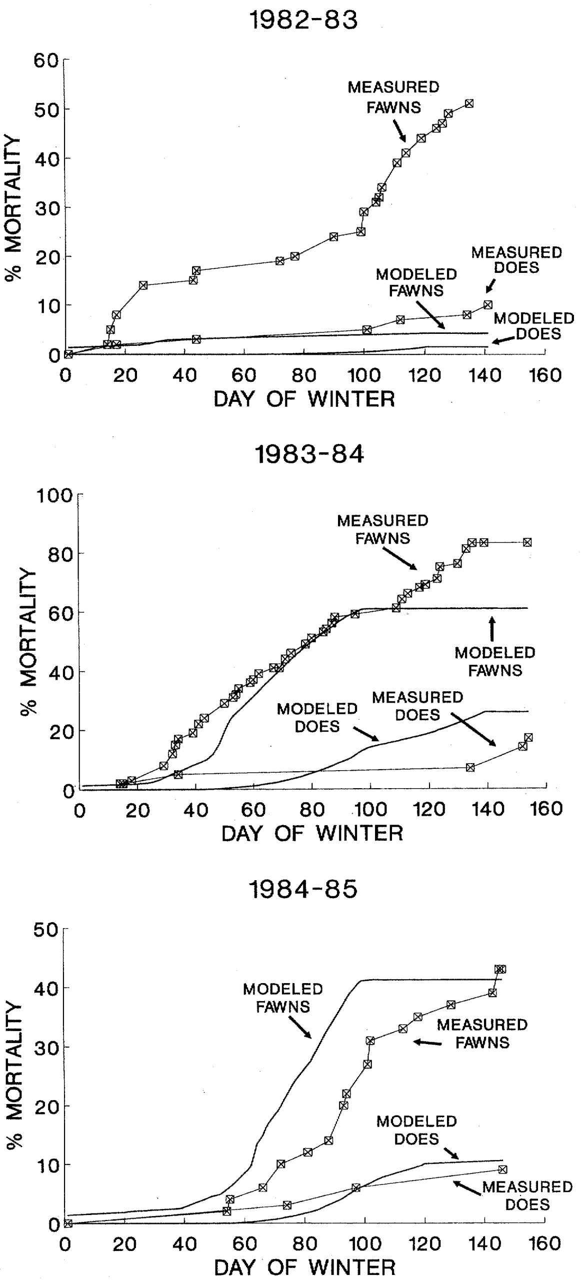


Fig. 6. Validation of model predictions of cumulative mortality in mule deer does and fawns in the Piceance Basin in northwestern Colorado during 1982–85. Field estimates of daily mortality from G. C. White, Colo. State Univ., unpubl. data.

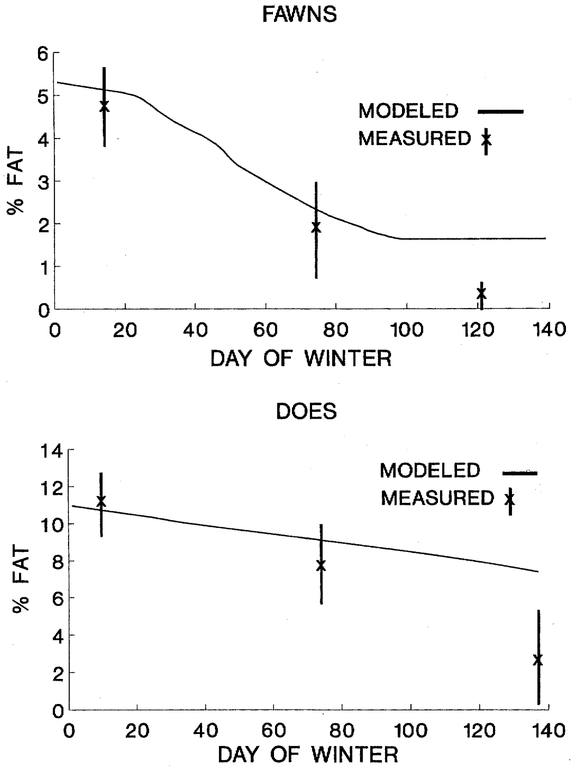


Fig. 7. Validation of model predictions of percent body fat in the average mule deer doe and fawn from the Piceance Basin in northwestern Colorado. Field data taken from Torbit et al. (1988).

more clearly than total costs did. However, because total daily intake was a function of initial body weight rather than current body weight, expressing energy intake on the basis of metabolic body size (which changes as the animal loses weight) would be misleading because lighter animals would appear to have greater intakes than heavier ones.

Predictions of weight-specific energy costs of thermoregulation increased by more than 10 times in does and increased 45 fold in fawns during a severe winter

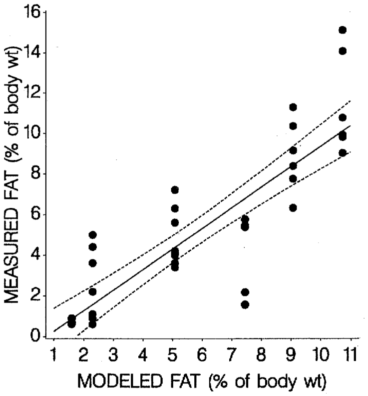


Fig. 8. Measured values for fatness of does and fawns regressed against model predictions of fatness. Equation is given by $Y = -0.75 + 1.01X$ ($r^2 = 0.72$, $P = 0.0001$). Dashed lines show 95% confidence intervals on the mean prediction of measured fatness.

Table 3. Simulated energy budget for mule deer does and fawns during mild and severe winters,[a] Piceance Basin, Colorado.

| | Energy costs (Kcal) | | Energy costs (Kcal/kg$^{0.75}$) | | % of total | |
|---|---|---|---|---|---|---|
| | Severe | Mild | Severe | Mild | Severe | Mild |
| Does | | | | | | |
| Resting | | | | | | |
| Lying | 121,336 | 132,017 | 6,521 | 6,575 | 65.1 | 68.4 |
| Thermoregulation | 4,366 | 329 | 222 | 16 | 2.3 | 0.2 |
| Ruminating | 1,018 | 1,098 | 55 | 55 | 0.5 | 0.6 |
| Activity | | | | | | |
| Posture | 41,516 | 43,350 | 2,230 | 2,159 | 22.3 | 22.5 |
| Net locomotion | 2,076 | 2,149 | 112 | 107 | 1.1 | 1.1 |
| Net locomotion (snow)[b] | 1,708 | 27 | 91 | 1 | 0.9 | 0.0 |
| Thermoregulation | 1,021 | 52 | 30 | 1 | 0.5 | 0.0 |
| Eating | 9,314 | 9,963 | 499 | 496 | 5.0 | 5.2 |
| Other | | | | | | |
| Gestation | 4,074 | 4,074 | 238 | 212 | 2.2 | 2.1 |
| Total | 186,549 | 193,037 | 10,019 | 9,621 | | |
| Fawns | | | | | | |
| Resting | | | | | | |
| Lying | 83,059 | 92,230 | 8,324 | 8,368 | 76.5 | 78.7 |
| Thermoregulation | 1,669 | 49 | 161 | 4 | 1.5 | 0.0 |
| Ruminating | 648 | 716 | 65 | 65 | 0.6 | 0.6 |
| Activity | | | | | | |
| Posture | 18,789 | 20,092 | 1,882 | 1,823 | 17.3 | 17.1 |
| Net locomotion | 852 | 901 | 85 | 82 | 0.8 | 0.8 |
| Net locomotion (snow)[b] | 213 | 7 | 53 | 1 | 0.5 | 0.0 |
| Thermoregulation | 213 | 0.0 | 20 | 0.0 | 0.2 | 2.7 |
| Eating | 2,880 | 3,181 | 288 | 289 | 2.7 | 2.7 |
| Other | | | | | | |
| Gestation | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Total | 108,641 | 117,176 | 10,879 | 10,632 | | |

[a] Input data for severe winter taken from daily weather records for 1978–79 and from records for 1976–77 for mild winter (Table 2).

[b] Net cost of traveling in snow above locomotion cost on bare ground.

(1978–79) relative to a mild one (1976–77) (Table 3). During a severe winter, ambient temperatures exceeded the resting lower critical temperature of mule deer during almost 9 of every 10 hours ($T > LCT_l$, 89% of the time for does, 87% for fawns). Because thermoregulation costs remained a relatively small proportion of the animal's overall energy budget, energy expended to meet thermoregulation costs during a severe winter increased total weight specific costs by only 4% in does and 2% in fawns relative to their expenditures during a mild winter. However, although thermoregulation costs remained a small part of the animal's total expenditure during a severe winter, offsetting these costs would nevertheless require catabolizing a substantial fraction of the animal's energy reserves (9% in does, 15% in fawns) if those costs could not be offset by dietary energy.

Effects of a severe winter on activity costs also were relatively minor (Table 3). Energy costs of walking in snow contributed a small portion of the animal's total energy budget, even when snows were deep. Energy expenditure for travel in snow was unimportant because of the slow travel speeds of simulated mule deer during foraging (1.5 m/min). At these speeds, the influence of snow on travel costs is small (Parker et al. 1984). Consequently, the single model parameter that required a "guess" for initial conditions (RMUL) exerted a largely trivial influence on model behavior.

Severe winter weather had greater im-

Table 4. Simulated intake of dry matter and metabolizable energy (ME) of mule deer does and fawns during a mild and severe winter,[a] Piceance Basin, Colorado.

| Source | Dry matter (kg) | | ME (Kcal) | | % of total ME | |
|---|---|---|---|---|---|---|
| | Severe | Mild | Severe | Mild | Severe | Mild |
| Does | | | | | | |
| Herbs | 16.4 | 98.1 | 22,659 | 135,089 | 17.0 | 83.8 |
| Shrubs | 107.0 | 25.4 | 110,521 | 26,199 | 83.0 | 16.2 |
| Total | 123.4 | 123.4 | 133,183 | 161,293 | | |
| Fawns | | | | | | |
| Herbs | 11.7 | 76.0 | 16,105 | 96,022 | 17.0 | 83.8 |
| Shrubs | 76.0 | 18.0 | 78,556 | 18,623 | 83.0 | 16.2 |
| Total | 87.7 | 87.7 | 94,663 | 114,644 | | |

[a] Input data for severe winter taken from daily weather records for 1978–79 and from records for 1976–77 for mild winter.

pact on energy intake than energy expenditure. Although weather during a severe winter did not change the total amount of dry matter consumed by mule deer relative to their consumption during a mild winter, it markedly reduced total energy intake (Table 4). These reductions resulted from an increased proportion of shrubs in the diet and consequent reductions in diet digestibility.

Severe winter weather can accelerate catabolism of reserves by retarding the animal's rate of energy intake and by accelerating its rate of expenditure. Seventy-five percent of the difference in energy balance between a mild and a severe winter was attributable to reductions in energy intake (Fig. 9). Thus, simulated energy balance and starvation mortality in mule deer during winter were strongly controlled by the number of days that snow conditions forced animals to consume diets containing low levels of available energy.

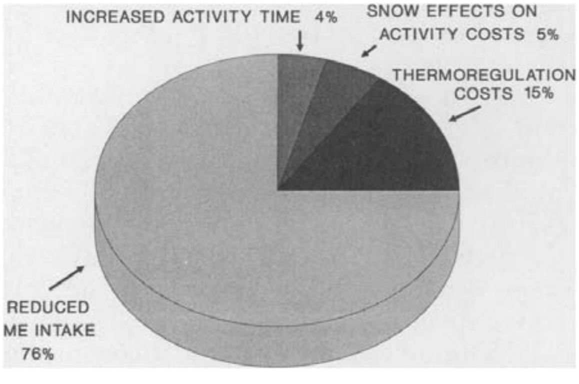


Fig. 9. Influences of winter weather on simulated energy balance of the average mule deer doe. Percentages give the proportion of the difference in energy balance between mild and severe winters that was attributable to effects of weather on energy expenditure and intake. Increased activity time represents the elevation in energy expenditure required by spending more time feeding; snow effects on activity reflect the elevation in energy expenditure required to travel through snow independent of increases in activity time.

## Model Experiments

*Change Food Quantity and Animal Density.*—Changing input weather data from a mild to a severe winter caused a greater change in mortality in does and fawns than was caused by a 10-fold change in the amount of food available to each deer at the beginning of winter (Fig. 10). Increasing food supplies above 200 kg/ha exerted negligible effects on simulated mortality during mild and severe winters. Changing deer density did not change the relationship between food supply and mortality; model predictions were relatively insensitive to deer density except when prewinter food supplies were reduced to 75 kg/ha and deer densities were increased to 60 animals/km$^2$. However, under these conditions, the entire standing crop of herbs was consumed and mortality accelerated rapidly. When biomass exceeded 400 kg/ha, >75% of the standing crop of shrubs and 50% of the herbs remained uneaten at the end of winter, even in the face of exceptionally high densities of deer (Fig. 11).

Mortality was relatively insensitive to initial food supply and deer density because the only mechanism relating these

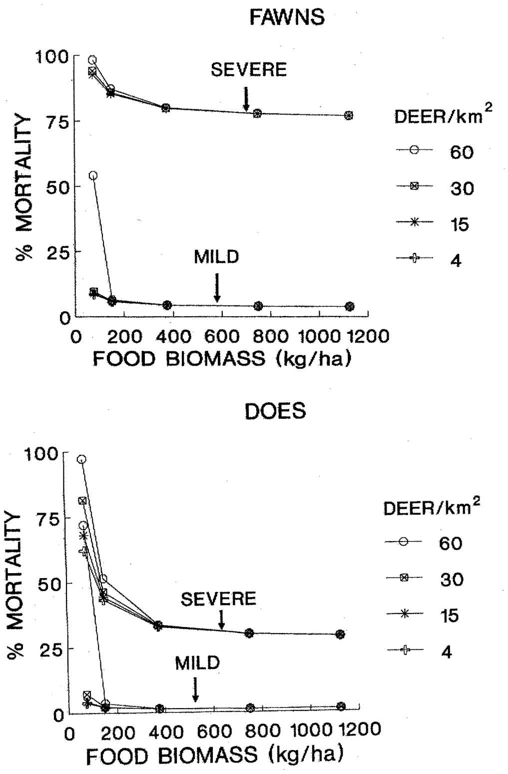


Fig. 10. Simulated mortality resulting from starvation of mule deer does and fawns relative to initial conditions for total food biomass and deer density during mild and severe winters. I assume that food supply is composed of one-third herbs and two-thirds shrubs at all biomass levels.

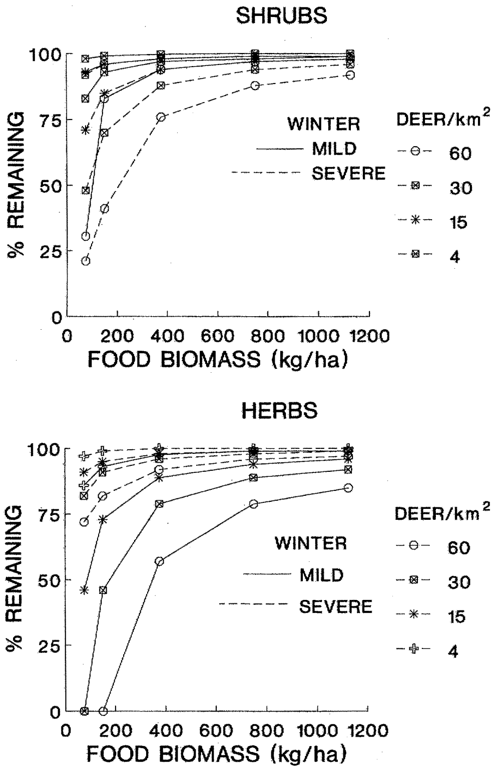


Fig. 11. Simulated proportion of the initial standing crop of shrubs and herbs remaining at the end of mild and severe winters relative to initial conditions for forage biomass and deer density. I assume that forage biomass is composed of one-third herbs and two-thirds shrubs at all biomass levels.

parameters to energy balance was the influence of food biomass on eating rate. Because this relationship is asymptotic, increases in the amount of food available to each deer caused by increasing initial food supply or reducing deer densities failed to influence energy balance unless initial food supplies fell below the asymptote in the representation of dry matter intake rate as a function of quantity.

*Improve the Nutritional Quality of Forage.*—Model predictions were highly sensitive to changes in initial conditions influencing energy gain, and these influences showed strong interactions. During a severe winter, the effect of digestibility of herbs was negligible, but each percentage point increase in the digestibility of shrubs in the average doe's diet resulted in about 10% points less mortality (Fig. 12). During mild winters, the influence of the digestibility of shrubs depended strongly on the digestibility of herbs (Fig. 12). Increasing digestibility of herbs above 40% had almost no impact on mortality during a mild winter regardless of shrub digestibility. Although mortality levels for fawns were consistently higher than those seen in does, the effects of changes in digestibility were otherwise similar.

Changing daily dry matter intake (DMICO) caused fundamental shifts in model predictions (Fig. 13). The magnitude of these changes depended on the value of maximum instantaneous intake (CHEWMAX). When CHEWMAX exceeded about 2.5 g/minute, the model was more sensitive to the limit on total daily intake (DMICO) than to CHEWMAX; below that point, CHEWMAX was the more sensitive variable. Thus, the interaction between DMICO and CHEWMAX was strongest in the vicinity of values of 2.5 g/minute for CHEWMAX. This was the case because when CHEWMAX declined below 2.5 g/minute, it became increasing-

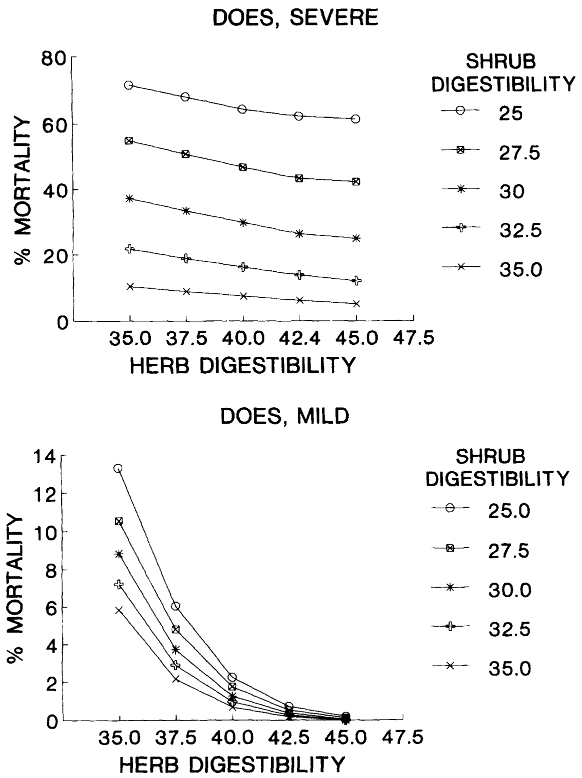


Fig. 12. Simulated mortality due to starvation of mule deer does during a severe and a mild winter relative to initial conditions for dry matter digestibility of herbs and shrubs.

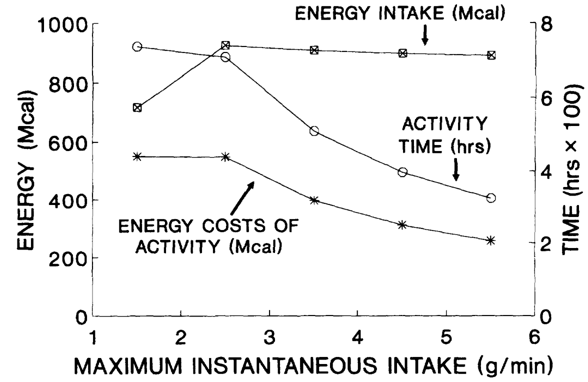


Fig. 14. Simulated overwinter activity time, energy expenditure for activity, and energy intake of the average mule deer doe relative to maximum instantaneous intake during a severe winter. Curves based on daily intake rate of 1.7% of body mass/day.

ly difficult for simulated deer to make an energetic profit by feeding (Fig. 14). At 2.5 g/minute maximum intake, energy costs of feeding exceeded the energy gains obtainable from feeding about 1% of the time, but when CHEWMAX was 1.5 g/minute, deer failed to profit from feeding about 30% of the time. Whenever the costs of feeding exceeded the energy gained from feeding, dry matter intake was reduced to zero and energy intake dropped sharply. However, whenever feeding was profitable, decreasing values of CHEWMAX increased time spent feeding and, hence, energy expenditure.

Achieved levels of daily dry matter intake were not constrained by the time available for feeding until the maximum daily intake (DMICO) exceeded 2.5% of body weight or until CHEWMAX fell to 0.75 g/minute. Thus, whenever daily intake was > 2.5% of body weight or CHEWMAX was < 0.75 g/minute, the animal could not compensate for a reduced rate of feeding by increasing feeding time.

*Alter Snow Distribution and Accumulation.*—Proportional changes in snow depth caused virtually no change in mortality of does or fawns during a mild winter (Fig. 15). This was the case because during much of the winter, there was no snow cover and, consequently, percentage changes in snow depth remained equal to zero. However, changing the snow regime for a mild winter to the severe case without altering temperatures caused major increments in mortality relative to the baseline output for a mild winter (72.1% vs. 4.2% in fawns, 22.7% vs. 1.3% in does). Reducing snow accumulation during a severe winter by 30% reduced mortality by almost 50% in does and fawns. Most of this reduction was caused by increasing the availability of forage rather than by re-

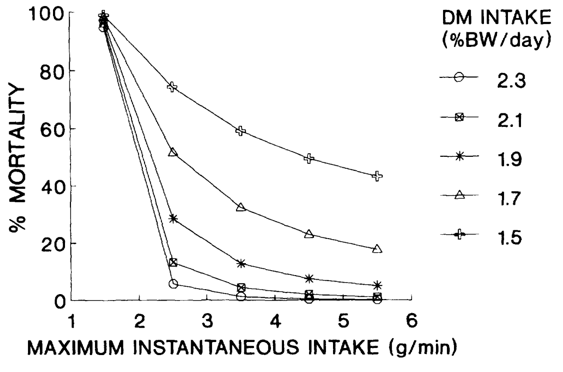


Fig. 13. Simulated mortality due to starvation of mule deer does relative to initial conditions for daily dry matter intake (% of body mass/day) and maximum instantaneous intake (g/min).

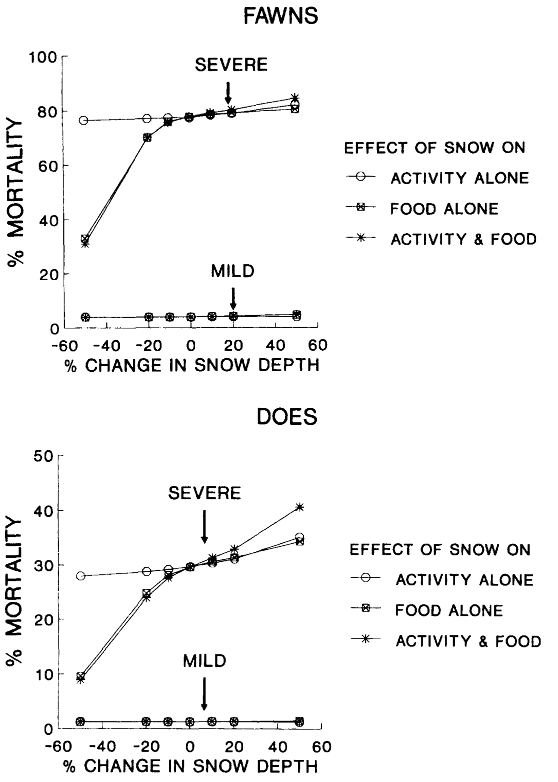


Fig. 15. Simulated mortality due to starvation of mule deer does and fawns relative to changes in daily snow depth during a mild and a severe winter. Curves represent separate and combined effects of snow on availability of forage and energy costs of activity. Curve for effects of snow on energy expenditure assumes no influence of snow on energy intake; curve for effects on food alone assumes no effect of snow on energy expenditure.

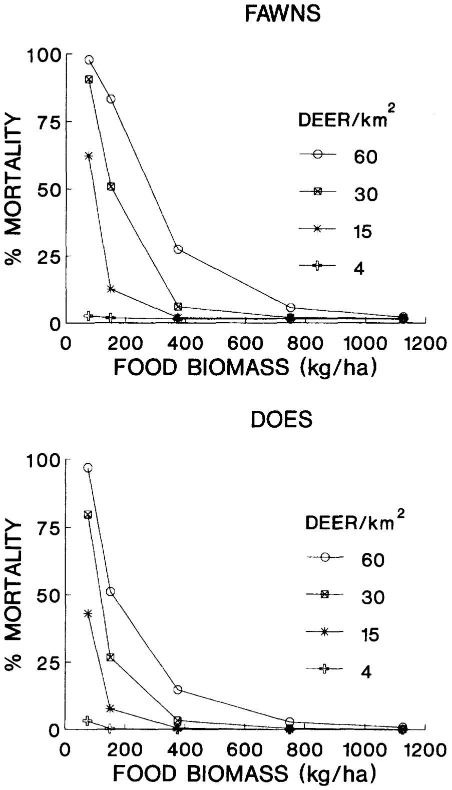


Fig. 16. Simulated mortality due to starvation of mule deer does and fawns during a severe winter relative to initial conditions for forage biomass and deer density. Forage biomass is modeled as a density function of dry matter digestibility and forage availability (Fig. 1). I assume the total food biomass is composed of one-third herbs and two-thirds shrubs.

ducing energy costs of activity. Simulated increases in snow depths above baseline values for a severe winter failed to substantially increase mortality. This was the case because snow depths in model experiments never exceed the height of the shrub layer. If this had occurred, mortality would have rapidly increased to 100% in both does and fawns.

*Interactions of Animal Density with Quantity, Quality, and Availability of Forage.*—Animal density and food biomass exerted strong control on mortality (Fig. 16) when the digestibility and availability of food was variable (Fig. 2). When food biomass fell below 400 kg/ha, differences in mortality due to differences in density within a severe winter (Fig. 16) nearly equaled the differences in mortality between a mild and severe winter at the same density (Fig. 10). The greatest effects of density were seen at low biomass, and the greatest effects of biomass were seen at high density. Given sufficiently low density (3.75 deer/km$^2$), winter mortality was virtually eliminated in both does and fawns even during a severe winter. The increased sensitivity of model predictions to changes in deer density and food amount resulted from coupling these parameters to the digestibility of deer diets, a link that was achieved when food supplies were represented as a distribution of varying quality, but was not present when food supplies were represented without variation in their nutritional value.

*Enhance Thermal Cover.*—Increasing ambient temperatures above baseline values had negligible effects on mortality of does and fawns during mild and severe winters (Fig. 17). However, reducing temperatures below those in baseline runs increased mortality during a severe winter,

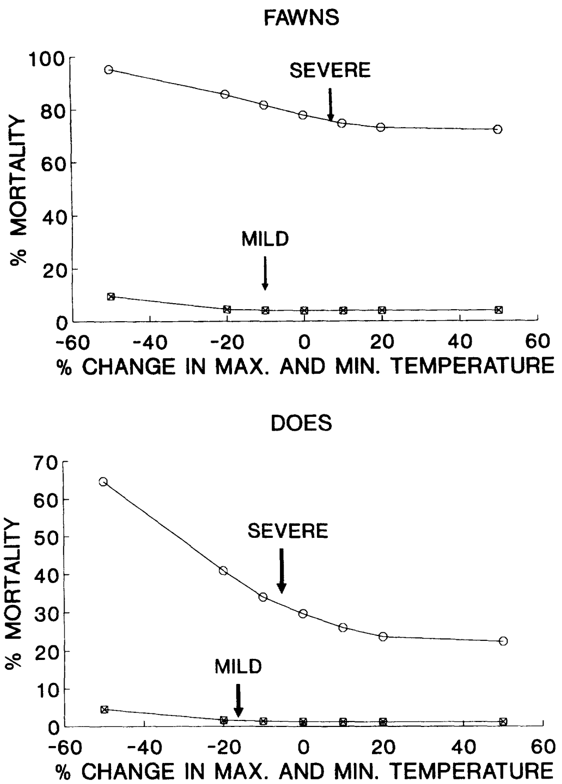


Fig. 17. Simulated mortality due to starvation in mule deer does and fawns during mild and severe winters relative to changes in maximum and minimum daily temperatures.

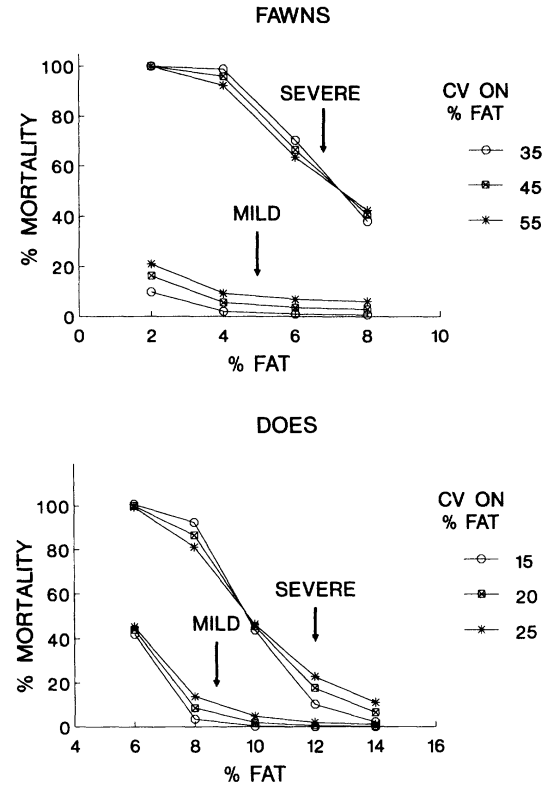


Fig. 18. Simulated mortality due to starvation in mule deer does and fawns during mild and severe winters relative to initial conditions for average percent body fat and its coefficient of variation.

particularly in does. The steep increase in doe mortality is attributable to the relatively low variance in their fat reserves (CV = 21%), which caused the shape of their fat reserve distribution to be narrow. As a result of this shape, small changes in values for overwinter energy balance in the vicinity of the rising portion of the fat reserve curve caused rapid increases in mortality. This was less true for fawns who had a high variance in fat reserves (CV = 45%), and hence, a flatter, broader, distribution. It should be remembered, however, that the baseline temperatures in these simulations (0% change) were taken from an exceptionally severe winter. The extreme temperature regime (−50% change) is probably only encountered at the northern limits of mule deer range.

Changing input data for a mild winter to reflect severe temperatures with mild snow depths caused small increases in mortality relative to the baseline simulations for a mild winter (2.3% vs. 1.3% in does, 5.7% vs. 4.2% in fawns). This was the case because even during mild winters, temperatures are not markedly different from those encountered during severe ones (Table 2) and because energy costs of thermoregulation were a relatively small portion of the animal's total energy expenditure (Table 3).

*Improve Condition of Animals in Autumn.*—Predictions of starvation mortality were extremely sensitive to changes in the fatness of does and fawns at the beginning of winter (Fig. 18). Within the range of 8–12% body fat in does and 4–8% in fawns, a single percentage point change in fatness at the beginning of a severe winter shifted mortality by about 15% points at its end. Outside that range, the effect of fatness was less dramatic. During a mild winter, mortality was low and largely uninfluenced by fatness until the percentage of body fat fell below about 9% in does and below about 4% in fawns.

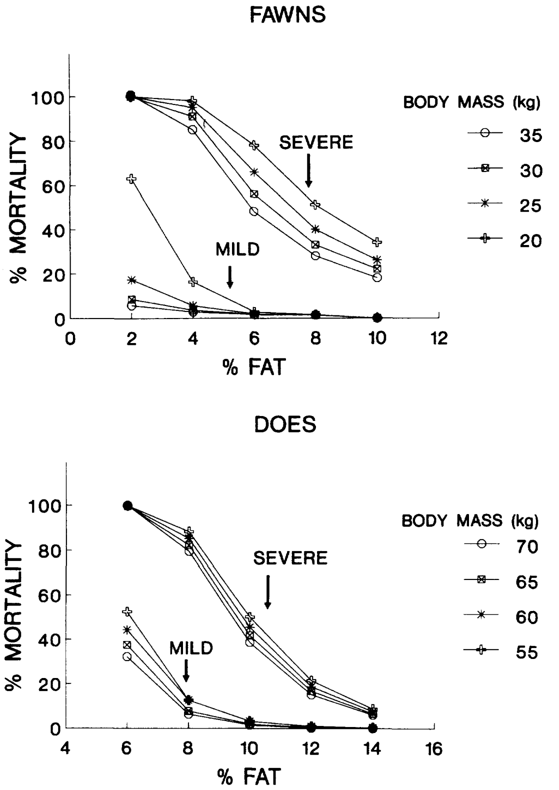


Fig. 19. Simulated mortality due to starvation in mule deer does and fawns during mild and severe winters relative to initial conditions for average % body fat and body mass.

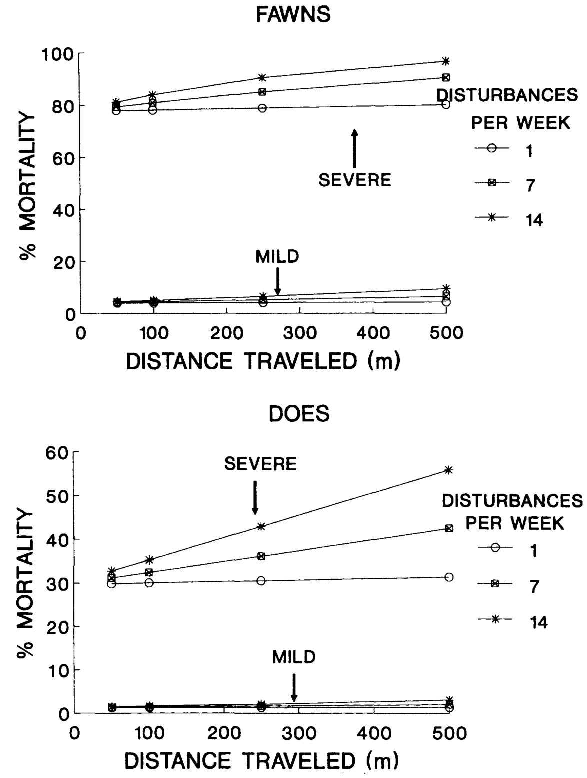


Fig. 20. Simulated mortality due to starvation in mule deer does and fawns during mild and severe winters relative to frequency of disturbance and distance traveled per disturbing event.

The effect of average fatness on population mortality depended on the variation in fat reserves in the population. Changing coefficients of variation in percent fat from 35% to 55% in fawns caused an almost 3-fold increase in mortality in fawns during a mild winter. The intersection of curves representing different coefficients of variation for fat occurs at exactly 50% mortality in the population (Fig. 18). This point, in turn, corresponded to the level of fatness that provided calories equal to those needed to offset energy deficits in the average animal. To survive a severe winter, the average fawn required less prewinter body fat (ca 7.5%) than the average doe (ca 10%) by virtue of its higher dry matter intake rate (2.9% of body weight for fawns, 1.7% for does). However, simulated mortality was consistently higher for fawns because their realized fat levels (5% of body mass) were well below their average requirement, whereas fat levels in simulated does (11% of body mass) exceeded it.

The effect of fat reserves depended on body size, particularly in fawns (Fig. 19). This dependence resulted from the effects of body size on total calories in fat, as well as its effects on energy intake and expenditure. Decreasing body size tended to elevate mortality rates at given fat level, but this tendency was greatest at intermediate values for body fat. Mortality rate was less sensitive to effects of body weight at high and low fat levels.

*Reduce Disturbance.*—Daily disturbance markedly increased simulated mortality in does and fawns during a severe winter (Fig. 20). The extreme case (2 disturbances/day, each causing animals to move 500 m) almost doubled mortality of does. Mortality was insensitive to disturbance during a mild winter.

*Provide Supplemental Feed.*—Predictions of mortality in does and fawns responded sharply to simulated supplemental feeding during a severe winter (Fig. 21). If feeding was begun by 1 February,

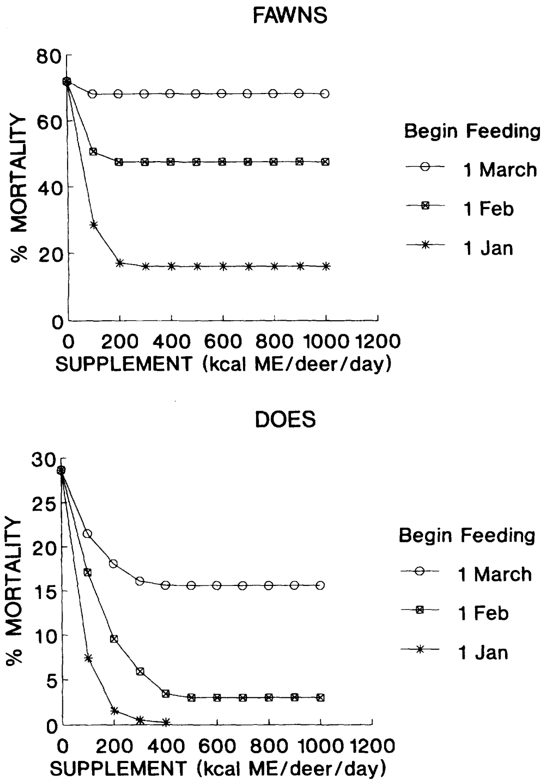


Fig. 21. Simulated mortality due to starvation in mule deer does and fawns during a severe winter relative to level of supplemental feeding and its initiation date.

mortality could be virtually eliminated in adult does and reduced to <20% in fawns by feeding rations providing 200 kcal/kg$^{0.75}$/day. However, if initiating feeding was delayed beyond early February, it rapidly became impossible to avert significant mortality regardless of feeding level. These simulations implicitly assumed that animals have reasonable access to shrubs (Table 1). When shrubs become less available as a result of a lower shrub canopy, lower initial biomass, or deeper snow than was the case in these simulations, more supplement will have to be fed at earlier dates to reduce mortality significantly.

## DISCUSSION

Simulation models have become widely accepted as useful adjuncts to traditional analysis tools in wildlife management (*see* reviews of Connolly 1978, Grant 1986, Starfield and Bleloch 1986, Walters 1986). To be most useful in this role, a simulation model must be predictive, revealing, and accessible. A model should provide a reasonable level of predictive power, thereby reducing uncertainty about the biological consequences of decisions. Simple regression equations can predict mortality in mule deer based on environmental input at a high level of precision and can achieve those predictions with far less complexity than is required by a simulation approach (Bartmann and Bowden 1984). However, a successful simulation model represents plausible mechanisms causing mortality and, in so doing, reveals inferences that would not otherwise emerge from the individual studies upon which the model is based or from purely predictive, regression approaches. These inferences, in turn, touch on many decisions in habitat and population management.

To influence those decisions, however, a successful model must be accessible—it must be constructed to allow its use by persons unfamiliar with computer simulations, as well as those accustomed to them, and should be driven by input data that can be obtained with a reasonable investment. There is a fundamental conflict between realism and utility in simulation models; increased biological realism usually must be bought with more detailed input, obtainable only at increased expense. Thus, keeping in mind that models are first of all abstractions, the most useful models will achieve a careful compromise between the realism of the natural world and the input data needed to represent it. There are several published models that simulate energy balance in cervids (Swift 1983, Boertje 1985, Hudson and White 1985*a*, Fancy 1986). Their utility in influencing management decisions has been limited, however, by an absence of formal validation (but *see* Fancy 1986), by formidable input requirements (e.g., Swift 1983), and by implementations that require the author's participation or a relatively high level of programming skill by the user to manipulate the model.

### Model Validation

Agreement of the predictions of my model with results of field surveys does not permit the conclusion that the model can accurately predict mortality in mule deer populations. Field measurements have their own biases. Helicopter census of prewinter population size probably underestimates the denominator in mortality estimates on shrub–woodland ranges (Bartmann et al. 1986), and removal of carcasses by predators may bias estimates of the numerator (Bartmann 1984). Telemetry studies of mortality are less subject to bias (although the effect of stress of capture and handling is not well understood), and it is encouraging that model predictions mimicked results of these studies as well as field surveys during most years. However, despite sources of error in data and occasional lack-of-fit in model predictions to those data, the resemblance of the estimates of the model to field measurements allows reasonable confidence in the ability of the model to represent processes of starvation in mule deer and to offer predictions that approximate what can be obtained by widely used, empirical approaches.

The agreement of model predictions with field data on mortality in mule deer does from 2 different winter ranges emphasizes the importance of starvation as cause of death, at least in adult females. If other sources are strongly operative, sources not represented in the model, they appear to be compensatory with starvation; otherwise, the model's predictions of starvation mortality would not track field estimates of total mortality as closely as they did.

The agreement of model predictions with empirical data, although reasonably close, was not perfect. These imperfections are revealing. The poorest fit between observed and predicted values occurred during 1982–83 in the Piceance Basin. Diarrhea was observed in many of the fawns collared in the telemetry studies of mortality during that year (L. H. Carpenter, Colo. Div. Wildl., pers. commun.). As a result, animals may have died of disease rather than starvation. This illustrates that although starvation and its compensatory sources of mortality may be the usual cause of death on these winter ranges, other sources may periodically predominate and may be additive to starvation losses.

The model frequently underestimated mortality rates in fawns and overestimated condition of does and fawns at the end of winter. Observed daily mortality frequently showed a surge of deaths in fawns at the end of winter that was not tracked by model predictions (Fig. 6). These discrepancies suggest that processes that are influential in nature are not represented in the model. Carry-over effects of severe weather on animal condition between years may be one such process. Measured mortality rates frequently exceeded model predictions of mortality during the years immediately following severe winters. This suggests that the loss of condition incurred by deer during extreme weather may persist into subsequent years, even when those later years are relatively mild.

Several processes influencing energy intake were not represented in the model and probably should be included in later versions. Snow conditions on winter ranges are exceedingly dynamic during late winter and early spring; crusting and changes in snow density and moisture content contribute to these dynamics, which, in turn, may profoundly affect the availability of forage and the energy costs of activity (Parker et al. 1984; Fancy and White 1985*b*,*c*). Although daily snow density can be input to the model, validation runs assumed a constant density in the absence of such data. Thus, because these changes in snow characteristics may magnify energy deficits, they also may explain the divergence between model predictions and field measurements during late winter, particularly the model's failure to mimic a late season acceleration in fawn mortality. Moreover, validation runs were set up such that forage quality remained constant throughout winter. If deer consumed the most nutritious foods early in the season, observed mortality could increase dramatically when the supply of those foods was exhausted. Seasonal changes in intake rates of adults (Wood et al. 1962, Nordan et al. 1968, McEwan 1975, Bahnak et al. 1981) offer another potentially influential process not incorporated in the model. Observed fat reserves in Piceance does may have been lower than predicted ones during a mild winter (Fig. 7) as a result of seasonality in metabolism that caused weight losses independent of those predicted by the model.

## Model Experiments

A pivotal revelation of the modeling effort was that processes controlling energy intake were generally more influential in determining starvation mortality than were processes controlling energy expenditure. A similar outcome has been seen in other simulation studies (Swift et al. 1980, Wickstrom et al. 1984, Fancy 1986). However, it can be argued that model predictions of energy expended for thermoregulation underestimate the true expenditure because simulations used ambient temperatures rather than operant temperatures as input and thus failed to specifically represent conductive, convective, and radiative heat losses (Moen 1968*a,b,c*). The model's algorithm for estimating thermoregulation costs is, indeed, simplified, but it is uncertain whether this simplification caused under- or overestimation of true energy costs.

To the extent that model predictions exceeded the true costs, we can have greater confidence in the conclusion that the real costs are not dominant components of the energy budget. Major overestimation of thermoregulation costs could result from the model's failure to represent heat gains from solar radiation during the day. Mule deer that were shivering before sunrise stopped shivering thereafter, with no change in measured ambient temperature (Parker and Robbins 1984). Other sources of overestimation include the animal's selection of favorable microclimates to mitigate heat loss. Although these sources of energy gain may fail to compensate for unrepresented sources of energy losses (conduction, convection, radiation), I believe the model's fundamental conclusions on the importance of thermoregulation remain robust. Major elevations in temperature regimes for mild and severe winters failed to substantially perturb model predictions of mortality. Regression studies also revealed that winter temperatures have a minor impact on mortality in mule deer (Bartmann and Bowden 1984).

In practical terms, it appears that enhancing thermal cover on shrub–steppe and shrub–woodland winter ranges will be ineffectual in improving condition of mule deer. This prediction has been corroborated empirically (D. J. Freddy, Colo. Div. Wildl., unpubl. data). However, I observed important thresholds in the relationship between simulated mortality and temperature, particularly for does (Fig. 15). These suggest that cover may be substantially more important at more northerly latitudes. Moreover, these thresholds imply that loss of existing cover (as opposed to cover enhancement) could markedly alter patterns of mortality.

Given the sensitivity of model predictions to variation in energy intake, it is important to identify variables that influence this process. Changing initial conditions for 3 variables (maximum daily intake of dry matter, maximum instantaneous intake of dry matter, and dry matter digestibility) caused qualitative changes in model behavior. All of these variables, in turn, respond to physical characteristics of forages, particularly the thickness of forage cell wall and its lignification (Spalinger et al. 1986, 1988; Baker and Hobbs 1987). These physical characteristics are relatively homogeneous within major forage groups (mature and senescent forbs, grasses, and leaves and stems of shrubs). This suggests that physical characteristics of diets that result from particular mixtures of forages should be used to drive energy intake. However, representing the physiological influence of forage physical structure on energy intake (even at the relatively crude level at which we currently understand that influence) depends first on understanding feeding behavior. We cannot predict the consequences of diet choices until we can predict the choices themselves, and, at the moment, the former is better understood than the latter.

Until this is achieved, I surmise that because variables controlling energy intake would move in the direction of reducing mortality and enhancing animal condition whenever diets contain low levels of cell wall, managers should emphasize habitat improvement prescriptions that offer palatable forages with low cell-wall content to wintering mule deer. These include immature grasses and leaves of shrubs and forbs. It should be emphasized that these need to be present only in relatively small amounts (Figs. 2, 16) to have a substantial impact on winter mortality. If snow accumulation renders such forage unavailable, then habitat managers should look to transition ranges to improve fat reserves of animals before winter begins.

Body fat content emerged as a highly influential variable in the model (Figs. 18, 19). This emphasizes that application of the model will depend on obtaining reasonable estimates of fat levels in the population of interest. Fortunately, recently developed regressions between kidney fat and whole body fat make such determinations feasible on a relatively large scale (Torbit et al. 1988).

The influence of fat reserves on mortality depended on body size, particularly in fawns (Fig. 19). Small increases in body fat caused large increases in survival of small fawns, but increasing body size of lean fawns conveyed relatively small advantages. The survival value of increasing body size in simulated deer with high fat levels resulted from the scaling of intake rate and energy expenditure relative to body size. Increasing body size elevated energy intake (which scaled to $BW^{1.0}$) more rapidly than energy requirements (which scaled to $BW^{0.75}$). Although increased body mass clearly conveys a survival advantage at a given level of body fat, the interaction of size and fatness illustrates why body size is an imprecise predictor of survival in mule deer fawns (White et al. 1987:fig. 2). The spread of points in Figure 19 illustrates that body size will be poorly related to survival if fat levels vary among animals of different size within age classes. Body size is apparently not well correlated with fatness within age classes of mule deer (Torbit et al. 1988:fig. 1).

Increasing food amount and reducing animal numbers are the predominant tools of mule deer management in the West. At first look, the model seems to suggest that these frequently used approaches will be ineffectual at reducing mortality (Fig. 10). Empirical evidence offers limited support for this suggestion. Bartmann and Bowden (1984) failed to find any relationship between prewinter population density of mule deer and the rate of overwinter mortality in those populations (but also *see* Gilbert et al. 1970:22). Moreover, during a severe winter, Baker and Hobbs (1985) observed exceedingly high levels of mortality in mule deer using sagebrush range that had been extensively treated to improve its value as winter habitat for mule deer.

Does this mean that winter mortality operates independently of deer density? The model does not represent successional changes in vegetation resulting from effects of feeding by deer, and consequently is insensitive to an important consequence of increasing density. Successional effects operate over several years; the inferences of the model are limited to the effects of density on mortality during a single year. Within a given year, however, the model suggests mortality rates will be density independent whenever there is a low variance in the quality and/or availability of food supplies, but will be strongly influenced by density whenever those resources are variable. This is the case because under most conditions changes in food supplies or deer density must influence the quality of deer diets if those changes are to influence mortality.

In practical terms, this means that population management has the potential to reduce mortality rates on ranges with a high diversity of forages offered on topography that causes differences in the effects of snow on access to them. On ranges with low forage diversity and homogenous availability, harvest will probably fail to reduce the proportion of the population that starves. Moreover, given the relatively small impact of deer on total forage supplies (Fig. 11), it may well be that long-term successional effects also will depend on the presence of a reasonable level of variation in forage resources. It follows that estimating the average value of food resources and their average biomass on the landscape is not sufficient to evaluate the quality of deer habitats or to prescribe treatments to enhance them. Instead, habitat evaluation and improvement depend on understanding the distribution relating quality and availability of deer foods to their biomass (Hobbs and Swift 1985, Hanley and Rodgers 1989).

## CONCLUSIONS

Processes influencing energy intake exert a much greater impact on energy balance of mule deer during winter than processes affecting their energy expenditure. Although energy expenditure in ungulates has been investigated with great cleverness and care (*see* reviews in Hudson and White 1985*b*), controls on energy intake rarely have been studied in a way that makes them useful in predictive models. Future progress in modeling energetics of mule deer will depend on research revealing mechanisms regulating diet selection and feeding behavior, rather than merely describing their outcomes.

The predictions of the model, as well as other, more empirical results (Wickstrom et al. 1984, Spalinger et al. 1988), suggest that forage quantity will rarely influence the daily dry matter intake of mule deer. Thus, increasing forage amount will probably not improve energy balance in deer, unless those increases are accompanied by changes in the availability or nutritional value of forage. Small improvements in the condition of animals at the beginning of winter, or enhancements in forage quality that provide deer greater energy intake during winter, are likely to pay large dividends in reducing winter mortality. Reducing population size will improve animal condition and reduce mortality only when food resources are heterogenous or are exceptionally rare.

Mortality resulting from starvation is a process operating at several levels of ecological organization. Energy balance and its component processes can be represented best at the level of the individual. Variation in the impact of energy balance, as seen in its effect on mortality rates, is determined by the distribution of energy reserves among individuals and, hence, operates at the level of the population. The quantity and quality of food available to the individual is determined by the composition and productivity of plant communities and the effects of populations on them and, thus, acts at the level of the ecosystem. A thorny problem in wildlife management has been bringing information obtained at these different levels to bear on the specific, focused decisions needed to effectively manipulate animal populations and the habitats they use. The most important result of this model is the illustration that information obtained for many different reasons, in different places, using different approaches, can be assembled such that useful predictions emerge—predictions that mimic the behavior of the natural world in a reasonable way. These predictions can enhance decisions on management of mule deer.

## LITERATURE CITED

ADAMCZEWSKI, J. Z., C. C. GATES, B. M. SOUTAR, AND R. J. HUDSON. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. Can. J. Zool. 66:1986–1996.

ALLDREDGE, A. W., J. F. LIPSCOMB, AND F. W. WHICKER. 1974. Forage intake rates of mule deer estimated with fallout cesium-137. J. Wildl. Manage. 38:508–516.

AMMANN, A. P., R. L. COWAN, C. L. MOTHERSHEAD, AND B. R. BAUMGARDT. 1973. Dry matter and energy intake in relation to digestibility in white-tailed deer. J. Wildl. Manage. 37:195–201.

BAHNAK, B. B., J. C. HOLLAND, L. J. VERME, AND J. J. OZOGA. 1981. Seasonal and nutritional influences on growth hormone and thyroid activity in white-tailed deer. J. Wildl. Manage. 45:140–147.

BAKER, D. L., AND N. T. HOBBS. 1985. Emergency feeding of mule deer during winter: tests of a supplemental ration. J. Wildl. Manage. 49:934–942.

———, AND ———. 1987. Strategies of digestion: digestive efficiency and retention time of forage diets in montane ungulates. Can. J. Zool. 65:1978–1984.

BARTMANN, R. M. 1983. Composition and quality of mule deer diets on pinyon–juniper winter range, Colorado. J. Range Manage. 36:534–541.

———. 1984. Estimating mule deer winter mortality in Colorado. J. Wildl. Manage. 48:262–267.

———, AND D. C. BOWDEN. 1984. Predicting mule deer mortality from weather data in Colorado. Wildl. Soc. Bull. 12:246–248.

———, L. H. CARPENTER, R. A. GARROTT, AND D. C. BOWDEN. 1986. Accuracy of helicopter counts of mule deer in pinyon–juniper woodland. Wildl. Soc. Bull. 14:356–363.

BLACK, H., R. J. SCHERZINGER, AND J. W. THOMAS. 1975. Relationships of Rocky Mountain elk and Rocky Mountain mule deer to timber management in the Blue Mountains of Oregon and Washington. Pages 11–31 *in* Elk-logging-roads symposium proceedings. U.S. For. Serv., For. Wildl. and Range Exp. Stn. and Univ. Idaho, Moscow.

BOERTJE, R. D. 1985. An energy model for adult female caribou of the Denali herd, Alaska. J. Range Manage. 38:468–472.

CARPENTER, L. H. 1976. Middle park cooperative deer study—deer habitat evaluation. Colo. Div. Wildl. Game Res. Rep. July Part 2:283–289.

———, D. L. BAKER, AND R. B. GILL. 1980. Test of a nutritionally based big game habitat evaluation system. Colo. Div. Wildl. Unpubl. Spec. Rep. 95pp. (Mimeogr.)

———, O. C. WALLMO, AND R. B. GILL. 1979. Forage diversity and dietary selection by wintering mule deer. J. Range Manage. 32:226–229.

CHAPPEL, R. W., AND R. J. HUDSON. 1979. Energy costs of standing in Rocky Mountain bighorn sheep. J. Wildl. Manage. 43:261–263.

CLARK, W. R., AND G. S. INNIS. 1982. Forage interactions and black-tailed jack rabbit population dynamics: a simulation model. J. Wildl. Manage. 46:1018–1035.

CONNOLLY, G. E. 1978. Predator control and coyote populations: a review of simulation models. Pages 327–345 *in* M. Beckoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York, N.Y.

———. 1981. Limiting factors and population regulation. Pages 287–347 *in* O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

EBERHARDT, L. E., E. H. HANSON, AND L. L. CADWELL. 1984. Movement and activity patterns of mule deer in the sagebrush–steppe region. J. Mammal. 65:404–409.

FANCY, S. G. 1986. Daily energy budgets of caribou: a simulation approach. Ph.D. Thesis, Univ. Alaska, Fairbanks, 266pp.

———, AND R. G. WHITE. 1985*a*. Incremental cost of activity. Pages 143–160 *in* R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Fla.

———, AND ———. 1985*b*. Energy expenditure for locomotion by barren-ground caribou. Can. J. Zool. 65:122–128.

———, AND ———. 1985*c*. Energy expenditures by caribou while cratering in snow. J. Wildl. Manage. 49:987–993.

FREDDY, D. J., M. W. BRONAUGH, AND M. C. FOWLER. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. Wildl. Soc. Bull. 14:63–68.

FREDERICK, R. B., W. R. CLARK, AND E. E. KLASS. 1987. Behavior, energetics, and management of refuging waterfowl: a simulation model. Wildl. Monogr. 96. 35pp.

GATES, C. C., AND R. J. HUDSON. 1979. Effects of posture and activity on metabolic responses of wapiti to cold. J. Wildl. Manage. 43:564–565.

GILBERT, P. F., O. C. WALLMO, AND R. B. GILL. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. J. Wildl. Manage. 34:15–23.

GILL, R. B. 1971. Middle Park deer study: productivity and mortality. Colo. Div. Wildl. Game Res. Rep. July Part 2:189–207.

GOLLEY, F. B. 1961. Energy value of ecological materials. Ecology 42:581–584.

GRANT, W. E. 1986. Systems analysis and simulation in wildlife and fisheries sciences. John Wiley and Sons, New York, N.Y. 338pp.

HANLEY, T. A. 1982. The nutritional basis for food selection by ungulates. J. Range Manage. 35:146–151.

———. 1984. Relationships between sitka black-tailed deer and their habitat. USDA For. Serv. Gen. Tech. Rep. PNW-168. 22pp.

———, F. L. BUNNELL, E. E. STARKEY, S. K. STEVENSON, AND A. S. HARESTAD. 1984. Habitat relationships of Cervidae (deer) in old-growth forests. Proc. Soc. Am. For. 1983:361–367.

———, AND J. J. RODGERS. 1989. Estimating carrying capacity with simultaneous nutritional constraints. USDA For. Serv. Note PNW-In Press.

HOBBS, N. T., D. L. BAKER, J. E. ELLIS, D. W. SWIFT, AND R. A. GREEN. 1982. Energy and nitrogen based estimates of elk winter range carrying capacity. J. Wildl. Manage. 46:12–21.

———, ———, AND R. B. GILL. 1983. Comparative nutritional ecology of montane ungulates during winter. J. Wildl. Manage. 47:1–16.

———, AND R. A. SPOWART. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. J. Wildl. Manage. 48:551–560.

———, AND D. M. SWIFT. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. J. Wildl. Manage. 49:814–822.

HUDSON, R. J., AND W. G. WATKINS. 1986. Foraging rates of wapiti on green and cured pastures. Can. J. Zool. 64:1705–1708.

———, AND R. G. WHITE. 1985*a*. Computer simulation of energy budgets. Pages 261–290 *in* R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Fla.

———, AND ———, editors. 1985*b*. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Fla. 314pp.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187–211.

KLEIBER, M. K. 1975. The fire of life. Robert E. Krieger Co., New York, N.Y. 454pp.

LOVELESS, C. M. 1967. Ecological characteristics of a mule deer winter range. Colo. Div. Game, Fish, and Parks Tech. Bull. 20. 124pp.

MALOIY, G. M. O. 1968. The physiology of digestion and metabolism in the red deer. Ph.D. Thesis, Univ. Aberdeen, Scotland. 165pp.

MAUTZ, W. W. 1978. Nutrition and carrying capacity. Pages 321–348 *in* J. L. Schmidt and D. L. Gilbert, eds. Big game of North America: ecology and management. Stackpole Books, Harrisburg, Pa.

———, AND J. FAIR. 1980. Energy expenditure and heart rate for activities of white-tailed deer. J. Wildl. Manage. 44:333–342.

MCEWAN, E. H. 1975. The adaptive significance of the growth patterns in Cervidae compared with other ungulate species. Zool. Zh. 54:1221–1232.

MILCHUNAS, D. G., M. I. DYER, O. C. WALLMO, AND D. E. JOHNSON. 1978. *In-vivo/in-vitro* relationships of Colorado mule deer forages. Colo. Div. Wildl. Spec. Rep. 43. 44pp.

MILLER, F. L. 1970. Distribution patterns of black-tailed deer (*Odocoileus hemionus columbianus*) in relation to environment. J. Mammal. 51:248–260.

MOEN, A. N. 1968*a*. Energy exchange of white-tailed deer, western Minnesota. Ecology 49:676–682.

———. 1968*b*. Surface temperatures and radiant heat loss from white-tailed deer. J. Wildl. Manage. 32:338–344.

———. 1968*c*. The critical thermal environment: a new look at an old concept. BioScience 18: 1041–1043.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1967–85. Climatological data: Colorado. Vols. 72–90. Environ. Data Serv., Natl. Climatic Center, Asheville, N.C.

NORDAN, H. C., I. MCT. COWAN, AND A. J. WOOD. 1968. Nutritional requirements and growth of black-tailed deer (*Odocoileus hemionus columbianus*) in captivity. Pages 89–100 *in* M. A. Crawford, ed. Symp. Zool. Soc. London, No. 21.

OWEN, O. E., P. FELIG, A. P. MORGA, J. WAHRE, AND G. F. CAHILL, JR. 1969. Liver and kidney metabolism during prolonged starvation. J. Clin. Invest. 48:574–583.

PARKER, K. L., AND C. T. ROBBINS. 1984. Thermoregulation in mule deer and elk. Can. J. Zool. 62:1409–1422.

———, AND ———. 1985. Thermoregulation in ungulates. Pages 161–182 *in* R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Fla.

———, ———, AND T. A. HANLEY. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474–488.

PARTON, W. H., AND J. A. LOGAN. 1981. A model for diurnal variation in soil and air temperature. Agric. Meteorol. 23:205–216.

REGELIN, W. L., J. C. NAGY, AND O. C. WALLMO. 1977. Effects of snow drifts on mountain shrub communities. Int. Congr. Game Biol. 13:414–419.

———, AND O. C. WALLMO. 1975. Carbon black increases snow melt and forage availability on deer winter range in Colorado. USDA For. Serv. Res. Note RM-296. 4pp.

RENECKER, L. A., AND R. J. HUDSON. 1978. Effect of posture, feeding, low temperature, and wind on energy expenditures of moose calves. Proc. North Am. Moose Conf. Workshop 14:126–140.

———, AND ———. 1986. Seasonal foraging rates of moose in aspen boreal habitats. J. Wildl. Manage. 50:143–147.

ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, N.Y. 336pp.

ROMESBURG, H. C. 1981. Wildlife science: gaining reliable knowledge. J. Wildl. Manage. 45:293–314.

SHORT, H. L. 1979. Deer in Arizona and New Mexico: their ecology and a theory explaining recent population declines. USDA For. Serv. Gen. Tech. Rep. 70. 25pp.

SIBBALD, A. R., T. J. MAXWELL, AND J. EADIE. 1979. A conceptual approach to modelling of herbage intake by hill sheep. Agric. Syst. 4:119–133.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative zoology. Harcourt, Brace, and World, New York, N.Y. 440pp.

SPALINGER, D. E., T. A. HANLEY, AND C. T. ROBBINS. 1988. Analysis of the functional response in foraging in the Sitka black-tailed deer. Ecology 69: 1166–1175.

———, C. T. ROBBINS, AND T. A. HANLEY. 1986. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. Can. J. Zool. 64:312–321.

STARFIELD, A. M., AND A. L. BLELOCH. 1986. Building models for conservation and wildlife management. Macmillian Publ. Co., New York, N.Y. 253pp.

STEINHORST, R. K., W. H. HUNT, G. S. INNIS, AND K. P. HAYDOCK. 1978. Sensitivity analysis of the ELM model. Pages 232–255 *in* G. S. Innis, ed. Grassland simulation model. Springer-Verlag, New York, N.Y.

SWEENEY, J. M., AND J. R. SWEENEY. 1984. Snow depth influencing winter movements of elk. J. Mammal. 65:524–526.

SWIFT, D. M. 1983. A simulation model of energy and nitrogen balance for free-ranging ruminants. J. Wildl. Manage. 47:620–645.

———, J. E. ELLIS, AND N. T. HOBBS. 1980. Energy and nitrogen requirements of North American cervids in winter: a simulation study. Proc. Int. Reindeer and Caribou Symp. 2:244–251.

TORBIT, S. C., L. H. CARPENTER, A. W. ALLDREDGE, AND D. M. SWIFT. 1985*a*. Mule deer body composition—a comparison of methods. J. Wildl. Manage. 49:86–91.

———, ———, R. M. BARTMANN, AND A. W. ALLDREDGE. 1988. Calibration of body composition indices in wintering mule deer. J. Wildl. Manage. 52:582–588.

———, ———, D. M. SWIFT, AND A. W. ALLDREDGE. 1985*b*. Differential loss of fat and protein by mule deer during winter. J. Wildl. Manage. 49:80–85.

WALLMO, O. C., L. H. CARPENTER, W. L. REGELIN, R. B. GILL, AND D. L. BAKER. 1977. Evaluation of deer habitat on a nutritional basis. J. Range Manage. 30:122–127.

———, A. LECOUNT, AND S. L. BROWNLEE. 1981. Habitat evaluation and management. Pages 287–347 *in* O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

WALTERS, C. J. 1986. Adaptive management of renewable resources. MacMillian Publ. Co., New York, N.Y. 300pp.

WEINS, J. A., AND G. S. INNIS. 1974. Estimation of energy flow in bird communities: a population bioenergetics model. Ecology 55:730–746.

WESLEY, D. E., K. L. KNOX, AND J. G. NAGY. 1973. Energy metabolism of pronghorn antelopes. J. Wildl. Manage. 37:563–573.

WHITE, G. C., AND R. M. BARTMANN. 1983. Estimation of survival rates of band recoveries of mule deer in Colorado. J. Wildl. Manage. 47: 506–511.

———, T. A. GARROTT, R. M. BARTMANN, L. H. CARPENTER, AND A. W. ALLDREDGE. 1987. Survival of mule deer in northwest Colorado. J. Wildl. Manage. 51:852–859.

WHITE, R. G., AND M. K. YOUSEF. 1978. Energy expenditure in reindeer walking on roads and on tundra. Can. J. Zool. 56:215–223.

WICKSTROM, M. L., C. T. ROBBINS, T. A. HANLEY, D. E. SPALINGER, AND S. M. PARISH. 1984. Food intake and foraging energetics of elk and mule deer. J. Wildl. Manage. 48:1285–1301.

WOOD, A. J., I. MCT. COWAN, AND H. C. NORDAN. 1962. Periodicity of growth in ungulates as shown by the deer of the genus *Odocoileus*. Can. J. Zool. 41:593–603.

WUNDER, B. A. 1978. Implications of a conceptual model for the allocation of energy resources by small mammals. Pages 68–75 *in* Populations of small mammals under natural conditions. Pymatuning Lab. Ecol., Univ. Pittsburgh, Pa., Spec. Publ. Ser. 5.

*Received 22 July 1988.*
*Accepted 22 January 1989.*

## APPENDIX

DEER9 is a simulation model of energy balance in mule deer that predicts animal condition and starvation mortality during winter. It requires at least 256K of available RAM. A graphics card and math-coprocessor are highly desirable. The model is built to allow use by persons with minimal computer experience, but the user should be familiar with DOS commands and with using prompted programs.

*Obtaining the Model.*—Model files can be transferred by modem over BITNET by contacting the author (NTHOBBS @ CSUGOLD). Provide your BITNET name and address, and I will respond. Alternatively, you can send me a 5.5-inch diskette and a suitable, self-addressed mailer.

*Model Files.*—Running the model requires only 1 file (DEER9.EXE), but others can be helpful. Source code is contained in DEER9.SRC to allow the user to modify the program. Two data files (SEVERE.DAT and MILD.DAT) were used in model experiments and provide example input for winters with high and low mortality. README.TXT contains notes on revisions, etc. A couple of files are needed to allow graphic output on monochrome monitors with Hercules cards (HGC.EXE and INIT10.COM).

*Installing the Model.*—Before using the model, be sure that the DOS ANSI.SYS driver is installed in your CONFIG.SYS file. See your DOS manual for instructions on setting-up this driver. If it is not installed, the model will run, but you are likely to get some strange color combinations in the screen output.

The model can be installed on a hard disk or run from the diskette drive. For hard disk users, copy the above files to the directory where you want the model and data to reside. Make that directory the default. For diskette drive users, put your working diskette (a backup copy is advisable) in a drive, and make it the default. In both cases, once the model is installed and the default drive or directory is chosen, you can begin a simulation by entering DEER9, followed by a return.

*Running a Simulation.*—You will need to respond to several questions to set up a simulation. Your responses can be the first letter of the appropriate word (i.e., *y* for yes) or the full word. The model is not sensitive to case; you can use capital letters or small ones. However, whenever you are asked to enter numerical data, it is *imperative* (*!!!!*) that all entries include a decimal point (i.e., 10.0 rather than 10). If a simulation results in suspiciously high mortality, the first thing to check is decimal points in the input. At any time, you can exit the program by simultaneously pressing the control and break key or, if you have it, the system request key. However, *if you exit using control break while graphs are displayed, you will probably have to reboot your computer to return to a normal screen.*

*Prompts for Monitor.*—You will first be asked about your monitor. Respond as prompted with an *e, c,* or *m* followed by a return. If you have a monochrome monitor, you will be asked about your graphics card (IBM or Hercules). If you have a Hercules card, you will be given 2 prompts to enter the commands HGC FULL and INT10. VGA monitors are not supported, but probably will be in the near future.

*Entering Weather Data.*—At the prompt, you will first need to specify the units on weather data (English or metric). If you plan to use the input data files included on the distribution diskette, specify English units. In any case, units should not be mixed (i.e., no Celsius for temperature combined with inches for snow depth). You will be asked how you want to enter weather data—from a file (respond *f*) or from the keyboard (respond *k*). If you choose the keyboard, you will be given 3 choices for data entry (enter data, revise estimates, or leave as is). If this is your first run of the model in a session, you must respond *e* for enter data. However, if this is a repeat run, you can revise the weather input to reflect milder or more severe conditions (enter *r*). This choice was specifically designed to facilitate decisions on supplemental feeding given that you have some data for conditions observed up to the present date and some projections for what is likely to occur for the rest of the winter. Finally by choosing *l* (leave as is), it is also possible to leave the weather data unchanged and run another simulation altering other inputs. At this point, you will be prompted for information about the length of the simulation (no. of days, etc.) and then asked for daily weather input. Temperature and snow depth information should reflect the conditions deer experience as closely as possible. This is to say it would be best to get snow depth information from areas of deer concentration.

It is also possible to enter daily weather data from a data file. You will be prompted for a file name and path to its location. This file should be formatted as follows:

| | |
|---|---|
| col 2–5: | year (e.g., 1979, integer) |
| col 9–10: | month (right justified integer) |
| col 14–15: | day (right justified integer) |
| col 16–25: | maximum temperature (anywhere in field, with decimal) |
| col 26–35: | minimum temperature (anywhere in field, with decimal) |
| col 36–45: | snow depth (anywhere in field, with decimal). |

Units must be uniform (i.e., no mixture of English and metric). Be certain that the file is flat ASCII. This is particularly important if you use a word processor to build it. It should contain no column headings. The last day of the simulation should be March 31 (shown by a 3 in column 10 and a 31 in column 14–15). If you want to run simulations beyond March, that is acceptable; just make March 31 = 32 and the last day of the simulation = March 31. It is possible to run up to 20 years of simulations by making a contiguous data file.

*Entering Habitat Data.*—You will be asked if you want to change the default data that describe the food supply and the deer population. Default values are those given in Table 1. Although not all of these can be changed by the user, the major ones are available to you. If you want to change these parameters, respond *y* to the question on defaults, and a menu will appear offering you choices. Choose a parameter you wish to change and enter its number at the prompt at the bottom of the menu. A window will then open describing the parameter, its units, and default values. You can change its value in this window.

All units must be the same as those shown in the window. If you decide you do not want to change the default value once the window has appeared, simply press the return key to get back to the menu. When you are done with changes, enter the number for exit. One other point—the code has traps for zeros that result when you press the return key alone. These traps preserve the default values and give you an easy way to return to the menu without changing a parameter. However, if you really want to enter a zero value, simply enter a number close to it (e.g., 0.000001).

*Entering Data on Attributes of Deer.*—You will be asked if you want to simulate a doe or a fawn. It is not possible to simulate both at once. Using a menu process identical to the one just described, you can then change default parameters describing the average animal if you wish to do so.

*Output Options.*—Respond to questions on graphics and tables. If your computer is not 100% IBM compatible, you probably cannot get graphic output and should opt for tables alone.

*Running the Simulation.*—The simulation will execute. If you do not have a math-coprocessor, it takes as long as 35 minutes/year of input data on an XT; with a coprocessor on an AT, it takes about 35 seconds.

*Printing.*—You can choose to have tables routed to your printer. If you want graphs printed, give the DOS command "graphics" before running the simulation. Then use your print screen key. Tables are printed for you if you respond *y* to the prompt.

*Repeat Simulations.*—You can run another simulation without entering new weather data, revise the data, or leave the program.

Reproductive Success of Elk Following Disturbance by Humans during Calving Season
Author(s): Gregory E. Phillips and A. William Alldredge
Source: *The Journal of Wildlife Management*, Vol. 64, No. 2 (Apr., 2000), pp. 521-530
Published by: Wiley on behalf of the Wildlife Society
Stable URL: http://www.jstor.org/stable/3803250
Accessed: 05-01-2018 23:18 UTC

# REPRODUCTIVE SUCCESS OF ELK FOLLOWING DISTURBANCE BY HUMANS DURING CALVING SEASON

GREGORY E. PHILLIPS,[1] Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA
A. WILLIAM ALLDREDGE, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA

***Abstract:*** Restricting human activity in elk (*Cervus elaphus*) calving areas during calving season can be controversial because of increasing human uses of elk habitat, and little evidence exists to evaluate impacts of these activities on elk populations. We evaluated effects of human-induced disturbance on reproductive success of radiocollared adult female elk using a control–treatment study in central Colorado. Data were collected during 1 pretreatment year and 2 treatment years. Treatment elk were repeatedly approached and displaced by study personnel throughout a 3–4-week period of peak calving during both treatment years, while control elk did not receive treatment. We observed elk on alpine summer ranges in July and August on both areas to estimate the proportion of marked cows maintaining a calf. Calf/cow proportions for the control area remained stable, but those for the treatment area declined each year. Average number of disturbances/elk/year effectively modeled variation in calf/cow proportions, supporting treatment as the cause of declining calf/cow proportions. Average decrease in calf/cow proportion in the treatment group was 0.225. Modeling indicated that estimated annual population growth on both study areas was 7% without treatment application, given that existing human activities cause some unknown level of calving-season disturbance. With an average of 10 disturbances/cow above ambient levels, our model projected no growth. Our results support maintaining disturbance-free areas for elk during parturitional periods.

***JOURNAL OF WILDLIFE MANAGEMENT 64(2):521–530***

***Key words:*** *Cervus elaphus*, elk, human disturbance, productivity, recreation, reproductive success.

Recently born elk calves are particularly susceptible to malnutrition and predation (Schlegel 1976, Taber et al. 1982:286, Bear 1989, Singer et al. 1997). Human-induced disturbance during calving season may exacerbate elk vulnerability, and restricting humans in parturitional habitats during calving season has been recommended to minimize impacts (Towry 1987). Seasonal closures may, however, conflict with human demands on these habitats, but little evidence exists to support or refute the need to protect elk from humans during calving season.

Previous studies have described displacement or alteration of elk spatial use patterns associated with activities such as vehicular traffic (Czech 1991, Cole et al. 1997), logging (Edge et al. 1985, Czech 1991), mining (Kuck et al. 1985, Johnson 1986), recreation (Berwick et al. 1986, Cassirer et al. 1992), and development (Berwick et al. 1986, Morrison et al. 1995). However, few studies have directly evaluated effects of calving-season disturbance on calf production. Johnson (1986) found no significant difference in reproduction (July calf:cow ratios) between elk using 3 surface-coal-mine areas and 3 control areas. Kuck et al. (1985) approached and displaced radiocollared calves in summer and reported no abandonment or mortality of collared calves, but small sample sizes provided low statistical power to detect an effect of disturbance on calf survival.

We hypothesized that human-induced disturbance of elk during calving season would reduce reproductive success (number of offspring of an individual surviving at a given time; Lincoln et al. 1998:261). We used control and treatment groups of elk to test our hypothesis by applying a disturbance treatment during calving season and comparing subsequent levels of reproductive success between groups.

## STUDY AREA

Our study was conducted in 2 geographically contiguous areas in central Colorado, approximately 160 km west of Denver: Beaver Creek and Vail (Fig. 1). Elevations ranged from 2,250 m to 4,150 m at Beaver Creek, and 2,400 m to 4,000 m at Vail. Ecosystem types on both areas included alpine tundra, subalpine and montane forest, montane shrubland, and riparian (Fitzgerald et al. 1994). Additional study area descriptions were provided by de Vergie (1989), Morrison (1992), and Morrison et al. (1995).

Portions of the Interstate-70 corridor are

---

[1] E-mail: gephillips@earthlink.net

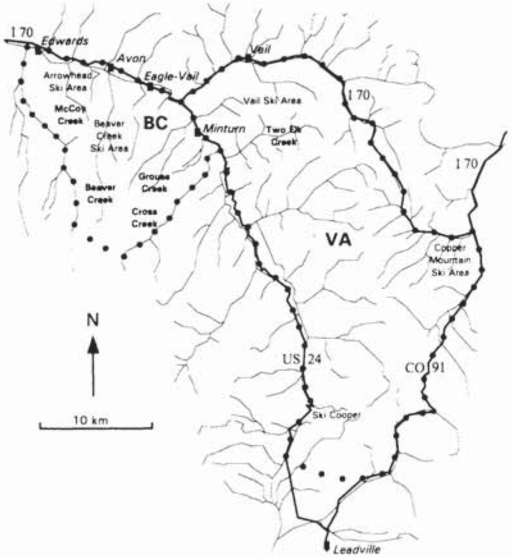


Fig. 1. Location of Beaver Creek (BC) and Vail (VA) study areas in central Colorado. Approximate boundaries of study areas shown by dotted lines.

heavily developed along the northern perimeter of both areas. Edwards, Avon, and Eagle–Vail occur north of the Beaver Creek study area along Interstate 70. Although shown as points (Fig. 1), these communities extend along the valley floor in a nearly continuous strip from about 2 km west of the intersection of Interstate 70 and U.S. Highway 24, westward beyond Edwards. Similarly, the town of Vail covers an approximately 12-km strip along Interstate 70 on the north boundary of the Vail study area. Minturn lies between Beaver Creek and Vail study areas along U.S. Highway 24 from Grouse Creek to Cross Creek. Both areas contain ski resorts: Copper Mountain, Vail, and Ski Cooper on the Vail study area, and Beaver Creek and Arrowhead on the Beaver Creek study area. Copper Mountain, Vail, and Beaver Creek Ski Areas are year-around resorts. National Forest lands within both study areas are popular destinations for recreationists engaged in backcountry activities. Because of land management policies in effect prior to, and throughout, our study the Two Elk Creek drainage, upper sections of McCoy Creek, and parts of the Beaver Creek drainage were closed to public access in May and June to protect elk during calving.

Beaver Creek and Vail study areas were well suited for use as treatment and control areas because of ecological and land use similarities, and both contained large, extensively studied elk herds. de Vergie (1989) reported that most elk on Beaver Creek and Vail occupied either one or the other area, and rarely crossed U.S. Highway 24, implying that Beaver Creek and Vail elk herds were sufficiently segregated to afford a treatment–control experimental opportunity. Cows captured on winter ranges in de Vergie's (1989) study used open alpine areas during summer, which would facilitate daily observation of marked cows for our study.

## METHODS

We maintained samples of marked adult female elk on Beaver Creek and Vail study areas from 1995 to 1997 (71–85 elk/area/yr), and applied a disturbance treatment to marked elk within the Beaver Creek study area during the peak calving period in 1996 and 1997. No treatment was applied to Beaver Creek elk in 1995 or to Vail elk in all 3 years. We ascertained presence or absence of a calf for individual marked adult cows by visual observation in July and August to estimate annual proportions of marked cows maintaining a calf on each area (calf/cow proportion). We compared treatment–control differences in calf/cow proportions for 1 year of pretreatment data and 2 years of treatment data to estimate effects of disturbance.

### Capturing and Marking Adult Female Elk

We used helicopter net-gunning to capture a representative sample of adult female elk at specified locations spread across both study areas (Phillips 1998). Elk were fitted with frequency-specific transmitters on neck collars containing 2 plastic identification sleeves marked with unique alpha-numeric codes of 76-mm-high black characters on a white background (Freddy 1993). Elk were also marked with unique combinations of colored plastic livestock ear tags (76 mm × 76 mm).

### Disturbance Treatments on Beaver Creek Study Area

We applied a treatment of simulated recreational hiking to radiocollared elk on the Beaver Creek area by approaching a radiocollared animal until she was displaced. The rationale behind our disturbance treatment was that a small number of people targeting a specific sample of animals (through the use of telemetry equipment) could create an effect equal to a greater number of recreationists hiking through the area.

Based on estimated parturition and conception dates for elk in Colorado (Bear 1989, Freddy 1989, Byrne 1990), and a median gestation period of 255 days (Bubenik 1982:171), we expected that 80–90% of calves would be born from 26 May to 19 June. These dates bounded our treatment period in 1996, but to increase treatment efficacy, we expanded the treatment period by 7 days in 1997 to 19 May through 19 June.

We used twice-weekly aerial telemetry to locate elk during the treatment period and to allocate treatment effort. Up to 9 technicians using telemetry receivers were assigned to areas of high elk densities for 24 days in 1996 and 30 days in 1997. We documented each disturbance by recording animal identification, time, location, and visual and telemetry evidence demonstrating that the target animal had been treated. We concluded that a treatment occurred when nearby elk were seen or heard running away, telemetry evidence supported the proximity of the target animal at time of treatment, and posttreatment telemetry evidence demonstrated a fading signal in the same direction that elk were seen or heard to move (Phillips 1998).

### Estimating Calf Status of Marked Elk

We observed marked adult female elk on Beaver Creek and Vail study areas each year during July and August to determine presence or absence of a calf. Observations were generally made from dawn to 1000 hr, and 1600 hr to dark at points that provided extensive views of alpine summer range where risk of disturbing elk was minimal. We recorded length of time that each marked cow was continuously visible and monitored. We documented time and duration of nursing and licking bouts, along with other types of interactions between cows and calves. Individual observation periods generally occurred over several days, were at numerous locations, and varied from several seconds to several hours, depending on animal movements, vegetation cover, terrain, and weather.

Calf status (CS) was determined for as many marked elk as possible, where CS1 denotes presence of a calf and CS0 denotes absence of a calf. Twinning occurs in elk but is generally <1% (Bubenik 1982:170, Taber et al. 1982: 280). Our use of a binary response variable for calf status implies 1 calf or no calf. If twinning rates were unusually high, bias could result from interpreting calf/cow proportions as the number of calves/cow, rather than the proportion of cows maintaining a calf (or calves). We could not determine presence of twins for marked cows because calves were not individually identifiable, but we did not observe any marked cows nurse 2 calves simultaneously or different calves, sequentially. We believe that calf/cow proportions can be interpreted as the number of calves/cow with negligible risk of bias from cows maintaining 2 calves. Our July–August calf/cow proportions are, therefore, conceptually similar to the summer calf production rate of Singer et al. (1997).

We concluded that a maternal bond existed between cow and calf if the cow nursed a calf for ≥10 sec, or if a cow exhibited "strong calf association", including licking bouts with a calf or traveling as a unit (Phillips 1998). Implicit here was an assumption that such behaviors are rare between cows and calves not maternally related (Geist 1982). Female red deer (*Cervus elaphus*) with calves infrequently allow a strange calf to nurse, but usually drive them away (Lowe 1966). We commonly observed cows reject nursing attempts by calves, although some calves were persistent in their attempts. These interactions were characterized by aggressive or avoidance behaviors by the cow toward the calf, similar to those described by Altmann (1952). Strong calf association was more subjective than nursing, but provided reliable CS1 evidence. We were looking for a distinctive attentiveness between cow and calf, especially when alarmed, that was not present in casual calf–cow interactions. Usually, most cows that exhibited strong calf association were later seen nursing a calf.

Concluding that a cow did not have a calf was not definitive because it was impossible to continuously observe individuals long enough to conclude CS0 with certainty. We obtained CS0 evidence (actually a lack of CS1 evidence) by accumulating blocks of uninterrupted observation time (several sec to several hr), within which a particular cow did not associate with calves. Observation data from summer 1995, comprised of discrete blocks of continuous observation time, indicated that approximately 95% of CS1 cows were detected within 350 min of cumulative observation time, and that longer observations provided rapidly diminishing returns (Phillips 1998). Cows that showed no strong calf association were included in analysis as CS0 only if total cumulative observation time was ≥350 min. Use of an arbitrary cutoff time introduces bias from excluding individuals with <350 min of observation time and no strong calf association. To balance this bias, we constrained evidence of calf association to occur within 350 min to classify an individual as CS1, i.e., cows were classified as CS0 if CS1 evidence was observed after 350 min of total observation time, but not within 350 min of observation. Only 8 CS0 classifications (2% of all classified individuals) resulted from this constraint.

### Analysis of Calf-status and Treatment-effort Data

We used a generalized linear mixed model approach, incorporated in the GLIMMIX macro of SAS Version 6.12 (Littell et al. 1996), to analyze calf-status and treatment-effort data. Error type was specified as binomial, and we used the logit link function to linearize the dependent variable and to scale estimates of calf/cow proportions between 0 and 1. The form of the general model was

$$\text{logit}(R_{ijk}) = m + \text{area}_i + \text{year}_j + (\text{area} \times \text{year})_{ij} + \text{indv(area)}_{ik},$$

where $\text{logit}(R_{ijk}) = \log_e[R_{ijk}/(1 - R_{ijk})]$; $R_{ijk}$ = probability that a specific individual $k$, given area $i$ and year $j$, maintained a calf during the July–August observation period; $m$ = intercept; $\text{area}_i$ = fixed effect of the $i^{th}$ area, $i = 1, 2$ (Beaver Creek and Vail, respectively); $\text{year}_j$ = fixed effect of the $j^{th}$ year, $j = 1, 2, 3$ (1995, 1996, and 1997, respectively); $(\text{area} \times \text{year})_{ij} = ij^{th}$ area-by-year interaction fixed effect; and $\text{indv(area)}_{ik}$ = random effect of the $k^{th}$ marked elk, nested within the $i^{th}$ area, $k = 1, 2 \ldots 184$.

Individual marked elk, sampled from the larger population of interest (all elk on Beaver Creek and Vail study areas), were the unit of analysis and were treated as a random-effects term. Modeling individuals as a random effect allowed for partitioning overall variance of calf-status data into components. With a separate estimate of the indv(area) variance component, $\hat{\sigma}^2_I$, the remaining variance is partitioned among fixed effects. Fixed effects are more appropriately interpreted when also accounting for random effects. Significance of $\hat{\sigma}^2_I$ was evaluated with a likelihood-ratio test between the general model and a reduced model without indv(area) (Lebreton et al. 1992:80).

We used deviance divided by degrees of freedom (DEV/df) as a general index for goodness of fit and overdispersion. We also used DEV as a goodness-of-fit statistic approximately distributed $\chi^2_{df}$ with df = $n - p$, where $n$ = number of observations and $p$ = number of independent fixed-effects parameters in the model (Littell et al. 1996:432,445). The GLIMMIX macro uses the residual estimate as an extra dispersion (ED) scale parameter to indicate if the observed conditional variance of the errors is different than theory. Overdispersion is indicated when ED > 1 and underdispersion when ED < 1. By default, GLIMMIX adjusts the analysis for ED, but ED can be set to 1.0 to prevent this adjustment.

Estimated annual calf/cow proportions for each study area (area-by-year $\hat{R}_{ij}$) and 95% confidence limits were obtained from back transformations of logit-scale area-by-year means and 95% confidence limits using the inverse logit link function (Littell et al. 1996:431). The area × year interaction effect and contrasts of annual differences between Beaver Creek and Vail area-by-year calf/cow proportions were examined for evidence of treatment effect. Our research hypothesis was that treatment-group $\hat{R}_{ij}$ (that is, $\hat{R}_{12}$ and $\hat{R}_{13}$) would decline relative to control values, after accounting for pretreatment differences. The contrast used to test the null hypothesis of no treatment effect was

$$[(R_{12} - R_{22}) + (R_{13} - R_{23})]/2 - (R_{11} - R_{21}) = 0$$

(average treatment effect).

This contrast states that the average difference between treatment and control calf/cow proportions during treatment years was the same as for the pretreatment year. Substitution of corresponding $\hat{R}_{ij}$ for each $R_{ij}$ in the contrast provides an estimate of the average treatment effect adjusted for pretreatment difference between Beaver Creek and Vail. A negative estimate corresponds with reduced average calf/cow proportions for the treatment group during 1996 and 1997.

Level of treatment effort represents a potential mechanism (magnitude of disturbance) to explain variation in the data, especially interaction effects. We determined the average number of treatments/individual for each area-by-year group and used these values as individual-specific covariates ("group-average" covariate). We replaced the area × year interaction in the general model with a term for the group-average covariate. This approach modeled the linear relationship between group-average number of treatments/cow and average calf/cow proportions, among area-by-year groups. We assessed efficacy of the group-average covariate relative to the interaction term using an analysis-of-deviance $F$-test and degrees of freedom appropriate when considering area-by-year groups, rather than individuals, as units of analysis (Skalski et al. 1993). An $F$-test was more appropriate than a likelihood-ratio test for this approach because it explicitly accounted for small denominator degrees of freedom resulting from the reduced sample size of 6 area-by-year cells. The structure of the $F$-statistic was

$$F = [(\mathrm{DEV}_{\mathrm{red}} - \mathrm{DEV}_{\mathrm{cov}})/(\mathrm{df}_{\mathrm{red}} - \mathrm{df}_{\mathrm{cov}})] \div [(\mathrm{DEV}_{\mathrm{cov}} - \mathrm{DEV}_{\mathrm{gen}})/(\mathrm{df}_{\mathrm{cov}} - \mathrm{df}_{\mathrm{gen}})],$$

where $\mathrm{DEV}_{\mathrm{red}}$ = deviance of the reduced model containing $m$, area, year, and indv(area); $\mathrm{DEV}_{\mathrm{cov}}$ = deviance of the model containing $m$, area, year, treatment effort covariate, and indv(area); $\mathrm{DEV}_{\mathrm{gen}}$ = deviance of the general model; $\mathrm{df}_{\mathrm{red}}$ = degrees of freedom for the reduced model; $\mathrm{df}_{\mathrm{cov}}$ = degrees of freedom for the covariate model; and $\mathrm{df}_{\mathrm{gen}}$ = degrees of freedom for the general model.

This $F$-test did not evaluate whether the covariate explained a significant amount of deviance when added to the reduced model. Rather, it tested how well the covariate served as a surrogate for the interaction term. The null hypothesis was that the covariate did not adequately substitute for the interaction in accounting for variation in area-by-year calf/cow proportions. We also computed the percentage of deviance explained by the covariate relative to the interaction term by

$$(\mathrm{DEV}_{\mathrm{red}} - \mathrm{DEV}_{\mathrm{cov}})/(\mathrm{DEV}_{\mathrm{red}} - \mathrm{DEV}_{\mathrm{gen}}) \times 100.$$

### Modeling Population Dynamics with Effects of Calving-season Disturbance

We explored the potential impact on population growth of various levels of disturbance, by incorporating the group-average covariate model as a predictor of prehunt calf/cow proportions in a density-independent population-dynamics model for elk. We parameterized the model using information from our study and others conducted in Colorado, and from Colorado Division of Wildlife 1986–95 harvest data (Phillips and Alldredge 1999). Because Beaver Creek and Vail study areas are popular with recreationists, and because large areas of each were open to human access during our study, some unknown level of disturbance probably occurred that was not caused by our treatment effort. Inclusion of the covariate model within the population model reflects potential changes in population growth if calving-season disturbances increase relative to levels that existed for non-treatment elk during our study.

## RESULTS

We documented 407 and 691 reliable treatment events on the Beaver Creek study area in 1996 and 1997, respectively. Average numbers of treatments/Beaver Creek individual were 5.4 in 1996, and 8.3 in 1997. We estimated calf status for >75% of marked cows/area throughout the study. Final sample sizes for calf status of marked cows were 59, 61, and 73 for Beaver Creek, and 54, 62, and 70 for Vail in 1995, 1996, and 1997, respectively.

We first fitted the general model without controlling the ED-scale parameter to evaluate lack of fit and overdispersion. Values of DEV (417.3, df = 372, $P = 0.052$), DEV/df (1.12), and ED scale (0.89) provided little evidence of lack of fit or overdispersion, so we set ED scale = 1.0 for further analysis.

A significant component of overall variation in probability of having a calf was explained by the random effects of individual elk (indv(area) likelihood-ratio test $\chi^2_1 = 47.9$, $P < 0.001$), and the random effects term was retained in the model. The GLIMMIX macro provides estimates of random-effects variance components in the logit scale, only: $\hat{\sigma}^2_I = 0.300$, SE = 0.241, 95% CI = 0.098–3.866.

Differences between Beaver Creek and Vail calf/cow proportions were not the same for each year of the study (area × year interaction, $\chi^2_2 = 14.0$, $P < 0.001$). After adjusting for pretreatment differences, estimated average treatment effect was −0.225 (contrast $F_{1,191} = 3.94$, $P = 0.024$), indicating that average calf production was 0.225 calves/cow lower for treatment elk than for control elk in 1996 and 1997. Final estimates of annual area-specific calf/cow proportions were obtained using the general model (Table 1). Confidence intervals are asymmetric because the transformation from logit scale to biological scale is nonlinear.

Average number of disturbances/elk/year did a good job of explaining the declining trend in Beaver Creek calf/cow proportions (Fig. 2). The

**Table 1. Estimates of July–August calf/cow proportions[a] for samples of marked adult female elk on Beaver Creek (BC) and Vail (VA) study areas, Colorado, 1995–97.**

| | | Biological scale[b] | | Logit scale[c] | |
|---|---|---|---|---|---|
| Year | Area | Mean | CI | Mean | SE |
| 1995[d] | BC | 0.646 | 0.512–0.761 | 0.6035 | 0.2822 |
| | VA | 0.627 | 0.486–0.750 | 0.5194 | 0.2924 |
| 1996 | BC[e] | 0.524 | 0.394–0.651 | 0.0972 | 0.2670 |
| | VA | 0.631 | 0.500–0.746 | 0.5368 | 0.2730 |
| 1997 | BC[e] | 0.398 | 0.288–0.519 | −0.4147 | 0.2487 |
| | VA | 0.703 | 0.582–0.802 | 0.8637 | 0.2698 |

[a] Proportion of marked cows maintaining a calf, or calves/cow assuming a negligible rate of twinning.

[b] Mean calf/cow proportion, and 95% CI back-transformed from logit scale to biological scale (0–1 calves/cow), using the inverse logit link function (Littell et al. 1996:431).

[c] Logit-scale mean and SE provided for CI computation using 1-sided Student's $t$-statistic and 191 df.

[d] Pretreatment year.

[e] Disturbance treatment applied to Beaver Creek elk in 1996–97.

group-average covariate representing treatment effort (5.4 and 8.3 treatments/Beaver Creek cow in 1996 and 1997, respectively, and 0 treatments/cow for all other area-by-year cells) was 95% as effective as the area × year interaction at explaining deviance in our data, but due to small sample size ($n = 6$ area-by-year cells) and low degrees of freedom, it appeared that the covariate term did not adequately substitute for the interaction term ($F_{1,1} = 17.226$, $P = 0.075$). Removal of nonsignificant area and year main effects provided more parsimonious covariate and reduced models, indicating that the covariate term adequately substituted for main-effects and interaction terms ($F_{1,4} = 10.962$, $P = 0.015$). The final model relating calf/cow proportions and treatment effort was

$$\text{logit}(\hat{R}) = 0.6485 - 0.1211 \times T,$$

where $T$ = group-specific average number of treatments/cow for each year, and standard errors were 0.1410 and 0.0319 for intercept and slope, respectively.

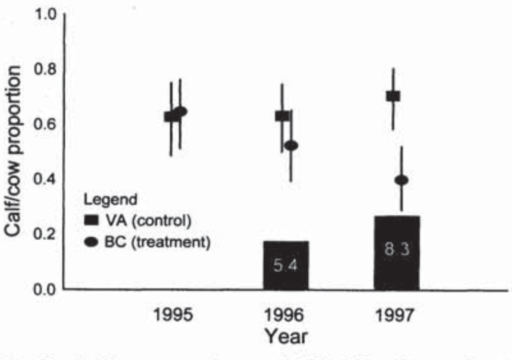


Fig. 2. Calf/cow proportions and 95% CI for Beaver Creek (BC) and Vail (VA) study areas (symbols), and average number of reliable BC disturbance treatments/marked cow (histogram). No treatments were applied in 1995.

Population modeling using a calf/cow proportion of 0.657 (treatment-effort covariate model output for 0 disturbances) indicated an annual growth rate of 7%. This growth rate includes the effect of some unknown level of disturbance of Beaver Creek and Vail elk from existing levels of human activity during calving season, but not treatment disturbance. Adding 10 calving-season disturbances/cow to ambient disturbance levels produced no growth (at 0.363 calves/cow), and >10 disturbances caused population decline. Although our model is approximate, it suggests that 1997 treatment levels were nearly high enough to curtail population growth (1% annual population growth at 8.3 disturbances/cow).

## DISCUSSION

Calf/cow proportions were similar on both study areas in the pretreatment year (1995) and remained relatively stable for Vail throughout our study. However, Beaver Creek calf/cow proportions declined steadily in 1996 and 1997, as would be expected if reproductive success were inversely related to treatment effort (Table 1, Fig. 2). Statistically significant area × year interaction and contrast of average treatment effect suggest the declining trend in Beaver Creek calf-cow proportions was not due to sampling variation, rather, that some factor(s) in the environment caused this decline.

Under our research hypothesis, the probability of a cow successfully raising a calf should be inversely related to the number of times she was disturbed by humans. A strong relationship would be expected assuming that all disturbance events were of equal intensity; all cows were similar in their ability to successfully raise a calf in the presence of disturbance; the true number of disturbances/cow was measured (or at least measured in proportion to their true occurrence); that numbers of cows were uniformly distributed with respect to number of disturbances/cow; and that a measurement of disturbance for a cow could serve as a measure (or index) of disturbance and survival probability for her calf. We believe that violations of these assumptions introduced error variation into the disturbance numbers we documented, rendering these data ineffective as individual-specific covariates. However, we believe that use of mean numbers of treatments/cow/group allowed many of these errors to "average out", providing a reliable index to treatment level. The group-average treatment-effort covariate substituted almost completely for the area × year interaction in the general model, meaning that average annual levels of treatment effort explained variation between area-by-year calf/cow proportions nearly as well as the most important term in the general model. Our results do not prove cause and effect, but they support treatment as a causal mechanism for decreased reproductive success on the Beaver Creek study area in 1996 and 1997.

Use of a control, acquisition of pretreatment data to contrast with treatment data, and implementation of a manipulative treatment effort are elements of our study design that strengthen a cause-and-effect conclusion. However, Hurlbert (1984) and Manly (1992) caution that when design is unreplicated and treatment not randomly allocated, as in our study, other factors may contribute to observed results.

To minimize the potential for inherently different levels of reproductive success for control and treatment elk, we selected adjacent study areas that were similar in ecological and land use characteristics. There was no reason to expect gross differences in elk population parameters between these areas and pretreatment calf/cow proportions were similar for both. We further attempted to minimize confounding effects by estimating calf/cow proportions in July and August to eliminate effects of hunting mortality, and by selecting adult elk for samples to minimize variability in reproductive success due to inclusion of yearlings (Freddy 1987:21,22).

We assumed that treatment activity during calving would not make elk more secretive and less observable during the observation period because all observations were temporally separated, and most were spatially separated, from treatments (Phillips 1998). Violation of this assumption would introduce unknown variance components in calf/cow proportion estimates, potentially affecting tests of main and interaction fixed effects. The contrast used to test for average treatment effect was based on within-year differences between calf/cow proportions, so nonconstant observability across years factored out if observability between Beaver Creek and Vail remained similar within years.

We tested for differences between year-specific cumulative distributions of 2 measures of observability for Beaver Creek and Vail: total observation time/marked cow, and total observation time required to determine a cow had a calf, and compared annual group-total observation time and percentage of marked cows classified for calf status between Beaver Creek and Vail study areas. We found no evidence that observability of marked cows, or interactions with their calves, decreased in response to treatment (Phillips 1998).

Additional evidence suggested that the low Beaver Creek calf/cow proportion in 1997 resulted from increased calf mortality rather than reduced observability. On Beaver Creek, 2, 3, and 10 marked cows, and on Vail, 1, 0, and 0 marked cows were observed nursing yearlings (but not calves) in 1995, 1996, and 1997, respectively (Phillips 1998). Potential hypotheses explaining yearling nursings include: a nonpregnant female may continue to nurse a calf through winter and the following summer (Darling 1936, 1937; Lowe 1966), and a cow that loses her calf may continue to lactate and resume nursing her previous calf (Altmann 1952, 1963).

Prolonged lactation of nonpregnant cows has been documented for mild maritime climates, but we found no evidence documenting this behavior in harsher continental climates (typified by our study areas) where earlier weaning of calves may be expected due to greater physiological stress in winter (Smith 1974). The relatively low yearling nursing rates for marked cows in all area-by-year groups, except Beaver Creek 1997, suggest that most elk on our study areas did not routinely nurse calves through winter and the following summer. Under hypothesis 1, increased yearling nursings observed on Beaver Creek in 1997 would result from lower conception rates in 1996. Hunting pressure, potentially a disruptive factor during the rut, probably was not greater in 1996 than 1995 because hunting mortalities of marked elk did not increase in 1996 (4 marked Beaver Creek cows in both years). We have no reason to believe that conception rates in Beaver Creek were different for 1995 and 1996, and therefore, no reason to expect increased rates of prolonged lactation by nonpregnant cows from 1996 to 1997. There is reason to expect an increase in calf mortality rate because 1997 was the year we applied the strongest disturbance treatment. Observed rates of yearling nursing may, therefore, indicate increased calf mortality on Beaver Creek in 1997, consistent with arguments that we documented declining calf/cow proportions instead of declining elk observability.

By targeting adult cows for treatment, we probably also disturbed their calves, and it is likely that we disturbed more calves than we saw. We occasionally observed lone calves without seeing any nearby adult elk. Some calves exhibited classic "hider" behavior (Lent 1974: 22–27, Geist 1982:237) but others stood and ran. Some that ran appeared neither comfortable nor competent in that activity. Although we did not touch calves or remain near them for more than a few minutes, such encounters probably increased calf energy requirements and risk of detection by predators, because disturbed calves move greater distances than undisturbed calves (Kuck et al. 1985).

We did not evaluate mechanisms for calf mortality, but studies reporting causes of mortality of radiocollared neonatal elk calves implicate predation as the primary proximate factor. Bear (1989) reported that coyotes (*Canis latrans*) were the main predators on calves of all ages. Black bears (*Ursus americanus*) were the main predators of neonatal calves in a 3-year study in northcentral Idaho (Schlegel 1976), and grizzly bears (*Ursus arctos*) and coyotes were the main predators of calves in summer during 1987–90 in Yellowstone National Park (Singer et al. 1997). We commonly saw and heard coyotes on the Beaver Creek study area during the treatment period, once observed a mountain lion (*Felis concolor*), and saw black bears on several occasions. We also found 2 elk calves killed by black bears on the Beaver Creek study area. We speculate that predation may have been the primary proximate factor in reducing calf/cow proportions on Beaver Creek during treatment years. Disturbance may have increased vulnerability to predation either through increased calf movement, nutritional stress, desertion, or a combination of these factors.

## MANAGEMENT IMPLICATIONS

Our study demonstrates the potential magnitude of impact to elk populations from high levels of recreational activity during calving season if people are dispersed across calving areas. However, large numbers of recreationists, traveling randomly and covering long distances, would be necessary to produce levels of disturbance similar to our treatment effort. Most of our treatments occurred away from recreational trails, and off-trail recreation on the Beaver Creek study area during calving season appeared to be minimal in both 1996 and 1997, even though large areas used by elk during calving season were open to the public. It appeared that elk and humans (other than project personnel) were spatially segregated, suggesting that elk avoid areas of human activity.

Our study did not specifically address the effects of trail-based recreational disturbance on elk. Effects of trail density and location, activity type, and trail-user volume on elk populations should be studied. Until such studies are done, however, maintaining low trail densities in traditional calving areas and selective use of calving-season closures seem justified to ensure that adequate areas of calving habitat remain undisturbed.

To ignore potential effects of human-induced disturbance of elk during calving season is to risk declining reproductive success in elk populations. If elk are left inadequate calving-season habitat and can no longer escape disturbance, either from over development of backcountry access corridors or from high levels of off-trail activity, then populations may decline. It is difficult to predict whether a declining population will eventually stabilize or become extirpated; even more difficult to curtail human activities once they become traditional, or to recover wildlife habitats once they are lost. To ensure a future for elk, it is prudent to plan for recreational developments that minimally impact populations.

## ACKNOWLEDGMENTS

The project was funded by Vail Associates, of Vail, Colorado, The Rocky Mountain Elk Foundation, and Colorado Division of Wildlife. R. M. Stephens was our full-time technician. T. Allender, W. W. Andree, K. P. Burnham, A. E. Byrne, P. C. Chapman, J. H. Ellenberger, L. C. Evans, D. J. Freddy, D. D. Hosler, T. L. Johnson, T. Johnston, S. F. Steinert, D. M. Swift, P. Testwuide, R. W. Thompson, G. C. White, and K. R. Wilson provided technical, logistic, and administrative support and assistance. We thank D. H. France, A. McGraw, J. Parrish, A. Vourax, and D. Younkin for safe and productive flights. J. A. Alldredge, J. G. Alldredge, R. D. Bartling, J. Cary, C. Chalcraft, S. T. Conrad, B. Edmiston, E. J. Holborn, C. A. Jewett, B. P. Jones, D. J. McGraw, C. M. Roe, J. D. Sechrist, K. J. Shively, T. M. Stephens, R. Swygman, R. J. West, C. C. Willard, and S. L. Yerian were summer technicians. Volunteers included K. Bilby, K. Blankenhagen, W. Broderick, S. Broderick, B. Caron, W. Chunko, W. Estes, J. R. Morrison, M. L. Petersburg, and M. Weitzel. Adventure Medical Kits, Adventure Outfitters, Cabela's, Coleman, Kowa Optimed, Patagonia, and Sierra Designs donated equipment. R. M. Bartmann, D. J. Freddy, and G. C. White provided constructive reviews of the manuscript. Our study plan, including capture and handling protocols, was approved by Colorado State University Institutional Animal Care and Use Committee under protocol number 94078A.

## LITERATURE CITED

ALTMANN, M. 1952. Social behavior of elk, *Cervus canadensis nelsoni*, in the Jackson Hole area of Wyoming. Behaviour 4:116–143.

———. 1963. Naturalistic studies of maternal care in moose and elk. Pages 233–253 *in* H. L. Rheingold, editor. Maternal behavior in mammals. John Wiley & Sons, New York, New York, USA.

BEAR, G. D. 1989. Seasonal distribution and population characteristics of elk in Estes Valley, Colorado. Colorado Division of Wildlife Special Report 65.

BERWICK, S., K. MCNAMARA, AND D. DANEKE. 1986. The effects of recreation, illegal harvest, and development on elk near Aspen, Colorado. Pages 270–275 *in* R. D. Comer, T. G. Baumann, P. Davis, J. W. Monarch, J. Todd, S. VanGytenbeek, D. Wills, and J. Woodling, editors. Proceedings of the issues and technology in the management of impacted western wildlife symposium. Thorne Ecological Institute, Boulder, Colorado, USA.

BUBENIK, A. B. 1982. Physiology. Pages 125–179 *in* J. W. Thomas and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

BYRNE, G. 1990. 1990 elk fetus report. Colorado Division of Wildlife, September 6, Glenwood Springs, Colorado, USA.

CASSIRER, E. F., D. J. FREDDY, AND E. D. ABLES. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. Wildlife Society Bulletin 20:375–381.

COLE, E. K., M. D. POPE, AND R. G. ANTHONY. 1997. Effects of road management on movement and survival of Roosevelt elk. Journal of Wildlife Management 61:1115–1126.

CZECH, B. 1991. Elk behavior in response to human disturbance at Mount St. Helens National Volcanic Monument. Applied Animal Behaviour Science 29:269–277.

DARLING, F. F. 1936. Red deer in Scotland. Geographical Magazine July:204–216.

———. 1937. A herd of red deer. Oxford University Press, London, United Kingdom.

DE VERGIE, W. J. 1989. Elk movements, dispersal, and winter range carrying capacity in the upper Eagle River Valley, Colorado. Thesis, Colorado State University, Fort Collins, Colorado, USA.

EDGE, W. D., C. L. MARCUM, AND S. L. OLSON. 1985. Effects of logging activities on home-range fidelity of elk. Journal of Wildlife Management 49:741–744.

FITZGERALD, J. P., C. A. MEANEY, AND D. M. ARMSTRONG. 1994. Mammals of Colorado. University Press of Colorado, Niwot, Colorado, USA.

FREDDY, D. J. 1987. The White River elk herd: a perspective, 1960–85. Colorado Division of Wildlife Technical Publication 37.

———. 1989. Effect of elk harvest systems on elk breeding biology. Colorado Division of Wildlife Research Report, July, Glenwood Springs, Colorado, USA.

———. 1993. Estimating survival rates of elk and developing techniques to estimate population size. Colorado Division of Wildlife Research Report, July.

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

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

JOHNSON, T. K. 1986. Impacts of surface coal mining on calving elk. Pages 255–269 *in* R. D. Comer, T. G. Baumann, P. Davis, J. W. Monarch, J. Todd, S. VanGytenbeek, D. Wills, and J. Woodling, editors. Proceedings of the issues and technology in the management of impacted western wildlife symposium. Thorne Ecological Institute, Boulder, Colorado, USA.

KUCK, L., G. L. HOMPLAND, AND E. H. MERRILL. 1985. Elk calf response to simulated mine disturbance in southeast Idaho. Journal of Wildlife Management 49:751–757.

LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

LENT, P. C. 1974. Mother-infant relationships in ungulates. Pages 14–55 *in* V. Geist and F. Walther, editors. Symposium on the behaviour of ungulates and its relation to management. International Union for Conservation of Nature and Natural Resources, New Series Number 24.

LINCOLN, R. J., G. A. BOXSHALL, AND P. F. CLARK. 1998. A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge, United Kingdom.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.

LOWE, V. P. W. 1966. Observations on the dispersal of red deer on Rhum. Pages 211–228 *in* P. A. Jewell and C. Loizos, editors. Play, exploration and territory in mammals. Academic Press, New York, New York, USA.

MANLY, B. F. J. 1992. The design and analysis of research studies. Cambridge University Press, Cambridge, United Kingdom.

MORRISON, J. R. 1992. The effects of ski area expansion on elk, and accuracy of 2 telemetry systems in mountainous terrain. Thesis, Colorado State University, Fort Collins, Colorado, USA.

———, W. J. DE VERGIE, A. W. ALLDREDGE, A. E. BYRNE, AND W. W. ANDREE. 1995. The effects of ski area expansion on elk. Wildlife Society Bulletin 23:481–489.

PHILLIPS, G. E. 1998. Effects of human-induced disturbance during calving season on reproductive success of elk in the upper Eagle River Valley, Colorado. Dissertation, Colorado State University, Fort Collins, Colorado, USA.

———, AND A. W. ALLDREDGE. 1999. Upper Eagle River Valley elk study, 1994–1997 final report. Colorado State University, Fort Collins, Colorado, USA.

SCHLEGEL, M. 1976. Factors affecting calf elk survival in northcentral Idaho—a progress report. Proceedings of the Annual Conference of Western Association of State Game and Fish Commissioners 56:342–355.

SINGER, F. J., A. HARTING, K. K. SYMONDS, AND M. B. COUGHENOUR. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12–25.

SKALSKI, J. R., A. HOFFMANN, AND S. G. SMITH. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. Pages 9–28 *in* J.-D. Lebreton and S. G. Smith, editors. Marked individuals in the study of bird population. Birkhauser Verlag, Basel, Switzerland.

SMITH, M. C. T. 1974. Biology and management of the wapiti (*Cervus elaphus nelsoni*) of Fiordland, New Zealand. New Zealand Deerstalkers Association, Wellington, New Zealand.

TABER, R. D., K. RAEDEKE, AND D. A. MCCAUGHRAN. 1982. Population characteristics. Pages 279–298 *in* J. W. Thomas and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

TOWRY, R. K. JR. 1987. Wildlife habitat requirements. Pages 72–209 *in* R. L. Hoover and D. L. Wills, editors. Managing forested lands for wildlife. Colorado Division of Wildlife, Denver, Colorado, USA.

*Received 17 February 1999.*
*Accepted 5 October 1999.*
*Associate Editor: Krausman.*

esa ECOSPHERE

# Analyzing animal movement patterns using potential functions

HAIGANOUSH K. PREISLER,[1],† ALAN A. AGER,[2] AND MICHAEL J. WISDOM[2]

[1]*Pacific Southwest Research Station, UDSA Forest Service, Albany, California 94710 USA*
[2]*Pacific Northwest Research Station, USDA Forest Service, La Grande, Oregon 97850 USA*

**Citation:** Preisler, H. K., A. A. Ager, and M. J. Wisdom. 2013. Analyzing animal movement patterns using potential functions. Ecosphere 4(3):32. http://dx.doi.org/10.1890/ES12-00286.1

**Abstract.** The advent of GPS technology has made it possible to study human-wildlife interactions on large landscapes and quantify behavioral responses to recreation and other anthropogenic disturbances at increasingly fine scales. Of particular interest are the potential impacts on habitat use patterns, energetics, and cascading impacts on fecundity and other life history traits for key wildlife species that are exposed to human activities. Statistical models quantifying effects of human activity on animal movement on a heterogeneous landscape are essential for understanding these potential impacts. Here we present a statistical framework for analyzing movement data that is based on the concept of a potential surface. The potential surface is motivated by the assumption that animals are moving on a space-time surface with regions or points of attraction or of repulsion. We demonstrate the use of the technique by analyzing movement data from a long-term controlled experiment to evaluate the responses of free ranging Rocky Mountain elk (*Cervus elaphus*) to anthropogenic disturbances that vary in time and space. Our results demonstrated a strong avoidance of elk to all-terrain vehicles detected up to one km from the disturbance. Elk avoidance of mountain bikers was detected up to 500 m, and avoidance of hikers and horseback riders was detected to 200 m.

**Key words:** *Cervus elaphus*; gradient system; movement; potential function; R code; Rocky Mountain elk; Starkey Experimental Forest and Range; stochastic differential equation.

**Received** 11 September 2012; revised 10 January 2013; accepted 11 January 2013; **published** 04 March 2013. Corresponding Editor: R. Parmenter.

† **E-mail:** hpreisler@fs.fed.us

## INTRODUCTION

Fine scale data-logging technology, such as global positioning systems (GPS), has stimulated many new approaches for analyzing and modeling movement patterns of free-ranging animals. Models of animal movements provide a quantitative framework to analyze spatiotemporal effects of anthropogenic disturbances, predators, and conspecifics. Of particular interest are the connections between movements and habitat use, energetics, and life history traits for keystone wildlife species that are increasingly exposed to human activities (Sawyer and Kaufman 2011).

Dynamics of free-ranging animal movements are complex, even without consideration of anthropogenic impacts. A wide range of models have been formulated and applied to animal movement. Most methods involve a Markov process such as uncorrelated or simply correlated random walk where the location of an animal at each step depends on the location in the previous step (Turchin 1998, Okubo and Levin 2001, Morales et al. 2004, Codling and Hill 2005, Smouse et al. 2010). Other processes include the Brownian Bridges models where the continuous movement paths are estimated assuming conditional random walk between successive locations

(Horne et al. 2007, Sawyer et al. 2009). State-space or hidden Markov models assume locations of animals are a function of the unobserved state of the system (location or velocity) at a previous general time (Johnson et al. 2008, Dowd and Joy 2011). Other models have been explored for modeling movement using mechanistic models that incorporate effects of explanatory variables, such as human disturbances and landscape features (Forester et al. 2007, McClintock et al. 2012). The approaches listed above model the stochastic differential equations of motion (SDE), or the velocity of the motion, as a function of explanatory variables. Our present work is based on the idea of potential functions that are used to motivate specific functional forms for the SDEs. This framework may be used in conjunction with other methods, such as state-space models, by presenting a mechanism for arriving at an equation for the expected step sizes of movement. Potential functions are motivated by methods from physics where the motion of a physical particle is modeled as being affected by its location on a potential surface and by its relative distances from other particles, regions, or barriers (Hirsch et al. 2004, Taylor 2004). An attractive feature of the potential function approach is the ease with which multiple factors affecting motion (e.g., foraging behavior, topography, human disturbance) can be incorporated into a mechanistic model and then parameterized via a regression routine. The estimation methods assume a Markovian/diffusion process which is then generalized to more realistic stochastic processes by introducing, for example, serial correlations in the error term. Our goals in the current paper are to (1) provide ecologists an overview of the potential function modeling approach, (2) demonstrate its practical implementation with readily-available regression routines (e.g., open access R programing software), (3) extend the techniques presented in our previous work (Brillinger et al. 2004, Brillinger 2010, Brillinger et al. 2011) to accommodate serial correlations, and (4) use the technique to study movements from a long-term controlled experiment for evaluating responses of free ranging Rocky Mountain elk (*Cervus elaphus*) to multiple anthropogenic disturbances, including all-terrain vehicle (ATV) riding, hiking, mountain biking, and horseback riding (Wisdom et al. 2004, Naylor et al. 2009).

## THE POTENTIAL FUNCTION APPROACH

Our approach is motivated by the assumption that particles are moving on a space-time surface containing regions or points of attraction and repulsion. This potential field is similar to a topographic surface under the influence of gravity where objects are attracted to low points or hollows and repelled from high points or hills. A simple example with a point of attraction at (0, 0) is provided by the potential $H(x, y) = (x^2 + y^2)$ where a particle at $(x, y)$ moves directly to (0, 0) on the surface (Fig. 1a). Next, if some random noise or perturbation is added to the potential, for example by shaking the surface, then the particle will still drift toward the point with lowest potential but with the path not straight but wiggling with an amplitude dependent on the level of the noise (see Fig. 1b, c). A second elementary example is provided by a process where a particle moves on a flat potential surface by means of statistically independent random steps, i.e., a random walk process with no drift.

An analytic foundation for this modeling framework is provided by a formal relationship between the potential surface and the velocity of the particle at a given location $(x, y)$ and time $t$. In Newtonian physics, the velocity of a particle at location $(x, y)$ is given by the negative of the gradient of the potential function at $(x, y)$. The gradient of a surface is defined by the slopes in the $x$- and $y$-directions, that is grad $H = (\partial H/\partial x, \partial H/\partial y)$. For example, for the potential surface in Fig. 1 with a point of attraction at (0, 0) the potential function $H(x, y) = (x^2 + y^2)$, and the velocity of the particle, as given by the speeds in the $x$- and $y$-directions are:

$$\partial x/\partial t = -\frac{\partial H(x,y)}{\partial x} = -2x;$$
$$\partial y/\partial t = -\frac{\partial H(x,y)}{\partial y} = -2y. \qquad (1)$$

The minus signs in Eq. 1 are traditional. Eq. 1 provides one example of a gradient system (see Hirsch and Smale 1974:199–204). Other examples of parametric potential functions and the corresponding surfaces are provided in Fig. 2. The potential can be any differentiable function, including non-parametric smooth functions that

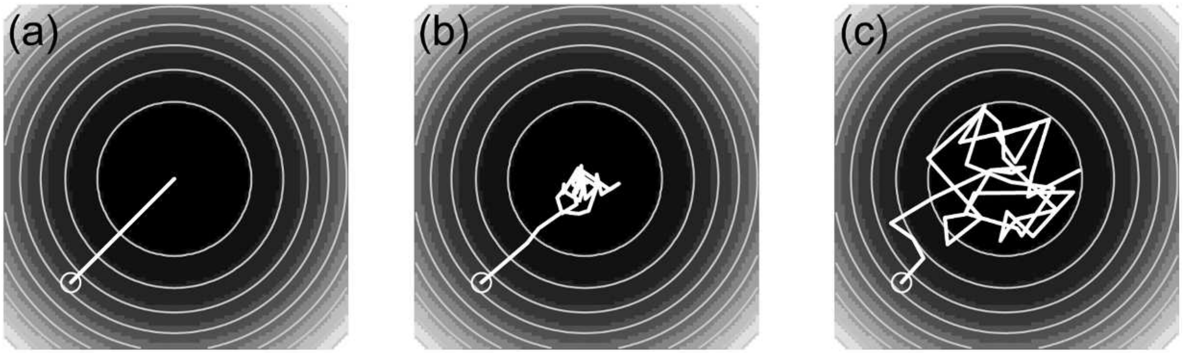
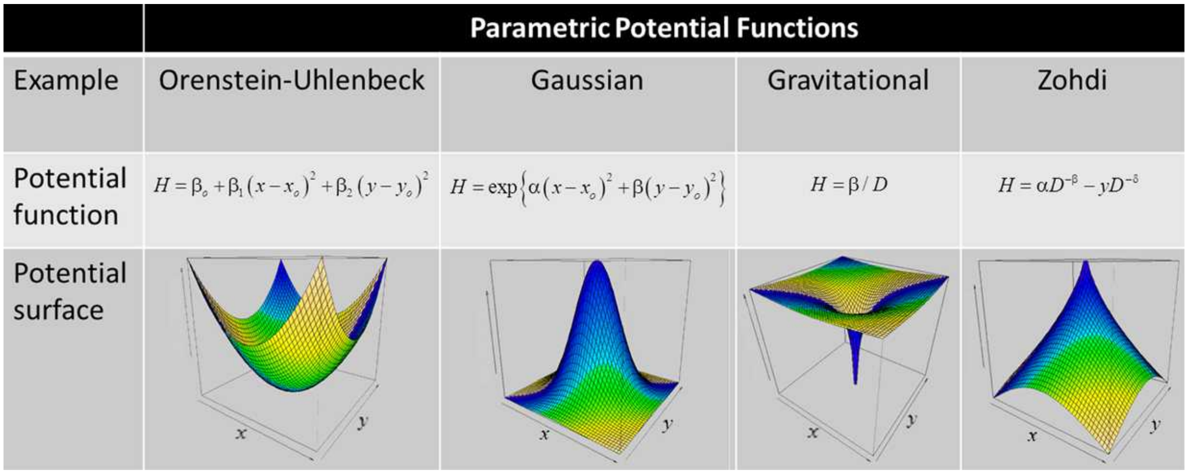


Fig. 1. Tracks of a particle moving in a potential with a point of attraction (lowest point) at the center of the surface. Tracks in the three panels were generated by adding various amounts of random noise to the same potential. (a) No noise; (b) some random noise (small variance); (c) larger amount of random noise (larger variance). In each panel the starting point is indicated by the open circle.

are estimated from the data.

Eq. 1 is important because while the potential itself may not be directly observable, the step sizes in the *x*- and *y*-directions, and thereby the approximate velocity of the animal, is observable. Consequently, if we assume the existence of a potential affecting the movements of an animal (up to random fluctuations) then it may be estimated, given observations on consecutive locations. This approach assumes that the potential function is differentiable. Complicated potential surfaces may be modeled and assessed using this framework. For example, there may be multiple regions of attraction where animals prefer to forage, versus regions of repulsion where human disturbances are frequent. A potential surface that integrates multiple factors affecting movement is developed by adding separate surfaces describing each of the attractions and repulsions together (Fig. 3 and Eq. 6). Potential functions may also be used to model animal movement as they are attracted to, or repulsed from, a moving entity (e.g., predator, hunter, vehicle). Brillinger et al. (2011) considered



| | Parametric Potential Functions | | | |
|---|---|---|---|---|
| Example | Orenstein-Uhlenbeck | Gaussian | Gravitational | Zohdi |
| Potential function | $H=\beta_o+\beta_1(x-x_o)^2+\beta_2(y-y_o)^2$ | $H=\exp\left\{\alpha(x-x_o)^2+\beta(y-y_o)^2\right\}$ | $H=\beta/D$ | $H=\alpha D^{-\beta}-yD^{-\delta}$ |
| Potential surface | | | | |

Fig. 2. Four examples of parametric potential functions, with one point of attraction or repulsion at ($x_0$, $y_0$), and plots of the corresponding surfaces for specific values of the parameters (α, β, δ). $D=\sqrt{(x-x_0)^2+(y-y_0)^2}$. An example of the use of the Zohdi function is found in Zohdi (2003, 2009) and Brillinger et al. (2011).

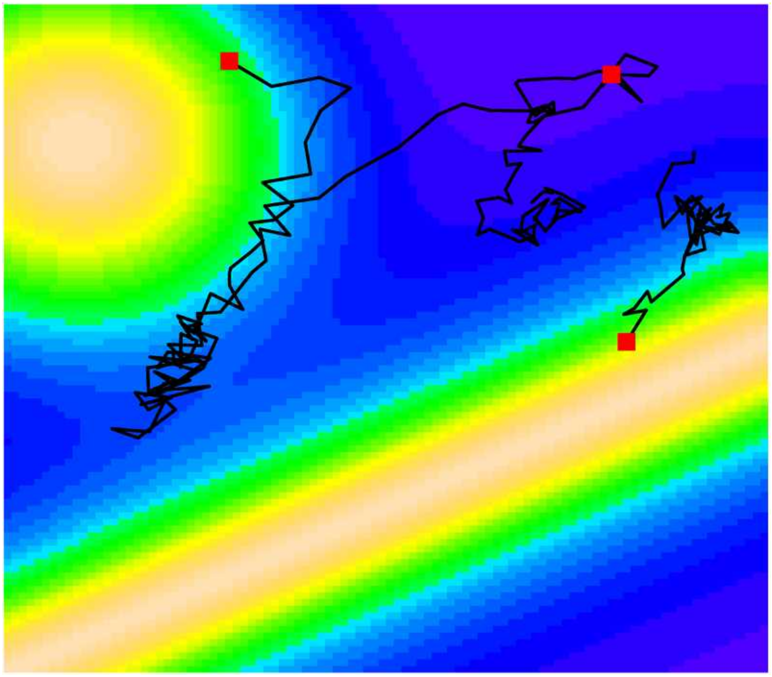


Fig. 3. An example of a potential surface with two repulsion regions and simulated movement tracks within this surface. Red squares are the starting points of the tracks. The highest background values (pink then orange) indicate ridges (high potential), followed by yellow then green and finally blue then purple indicating valleys (low potential regions).

the case of modeling attraction between a given animal and conspecifics. When the point of attraction or repulsion is moving (e.g., person or conspecific) then the potential surface that defines the regions of attraction/repulsion are changing as well.

## STOCHASTIC DIFFERENTIAL EQUATIONS

The potential function allows one to model the deterministic component (expected velocity) of movement in terms of biologically meaningful parameters. The stochastic component of the movement is modeled by adding a random term to the differential equations defining the velocity of the particle at time *t*. Specifically, the stochastic differential equation (SDE) is:

$$dr(t) = \mu(r,t)dt + \Sigma(r,t)\mathrm{d}\mathbf{V}(t) \qquad (2)$$

where $d\boldsymbol{r}(t) = \{\partial x, \partial y\}$; $\boldsymbol{\mu}(t)$ is minus the gradient of the potential surface of the expected drift or movement direction of the particle in the next increment of time; $\boldsymbol{\Sigma}(\boldsymbol{r}, t)$ is a real valued matrix specifying the correlation between the steps in the *x* and *y*-directions; and $d\boldsymbol{V}(t)$ is a continuous-time stochastic process with expected value of zero. The SDE formulation with Brownian driver, i.e., $d\boldsymbol{V}(t) = d\boldsymbol{B}(t)$ leads to a continuous time random walk under assumptions. Eq. 2 is the basis for the discrete time formulation used in this paper for estimation purposes. The Brownian driver can take on many forms (Table 1), including auto-correlated time series.

## STATIONARY DISTRIBUTIONS AND POTENTIAL FUNCTIONS

Animal movement studies are sometimes concerned with the estimation of the home range, i.e., spatial extent of an animal's movement, or the stationary distribution of animal locations, sometimes referred to as the utilization distribution (Millspaugh et al. 2006). In special cases, in particular when the potential function *H* does not depend on time *t* and $\boldsymbol{\Sigma} = \sigma^2\boldsymbol{I}$, the stationary distributions may be shown to be

Table 1. Examples of stochastic processes.

| Example | $\boldsymbol{\mu}(x(t), y(t))$ | $d\mathbf{V}(t) = \{dV_x, dV_y\}$ |
|---|---|---|
| Random walk | **0** | $V_x$ , $V_y$ independent Brownian processes |
| Biased random walk | Constant (not zero) vector **A** | $V_x$, $V_y$ independent Brownian processes |
| O-U process with point of attraction at ***a*** | $A\|\|r(t) - a\|\|$ | $V_x$, $V_y$ independent Brownian processes |
| Correlated random walk (consecutive moves are correlated)† | **0** | $V_x$, $V_y$ positively correlated processes |
| Levy process (Brownian process with jumps)‡ | Any parametric or non-parametric smooth function | $V_x$, $V_y$ Brownian plus marked Poisson process |

† Note that in both O-U process and correlated random walk (CRW) animals are moving with persistence in a given direction. That is, consecutive moves are correlated. However, in an O-U process the persistence is towards a point of attraction/repulsion.

‡ Jumps occur at random time points as characterized by a Poisson process.

$$\pi(r) = k\exp\{-2H(r)/\sigma^2\}. \tag{3}$$

The constant $k$ is to make $\pi(\boldsymbol{r})$ integrate to 1. The potential function in this case is the logarithm of the stationary distribution (up to a constant). For example, if the potential function leads to the Ornstein-Uhlenbeck equations then the stationary distribution is the two-dimensional Gaussian density function with the mode of the distribution located at the point of attraction of the Ornstein-Uhlenbeck process.

## ESTIMATION METHODS

There is substantial literature devoted to the topic of inference from stochastic differential equations (Sorensen 1997, Prakasa Rao 1999). Given a set of discrete observations on animal locations, the potential function and its gradients in continuous time (velocity) are used as a framework to build the discrete difference equation used in a regression model. Estimation is set in terms of the discrete approximation of the velocity in Eq. 2 as given by

$$\frac{[r(t_{i+1}) - r(t_i)]}{[t_{i+1} - t_i]} \approx \mu\Big(r(t_i)\Big) + \boldsymbol{\Sigma}\mathbf{Z}_{i+1}/\sqrt{t_{i+1} - t_i} \tag{4}$$

with $\mathbf{Z}_i$ a standard bivariate random vector with variance-covariance matrix given by $\boldsymbol{\Sigma}$. The term $\sqrt{t_{i+1} - t_i}$ is needed because the variance-covariance matrix of the real valued continuous process, $d\mathbf{V}$, is $\boldsymbol{\Sigma}dt$.

Given observed locations ($x_i$, $y_i$) for what may be unequally spaced times $t_1 < t_2 < \ldots < t_i < \ldots < t_m$, parameters, $\boldsymbol{\Theta}$, of a differentiable function, $H(x, y|\Theta)$, may be estimated by the regression model

$$\begin{aligned} \frac{\Delta x_i}{\Delta t_i} &= H_x(x_i, y_i|\Theta) + \varepsilon_i \\ \frac{\Delta y_i}{\Delta t_i} &= H_y(x_i, y_i|\Theta) + \gamma_i \end{aligned} \tag{5}$$

where; $\Delta x_i = (x_{i+1} - x_i)$; $\Delta y_i = (y_{i+1} - y_i)$; $\Delta t_i = (t_{i+1} - t_i)$; $H_x$, $H_y$ are the partial derivatives of $H(x, y|\Theta)$ with respect to $x$ and $y$ and where $\varepsilon$ and $\gamma$ are random noises. In the case where the error terms $\varepsilon_i$ and $\gamma_i$ are independent, ordinary least squares regression routines may be used to estimate the parameters. The error terms may not be independent if the step sizes, $\Delta x_i$, $\Delta y_i$, are correlated, $\mathrm{cov}(\varepsilon_i, \gamma_i) \neq 0$, or if the sample includes observations on more than one subject/animal resulting in within subject correlated errors. Observation error in our study was assumed to be negligible relative to the stochastic error, although this assumption needs to be carefully examined on a study by study basis (see *The Data* section). Finally, serial correlation may necessitate the use of an autoregressive model.

The gradient of the potential surface, when displayed as a vector field of arrows, provides an estimate of the average velocity of an animal at a point. Sometimes the average velocity of animals is of interest in itself. One may use a nonparametric smooth function of location to estimate the discrete velocities without relating them to a specific parametric potential surface. Estimation in this case can be carried out using the two-dimensional tensor spline functions (Wood 2006) or a two-dimensional locally weighted regression routine (Hastie and Tibshirani 1990).

## An Example on Elk Movement

### The experiment and the data

Here we demonstrate potential functions that describe the strength of repulsion between elk and four different human activities (riding an All-terrain vehicle (ATV), biking, hiking, and equestrian riding), using data from a controlled landscape experiment at the Starkey Experimental Forest and Range in eastern Oregon (Wisdom et al. 2004, Preisler et al. 2006, Naylor et al. 2009). In this experiment, 25 elk were followed (using Loran-C technology and GPS collars) during summer for four years (2002–2005). The purpose of the study was to understand responses of elk to four distinct recreational disturbances (henceforth treatments). During 2002–2004, each treatment was implemented for five days followed by a nine-day control period where all human activities were excluded. For each 5-d treatment period, two recreationists, moving independently, implemented one type of disturbance (ATV riding, mountain biking, hiking, or horseback riding). Each type of disturbance was implemented on 32 km of trails twice daily, once in the morning (approximately 08:00 to 12:00 local time) and once in the afternoon (approximately 1300 to 1700 local time) (Wisdom et al. 2004, Naylor et al. 2009). Each pair of recreationists was equipped with a GPS unit that tracked their locations on a continual basis (Wisdom et al. 2004). Data used in our analysis were limited to cases with elapsed time between consecutive observations less than 15 min. The median time between observations was 5 min with 85% less than 5.5 min. The mean error associated with the telemetry locations was <20 m for the GPS data (92% of the data used) and <50 m for the Loran-C data. Consequently, the assumption of negligible measurement error in the model was not unreasonable. For each elk observation, the distance to the disturbance associated with the step size between time $t$ and $t+\Delta$ was calculated by using the nearest GPS location of the disturbance within 5 min of the observed elk location at time $t$. In 2005, treatments were excluded from the study area and elk location data were obtained to analyze movement patterns in the absence of human activities.

### Estimation

We assumed that elk are moving on a hypothetical potential surface as they react to two outside forces: (1) attraction towards unknown foraging and resting areas, and (2) reaction to a human disturbance. The potential function for this model is given by

$$H[x(t),y(t)] = H_1[x(t),y(t)] + H_2[d(x(t),y(t))] \quad (6)$$

where $H_1[x(t), y(t)]$ is assumed to be a nonparametric smooth function of the elk location $\{x(t), y(t)\}$ describing the regions of attraction for elk during different periods of the day (movement towards foraging or resting grounds). $H_2[x(t), y(t)]$ is assumed to be a parametric function of the distance, $d(x(t), y(t))$, between the animal and the disturbance at time $t$. Specifically, we used a fourth-degree polynomial

$$\begin{aligned} H_2\Big(d(x(t),y(t)|\Theta\Big) &= \beta_o + \beta_1 d + \beta_2 d^2 + \beta_3 d^3 + \beta_4 d^4 \\ &\qquad \text{for } d < \infty \\ H_2(\infty|\Theta) = \alpha &\qquad \text{for } d = \infty \end{aligned} \quad (7)$$

where

$$d = \sqrt{(x - z_x)^2 + (y - z_y)^2}$$

is the distance between the location $(x_, y)$ of the elk and the location $(z_{x\,,}\, z_y)$ of the disturbance at a given time $t$. The distance between an elk and a human disturbance is set to ∞ when there is no human activity in the region. The degree of the polynomial was arbitrary, and the parameters, $\beta_0, \ldots, \beta_4$, individually have no physical interpretation. We simply required an equation for the potential surface that could accommodate most non-linear shapes. The potential surface as a whole, rather than the individual parameters, is what provides the interpretation. Note that, given a distance between an elk and a disturbance, the potential function term $H_2[x(t), y(t)]$ in Eq. 7 is assumed to be independent of time of day. On the other hand we assumed that $H_1[x(t), y(t)]$ is independent of time only within each of four day-time periods discussed below. These time periods corresponded to two distinct daily periods of maximum time spent foraging (04:00–

07:00 h and17:00–20:00 h) and two distinct periods of maximum time spent resting (08:00–16:00 h and 21:00–03:00 h) (Ager et al. 2003). These distinct time periods were based on results of activity monitoring by Naylor et al. (2009) for elk in the northeast pasture. Treatments were implemented only during one of the four periods (08:00–16:00 h).

The regression equations used for estimation purposes were motivated by Eqs. 6 and 7. They are the discrete approximations (difference equations) of their partial derivatives with respect to $x$ and $y$. For $d < \infty$, i.e., for days with human disturbance, the difference equations are given by

$$\begin{aligned}\frac{\Delta x_i}{\Delta t_i} &= -H_{1x}(x,y) - (\beta_1 + 2\beta_2 d_i + 3\beta_3 d_i^2 + 4\beta_4 d_i^3) \\ &\quad \times (x_i - z_{x,i})/d_i + \varepsilon_i \\ \frac{\Delta y_i}{\Delta t_i} &= -H_{1y}(x,y) - (\beta_1 + 2\beta_2 d_i + 3\beta_3 d_i^2 + 4\beta_4 d_i^3) \\ &\quad \times (y_i - z_{y,i})/d_i + \gamma_i \qquad (8)\end{aligned}$$

and for control days ($d = \infty$) are given by

$$\begin{aligned}\frac{\Delta x_i}{\Delta t_i} &= -H_{1x}(x,y) + \varepsilon_i \\ \frac{\Delta y_i}{\Delta t_i} &= -H_{1y}(x,y) + \gamma_i\end{aligned} \qquad (9)$$

$H_{1x}$, $H_{1y}$ are nonparametric smooth functions such as a locally weighted regression function or a two dimensional spline. The estimation process involved, first, using the control data collected in 2005 and the difference equations in Eq. 9 to obtain separate estimates of the diurnal movement patterns of elk for each of the four time periods described above. Next, Eq. 8 is used, with $H_{1x}$, $H_{1y}$ replaced by their estimated values, $\hat{H}_{1x}, \hat{H}_{1y}$, from the first stage, to estimate the parameters $\{\beta_1, \ldots, \beta_4\}$. The R-code for estimating the regression parameters $\{\beta_1, \ldots, \beta_4\}$, is given in the Supplement. Parameter estimates were then used in Eq. 7 to develop an estimate of the potential surface up to the constant parameter, $\beta_0$. Standard errors for the potential surface were evaluated from the estimated SEs of the individual parameters, $\{\beta_1, \ldots, \beta_4\}$, and those for $\hat{H}_{1x}, \hat{H}_{1y}$, using the delta-method.

## RESULTS

### *Stochastic terms*

Correlations between the step sizes in the $x$- and $y$-directions were negligible for both control days and treatment days with $\rho(\varepsilon_i, \gamma_i)$ equal to 0.035 for control and −0.003 for treatment. Therefore, the matrix $\boldsymbol{\Sigma}$ in Eq. 2 was set to the diagonal matrix $\sigma^2\mathbf{I}$. The serial correlations $\rho(\varepsilon_i, \varepsilon_{i-1})$, $\rho(\gamma_i, \gamma_{i-1})$ ranged between 0.21 and 0.36 for the four time periods during control days and between 0.32 and 0.52 for the four disturbances during treatment days. The larger values tended to be for serial correlations in the $y$-direction. The estimated serial correlations are an indication that the underlying continuous process is not Markovian because there is some evidence that an elk's location at time $t$ depends not only on its location at $t - 1$ (Markov process) but also on its location two periods ago.

### *Diurnal movement patterns during control days*

Plots of the estimated gradient of the potential function (movement arrows) evaluated using the control data (Fig. 4) demonstrate significant directional movement patterns. Arrows in Fig. 4 were plotted as a random sample of all locations where elk were detected during control days. Only arrows that were significantly greater than zero (arrow length >2 SE) were plotted. The estimated movement arrows revealed daily cycles of spatial movement patterns from resting to foraging areas and back. For example, during the early morning hours (04:00–07:00), elk appeared to be moving to preferred foraging areas, as depicted by movements to the northeast and away from the southern and eastern areas. Significant movement patterns were not evident during the night (21:00–03:00) nor daytime (08:00–16:00) periods when elk typically rest and ruminate. At dusk (16:00–20:00), elk again appeared to move from foraging areas to rest areas along the border fence in the west and south.

### *Movements with respect to disturbance*

As noted above, treatments were introduced into the experimental region only during the day time hours 08:00–16:00. Undisturbed elk exhibited seemingly random movement and regions of attraction or repulsion were not apparent, con-

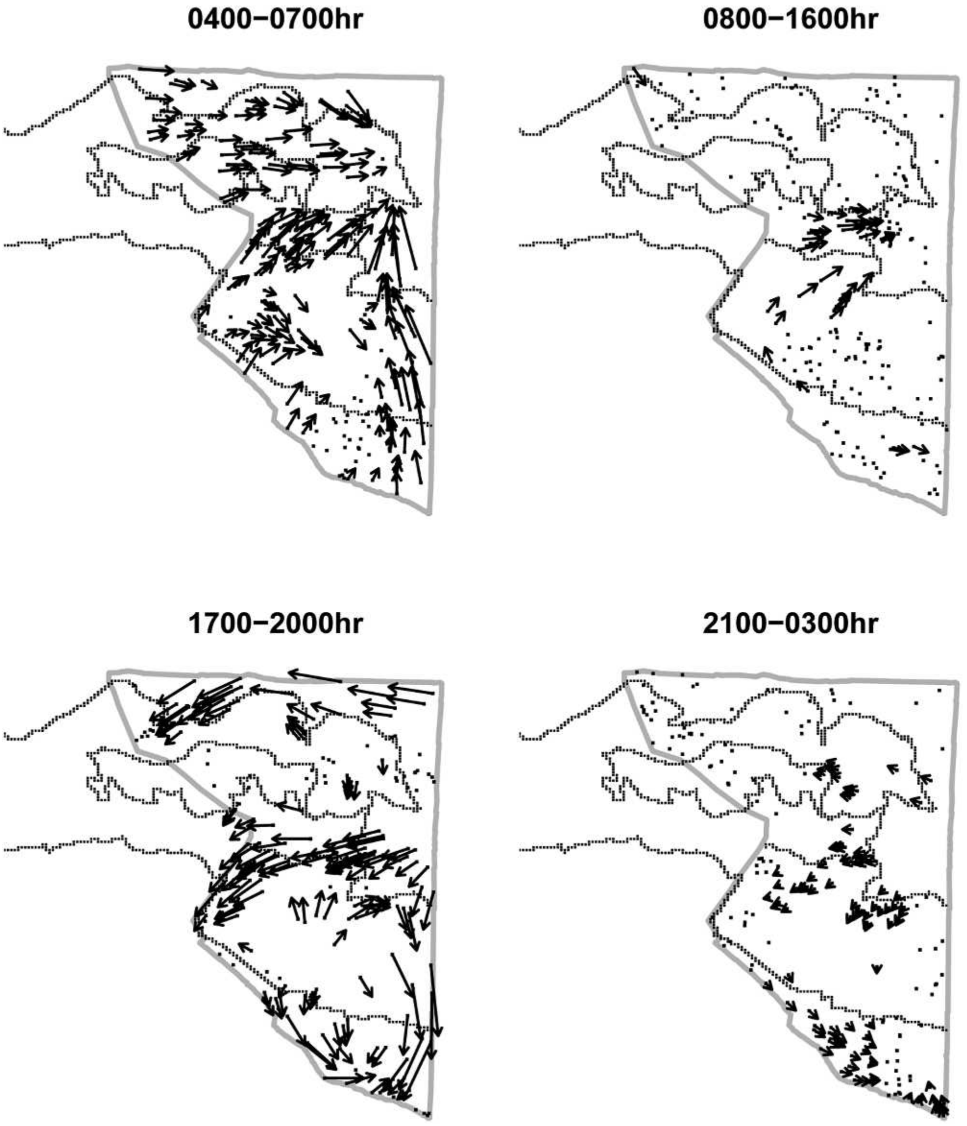


Fig. 4. Estimated (smoothed) movement vectors for four periods of the day in the absence of human disturbances. Speed of movement is proportional to the length of the movement arrows. The two time intervals on the left are associated with periods of maximum crepuscular movements to and from foraging areas. The two time intervals on the right are associated with periods of rest and rumination.

trary to the pattern seen during the early morning (04:00–07:00) or evening hours (Fig. 4). Accordingly, it seemed reasonable to use a model with the non-parametric term $H_1[x(t), y(t)]$ in Eq. 6 set to a constant, and consequently, its partial derivatives, $H_{1x}$, $H_{1y}$, in Eq. 8 are zero. The exact model fitted to the data on treatment days is shown in the R-code given in the Supplement. The estimated parameter values for $\{\beta_1, ..., \beta_4\}$ were next used in Eq. 7 to produce Fig. 5 depicting the height of the potential surface as a function of the distance between elk and the four disturbances. The estimated curves in Fig. 5 seem to indicate that elk within a few hundred meters of any of the four disturbances were, on average, moving away (repelled) from the disturbance. The repulsion appeared to be strongest in terms of both magnitude and

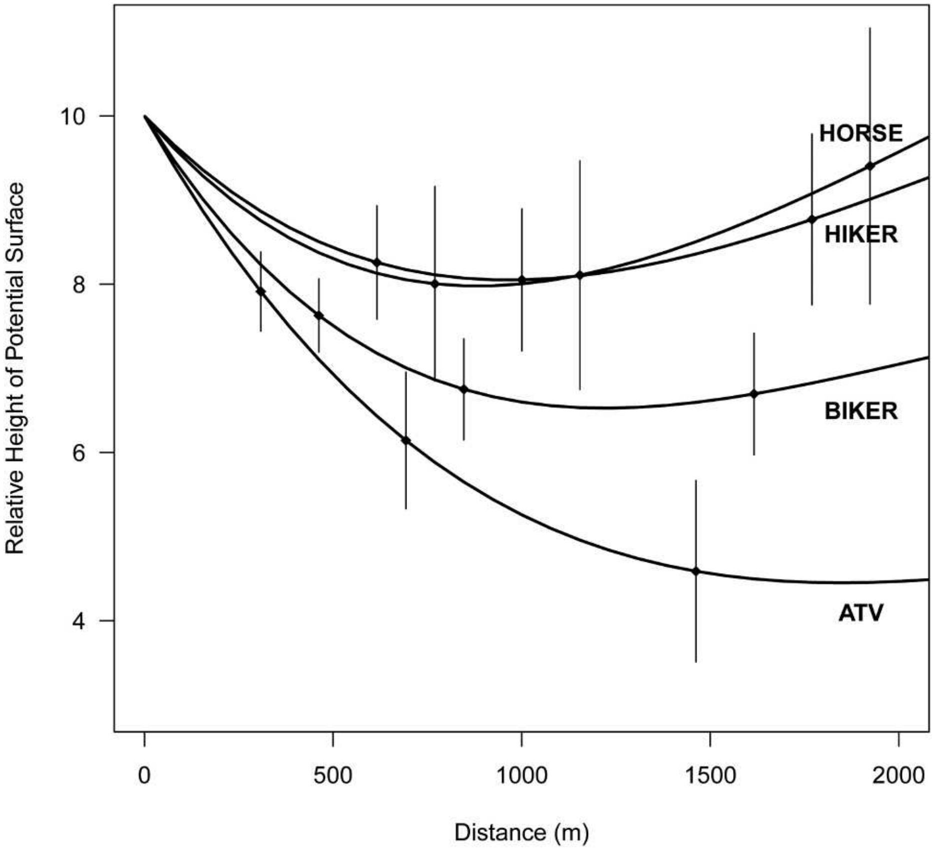


Fig. 5. Estimated height of the potential surfaces as a function of the distance to each of the four disturbances, ATV riding (ATV), bike riding (BIK), hiking (HIK) and horseback riding (HRS). Vertical lines are ±2 SE bounds.

distance for the ATV treatment, with some repulsion observed up to 1.0 km. Repulsion from bikers was detected up to about 500 m, after which the function is not significantly different from a horizontal line. The smallest estimated repulsion effect was observed between elk and hikers and elk and horseback riders, with significant repulsion observed only up to about 200 m.

Potential surfaces were next evaluated for treatments at selected locations along the treatment routes. This type of analysis can be used to predict the potential impact of human activities at specific locations. A map of the study area and the treatment routes is shown in Fig. 6. Overlaid on the maps are the estimated potential functions assuming the disturbance is at a particular location on the route. When an ATV was at the indicated location, the estimated potential function decreased from a value of 10.0 to 4.0. These values are significantly higher than the minimum level (grey, flat area) was; according to our potential function model, elk appear to be feeling no force of attraction or repulsion. When the disturbance was a hiker or a horseback rider, the repulsion appeared much less and the potential surface is mostly flat (Figs. 4 and 5) with no regions of attraction or repulsion, i.e., similar to days when no human disturbance was allowed in the study area.

## DISCUSSION

We have presented a framework for studying the movement of animals (in particular attraction and repulsion) that couples a conceptual model of behavior with statistical methods and estimation procedures. In this framework, motion of an animal is assumed to be affected by its location relative to surrounding biophysical factors, in-

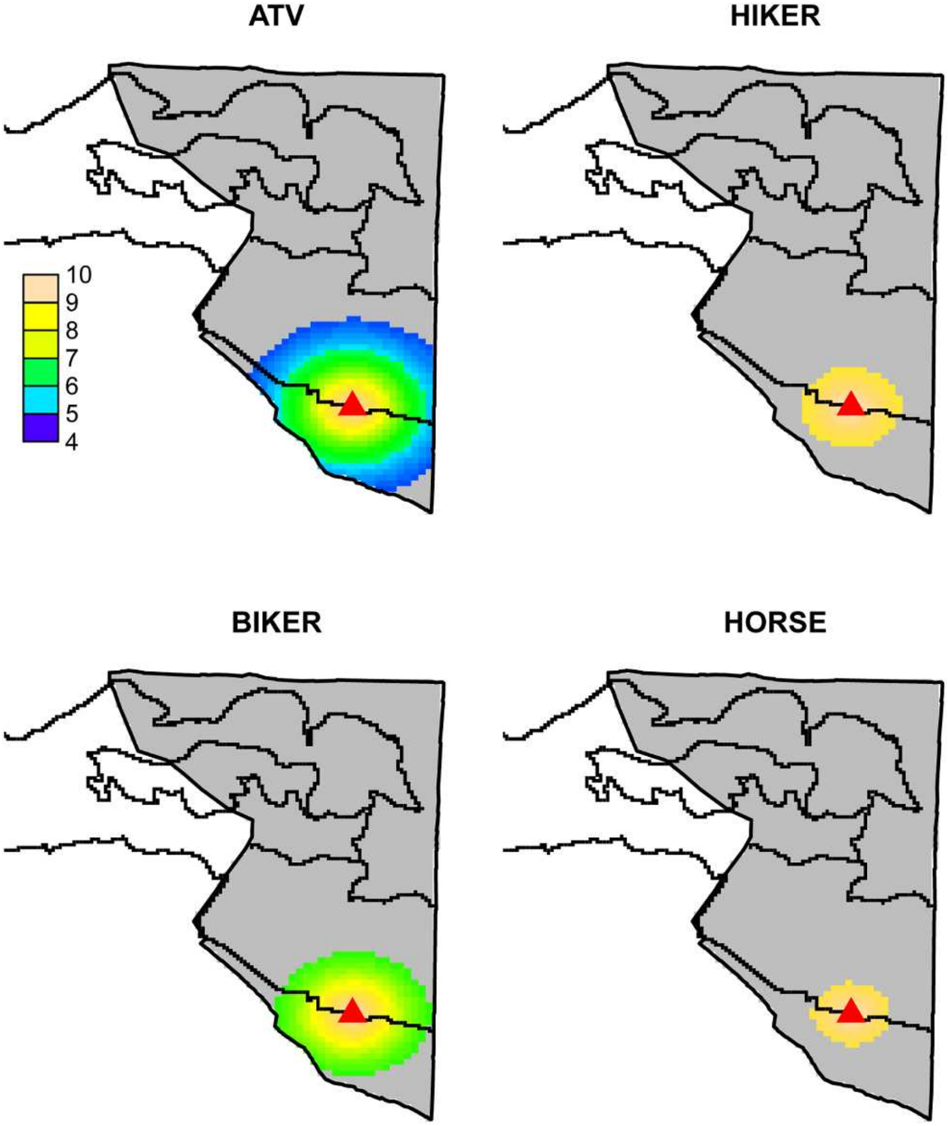


Fig. 6. Estimated potential surfaces when the human disturbance was located at a particular point (red triangle) on the route within the study area. The grey areas indicate regions where the potential surface is approximately flat.

cluding conspecifics, predators, humans, or sources of food. We also provided example SDEs and accompanying R scripts (Supplemental Material) that can be modified to implement the framework as part of other movement studies concerned with detecting and quantifying landscape patterns of movements and their timing with respect to different behavioral states (e.g., foraging, migration, avoidance).

Our methods were initially developed to explain animal movement in terms of human and ecological disturbances, and the example we presented concerned quantifying the strength of repulsion of elk from four different human disturbances. This is in contrast to a number of other recent studies that characterized temporal changes in movement patterns associated with different behavioral states (Forester et al. 2007, Dowd and Joy 2011). Potential surfaces can be applied to studies used to model animal interactions with patch boundaries and core area by including locational variables like distance to patch edge or centroid. State changes can be then modeled as a bivariate function that includes both distance metrics and time as the explanatory variables. Time steps can be hour of day or season in year (or both) depending on the temporal scale of the data and the movement behavior in question. An example of fitting such a potential function is given in Preisler et al. (2004) where the effect of habitat features, such as refugia from roads, food patches, streams and canyons on movement were studied by time of day and season. In movement studies on marine mammals, for example, where sea surface temperature can be an important explanatory variable (e.g., Jonsen et al. 2003), a univariate function of the changing temperature, $H(T(t))$, can be used as a potential function, with points of attraction (valleys in the potential surface) being regions with higher temperatures. One may use a polynomial function with temperature, $T$, as an explanatory variable. Note that in this example temperature is a function of time, thus it is possible to represent time in the model (i.e., a potential function varying in time) without having to include it explicitly in the equation. In Brillinger et al. (2008) the authors study the movement of Hawaiian monk seals (*Monachus schauinslandi*) using a time varying potential function with two points of attraction to describe the migration of the seal as it moves between a foraging region in the sea and resting areas on land.

The complexity of the stochastic component of a movement model is determined by the data at hand. In our elk example, serial correlation was detected beyond that of a Markov process and an autoregressive model was employed. A Lévy process (diffusion process with jumps) can be useful for studying reactions of animals to outside stimuli (e.g., cars, or other animals). However, it was not used in the present study because locations and times of the disturbances were known. More complicated error structures, such as when measurement errors are too large to ignore, may necessitate the use of a linear or non-linear state-space model. However, one may still base the form of the difference equation on a function derived from a hypothesized potential function.

Brownian-bridges are another technique that has been used to analyze movements. In particular, when the animal's location is known at a sequence of locations, one can estimate positions in between using Brownian bridges (Horne et al. 2007), and then estimate the utilization distribution as a function of location-specific habitat variables. Eq. 3 of our model shows the relationship between the utilization distribution and a potential function independent of time. Thus Brownian-bridges models may be linked to a particular form of a potential function.

Elapsed time between consecutive observations was small (~5 min) in the present study. However, the utility of potential function models is not limited to high frequency data; the approach can be applied to whatever spatiotemporal scale is of interest. In the present study short-term responses to human disturbances were of interest, whereas in the Hawaiian monk seal example (Brillinger et al. 2008) the data were daily observations. In an example on the transition of Sierra Nevada yellow-legged frogs (*Rana sierrae*) to breeding, feeding and overwintering locations the time steps were months (Matthews and Preisler 2010). One can also interpolate between consecutively observed locations to increase the temporal resolution of location data using Brownian bridges (Horne et al. 2007) or simple linear or spline interpolation (Brillinger et al. 2011).

Our work is motivated in part by the fact that models for analyzing movement trajectories can provide ecologists with valuable insights into the behavioral mechanisms that control movement parameters. The study of movement is fundamental to understanding individual and population responses to emergent anthropogenic and natural disturbance. Recent studies have followed three lines of investigation (Schick et al. 2008), namely: (1) modeling for realistic movement, (2) animal-environment interactions, and (3) inferring movement when the data are incomplete. We offer a stochastic model that can be applied to all three lines of investigation. SDEs can be used to statistically model the ecology of animal movement and associated behavioral states in continuous time, as seen in our maps of movement vectors. The approach also encapsulates basic mechanisms of movement, namely, internal state, navigation, and external influences (Nathan et al. 2008 ) as time-space explanatories. Moreover, the potential function surfaces can have underlying biological meaning that can lead to insights about the factors that control movement patterns, such as energetic considerations and habitat quality. For example, conditions of high habitat quality and low energetic cost to an animal would be indicated by a potential surface and movement vector of animal use that is concentrated in small areas, centered on the best habitats. By contrast, conditions of low habitat quality and high energetic cost would be indicated by a potential surface and movement vectors where animal use is substantially less concentrated and more widely distributed across a larger area. Similarly, environmental conditions that cause animal repulsion (e.g., roads, human activities) can be accurately mapped and quantified, as shown by the patterns of animal avoidance in the present study (Figs. 4 and 5).

Deriving ecological inferences from animal movement data has been difficult, in part because it is a multistate, stochastic process (McClintock et al. 2012). Elk, like many ungulates, exhibit pronounced switching behavior between fine- and broad-scale movements, corresponding to crepuscular transitions in habitat preferences (Ager et al. 2003). Different landscape features and associated scales of perception may be responsible for decision making and navigation during these phases. State-space models are one approach to handle multiphasic movements where both time-dependent and time-independent factors must be considered (Forester et al. 2007). More recently, nested, discrete, multi-state movement models have been proposed as a simplified framework to facilitate the analyses of the growing body of movement data (McClintock et al. 2012). We submit that SDEs derived from potential functions enhance the above approaches by connecting a physical model to the discrete difference equations that may then be readily estimated with existing statistical packages.

## ACKNOWLEDGMENTS

We thank Professor David Brillinger for his comments and help during the preparation of this manuscript. We thank Jennifer Hafer and Bridgett Naylor for data preparation and management. We are also thankful to two referees and the associate editor for their valuable comments on the manuscript. Special thanks go to Michelle Day for her help with Fig. 2 and other copy editing issues. This research was supported with funding from the Oregon Department of Parks and Recreation and the USDA Forest Service Pacific Northwest and Pacific Southwest Research Stations.

## LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female rocky mountain elk and mule deer. Journal of Mammalogy 84:1076–1088.

Brillinger, D. R. 2010. Modelling spatial trajectories. Pages 463–474 *in* A. Gelfand, P. Diggle, P. Guttorp, and M. Fuentes, editors. Handbook of spatial statistics. CRC Press, Boca Raton, Florida, USA.

Brillinger, D. R., H. K. Preisler, A. A. Ager, and J. G. Kie. 2004. An exploratory data analysis (EDA) of the paths of moving animals. Journal of Statistical Planning and Inference 122:43–63.

Brillinger, D. R., H. K. Preisler, and M. J. Wisdom. 2011. Modelling particles moving in a potential field with pairwise interactions and an application. Brazilian Journal of Probability and Statistics 25:421–436.

Brillinger, D. R., B. S. Stewart, and C. L. Littnan. 2008. Three months journeying of a Hawaiian monk seal. Institute of Mathematical Statistics Collection. Probability and Statistics: Essays in Honor of David A. Freedman **2**:246–264.

Codling, E. A., and N. A. Hill. 2005. Sampling rate effects on measurements of correlated and biased random walks. Journal of Theoretical Biology 233:573–588.

Dowd, M., and R. Joy. 2011. Estimating behavioral parameters in animal movement models using a state-augmented particle filter. Ecology 92:568–575.

Forester, J. D., A. R. Ives, M. G. Turner, D. P. Anderson, D. Fortin, H. L. Beyer, D. W. Smith, and M. S. Boyce. 2007. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecological Monographs 77:285–299.

Hastie, T. J., and R. J. Tibshirani. 1990. Generalized additive models. Chapman & Hall, New York, New York, USA.

Hirsch, M. W., and S. Smale. 1974. Differential equations, dynamical systems, and linear algebra. Academic Press, New York, New York, USA.

Hirsch, M. W., S. Smale, and R. L. Devaney. 2004. Differential equations, dynamical systems, and an introduction to chaos. Academic Press, Elsevier, Waltham, Massachusetts, USA.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

Johnson, D. S., J. M. London, M. A. Lea, and J. W. Durban. 2008. Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–1215.

Jonsen, I. D., R. A. Myers, and J. M. Flemming. 2003. Metaanalysis of animal movement using state-space models. Ecology 84:3005–3063.

Matthews, K. R., and H. K. Preisler. 2010. Site fidelity of the declining amphibian *Rana sierrae* (Sierra Nevada yellow-legged frog). Canadian Journal of Fisheries and Aquatic Sciences 67:243–255.

McClintock, B. T., R. King, L. Thomas, J. Matthiopoulos, B. J. McConnell, and J. M. Morales. 2012. A general discrete-time modeling framework for animal movement using multistate random walks. Ecological Monographs 82:335–349.

Millspaugh, J. J., R. M. Nielson, L. L. McDonald, J. M. Marzluff, R. A. Gitzen, C. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384–395.

Morales, J. M., T. Haydon, J. Frair, K. F. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: Building movement models as mixtures of random walks. Ecology 85:2436–2445.

Nathan, R., W. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences USA 105:19052–19059.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management 37:328–338.

Okubo, A., and S. A. Levin. 2001. Diffusion and ecological problems: modern perspectives. Springer-Verlag, New York, New York, USA.

Prakasa Rao, B. L. S. 1999. Statistical inference for diffusion type processes. Arnold, London, UK.

Preisler, H. K., A. A. Ager, B. K. Johnson, and J. G. Kie. 2004. Modeling animal movements using stochastic differential equations. Environmetrics 15:643–657.

Preisler, H. K., A. A. Ager, and M. J. Wisdom. 2006. Statistical methods for analyzing responses of wildlife to human disturbance. Journal of Applied Ecology 43:164–172.

Sawyer, H., and M. J. Kaufman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078–1087.

Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.

Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark. 2008. Understanding movement data and movement processes: current and emerging directions. Ecology Letters 11:1338–1350.

Smouse, P. E., S. Focardi, P. R. Moorcroft, J. G. Kie, J. D. Forester, and J. M. Morales. 2010. Stochastic modelling of animal movement. Philosophical Transactions of the Royal Society 365:2201–2211.

Sorensen, M. 1997. Estimating functions for discretely observed diffusions: A review. IMS Lecture Notes Monograph Series 32:305–325.

Taylor, J. R. 2004. Classical mechanics. University Science Books, Sausalito, California, USA.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, Massachusetts, USA.

Wisdom, M. J., A. A. Ager, H. K. Preisler, N. J. Cimon, and B. K. Johnson. 2004. Effects of off-road recreation on mule deer and elk. Transactions, North American Wildlife and Natural Resources Conference 69:531–550.

Wood, S. N. 2006. Low rank scale invariant tensor product smooths for generalized additive mixed models. Biometrics 62:1025–1036.

Zohdi, T. L. 2003. Computational designth of swarms. International Journal for Numerical Methods in Engineering 57:2205–2219.

Zohdi, T. L. 2009. Mechanistic modeling of swarms. Computational Methods in Applied Mechanical Engineering 198:2039–2051.

## SUPPLEMENTAL MATERIAL

### SUPPLEMENT

R script and resulting output for estimating the potential surface described in Eq. 3 with data from elk during ATV treatment days (*Ecological Archives* C004-002-S1).

Copyright © 2011 by the author(s). Published here under license by the Resilience Alliance.
Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. *Ecology and Society* **16**(3): 16.
http://dx.doi.org/10.5751/ES-04251-160316

*Research*

# Human Activity Differentially Redistributes Large Mammals in the Canadian Rockies National Parks

*James Kimo Rogala* [1,2], *Mark Hebblewhite* [3], *Jesse Whittington* [1], *Cliff A. White* [1], *Jenny Coleshill* [2], *and Marco Musiani* [2]

ABSTRACT. National parks are important for conservation of species such as wolves (*Canis lupus*) and elk (*Cervus canadensis*). However, topography, vegetation conditions, and anthropogenic infrastructure within parks may limit available habitat. Human activity on trails and roads may lead to indirect habitat loss, further limiting available habitat. Predators and prey may respond differentially to human activity, potentially disrupting ecological processes. However, research on such impacts to wildlife is incomplete, especially at fine spatial and temporal scales. Our research investigated the relationship between wolf and elk distribution and human activity using fine-scale Global Positioning System (GPS) wildlife telemetry locations and hourly human activity measures on trails and roads in Banff, Kootenay, and Yoho National Parks, Canada. We observed a complex interaction between the distance animals were located from trails and human activity level resulting in species adopting both mutual avoidance and differential response behaviors. In areas < 50 m from trails human activity led to a mutual avoidance response by both wolves and elk. In areas 50 - 400 m from trails low levels of human activity led to differential responses; wolves avoided these areas, whereas elk appeared to use these areas as a predation refugia. These differential impacts on elk and wolves may have important implications for trophic dynamics. As human activity increased above two people/hour, areas 50 - 400 m from trails were mutually avoided by both species, resulting in the indirect loss of important montane habitat. If park managers are concerned with human impacts on wolves and elk, or on these species' trophic interactions with other species, they can monitor locations near trails and roads and consider hourly changes of human activity levels in areas important to wildlife.

Key Words: *Banff National Park; conditional logistic regression; elk; human activity; resource selection; trails; wolves; Yellowstone National Park*

## INTRODUCTION

Habitat loss from an increasing and expanding human population is the greatest threat to a wide diversity of species (Wilcove et al. 1998, Brooks et al. 2002). The establishment of parks has been an important strategy to prevent direct habitat loss and to preserve biologically important flora and fauna (Margules and Pressey 2000). However, parks may be susceptible to habitat degradation or indirect habitat loss from both natural and anthropogenic disturbances (Peters and Darling 1985, Baker 1992, Hobbs and Huenneke 1992). For example, many wildlife species in mountainous areas are affected by topographical fragmentation and indirect habitat loss by steep rugged mountain ranges. Additionally, anthropogenic infrastructure and human activity in mountainous landscapes are primarily located on valley bottoms, which often contain the most productive habitat for wildlife species, further increasing fragmentation and limiting available habitat (Gibeau et al. 1996, Paquet et al. 1996).

Recreation and transportation may have an array of immediate and long-term impacts on species within wilderness parks (Boyle and Samson 1985, Forman and Alexander 1998, Trombulak and Frissell 2000). Activities such as hiking and biking on trails, and vehicle activity on roads may affect a wide range of species such as moose (*Alces alces*; Yost and Wright 2001), mule deer (*Odocoileus hemionus*; Freddy et al. 1986), bobcats (*Lynx rufus*) and coyotes (*Canis*

---

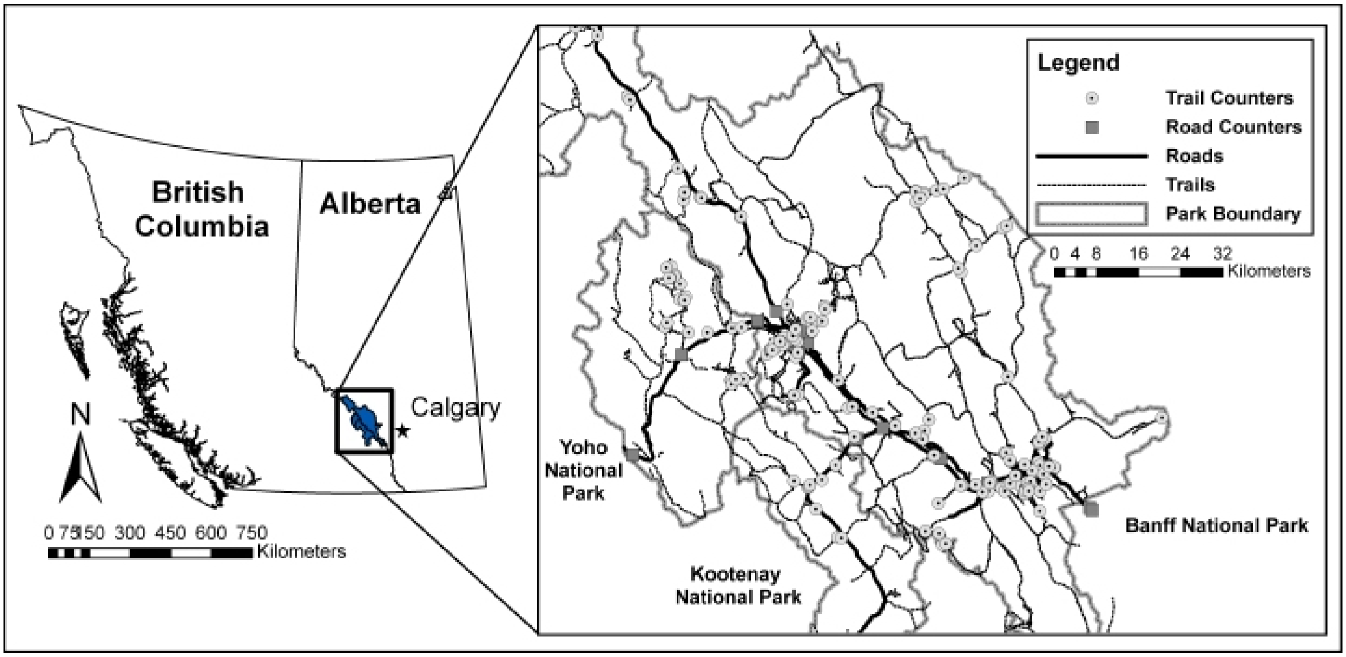
[1]Parks Canada, [2]University of Calgary, [3]University of Montana

*latrans*; George and Crooks 2006), bighorn sheep (*Ovis canadensis*; Keller and Bender 2007), bison (*Bison bison)* and pronghorn (*Antilocapra americana*; Taylor and Knight 2003), small mammals (Oxley et al. 1974), Brown-headed Cowbirds (*Molothrus ater*), bald eagles (*Haliaeetus leucocephalus*; Buehler et al. 1991, Miller et al. 1998), and black bears (*Ursus americanus*; Kasworm and Manley 1990). For many of these species, wildlife use near human activity decreased substantially, often leading to indirect habitat loss. For example, avoidance of human activity by woodland caribou (*Rangifer tarandus caribou*) on seismic exploration lines and roads resulted in loss of up to 48% of habitat in Alberta, Canada (Dyer et al. 2001). However, in other systems, wildlife species differentially responded to human activity according to trophic level. For example, in Grand Teton National Park, Berger (2007) found that grizzly bear avoidance of human activity because of presumed higher risk of mortality (e.g., Nielsen et al. 2004), created a refugia for female moose and their calves. This suggests a cascading top-down trophic interaction hypothesis whereby carnivores but not their prey avoided human activity, resulting in a refugia for prey. These indirect human effects on trophic dynamics could lead to human mediated trophic cascades on plant communities and species dependent upon those plants (e.g., Hebblewhite et al. 2005). Understanding how increasing human activity affects the intensity and extent of habitat use by different trophic levels has important implications for land managers and for indirect habitat loss mitigation strategies.

Indirect habitat loss caused by avoidance of trails and roads has been documented for wolves (*Canis lupus*; Theuerkauf et al. 2003, Whittington et al. 2004, Hebblewhite and Merrill 2008), consistent with this species treating human disturbance as predation risk, perhaps because of higher mortality near humans despite protection (Hebblewhite et al. 2003). For elk (*Cervus canadensis*), however, responses were more variable; where some authors reported avoidance (Cassirer et al. 1992, Gagnon et al. 2007), others reported selection for areas near human activity (Hebblewhite et al. 2005), suggesting that both avoidance and trophic interaction may occur in different populations. However, most previous research on the effects of human activities on wolf and elk selection has occurred at relatively coarse spatial-temporal scales. For example, previous research that has used human activity models at broad spatial scales includes Theuerkauf et al. (2001), Anderson et al. (2005), and Shively et al. (2005). Research using human activity models at broad temporal scales, i.e., summer vs. winter, includes Jedrzejewski et al. (2001) and Sawyer et al. (2007). Other research has compared human activity levels between circadian cycles, i.e., day vs. night (Schultz and Bailey 1978, Ciucci et al. 1997, Ager et al. 2003, Theuerkauf et al. 2003) or between different activity-level trails/roads, i.e., high vs. low activity (Rost and Bailey 1979, Thurber et al. 1994, Ager et al. 2003). These analyses assume a constant response across spatio-temporal scales, and may obscure the true relationship between humans and wildlife. Human activity levels vary both spatially and temporally. For example, if a species response to human activity is measured at the temporal scale of day vs. night across the entire study area, there may be locations within the study where the daytime human activity level, i.e., a low activity road, equals the nighttime level, i.e. a high-activity road. In this case, research may incorrectly assume that these two roads incur similar responses by wildlife during the day or night. To identify fine-scale wildlife responses to human activity levels, researchers would ideally use temporally varying human activity levels spatially across many different trails and roads. Such an approach would allow researchers to understand whether wildlife were able to distinguish changes in human activity levels at finer spatio-temporal scales, i.e., within the circadian cycle at individual trails and roads. As a result, managers could potentially mitigate the negative effects of human activity by managing the timing and amount of human activity.

Our research investigates the relationship between modeled fine-scale (hourly) human activity levels on roads and trails and the distribution of wolves and elk near these linear features. Specifically, we tested the effects of modeled hourly human activity on wolf and elk use of areas adjacent to trails and roads across three mountainous national parks of the Canadian Rockies. We tested the hypothesis that humans had an equal effect on both species, vs. the trophic interaction hypothesis of Berger et al. (2001), whereby wolves but not elk would avoid human activity, thus providing elk with a ‘human’ shield. We test these hypotheses using GPS radio telemetry from 32 individuals of the two species in a paired-logistic resource selection function framework (Compton et al. 2002). Finally, we tested for thresholds in the response of wildlife to human activity levels. Our study is among the first to

**Fig. 1**. Location of study area: Banff, Kootenay, and Yoho National Parks within the provinces of British Columbia and Alberta, Canada.



combine GPS collars with hourly human activity data to test for fine-scale wildlife-human interactions.

## METHODS

### Study area

Banff, Kootenay, and Yoho National Parks are located in the Canadian Rocky Mountains approximately 150 km west of Calgary (Fig. 1). They are adjacent parks covering 9360 km² in southwestern Alberta and southeastern British Columbia. The topography of the area is mountainous with rugged slopes, steep-sided ravines, and flat valley bottoms. Ecoregions include montane, subalpine, and alpine, which correspond to increasing elevation and decreasing productivity (Holland and Coen 1983). Vegetation in the area includes lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), poplar (*Populus sp.*), and Douglas fir (*Pseudotsuga menziesii*; Holroyd and Van Tighem 1983). In addition to our research species, wildlife in the area includes black bear, grizzly bear (*Ursus arctos*), cougar (*Puma concolor*), lynx (*Felis lynx*), coyote, wolverine (*Gulo gulo*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemonius*), bighorn sheep, and moose. For more details, see Hebblewhite et al. (2005).

### Human activity

Humans have widespread presence in the three national parks primarily at valley bottoms and in particular the Bow River Valley. The Canadian Pacific Railway line, Trans Canada Highway (TCH), Highways 93 and 1A, and other lesser-used, secondary two-lane paved roads run through the national parks. Approximately 5 - 6 million people travel through the area annually (Green at al. 1996). Vehicle volumes during 1997-2004 ranged from 50,000 to 800,000 vehicles per month along the TCH, 25,000 to 150,000 vehicles per month along Highway 93, and 4,000 to 100,000 vehicles per month along Highway 1A (Parks Canada, *unpublished data*). Facilities include the towns of

Lake Louise and Banff, three ski hills, campgrounds, a golf course, and other tourism related developments. An extensive network of trails along valley bottoms is primarily used for hiking with some biking and equestrian use. In the winter, trails are used for skiing, snowshoeing, and hiking for recreation and access routes for other mountaineering activities. Human activity levels on various trails in the summer range from 100 to 70,000 per month along the Bow River Valley and 0 to 1000 per month in backcountry areas (Parks Canada, *unpublished data*). Volumes in the winter decrease dramatically with backcountry locations receiving almost no human activity.

To model hourly human activity we obtained data on trails and roads in Banff, Kootenay, and Yoho National Parks from Parks Canada (Fig. 1). Data on 137 trails were gathered using passive (Trafx Research Ltd., Canmore, Alberta, Canada) and active (Goodson & Associates, Inc., Lenexa, Kansas, USA) infrared counters deployed along trails between 2000 and 2007 (Watson et al. 2000, Cessford and Muhar 2003). We accounted for possible over counting due to false triggers, for example, movements of vegetation by wind, by deleting counts that were > 50% higher than any other counts on that trail if local park experts also indicated such counts as inexplicably high. Additionally, we only used data from infrared counters that were evaluated by field personnel as reliable. Examples of unreliable infrared counters include those temporarily covered by branches, blocked by spider webs, tampered with, or experiencing malfunctioning hardware issues. Deleted or lost data occurred in < 1% of the documentation period for all counters. We further assessed data reliability by setting up infrared cameras (Reconyx LLP, Holmen, Wisconsin, USA) simultaneously along infrared counters at five trails. The mean hourly count using infrared cameras on the five documented trails was 0.27 (se = 0.11) user/hour less than counts documented by infrared counters. The observed hourly human trail activity in our data ranged from 0 - 1500 users/hour and averaged 1.1 user/hour. We concluded that the slight overestimation (0.27 user/hour) of infrared counters resulted in conservative estimates of wildlife and trails in our study. To quantify vehicle activity on roads in the study area, hourly road count data was obtained from the Parks Canada Traffic Count database (Parks Canada, *unpublished data*).

## Wildlife data and habitat selection

We obtained wolf and elk Global Positioning System (GPS) telemetry locations from previous research in the study area (Hebblewhite and Merrill 2007, Hebblewhite et al. 2008). Twelve wolves (nine females and three males) from four packs were captured between 2002-2004 using modified foot-hold traps in the summer and helicopter net-gunning and limited aerial darting during the winter, and were outfitted with GPS radio-telemetry collars (GPS3300 model, LOTEK Inc., Newmarket, Ontario, Canada). Wolf location data was collected between December 2002 and July 2005. Twenty female elk were captured between 2002-2004 using corral traps or net-gunning and outfitted with GPS radio-telemetry collars (GPS3300 and 4400 collars, LOTEK Inc., Newmarket, Ontario, Canada). Elk location data were collected between June 2002 and October 2004. Details of wolf and elk capture and monitoring procedures can be found in Hebblewhite and Merrill (2007) and Hebblewhite et al. (2008), respectively. Capture and handling methods were approved under Banff National Park Permit Number B-1994-29 and University of Alberta Animal Care protocol ID# 35112. All collars were programmed to acquire locations every two hours, which was considered sufficiently temporally accurate to estimate movement parameters of wildlife (Jerde and Visscher 2005).

We investigated resource selection as a function of human activity along roads and trails for these two species using paired or matched-case control logistic regression (Hosmer and Lemeshow 2000, Compton et al. 2002, Whittington et al. 2005). Matched-case control logistic regression, also known as conditional logistic regression, is quickly becoming the recommended method for evaluating resource selection because it appropriately measures availability from a mechanistically biological perspective (Moorcroft and Barnett 2008), and results in robust relative probabilities of selection in a used-availability design (Keating and Cherry 2004). We compared resource selection between telemetry locations and availability measured using 10 random locations paired to each observation. We derived the 10 random locations from the empirical step length and turning angle distribution between consecutive two-hour locations in a classic matched-case control design (Fortin et al. 2005). The distributions for elk were averaged across all individuals, but to account for possible differences between wolf packs, we used step length and turning angle distributions from each individual pack. We created random locations using Hawth's Analysis Tools (Beyer 2004) and ArcMap 9.2 (ESRI Inc. 2006), and ensured that each available location did not occur outside the study area. We assigned the date and time of each animal location to the paired random locations. Although habitat induced fix-rate bias is a concern in habitat selection studies (D'Eon et al. 2002, Frair et al. 2004, Hebblewhite et al. 2007), habitat induced GPS-bias was not incorporated into analyses for wolves and elk because rates were < 10% (Hebblewhite et al. 2007).

## Model variables

In order to model the effects of human activity on wildlife distribution at different distances from trails and roads, we categorized distances to roads and trails using the following distance categories: 0 - 50 m, 51 - 200 m, 201 - 400 m, 401 - 600 m, 601 - 800 m, and > 800 m. The 0 - 50 m distance represents an animal being on or immediately adjacent to a road or trail. We chose a 50 m distance as a balance in GPS location accuracy (see Hebblewhite 2006) such that it incorporates an area large enough to include the bulk of locations when an animal is on a trail or road and small enough to minimally include locations away from a trail. In addition, given the temporal resolution of the human activity dataset (+/-1 hour), using categories for distances to trails/ roads seemed appropriate. In sum, using a continuous variable for distance would have exaggerated the inference warranted from wildlife locations' accuracy and from the resolution of the human influence data. We used 800 m as the upper range to include the area an animal may be displaced to when disturbed. We used 800 m as the reference category because it was furthest away from human linear features and therefore likely the least affected by human activity. Modeled hourly human activity counts on the trail or road nearest to observed telemetry and random locations were derived using the rules listed below and similar to the human activity model described in Musiani et al. (2010, see also Shepherd and Whittington 2006). Observed human activity counts from the telemetry location date and hour-of-day were obtained from the nearest trail and road (100% of road data, 28% of trail data). If this was not available, we used the mean of previous years of human activity of the observed telemetry location month, week, day-of-week, and hour-of-day from the nearest trail or road (57% of trail data). If this was not available, we used the average human activity value of the observed telemetry location date and hour-of-day for similar trails and roads (15% of trail data). Similar trails and roads were defined on a monthly log-scale by Green et al. (1996).

In addition to human activity, we addressed possible confounding effects of other resources by including covariates commonly known to be important predictors of species occurrence in other studies (Mysterud and Ims 1998). We included these covariates in models whether or not they improved model performance to isolate the effects of human activity and distance to trails and roads on species' behaviors. These covariates included slope, elevation, and cover for wolves (Massolo and Meriggi 1998, Kunkel and Pletscher 2000, Ciucci et al. 2003, Mech and Boitani 2003, Oakleaf et al. 2006); and elevation, slope, and greenness as measured by the Normalized Difference Vegetation Index (NDVI; Pettorelli et al. 2005) for elk (Toweill and Thomas 2002, Fortin et al. 2005, Mao et al. 2005, Hebblewhite 2006, Stubblefield et al. 2006). Cover and greenness were derived from Landsat 7 TM satellite imagery (McDermid et al. 2005). Greenness is the measure of herbaceous phytomass and correlates to primary productivity and biomass. Elevation and slope were derived from a 30 $m^2$ Digital Elevation Model (DEM) of the study area.

## Analysis

We tested for wolf and elk selection of areas near trails and roads using separate models for trails and road. We assessed species' responses to these features by comparing models with and without distance, level of human activity, and their interaction. We compared nested models using likelihood ratio tests. We assessed multicollinearity of model variables using the variance inflation factor (VIF), which is a measure of the amount of multicollinearity in a set of multiple regression variables; VIF values > 10 indicate collinearity. We examined the spatial effects of increasing human activity by estimating relative predicted probabilities of occurrence vs. human activity for each distance category. For each specific level of trail activity the predicted probability for a given distance category was the probability of wildlife occurrence in that distance category compared with other distance categories. The cumulative predicted probabilities of all distance categories for a specific level of trail activity summed to one. We graphed relative

**Table 1.** Likelihood ratio test and P-value (significance at < 0.05) results of distance-to-trail/road categorical variable and distance-to-trail/road*hourly trail/road activity categorical interaction variable using nested models for each species. Mean Spearman's rho and P-value of 5-fold cross validation tests performed on models with significant interaction variables.

| | | Trails | | Roads | |
|---|---|---|---|---|---|
| Explanatory Variable | | Wolf | Elk | Wolf | Elk |
| L-R Test of Distance | $\chi^2$ | 33.92 | 58.88 | 28.00 | 9.23 |
| | *P* | < 0.000 | < 0.000 | < 0.000 | 0.100 |
| L-R Test of Distance * Activity | $\chi^2$ | 12.39 | 44.63 | 17.18 | 11.25 |
| | *P* | 0.030 | < 0.000 | 0.004 | 0.047 |
| K-fold Cross Validation of Model | $\mu$ rho | 0.971 | 0.905 | 0.959 | 0.314 |
| | $\mu$ *P* | < 0.000 | 0.002 | < 0.000 | 0.396 |

predicted probabilities of occurrence by human activity for each distance category using a linear stretch to scale the relative predicted probabilities between 0 and 1 (Johnson et al. 2004). We assessed the magnitude of response using the derivatives of relative predicted probabilities (Long and Freese 2006).

We used Stata 10 (Stata Corp. L.P. 2008) for statistical analysis. Matched case-control logistic regression was performed using robust variance estimates (Huber-White sandwich estimator) to account for autocorrelation in GPS data (Nielson et al. 2002). For studies in which unbalanced samples occur, sample weighting can be used to rectify unequal observations (Long and Freese 2006). Our research had unequal telemetry observations per animal for elk and per pack for wolves, potentially leading to greater leverage for those animals or packs with more observations. To rectify this, we inversely weighted observations by each animal's or pack's proportion of the total observations, so that all animals for elk or packs for wolves had the same statistical weight in analysis (Long and Freese 2006).

We performed a Spearman's rank correlation based on a case-control k-fold cross validation (k=5) to assess the predictive capability of each model (Boyce et al. 2002, Fortin et al. 2009). The 5-fold cross validation used 80% of the data to create a model that predicted the frequency of occurrence of the withheld 20% using bins that represented the range of predicted RSF scores; the process was repeated five times replacing the withheld 20%.

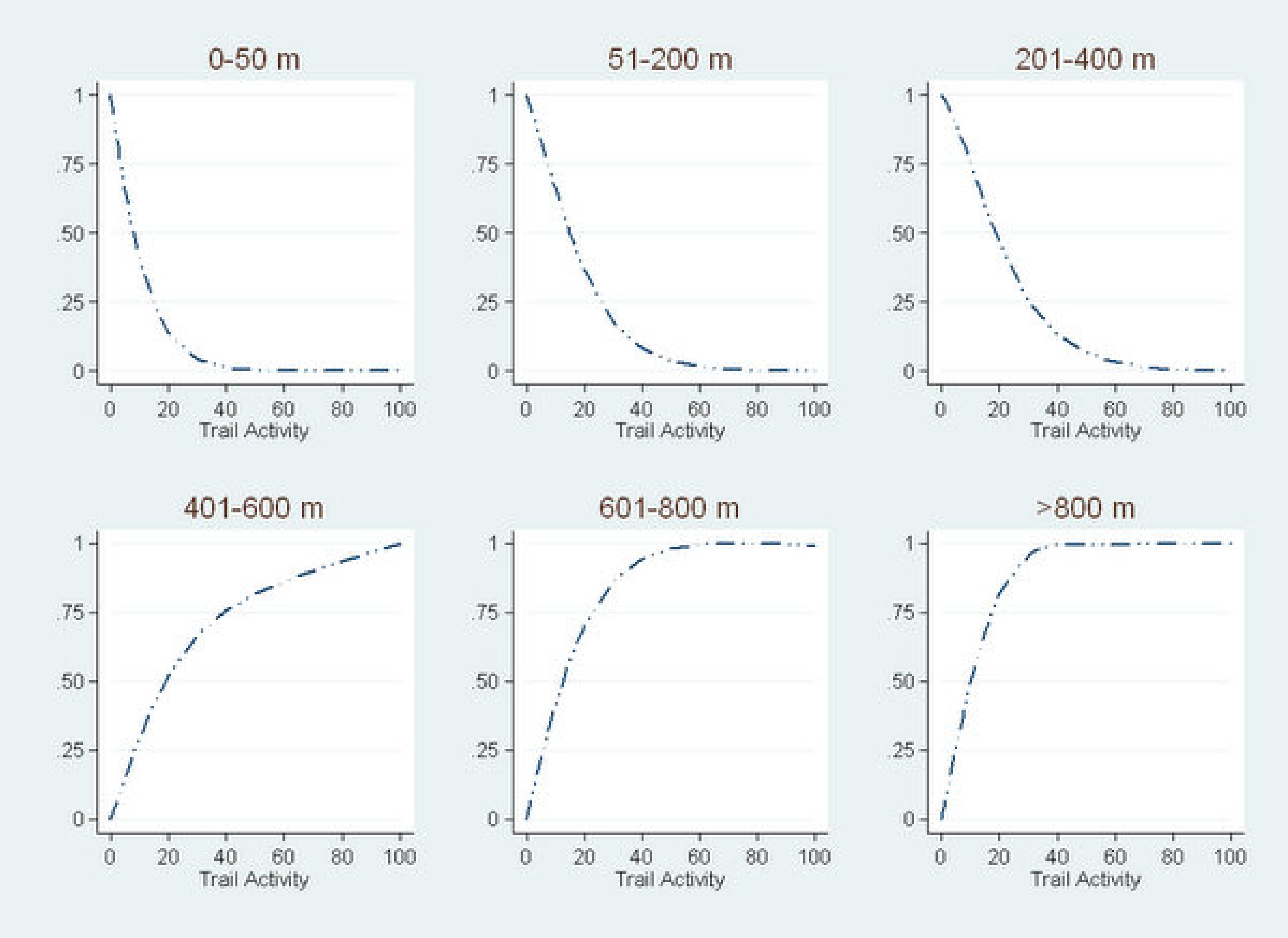
## RESULTS

### Wolf responses to trails

Wolf use of areas near trails was affected by distance to human activity and trail activity level. The distance-to-trail variable improved model performance ($\chi^2 = 33.9$, $P < 0.0005$; Table 1), and the interaction variable distance-to-trail*trail activity further improved model performance ($\chi^2 = 12.4$, $P = 0.030$; Table 1). Wolf response to increasing trail activity for distance classes < 400 m differed from distances > 800 m ($P < 0.05$, Appendix Table A1.1), whereas wolves showed neither selection nor avoidance for distance classes > 400 m regardless of human activity.

As trail activity increased, wolf selection of areas in distances 0 - 50 m, 51 - 200 m, and 201 - 400 m

**Fig. 2.** Graphs of the change in wolf relative probability of use as a function of increasing trail activity within six ‘distance-to-trail’ categories. The x-axis is hourly trail activity and y-axis is relative probability of use. A linear stretch was used to scale the predicted values between 0 and 1 following Johnson et al. (2004).



decreased (Fig. 2). Conversely, wolf selection of areas in distances 401 - 600 m, 601 - 800 m, and > 800 m increased with increasing trail activity (Fig. 2). Wolf response changed from avoidance of distances < 400 m to attraction of distances > 400 m with increasing trail activity, because wolves may move from areas < 400 m to > 400 m from trails. Wolf responses to increasing trail activity leveled off for all distances at higher trail activity levels (Fig. 2). Derivatives were lowest (decreasing slope) in areas near trails, suggesting wolves had a stronger and quicker avoidance of human activity near trails (Table 2). Elevation, slope, and cover were strong predictors of wolf occurrence ($P < 0.05$, Appendix Table A1.1). The mean VIF for all variables was 1.23 and no VIF was greater than 2, indicating minimal collinearity. The 5-fold cross validation had a mean Spearman’s rank correlation of 0.97 ($P < 0.0005$) indicating that the model predicted the distribution of wolves accurately (Table 1).

**Table 2.** Hourly human activity at the peak negative derivative. 'Peak derivative level' represents the greatest rate of negative change in probability of use of locations within listed distances-to-trails/roads. Distance-to-trail/road categories that did not have negative derivatives were not included. † = Derivative was continuously negative. N/A = Not applicable.

| Species | Human Activity Type | Distance from Trail or Road (m) | Peak Negative Derivative Level | Hourly Human Activity Level at Peak Negative Derivative | Hourly Human Activity Level When Species Began Avoidance |
|---|---|---|---|---|---|
| Elk | Trail | 0-50 | -0.05116 | < 1 | † |
| | | 51-200 | -0.00477 | 8 | 1 |
| | | 201-400 | -0.00463 | 10 | 2 |
| | | 401-600 | -0.00355 | 45 | 12 |
| | | 601-800 | -0.00345 | 45 | 12 |
| Wolves | Trail | 0-50 | -0.01540 | < 1 | N/A |
| | | 51-200 | -0.00639 | 8 | N/A |
| | | 201-400 | -0.00540 | 10 | N/A |
| | Road | 0-50 | -0.00026 | 25 | N/A |
| | | 51-200 | -0.00008 | 700 | N/A |
| | | 201-400 | -0.00001 | 1500 | N/A |

### Wolf responses to roads

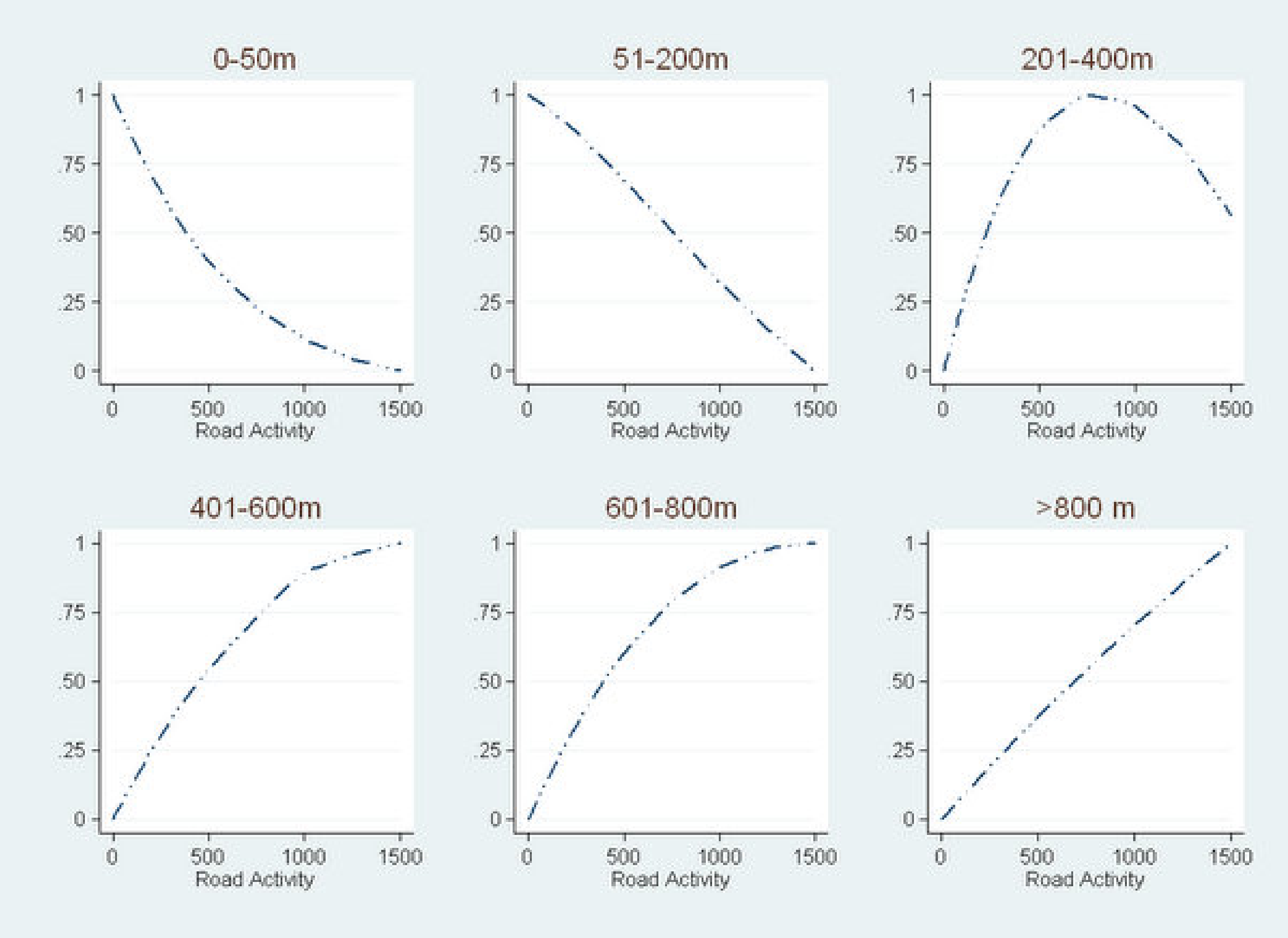
The distance-to-road variable improved model performance ($\chi^2 = 28.0$, $P < 0.0005$; Table 1). The interaction variable distance-to-road*road activity further improved model performance ($\chi^2 = 17.2$, $P = 0.004$; Table 1). Wolf response to increasing road activity at distances 0 - 200 m was significantly different than for distances > 800 m ($P < 0.05$, Appendix Table A1.2).

As road activity increased, wolf selection progressively changed from avoidance (< 200 m) to neutral (201 - 400 m) to attraction (> 400 m; Fig. 3), suggesting that wolves at distances < 200 m move to distances > 400 m as road activity increases. Wolf selection for the 201 - 400 m distance changed from mild attraction to mild avoidance at the road activity level of ~1500 vehicles/hr (Table 2). Derivatives were lowest near roads, suggesting a greater avoidance response to human activity when animals were nearer to roads (Table 2). Elevation, slope, and cover were strong predictors of wolf occurrence ($P < 0.05$, Appendix Table A1.2). The mean VIF for all variables was 1.81 and no VIF was greater than 4, indicating minimal collinearity. The 5-fold cross validation had a mean Spearman's rank correlation of 0.96 ($P < 0.0005$) indicating that the model consistently predicted the distribution of wolves (Table 1).

### Elk responses to trails

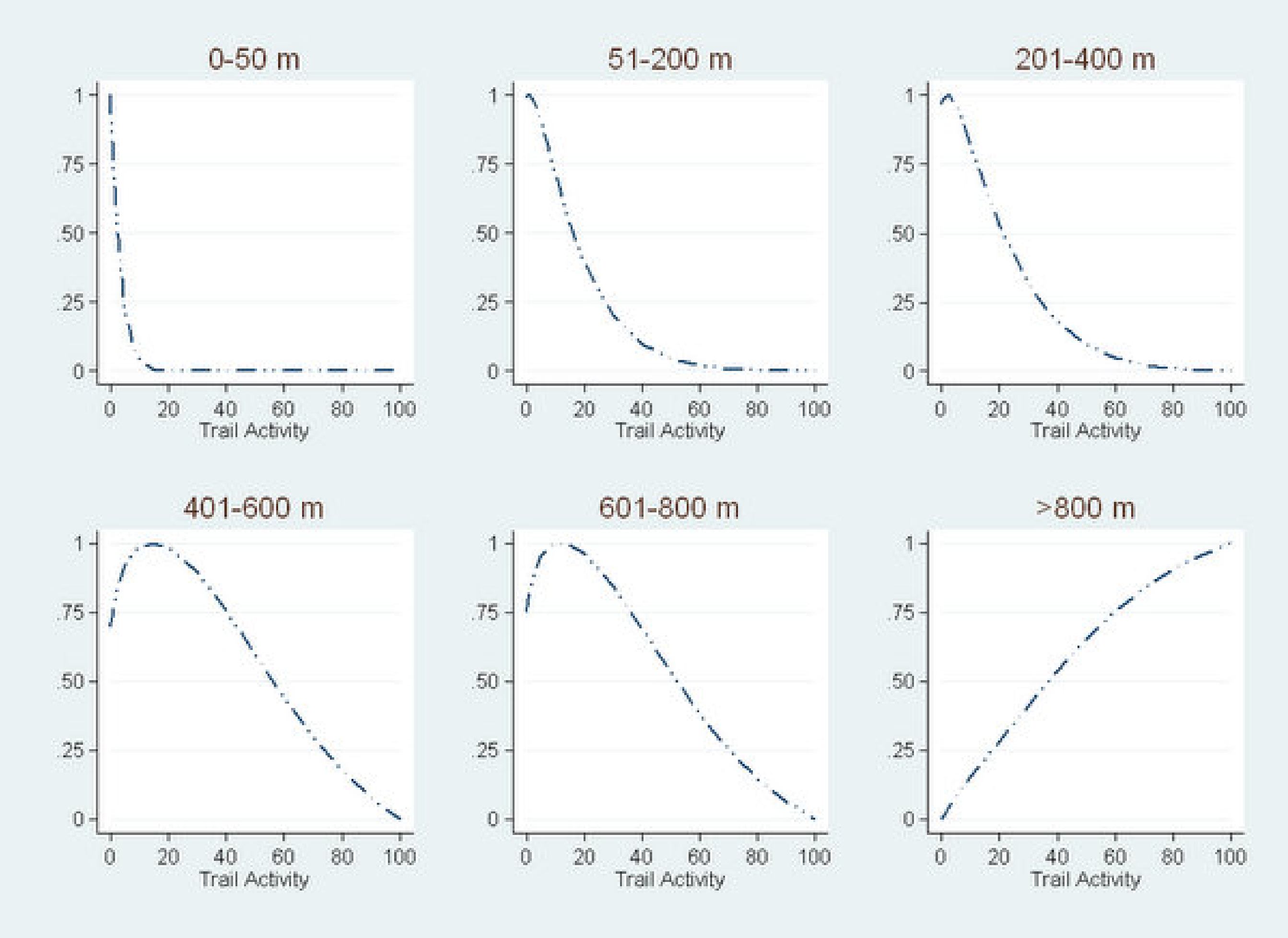
The categorical distance-to-trail variable improved model performance ($\chi^2 = 58.88$, $P < 0.05$; Table 1). The interaction variable distance-to-trail*trail activity further improved model performance ($\chi^2 = 44.63$, $P = 0.05$; Table 1). Elk response to increasing trail activity at distances 201 - 400 m and 601 - 800 m was significantly different than for distances > 800 m ($P < 0.05$, Appendix Table A1.3).

**Fig. 3.** Graphs of the change in wolf relative probability of use as a function of increasing road activity within six ‘distance-to-road’ categories. The x-axis is hourly road activity and y-axis is relative probability of use. A linear stretch was used to scale the predicted values between 0 and 1 following Johnson et al. (2004).



As trail activity increased, elk selection of locations in distance 0 - 50 m immediately and sharply decreased, than leveled off at between 10 - 20 users/hour (Fig. 4). Elk responded to increasing trail activity at distances 51 - 400 m initially with mild attraction; then avoided these distances when trail activity reached one to two users/hr (Table 2, Fig. 4). Similarly, elk at distances 401 - 800 m responded to increasing trail activity with attraction; then avoided these distances when trail activity reached ~12 users/hr. Derivatives were lowest near trails, suggesting a greater avoidance response to human activity when animals were nearer to trails (Table 2). Elevation, slope, and greenness were strong predictors of elk occurrence ($P < 0.05$, Appendix Table A1.3). The mean VIF for all variables was 1.34 and no VIF was greater than 3, indicating minimal collinearity. The 5-fold cross validation had a mean Spearman’s rank correlation of 0.91 ($P = 0.002$) indicating that the model consistently predicted the distribution of elk (Table 1).

**Fig. 4.** Graphs of the change in elk relative probability of use as a function of increasing trail activity within six ‘distance-to-trail’ categories. The x-axis is hourly trail activity and y-axis is relative probability of use. A linear stretch was used to scale the predicted values between 0 and 1 following Johnson et al. (2004).



### Elk responses to roads

The categorical distance-to-road variable did not on its own improve model performance ($\chi^2 = 9.23$, $P = 0.100$; Table 1). However, the interaction variable distance-to-roads*road activity was a predictor of elk occurrence ($\chi^2 = 11.25$, $P = 0.047$; Table 1). Elk selected for lower elevations and higher greenness ($P < 0.05$, Appendix Table A1.4) but not lower slopes ($P > 0.05$, Appendix Table A1.4). The mean VIF for all variables was 1.63 and no VIF was greater than 3, indicating minimal collinearity. The 5-fold cross validation had a mean Spearman’s rank correlation of 0.31 ($P = 0.396$) indicating that the model did not consistently predict the distribution of elk (Table 1). As the model did not consistently predict elk distribution, relative predicted probabilities were not calculated for the elk near roads model.

## DISCUSSION

### Wolf and elk avoidance of human activity

Our study documented clear changes in habitat selection patterns by wolves and elk in response to increased human activity with marked implications for their ecology and community interactions. We found wolves and elk selected areas farther away from trails and roads with increasing human activity (Figs. 2-4). For example, as human activity increased, wolf relative probability of use decreased in areas < 400 m and increased in areas > 400 m from trails. Similarly, elk responded to increasing human activity on trails by progressively decreasing their relative probability of use in areas < 800 m. In particular, elk seemed to prefer areas at distances 401 - 800 m from trails (medium distances) over those > 800 m at low levels of human activity. However, those elk located at medium distances from trails were avoiding human activity as it increased. In accordance with our findings, previous research observed that wolves in Jasper National Park, Canada more strongly selected low activity trails compared with high activity trails (Whittington et al. 2005), wolves in Scandinavia fled from an approaching human when between 17 and 310 m away (Karlsson et al. 2007), and wolves in Finland showed greatest human-avoidance at the most heavily used roads (Kaartinen et al. 2005). Elk and other ungulates have displayed similar behavior in response to increasing human activity. For example, Wisdom et al. (2004) found that elk were provoked to flee more frequently during higher levels of trail activity and Keller and Bender (2007) found that increased human presence negatively affected bighorn sheep use of a preferred mineral lick site. Our research found insufficient evidence of elk response to road activity. In contrast to this, other research has found negative effects of road activity on elk and other ungulates. In other studies, elk occurred at greater distances to open than closed roads (Ager et al. 2003) and were found to decrease their use in areas < 200 m from roads at increasing vehicle activity (Gagnon et al. 2007). Similarly, Dussault et al. (2007) found that moose increased their movement rates near roads and Papouchis et al. (2001) found that bighorn sheep were found 39% farther from roads in a high-use area than in a low-use area. A possible reason for this contrast may be the mountainous topography of our study area in which both roads and optimal elk foraging habitat might occur at valley bottoms (Dodd et al. 2007).

We found that wolves and elk located closer to trails or roads displayed greater avoidance rates at similar human activity levels than those farther away. For example, wolves and elk at locations 0 - 50 m from trails reduced their relative probability of occurrence at a faster rate than those at 51 - 200 m as human activity increased. Similarly, Wisdom et al. (2004) documented elk movement rates and flight response probabilities were substantially higher during higher levels of trail activity in Oregon. By identifying derivatives of relative probability of use, we also found that at closer distances to trails, and roads for wolves, smaller human activity levels were required to invoke avoidance responses.

Human activity may be an important factor in predator-prey interactions (Kunkel and Pletscher 2000, Hebblewhite et al. 2005, Hebblewhite and Merrill 2008). Previous research has found that human activity may lead to universal avoidance. For example, Mech and Boitani (2003) found that wolves learned to avoid humans to decrease their own mortality risk and Cassirer et al. (1992) found elk avoided even small numbers of humans. Conversely, in other systems a differential response to human activity according to trophic level resulted in cascading trophic interactions (Hebblewhite et al. 2005, Berger 2007).

We observed a complex interaction between the distance animals were located from trails and human activity levels resulting in species adopting both mutual avoidance and differential response behaviors. Close distances to trails appeared to mediate a mutual avoidance response by both wolves and elk. Both species avoided areas 50 m or less from trails in response to low levels of human activity. Wolf and elk responses in areas between 50 - 400 m from trails were dependent on the level of human activity. At low levels of human activity differential responses could be mediating trophic interactions. Wolves responded to low levels of human activity by avoiding areas 50 - 400 m. Conversely, elk responded to similar levels of human activity by initially increasing their use in these areas, perhaps taking advantage of the refugia created from the reduced likelihood of predators in general. Consistent with this interpretation, wolf avoidance of human activity has been described in many other systems (Thurber et al. 1994, Theuerkauf et al. 2003, Kaartinen et al. 2005, Whittington et al. 2005), and a study conducted in the study area (Hebblewhite and Merrill 2007) showed that ungulates can exploit this to reduce their own predation risk. In our study area, wolves are the main predators of elk (Hebblewhite et al. 2002). However, elk might need to minimize the risk of being predated upon also by other predators, including cougars (Kortello et al. 2007) and black and grizzly bears (Herrero 2005). Whereas little is known for cougars and black bears, a large body of information demonstrates grizzly bear spatial avoidance of humans at higher levels of use in the study area (Gibeau et al. 2002, Chruszcz et al. 2003). Therefore, similar speculation is warranted for wolves, grizzly bears, and perhaps other predators of elk, because large mammalian predators are known to avoid humans in other areas (Kasworm and Manley 1990, Trombulak and Frissell 2000, George and Crooks 2006). However, once human activity levels were greater than two persons per hour, wolves and elk once again responded with mutual avoidance of areas 50 - 400 m from trails, resulting in the indirect loss of important montane habitat.

During low human activity, wolves in our study were more likely to be at locations between 0 - 50 m than distances > 400 m from trails (Appendix Table A1.5). This corroborates previous findings indicating that wolves may use linear features with low levels of human activity for travel routes (Thurber et al. 1994, Callaghan 2002) because these features may allow wolves ease of travel (James and Stuart-Smith 2000). Other research conducted in the Canadian Rocky Mountains similarly found wolves preferred areas < 25 m from roads and trails (Whittington et al. 2005). Wolves preferring to travel on or near linear features for short durations (under two hours) might explain our research not detecting a significant selection for areas 0 - 50 m compared with areas 51 - 400 m from trails (Whittington et al. 2004).

## Confounding factors in human effects on habitat use

Trails and roads in our study area often occur in high quality habitat along valley bottoms and often near streams and rivers. We included elevation as a covariate to control for this effect, however wolf and elk use of high quality habitat and narrow travel corridors near roads and trails could have reduced the displacement effects we observed (Kunkel and Pletscher 2000, Hebblewhite et al. 2005). Interestingly, trails had a stronger spatial effect on wolf and elk resource selection than roads. One reason for this result could be that animals in our study area regularly used wildlife crossing structures to cross the Trans Canada Highway (Clevenger et al. 2001) perhaps resulting in less apprehension of approaching and crossing roads. In addition, hiding cover and topographical features may be important factors that affect animal response (Hewison et al. 2001, Ager et al. 2003). For example, in the presence of hiding cover or nearby ridges wildlife may be more likely to tolerate being closer to human presence (Cassirer et al. 1992). It is possible that some animals in our study exhibited attenuated responses to human activity because of such features, which were not accounted for by our methodological approach.

We attempted to account for confounding factors by including the commonly found habitat and topographical factors important to each species. However, other factors such as snow conditions, topography, or variability in individual behavior may have affected our results (Hebblewhite and Merrill 2008). For example, Cassirer et al. (1992) observed that the distance moved by elk in Yellowstone National Park after being disturbed by cross country skiers ranged widely and was related to distance to nearest ridge. Future research might investigate the relative importance of other covariates with human activity at increasing distances to roads and trails to assess their relative importance to selection (Rowland et al. 2000). We used the human activity level of the nearest trail/road to a wildlife telemetry location as an indicator of human presence when assessing effects to wildlife. We acknowledge that wildlife may have been affected by other trails/roads further away from our documented trail/road, but with higher human activity levels. Such additional effects on wildlife movements in theory have the potential to confound, attenuate, or obscure the responses found in this study. Trails in our mountainous study area generally occurred on valley bottoms that were > 2 km from their nearest trail. Consequently, the disturbance effects produced by the second nearest trail or road might have been eliminated or at least attenuated, because of the rugged mountainous terrain of our study area separating trails, resulting in topographic obstacles existing between wildlife and multiple locations of human use. Wildlife locations that occurred near trail intersections may have incurred effects from both trails. We believe these effects were minimal in our research, considering that opportunities where a high activity trail intersects with or occurs within close proximity of a low activity trail were very few in our study area. In fact, high activity trails/roads occurred in proximity to other high activity trails/roads, as was similar for low-use areas. Future research might investigate cumulative disturbance from human activity also incorporating approaches such as density indexes over the landscape.

## Implications

Our study documented marked responses to human activity by a top predator and by a dominant herbivore species (Witmer and deCalesta 1985, Thurber et al. 1994, Shepherd and Whittington 2006). The responses to human activity we documented for wolves and elk may have energetic costs similar to anti-predator behaviors (Frid and Dill 2002). Duchesne et al. (2000) observed that woodland caribou increased time spent in vigilance behavior at the expense of foraging as eco-tourist visits increased in the Charlevoix Biosphere Reserve, Canada. Cassirer et al. (1992) estimated that elk needed to consume an additional 295 g/day of forage to compensate for movement away from cross country skiers in Yellowstone National Park. Greater energy requirements and reduced foraging time caused by anthropogenic disturbance can impair animal fitness (Frid and Dill 2002). Our research did not directly investigate energetic costs. However, proper identification and management of human disturbance near trails and roads may be important to mitigate a possible predation risk response and its associated effects.

The human mediated changes in both human-wildlife and predator-prey interactions may lead to undesirable consequences. Differential habituation among and within species may lead to changes in predator-prey dynamics (Caro 2005). For example, differential displacement away from human presence resulted in unequal predation risks of migrant vs. resident elk in our study area (Robinson et al. 2010). Additionally, wolf exclusion caused by humans led to changes in elk population dynamics (Hebblewhite et al. 2002) and cascading trophic effects on aspen (*Populus tremuloides*), willow (*Salix* spp.), beaver (*Castor Canadensis*), and songbirds (Hebblewhite et al. 2005). In this view, the role of humans may equally apply to wolves, elk, and to other potential species affected as humans may de facto serve the role of the nonconsumptive keystone predator (Boyle and Samson 1985).

Our research documented differential influences on wolves and elk that were dependent on the level of human activity, with the latter possibly benefiting from predator displacement by humans. Studies could be conducted in the future on other carnivore and herbivore species to highlight similar mechanisms across ecosystems. Additionally, future research focusing on the likelihood of returning to disturbance areas would be useful to further address possible long term behavioral consequences attributed to human activity because some studies have suggested persistent low levels of disturbance may lessen the likelihood of returning to previously used areas (Kuck et al. 1985) and lead to permanent shifts in habitat use (Rowland et al. 2000), whereas other studies found animals returned when activity lowered or desisted (Casirer et al. 1992, Gagnon et al 2007).

Understanding how human activity affects species distribution has great importance in areas such as ours where topography limits suitable habitat. Suitable habitat is limited by rock, ice, and steep rugged terrain in the mountainous landscape of Banff, Kootenay, and Yoho National Parks (Gibeau et al. 2001). The anthropogenic infrastructure that is required to support a town, transportation, and tourism related industry also reduces suitable habitat on valley bottoms in mountainous areas. The combination of these conditions may threaten species viability via higher rates of mortality (Benn and Herrero 2002, McNay 2002), habitat fragmentation (Alexander et al. 2005), and reduced habitat security and species resiliency (Weaver et al. 1996, Gibeau et al. 2001). Additional disturbance initiated by human activity, as documented in our study, at otherwise suitable habitats surrounding trails and roads that often occur on valley bottoms may further reduce species viability.

The circadian cycle has been the finest temporal scale used by previous studies that associate wildlife distribution to human activity. Our research documented that wildlife avoidance occurs at finer spatio-temporal scales than previously studied. We found that wolf and elk selection of locations near trails and roads was dependent on hourly human activity levels and the distance to the human linear feature. A failure to properly address the scale at which wildlife respond to human activity could lead to mistaken conclusions about habitat selection. Proper assessment of the relationship between fine-scale human activity and wildlife distribution may have important implications for animal energy budgets, human-wildlife and predator-prey interactions, ecological trophic cascades, and wildlife viability.

*Responses to this article can be read online at:*
*http://www.ecologyandsociety.org/vol16/iss3/art16/responses/*

---

## Acknowledgments:

*We thank our funding partners: Parks Canada, the University of Calgary, ACA Challenge Grants in Biodiversity, ACA Grant Eligible Conservation Fund, Foothills Model Forest-Chisholm-Dogrib Fire initiative grants, Sundre Forest Products LTD., Canon National Parks Science Scholarship for the Americas, Rocky Mountain Elk Foundation, University of Alberta, and a NSERC Discovery grant. We would also like to acknowledge the following for their input and advice toward this project: Cormack Gates, Tom Hurd, Alessandro Massolo, Tom Davidson, Tao Gui, Cathy Hourigan, Greg McDermid, Jean-Gabriel Hasbani, Kathy Rettie, Mike Gibeau, Gordon Stenhouse, Parks Canada, Alberta Sustainable Resource Development, Tyler Muhly, Joann Skilnik, Paul Paquet, Sk. Morshed Anwar, Rick Smee, Darren Labonte, James R. Allen, Tom Daniels, Barry McElhinney, Ian Pengelly, Darrel Zell, Johnny and Marie Nylund, Rick and Jean Smith, and finally the two anonymous reviewers for their invaluable comments on the manuscript.*

---

## LITERATURE CITED

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *Journal of Mammalogy* 84(3):1076-1088. http://dx.doi.org/10.1644/BBa-020

Alexander, S. M., N. M. Waters, and P. C. Paquet. 2005. Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. *Canadian Geographer* 49(4):321-331. http://dx.doi.org/10.1111/j.0008-3658.2005.00099.x

Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management* 69:298-310. http://dx.doi.org/10.2193/0022-541X(2005)069<0298:SSRSBR>2.0.CO;2

Baker, W. L. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. *Landscape Ecology* 7(3):181-194. http://dx.doi.org/10.1007/BF00133309

Benn, B., and S. Herrero. 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971-98. *Ursus* 13:213-221.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Royal Society: Biology Letters* 3(6):620-623. http://dx.doi.org/10.1098/rsbl.2007.0415

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications* 11(4):947-960. http://dx.doi.org/10.2307/3061004

Beyer, H. L. 2004. Hawth’s analysis tools for ArcGIS. [online] URL: http://www.spatialecology.com/index.php

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157(2-3):281-300. http://dx.doi.org/10.1016/S0304-3800(02)00200-4

Boyle, S. A., and F. B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin* 13(2):110-116.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16(4):909-923. http://dx.doi.org/10.1046/j.1523-1739.2002.00530.x

Buehler, D. A., T. J. Mersmann, J. D. Fraser, and J. K. D. Seegar. 1991. Effects of human activity on Bald Eagle distribution on the northern Chesapeake Bay. *Journal of Wildlife Management* 55(2):282-290. http://dx.doi.org/10.2307/3809151

Callaghan, C. J. 2002. *The ecology of gray wolf* (Canis lupus) *habitat use, survival, and persistence in the central Rocky Mountains, Canada.* Dissertation. Faculty of Graduate Studies, University of Guelph, Guelph, Ontario, Canada.

Caro, T. 2005. *Antipredator defenses in birds and mammals*. University of Chicago Press, Chicago, Illinois, USA.

Cassirer, E. F., D. J. Freddy, and E. D. Ables. 1992. Elk responses to disturbance by cross-country skiers in Yellowstone National Park. *Wildlife Society Bulletin* 20(4):375-381.

Cessford, G., and A. Muhar. 2003. Monitoring options for visitor numbers in national parks and natural areas. *Journal for Nature Conservation* 11 (4):240-250. http://dx.doi.org/10.1078/1617-1381-00055

Ciucci, P., L. Boitani, F. Francisci, and G. Andreoli. 1997. Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology* 243 (4):803-819. http://dx.doi.org/10.1111/j.1469-7998.1997.tb01977.x

Ciucci, P., L. Boitani, and M. Masi. 2003. Winter habitat and travel route selection by wolves in the northern Apennines, Italy. *Ecography* 26 (2):223-235. http://dx.doi.org/10.1034/j.1600-0587.2003.03353.x

Clevenger, A. P., B. Chruszcz, and K. E. Gunson. 2001. Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin* 29 (2):646-653.

Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83(3):833-843. http://dx.doi.org/10.2307/3071885

Chruszcz, B., A. P. Clevenger, K. E. Gunson, and M. L. Gibeau. 2003. Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology* 81(8):1378-1391. http://dx.doi.org/10.1139/z03-123

D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30 (2):430-439.

Dodd, N. L., J. W. Gagnon, S. Boe, and R. E. Schweinsburg. 2007. Assessment of elk highway permeability by using global positioning system telemetry. *Journal of Wildlife Management* 71 (4):1107-1117. http://dx.doi.org/10.2193/2006-106

Duchesne, M., S. D. Côté, and C. Barrette. 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. *Biological Conservation* 96(3):311-317. http://dx.doi.org/10.1016/S0006-3207(00)00082-3

Dussault, C., J.-P. Ouellet, C. Laurian, R. Courtois, M. Poulin, and L. Breton. 2007. Moose movement rates along highways and crossing probability models. *Journal of Wildlife Management* 71 (7):2338-2345. http://dx.doi.org/10.2193/2006-499

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management* 65(3):531-542. http://dx.doi.org/10.2307/3803106

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29(1):207-231. http://dx.doi.org/10.1146/annurev.ecolsys.29.1.207

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320-1330. http://dx.doi.org/10.1890/04-0953

Fortin, D., M.-E. Fortin, H. L. Beyer, T. Duchesne, S. Courant, and K. Dancose. 2009. Group-size-mediated habitat selection and group fusion—fission dynamics of bison under predation risk. *Ecology* 90(9):2480-2490. http://dx.doi.org/10.1890/08-0345.1

Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41(2):201-212. http://dx.doi.org/10.1111/j.0021-8901.2004.00902.x

Freddy, D. J., W. M. Bronaugh, and M. C. Fowler. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. *Wildlife Society Bulletin* 14(1):63-68.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6(1): 11. [online] URL: http://www.consecol.org/vol6/iss1/art11/

Gagnon, J. W., T. C. Theimer, N. L. Dodd, S. Boe, and R. E. Schweinsburg. 2007. Traffic volume alters elk distribution and highway crossings in Arizona. *Journal of Wildlife Management* 71(7):2318-2323. http://dx.doi.org/10.2193/2006-224

George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. *Biological Conservation* 133(1):107-117. http://dx.doi.org/10.1016/j.biocon.2006.05.024

Gibeau, M. L., A. P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation* 103(2):227-236. http://dx.doi.org/10.1016/S0006-3207(01)00131-8

Gibeau, M. L., S. Herrero, J. Kansas, and B. Benn. 1996. Grizzly bear population and habitat status in Banff National Park. Chapter 6 *in* J. Green, C. Pacas, L. Cornwell, and S. Bayley, editors. *Ecological outlooks project. A cumulative effects assessment and futures outlook of the Banff Bow Valley.* Prepared for the Banff Bow Valley study, Department of Canadian Heritage, Ottawa, Ontario, Canada.

Gibeau, M. L., S. Herrero, B. N. McLellan, and J. G. Woods. 2001. Managing for grizzly bear security areas in Banff National Park and the central Canadian Rocky Mountains. *Ursus* 12:121-130.

Green, J., C. Pacas, L. Cornwell, and S. E. Bayley. 1996. *Ecological outlook cumulative effects assessment and futures outlook of the Banff Bow Valley: final report.* Department of Canadian Heritage, Ottawa, Ontario, Canada.

Hebblewhite, M. 2006. *Linking predation risk and forage to ungulate population dynamics.* Dissertation. Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

Hebblewhite, M., and E. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152(2):377-387. http://dx.doi.org/10.1007/s00442-007-0661-y

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45(3):834-844. http://dx.doi.org/10.1111/j.1365-2664.2008.01466.x

Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78(2)141-166. http://dx.doi.org/10.1890/06-1708.1

Hebblewhite, M., M. Percy, and E. H. Merrill. 2007. Are all global positioning system collars created equal? Correcting habitat-induced bias using three brands in the central Canadian Rockies. *Journal of Wildlife Management* 71(6):2026-2033. http://dx.doi.org/10.2193/2006-238

Hebblewhite, M., M. Percy, and R. Serrouya. 2003. Black bear (*Ursus americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta. *Biological Conservation* 112(3):415-425. http://dx.doi.org/10.1016/S0006-3207(02)00341-5

Hebblewhite, M., D. H. Pletscher, and P. C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology* 80(5):789-799. http://dx.doi.org/10.1139/z02-058

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86(8):2135-2144. http://dx.doi.org/10.1890/04-1269

Herrero, S., editor. 2005. *Biology, demography, ecology and management of grizzly bears in and around Banff National Park and Kananaskis Country: the final report of the Eastern Slopes Grizzly Bear Project.* Faculty of Environmental Design, University of Calgary, Calgary, Alberta, Canada.

Hewison, A. J. M., J. P. Vincent, J. Joachim, J. M. Angibault, B. Cargnelutti, and C. Cibien. 2001. The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. *Canadian Journal of Zoology* 79(4):679-689. http://dx.doi.org/10.1139/z01-032

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6(3):324-337. http://dx.doi.org/10.1046/j.1523-1739.1992.06030324.x

Holland, W. D., and G. M. Coen, editors. 1983. *Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 1: summary.* Alberta Institute of Pedology, Edmonton, Alberta, Canada.

Holroyd, G. L., and K. J. Van Tighem. 1983. *Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume 3: the wildlife inventory.* Canadian Wildlife Service, Edmonton, Alberta, Canada.

Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression.* Second edition. John Wiley and Sons, New York, New York, USA. http://dx.doi.org/http://dx.doi.org/10.1002/0471722146

James, A. R. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64 (1):154-159. http://dx.doi.org/10.2307/3802985

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, and H. Okarma. 2001. Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. *Canadian Journal of Zoology* 79:1993-2004.

Jerde, C. L., and D. R. Visscher. 2005. GPS measurement error influences on movement model parameterization. *Ecological Applications* 15(3) 806-810. http://dx.doi.org/10.1890/04-0895

Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* 41(2):238-251. http://dx.doi.org/10.1111/j.0021-8901.2004.00899.x

Kaartinen, S., I. Kojola, and A. Colpaert. 2005. Finnish wolves avoid roads and settlements. *Annales Zoologici Fennici* 42:523-532.

Karlsson, J., M. Eriksson, and O. Liberg. 2007. At what distance do wolves move away from an approaching human? *Canadian Journal of Zoology* 85(11):1193-1197. http://dx.doi.org/10.1139/Z07-099

Kasworm, W. F., and T. L. Manley. 1990. Road and trail influences on grizzly bears and black bears in Northwest Montana. *Bears: Their Biology and Management* 8:79-84. http://dx.doi.org/10.2307/3872905

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management* 68:774-789. http://dx.doi.org/10.2193/0022-541X(2004)068[0774:UAIOLR]2.0.CO;2

Keller, B. J., and L. C. Bender. 2007 Bighorn sheep response to road-related disturbances in Rocky Mountain National Park, Colorado. *Journal of Wildlife Management* 71(7):2329-2337. http://dx.doi.org/10.2193/2006-486

Kortello, A. D., T. E. Hurd, and D. L. Murray. 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. *Ecoscience* 14(2):214-222. http://dx.doi.org/10.2980/1195-6860(2007)14[214:IBCPCA]2.0.CO;2

Kuck, L., G. L. Hompland, and E. H. Merrill. 1985. Elk calf response to simulated mine disturbance. *Journal of Wildlife Management* 49(3):751-757. http://dx.doi.org/10.2307/3801706

Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78(1):150-157. http://dx.doi.org/10.1139/z99-181

Long, J. S., and J. Freese. 2006. *Regression models for categorical dependent variables using Stata* Second edition. Stata Press, College Station, Texas, USA.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69(4):1691-1707. http://dx.doi.org/10.2193/0022-541X(2005)69[1691:HSBEBA]2.0.CO;2

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253. http://dx.doi.org/10.1038/35012251

Massolo, A., and A. Meriggi. 1998. Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. *Ecography* 21(2):97-107. http://dx.doi.org/10.1111/j.1600-0587.1998.tb00663.x

McDermid, G. J., S. E. Franklin, and E. F. LeDrew. 2005. Remote sensing for large-area habitat mapping. *Progress in Physical Geography* 29 (4):449-474. http://dx.doi.org/10.1191/0309133305pp455ra

McNay, M. E. 2002. *Wolf-human interactions in Alaska and Canada: a review of the case history.* Wildlife Technical Bulletin 13. Alaska Department of Fish and Game, Juneau, Alaska, USA.

Mech, L. D., and L. E. Boitani. 2003. *Wolves: behavior, ecology, and conservation.* The University of Chicago Press, Chicago, Illinois, USA.

Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. *Ecological Applications* 8(1):162-169. http://dx.doi.org/10.1016/S1240-1307(98)80058-7

Moorcroft, P. R., and A. Barnett. 2008. Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* 89 (4):1112-1119. http://dx.doi.org/10.1890/06-1985.1

Musiani, M., S. M. Anwar, G. J. McDermid, M. Hebblewhite, and D. J. Marceau. 2010. How humans shape wolf behavior in Banff and Kootenay National Parks, Canada. *Ecological Modelling* 221 (19):2374-2387. http://dx.doi.org/10.1016/j.ecolmodel.2010.06.019

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79 (4):1435-1441. http://dx.doi.org/10.2307/176754

Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus* 13:45-56.

Nielsen, S. E., S. Herrero, M. S. Boyce, R. D. Mace, B. Benn, M. L. Gibeau, and S. Jevons. 2004. Modelling the spatial distribution of human-caused grizzly bear mortalities in the central Rockies ecosystem of Canada. *Biological Conservation* 120 (1):101-113. http://dx.doi.org/10.1016/j.biocon.2004.02.020

Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection by recolonizing wolves in the northern Rocky Mountains of the United States. *Journal of Wildlife Management* 70(2):554-563. http://dx.doi.org/10.2193/0022-541X(2006)70[554:HSBRWI]2.0.CO;2

Oxley, D. J., M. B. Fenton, and G. R. Carmody. 1974. The effects of roads on populations of small mammals. *Journal of Applied Ecology* 11(1):51-59. http://dx.doi.org/10.2307/2402004

Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. *Journal of Wildlife Management* 65(3):573-582. http://dx.doi.org/10.2307/3803110

Paquet, P. C., J. Wierchowski, and C. Callaghan. 1996. Effects of human activity on gray wolves wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 *in* J. Green, C. Pacas, L. Cornwell, and S. Bayley, editors. *Ecological outlooks project. A cumulative effects assessment and futures outlook for the Banff Bow Valley.* Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, Ontario, Canada.

Peters, R. L., and J. D. S. Darling. 1985. The greenhouse effect and nature reserves. *BioScience* 35(11):707-717. http://dx.doi.org/10.2307/1310052

Petorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution* 20(9):503–510. http://dx.doi.org/10.1016/j.tree.2005.05.011

Robinson, G. G., M. Hebblewhite, and E. H. Merrill. 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia* 163(1):265-275. http://dx.doi.org/10.1007/s00442-010-1620-6

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management* 43(3):634-641. http://dx.doi.org/10.2307/3808741

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64(3):672-684. http://dx.doi.org/10.2307/3802737

Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. *Journal of Wildlife Management* 71 (3):868-874. http://dx.doi.org/10.2193/2006-131

Schultz, R. D., and J. A. Bailey. 1978. Responses of national park elk to human activity. *Journal of Wildlife Management* 42(1):91-100. http://dx.doi.org/10.2307/3800694

Shepherd, B., and J. Whittington. 2006. Response of wolves to corridor restoration and human use management. *Ecology and Society* 11(2): 1. [online] URL: http://www.ecologyandsociety.org/vol11/iss2/art1/

Shively, K. J., A. W. Alldredge, and G. E. Phillips. 2005. Elk reproductive response to removal of calving season disturbance by humans. *Journal of Wildlife Management* 69(3):1073-1080. http://dx.doi.org/10.2193/0022-541X(2005)069[1073:ERRTRO]2.0.CO;2

Stubblefield, C. H., K. T. Vierling, and M. A. Rumble. 2006. Landscape-scale attributes of elk centers of activity in the central Black Hills of South Dakota. *Journal of Wildlife Management* 70 (4):1060-1069. http://dx.doi.org/10.2193/0022-541X(2006)70[1060:LAOECO]2.0.CO;2

Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications* 13(4):951-963. http://dx.doi.org/10.1890/1051-0761(2003)13[951:WRTRAA]2.0.CO;2

Theuerkauf, J., W. Jedrzejewski, K. Schmidt, and R. Gula. 2001. Impact of human activity on daily movement patterns of wolves(*Canis lupus*) in the Bialowieza Forest, Poland. Pages 206-208 *in* R. Field, R. J. Warren, H. Okarma, and P. R. Sievert, editors. *Wildlife, land, and people: priorities for the 21st century: Proceedings of the Second International Wildlife Management Congress.* The Wildlife Society, Bethesda, Maryland, USA.

Theuerkauf, J., W. Jedrzejewski, K. Schmidt, and R. Gula. 2003. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). *Journal of Wildlife Management* 67 (4):706-716. http://dx.doi.org/10.2307/3802677

Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* 22:61-67.

Toweill, D. E., and J. W. E. Thomas. 2002. *North American elk: ecology and management.* Smithsonian Institute Press, Washington, D.C., USA.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14 (1):18-30. http://dx.doi.org/10.1046/j.1523-1739.2000.99084.x

Watson, A. E., D. N. Cole, D. L. Turner, and P. S. Reynolds. 2000. Wilderness recreation use estimation: a handbook of methods and systems. U. S. Forest Service, General Technical Report RMRS-GTR-56. Rocky Mountain Research Station, Ogden, Utah, USA.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10(4):964-976. http://dx.doi.org/10.1046/j.1523-1739.1996.10040964.x

Whittington, J., C. C. St. Clair, and G. Mercer. 2004. Path tortuosity and the permeability of roads and trails to wolf movement. *Ecology and Society* 9(1): 4. [online] URL: http://www.ecologyandsociety.org/vol9/iss1/art4/

Whittington, J., C. C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* 15 (2):543-553. http://dx.doi.org/10.1890/03-5317

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48 (8):607-615. http://dx.doi.org/10.2307/1313420

Wisdom, M. J., A. A. Ager, H. K. Preisler, N. J. Cimon, and B. K. Johnson. 2004. Effects of off-road recreation on mule deer and elk. *Transactions of the 69th North American Wildlife and Natural Resource Conference.* 531-550.

Witmer, G. W., and D. S. deCalesta. 1985. Effect of forest roads on habitat use by roosevelt elk. *Northwest Science* 59:122-125.

Yost, A. C., and R. G. Wright. 2001. Moose, caribou, and grizzly bear distribution in relation to road traffic in Denali National Park, Alaska. *Arctic* 54:41-48.

---

**APPENDIX 1.** Model results. * = reference category.

**Table A1.1.** Model results for wolves and trails. Results predict wolf occurrence near trails using matched case-control logistic regression.

| **Variable** | **Coeff.** | **Robust SE** | **z** | **P-value** |
|---|---|---|---|---|
| Cover | -0.084 | 0.036 | -2.29 | 0.022 |
| Elevation | -0.002 | <0.001 | -15.32 | <0.001 |
| Slope | -0.041 | 0.002 | -16.94 | <0.001 |
| Trail Activity | 0.001 | 0.003 | 0.38 | 0.705 |
| 0-50 m | 0.320 | 0.079 | 4.07 | <0.001 |
| 51-200 m | 0.233 | 0.062 | 3.75 | <0.001 |
| 201-400 m | 0.226 | 0.060 | 3.77 | <0.001 |
| 401-600 m | 0.017 | 0.061 | 0.28 | 0.779 |
| 601-800 m | 0.039 | 0.063 | 0.63 | 0.531 |
| >800 m | * | * | * | * |
| 0-50 m*Trail Activity | -0.129 | 0.062 | -2.08 | 0.037 |
| 51-200 m*Trail Activity | -0.079 | 0.040 | -1.98 | 0.048 |
| 201-400 m*Trail Activity | -0.067 | 0.033 | -2.03 | 0.042 |
| 401-600 m*Trail Activity | 0.005 | 0.011 | 0.44 | 0.658 |
| 601-800 m*Trail Activity | 0.003 | 0.003 | 0.80 | 0.424 |
| >800 m*Trail Activity | * | * | * | * |

**Table A1.2**. Model results for wolves near roads. Results predict wolf occurrence near roads using matched case-control logistic regression.

| **Variable** | **Coeff.** | **Robust SE** | **z** | **P-value** |
|---|---|---|---|---|
| Cover | -0.091 | 0.042 | -2.18 | 0.029 |
| Elevation | -0.002 | <0.001 | -12.58 | <0.001 |
| Slope | -0.048 | 0.003 | -17.02 | <0.001 |
| Road Activity | 0.004 | <0.001 | 4.89 | <0.001 |
| 0-50 m | 0.279 | 0.144 | 1.94 | 0.052 |
| 51-200 m | 0.418 | 0.112 | 3.74 | <0.001 |

(con'd)

| | | | | |
|---|---|---|---|---|
| 201-400 m | 0.355 | 0.107 | 3.31 | 0.001 |
| 401-600 m | 0.182 | 0.120 | 1.51 | 0.130 |
| 601-800 m | 0.060 | 0.143 | 0.42 | 0.677 |
| >800 m | * | * | * | * |
| 0-50 m*Road Activity | -0.002 | 0.001 | -2.94 | 0.003 |
| 51-200 m*Road Activity | -0.001 | <0.001 | -1.96 | 0.049 |
| 201-400 m*Road Activity | <0.001 | <0.001 | -0.81 | 0.418 |
| 401-600 m*Road Activity | <0.001 | <0.001 | -0.32 | 0.747 |
| 601-800 m*Road Activity | <0.001 | <0.001 | -0.50 | 0.617 |
| >800 m*Road Activity | * | * | * | * |

**Table A1.3**. Model results for elk near trails. Results predict elk occurrence near trails using matched case-control logistic regression.

| **Variable** | **Coeff.** | **Robust SE** | **z** | **P-value** |
|---|---|---|---|---|
| Elevation | <-0.001 | <0.001 | -0.52 | 0.605 |
| Slope | -0.018 | 0.003 | -5.34 | <0.001 |
| Greenness | 0.168 | 0.023 | 7.35 | <0.001 |
| Trail Activity | 0.026 | 0.019 | 1.36 | 0.173 |
| 0-50 m | 0.229 | 0.391 | 0.59 | 0.558 |
| 51-200 m | -0.142 | 0.196 | -0.72 | 0.471 |
| 201-400 m | 0.027 | 0.121 | 0.22 | 0.822 |
| 401-600 m | 0.362 | 0.117 | 3.10 | 0.002 |
| 601-800 m | 0.324 | 0.113 | 2.86 | 0.004 |
| >800 m | * | * | * | * |
| 0-50 m*Trail Activity | -0.350 | 0.277 | -1.26 | 0.206 |
| 51-200 m*Trail Activity | -0.091 | 0.050 | -1.78 | 0.075 |
| 201-400 m*Trail Activity | -0.071 | 0.030 | -2.37 | 0.018 |
| 401-600 m*Trail Activity | -0.028 | 0.029 | -0.98 | 0.329 |
| 601-800 m*Trail Activity | -0.033 | 0.016 | -2.03 | 0.042 |
| >800 m*Trail Activity | * | * | * | * |

(con'd)

**Table A1.4** . Model results for elk near roads. Results predict elk occurrence near roads using matched case-control logistic regression.

| **Variable** | **Coeff.** | **Robust SE** | **z** | **P-value** |
|---|---|---|---|---|
| Elevation | -0.002 | <0.001 | -5.71 | <0.001 |
| Slope | 0.001 | 0.005 | 0.11 | 0.916 |
| Greenness | 0.211 | 0.026 | 8.11 | <0.001 |
| Road Activity | -0.001 | 0.001 | -1.80 | 0.071 |
| 0-50 m | 0.103 | 0.219 | 0.47 | 0.637 |
| 51-200 m | 0.017 | 0.138 | 0.12 | 0.903 |
| 201-400 m | 0.153 | 0.126 | 1.22 | 0.223 |
| 401-600 m | 0.100 | 0.118 | 0.84 | 0.400 |
| 601-800 m | 0.228 | 0.106 | 2.16 | 0.031 |
| >800 m | * | * | * | * |
| 0-50 m*Road Activity | -0.006 | 0.002 | -2.53 | 0.011 |
| 51-200 m*Road Activity | -0.001 | 0.001 | 1.26 | 0.208 |
| 201-400 m*Road Activity | <-0.001 | 0.001 | -0.02 | 0.988 |
| 401-600 m*Road Activity | <0.001 | 0.001 | 0.16 | 0.870 |
| 601-800 m*Road Activity | <-0.001 | 0.001 | -0.28 | 0.779 |
| >800 m*Road Activity | * | * | * | * |

**Table A1.5**. Model results for wolves on trails. Results predict wolf occurrence near trails using matched case-control logistic regression and 0-50 m as the reference category.

| **Variable** | **Coeff.** | **Robust SE** | **z** | **P-value** |
|---|---|---|---|---|
| Cover | -0.084 | 0.036 | -2.29 | 0.022 |
| Elevation | -0.002 | <0.001 | -15.32 | <0.001 |
| Slope | -0.041 | 0.002 | -16.94 | <0.001 |
| Trail Activity | -0.127 | 0.061 | -2.06 | 0.039 |
| 0-50 m | * | * | * | * |
| 51-200 m | -0.086 | 0.066 | -1.31 | 0.192 |

(con'd)

| | | | | |
|---|---|---|---|---|
| 201-400 m | -0.094 | 0.073 | -1.29 | 0.198 |
| 401-600 m | -0.302 | 0.081 | -3.76 | <0.001 |
| 601-800 m | -0.281 | 0.086 | -3.25 | 0.001 |
| >800 m | -0.320 | 0.079 | -4.07 | <0.001 |
| 0-50 m*Trail Activity | * | * | * | * |
| 51-200 m*Trail Activity | 0.049 | 0.063 | 0.78 | 0.433 |
| 201-400 m*Trail Activity | 0.061 | 0.066 | 0.93 | 0.355 |
| 401-600 m*Trail Activity | 0.134 | 0.063 | 2.13 | 0.034 |
| 601-800 m*Trail Activity | 0.131 | 0.062 | 2.12 | 0.034 |
| >800 m*Trail Activity | 0.129 | 0.062 | 2.08 | 0.037 |

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

Mary M. Rowland[1], Michael J. Wisdom, Bruce K. Johnson, and Mark A. Penninger

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 effects 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), Gucinski 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.

---

[1] Suggested citation: M. M. Rowland, M. J. Wisdom, B. K. Johnson, and M. A. Penninger. 2005. Effects of Roads on Elk: Implications for Management in Forested Ecosystems. Pages 42-52 *in* Wisdom, M. J., technical editor, The Starkey Project: a synthesis of long-term studies of elk and mule deer. Reprinted from the 2004 Transactions of the North American Wildlife and Natural Resources Conference, Alliance Communications Group, Lawrence, Kansas, USA.

## 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, Leptich 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 downfall (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 generally 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 commonly 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 Millspaugh 1999, Johnson et al. 2000).

Land managers in turn have incorporated concerns about elk and roads into formal 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/km$^2$) in general, but no more than 1.5 miles per square mile (0.9 km/km$^2$) 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/km$^2$), 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).

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 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.”

## Acknowledgments

We thank J. G. Kie, G. J. Roloff, and B. C. Wales for reviewing earlier drafts of this manuscript. C. Whitlock provided information about the Dark Meadow project and planning for the Wallow-Whitman National Forest and B. Fischer prepared the figures. Funding for the Starkey roads study was provided by the Oregon Department of Fish and Wildlife and the U.S. Department of Agriculture, Forest Service.

## Literature Cited

Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *Journal of Mammalogy* 84:1076-1088.

Benkobi, L., M. A. Rumble, G. C. Brundige, and J. J. Millspaugh. 2004. *Refinement of the Arc-Habcap model to predict habitat effectiveness for elk*. U. S. Department of Agriculture, Forest Service, Research Paper RMRS-RP-51, Fort Collins, Colorado.

Bettinger, P., K. Boston, and J. Sessions. 1999. Combinatorial optimization of elk habitat effectiveness and timber harvest volume. *Environmental Modeling and Assessment* 4:143-153.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. *Journal of Wildlife Management* 61:1115-1126.

Cooper, A. B., and J. J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. *Ecological Applications* 80:566-575.

Didier, K. A., and W. F. Porter. 1999. Large-scale assessment of potential habitat to restore elk to New York State. *Wildlife Society Bulletin* 27:409-418.

Edge, W. D., and C. L. Marcum. 1991. Topography ameliorates the effects of roads and human disturbance on elk. In *Proceedings Elk Vulnerability Symposium*, eds. A. G. Christensen, L. J. Lyon, and T. N. Lonner, 132-137. Bozeman: Montana State University.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207-231.

Forman, R. T. T., D. Sperling, J. A. Bissonette et al. 2003. *Road ecology: science and solutions*. Washington, DC: Island Press.

Gaines, W. L., P. H. Singleton, and R. C. Ross. 2003. *Assessing the cumulative effects of linear recreation routes on wildlife habitats on the Okanogan and Wenatchee National Forests*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-586, Portland, Oregon.

Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17:420-432.

Gratson, M. W., and C. Whitman. 2000b. Characteristics of Idaho elk hunters relative to road access on public lands. *Wildlife Society Bulletin* 28:1016-1022.

Gratson, M. W., and C. Whitman. 2000a. Road closures and density and success of elk hunters in Idaho. *Wildlife Society Bulletin* 28:302-10.

Gucinski, H., M. H. Brooks, M. J. Furniss, and R. R. Ziemer. 2001. *Forest roads: a synthesis of scientific information*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-509, Portland, Oregon.

Havlick, D. G. 2002. *No place distant: Roads and motorized recreation on America's public lands*. Washington, DC: Island Press.

Hayes, S. G., D. J. Leptich, and P. Zager. 2002. Proximate factors affecting male elk hunting mortality in northern Idaho. *Journal of Wildlife Management* 66:491-499.

Hieb, S. R., ed. 1976. *Proceedings of the elk-logging-roads symposium*. Moscow: Forest, Wildlife, and Range Experimental Station, University of Idaho.

Hillis, J. M., M. J. Thompson, J. E. Canfield, L. J. Lyon, and T. N. Lonner. 1991. Defining elk security: the Hillis paradigm. In *Proceedings Elk Vulnerability Symposium,* eds. A. G. Christensen, L. J. Lyon, and T. N. Lonner, 38-43. Bozeman: Montana State University.

Hitchcock, M., and A. Ager. 1992. *Microcomputer software for calculating an elk habitat effectiveness index on Blue Mountain winter range*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-301, Portland, Oregon.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. *Journal of Wildlife Management* 64:685-697.

Leege, T. A. 1984. *Guidelines for evaluating and managing summer elk habitat in northern Idaho*. Idaho Department of Fish and Game, Wildlife Bulletin 11, Boise, Idaho.

Leptich, D. J., and P. Zager. 1991. Road access management effects on elk mortality and population dynamics. In *Proceedings Elk Vulnerability Symposium*, eds. A. G. Christensen, L. J. Lyon, and T. N. Lonner, 126-131. Bozeman: Montana State University.

Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. *Journal of Forestry* 79:658-660.

Lyon, L. J. 1983. Road density models for describing habitat effectiveness for elk. *Journal of Forestry* 81:592-595.

Lyon, L. J. 1984. *Field tests of elk/timber coordination guidelines*. U.S. Department of Agriculture, Forest Service, Research Paper INT-RP-325, Ogden, Utah.

Lyon, L. J., and A. G. Christensen. 1992. *A partial glossary of elk management terms*. U.S. Department of Agriculture, Forest Service, General Technical Report INT-GTR-288, Portland, Oregon.

Lyon, L. J., and A. G. Christensen. 2002. Elk and land management. In *North American elk: ecology and management*, eds. D. E. Toweill and J. W. Thomas, 557-581. Washington, DC: Smithsonian Institution Press.

Lyon, L. J., T. N. Lonner, J. P. Weigand, C. L. Marcum, W. D. Edge, J. D. Jones, D. W. McCleerey, and L. L. Hicks. 1985. *Coordinating elk and timber management: Final report of the Montana Cooperative Elk-Logging Study*. Helena: Montana Department of Fish, Wildlife, and Parks.

Marcum, C. L., and W. D. Edge. 1991. Sexual differences in distribution of elk relative to roads and logged areas in Montana. In *Proceedings Elk Vulnerability Symposium*, eds. A. G. Christensen, L. J. Lyon, and T. N. Lonner, 142-148. Bozeman: Montana State University.

McCorquodale, S. M., R. Wiseman, and C. L. Marcum. 2003. Survival and harvest vulnerability of elk in the Cascade Range of Washington. *Journal of Wildlife Management* 67:248-257.

Millspaugh, J. J. 1999. Behavioral and physiological response of elk to human activities in the southern Black Hills, South Dakota. Ph.D. dissertation, University of Washington, Seattle.

Millspaugh, J. J., R. J. Woods, K. E. Hunt, K. J. Raedeke, G. C. Brundige, B. E. Washburn, and S. K. Wasser. 2001. Fecal glucocorticoid assays and the physiological stress response in elk. *Wildlife Society Bulletin* 29:899-907.

Perry, C., and R. Overly. 1977. *Impact of roads on big game distribution in portions of the Blue Mountains of Washington*. Washington Game Department, Bulletin No. 11, Olympia, Washington.

Roloff, G. J. 1998. Habitat potential model for Rocky Mountain elk. In *Proceedings 1997 Deer/Elk Workshop*, *Rio Rico, Arizona*, ed. J. C. deVos, Jr., 158-175. Phoenix: Arizona Game and Fish Department.

Roloff, G. J., B. Carroll, and S. Scharosch. 1999. A decision support system for incorporating wildlife habitat quality into forest planning. *Western Journal of Applied Forestry* 14:91-99.

Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for elk. *Journal of Wildlife Management* 65:899-914.

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management* 43:634-641.

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

Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64:672-684.

Thomas, J. W., H. Black, Jr., R. J. Scherzinger, and R. J. Pedersen. 1979. Deer and elk. In *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington,* ed. J. W. Thomas, 104-127. U.S. Department of Agriculture, Forest Service, Agricultural Handbook No. 553. Portland, Oregon.

Thomas, J. W., D. A. Leckenby, M. Henjum, R. J. Pedersen, and L. D. Bryant. 1988. *Habitat-effectiveness index for elk on Blue Mountain winter ranges*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-218, Portland, Oregon.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18-30.

Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of northcentral Idaho. *Journal of Wildlife Management* 57:495-502.

U.S. Department of Agriculture, Forest Service. 1990a. *Umatilla National Forest Land and Resource Management Plan*. Pendleton, Oregon.

U.S. Department of Agriculture, Forest Service. 1990b. *Wallowa-Whitman National Forest Land and Resource Management Plan*. Baker City, Oregon.

U.S. Department of Agriculture, Forest Service. 2003. *Dark Meadow restoration environmental assessment*. La Grande Ranger District, Wallowa-Whitman National Forest, La Grande, Oregon.

U.S. Government, Office of the Federal Register. 2001. *Rules and regulations*. Federal Register 66: 9 (Jan. 12, 2001): 3244-3273.

Weber, K. T., C. L. Marcum, M. G. Burcham, and L. J. Lyon. 2000. Landscape influences on elk vulnerability to hunting. *Intermountain Journal of Science* 6:86-94.

Wertz, T. L., A. Blumton, and L. E. Erickson. 2004. Conflict resolution by adaptive management: moving elk where they want to go. In *Proceedings 2001 Western States and Provinces Deer and Elk*

*Workshop*, ed. J. Mortensen, D. G. Whittaker, E. C. Meslow et al., 59-66. Salem: Oregon Department of Fish and Wildlife.

Wisdom, M. J. 1998. Assessing life-stage importance and resource selection for conservation of selected vertebrates. Ph.D. dissertation, University of Idaho, Moscow.

Wisdom, M. J., A. A. Ager, H. K. Preisler, N. J. Cimon, and B. K. Johnson. 2004a. Effects of off-road recreation on mule deer and elk. *Transactions of the North American Wildlife and Natural Resources Conference* 69:531-550.

Wisdom, M. J., L. R. Bright, C. G. Carey, W. W. Hines, R. J. Pedersen, D. A. Smithey, J. W. Thomas, and G. W. Witmer. 1986. *A model to evaluate elk habitat in western Oregon*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Publication No. R6-F&WL-216-1986, Portland, Oregon.

Wisdom, M. J., N. J. Cimon, B. K. Johnson, E. O. Garton, and J. W. Thomas. 2004b. Spatial partitioning by mule deer and elk in relation to traffic. *Transactions of the North American Wildlife and Natural Resources Conference* 69:509-530.

Witmer, G. W., and D. S. deCalesta. 1985. Effect of forest roads on habitat use by Roosevelt elk. *Northwest Science* 59:122-125.

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 mi/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.

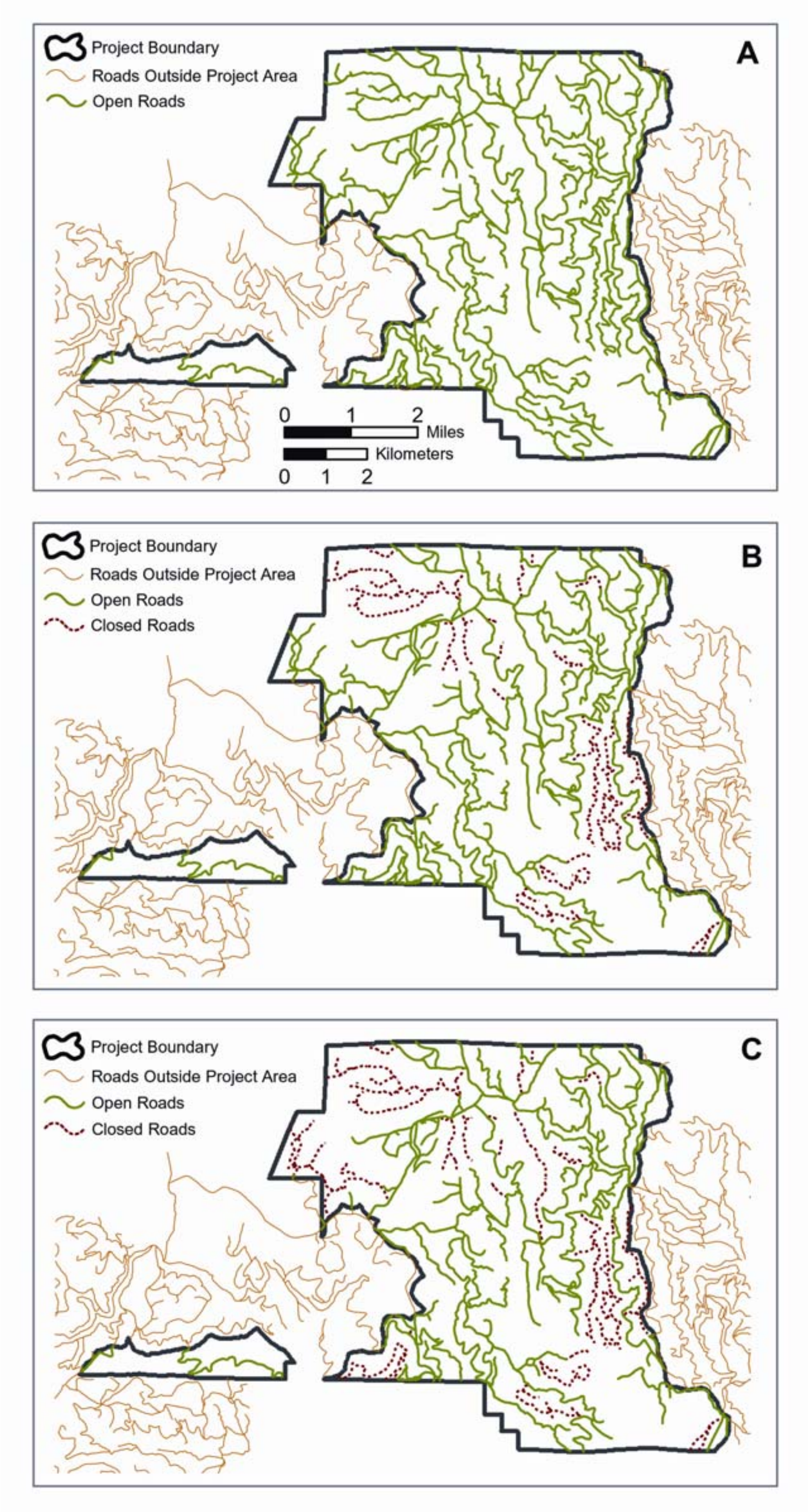


Figure 1. Open roads under three alternatives of the Dark Meadow Restoration Project, Wallowa-Whitman National Forest, northeastern Oregon: the “no action” alternative (A); Alternative 1 (B); and Alternative 2 (C). Open roads were defined as any road available to motorized traffic, including roads officially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

Elk Distribution and Modeling in Relation to Roads
Author(s): Mary M. Rowland, Michael J. Wisdom, Bruce K. Johnson, John G. Kie
Source: *The Journal of Wildlife Management*, Vol. 64, No. 3 (Jul., 2000), pp. 672-684
Published by: Allen Press
Stable URL: http://www.jstor.org/stable/3802737
Accessed: 08/01/2009 11:26

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=acg.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

*Allen Press* is collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management.*

http://www.jstor.org

TER. 1999. Declining survival of ring-necked pheasant chicks in Illinois in the late 1900s. Journal of Wildlife Management 63:705–710.

———, ———, ———, AND ———. 2000. Annual set-aside programs and habitat quality in Illinois and the Midwest: a long-term perspective. Wildlife Society Bulletin 28:347–354.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

*Received 2 February 1999.*
*Accepted 2 February 2000.*
*Associate Editor: Dabbert.*

# ELK DISTRIBUTION AND MODELING IN RELATION TO ROADS

MARY M. ROWLAND,[1] Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA
MICHAEL J. WISDOM, U.S. Forest Service, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA
BRUCE K. JOHNSON, Oregon Department of Fish and Wildlife, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA
JOHN G. KIE, U.S. Forest Service, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA

***Abstract:*** We tested performance of 3 aspects of an elk (*Cervus elaphus*)–road density model that has been used extensively throughout western North America but has not been sufficiently validated. First, we tested the hypothesis that elk selection of habitats increases with increasing distance away from open roads. This forms the empirical basis for the model. Second, we compared the model's predictions of relative elk habitat selection, or habitat effectiveness (HE), with observed values at varying levels of road density. And third, we examined the potentially confounding effects of different spatial patterns of roads on model predictions. We conducted our study during spring and summer, 1993–95, at the Starkey Experimental Forest and Range (Starkey), northeast Oregon. Selection ratios were calculated using >100,000 recorded locations of 89 radio-collared female elk, with locations mapped in relation to 0.1-km-wide distance bands away from open roads. Selection ratios increased with increasing distance from open roads, and varied between seasons, but not among years or individual animals. Linear regression models, using distance to open roads as a predictor, accounted for significant variation in selection ratios during spring and summer. Model predictions of HE, as measured by number of elk locations, corresponded only weakly, however, with observed values of HE. The contradictory results of these 2 analyses may be explained in part by our simulation results, which showed that potential reductions in elk HE vary strongly with the spatial pattern of roads, which is not measured by the elk–road density model. Our results suggest that (1) management of roads and related human activities during spring and summer should remain an important consideration for modeling and managing the elk resource; and (2) a spatially explicit road component is needed for elk habitat models.

***JOURNAL OF WILDLIFE MANAGEMENT 64(3):672–684***

***Key words:*** *Cervus elaphus,* disturbance, elk, forest management, habitat effectiveness models, Oregon, radiotelemetry, roads, road density, Starkey Project.

Shifts in elk distribution away from roads used by motorized vehicles have been documented across many areas of the western United States (Hieb 1976, Perry and Overly 1977, Lyon 1979, Rost and Bailey 1979, Witmer and deCalesta 1985). Such shifts may reduce carrying capacity of some areas (Wisdom and Thomas 1996) and redistribute elk from public to private lands (Wertz et al. 1996). Roads and associated disturbances have been presumed to be the primary agent driving elk distribution across seasons and landscapes (Leege 1984, Lyon 1984, Lyon et al. 1985). To better quantify this relation, an elk–road density model was developed (Thomas et al. 1979, Lyon 1983) that has been used extensively throughout the intermountain west as a component of elk habitat effectiveness models (Leege 1984; Thomas et al. 1979, 1988; Wisdom et al. 1986).

Habitat effectiveness for elk has been defined as the "percentage of available habitat that is usable by elk outside the hunting season" (Lyon and Christensen 1992:4). The road component of HE models was developed by manipulating data based on indices of elk use (pellet group

---

[1] E-mail: mrowland@eou.edu

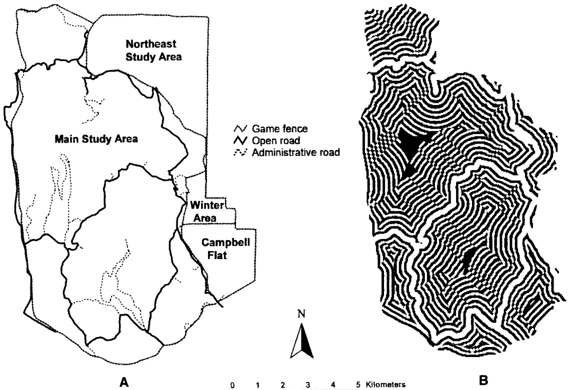


Fig. 1. Study area and roads in the Starkey Experimental Forest and Range, Oregon (A), and delineation of 0.1-km distance bands buffered from open roads (B) for evaluation of elk distribution in relation to roads, 1993–95. In "B" all pixels >1.9 km from an open road were combined in band 2.0; broad, light gray band indicates open road and 0.1 km on either side of road.

densities) in relation to distance from open roads, but not in relation to open road densities (Lyon 1979, 1983). Although the road density variable and other components of elk HE models have undergone only limited validation (Lyon 1984), these models and their variants have been used extensively in National Forest System planning and management (Edge et al. 1990, Christensen et al. 1993). In addition, the prediction of HE for the elk–road density model assumes no change in HE with variation in the underlying spatial pattern of roads, despite substantial differences in existing road patterns on landscapes where the model is used.

Widespread use of the elk–road density model is likely to continue: elk remain a focal species in land and resource management of National Forests in the interior northwest (Edge et al. 1990, Groves and Unsworth 1993) and are of considerable economic importance (Duffield and Holliman 1988, Loomis et al. 1988, Bolon 1994). Land management plans for National Forests often include specific standards for elk HE values related to road densities or other road management criteria (Carter 1992). Moreover, roads are of increasing concern for wildlife occurring on public lands in the interior northwest (Wisdom et al. 2000), as well as for terrestrial and aquatic communities worldwide (Trombulak and Frissell 2000). Better quantification of effects of roads on elk and other wildlife is needed, because road-related mitigation for wildlife is costly and logistically challenging. Closing or obliterating roads to reduce vehicle access can cost millions of dollars and be politically unpopular; likewise, maintaining open roads may be expensive and controversial.

In response to a long-standing need for validation, we tested performance of 3 aspects of the elk–road density model of Lyon (1983). Our specific objectives were to (1) test the hypothesis that the degree of selection of habitats by elk increases with increasing distance from open roads (test of elk–distance from roads hypothesis), (2) compare model predictions of HE with observed values (evaluation of HE model predictions), and (3) examine potentially confounding effects of different spatial patterns of roads on model performance (simulation of spatial-pattern effect).

## STUDY AREA

The Starkey Experimental Forest and Range is a research area of about 101 km$^2$ in northeast Oregon (Fig. 1A). The Starkey Project was initiated there in 1987; its primary purpose is to support long-term studies of elk, mule deer (*Odocoileus hemionus*), and cattle on summer range in relation to timber and grazing management, recreation, impacts of roads, and road-associated human activities (Rowland et al. 1997). The Starkey area is particularly useful for such ungulate research because it reflects "the history of resource exploitation typical of the ponderosa pine-bunchgrass forests" (Skovlin 1991:1). Also, traffic levels, recreational activities (including hunting), cattle grazing, and timber management resemble patterns of use on adjacent public lands (Skovlin 1991, Rowland et al. 1997).

To support ungulate research objectives, most of Starkey is enclosed by ungulate-proof fence of New Zealand woven-wire (Bryant et al. 1993, Rowland et al. 1997). Starkey has been divided into 4 areas, each fenced separately (Fig. 1A). Two areas called main (77.6 km$^2$) and northeast (14.5 km$^2$) are used for telemetry studies during spring–fall and contain known population densities of mule deer and elk that are managed to meet study objectives (Rowland et al. 1997). Starkey also contains a 265-ha winter area (Fig. 1A), where ungulates are fed at a maintenance level from December to April (Wisdom et al. 1993, Rowland et al. 1997).

Our study was confined to the main area, where about 430 adult elk were present from early April until mid-December each year during our study (1993–95), along with 540 domestic cow–calf pairs and 270 adult mule deer. Densities of adult elk in the study area (5.5/km$^2$) were similar to those in occupied elk habitat on adjacent public lands (B. K. Johnson, unpublished data). Moreover, habitat available to elk in the main study area was 2–4 times larger than typical summer home ranges of elk in the Blue Mountains (20–29 km$^2$; Leckenby 1984), thus providing study animals with large-scale habitat choices commensurate with those of free-ranging herds.

During our study, about 44 of 201 km of roads (22%) were open to the public (Fig. 1A). Open roads crossed a variety of slopes, but most were built on gentle terrain (mean slope = 12%). All open roads were single lane (3.5–4.5 m wide) and primarily graveled. Starkey roads are similar to those on adjacent National Forest lands (R. K. Nielsen, U.S. Forest Service, personal communication), and are comparable to the secondary roads defined by Perry and Overly (1977) in their analysis of elk–road relations in the Blue Mountains of Washington and to roads used by Lyon (1983) in his development and refinement of the elk–roads model. The majority of Starkey roads (78%) were closed to the public; however, about one-half of the closed roads were open for administrative use. Administrative roads were typically narrower and only occasionally graveled.

Over 70 traffic counters monitor traffic rates at Starkey (Rowland et al. 1997). Daytime traffic rates on open roads were usually 1–4 vehicles/12 hr, but sometimes exceeded 50 vehicles/12 hr on certain road segments (M. J. Wisdom, unpublished data). Summer traffic rates were consistently higher than those in spring. Traffic rates on administrative roads were much lower than those on open roads, generally ≤1 vehicle/12 hr.

Total road density in the main study area was 2.6 km/km$^2$, with about 0.6 km/km$^2$ of open roads; road densities were constant during the 3 years of this study. Open road density on National Forests surrounding Starkey was about 1.3 km/km$^2$, and is steadily declining with intentional closure of roads to meet travel management plan objectives (U.S. Forest Service 1990).

## METHODS

### Characterizing Road Location and Type

Road locations were verified with a differentially corrected global positioning system (DGPS), mapped as a vector layer, and rasterized in a spatial database of 30- × 30-m pixels (Rowland et al. 1998). Road data, both spatial and attribute, were entered in a geographic information system (GIS) and digitized into Universal Transverse Mercator Grid System (UTM) coordinates. Three types of roads were designated in the database: open (open to the public); closed (no known vehicle use or physically barricaded); and administrative (restricted vehicle use, not open to the public).

### Monitoring Animal Movements

Elk were trapped each year in the winter area (Fig. 1A), as well as in 2 corral traps placed in the main area (Rowland et al. 1997). All animal handling and feeding followed protocols approved by an Institutional Animal Care and Use Committee (Wisdom et al. 1993). Radiocollars were placed on female elk in spring before animals were released into different study areas. Whenever possible, collars were placed on elk that were tracked the previous year. Collars functioned for about 2.5 years, but were replaced whenever an elk was recaptured. The percentage of female elk monitored, relative to the total adult female population in the study area, ranged from 12–19% during our study.

Locations were generated with the use of a LORAN-C automated telemetry system (Dana et al. 1989, Findholt et al. 1996, Rowland et al. 1997, Johnson et al. 1998). The telemetry system was activated each year from early April until mid-December. Each telemetry location was assigned to UTM coordinates of the associated 30- × 30-m pixel. Locations were 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). Mean (±SE) position error for locations was 53 ± 5.9 m (Findholt et al. 1996).

Elk locations for our analyses were collected during spring (mid-Apr to mid-Jun) and summer (mid-Jun to mid-Aug) 1993–95, resulting in 6 sampling periods (2 seasons × 3 yr). We did not analyze locations obtained in the fall when hunts were conducted to eliminate potentially confounding effects of increased traffic rates and hunter behavior on elk. Moreover, the elk–road density model was developed primarily from data collected outside the hunting season (Lyon 1983).

More than 100,000 locations were recorded for 32–53 elk that were monitored during these 6 sampling periods, with 1 location/elk systematically collected about every 3–5 hr. Mean (±SE) time interval between locations (3.7 ± 0.6 hr) was similar among elk, and locations from each elk were typically spread evenly across each sampling period. Each elk in our analyses had ≥100 locations per sampling period; however, mean (±SE) number of locations per animal in a period was substantially larger, ranging from 247 ± 15 ($n$ = 36) to 912 ± 40 ($n$ = 33). Turnover rate among radiocollared animals in our samples was >50% (i.e., less than half the elk in our spring samples were also included the previous summer). Only 4 elk from the spring 1993 sample remained in the summer 1995 sample.

## Testing the Elk–distance from Roads Hypothesis

All 86,000 of the 30- × 30-m pixels in the main study area were buffered against open roads with the spatial analysis software UTOOLS (Ager and McGaughey 1997) to calculate the distance from recorded elk locations to the nearest open road. Distances were straight-line and represented minimum values. Roads in an 800-m-wide band surrounding the study area were included in the buffer routine to account for open roads outside the fence that might have influenced distributions of elk within the fence (Fig. 1A). Pixels were subsequently grouped into 20 distance bands, each 0.1 km wide (Table 1; Fig.1B). The maximum distance from any pixel to an open road was 2.4 km. For distance-to-roads analysis, locations for each elk were assigned to the appropriate distance band and summed by band for each sampling period.

Each radiocollared elk was treated as a sample unit. This eliminated problems of non-independence that may arise if individual locations are considered samples (e.g., serial correlation of locations collected sequentially from an animal), or if locations are pooled across animals that have different patterns of habitat use (Aebischer et al. 1993, Otis and White 1999). We calculated a selection ratio, USEAVAIL, based on distance bands as our response variable: USEAVAIL = PROPUSE/PROPAVAIL, where PROPUSE is the proportion of use, or number of radiolocations of an elk in a distance band (OBSERVATIONS) divided by the total number of locations for that elk in the sampling period (TOTAL), and PROPAVAIL is the proportional availability of a distance band, i.e., band area divided by total study area. PROPAVAIL was constant across sampling periods and elk. Our ratio is similar to forage selection ratios commonly used in resource selection studies (Manly et al. 1993).

Table 1. Area (ha) in distance bands created for evaluation of elk distribution in relation to distance from open roads, Starkey Experimental Forest and Range, Oregon, 1993–95.

| Distance band[a] | Area | Study area (%) |
|---|---|---|
| 0.1 | 961 | 12.4 |
| 0.2 | 774 | 10.0 |
| 0.3 | 806 | 10.4 |
| 0.4 | 618 | 8.0 |
| 0.5 | 634 | 8.2 |
| 0.6 | 585 | 7.6 |
| 0.7 | 480 | 6.2 |
| 0.8 | 388 | 5.0 |
| 0.9 | 392 | 5.1 |
| 1.0 | 331 | 4.3 |
| 1.1 | 265 | 3.4 |
| 1.2 | 279 | 3.6 |
| 1.3 | 245 | 3.2 |
| 1.4 | 212 | 2.7 |
| 1.5 | 179 | 2.3 |
| 1.6 | 148 | 1.9 |
| 1.7 | 123 | 1.6 |
| 1.8 | 90 | 1.2 |
| 1.9 | 86 | 1.1 |
| 2.0 | 172 | 1.9 |

[a] Distance bands are in 0.1-km increments. Band 0.1 includes all pixels from 0–100 m from an open road; band 2.0 includes all pixels > 1.9 km from an open road.

Because our dependent variable was a ratio of 2 proportions and violated assumptions of normality and equal variance, we performed an arcsine transformation of the numerator (PROPUSE) to allow for standard statistical analysis (Zar 1984:240):

$$\text{USEAVAIL} = \{\sin^{-1}[(\text{OBSERVATIONS} + 0.375) \div (\text{TOTAL} + 0.75)]^{1/2}\}/\text{PROPAVAIL}$$

The denominator, PROPAVAIL, did not require transformation because it remained constant for each band among seasons and years. Our transformation succeeded in normalizing selection ratios across distance bands, as well as in stabilizing variances.

The transformed selection ratio also was weighted to (1) account for unequal number of locations among elk (i.e., estimates for more frequently located elk were more precise), and (2) restabilize the variance after dividing the transformed PROPUSE by PROPAVAIL (D. B. Marx, University of Nebraska, personal communication):

$$\text{WEIGHT} = \text{PROPAVAIL}(\text{TOTAL})^{1/2}$$

We first tested whether selection ratios (response variable) varied among distance bands or animals (nested within yr) for each sampling period using analysis of variance (ANOVA; PROC GLM, unbalanced design; SAS Institute 1989). Next we pooled all data to test for effects of distance band, animal, year, and season (main effects) on selection ratios with a factorial ANOVA for unbalanced designs. Additional ANOVAs were used to test for year effect within linear models for each season. To overcome the problem of variable sample size for our unbalanced design, we used least square means to test for differences in USEAVAIL among years when a year effect was significant (PROC GLM; SAS Institute 1989).

To develop predictive models for elk selection in relation to distance from roads, we explored the mathematical relation between selection ratio (USEAVAIL), animal, and distance band for each sampling period, including use of polynomial terms up to the 5th degree for distance band (PROC GLM; SAS Institute 1989). We found that the more complex models were statistically significant in all periods ($P < 0.001$ for cubic or higher order terms for distance band), but the simple linear term for distance band also was significant and accounted for 90–97% of the model sum of squares. Consequently, we estimated model parameters for only simple linear models for both seasons (i.e., USEAVAIL on distance band as a continuous variable).

Variance of USEAVAIL was markedly higher in the outer distance bands, despite the transformations, and mean USEAVAIL declined in the outermost 1 or 2 bands in every period. Bands 1.9 and 2.0 were isolated (Fig. 1B), and thus likely to be largely unavailable to many elk in our study area. Consequently, we omitted these 2 bands (which together composed only 3% of the study area) from our model fitting to better define relations within the first 1.8 km from open roads. Statistical inferences for all tests involving distance bands were based on transformed, weighted selection ratios; we considered probabilities $\leq 0.05$ to be statistically significant.

Table 2. Characteristics of elk analysis units used in tests of elk distribution in relation to open road density, Starkey Experimental Forest and Range, Oregon, 1993–95.

| Elk analysis unit | Area (ha) | Open road density (km/km$^2$)[a] DEN1 | Open road density (km/km$^2$)[a] DEN2 |
|---|---|---|---|
| 1 | 502 | 0.93 | 0.51 |
| 2 | 560 | 0.10 | 0.05 |
| 3 | 487 | 1.54 | 0.39 |
| 4 | 579 | 1.56 | 1.28 |
| 5 | 620 | 1.33 | 0.13 |
| 6 | 423 | 0.17 | 0.08 |
| 7 | 466 | 1.39 | 1.12 |
| 8 | 449 | 0.50 | 0.44 |
| 9 | 504 | 1.28 | 1.05 |
| 10 | 548 | 1.06 | 0.91 |
| 11 | 464 | 1.17 | 0.00 |
| 12 | 650 | 1.59 | 1.03 |
| 13 | 543 | 1.09 | 0.63 |
| 14 | 477 | 1.59 | 0.69 |
| 15 | 469 | 0.69 | 0.00 |

[a] Open road densities were calculated with 2 definitions of open roads: in DEN1, open roads included administrative roads and roads open to the public; in DEN2, open roads included only those roads open to the public.

## Evaluating HE Model Predictions

To compare HE values predicted by the elk–road density model with observed values of HE from our study animals, we partitioned the study area into 15 elk analysis units that ranged in size from 423 to 650 ha. Units were placed within the 3 major subwatersheds in the study area (i.e., units did not cross subwatershed boundaries) and spanned a range of road densities (Table 2). Road densities were calculated using ARC/INFO software (Environmental Systems Research Institute 1990) by overlaying the roads vector layer with a polygon map layer of the elk analysis units. Open roads for our analysis were defined in 2 ways: (1) roads open to both public and occasional administrative use, where administrative use was limited to research activities and roads and facilities maintenance (DEN1); and (2) only those roads open to public use (DEN2).

To evaluate model predictions, we first calculated HE scores in each of our 15 units using 3 equations developed by Lyon (1983) as a "single nonlinear function." (The original equations reported in Hitchcock and Ager [1992:3] were in English units; here we present their metric equivalents.) The HE was determined as follows, where DEN = open road density in km/km$^2$: (1) if $\text{DEN} < 0.68$, $\text{HE} = 0.4 + (1 - 0.2688\ \text{DEN})^6 \times 0.6$; (2) if $0.68 \leq \text{DEN} < 1.24$, $\text{HE} = 0.486 + 0.1667(1.24 - \text{DEN})$; and (3) if

$1.24 \leq \mathrm{DEN} \leq 3.72$, $\mathrm{HE} = 0.104 + 0.154(3.72 - \mathrm{DEN})$. We calculated 2 HE scores for each unit: the first (HE1) used the density of both administrative roads and those open to the public (DEN1), and the second (HE2) used the density of only those roads open to the public (DEN2). We included both administrative and open roads to more closely match the original definitions used when the elk–road models were developed; an open road was considered one accessible to motor vehicle traffic (Lyon 1979).

For regression analysis, we pooled elk locations (dependent variable) across animals within units (i.e., elk analysis units were sampling units; PROC REG, SAS Institute 1989). Spring and summer data were analyzed separately because prior investigation of elk in relation to open roads at Starkey revealed seasonal differences in distributions (M. M. Rowland, unpublished data). Numbers of elk locations were weighted first by unit area, because units were unequal in size (Table 2), and second by total number of elk locations per period, to account for varying numbers of elk locations among periods. We hypothesized that number of elk locations would be a linearly increasing function of HE, as predicted by the model.

Because locations were pooled across elk having an unequal number of locations, we explored the distribution of locations among grids. In no case did elk occur in a single unit in a period, nor did any individual elk dominate the analyses (e.g., by having as many as twice the mean number of locations for that sampling period). Mean number of units occupied by an elk in a sampling period ranged from 7.6 to 9.2 of the 15 units available. The median number of locations for elk either equaled (2 periods) or exceeded (4 periods) the mean (i.e., the distribution of number of locations was skewed more toward animals with fewer, rather than more, locations).

### Measuring Effects of Other Environmental Variables

To address potentially confounding effects of other variables on our analysis of elk distribution in relation to roads, we calculated mean values (across all 30- × 30-m pixels) for 3 environmental variables in each distance band and elk analysis unit: tree canopy cover (%), defined as summed canopy closure for all trees with stem diameter >13 cm; slope (%); and elevation (m). We included these variables because these 3 were most likely to be correlated with locations of roads, and slope and canopy cover have previously been identified as significant variables in other analyses of elk habitat use (Edge et al. 1987, Unsworth et al. 1998). We computed Pearson correlation coefficients (PROC CORR; SAS Institute 1985) to test for associations between these 3 variables and variables used in our test of the elk–distance from roads hypothesis and in our evaluation of HE model predictions.

### Simulating Effects of Road Density Patterns

Pattern and spatial distribution of roads may influence the relative area affected in relation to use by elk. We explored the relation between open road density, road pattern, and potential habitat loss by creating 9 hypothetical analysis units, each 10.4 km$^2$. We created a unique vector map for each unit by assigning 3 road densities (0.6, 1.9, and 3.1 km/km$^2$) across the units; each density was represented by 3 road patterns (even, random, and clumped). Roads were placed east–west and north–south, at right angles to one another (Fig. 2). For the even road pattern, roads were placed at regular intervals across the landscape; clumped roads were placed at 400-m intervals and were clustered in 1 corner of the units (Fig. 2). Starting points for randomly placed roads were drawn from a random numbers table. The vector maps were then rasterized and a 250-m horizontal buffer extended on both sides of all road segments to represent the zone of potential habitat loss to elk. This distance was selected based on work by Wisdom (1998) on the mean difference between all pixels at Starkey, in relation to distance to open roads, and pixels with elk locations. Finally, we calculated the proportion of area in the zone of potential habitat loss for each of the 9 units, as well as the size of the largest block of continuous habitat unaffected by roads.

## RESULTS

### Elk–distance from Roads Hypothesis

The ratio USEAVAIL differed among bands ($P < 0.001$) but not among animals ($P > 0.953$) in each sampling period under the ANOVA. For data pooled across years and seasons ($n = 4{,}660$ elk–band–sampling period combinations), the overall ANOVA accounted for >50% of the var-

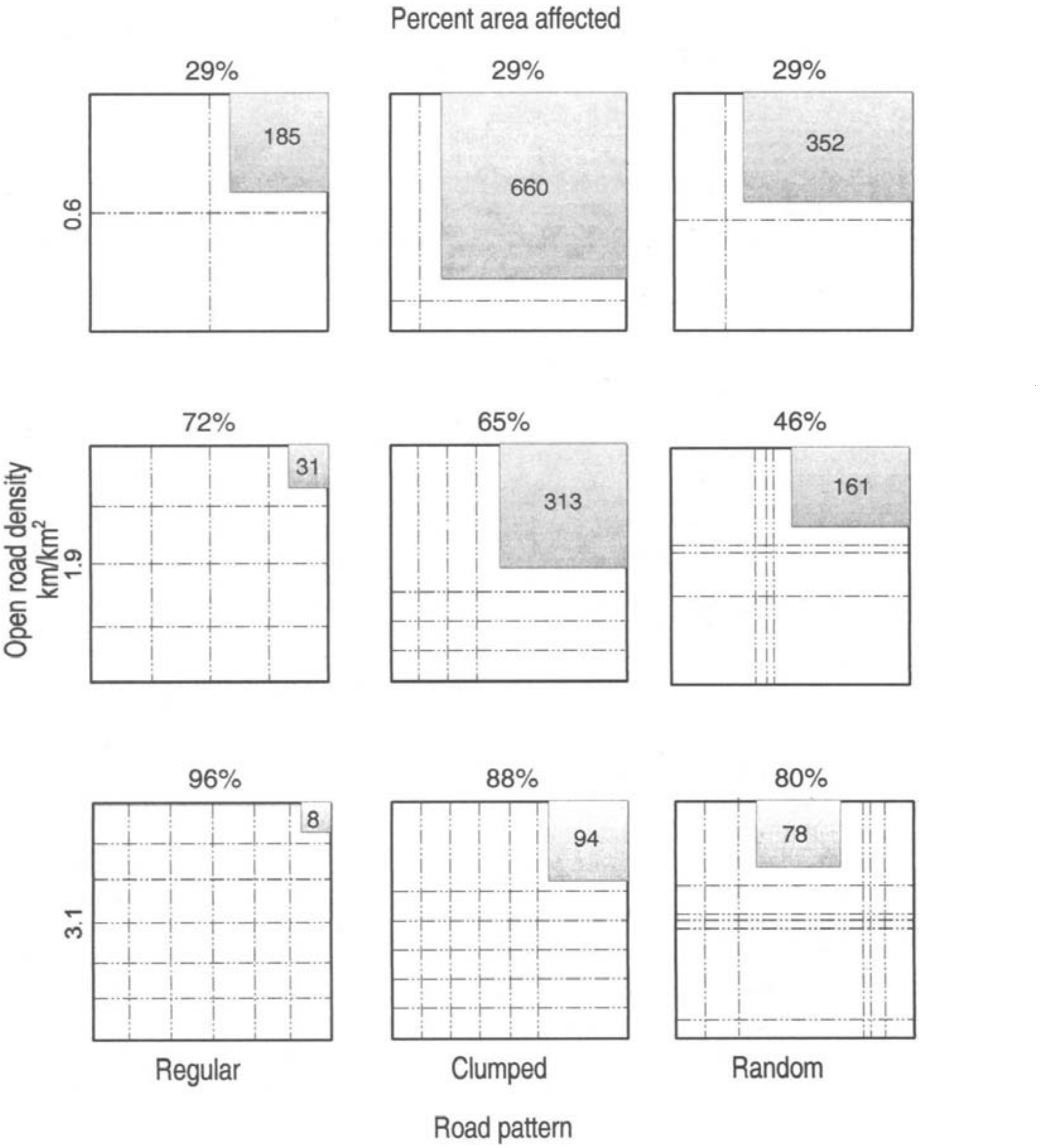


Fig. 2. Effect of road pattern and road density on area of potential habitat loss in 9 hypothetical elk analysis units. Buffer distance for road effect was 250 m on either side of roads (depicted by dashed lines). Shaded areas are largest continuous blocks of habitat unaffected by roads (ha). Total percentage of area affected by roads is reported above each unit.

iation in USEAVAIL ($F_{240,\ 4,419}$ = 22.99, $r^2$ = 0.56, $P < 0.001$). The ratio USEAVAIL differed by distance band ($F_{19,\ 4,419}$ = 261.33, $P <$ 0.001), season ($F_{1,\ 4,419}$ = 76.06, $P < 0.001$), season × distance band ($F_{19,\ 4,419}$ = 8.76, $P <$ 0.001), and year × distance band ($F_{38,\ 4,419}$ = 1.59, $P$ = 0.012), but not by year ($F_{2,\ 4,419}$ = 0.79, $P$ = 0.455) or animal ($F_{121,\ 4,419}$ = 0.64, $P$ = 0.999).

For ANOVAs run for each season separately, USEAVAIL differed in spring by distance band (linear term only; $F_{1,\ 2,071}$ = 1,819.09, $P <$ 0.001), but not by year ($F_{2,\ 2,071}$ = 0.70, $P$ = 0.498), animal ($F_{119,\ 2,071}$ = 0.41, $P$ = 1.000), or distance band × year ($F_{2,\ 2,071}$ = 1.10, $P$ = 0.333). In contrast to spring results, USEAVAIL differed among years in summer ($F_{2,\ 1,884}$ = 9.28, $P < 0.001$; Fig. 3) and by distance band × year ($F_{2,\ 1,884}$ = 13.46, $P < 0.001$). Similar to spring, selection ratios varied by distance band ($F_{1,\ 1,884}$ = 3,455.80, $P < 0.001$), but not by animal ($F_{108,\ 1,884}$ = 0.25, $P$ = 1.000).

In the linear regression model developed for spring, selection ratios increased steadily as distance from road increased ($r^2$ = 0.50, $P <$ 0.001; Fig. 3). For the 3 summer regression

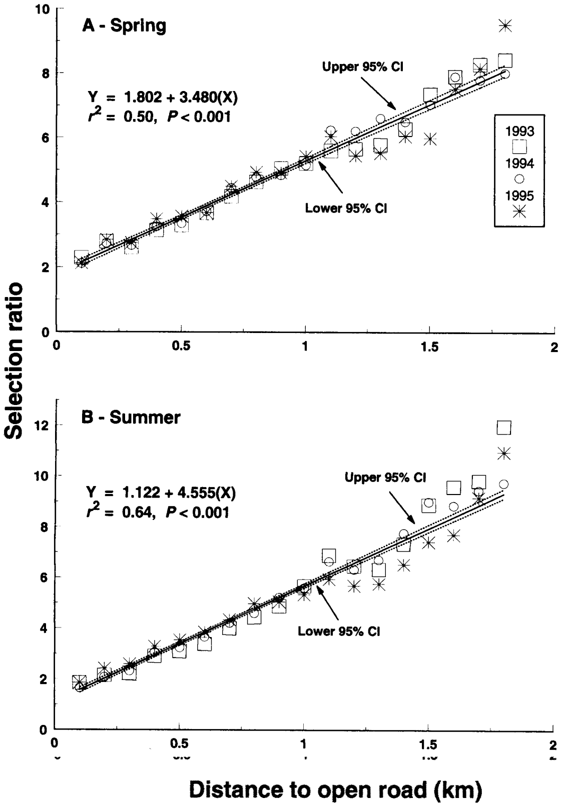


Fig. 3. Selection ratios (transformed and weighted USEAVAIL) of elk in relation to distance from open roads during spring (A) and summer (B), Starkey Experimental Forest and Range, Oregon, 1993–95 (see text for complete definition of USEAVAIL). Solid lines represent regression models for data pooled across years; dashed lines represent upper and lower bounds of the 95% confidence intervals for expected values (means) of USEAVAIL. Data points represent mean selection ratios observed for each year, by distance band. A USEAVAIL value of about 3 is equivalent to an untransformed selection ratio of 1 (i.e., no evidence of selection).

models, a positive, linear relation was found between USEAVAIL and distance band ($r^2$ = 0.64, $P < 0.001$; Fig. 3, combined model). Linear models for summer 1993 and 1994 were similar ($P$ = 0.947), but 1995 differed from 1993 ($P$ = 0.014) and from 1994 ($P$ = 0.017). Slope of the 1995 model (3.97) was less than that of 1993 (4.88) or 1994 (4.76).

## HE Model Predictions

Road densities among units ranged from 0.1–1.6 km/km² for DEN1, and 0 to 1.3 km/km² for DEN2 (Table 2). Corresponding HE1 scores ranged from 0.43 to 0.91 with both types of roads considered open, and from 0.48 to 1.00 for HE2 scores (Fig. 4). The maximum HE score (1.0) was associated with a wide range of elk numbers across the 6 sampling periods (6,497–10,190), as was the lowest score of 0.43 (507–9,202). We observed no linear relation ($P > 0.05$) between numbers of elk locations and HE, with the exception of HE2 in summer, when a weak correspondence was detected ($r^2$ = 0.124, $P$ = 0.010, Y = 1,041 + 4,860X; Fig. 4).

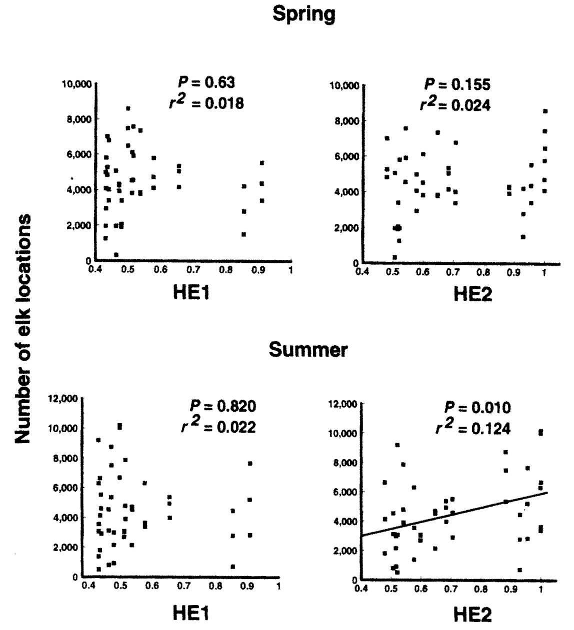


Fig. 4. Numbers of elk locations versus habitat effectiveness (HE) scores in 15 elk analysis units in the Starkey Experimental Forest and Range, Oregon, spring and summer 1993–95. The HE scores were calculated using 2 definitions of open roads: HE1 includes both administrative roads and roads open to the public; HE2 includes only roads open to the public (see text for equations for HE). Elk locations were weighted by size of units as well as number of locations per period, and pooled across animals. Regression equation for HE2 in summer: Y = 1,041 + 4,860X.

## Environmental Variables

Mean (±SE) slope was 21.5 ± 1.3% ($n$ = 20, range = 13.2–31.8) across distance bands, and was positively correlated with distance to open roads ($r$ = 0.994, $P < 0.001$). Slope averaged 18.1 ± 1.5% in the 15 elk analysis units ($n$ = 15, range = 7.7–27.9); a weak, negative correlation was found between slope and open road density ($r$ = −0.472, $P$ = 0.076). Mean (±SE) elevation (1,355 ± 2.59 m; range = 1,328–1,374 m) decreased as distance to roads increased ($r$ = −0.878, $P < 0.001$). Elevation in elk analysis units (1,358 ± 18.5 m; range = 1,210–1,458 m) was not correlated with open road density. Tree canopy cover was uniform ($P > 0.3$) across distance bands (28.0 ± 0.4%, range = 25.3–33.3%) and analysis units (27.6 ± 1.2%, range = 20.4–36.3%).

### Simulating Road Density Patterns

Road pattern visibly affected potential habitat loss in our simulated elk habitats (Fig. 2). Regularly spaced roads had the greatest percentage of habitat influenced by roads, and randomly spaced roads the least. Moreover, clumped patterns produced comparatively larger continuous blocks of habitat unaffected by roads. For example, a clumped pattern of open roads at a density of 3.1 km/km$^2$ supported a block of unroaded habitat >3 times larger than that remaining in a unit with a regular pattern of roads and a density of only 1.9 km/km$^2$ (Fig. 2).

## DISCUSSION

### Elk–distance from Roads Hypothesis

Female elk within Starkey consistently selected areas away from open roads in both spring and summer, corroborating the empirical basis for the elk–roads model (Lyon 1983) and other studies (Hieb 1976, Perry and Overly 1977, Rost and Bailey 1979). Although we observed a strong linear increase in elk selection ratios throughout the range of distances used in regression analyses (0–1.8 km), variance of USEAVAIL increased as distance from roads increased. Presumably, as elk were further removed from road-related human activities, other factors (e.g., amount and quality of forage) more strongly influenced their distribution (Wisdom 1998, B. K. Johnson, unpublished data).

Precisely defining the distance at which road effects dissipated in our study area was infeasible due to the relative rarity of areas located far from roads (Table 1, Fig. 1B). The isolation of bands 1.9 and 2.0, which occurred in only 2 patches, may have rendered these areas largely unavailable to elk in our study. More than 40% of the occurrences of zero use in our data set were in the outer 2 bands, leading to depression of mean USEAVAIL values in these bands and less precise estimates of USEAVAIL as distance from roads increased.

We observed more pronounced selection away from roads in bands closest to roads during summer (as evidenced by lower values for USEAVAIL) and a steeper slope for the summer model compared to results for spring (Fig. 3). These seasonal differences could be explained by higher traffic rates during summer (M. J. Wisdom, unpublished data), when cattle are brought to Starkey and recreational use and research activities increase. These differences did not appear to be related to elk avoidance of cattle during summer, as cattle distributions within Starkey show no relation to distribution of open roads (B. K. Johnson, unpublished data). Also, stronger selection for areas away from roads in summer was not caused by roads being located disproportionately in more open habitat types (e.g., grasslands), where forage would be expected to cure earlier than in more shaded sites. Open roads at Starkey traverse a variety of habitat types; however, the relative proportions of vegetation types in which roads occur are identical to the relative proportions of these types within the study area as a whole (M. M. Rowland, unpublished data).

Differences among years in our linear models for summer were less easily explained. Selection ratios were similar among years until about 1.2 km, where models diverged for unknown reasons, resulting in a significant distance band × year interaction (Fig. 3). Although the summer 1995 model was statistically different from the 1993 and 1994 models, the pattern of increasing elk selection with increasing distance from open roads was qualitatively similar in all 3 years. Thus, annual differences in elk selections may have had little biological significance.

### HE Model Predictions and Road Density

Despite the strong relation we detected between elk selection and distance from open roads, little or no significant relations appear to exist between number of elk locations and HE scores based on road densities. The 1 significant regression we obtained (summer-HE2) explained only 12% of the variation in elk numbers among analysis units. We believe this anomaly was largely due to differences in spatial scales associated with the 2 road metrics. That is, elk at Starkey appeared to demonstrate selection at the scale of our distance bands; however, selection away from roads was not detectable at the scale of our analysis units when HE values based on road density were used as a predictor. Apparently elk were able to select areas away from roads, yet still occur in large numbers in units with relatively high open road densities (e.g., 1.5 km/km$^2$). Similarly, Robel et al. (1993) found that inappropriate scale of model variables was likely to have caused the lack of correlation they observed between habitat suitability values for beaver (*Castor canadensis*) and densities of beaver colonies.

The conversion of data originally based on distance-to-roads to a larger scale based on open road densities may partially explain this contradiction. The original HE models for elk (Lyon 1979, 1983; Thomas et al. 1979) were developed using road densities, rather than distance-to-roads, because road density models could quantify habitat loss and account for the combined influence of multiple roads on elk (Lyon 1979). Furthermore, road densities were easily calculated for model input. Original linear models predicting HE from open road density assumed a cumulative effect of multiple roads on elk habitat, but such calculations may have overestimated losses in effective habitat, especially at higher road densities (Lyon 1979). Later models were less conservative and incorporated a "no overlap" rule, in which effects from one road were assumed to terminate at the midpoint between roads (Lyon 1983). Scaling up of the original distance-to-roads data in this manner, with its associated assumptions about elk behavior between roads and loss of habitat, may have obscured the true relation between elk distribution and roads. The use of distance bands may offer managers a more spatially appropriate scale for predicting road effects than do traditional road density models or analyses of habitats used versus those available (often described by sampling random points).

Our simulation of road pattern and its effect on potential habitat loss may offer further insight into lack of agreement between HE scores and elk numbers (Fig. 2). This exercise demonstrated that it is possible to have an area with relatively high road density, but habitat loss equivalent to an area with lower road density, depending on the spatial distribution of roads. We therefore recommend that spatial distribution of roads be considered when evaluating management units by HE scores, especially in areas with relatively few roads.

Size of our analysis units was a potential problem. Our units were small ($\bar{x}$ = 515 ha), whereas Lyon (1983) recommended analysis areas of 800–1,200 ha. We partitioned our study area to capture a range of road densities within Starkey, and in particular to obtain several units with densities <0.6 km/km$^2$, because HE declines rapidly in this portion of the model. However, we repeated our regression analysis with the study area subdivided into 7 larger analysis units ($\bar{x}$ = 1,100 ha), and obtained similar results (M. M. Rowland, unpublished data).

Population density may also affect elk response to roads at the scale of our HE model predictions; the relationships we detected are likely to change as animal density changes. Elk density in our study area was about 5.5/km$^2$. At lower densities, fewer elk may have remained in analysis units with high road densities, leading to improved performance of the model. However, the original elk–road density model implicitly assumed that predictions of HE were robust to variations in elk density.

Lastly, the lack of correlation between predicted and observed HE may be caused in part by the wide range of traffic rates associated with open roads at Starkey, and thus, differences in actual disturbance associated with roads in our 15 analysis units (Wisdom 1998). Some open road segments, such as those near the main entrance gate, receive far more traffic than segments in more remote portions of the study area, though all are open to the public.

Although models that predict changes in HE or selection ratios of elk in relation to roads are useful in analyzing effects of management prescriptions, a more fundamental question is how road-related disturbance influences elk fitness and survival, as well as plant community health. Vulnerability of elk to hunter harvest is closely associated with presence of roads (Christensen et al. 1991, Unsworth et al. 1993). In western Oregon, Cole et al. (1997) found that energetic costs of female Roosevelt elk (*C. e. roosevelti*) were reduced following road closures, and elk survival increased. Harassment of wildlife, such as that caused by traffic on roads, can lead to population reductions due to increased energetic costs and less access to favored resources (Geist 1978).

Furthermore, persistent road-mediated disturbance may lead to permanent shifts in habitat use by elk away from roads and thereby effect greater levels of herbivory in some sites. Large ungulates such as elk can have profound effects on ecosystem processes and components (Hobbs 1996, Augustine and McNaughton 1998). Given the widespread distribution of elk in the intermountain west, as well as the extensive road network on both public and private lands in this region, such effects could be substantial.

### Environmental Variables

Correlation tests revealed that slope increased as distance to roads increased, and decreased with increasing open–road density. In addition, elevation was lower as distance to roads increased. These results reflect the location of most open roads in Starkey on gentle slopes and upper portions of drainages. Selection ratios for elk in the farthest bands may have been even higher had slopes not been steeper there, because elk often prefer gentler slopes (Hershey and Leege 1982, Irwin and Peek 1983, Edge et al. 1987). However, the range of differences in both slope and elevation in our study area were probably not ecologically significant for elk; mean elevation across our bands only varied from 1,328 to 1,374 m, and slope from 13 to 32%.

Tree canopy cover was consistent across Starkey and not correlated with distance to roads or open road density. Unsworth et al. (1998) found that elk in roaded areas tended to use habitats with greater canopy cover relative to unroaded areas. Some elk habitat models scale effects of roads on HE by security cover or tree canopy–cover classes (Lyon 1979, Roloff 1998). Such an adjustment was unnecessary, however, in our study area.

## MANAGEMENT IMPLICATIONS

Our results support long-standing efforts by elk managers to mitigate negative effects of road-related human activities on elk distributions in forested ecosystems. We recommend retention of a road component in HE models for elk. However, our results suggest that a spatially explicit roads variable may be more appropriate, based on distance bands buffered from open roads, rather than road density alone. With the advent of GIS, assessment areas can easily be buffered into bands at prescribed distances from roads and assigned appropriate scores, as recommended in a draft habitat potential model for elk (Roloff 1998). Our study, combined with several previous studies, suggests that substantial shifts in elk distribution away from open roads are a widespread phenomenon. Because of the potential for effects of road densities at the landscape level on carrying capacity, managers and researchers would benefit from joint efforts to establish cause–effect relationships among elk distribution, open roads, and elk carrying capacity using large-scale management experiments replicated across a diversity of elk habitats in the western United States.

## ACKNOWLEDGMENTS

The Starkey Project is supported financially by the Oregon Department of Fish and Wildlife, Federal Aid in Wildlife Restoration, and the U.S. Forest Service, Pacific Northwest Research Station and Pacific Northwest Region. A. A. Ager, N. J. Cimon, P. K. Coe, R. J. Stussy, and D. L. White assisted with data analysis and graphics production. D. B. Marx and T. Max guided statistical analysis. We thank J. H. Noyes, W. D. Edge, and 2 anonymous reviewers for helpful comments on previous drafts of this manuscript, D. H. Johnson for assistance with equation conversions, and J. W. Thomas for his unceasing work in the establishment of the Starkey Project.

## LITERATURE CITED

AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313–1325.

AGER, A. A., AND R. J. MCGAUGHEY. 1997. UTOOLS: microcomputer software for spatial analysis and landscape visualization. U.S. Forest Service General Technical Report PNW-GTR-397.

AUGUSTINE, D. J., AND S. J. MCNAUGHTON. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165–1183.

BOLON, N. A. 1994. Estimates of the values of elk in the Blue Mountains of Oregon and Washington: evidence from the existing literature. U.S. Forest Service General Technical Report PNW-GTR-316.

BRYANT, L. D., J. W. THOMAS, AND M. M. ROWLAND. 1993. Techniques to construct New Zealand elk-proof fence. U.S. Forest Service General Technical Report PNW-GTR-313.

CARTER, B. 1992. User's guide for forest plan implementation. Forest plans covered: Umatilla, Wallowa-Whitman, Malheur. U.S. Forest Service, Umatilla National Forest, Pendleton, Oregon, USA.

CHRISTENSEN, A. G., L. J. LYON, AND T. N. LONNER, compilers. 1991. Proceedings of a symposium on elk vulnerability. Montana State University, Bozeman, Montana, USA.

———, ———, AND J. W. UNSWORTH. 1993. Elk management in the Northern Region: considerations in forest plan updates or revisions. U.S. Forest Service General Technical Report INT-303.

COLE, E. K., M. D. POPE, AND R. G. ANTHONY. 1997. Effects of road management on movement and survival of Roosevelt elk. Journal of Wildlife Management 61:1115–1126.

DANA, P. H., W. FOWLER, AND D. HINDMAN. 1989. Automated animal-tracking system: tracking elk with retransmitted Loran-C. Pages 53–61 *in* J. M. Beukers, editor. Proceedings of the 18th annual technical symposium of the International Loran Association. International Loran Association, Santa Barbara, California, USA.

DUFFIELD, J., AND J. HOLLIMAN. 1988. The net economic value of elk hunting in Montana. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

EDGE, W. D., C. L. MARCUM, AND S. L. OLSON-EDGE. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. Journal of Wildlife Management 51:844–851.

———, S. L. OLSON-EDGE, AND L. L. IRWIN. 1990. Planning for wildlife in national forests: elk and mule deer habitats as an example. Wildlife Society Bulletin 18:87–98.

ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 1990. PC ARC/INFO starter kit users guide. Environmental Systems Research Institute, Redlands, California, USA.

FINDHOLT, S. L., B. K. JOHNSON, L. D. BRYANT, AND J. W. THOMAS. 1996. Corrections for position bias of a Loran-C radio-telemetry system using DGPS. Northwest Science 70:273–280.

GEIST, V. 1978. Behavior. Pages 283–296 *in* J. L. Schmidt and D. L. Gilbert, editors. Big game of North America. Stackpole Books, Harrisburg, Pennsylvania, USA.

GROVES, C. R., AND J. W. UNSWORTH. 1993. Wapiti and warblers: integrating game and nongame management in Idaho. Pages 408–417 *in* D. M. Finch and P. W. Stangel, editors. Status and management of neotropical migratory birds. U.S. Forest Service General Technical Report RM-229.

HERSHEY, T. J., AND T. A. LEEGE. 1982. Elk movements and habitat use on a managed forest in north-central Idaho. Idaho Department of Fish and Game Wildlife Bulletin Number 10.

HIEB, S. R., editor. 1976. Proceedings of the elk-logging-roads symposium. Forest, Wildlife, and Range Experiment Station, University of Idaho, Moscow, Idaho, USA.

HITCHCOCK, M., AND A. AGER. 1992. Microcomputer software for calculating an elk habitat effectiveness index on Blue Mountain winter range. U.S. Forest Service General Technical Report PNW-GTR-301.

HOBBS, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

IRWIN, L. L., AND J. M. PEEK. 1983. Elk habitat use relative to forest succession in Idaho. Journal of Wildlife Management 47:664–672.

JOHNSON, B. K., A. A. AGER, S. L. FINDHOLT, M. J. WISDOM, D. B. MARX, J. W. KERN, AND L. D. BRYANT. 1998. Mitigating spatial differences in observation rate of automated telemetry systems. Journal of Wildlife Management 62:958–967.

LECKENBY, D. A. 1984. Elk use and availability of cover and forage habitat components in the Blue Mountains, northeast Oregon, 1976–1982. Oregon Department of Fish and Wildlife, Wildlife Research Report Number 14.

LEEGE, T. A. 1984. Guidelines for evaluating and managing summer elk habitat in northern Idaho. Idaho Department of Fish and Game Wildlife Bulletin Number 11.

LOOMIS, J., J. COOPER, AND S. ALLEN. 1988. The Montana elk hunting experience: a contingent valuation assessment of economic benefits to hunters. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

LYON, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. Journal of Forestry 79:658–660.

———. 1983. Road density models describing habitat effectiveness for elk. Journal of Forestry 81:592–595.

———. 1984. Field tests of elk/timber coordination guidelines. U.S. Forest Service Research Paper INT-325.

———, AND A. G. CHRISTENSEN. 1992. A partial glossary of elk management terms. U.S. Forest Service General Technical Report INT-288.

———, T. N. LONNER, J. P. WEIGAND, C. L. MARCUM, W. D. EDGE, J. D. JONES, D. W. MCCLEEREY, AND L. L. HICKS. 1985. Coordinating elk and timber management. Final report of the Montana Cooperative Elk-Logging Study 1970–1985. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

MANLY, B., L. MCDONALD, AND D. THOMAS. 1993. Resource selection by animals. Chapman & Hall, London, United Kingdom.

OTIS, D. L., AND G. C. WHITE. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039–1044.

PERRY, C., AND R. OVERLY. 1977. Impact of roads on big game distribution in portions of the Blue Mountains of Washington. Washington Game Department Bulletin Number 11.

ROBEL, R. J., L. B. FOX, AND K. E. KEMP. 1993. Relationship between habitat suitability index values and ground counts of beaver colonies in Kansas. Wildlife Society Bulletin 21:415–421.

ROLOFF, G. J. 1998. Habitat potential model for Rocky Mountain elk. Pages 158–175 *in* J. C. deVos, Jr., editor. Proceedings of the 1997 deer/elk workshop. Arizona Game and Fish Department, Phoenix, Arizona, USA.

ROST, G. R., AND J. A. BAILEY. 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43:634–641.

ROWLAND, M. M., L. D. BRYANT, B. K. JOHNSON, J. H. NOYES, M. J. WISDOM, AND J. W. THOMAS. 1997. The Starkey Project: history, facilities, and data collection methods for ungulate research. U.S. Forest Service General Technical Report PNW-GTR-396.

———, P. K. COE, R. J. STUSSY, A. A. AGER, N. J. CIMON, B. K. JOHNSON, AND M. J. WISDOM. 1998. The Starkey habitat database for ungulate research: construction, documentation, and use. U.S. Forest Service General Technical Report PNW-GTR-430.

SAS INSTITUTE. 1985. SAS procedures guide for personal computers. Version 6 edition. SAS Institute, Cary, North Carolina, USA.

———. 1989. SAS/STAT user's guide. Version 6.

Fourth edition. Volume 2. SAS Institute, Cary, North Carolina, USA.

SKOVLIN, J. M. 1991. Fifty years of research progress: a historical document on the Starkey Experimental Forest and Range. U.S. Forest Service General Technical Report PNW-GTR-266.

THOMAS, J. W., H. BLACK, JR., R. J. SCHERZINGER, AND R. J. PEDERSEN. 1979. Deer and elk. Pages 104–127 *in* J. W. Thomas, technical editor. Wildlife habitats in managed forests–the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture Agricultural Handbook 553.

———, D. A. LECKENBY, M. HENJUM, R. J. PEDERSEN, AND L. D. BRYANT. 1988. Habitat-effectiveness index for elk on Blue Mountain winter ranges. U.S. Forest Service General Technical Report PNW-GTR-218.

TROMBULAK, S. C., AND C. A. FRISSELL. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

U.S. FOREST SERVICE. 1990. Final North Fork John Day motorized access and travel management program. U.S. Forest Service, Umatilla National Forest, Pendleton, Oregon, USA.

UNSWORTH, J. W., L. KUCK, E. O. GARTON, AND B. R. BUTTERFIELD. 1998. Elk habitat selection on the Clearwater National Forest, Idaho. Journal of Wildlife Management 62:1255–1263.

WERTZ, T. L., A. BLUMTON, L. E. ERICKSON, L. M. KEMP, AND T. THOMAS. 1996. Strategies to keep wildlife where you want them—do they work? Pages 70–72 *in* K. Evans, compiler. Sharing common ground on western rangelands: proceedings of a livestock/big game symposium. U.S. Forest Service General Technical Report INT-GTR-343.

WISDOM, M. J. 1998. Assessing life-stage importance and resource selection for conservation of selected vertebrates. Dissertation, University of Idaho, Moscow, Idaho, USA.

———, L. R. BRIGHT, C. G. CAREY, W. W. HINES, R. J. PEDERSEN, D. A. SMITHEY, J. W. THOMAS, AND G. W. WITMER. 1986. A model to evaluate elk habitat in western Oregon. U.S. Forest Service, Pacific Northwest Region R6-F&WL-216-1986.

———, J. G. COOK, M. M. ROWLAND, AND J. H. NOYES. 1993. Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range. U.S. Forest Service General Technical Report PNW-GTR-311.

———, R. S. HOLTHAUSEN, B. C. WALES, C. D. HARGIS, V. A. SAAB, D. C. LEE, W. J. HANN, T. D. RICH, M. M. ROWLAND, W. J. MURPHY, AND M. R. EAMES. 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia Basin: broad-scale trends and management implications. U.S. Forest Service General Technical Report PNW-GTR-485.

———, AND J. W. THOMAS. 1996. Elk. Pages 157–181 *in* P. R. Krausman, editor. Rangeland wildlife. Society for Range Management, Denver, Colorado, USA.

WITMER, G. W., AND D. S. DECALESTA. 1985. Effect of forest roads on habitat use by Roosevelt elk. Northwest Science 59:122–125.

ZAR, J. H. 1984. Biostatistical analysis. Second edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.

*Received 26 July 1999.*
*Accepted 9 February 2000.*
*Associate Editor: Boutin.*

50 YEARS WITH IMPACT Journal of Applied Ecology 1913 British Ecological Society 2013 CELEBRATING 100 YEARS

*Journal of Applied Ecology* 2013, **50,** 68–78 doi: 10.1111/1365-2664.12013

# A framework for understanding semi-permeable barrier effects on migratory ungulates

**Hall Sawyer[1]*, Matthew J. Kauffman[2], Arthur D. Middleton[3,4], Thomas A. Morrison[3], Ryan M. Nielson[1] and Teal B. Wyckoff[3,5]**

*[1]Western Ecosystems Technology, Inc., 200 South 2nd St., Suite B, Laramie, WY, 82070, USA; [2]US Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, 82071, USA; [3]Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY, 82071, USA; [4]Program in Ecology, University of Wyoming, Laramie, WY, 82071, USA; and [5]Wyoming Geographic Information Science Center, University of Wyoming, Laramie, WY, 82071, USA*

---

## Summary

**1.** Impermeable barriers to migration can greatly constrain the set of possible routes and ranges used by migrating animals. For ungulates, however, many forms of development are semi-permeable, and making informed management decisions about their potential impacts to the persistence of migration routes is difficult because our knowledge of how semi-permeable barriers affect migratory behaviour and function is limited.

**2.** Here, we propose a general framework to advance the understanding of barrier effects on ungulate migration by emphasizing the need to (i) quantify potential barriers in terms that allow behavioural thresholds to be considered, (ii) identify and measure behavioural responses to semi-permeable barriers and (iii) consider the functional attributes of the migratory landscape (e.g. stopovers) and how the benefits of migration might be reduced by behavioural changes.

**3.** We used global position system (GPS) data collected from two subpopulations of mule deer *Odocoileus hemionus* to evaluate how different levels of gas development influenced migratory behaviour, including movement rates and stopover use at the individual level, and intensity of use and width of migration route at the population level. We then characterized the functional landscape of migration routes as either stopover habitat or movement corridors and examined how the observed behavioural changes affected the functionality of the migration route in terms of stopover use.

**4.** We found migratory behaviour to vary with development intensity. Our results suggest that mule deer can migrate through moderate levels of development without any noticeable effects on migratory behaviour. However, in areas with more intensive development, animals often detoured from established routes, increased their rate of movement and reduced stopover use, while the overall use and width of migration routes decreased.

**5.** *Synthesis and applications*. In contrast to impermeable barriers that impede animal movement, semi-permeable barriers allow animals to maintain connectivity between their seasonal ranges. Our results identify the mechanisms (e.g. detouring, increased movement rates, reduced stopover use) by which semi-permeable barriers affect the functionality of ungulate migration routes and emphasize that the management of semi-permeable barriers may play a key role in the conservation of migratory ungulate populations.

**Key-words:** Brownian bridge movement model, connectivity, migration routes, mule deer, stopovers

---

*Correspondence author. E-mail: hsawyer@west-inc.com

## Introduction

Migration is unique among animal movement strategies because of the impressive distances that animals travel, the predictability of their return and, for many species, the sheer number of individuals involved (Dingle 1996; Milner-Gulland, Fryxell & Sinclair 2011). Migratory ungulates have received much attention because of their role as drivers of ecosystem processes (McNaughton 1985; Hobbs 1996), their value to humans as harvestable resources (Vors & Boyce 2009) and their potential as flagship species for landscape-level conservation (Thirgood *et al.* 2004). Recent global declines in the abundance and distribution of migratory ungulates (Berger 2004; Bolger *et al.* 2008; Harris *et al.* 2009) underscore the need to better understand the consequences of disruptions to migratory behaviour. Declines in migratory ungulates have been clearly linked to excessive harvest and land-use changes (e.g. agricultural development) on seasonal ranges (Bolger *et al.* 2008), but neither overharvest nor fragmentation of seasonal ranges actually affect the migration route itself. In contrast, anthropogenic features, such as roads, fences, power lines and pipelines, often overlap or bisect migration routes and are commonly cited as sources of habitat fragmentation or barriers with the potential to impede animal movement (Bolger *et al.* 2008; Harris *et al.* 2009; Dobson *et al.* 2010). Despite this recognition, our knowledge of how such barriers affect migration when they overlap with a migration route is limited.

It is clear that impermeable barriers, such as game-proof fences, inhibit the connectivity of migration routes, such that entire seasonal ranges become inaccessible. A total loss of connectivity presumably eliminates the ecological benefits of migration, which can include tracking gradients in high-quality forage (McNaughton 1985; Wilmshurst *et al.* 1999), accessing water holes (Williamson & Williamson 1984; Bolger *et al.* 2008) and reducing predation (Fryxell & Sinclair 1988; Hebblewhite & Merrill 2007). In some cases, impermeable barriers have caused population declines that resulted in the loss of thousands of migratory ungulates (Williamson & Williamson 1984; Whyte & Joubert 1988; Spinage 1992; Ben-Shahar 1993).

Most anthropogenic features, however, are at least semi-permeable to ungulates, and the assumption that semi-permeable barriers elicit similar effects (i.e., loss of migration function, population declines) is not yet supported by empirical evidence, nor have the potential mechanisms for such effects been explored. While the emergence of corridor ecology research (e.g. Hilty, Lidicker & Merenlender 2006) has improved the awareness of barrier effects, most conservation attention has focused on impermeable barriers (e.g. Dobson *et al.* 2010; Holdo *et al.* 2011). This is due in part to the difficulties associated with studying subtle and potentially long-term behavioural changes in migratory animals. However, recent improvements in GPS technology have advanced the study of migratory animals, and rapid increases in energy and urban development have prompted new interest in understanding how migratory ungulates might be influenced when semi-permeable barriers are constructed within their routes.

To facilitate a mechanistic understanding of semi-permeable barrier effects, we distinguish here between 'connectivity' and the 'functional attributes' of a migration route. For our purposes, connectivity simply describes whether or not animals are able to move from one seasonal range to another, whereas the functional attributes of a route include access of locally important resources such as stopover sites, movement corridors and escape terrain, which allow animals to track vegetation phenology and balance predation risk (Fig. 1). Thus, when connectivity is lost due to construction of an impermeable

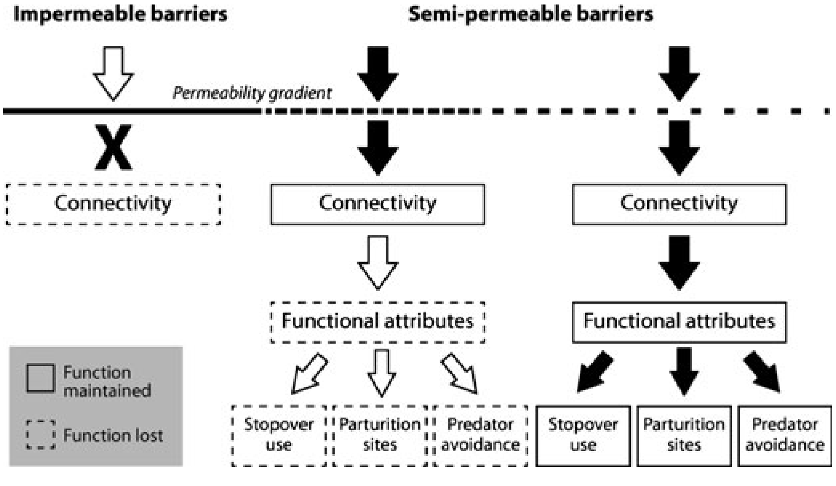


**Fig. 1.** Conceptual model that distinguishes between 'connectivity' and 'functional attributes' of a migration route and illustrates how each are affected by barriers (white arrows). Impermeable barriers impede connectivity such that animals can no longer migrate between seasonal ranges. In contrast, semi-permeable barriers often allow connectivity to be maintained, but the functional attributes of the migration route can be compromised, especially as permeability decreases.

barrier, the functional attributes of the migration route are also lost, along with the benefits of the seasonal range. Importantly, however, when connectivity remains intact because barriers are semi-permeable, the functional attributes of the migration routes may or may not be compromised. Thus, distinguishing between connectivity and functional attributes clarifies that impermeable and semi-permeable barriers may affect ungulate migration through different mechanisms.

Here, we propose a general framework to evaluate semi-permeable barrier effects on migratory ungulates, with the goal of expanding the discussion of barrier effects beyond the broad assumption that anthropogenic features will unconditionally impede migration. Our framework consists of three steps. First, the potential barrier is identified and measured in a way that facilitates the detection of development thresholds that alter behaviour. Roads, for example, are commonly viewed as potential barriers to migration (Dobson *et al.* 2010). However, a road or network of roads may not elicit a behavioural response until some threshold (e.g. road density, traffic levels, road width, etc.) is exceeded (Dyer *et al.* 2002; Frair *et al.* 2008). Thus, whether the potential barrier is a road, fence or other development, it should be measured in a way that considers likely thresholds. Second, the behavioural responses to a given anthropogenic feature are measured. We note that simply determining whether animals continue to migrate after construction of a potential barrier (e.g. Carruthers & Jakimchuk 1987; Ito *et al.* 2005) only provides information on connectivity and may overlook important behavioural changes. To examine whether semi-permeable barriers reduce the benefits of migration, specific migration behaviours (e.g. rate of movement, fidelity) must be quantified before and after the construction of the potential barrier (or in areas with and without barriers). These may include traditional metrics such as net-squared displacement and rate of movement, or the more advanced utilization distribution (UD) metrics now possible with movement-based kernel density estimation (MKDE; Benhamou 2011) and Brownian bridge movement models (BBMM; Horne *et al.* 2007; Kranstauber *et al.* 2012). Next, to predict how the observed behavioural changes may influence the functionality of the migration route, it is necessary to characterize functional attributes (e.g. stopover sites, escape terrain, parturition) of the migratory landscape. This third step highlights the importance of linking observed behavioural changes to functional attributes of the migratory landscape, thereby providing a means to evaluate how the benefits of migration may be altered by behavioural changes caused by barriers.

We illustrate our framework using empirical data from migratory mule deer *Odocoileus hemionus* in Wyoming, USA. Like many areas of western North America, ungulate ranges in Wyoming are experiencing unprecedented levels of energy development (Sawyer, Kauffman & Nielson 2009; Sawyer *et al.* 2009). Although the scale and intensity of development are rapidly increasing (Copeland *et al.* 2009), we know little about whether energy infrastructure alters migratory behaviour, the functionality of migration routes or the ecological benefits of migration. Here, we use GPS movement data to examine the behavioural response of two migratory mule deer populations to varying levels of energy development. Using migration routes identified prior to large-scale natural gas development as the baseline, our goal was to determine how mule deer migration was influenced by increased levels of gas development. We examined several complementary metrics of behavioural change and evaluated how they affected the functional attributes of the migratory landscape, with an emphasis on understanding how semi-permeable barriers alter the benefits of migration. By revealing differential responses of mule deer to varying levels of development, our findings highlight the importance of considering semi-permeable barriers in land-use planning – an urgent goal amid ongoing global declines in ungulate migration.

## Materials and methods

### STUDY AREA

Our study was conducted in the 1100-km$^2$ Atlantic Rim Project Area (ARPA), located in south-central Wyoming. The ARPA is generally characterized by rolling topography, prominent ridges and dry canyons dominated by sagebrush *Artemisia* sp., black greasewood *Sarcobatus vermiculatus* and other mixed shrubs *Purshia tridentata, Chrysothamnus* sp., *Cercocarpus* sp. Elevations range from 1920 to 2530 m. The ARPA contains two distinct mule deer winter ranges known as the Dad and Wild Horse winter ranges. The Dad winter range supports ~500–1000 mule deer, whereas the Wild Horse range supports ~1500–2000. Population-level migration routes for both winter ranges were identified in 2005 and 2006 (Sawyer *et al.* 2009), during a period of exploratory energy development that we refer to as Phase 1 (Figs 2 and 3). Shortly thereafter, the Bureau of Land Management (BLM) approved development of *c.* 2000 wells to extract coal-bed methane from the ARPA (BLM 2007). Although most of the development was planned for areas outside of mule deer migration routes, there were two areas where development overlapped with migration routes, including the 33·6-km$^2$ Dry Cow Creek located northeast of the Dad winter range (Fig. 2) and the 15·5-km$^2$ Wild Horse Basin located east of the Wild Horse winter range (Fig. 3).

### ANIMAL CAPTURE AND DATA COLLECTION

We captured 47 mule deer during Phase 1 and equipped animals with store-on-board GPS collars that collected locations every 2·5 h (Sawyer *et al.* 2009). Between February 2005 and November 2006, we collected 116 494 locations from the 47 deer to document spring and autumn migrations. We refer readers to Sawyer *et al.* (2009) for further details on Phase 1. During Phase 2, we captured 56 mule deer and equipped them with GPS collars programmed to collect locations every 2 hours during migration. Collars collected data for spring and autumn migrations of 2008,

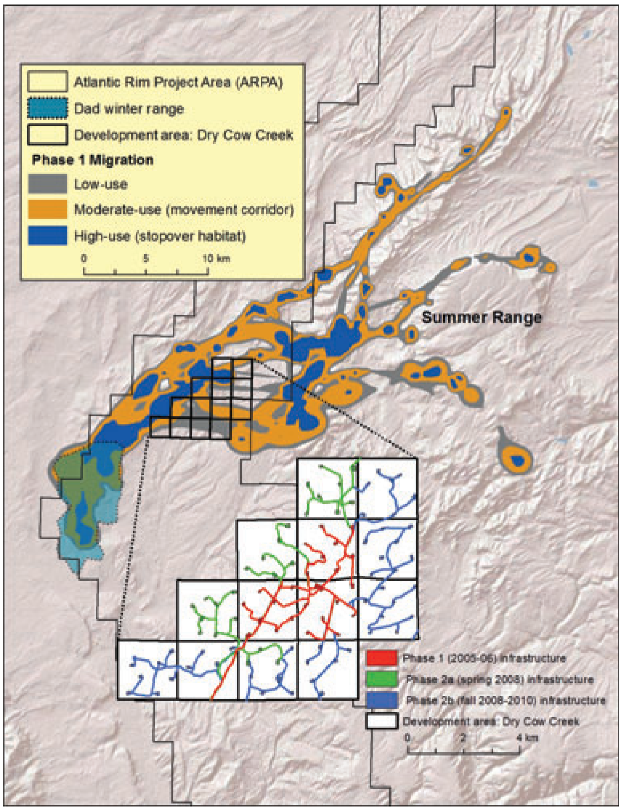


**Fig. 2.** Location of 33·6-km$^2$ Dry Cow Creek development area within the population-level migration route estimated for mule deer from the Dad winter range during Phase 1. Map insert shows the level of gas development in Dry Cow Creek during Phase 1 (2005–06), Phase 2a (spring 2008) and Phase 2b (autumn 2008–2010). Infrastructure includes roads (linear features) and gas pads (small squares).

2009 and 2010. During Phase 2, we recovered 191 302 GPS locations from 50 of the 56 marked animals. Of those 50 animals, 39 (26 in Wild Horse winter range and 13 in Dad winter range) lived long enough to complete at least one migration. Fix success of GPS collars was high (99%), so our analysis was not affected by missing locations.

### IDENTIFYING THE POTENTIAL BARRIER

A critical component of studying barrier effects is to quantify potential barriers in terms that allow thresholds to be considered (Dyer *et al.* 2002; Frair *et al.* 2008). The potential barriers in our study included road networks and well pads associated with gas development. We used 10-m resolution satellite imagery acquired from Spot Image Corporation (Chantilly, VA, USA) to quantify road and well pad densities during each phase of development. We recognize that roads and well pads can have varying levels of human disturbance (e.g. traffic), depending on the type of wells (e.g. drilling vs. producing) and associated production facilities (Sawyer, Kauffman & Nielson 2009). However, we did not distinguish between road and well pad types because all roads in our development areas were improved gravel and *c.* 10 m wide, and well pads were similar in size and type.

### DETECTING CHANGES IN MIGRATORY BEHAVIOUR

We sought to identify potential individual and population-level behavioural responses during migration. We calculated movement rates of mule deer ($n = 43$) through the development areas and used a standard two-sample $t$-test ($\alpha = 0{\cdot}10$) to determine whether movement rates varied between Phases 1 and 2. Movement rates were only calculated for animals that moved through development areas and were based on the movement sequence that included one location either side of the development area. To evaluate movement in the context of the larger migration route, we also calculated movement rates in undeveloped habitat, between the development areas and summer ranges. For a small sample of animals that collected data in both study phases ($n = 4$), we compared migration routes between years to assess whether animals detoured around the development area.

We used the Brownian bridge movement model (BBMM) to estimate population-level migration routes for GPS-collared deer from both the Dad and Wild Horse winter ranges. The BBMM uses time-specific location data to estimate a UD along a movement route, where the probability of being in an area is conditioned on the start and end locations, the elapsed time between locations and the speed of movement (Horne *et al.* 2007). We used the 'BBMM' package in R (R Foundation for Statistical Computing, Vienna, Austria) to estimate UDs for individual migration routes. Population-level migration routes were then estimated by averaging the individual UDs within each winter range and study phase. These population-level UDs provide a probabilistic measure of the migration route, where the height of UD reflects intensity of use and the contours of the UD delineate the surface area, or width of the route. Overall, the Phase 1 period (spring 2005–spring 2006) included 55 migrations (42 spring, 13 autumn) collected from 35 deer, whereas Phase 2 (spring 2008 –autumn 2010) included 86 migration routes (56 spring, 30 autumn) from 39 deer. The Phase 1 population-level migration

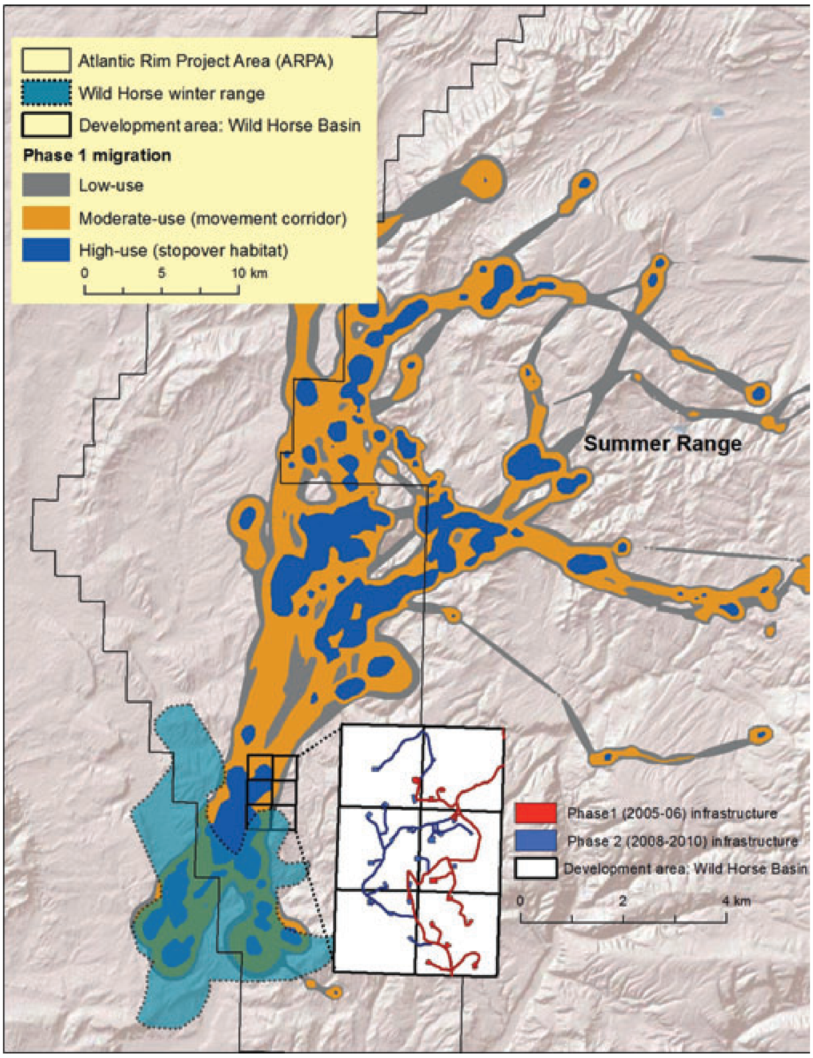


**Fig. 3.** Location of 15·5-km$^2$ Wild Horse Basin development area within the population-level migration route estimated for mule deer from the Dad winter range during Phase 1. Map insert shows the level of gas development in Wild Horse Basin during Phase 1 (2005–06) and Phase 2 (2008–2010). Infrastructure includes roads (linear features) and gas pads (small squares).

route for the Wild Horse winter range included 37 migrations by 23 deer, while the Dad winter range included 18 migrations by 12 deer (Figs 2 and 3). The Phase 2 population-level migration route for the Wild Horse winter range included 61 migrations by 23 deer. Phase 2 development in Dry Cow Creek was split into Phase 2a (spring 2008) and 2b (autumn 2008–autumn 2010), to account for the development activity during the summer of 2008. The population-level route for the Dad winter range included 12 migrations by 12 deer in Phase 2a, and 13 migrations by 9 deer in Phase 2b.

To evaluate whether the intensity of deer use (i.e. height of the UD) within migration routes changed in the development areas, we used the UD of migration routes estimated during Phase 1 as a reference and examined whether observed changes in the Dry Cow Creek and Wild Horse Basin were statistically different than those expected in a larger portion of the migration route. To do this, we designed a randomization procedure that estimated the expected change in deer use for a larger area (3 km buffer) surrounding both Dry Cow Creek and Wild Horse Basin development areas. For Dry Cow Creek, we randomly selected 13, 2·6-km$^2$ units (equal to the size of the development area) from a larger sample of 51 and then calculated the percentage change in UD volume relative to Phase 1. This process was conducted 500 times and provided an estimate of the amount of change expected in any combination of 13, 2·6-km$^2$ units sampled from the larger 132-km$^2$ area. A similar process was repeated in Wild Horse Basin, except we randomly selected 6, 2·6-km$^2$ units from a larger sample of 21. We calculated 90% confidence intervals to test whether the changes observed in the development areas were more or less than expected based on the permutation results. Our randomization analysis used the three-dimensional structure or volume of UDs to detect changes in population-level migration use and is conceptually similar to the volume of intersection method described by Millspaugh *et al.* (2004). We also calculated the change in the amount of migration surface area, as defined by the outer 99% contour of the population-level migration routes in the Dry Cow Creek and Wild Horse Basin during Phases 1 and 2. This simple, two-dimensional metric is useful for detecting change in the width of a migration route.

### IDENTIFYING FUNCTIONAL ATTRIBUTES OF THE MIGRATORY LANDSCAPE

For temperate ungulates that migrate along elevation gradients, functional attributes of the migratory landscape can be generally characterized as either stopover habitat where animals spend most of their time, or the intervening movement corridors where animals travel quickly (Sawyer *et al.* 2009; Sawyer & Kauffman 2011). We defined migratory segments as either stopover habitat or movement corridors, although we note that future studies may use or reveal additional functional attributes, such as parturition sites (e.g. Singh *et al.* 2010; Barbknecht *et al.* 2011). Stopover sites were classified as the highest 25% quartile in the UD, whereas the 50–75% quartiles were considered movement corridors (Sawyer *et al.* 2009). At the individual level, we calculated the area of stopover habitat for each deer ($n$ = 43) before and after development to assess whether this functional attribute was influenced by increased levels of development.

## Results

### IDENTIFYING THE POTENTIAL BARRIER

The Dry Cow Creek area was partially developed during Phase 1, with road and well pad densities of 0·56 km km$^{-2}$ and 0·77 km$^{-2}$, respectively. However, by the spring of 2008 (Phase 2a), road and well pad densities increased to 1·07 km km$^{-2}$ and 1·49 km$^{-2}$, respectively. Following construction in summer 2008 (Phase 2b), the road and well pad densities increased further to 1·92 km km$^{-2}$ and 2·82 km$^{-2}$, respectively (Fig. 2). Compared to Dry Cow Creek, gas development in Wild Horse Basin was smaller in size and intensity. Road and well pad densities during Phase 1 were 0·83 km km$^{-2}$ and 0·65 km$^{-2}$, respectively, and increased to 1·51 km km$^{-2}$ and 1·86 km$^{-2}$ during Phase 2 (Fig. 3).

### CHANGES IN MIGRATORY BEHAVIOUR

At the individual level, movement rates of deer in the Dry Cow Creek development steadily increased from 1·06 ± 0·26 km h$^{-1}$ (mean ± SE) in Phase 1 to 1·68 ± 0·21 in Phase 2a, and 1·94 ± 0·18 in Phase 2b (Fig. 4). Movement rates in Phase 2b were higher than those observed in Phase 1 ($t_{11}$ = −2·68, $P$ = 0·021). Concurrently, movement rates of deer after they had moved through the development area steadily decreased from 1·25 ± 0·12 in Phase 1 to 0·79 ± 0·27 in Phase 2a, and 0·21 ± 0·05 in Phase 2b (Fig. 4). The rate of deer movement in undeveloped areas was lower in Phase 2b compared with Phase 1 ($t_{11}$ = 7·68, $P$ < 0·001). Of the 4 deer that collected data in both Phase 2a and 2b, three animals appeared to alter their routes in response to development by diverging from the previous year's path near the development boundary and then moving back to the path *c.* 3–4 km beyond the development (Fig. 5). Overall, the detours used by these animals bypassed approximately 8 km of their original migration route. At the population level, the intensity of deer use, as indicated by the UD volume, declined by 10% and 53% in Phases 2a and 2b, respectively (Fig. 6). The 53% decrease was statistically significant and coincided with road and well pad densities of 1·92 km km$^{-2}$ and 2·82 km km$^{-2}$, respectively. Similarly, the surface area of migration routes in the Dry Cow Creek steadily decreased from 23·4 km$^2$ in Phase 1 to 21·5 km$^2$ in Phase 2a (−8%) and 15·4 km$^2$ in Phase 2b (−34%).

In contrast to the altered movement rates that followed development in the Dry Cow Creek, we did not detect any individual or population-level responses in the smaller and less concentrated development of Wild Horse Basin. Movement rates through the development area did not differ ($t_{17}$ = 0·56, $P$ = 0·579) between Phase 1 (1·24 ± 0·30 km

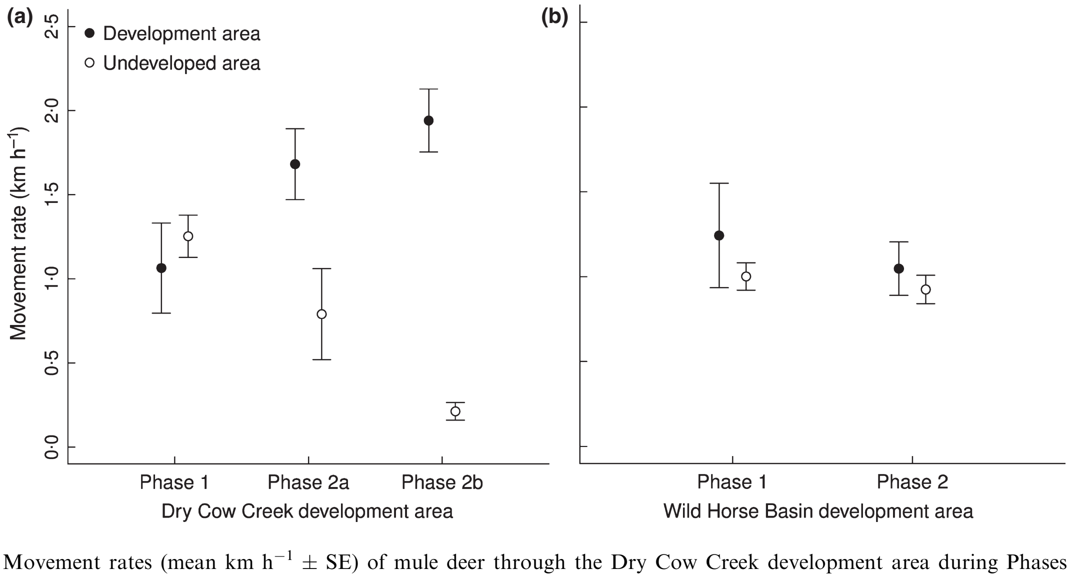


**Fig. 4.** (a) Movement rates (mean km h$^{-1}$ ± SE) of mule deer through the Dry Cow Creek development area during Phases 1, 2a and 2b. Movement rates through the developed area were higher during Phases 2a and 2b compared with Phase 1, whereas movement rates through undeveloped habitat decreased. (b) Movement rates of mule deer through the Wild Horse Basin development area during Phases 1 and 2. Movement rates through developed and undeveloped areas were similar in both phases.

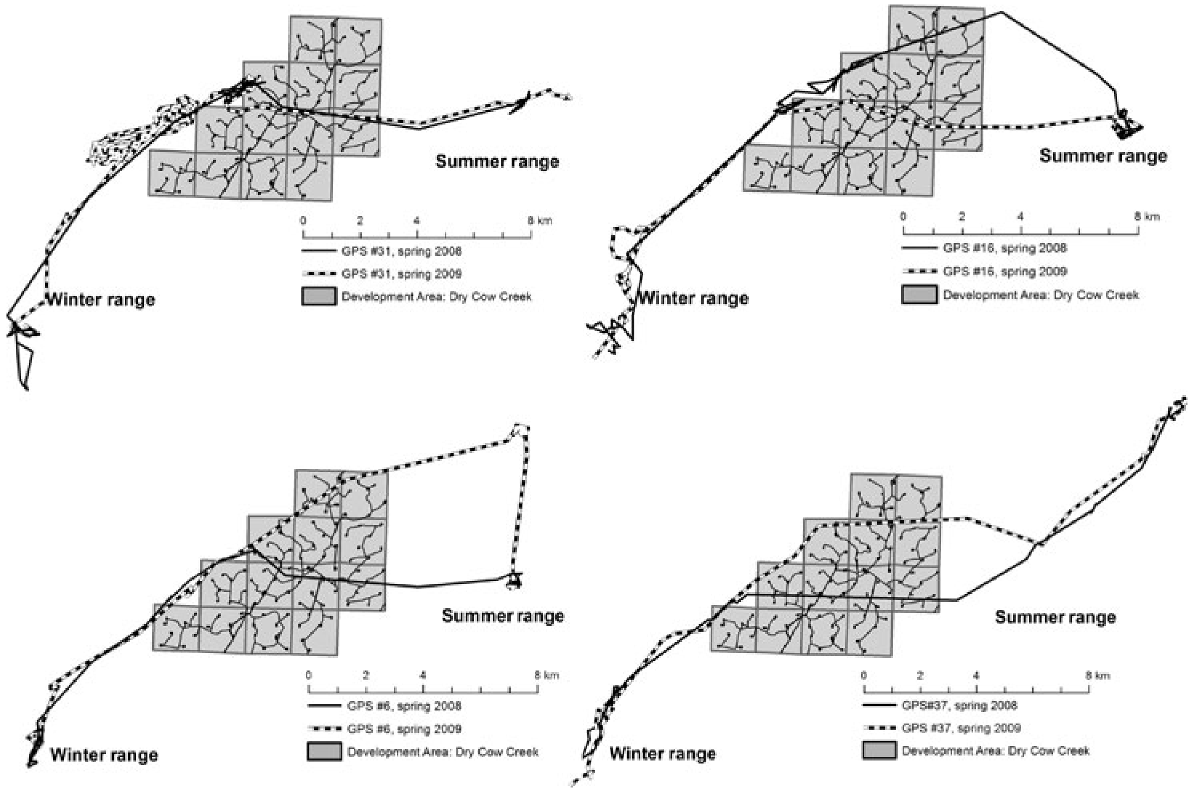


**Fig. 5.** Migration routes of four mule deer during Phase 2a and Phase 2b through the Dry Cow Creek development area. Deer #31 moved through the central portion of Dry Cow Creek in both Phases 2a and 2b, whereas Deer #16, #6 and #37 all show clear detours around or through different portions of the developed areas before and after development.

hr$^{-1}$; mean ± SE) and Phase 2 (1·05 ± 0·15; Fig. 4). Concurrently, movement rates outside of the development area also did not differ ($t_{17} = 0{\cdot}66$, $P = 0{\cdot}516$) between Phase 1 (1·00 ± 0·08 km hr$^{-1}$; mean ± SE) and Phase 2 (0·92 ± 0·08; Fig. 4). At the population level, the intensity of deer use decreased by 23% in Phase 2, but was within the confidence intervals of the expected variance in deer use (Fig. 6). The surface area of migration route was similar between Phase 1 (10·9 km$^2$) and Phase 2 (12·1 km$^2$).

### FUNCTIONAL ATTRIBUTES OF MIGRATORY LANDSCAPE

For individual deer migrating through Dry Cow Creek, the area of stopover habitat decreased as development increased, with an average of 1·63 ± 0·43 km$^2$ (mean ± SE) during Phase 1, 1·16 ± 0·38 km$^2$ in Phase 2a and 0·66 ± 0·19 km$^2$ in Phase 2b (Fig. 7). The area of stopover habitat used during Phase 2b was marginally lower than Phase 1 ($t_9 = 2{\cdot}04$, $P = 0{\cdot}07$). For individual deer migrating through Wild Horse Basin, the area of stopover habitat was similar ($t_{19} = -0{\cdot}611$, $P = 0{\cdot}548$) between Phase 1 (1·30 ± 0·34 km$^2$) and Phase 2 (1·63 ± 0·41 km$^2$; Fig. 7).

## Discussion

Sustaining migratory ungulate populations in the face of widespread development and land-use change poses difficult conservation challenges across the globe (Bolger *et al.* 2008; Harris *et al.* 2009). Increased levels of development create a variety of barriers (e.g. roads, pipelines, fences) that are semi-permeable to ungulates; yet, we know little about how these types of barriers influence migratory behaviour or the persistence of migratory populations. We found that changes in migratory behaviour of two mule deer populations in western Wyoming varied with the size and intensity of semi-permeable barriers associated with gas development. In migration routes exposed to a larger, more concentrated development (i.e. Dry Cow Creek), mule deer use declined by 53% and movement rates nearly doubled (1·06–1·94 km h$^{-1}$). The decline in deer use and accelerated movement rates reduced both the surface area of the migration route and area of stopover use. In contrast, we did not detect any changes in migratory behaviour through Wild Horse Basin, where the development area was smaller and infrastructure less concentrated. The intensity of deer use, surface area of the routes, movement rates of animals, and stopover use were similar before and after gas development. Presumably, the absence of any detectable response by migrating deer in this area was a function of permeability thresholds, due to either the lower level or smaller size of the development. Additionally, timing stipulations restricted development activities (i.e. drilling) in Wild Horse Basin between 1 November and 30 April – a time period that includes

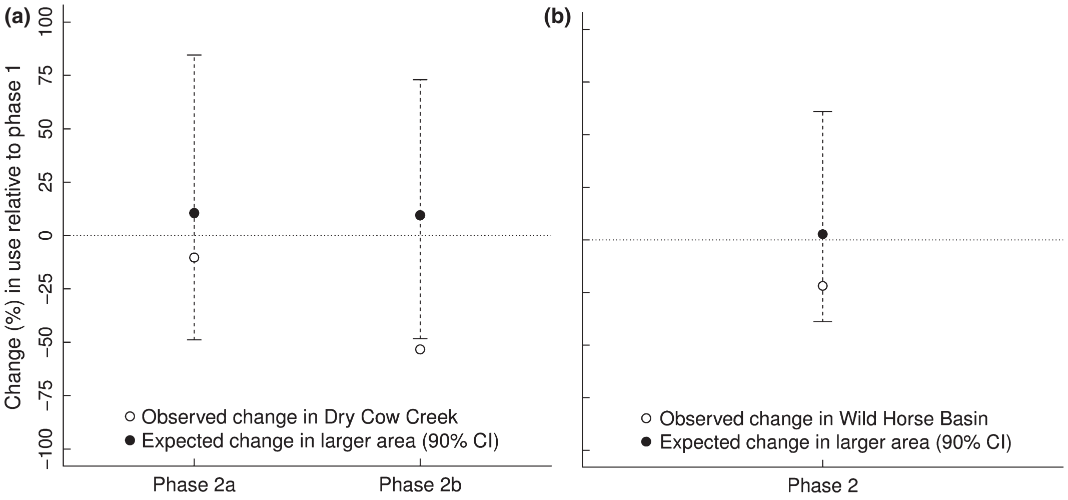


**Fig. 6.** (a) Change in population-level deer use in Dry Cow Creek development area during Phases 2a and 2b, relative to a larger 132-km$^2$ area and using Phase 1 as a reference level. (b) Change in population-level deer use in Wild Horse Basin development area during Phase 2, relative to a larger 54-km$^2$ area and using Phase 1 as a reference level.

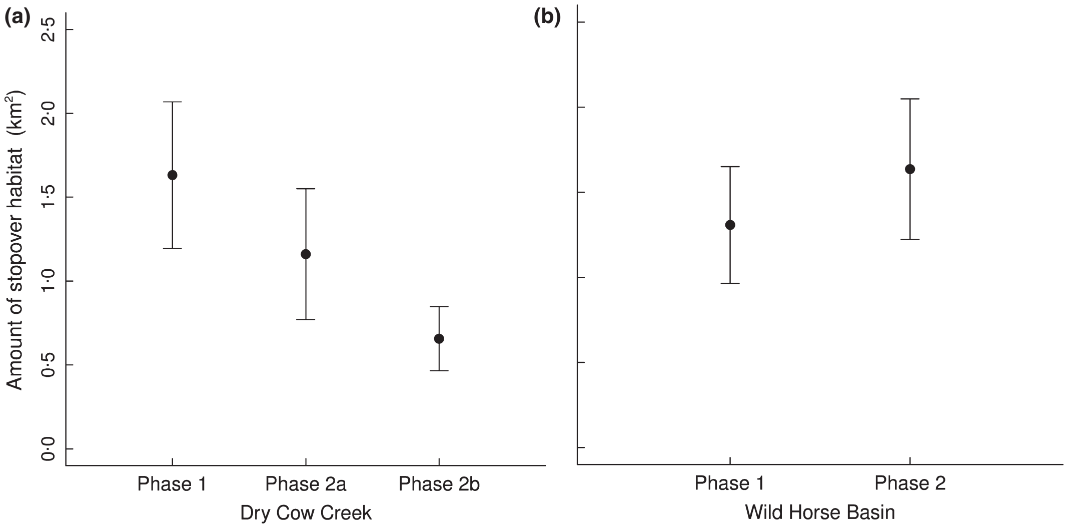


**Fig. 7.** (a) Area of stopover habitat (mean km$^2$ ± SE) used by mule deer in the Dry Cow Creek development area during Phases 1, 2a and 2b, and (b) Wild Horse Basin development area during Phases 1 and 2.

much of the spring and autumn migrations. Reducing traffic levels can reduce disturbance to mule deer (Sawyer, Kauffman & Nielson 2009), so these restrictions may have mitigated the potential barrier effects by minimizing disturbance to mule deer.

Our finding of individual and population-level responses to semi-permeable barriers makes clear that anthropogenic features can affect migration, even when connectivity between seasonal ranges is maintained. However, it is of interest whether these behavioural changes reduce the functionality of migration routes and ultimately, whether the functional loss could affect demography and persistence of migrants that use impacted routes. For example, stakeholders involved with this study have posed the question, 'Why does it matter if deer migrate more quickly through the development area?' Without a reasonable answer to this question, agencies and industry are less motivated to modify, or attempt to mitigate, development plans that overlap with ungulate migration routes. Recent work suggests mule deer spend 95% of the migration period in stopovers, essentially using them to slow down their migration to exploit forage quality gradients created by phenological delays associated with elevation (Sawyer & Kauffman 2011). Our analyses suggest that development within a route can increase movement rates and alter migration route function by reducing stopover use. Although only 15% of the migration route in Dry Cow Creek was classified as stopover habitat, a 60% (1·63–0·66 km$^2$) reduction in the size of these areas is concerning. Any behavioural change that impedes access to or discourages use of stopover habitat is likely to reduce the ability of animals to optimally forage and track vegetation phenology. Whether such a functional loss has measurable demographic consequences is unknown, but given the importance of summer nutrition for body condition and reproduction (Cook *et al.* 2004; Parker, Barboza & Gillingham 2009; Tollefson *et al.* 2010), lost foraging opportunities during migration certainly have the potential to incur energetic and demographic costs. Further study, as has been done with avian taxa (e.g. Hoye *et al.* 2012), is needed to link altered migratory behaviour by ungulates to fitness metrics (e.g. body condition, reproduction, survival).

Sawyer *et al.* (2009) suggest that semi-permeable barriers situated in movement corridors are less likely to impact migration route function than barriers in stopover areas, because animals do not rely on movement corridors as primary sources of forage. We caution, however, that changes in migratory behaviour within movement corridors have the potential to influence other, more subtle migration route functions. For example, it is possible that ungulates collect information on forage phenology while travelling through movement corridors to optimize the rate at which they access peak digestibility of forage (Sawyer & Kauffman 2011). Interestingly, our results suggest that when animals move more rapidly through developed areas, they tend to offset the quick movement by slowing down once they return to undeveloped habitat. This pattern is consistent with the hypothesis that increased movement rates create short-term phenological mismatches, and that animals attempt to correct for these mismatches by slowing down after moving through developed areas. Given the potential consequences of phenological mismatches (Post & Forchhammer 2008), this movement pattern warrants further research, especially in areas where development projects bisect long segments of migration routes. Of additional concern is that many migratory ungulates show high fidelity to migration routes (Berger, Cain & Berger 2006; Sawyer *et al.* 2009; Bunnefeld *et al.* 2011), and it is unknown how detours made along the route due to disturbance will influence movement rates and the ability of animals to track phenology. Certainly, when deer bypass 8 km of their traditional migration routes, like those in Dry Cow Creek, the functionality of that particular segment is effectively lost. Thus, there are a variety of mechanisms (i.e. increased movement rates and detouring) by which semi-permeable barriers may diminish the ability of migrants to track optimal forage conditions.

Most ungulate populations are partially migratory (Cagnacci *et al.* 2011; Hebblewhite & Merrill 2011), but the proportion of migratory animals is typically larger than the resident segment (Fryxell, Greever & Sinclair 1988; Bunnefeld *et al.* 2011). Our study was no exception, as only four of the 103 GPS-marked animals were resident. Recent studies suggest that the ratio of migratory to resident animals may shift when the benefits of migrating no longer exceed the benefits of a resident strategy (Hebblewhite & Merrill 2011). For example, elk populations have become increasingly resident in areas where differential levels of predation on neonates and changes in habitat quality favour the resident strategy (Hebblewhite *et al.* 2006; Hebblewhite & Merrill 2011; Middleton *et al.* in press). Our work highlights the possibility that, like changes in predation or habitat quality, the effects of semi-permeable barriers on migration route function have the potential to reduce the benefits of migration and favour resident animals. Given that ungulate migrations generally occur along traditional routes that are learned and passed on from mother to young (McCullough 1985; Sweanor & Sandegren 1988; Nelson & Mech 1999), it may be difficult to restore migratory landscapes by removing barriers once migratory subpopulations have dwindled (but see Bartlam-Brooks, Bonyongo & Harris 2011). In general, ungulates that demonstrate strong fidelity to narrow, linear pathways (Berger, Cain & Berger 2006; Sawyer & Kauffman 2011) may be more vulnerable to barrier effects than those exhibiting more nomadic migratory patterns, such as wildebeest *Connochaetes taurinus* (Holdo, Holt & Fryxell 2009) and Mongolian gazelles *Procapra gutturosa* (Mueller *et al.* 2011). However, in contrast to populations that follow distinct migration routes, mitigating the potential effects of semi-permeable barriers for nomadic populations will be difficult because of their unpredictable movements across the landscape (Mueller *et al.* 2011).

Ideally, our study would have followed the same animals through the entire study period, such that changes in individual movements could be more closely examined. For example, the 4 animals that collected data during two phases revealed that increased levels of development may lead to individual animals detouring and bypassing entire segments of their traditional routes. Other work has found that increased levels of human disturbance may interact with environmental conditions to discourage older individuals from migrating (Singh *et al.* 2012). Thus, we suspect that evaluating individual movements through time would provide more insight into the mechanistic drivers of the behavioural changes we observed and reduce the amount of variation in the metrics of interest. For future studies, we recommend the same animals be marked through the entire study period so that individual and population-level movement patterns can be examined in more detail. Also critical to detecting changes in behaviour is the collection of baseline data before intensive development. In our case, had state and federal agencies not required both pre- and post-development study phases, changes in migratory behaviour would have gone undocumented.

## CONCLUSIONS AND RECOMMENDATIONS

Managing migratory ungulates is especially difficult because of the long distances they move, often across a mix of land ownership and land-use practices. As energy development and other human disturbances expand, it is increasingly important to understand how migrating ungulates respond to the semi-permeable barriers. Our study suggests that increased levels of gas development in migration routes may encourage detouring, increase movement rates, reduce the area of stopover use by individuals and reduce the overall amount of deer use and constrict the size of migration routes at the population level. The existence of such behavioural changes suggests that certain levels of development, while still allowing connectivity between seasonal ranges, may nevertheless reduce route functionality and the benefits of migration. Ultimately, demographic costs associated with barriers are the most desirable currency in which to measure the effects of development on migratory ungulates. In the absence of such data, quantifying behavioural changes and functional attributes of the migratory landscape before and after development provides an intuitive first step for understanding the consequences of semi-permeable barriers for the persistence of migratory ungulates.

## Acknowledgements

This work was supported by the Bureau of Land Management, the Wyoming Game and Fish Department, the U.S. Geological Survey (Wyoming Landscape Conservation Initiative) and grants provided to Western Ecosystems Technology, Inc from Anadarko Petroleum Company. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U. S. Government. Comments from E. J. Milner-Gulland, G. Hopcraft, N. Korfanta and one anonymous reviewer improved the manuscript.

## References

Barbknecht, A.E., Fairbanks, W.S., Rogerson, J.D., Maichak, E.J., Scurlock, B.M. & Meadows, L.L. (2011) Elk parturition site selection at the local and landscape scales. *Journal of Wildlife Management*, **75**, 646–654.

Bartlam-Brooks, H.L.A., Bonyongo, M.C. & Harris, S. (2011) Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of a zebra *Equus burchelli* migration in Botswana. *Oryx*, **45**, 210–216.

Benhamou, S. (2011) Dynamic approach to space and habitat use based on biased random bridges. *PLoS ONE*, **6**, e14592.

Ben-Shahar, R. (1993) Does fencing reduce the carrying capacity for populations of large herbivores? *Journal of Tropical Ecology*, **9**, 249–253.

Berger, J. (2004) The last mile: how to sustain long-distance migration in mammals. *Conservation Biology*, **18**, 320–331.

Berger, J., Cain, S.L. & Berger, K.M. (2006) Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters*, **22**, 528–531.

Bolger, D.T., Newmark, W.D., Morrison, T.A. & Doak, D.F. (2008) The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, **11**, 63–77.

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J. & Ericsson, G. (2011) A model-driven approach to quantify migration patterns: individual, yearly and regional differences. *Journal of Animal Ecology*, **80**, 466–476.

Bureau of Land Management (2007) *Record of Decision: Environmental Impact Statement for the Atlantic Rim Natural Gas Field Development Project*. Rawlins Field Office, Rawlins, Wyoming.

Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A.J.M., Morellet, N., Kjellander, P., Linnell, J.D.C., Mysterud, A., Neteler, M., Delucchi, L., Ossi, F. & Urbano, F. (2011) Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos*, **120**, 1790–1802.

Carruthers, D.R. & Jakimchuk, R.D. (1987) Migratory movements of the Nelchina Caribou Herd in relation to the Trans-Alaska Pipeline. *Wildlife Society Bulletin*, **15**, 414–420.

Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T., Bryant, L.D. & Irwin, L.L. (2004) Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs*, **155**, 1–61.

Copeland, H.E., Doherty, K.E., Naugle, D.E., Pocewicz, A. & Kiesecker, J.M. (2009) Mapping oil and gas development potential in the US Intermountain West and estimating impacts to species. *PLoS ONE*, **4**, e7400. doi:10.1371/journal.pone.0007400.

Dingle, H. (1996) *Migration: The Biology of Life on the Move*. Oxford University Press, New York.

Dobson, A., Borner, M., Sinclair, A.R.E., *et al.* (2010) Road will ruin Serengeti. *Nature*, **467**, 272–273.

Dyer, S.J., O'Neill, J.P., Wasel, S.M. & Boutin, S. (2002) Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Canadian Journal of Zoology*, **80**, 839–845.

Frair, J.L., Merrill, E.H., Beyer, H.L. & Morales, J.M. (2008) Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology*, **45**, 1504–1513.

Fryxell, J.M., Greever, J. & Sinclair, A.R.E. (1988) Why are migratory ungulates so abundant? *American Naturalist*, **131**, 781–798.

Fryxell, J.M. & Sinclair, A.R.E. (1988) Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution*, **3**, 237–241.

Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromsigt, J.P.G.M. & Berger, J. (2009) Global decline in aggregated migrations of large terrestrial animals. *Endangered Species Research*, **7**, 55–76.

Hebblewhite, M. & Merrill, E.H. (2007) Multi-scale wolf predation risk for elk: does migration reduce risk? *Oecologia*, **152**, 377–387.

Hebblewhite, M. & Merrill, E.H. (2011) Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. *Oikos*, **120**, 1860–1870.

Hebblewhite, M., Merrill, E.H., Morgantini, L.E., White, C.A., Allen, J. R., Bruns, E., Thurston, L. & Hurd, T.E. (2006) Is the migratory behavior of montane elk herds in peril? The case of Alberta's Ya Ya Tinda elk herd. *Wildlife Society Bulletin*, **35**, 1280–1294.

Hilty, J.A., Lidicker Jr, W.Z. & Merenlender, A.M. (2006) *Corridor Ecology: The Science and Practice and Linking Landscapes for Biodiversity Conservation*. Island Press, Washington, USA.

Hobbs, N.T. (1996) Modification of ecosystems by ungulates. *Journal of Wildlife Management*, **60**, 69–713.

Holdo, R.M., Holt, R.D. & Fryxell, J.M. (2009) Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, **173**, 43–445.

Holdo, R.M., Fryxell, J.M., Sinclair, A.R.E., Dobson, A. & Holt, R.D. (2011) Predicted impact of barriers to migration on the Serengeti wildebeest population. *PLoS ONE*, **6**, e16370.

Horne, J.S., Garton, E.O., Krone, S.M. & Lewis, J.S. (2007) Analyzing animal movements using Brownian Bridges. *Ecology*, **88**, 2354–2363.

Hoye, B.J., Hahn, S., Nolet, B.A. & Klaassen, M. (2012) Habitat use throughout migration: linking consistency, prior breeding success and future breeding potential. *Journal of Animal Ecology*, **81**, 657–666.

Ito, T.Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A. & Jiang, Z. (2005) Preliminary evidence of a barrier effect of a railroad on the migration of Mongolian gazelles. *Conservation Biology*, **19**, 945–948.

Kranstauber, B., Kays, R., LaPoint, S.D., Wikelski, M. & Safi, K. (2012) A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, **81**, 738–746.

McCullough, D.R. (1985) Long range movements of large terrestrial animals. *Contributions in Marine Science Supplement*, **27**, 444–465.

McNaughton, S.J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, **55**, 260–294.

Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Cook, J.G., Cook, R.C., Nelson, A.A., Jimenez, M.D. & Klaver, R.W. Animal migration amid shifting patterns of phenology and predation: lessons learned from a Yellowstone elk herd. *Ecology*, in press.

Millspaugh, J.J., Gitzen, R.A., Kernohan, B.J., Larson, M.A. & Clay, C. L. (2004) Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin*, **32**, 148–157.

Milner-Gulland, E.J., Fryxell, J.M. & Sinclair, A.R.E. (2011) *Animal Migration*. Oxford University Press, Oxford.

Mueller, T., Olson, K.A., Dressler, G., Leimgruber, P., Fuller, T.K., Nicolson, C., Novaro, A.J., Bolgeri, M.J., Wattles, D., DeStefano, S., Calabrese, J.M. & Fagan, W.F. (2011) How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography*, **20**, 683–694.

Nelson, M.E. & Mech, L.D. (1999) Twenty-year home range dynamics of a white-tailed deer matriline. *Canadian Journal of Zoology*, **77**, 1128–1135.

Parker, K.L., Barboza, P.S. & Gillingham, M.P. (2009) Nutrition integrates environmental responses of ungulates. *Functional Ecology*, **23**, 57–69.

Post, E. & Forchhammer, M.C. (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B*, **363**, 2369–2375.

Sawyer, H. & Kauffman, M.J. (2011) Stopover ecology of a migratory ungulate. *Journal of Animal Ecology*, **80**, 1078–1087.

Sawyer, H., Kauffman, M.J. & Nielson, R.M. (2009) Influence of well pad activity on the winter habitat selection patterns of mule deer. *Journal of Wildlife Management*, **73**, 1052–1061.

Sawyer, H., Kauffman, M.J., Nielson, R.M. & Horne, J.S. (2009) Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, **19**, 2016–2025.

Singh, N.J., Grachev, I.A., Bekenov, A.B. & Milner-Gulland, E.J. (2010) Saiga antelope calving site selection is increasingly driven by human disturbance. *Biological Conservation*, **143**, 1770–1779.

Singh, N.J., Börger, L., Dettki, H., Bunnefeld, N. & Ericsson, G. (2012) From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, **22**, 2007–2020.

Spinage, C.A. (1992) The decline of the Kalahari wildebeest. *Oryx*, **26**, 147–150.

Sweanor, P.Y. & Sandegren, F. (1988) Migratory behavior of related moose. *Holarctic Ecology*, **11**, 190–193.

Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J., Sinclair, A.R.E. & Borner, M. (2004) Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation*, **7**, 113–120.

Tollefson, T.N., Shipley, L.A., Myers, W.L., Keisler, D.H. & Dasgupta, N. (2010) Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *Journal of Wildlife Management*, **74**, 974–986.

Vors, L.S. & Boyce, M.S. (2009) Global declines of caribou and reindeer. *Global Change Biology*, **15**, 2626–2633.

Whyte, I.J. & Joubert, S.C.J. (1988) Blue wildebeest population trends in the kruger national-park and the effects of fencing. *South African Journal of Wildlife Research*, **18**, 78–87.

Williamson, D. & Williamson, J. (1984) Botswana's fences and the depletion of the Kalahari's wildlife. *Oryx*, **18**, 218–222.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. & Henschel, C.P. (1999) Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, **77**, 1223–1232.

*Received 2 July 2012; accepted 24 October 2012*
*Handling Editor: Nathalie Pettorelli*

# ENERGY DEVELOPMENT GUIDELINES FOR MULE DEER

A Product of the
Mule Deer Working Group

Sponsored by the
Western Association of Fish and Wildlife Agencies

2011

## THE AUTHORS:

DARYL W. LUTZ
WYOMING GAME AND FISH DEPARTMENT
260 BUENA VISTA,
LANDER, WY 82520, USA

JAMES R. HEFFELFINGER
ARIZONA GAME AND FISH DEPARTMENT
555 N. GREASEWOOD ROAD
TUCSON, AZ 85745, USA

STEPHEN A. TESSMANN
WYOMING GAME AND FISH DEPARTMENT
5400 BISHOP BLVD.
CHEYENNE, WY 82006, USA

R. SCOTT GAMO
WYOMING GAME AND FISH DEPARTMENT
5400 BISHOP BLVD.
CHEYENNE, WY 82006, USA

STEVEN SIEGEL
NEVADA DEPARTMENT OF WILDLIFE
1100 VALLEY ROAD
RENO, NV 89512, USA

Mule Deer
Working Group

*Cover photos by Mark Gocke (oil/gas), Dana Wright (wind), Nadine Y. Barclay, U.S. Air Force (solar), and George Andrejko (mule deer).*

**Suggested Citation:** Lutz, D. W., J. R. Heffelfinger, S. A. Tessmann, R. S. Gamo, and S. Siegel. 2011. Energy Development Guidelines for Mule Deer. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, USA.

# TABLE OF CONTENTS

# PREFACE

The geographic scope, intensity, and pace of domestic energy development have potential to impact fish and wildlife habitats on a large scale. The capability of habitat to sustain wildlife into the future will depend on effective project planning and mitigation developed through constructive collaboration among federal land management agencies, state, provincial, and tribal wildlife management agencies, private landowners, industry, and other conservation partners.

This document establishes guidelines that will enable energy development to proceed in a manner reasonably compatible with habitat requirements of mule and black-tailed deer. These *Energy Development Guidelines for Mule Deer* will help resource managers focus on pre-project risk assessments, appropriate project designs, effective mitigation and reclamation, and adequate monitoring to better conserve mule deer habitats through adaptive management. Historically, the federal process of energy leasing and development has been too inflexible to apply best technology and information currently available. These guidelines represent the state of our knowledge at the time of publication, but it is the intent of the Mule Deer Working Group that they be promptly updated with all subsequent and pertinent research that becomes available to decision makers.

*Photo courtesy of George Andrejko/AZGFD*

# INTRODUCTION

Black-tailed and mule deer (collectively mule deer, *Odocoileus hemionus*) are icons of the North American West. Perhaps no animal better symbolizes the region in the minds of the American public. Because of their popularity and broad distribution, mule deer are one of the most economically and socially important animals in western North America. In a 2006 survey of wildlife-related recreation, the U. S. Fish and Wildlife Service (USFWS) reported nearly 3 million people hunted in the 19 western states (USFWS 2007). In 2006 alone, hunters were afield almost 50 million days and spent more than $7 billion on lodging, gas, and hunting-related equipment. Although the survey encompassed all forms of hunting, mule deer have traditionally been one of the most important game animals in the West. According to the same survey, 25.6 million residents in 19 western states spent more than $15.5 billion "watching wildlife" in 2006. The value of abundant wildlife populations cannot be overemphasized. Because mule deer are inextricably tied to the history, development, and future of the West, the species is one of the true barometers of ecological conditions in western North America.

Mule deer are distributed throughout western North America from the coastal islands of Alaska, to southern Baja Mexico and from the northern border of the Mexican state of Zacatecas to the Canadian provinces of Saskatchewan, Alberta, British Columbia, and the southern Yukon Territory. Within these broad latitudinal and geographic gradients, mule deer have developed incredibly diverse behavioral and ecological adaptations enabling the species to occupy a diversity of climatic regimes and vegetation associations.

Federal land management agencies regulate surface disturbing activities, including energy development, throughout much of the mule deer range in the West. In the eastern portions of mule deer range, private landowners control how habitat is managed. Mule deer habitats are increasingly vulnerable to unprecedented threats from a range of anthropogenic developments. If mule deer habitats are to be conserved, it is imperative that government agencies and private conservation organizations elevate their awareness of the species' key habitat requirements, engage in habitat restoration initiatives, and fully integrate effective habitat protection and mitigation practices into all land use decisions.

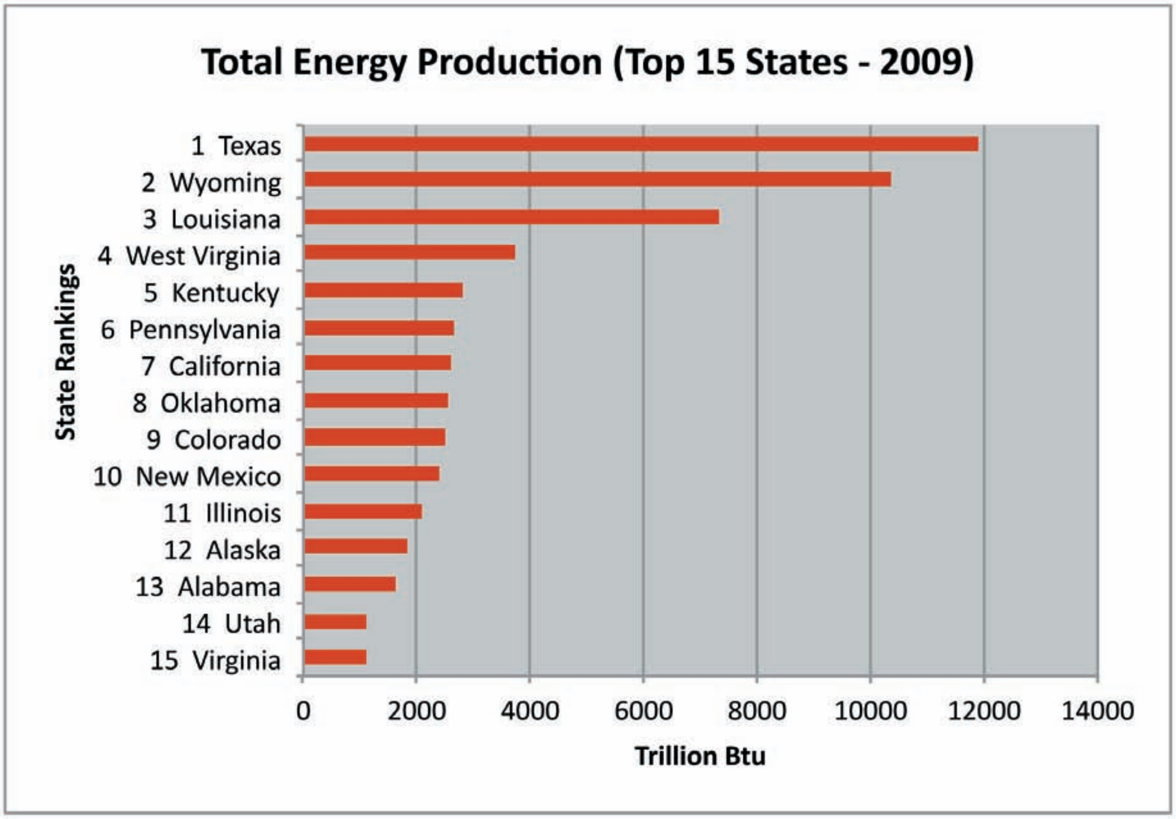
State wildlife agencies manage and regulate wildlife populations that are dependent on those habitats managed by the Federal land management agencies and private landowners. The Western Governors' Association (WGA) recognized the need to coordinate efforts to protect and maintain wildlife migration corridors and crucial habitats (WGA 2008). They approved Policy Resolution 07-01 to work "in partnership with important stakeholders, to identify key wildlife corridors and crucial wildlife habitats in the West and make recommendations on needed policy options and tools for preserving those landscapes." The WGA's *Wildlife Corridors Initiative*, is a multi-state and collaborative effort to improve knowledge and management of wildlife corridors and crucial habitat. The primary objective was to develop a tool for policy makers to integrate wildlife corridor and crucial habitat values into planning decisions, and promote best management practices for development to reduce harmful impacts on wildlife.

Energy consumption and production continue to be the focus of the nation's energy policy. According to the National Energy Policy (2001), "…if energy production increases at the same rate as during the last decade our projected energy needs will far outstrip expected levels of production. This imbalance, if allowed to continue, will inevitably undermine our economy, our standard of living, and our national security." As pressure mounts to locate and develop additional sources of domestic energy in the western states, careful attention must be given to how industry can maintain effective habitat conditions for mule deer. To best do that, rigorous research to determine population level effects of energy development on mule deer needs to continue as many questions remain unanswered. Hebblewhite (2011) observed many population level surveys have identified important changes, but the mechanisms of change remain speculative. He concludes research needs to occur to better achieve an evidence-based framework for mitigating development.

Sawyer et al. (2002) suggested habitat loss and fragmentation caused by extensive energy development could pose a serious threat to mule deer and pronghorn (*Antilocapra americana*) populations in western Wyoming. The national focus on energy independence should, at the same time, recognize the importance of maintaining intact wildlife habitats supporting diverse economic, recreational, social, and aesthetic values.

Areas of known or potential energy resources overlap much of what is considered important mule deer habitat. Development of those resources brings about habitat disturbance or loss due to construction of well pads, roads, pipelines, mine facilities, wind and solar farms, and other features. In addition, disturbances from vehicle traffic, noise, and human activities often displace mule deer to areas farther away from well pads (Sawyer et al. 2006). Presumably this displacement is to areas of less suitable habitat. This disturbance and displacement diverts time and energy away from foraging, resting, and other activities that improve physiological condition (Gill et al. 1996, Frid and Dill 2002). Therefore, there is the potential to decrease mule deer survival and recruitment rates and ultimately lead to population-level effects. Activities associated with energy exploration and development often preclude or inhibit use of winter ranges that are critically important to mule deer (Lutz et al. 2003, Sawyer et al. 2006). Roads and traffic also limit mule deer use of important habitats (Sawyer et al. 2009c). The impact of roads has been increasingly recognized in the past decade (Forman et al. 2003). In fact, highway-associated impacts are one of the most prevalent and widespread stressors affecting natural ecosystems in the U.S. (Noss and Cooperrider 1994, Trombulak and Frissell 2000, Farrell et al. 2002). These impacts are especially severe in the western states where oil and gas, and more recently wind and solar energy, are being developed rapidly at a time when mule deer populations are depressed (Heffelfinger and Messmer 2003, Lutz et al. 2003, Hebblewhite 2008).

While other energy sources such as nuclear and woody or cellulosic biomass conversion could present some issues or concerns, their impact on mule deer or mule deer habitat is not considered significant and therefore not addressed here. For purposes of this document we focus guidelines on the forms of energy development having significant effect on mule deer and their habitat.



*Nine of the top 15 energy producing states are in the West and provide habitats for black-tailed or mule deer (U.S. Energy Information Administration, http://www.eia.doe.gov/state/state_energy_rankings.cfm?keyid=89&orderid=1)*

# OIL AND GAS ENERGY DEVELOPMENT

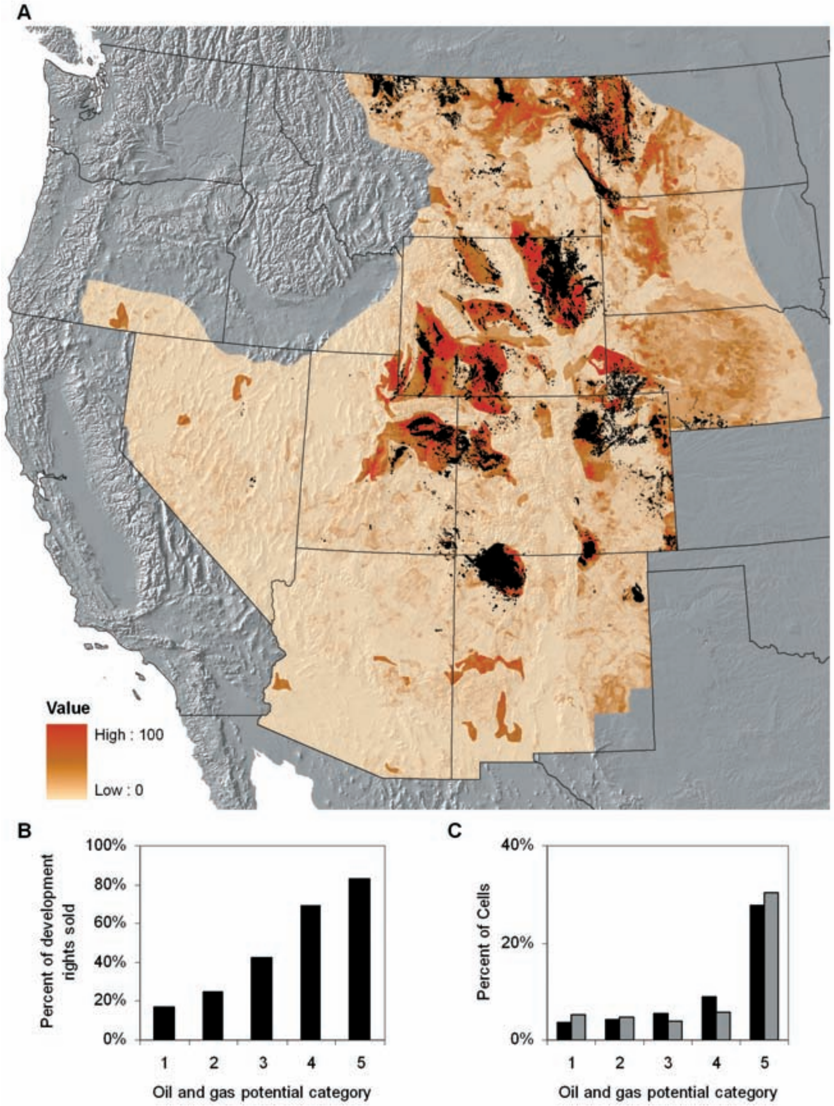
## BACKGROUND

Exploration and extraction of oil and gas resources continue to have a range of effects on mule deer habitats. Some types of disturbance can be positive if they improve vegetative structure or nutritional content. However, activities associated with extraction of energy resources often have adverse effects on mule deer. The severity of impact depends upon the amount and intensity of the disturbance, specific locations and arrangements of disturbance, and ecological significance of habitats affected. In Colorado, it has been demonstrated most mule deer populations are ultimately limited by habitat (Bartmann et al. 1992, White and Bartmann 1998, Bergmann et al. 2007, Bishop 2007, Watkins et al. 2007). Thus, small isolated disturbances within non-limiting habitats are of minor consequence within most ecosystems. However, larger-scale developments within habitats limiting the abundance and productivity of a mule deer population are a significant concern. Both direct and indirect impacts associated with energy and mineral development have the potential to affect ungulate population dynamics, especially when impacts are concentrated on winter ranges (Sawyer et al. 2002).

In order to meet their nutritional and energy needs, mule deer throughout most of North America depend on distinct seasonal ranges for summer (high elevation forests) and winter (low elevation shrub and grasslands). Migratory mule deer rely on networks of migration routes to transition between these critical areas (Sawyer et al. 2005). Oil and gas development not only removes habitats from these ranges, but may also displace deer from other preferred habitats (Sawyer et al. 2006) and create barriers that hinder migration and use of remaining habitats (Sawyer et al. 2009a). In some cases, construction activities might remove decadent vegetation and provide the opportunity to reclaim the area with improved forage.

Throughout the West, reservoirs of oil and gas commonly overlie important mule deer habitats, including winter ranges (Sawyer et al. 2006). Freddy et al. (1986) demonstrated that mule deer exhibit an alert-flight response at distances up to 0.08 and 0.12 mile from sources of noise and activity from snowmobiles and people afoot, respectively. Sawyer et al. (2006, 2009a, b) showed that high-use deer areas on winter range consistently occurred 1.2 to 1.8 miles away from well pads. Additionally, Sawyer et al. (2009a) found mule deer avoided all types of well pads, but selected areas farther from well pads with greater levels of human disturbance (i.e., traffic). They also concluded liquid gathering systems and directional drilling are effective practices to reduce human activity and surface disturbance during development. They suggested indirect habitat loss to mule deer may be reduced approximately 38-63% when liquids are collected in pipelines rather than stored at well pads and hauled away with tanker trucks. In western Wyoming, surface disturbance was reduced by 70-80% using directional drilling (Sawyer et al. 2009b).

A relatively new area of significant interest has been development of natural gas from coal beds. Depending on depth of the coal seam, coal bed natural gas (CBNG) production and coal mining activities can occur in the same general area, thus raising concerns about possible cumulative effects on mule deer and other wildlife. Development and extraction activities associated with CBNG,



*Oil and gas resource potential in the Intermountain West (Copeland et al. 2009)*

coal, and deep-well natural gas have potential for profound and long-term impacts on the environment. For the purpose of this discussion, oil and gas development includes those activities used to extract all hydro-carbon compounds such as natural gas, crude oil, coal bed methane, and oil shale.

Drilling operations during winter months (15 Nov – 30 Apr) causes measurably greater impact on mule deer compared to production and maintenance activities. Sawyer et al. (2009a) cautioned wintering mule deer are sensitive to drilling disturbance and that indirect habitat loss may increase by a factor of >3 when seasonal wildlife protection restrictions are waived. Wildlife managers should expect considerable short-term displacement of wintering mule deer if wide-spread, year-round drilling is permitted in crucial winter range and long-term displacement depending on the level of disturbance during well field operation.

**Impact Thresholds**
Impact thresholds are levels of development and disturbance that impair key habitat functions by directly eliminating habitat; disrupting wildlife access to, or use of habitat; or causing avoidance and stress (WGFD 2010a). Impact thresholds, appropriate management, and mitigation will vary depending on habitats affected. Our most pressing need is to address the species and habitat functions affected by impending, large-scale developments primarily in sagebrush-steppe ecosystems.

Impact thresholds are based on 2 quantitative measures: density of well pad locations and cumulative area of disturbances/mile$^2$. The cumulative area of disturbance represents direct loss of habitat. While evaluating impacts to sage-grouse, Naugle et al. (2006) concluded density of well pads is highly correlated with other features of development and therefore comprises a suitable index representing the extent of development. Although the density of well pads and cumulative acreage serve as a general index to well-field development and activities, thresholds based upon these alone may under-represent the actual level of disturbance (WGFD 2010a). Relative degrees of impact are described as follow:

**Low Impact—** One well pad location with total disturbance not exceeding 20 acres/mile$^2$. Habitat effectiveness is reduced within a zone surrounding each well, facility, and road corridor through human presence, vehicle traffic, and equipment activity.

**Moderate Impact—** Two to 4 well pad locations with total disturbance not exceeding 60 acres/mile$^2$. At this range of development, impact zones surrounding each well pad, facility and road corridor begin to overlap, thereby reducing habitat effectiveness over much larger, contiguous areas. Human, equipment and vehicular activity, noise, and dust are also more frequent and intensive and will impair the ability of animals to use critical areas (winter range, parturition grounds, etc.) and impacts will be much more difficult to mitigate. It may not be possible to fully mitigate impacts caused by higher well densities, particularly by developing habitat treatments on site. Habitat treatments will then generally be located in areas near, rather than within well fields to maintain the function and effectiveness of critical areas.

**High Impact—** Greater than 4 well pad locations or 60 acres of disturbance/mile$^2$. At this level of development, the function and effectiveness of habitat becomes compromised. Long-term consequences would likely include continued fragmentation and disintegration of habitat leading to decreased survival, productivity, and ultimately, loss of carrying capacity for the herd. This will result in a loss of ecological functions, recreation opportunity, and income to the economy. An additional consequence may include permanent loss of migration memory from large segments of unique, migratory mule deer herds.

## ISSUES AND CONCERNS

For purposes of these guidelines, impacts to mule deer from oil and gas development can be divided into the following general categories: 1) direct and indirect loss of habitat; 2) physiological stress, 3) disturbance and displacement; 4) habitat fragmentation and isolation; and 5) other secondary (offsite) effects.

*The presence of well pads, roads, pipelines, compressor stations, and out buildings directly removes habitat from use (Photo courtesy of New Mexico Department of Game and Fish [NMDGF]).*

### Direct and Indirect Loss of Habitat

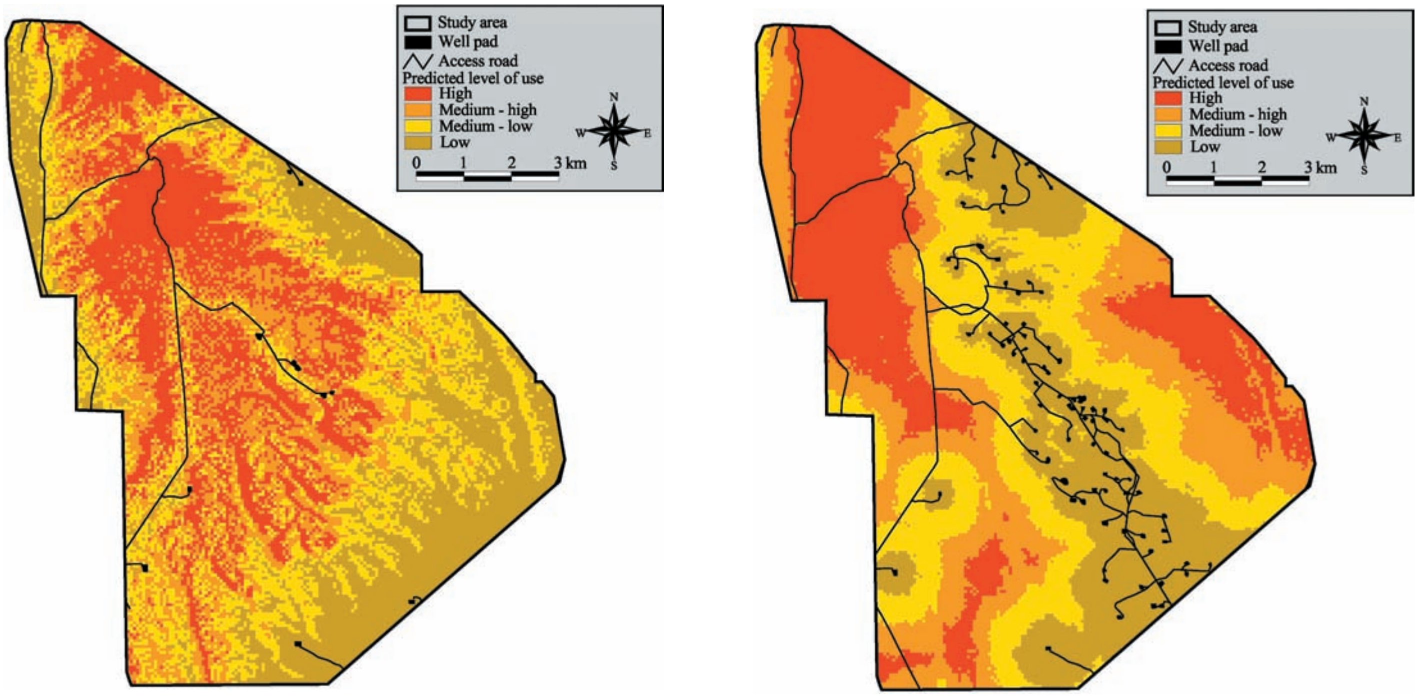
Direct loss of habitat results primarily from construction and production phases of development. The construction and subsequent presence of well pads, roads, pipelines, compressor stations, and out buildings directly removes habitat from use. Production activities require extensive infrastructure and depending upon scale, density, and arrangement of the developed area, indirect loss of habitat can be extensive (USDI 1999). As an example, within the Big Piney-LaBarge oil and gas field in Wyoming, the actual physical area of structures, roads, pipelines, pads, etc. covers approximately 7 miles$^2$. However, because of the arrangement of these structures, the entire 166 mile$^2$ landscape is within 0.5 mile of a road, and 160 miles$^2$ (97% of the landscape) is within 0.25 mile of a road or other structure (Stalling 2003).

Generally, it is possible to reclaim 50% of a disturbed area to minimal cover standards within 3-5 years after construction. However, re-establishing suitable habitat conditions (appropriate native species composition, diversity, structure, and age) may take 30–40 years (Young and Evans 1981, Bunting et al. 1987, Winward 1991), or may take well over 100 years (Baker 2006, Cooper et al. 2007). The remaining 50% of the disturbed area consists of the working surfaces of roads, well pads, and other facilities, and represents a much longer term loss of habitat (USDI 1999). Successful reclamation of sagebrush communities is difficult at best, as success is highly dependent upon amount and timing of precipitation. Sagebrush seed remains viable in salvaged topsoil for a comparatively brief period and reseeding is usually required if reclamation is conducted >1 year post-disturbance. Restoration of shrub habitats important to wintering deer is critical, but reclamation of these vegetation types in dry regions may not occur quickly (Baker 2006) and therefore any disturbance will likely represent a longer-term habitat loss.

### Physiological Stress

Animals become physiologically stressed when energy expenditures increase due to alarm or behavioral avoidance. These responses are generally attributed to interactions with humans or activities associated with human presence such as traffic, noise, pets, and etc. Physiological stress diverts time and energy away from critical activities such as foraging and resting important to maintain or improve fitness (Gill et al. 1996, Frid and Dill 2002). This seems especially critical to wintering deer whose nutritional condition is closely associated with survival (Sawyer et al. 2009a).

During winter months, additional stress can be particularly harmful because a deer's energy balance is already operating at a deficit (Wallmo et al. 1977). In addition, the diversion of energy reserves can be detrimental to other vital functions during the life cycle such as gestation and lactation. An environmental assessment of oil and gas development in the Glenwood Springs (CO) Resource Area expressed concern these impacts could ultimately have population effects through reduced production, survival, and recruitment (USDI 1999).



*Predicted levels of mule deer use before and after natural gas development in western Wyoming. Avoidance of well pads can create indirect habitat losses that are considerably larger than direct habitat loss (from Sawyer et al. 2006)*

### Disturbance and Displacement

Increased human presence and activity, equipment operation, vehicle traffic, and noise related to wells and compressor stations, etc. are primary factors leading to avoidance of a developed area by wildlife (Barber et al. 2010). The avoidance response by mule deer (indirect habitat loss) extends the influence of each well pad, road, and facility to surrounding habitats. In winter ranges of western Wyoming, mule deer were shown to prefer habitats 1.2 to 1.8 miles away from well pads (Sawyer et al. 2006, 2009b).

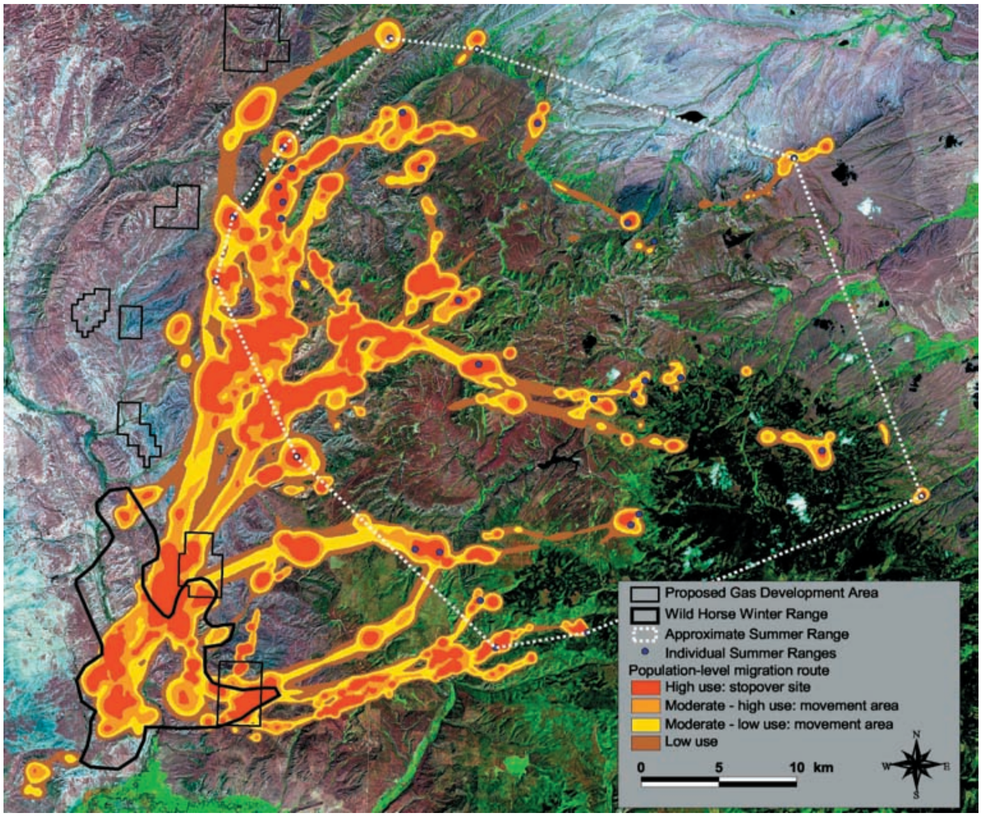
During all phases of well field development and operation, roads tend to be the most significant concern because they often remain open to unregulated use. This contributes to noise and increased human presence within the development area. Rost and Bailey (1979) documented an inverse relationship between habitat use by deer and elk and distance to roads. Sawyer et al. (2009a) found mule deer selected areas farther from well pads associated with higher levels of traffic, primarily heavy truck traffic used to remove condensate from producing wells. This 'displacement' effect can result in the under use of otherwise suitable habitats near infrastructure and disturbances and over use of habitats in more distant locations. Displacement also adds to the potential for depredation problems within nearby agricultural properties. Some other consequences of increased human presence include, but are not limited to, mortality and injury due to vehicle collisions, illegal hunting, and harassment from a variety of increasing recreational activities such as OHV use.

### Habitat Fragmentation and Isolation

Human caused habitat fragmentation creates landscapes fundamentally different from those shaped by natural processes to which species have adapted (Noss and Cooperrider 1994). Human caused changes often manifest as altered plant composition, often dominated by weedy and invasive species. This, in turn, changes the type and quality of the food base as well as the structure of the habitat. When the ability to move between important daily or seasonal habitats (e.g., parturition areas, winter range, etc.) is severely disrupted, abandonment of habitat ultimately could result.

When planning developments, it is critical to consider these corridors and how to avoid or mitigate impacts in order to sustain deer migration corridors (Merrill et al. 1994). Sawyer et al (2009c) recently developed a framework to identify and prioritize mule deer migration routes for landscape-level planning. Such a framework may improve

*The Rosa gas field in northwestern New Mexico shows an example of extreme impact. (Photo courtesy of NMDGF)*



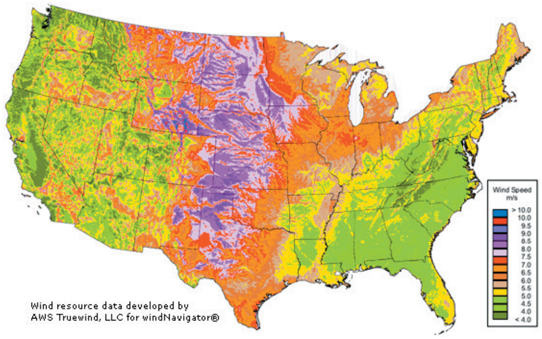
*Estimated migration routes for mule deer relative to proposed gas development in southwest Wyoming. High-use areas represent stopover sites presumably used as foraging and resting habitat, whereas moderate-use areas represent movement corridors (from Sawyer et al 2009c).*

both management and planning and ensure potential impacts to mule deer migration routes are minimized. In much of the Southwest, mule deer do not engage in predictable migrations, but may make long-distance "nomadic" movements based on seasonal variation in water and food availability. Flexibility in movement across ranges can be ultimately reflected in the survival and productivity of the deer population and likely enhances their ability to recover from population declines.

### Secondary Effects

The severity of activities associated with support or service industries linked to development often equals or exceeds that of the direct effects described above. These impacts are similar to those that occur during construction and operations. Additional human presence from increased support industries and community expansion will contribute to human-wildlife interactions and declines in mule deer habitat availability and quality.

Roads, pipelines, and transmission corridors not only remove habitat, but also have the potential to contaminate ground and surface water supplies. Noxious weeds introduced by equipment can infiltrate roadside impact zones and cause additional negative impacts such as non-native bacteria, viruses, insect pests, or chemical defense compounds with toxic or allergenic properties (NMDGF 2007). In addition, these invasive species can spread to adjoining native plant communities.



*Wind energy resource potential in the U. S. (U.S. Department of Energy, Natural Renewable Energy Laboratory)*

*Construction of wind turbines can create habitat disturbances similar to other forms of energy development. (Photo by J. Heffelfinger/AGFD*

Impervious roads and disturbed pipeline corridors increase surface water runoff which can reduce infiltration, lower the water table, and result in lower rangeland productivity. This problem will increase if the nation's energy infrastructure is expanded as recommended in the Energy Policy Act of 2005.

Activities occurring at the well site (drilling, pumping, etc.) or associated with product transportation to other destinations via pipeline or vehicle may lead to the release of a variety of toxic hydro-carbon based compounds. These compounds are common by-products and can pose serious health risks to not only employees, but also the environment and mule deer in the surrounding area. All these events can decrease the amount of area available to mule deer and other wildlife. Finally, potential exists for rendering an area useless to wildlife for an indeterminable amount of time unless careful consideration is given to planning and implementing quality mitigation and reclamation programs.

## WIND ENERGY DEVELOPMENT

### Background

Wind-energy development is a component of the nationwide effort to reduce dependence on foreign oil and minimize carbon emissions associated with energy derived from oil, gas, and coal. At the end of 2007 the U. S. had the second highest cumulative wind capacity globally. In 2009, the U.S. wind industry installed 10,010 megawatts (MW) of generating capacity, breaking U.S. installation records for the third year in a row. Wind power represented 39% of all U.S. electric generation capacity additions for the year (USDOE 2010). This rate of development is expected to continue, and perhaps to accelerate, as U.S. energy policy emphasizes independence from foreign oil and reduction of carbon emissions. The USFWS and members of the Wind Turbine Guidelines Advisory Committee (USFWS 2010) recognize wind-generated electrical energy is renewable, and is considered to be generally environmentally friendly. The U.S. Department of Energy (DOE) estimates that a single 1.5 megawatt (MW) wind turbine displaces 2,700 metric tons of $CO_2$/year compared with the current U.S. average utility fuel mix. Wind energy development is proceeding without basic fact-finding research on the environmental consequences and impacts to mule deer.

Although fossil fuel consumption and carbon emissions are largely confined to the manufacture, construction, and maintenance aspects of wind power generation, wind farms themselves are an intensive, industrial-scale use of the land and have the potential to impact mule deer habitats throughout the West. With current technology, individual turbines typically generate in the range of 1.5-2.0 megawatts each. Towers range from 212 to >260 feet tall with blade sweeps of 328 to >400 feet above ground level. For maximum generating efficiency, tower strings are separated by approximately 10 rotor diameters, and individual towers within strings are separated by 3 rotor diameters. Wind farms incorporate a road network to facilitate access for turbine maintenance. In addition, power lines provide connection to transfer stations that connect to nearby transmission lines. Based on other wildlife energy research (Sawyer et al. 2006, 2009a), associated infrastructure has potential to affect mule deer.

*The open areas mule deer occupy usually have high potential for wind energy development. (Photo by S. Gray, TPWD)*

## ISSUES AND CONCERNS

Little is known about the effect of wind power development on mule deer. Although research on avian species and bats has received much attention in recent years, very little research has been done to evaluate impacts on larger mammals. The USFWS (2011) states siting of a wind energy project is the most important element in avoiding effects to wildlife and their habitats. The direct impact from surface disturbance may be relatively small in scope as turbines and roads typically constitute a small total acreage within a development area (WGFD 2010b). However, indirect impacts affecting habitat use by ungulates may be much larger. Due to the acreages that large-scale wind projects encompass (10,000- to 100,000-acre project areas), the potential exists to displace mule deer from important seasonal habitats. If displacement does occur, it may affect migration routes, parturition areas and important summer ranges, all of which provide essential seasonal habitat components to maintain mule deer populations. Other indirect effects identified by the USFWS (2011) include introduction of invasive vegetation that result in alteration of fire cycles; increase in predators or predation pressure; decreased survival or reproduction; and decreased use of the habitat as a result of habitat fragmentation.

The transmission corridors that transfer energy production to electrical grids may represent a greater impact than the actual siting of wind turbines. Transmission corridors and any associated roads can cause direct mortality and remove habitat, but they also have the potential to fragment important habitat components. These corridors can also facilitate the spread of invasive species not native to that area (Gainer 1995, NMDGF 2007). The impact of associated corridors must be considered along with the area chosen for turbine placement when evaluating impacts (Kuvlesky et al. 2007).

Mule deer crucial habitats, especially winter ranges, are often characterized by open landscapes comprised of sagebrush-steppe or sagebrush-grassland habitat types. These areas often provide accessible lands with high potential for wind-energy development. Potential impacts to mule deer include direct and indirect habitat loss, displacement, and cumulative impacts associated with other nearby energy developments.

Mule deer have been observed to maintain populations in conjunction with coal mine development where the pace of development is slow and dependent upon bond release after successful reclamation (Medcraft and Clark 1986, Gamo and Anderson 2002). However, Sawyer and Nielson 2010) found mule deer numbers declined by 40-60% following intensive gas development of the winter range. Over a 9-year period, they found no evidence of similar mule deer declines in winter ranges adjacent to the gas field (Sawyer and Nielson 2010).

Wind energy development, like other forms of development, does include a certain amount of construction and resulting infrastructure (WGFD 2010b). Temporary and permanent roads are constructed, maintenance activities occur, and the landscape becomes fragmented. It is expected that mule deer will be displaced from habitats during construction. The impacts of long-term facility operation are unclear.

# SOLAR ENERGY DEVELOPMENT

## BACKGROUND

Solar energy development is also a component in the nationwide effort to secure a free fuel source and reduce carbon emissions associated with energy derived from oil, gas, and coal. Solar energy development in the U. S. is viewed as a source of "green" energy. Where solar energy is being developed, habitat loss for mule deer approaches 100% within the footprint of the project. Currently, identified solar projects in Arizona alone range in size from 2,000 to >25,000 acres and, in totality, encompass an estimated potential 800,000 acres resulting in significant habitat loss for wildlife (AGFD 2010).

### Photovoltaic

Photovoltaic (PV) solar systems are a series of small cells made of crystalline silicon or a thin film layer that are assembled into a panel of cells, and in turn several panels can be clustered into an array. These PV cells convert sunlight directly into electricity when the sun's photons agitate electrons in the PV cell, and electrons are then channeled directly as DC electrical current. The DC output may be converted to AC output. Photovoltaic systems have mainly been used to power small and medium-sized applications, such as supplementing energy for individual homes or facilities not connected to a main power grid. Recently, multi-megawatt PV plants are becoming more common. A proposed 550 MW power station in southern California encompassing 4,245 acres is characteristic of the trend toward larger PV stations throughout the country and world. Photovoltaic solar-energy development sites are an intensive, industrial-scale use of the land and have the potential to significantly impact mule deer and their habitats throughout the West. The advantage of PV systems from a wildlife perspective is that they use much less water than other solar technologies. No water is used to collect, transfer, or store energy; water is only needed to wash the PV panels. Although efficiency is increasing, the disadvantage is their lower productivity and greater land area required to produce the same amount of energy as more efficient systems.

*Nellis Air Force Base in Nevada is home to a PV system with 72,000 solar panels that produce 14 MW of electricity. (U.S. Air Force photo by Airman 1st Class N. Y. Barclay)*

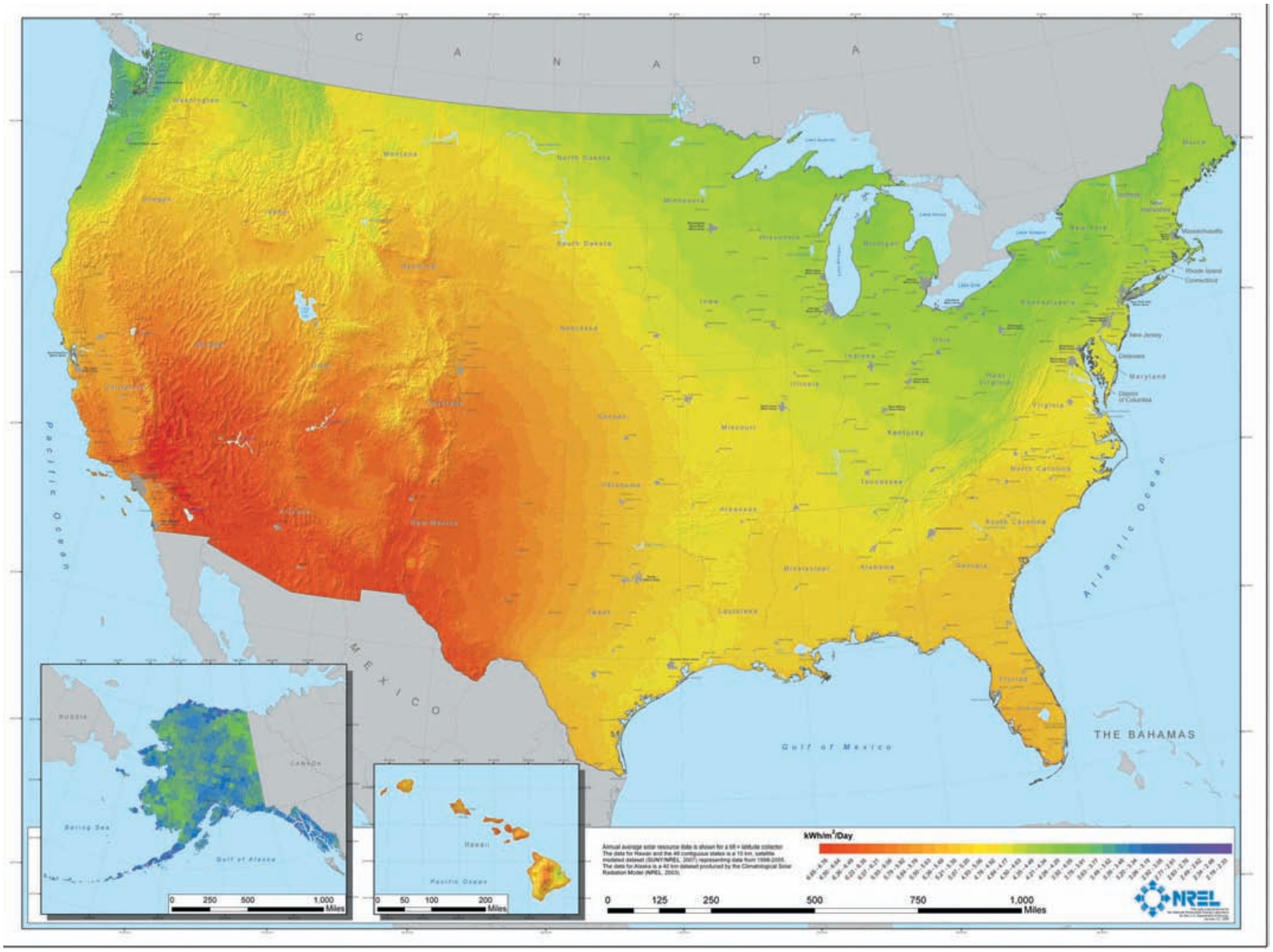
*Each of these Dish/Engine units produces 10 kW of power. (Photo courtesy of Sandia National Laboratory)*

### Concentrating Solar Power

Concentrating Solar Power (CSP) differs from PV in that it uses a reflective surface to concentrate solar energy to heat a liquid medium to generate steam that drives a turbine to generate electricity. If thermal energy storage is included in the system, electricity generated with CSP can be supplied to an electrical grid or stored for peak usage times, nighttime, or cloudy days. This is unlike PV which does not store energy. The Southwest holds potential to generate significant amounts of electricity with this technology. However, CSP technology requires more water for energy production and washing of mirrors.

### Dish/Engine Systems

Dish/Engine systems consist of a solar collector (usually a mirrored dish) that concentrates solar energy into a central power conversion unit (Stirling engine) in front of the dish. The concentrated sunlight heats a thermal receiver in the engine made of tubes filled with liquid such as helium or hydrogen. This heated gas (1,400° F) then moves pistons in the engine to directly generate electricity (DOE 2007). The dishes are designed to track movements of the sun throughout the day to assure maximum exposure. These units are well-suited for more dispersed applications because they generate relatively small amounts of energy (1-25 kW, DOE 2007). Of all the CSP technologies, Dish/Engine systems require the least amount of water, therefore minimizing impact to local hydrologic resources. However, these units can be installed on uneven ground and that could result in more solar development in important mule deer habitat.



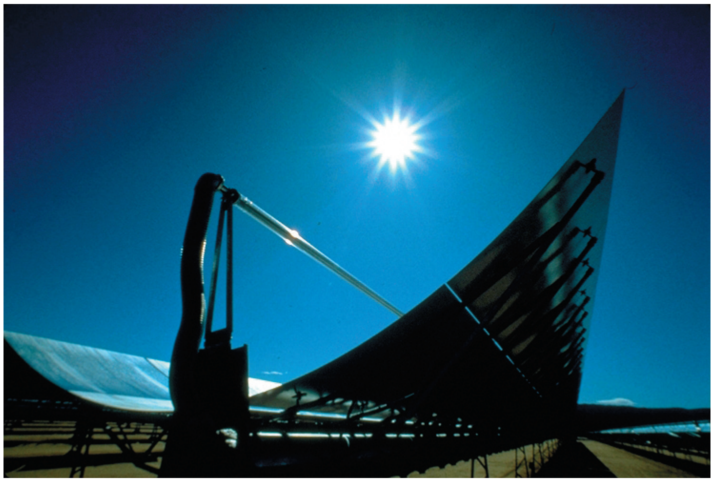
*Solar PV energy potential in the United States. (National Renewable Energy Laboratory, http://www.nrel.gov/gis/solar.html)*

**Parabolic Trough Systems**
These CSP systems use parallel rows of long trough mirrors to reflect sunlight onto a linear receiver containing a liquid (usually an organic oil). That liquid is then superheated (about 750°F) and used to create steam which turns turbines to generate electricity. Most Parabolic Trough Systems use long parabolic troughs to simply reflect light onto the oil filled tube, but a variation called the Fresnel Reflector system uses linear mirrors to reflect sunlight onto a linear receiver suspended above the mirrors. These linear structures are oriented north-south and tilt to track the sun across the sky throughout the day. Concentrating Solar Power technology can also be combined with natural gas, resulting in hybrid systems that can provide power at any time. Currently, the largest solar trough facility in the world is being constructed near Gila Bend, Arizona and has the potential to generate 250 MW of electricity.

**Power Tower Systems**
Power Tower systems consist of a tall tower supporting a thermal receiver surrounded by a large field of flat "heliostat" mirrors that track the sun's movement and keep solar energy focused on the receiver. The heat concentrated (1,050° F) in the receiver is used to generate steam, which turns turbines to generate electricity. The heat can be collected and transported by water, but newer designs are incorporating molten salt because of its superior thermal energy storage properties. Individual commercial plants can produce up to 200 MW of electricity. Both parabolic trough and power tower systems can be engineered with molten salt thermal storage so that the heat can be stored and then used later to generate electricity. Molten salt integrated in a tower system allows for significantly higher power plant operating temperatures and therefore higher generation efficiencies (i.e., lower cost of electrical generation) compared with direct steam towers or trough systems.

## ISSUES AND CONCERNS

Primary impacts to mule deer from solar energy development can be summarized into the following general categories: 1) direct loss of habitat; 2) habitat fragmentation; and 3) hydrologic changes. Each of these,



*A Parabolic Trough System uses a reflective trough to heat a tube filled with oil to produce steam to drive a turbine to generate electricity. (Photo courtesy of Sandia National Laboratory)*

*Compact Linear Fresnel reflectors and linear receiver. (Photo courtesy of Areva Media Department)*

*Abengoa's PS10 and PS20 power towers near Seville, Spain use reflectors that track the sun to concentrate the sun's energy to a focal point in the tower where liquid is heated to >1,000° F and used to generate electricity.*

alone or in conjunction with others, has the potential to significantly influence whether deer can maintain robust or depressed populations in the developed area or abandon it altogether.

### Direct Loss of Habitat

Wildlife habitat loss may result from construction of large-scale solar facilities. The largest contiguous loss of habitat would occur within the perimeter of the facility's security fence. Additional habitat loss may take place through the construction of new or expansion of existing substations, new transmission lines, and associated access roads (AGFD 2010). In addition, drainages are re-routed around large facilities eliminating critical desert dry wash woodlands used as refuge and spring foraging habitats. Finally, conversion of irrigated agriculture areas to solar facilities is eliminating important water sources in some areas, although water consumption for power generation is generally comparatively lower than for agricultural use.

### Habitat Fragmentation

Solar development will potentially disturb and fragment mule deer habitat during and after construction of a facility. The development of utility-scale solar fields and associated infrastructure including substations, transmission lines, and access roads will likely affect mule deer movement and habitat use (AGFD 2010). In California, several utility-scale facilities may be built adjacent to one another and are completely fenced which may impede mule deer movement over large areas. It is imperative wildlife movement corridors to and from crucial habitats are identified during pre-construction planning. These data could be used to establish the location of sensitive resources and recommend the most appropriate locations of roads, fences, and other infrastructure to minimize habitat fragmentation and disturbance.

### Hydrology

Much of the Southwest, where solar energy development potential is highest, also lacks abundant water resources. In this region, water is a very crucial component that can limit mule deer populations. Any changes to hydrologic resources, ground or surface water, have the potential to affect mule deer distribution and abundance. Solar energy development can impact hydrologic resources through development of the project footprint (e.g., land disturbance, erosion, changes in runoff patterns, and hydrological alterations), project emissions (e.g., sediment runoff, chemical spills, herbicide use, and water releases), and resource use (e.g., water extraction, diversion, or change in use; AGFD 2010). Though evaporation ponds are typically located within the fenced solar facility, mule deer are attracted to any form of open water and therefore are susceptible to inadvertent poisoning due to concentrated salts and other minerals.

Because of their thermal processes, Parabolic Trough and Power Tower systems may require large amounts of water to collect and transfer heat, cool and condense steam, and also to clean mirrored surfaces. A typical wet-cooled coal or nuclear power plant consumes 500 gallons of water per megawatt hour (gal/MWh), which is similar to the amount used by a Power Tower system (DOE 2007). A water-cooled parabolic trough plant consumes approximately 800 gal/MWh, and of this, 2% is used for mirror washing (DOE 2007). Recent advances in cooling technology have shown water usage in these plants can be reduced by up to 90% with a resultant increase in energy costs of 2-10% by using dry cooling or a hybrid of wet and dry cooling technologies (DOE 2007).

## GEOTHERMAL ENERGY DEVELOPMENT

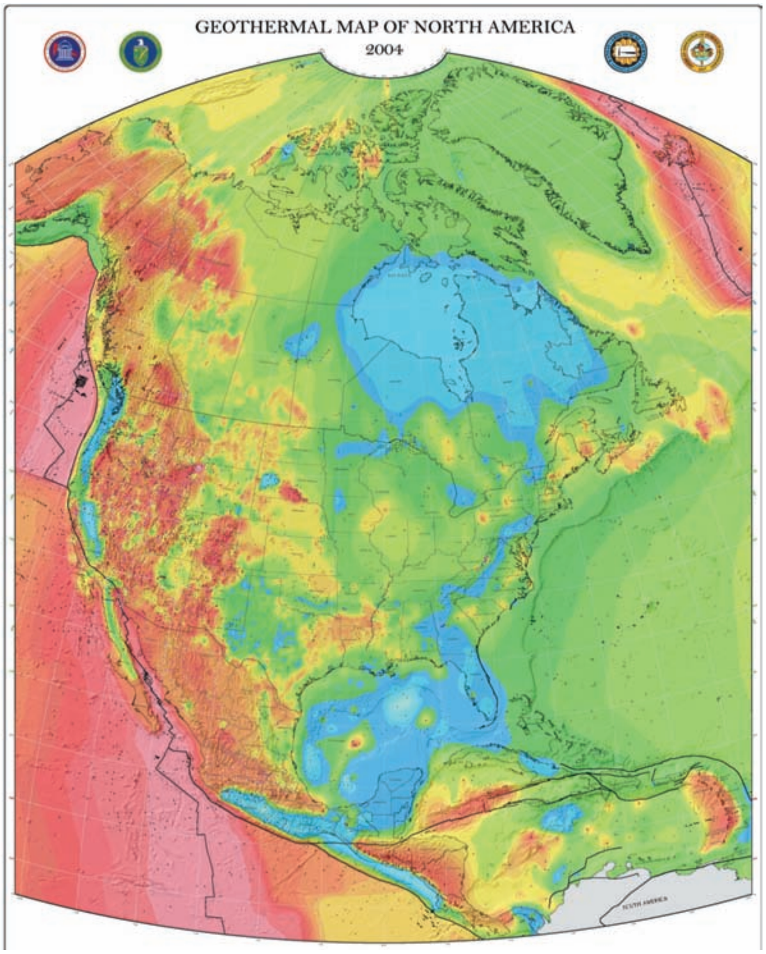
### Background

Geothermal energy development has increased 20% worldwide in the last five years (Holm et al. 2010). The 2010 figures reflect 10,715 MW on line, generating 67,246 gigawatt hours (GWh) of power with a projected growth to 18,500 MW by 2015. Seventy countries currently have geothermal power projects proposed or under development. Geothermal capacity increased by 530 MW in the U.S. over the past 5 years, the largest growth logged by any single country. From a continental perspective, the largest growth occurred in Europe and Africa. Although the growth is encouraging, overall the resource as a whole is under-utilized. Some countries are developing only a small amount of the geothermal resources available and a number of countries with resources are not developing them to any significant degree. World-wide, most of the new development is for use in direct heating or other direct use application.

In North America, development is concentrated in the western third of the continent from Alaska to southern Mexico. Some lesser resource potential occurs in the southeastern U. S.. In the U. S., the increase in geothermal development is primarily to supply off-site electrical grids. The increase in activity in the U.S. is tied to increased financial support and other incentives for development, such as the Renewable Energy Tax Credit. It is unknown how long this support will be sustained. Mexico continues to be a significant developer of geothermal power production and is currently ranked fourth in the world for installed capacity. Although Canada has not developed geothermal resources for power production, a number of projects are under consideration.

The DOE maintains a website listing incentives available in the U. S. (http://www.dsireusa.org/). A growing number of states are developing requirements (Renewable Portfolio Standards) for energy providers to include renewable energy as a percent of the power provided to their customers. This mix could include geothermal-sourced energy. A list of state standards is maintained by the DOE (http://apps1.eere.energy.gov/states/maps/renewable_portfolio_states.cfm).

In Section 225 of the Federal Energy Policy Act of 2005, the Secretaries of Interior and Agriculture were charged with developing a program to reduce (by 90 percent) the backlog of geothermal lease applications. In 2008, the Bureau of Land Management and U.S. Forest Service drafted a Programmatic Environmental Impact Statement (USDI and USDA 2008) addressing this issue. The EIS addresses alternatives that identify opportunities for development and areas with sensitive resources that should be avoided. Site-specific documentation is still required, but the programmatic EIS allows for the streamlining of the leasing process. Two primary



*Geothermal resources are concentrated primarily in western North America (Blackwell and Richards 2004). Energy potential ranges from very little (blue) to high (red).*

considerations determine whether a geothermal resource is suitable for development; the temperature of the resource and its extent or size. The temperature will determine how the resource could be used and the size will determine the longevity. A large amount of capital is needed to develop a resource, so developers must fully evaluate the overall value and potential before proceeding.

Depending upon its quality, a geothermal resource may produce steam (most desirable), hot water, or warm water (least desired). Current protocols are to reinject used geothermal fluids to replenish the resource, enabling it to last longer. This also allows for safe disposal of brine or high concentrations of dissolved and suspended solids, which had been a site management issue before reinjection became the standard procedure.

Geothermal resources have a range of uses, including power generation, domestic or industrial heating, recreation, fish farming and other types of aquaculture, greenhouse operation, commercial food processing, and others. Some geothermal resources have incorporated a clean surface water component which provides habitat for shorebirds and waterfowl and a source of drinkable water for larger game species and livestock.

Five components of geothermal development should be considered when assessing impacts: exploration, well drilling, power production or on-site use, transmission lines, and facility operation. Exploration usually involves site visits, drilling by a truck-mounted auger, some minimal site disturbance and noise. The effects at this early phase are short-term and temporary in nature. Well drilling results in moderate site disturbance and may include the construction of a flat well pad that could occupy 2-3 acres or more. A well casing and some apparatuses to control the well are left in place, usually within a fenced facility. Site disturbance should be temporary if the area is not needed for the development of facilities. The well site is usually connected to a primary use area by above-ground insulated piping. Existing access roads may be utilized or new roads constructed if no other access exists.

The construction of the power production or resource use facility (on-site heating, vegetable drying, electricity production, etc.) may permanently occupy ≥10 acres depending on the geothermal resource use and size of the facility. This area will represent a permanent loss of habitat (unless constructed in an area of low value initially, as recommended). Construction activity is relatively short-term, but has the potential to disturb wildlife through noise, human and vehicle presence, and habitat loss. These temporary use areas are generally reclaimed if not needed for operational activities.

*A flow test in progress at the Blue Mountain Geothermal site. The initial drilling of the wells may occupy only 2-3 acres, but this is the phase where most disturbance occurs. Photo courtesy of Bureau of Land Management, Nevada State Office.*

*After drilling, a fenced well casing and control equipment is left in place like this structure at the Salt Wells Geothermal well site near Fallon, Nevada (operated by ENEL North America, Inc.). Photo courtesy of Bureau of Land Management, Nevada State Office.*

*The Ormat Steamboat power station at the southern edge of Reno, NV with a large brown heat exchanger, above-ground piping, and access road visible. Photo courtesy of Bureau of Land Management, Nevada State Office.*

Associated linear project components such as power lines, pipelines, and roads create additional permanent impacts to mule deer habitat if existing linear disturbances are not followed. Depending upon where the facilities are sited and how they are constructed, they can result in temporary disturbance during construction as well as permanent habitat loss and fragmentation.

Site activity is greatly diminished during facility operation. The operation phase entails periodic human presence including intermittent noise and vehicle use. Depending upon the technology employed, if resources are captured and re-injected there may be a decrease in the amount of surface water available. Also, a portion of the facility may be fenced which may impede deer movements across the site.

## ISSUES AND CONCERNS

In general, geothermal resource development has minimal impact on mule deer. Sites are usually compact in contrast with other forms of energy development such as wind, solar, or fossil fuels. All temporary disturbance is reclaimed and long-term disturbance at the site (human presence, vehicles, or noise) should be minimal. There can be a few potential impacts to mule deer such as above ground pipelines and elevated noise levels (USDI and USDA 2008).

### Habitat Loss, Disturbance, and Fragmentation

Impacts of geothermal energy exploration, development and extraction in mule deer habitat can be similar to those caused by oil and gas development, albeit at a smaller scale. Although pertinent to this section, there is no need to reiterate similar issues and concerns related to the direct loss of habitat, physiological stress on deer, disturbance and displacement from important habitat, fragmentation and isolation of important habitat components, and secondary effects.

It is important to consider the total impact of the project, not only at the well site and power production area, but also from the transmission corridors and access roads used in construction and operation of facilities. These linear components are more likely to fragment habitat and could present a greater concern than the core facilities. These effects will not likely be as severe or extensive as experienced from oil and gas development, but should still be evaluated by resource managers on a case by case basis.

### Related Concerns

The Programmatic EIS for geothermal leasing (USDI and USDA 2008) identified several related concerns that may be an issue in some phases of geothermal energy development. Although direct habitat loss, disturbance, and fragmentation are the most obvious impacts of geothermal projects, invasive vegetation, fire, direct mortality, noise, and chemical contaminants warrant additional vigilance of managers.

Spread of invasive vegetation could result from construction activity, especially ground disturbance, vehicle traffic, or creation of new access routes. Once established, some invasive species have proven difficult or impossible to control. As demonstrated by several cases in the West, invasive plant species can alter entire vegetative communities, resulting poorer quality mule deer habitat on a landscape scale.

Fires accidentally ignited during construction or maintenance activities can alter the natural fire regime

and produce undesirable changes in plant communities. An increase in fire frequency provides opportunities for invasive plants to become established and may result in loss of desirable vegetation for many years. Once invasive species such as cheatgrass become established, the fire cycle and natural plant community may be permanently altered, especially in native shrub-dominated communities.

Additional issues include: 1) direct mortality of mule deer from vehicle collisions, open trenches or ditches, fencing and above-ground piping, 2) intermittent noise associated with construction activity and some operational activities (e.g., steam venting), and 3) infrequent exposure to contaminants such as vehicle fuels, herbicides, or accidental spills (USDI and USDA 2008).

*Photo courtesy of Tom Newman*

# CONSOLIDATED GUIDELINES

General guidelines and additional mitigation recommendations (Habitat Mitigation Options) are provided to minimize impacts of energy development on mule deer and their habitat. Recommendations are also categorized according to impact thresholds. When energy development is proposed on public lands, federal permitting agencies have the dual responsibility of authorizing the development while conserving surface resources, including wildlife and other environmental values.

## A. GENERAL GUIDELINES

1. Consult the appropriate wildlife and land management agencies at least 2 years prior to submitting project permit applications to allow time for appropriate studies and inventories to be conducted and site-specific recommendations developed (TWS 2008a).
2. Identify minimum quality and quantity of information necessary for analysis before a lease or annual permit for construction can be issued (WAFWA 2010).
3. Develop a map of important habitats and potential conflict areas. Developers should use the map as one of the first steps in pre-development planning to identify important, sensitive, or unique habitats and wildlife in the area (TWS 2008b).
4. Utilize the Decision Support System developed by the Western Governor's Association to coordinate planning.
5. Use the most current wildlife data and applicable plans to identify important wildlife habitat resources that should be conserved (WAFWA 2010).
6. Design configurations of energy development to avoid or reduce unnecessary disturbances, wildlife conflicts, and habitat impacts. Where possible, coordinate planning among companies operating in the same area to minimize the footprint of development (e.g., negotiate unitized field development plans, co-locate power lines and pipe lines in existing corridors).
7. Implement timing stipulations that minimize or prohibit activities during critical portions of the year.
8. At a minimum, construction activities should be suspended from November 15-April 30 on areas designated as crucial winter range. If project features will be sited within identified parturition areas, activities should be suspended from 1 May – 30 June (Pojar and Bowden 2004). Minimize disturbances and activities within producing well fields during the same timeframe. Include provisions in subcontractor agreements requiring adherence to the same seasonal use restrictions observed in company operations.
9. Avoid placing facilities in locations that bisect major migration corridors and other important habitats. Also, avoid unstable slopes and local factors that can cause soil instability (groundwater conditions, precipitation, seismic activity, slope angles, and geologic structure).
10. Plan the pattern and rate of development to avoid the most important habitats and generally reduce extent and severity of impacts (TWS 2008a). Implement phased development in smaller increments with concurrent reclamation of abandoned wells.
11. Disturb the minimum area (footprint) necessary to efficiently develop and operate the facility.
12. Design and implement habitat treatments sufficient to maintain habitat functions on-site. In cases where offsite mitigation would provide greater benefits than onsite mitigation, the offsite mitigation should be located within the same landscape unit indentified in consultation with the state or provincial wildlife agency. Habitat treatments should include appropriate options from Habitat Mitigation Options, selected through consultation with the state or provincial wildlife agency.
13. Mitigation should be planned to offset the loss of habitat effectiveness throughout the areas directly and indirectly affected by energy project development. Management practices identified in Habitat Mitigation Options may reduce the extent of habitat treatments needed to offset or mitigate the effect.
14. When it is not possible to avoid, minimize, or effectively mitigate impacts through other means create a Mitigation Trust Account. The operator would contribute funding to a mitigation trust account based on the estimated cost of habitat treatments or other mitigation needed to restore the functions and effectiveness of impacted habitats.
15. For mitigation planning purposes the acreage basis for mitigation will be the amount of surface that is directly disturbed plus the additional area on which habitat functions are impacted by noise, activities, and other disturbance effects. Mitigation recommendations may be refined and possibly standardized as habitat treatments are implemented and their effectiveness monitored.

**Oil, Gas, & Geothermal General**

16. When geological substrate and hydro-carbon resource types lend themselves to directional technologies, drill multiple wells from the same pad.
17. Utilize mats to support drill rigs in order to eliminate top-soil removal.
18. Locate drill pads, roads, and facilities in the least sensitive areas or cluster these features in locations already impacted.
19. Locate drill pads, pipelines, roads, and facilities below ridgelines or behind topographic features, where possible, to minimize visual and auditory effects, but away from streams, drainages, and riparian areas as well as important sources of forage, cover, and habitats important to different life cycle events (reproduction, winter, parturition, and rearing).

*Additional Guidelines for Moderate Impact Developments (2-4 well pad locations/mile$^2$ with no more than 60 acres of total disturbance).*

20. Apply all general guidelines prescribed above to retain as much effective habitat as possible.
21. Develop multiple wells from single pads by employing directional or horizontal drilling technologies and unitized development. The highest management priority within crucial winter range is to recover oil and gas resources with the least possible infrastructure and associated disturbance. Where several companies hold smaller, intermingled leases, the cumulative impact could be reduced substantially if the companies enter a cooperative agreement (called unitization) to directional drill from common well pads.
22. Use clustered development configurations. Locate well pads, facilities and roads in clustered configurations within the least sensitive habitats. Clustered configurations are a geographical and not necessarily a temporal (i.e., "phased development") consideration.
23. Install a liquid gathering system to convey liquids from producing wells to a centralized collection point. If fluids cannot be piped off site, enlarge storage tank capacity to minimize truck trips to ≤1/month and to eliminate trips during sensitive times of year. If the potential for production of liquids is unknown, but exceeds 1 truck trip/month after production begins, consider retrofit the field with pipelines or larger storage.
24. Install telemetry to remotely monitor instrumentation and reduce or eliminate travel required to manually inspect and read instruments.
25. Develop a travel plan that minimizes frequency of trips on well-field roads. Include provisions in subcontractor agreements requiring adherence to the same travel plan provisions observed in company operations.
26. As appropriate, gate and close newly constructed roads to public travel during sensitive times of year.
27. Implement a robust wildlife monitoring program such as the Before-After Control-Impact (BACI) research design to detect and evaluate ongoing effects such as mortalities, avoidance responses, distribution shifts, habituation, evidence of movement or migration barriers, and depressed productivity (e.g., low fawn:doe ratios), and to assess the effectiveness of mitigation. Monitor vegetation utilization within and outside the well field.
28. If it is not possible to maintain habitat effectiveness within or immediately adjacent to the well field, off-site and off-lease mitigation should be considered on a case-by-case basis. The primary emphasis of off-site or off-lease mitigation is to maintain habitat functions for the affected population or herd as close to the impacted site as possible and within the same landscape unit. Off-site and off-lease mitigation should only be considered when feasible mitigation options are not available within or immediately adjacent to the impacted area, or when the off-site or off-lease location would provide more effective mitigation than can be achieved on-site.

*Additional Guidelines for High Impact Developments ( >4 well pad locations/mile$^2$ or disturbance exceeding 60 acres).*

29. Adhere to all general guidelines and those applicable to "Moderate Impact Developments."
30. Develop the well field in smaller incremental phases (phased development) to reduce the overall impact of a high-density field. Although complex geological, technical, and regulatory issues may constrain the use of this strategy, it should be considered where feasible.
31. Opportunities may exist to partially offset the loss of crucial winter range by completing habitat rehabilitation and enhancement projects in appropriate locations outside the well field (off-site mitigation). This type of mitigation is difficult and should never be looked upon as a prescriptive solution to authorize high-density well fields in crucial winter range. The most effective solution is to avoid high-density developments. If avoidance is not feasible, plan effective habitat treatments in locations selected to minimize the loss of habitat function for the affected herd or population, within the same landscape unit.

**Wind and Solar**

32. Site wind and solar energy developments within areas already affected by other forms of development (e.g., urban areas, agricultural land, oil and gas fields, and existing or reclaimed mines). Avoid further fragmentation of intact native habitats.
33. Avoid locating wind and solar energy facilities within crucial mule deer winter ranges.

## B. ROADS

1. Use existing roads, no matter how primitive, where they exist in areas that do not impact wildlife habitat and are not within environmentally sensitive areas.
2. If new roads are needed, close unnecessary roads that impact important mule deer habitat.
3. Roads should not bisect or run immediately adjacent to any water feature, or prevent mule deer from reaching adjacent habitat.
4. Construct the minimum number and length of roads necessary.
5. Coordinate road construction and use among companies operating in the same area.
6. Design and construct roads to a minimum standard to accommodate their intended purpose.
7. Design roads with adequate structures or features to discourage off-road travel.

## C. TRANSMISSION CORRIDORS

1. Use existing utilities, power lines, roads, and pipeline corridors to the extent feasible.
2. Site new corridors in areas of already disturbed or poor quality mule deer habitat or adjacent to other linear disturbances.
3. Bury power lines whenever possible. All trenching should occur with concurrent back filling. All buried power lines should be placed in or adjacent to roads or other existing utility rights-of-way.
4. If fence construction is necessary, consult with the state or provincial wildlife agency to determine appropriate locations and designs based on wildlife resources of the site.
5. Construct above ground pipelines conveying geothermal fluids with sufficient ground clearance to allow adequate mule deer passage.
6. Conduct concurrent backfilling with trenching operations to minimize the amount of trench left open.

## D. NOISE AND LIGHTING

1. Minimize noise to the extent possible. All compressors, vehicles, and other sources of noise should be equipped with effective mufflers or noise suppression systems (e.g., "hospital mufflers").
2. Wind turbines and other non-motorized structures should be designed to minimize noise.
3. Whenever possible, use electric motors instead of diesel engines to power compression equipment.
4. Use topography to conceal facilities and reduce noise disturbance in areas of known importance.
5. Manage on-site lighting to minimize disturbance to mule deer.

## E. TRAFFIC AND HUMAN DISTURBANCE

1. Develop a travel plan that minimizes the amount of vehicular traffic required to monitor and maintain wells and other facilities (USDI 2005).
2. Limit traffic to the extent possible during high wildlife use hours (within 3 hours of sunrise and sunset).
3. Use pipelines (liquid gathering systems) to transport condensates off site.
4. Transmit instrumentation readings from remote monitoring stations to reduce maintenance traffic.
5. Post speed limits on all access and maintenance roads to reduce wildlife collisions and limit dust (30-40 mph is adequate in most cases).
6. Employees should be instructed to avoid walking away from vehicles or facilities into view of wildlife, especially during winter months.
7. Prohibit employees from carrying firearms in development fields or sites.
8. Institute a corporate-funded reward program for information leading to conviction of poachers, especially on winter range.

## F. HYDROLOGIC RESOURCES (AGFD 2010)

1. Prepare a water management plan in those regions and for those operations that discharge surplus water of questionable quality (e.g., Coal Bed Methane).
2. Develop a contingency plan to prevent potential groundwater and surface water contamination.
3. Develop a storm water management plan to ensure compliance with state, provincial, and federal regulations and prevent off-site migration of contaminated storm water or increased soil erosion.
4. Spread excess excavated soil to match surrounding topography or dispose of in a manner to minimize erosion and leaching of hazardous materials.
5. Incorporate best management practices for addressing hydro-modification impacts (e.g., retention basins for treatment of water from runoff and infiltration and recharge of the groundwater basin).
6. Refuel in a designated fueling area that includes a temporary berm to contain the spread of any potential spill.
7. Use drip pans during refueling and under fuel pump and valve mechanisms of any bulk fueling vehicles parked at the project site to contain accidental releases.
8. Identify sustainable yields of groundwater and nearby surface water bodies.
9. Limit the withdrawal of water at the facility so it does not exceed the sustainable yield in order to preserve natural discharge sites (springs), ponds, and wells that may provide sources of water and enhanced forage for mule deer.
10. Avoid streams, wetlands, and drainages where possible. Locate access roads to minimize stream crossings and cause the least impact where crossings cannot be avoided. Where access roads would cross a dry drainage, the road gradient should be 0% to avoid diverting surface waters from the channel. Cross water bodies at right angles to the channel and in locations producing minimum impact.
11. Develop a Stormwater Pollution Plan. The Environmental Protection Agency (EPA) website contains templates for such a plan: http://cfpub.epa.gov/npdes/stormwater/swppp.cfm.
12. Locate contaminated ponds in places wildlife tend to avoid, such as areas of high human use or highly disturbed areas.
13. Waste water contaminant ponds should be fenced to prevent mule deer access.
14. Monitor ponds to detect wildlife mortalities. Develop a contingency plan to handle wildlife mortality incidents (e.g., if a waterfowl die-off is observed contact state, provincial, or federal agencies as soon as possible and have a contingency plan to handle the situation).
15. Maintain existing surface waters that mule deer use as a water source. Consider constructing freshwater ponds or wetlands nearby to attract wildlife away from

potentially toxic evaporation ponds. Water sources should not be placed in areas where increased wildlife-vehicle collisions could occur.

16. Monitor toxicity of the ponds and prepare a mitigation plan to address any rise in toxicity levels. The plan should include short- and long-term measures to deter wildlife from the area.
17. Rely on “dry cooling” technology to reduce water consumption at solar facilities. If this is not feasible, the hybrid parallel wet-dry cooling method should be used.

## G. POLLUTANTS, TOXIC SUBSTANCES, DUST, EROSION, AND SEDIMENTATION

1. Avoid spilling or dumping oil or fuel (synthetic or hydrocarbon) or molten salts. Oil spills should be contained and all contaminated soil removed. Oil pits should not be used, but if absolutely necessary, they should be enclosed in netting and small-mesh fence. All netting and fence must be maintained and kept in serviceable condition.
2. Produced water from oil, gas, and geothermal facilities should not be pumped onto the surface except when beneficial for wildlife, provided water quality standards for wildlife and livestock are met. Produced water of suitable quality may also be used for supplemental irrigation to improve reclamation success.
3. Re-injection of water into Coal Bed Methane or geo-thermal sites should be considered when water quality is of concern.
4. Hydrogen sulfide should not be released into the environment.
5. If inorganic salts are spilled in solar operations, the molten material should be immediately cooled to a solid, contained within concrete dikes and curbing, and removed or recycled back into the system (AGFD 2010).
6. To contain hazardous materials such as arsenic, cadmium, or silicon, create a protocol for responsible disposal of decommissioned PV solar panels. Prior to facility construction, determine whether PV panel manufacturers provide an Extended Producer Responsibility (EPR) service which requires the manufacturer to take back their product, thus ensuring panels are recycled safely and responsibly, or recycle PV panels at existing responsible electronic waste recycling facilities or at facilities that recycle batteries containing lead and cadmium.

## H. MONITORING AND ENVIRONMENTAL RESPONSE

1. Monitor conditions or events that may indicate environmental problems (e.g., water quality in nearby rivers, streams, wells, etc.). Such conditions or events can include any significant chemical spill or leak, detection of multiple wildlife mortalities, sections of roads with frequent and recurrent wildlife collisions, poaching and harassment incidents, severe erosion into tributary drainages, migration impediments, wildlife entrapment, sick or injured wildlife, or other unusual observations.
2. Immediately report observations of potential wildlife problems to the state or provincial wildlife agency and, when applicable, federal agencies such as USFWS or EPA.
3. Apply GIS technologies to monitor the extent of disturbance annually and document the progression and footprint of disturbances. Use this spatial data to evaluate the cumulative effects of existing and proposed impacts. Release compilations and analyses of this information to resource management agencies at least annually.

## I. PUBLIC RECREATION AND ACCESS

1. Prior to finalizing development and travel management plans, state or provincial wildlife agencies should be consulted to ensure adverse impacts to hunting opportunity are prevented, minimized, or mitigated.
2. As projects are constructed, there is a possibility projects located over established roads may impede or restrict access to public lands. To guard against the creation of illegal roads and maintain access to public lands, coordinate with the appropriate landowners to create alternate travel routes. These alternate routes must be created in close proximity to the project and should be similar in function to the original routes. Signs should be installed to indicate public travel routes while project construction takes place and remain in place after project completion (AGFD 2010).
3. Hunting access should continue within developments on public lands and on private land with landowner permission.

## J. RESEARCH AND SPECIAL STUDIES

1. Where there are questions or uncertainties regarding cumulative impacts, the degree of impact to specific resources, or effectiveness of mitigation, industries and companies should fund special studies to collect data for evaluation and documentation.
2. Conduct research to better understand wind-energy development impacts. Research should primarily investigate deer distribution pre- and post-development, abundance, and demography. Research on habitat should document vegetation species composition, utilization rates, location of migration corridors, location of important seasonal habitats, and changes in habitat use and distribution of deer.
3. Use the Before-After Control-Impact (BACI) research design. Data should be collected ≥2 years prior to development and 3 years post-development to provide a quantitative basis for estimating development impacts.
4. Evaluate alteration of vegetation and micro-climate adjacent to energy development.
5. Evaluate movement and behavior patterns of mule deer pre- and post-construction, especially the impact on movement corridors.
6. More research is needed on population-level effects of energy development on mule deer.

## K. NOXIOUS WEEDS

1. Control noxious and invasive plants that appear along roads and at development sites and ancillary facilities (USDI 2005).
2. Designate specific areas to clean and sanitize all equipment brought in from other regions. Seeds and propagules of noxious plants are commonly imported by equipment and mud clinging to equipment.
3. Request employees to clean mud from footwear before traveling to the work site, to prevent importation of noxious weeds.

## L. INTERIM RECLAMATION

1. Establish effective, interim reclamation on all surfaces disturbed throughout the operational phase of the development.
2. Reclaim abandoned or decommissioned development sites concurrently with development of new sites.
3. Salvage topsoil from all construction and re-apply during interim reclamation.
4. Approved weed-free mulch application should be used in sensitive areas (dry, sandy, steep slopes).
5. A variety of native grasses, shrubs, and forbs endemic to the site should be used for revegetation. Non-native vegetation is discouraged and should not be used unless native forbs and grasses are not available or are ineffective in quickly recovering the site.
6. Continue to monitor and treat reclaimed surfaces until satisfactory plant cover is established.
7. Solar facilities need not be fenced. Native and preferred non-native forbs and grasses should be established to sustain use by wildlife during energy production.

## M. FINAL RECLAMATION

1. Develop a comprehensive reclamation plan addressing vegetation and hydrology considerations, which includes specifically measurable objectives for wildlife and habitat so success can be achieved during the production phase of development (WAFWA 2010).
2. Salvage topsoil during decommissioning operations and reapply to reclaimed surfaces.
3. All buildings, well heads, turbines, solar arrays, and ancillary facilities should be removed.
4. Replant a mixture of forbs, grasses, and shrubs that are native to the area and suitable for the specific ecological site.
5. Restore vegetation cover, composition, and diversity to achieve numeric standards commensurate with the ecological site.
6. Do not allow grazing on re-vegetated sites until the plants are established and can withstand herbivory as noted through monitoring.
7. Reevaluate the existing system of bonding. Bonds should be set at a level adequate to cover the company's liability for reclamation of the entire development project.

# HABITAT MITIGATION OPTIONS

The habitat enhancements suggested in this section are largely based on a similar document used successfully in Wyoming (WGFD 2010a). These represent options for companies and resource agencies to consider in designing an integrated mitigation plan to sustain mule deer habitat functions potentially affected by energy developments. The list is not exhaustive; many additional options and practices could also provide effective mitigation. Regional biologists, company personnel, and others may have alternative suggestions to address specific circumstances.

**Corporate-owned Lands under Conservation Management –** Management of corporate-owned or -controlled lands may be one of the best alternatives to achieve effective, long-term mitigation of energy development impacts. Availability of corporate-owned lands can provide managers with increased options and flexibility to mitigate impacts and potentially provide increased recreational access.

**Conservation Easements –** This concept includes numerous options and practices for mitigating impacts to the most crucial habitats. These options and practices include maintaining open space, excluding subdivisions, keeping an agricultural base of operations compatible with wildlife, excluding fencing or other developments that are restrictive to wildlife migration and movement, grazing management systems, etc. Where appropriate, conservation easements could be established through the formation of a land trust, or by earmarked contributions to an existing land trust. Depending upon the amount of property rights acquired, costs range from 35% to 95% of fee title acquisition. The mitigation would be in effect as long as the easement is held and monitored by the assignee. The intent is to maintain the easements at least throughout the time habitat functions are disrupted, including the time required for reclamation to mature.

**Grazing or AUM Management Program –** This practice could include many options, with the owner's or permittee's concurrence, to improve habitat quality for wildlife. Some options might include: 1) paying for private grazing AUMs to provide rest or treatments on public lands; 2) paying for a portion of the AUMs within an allotment; 3) providing for rest or treatments and once completed, turning the land back to grazing use; 4) purchase of AUMs to reduce grazing use on important habitats; or 5) establishing forage reserves (grass banks) to provide management flexibility for habitat treatments and livestock grazing. Other grazing management options include electric fencing to provide pasture systems, herding, water developments, etc. These could all be utilized to better manage grazing animals to improve range and habitat conditions.

**Habitat Improvements –** Several states and NGOs are currently implementing programs to acquire, protect, and improve to recover mule deer populations. The same habitat management practices could be applied as off-site mitigation where important habitats could potentially be improved to restore habitat functions impacted in other areas. Before habitat treatments are applied, qualified personnel should evaluate the prospective site to determine its condition, improvement potential, and ecologically appropriate treatments. Practitioners are encouraged to consult the Mule Deer Habitat Guidelines in their respective ecoregion for recommended practices (www.muledeerworkinggroup.com). Early consultation with the state or provincial wildlife management agency and land management agencies can greatly assist with the planning of effective habitat work and selection of appropriate treatments.

# LITERATURE CITED

**Arizona Game and Fish Department (AGFD). 2010.** Guidelines for solar development in Arizona. Arizona Game and Fish Department, Phoenix, USA.

**Baker, W. L. 2006.** Fire and restoration of sagebrush ecoystems. Wildlife Society Bulletin 34:177-185.

**Barber, J. R., K. R. Crooks, and K. M. Fristup. 2010.** The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology and Evolution 25:180-189.

**Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992.** Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121:1-39

**Bergman, E. J., C. J. Bishop, D. J. Freddy, and G. C. White. 2007.** Evaluation of winter range habitat treatments on over-winter survival and body condition of mule deer. Wildlife Research Report, Colorado Division of Wildlife, Fort Collins, USA.

**Bishop, C. J. 2007.** Effect of enhanced nutrition during winter on the Uncompahgre Plateau mule deer population. Dissertation, Colorado State University, Fort Collins, USA

**Blackwell, D. D., and M. Richards. 2004.** Subset of geothermal map of North America. American Association of Petroleum Geologists, Tulsa, Oklahoma, USA. <http://www.smu.edu/geothermal> Accessed 1 September 2010.

**Bunting, S. C., B. M. Kilgore, and C. L. Bushey. 1987.** Guidelines for prescribed burning sagebrush-grass rangelands in the northern Great Basin. U.S. Forest Service General Technical Report INT-231, Ogden, Utah, USA.

**Cooper, S. V., P. Lesica, and G. M. Kudray. 2007.** Post-fire recovery of Wyoming big sagebrush shrub-steppe in central and southeast Montana. Report to the U.S. Department of the Interior, Bureau of Land Management, State Office. Montana Natural Heritage Program, Helena, USA.

**Copeland, H. E., K. E. Doherty, D. E. Naugle, A. Pocewicz, and J. M. Kiesecker. 2009.** Mapping oil and gas development potential in the U.S. Intermountain West and estimating impacts to species. PLoS ONE 4(10): e7400. doi:10.1371/journal.pone.0007400

**Energy Policy Act of 2005.** 2005. Energy policy act of 2005. <www.epa.gov/oust/fedlaws/publ_109-058.pdf> Accessed 17 Dec 2010.

**Farrell, J. E., L. R. Irby, and P. T. McGowen. 2002.** Strategies for ungulate-vehicle collision mitigation. Intermountain Journal of Sciences 8:1-18.

**Freddy, D. J., W. M. Bronaugh, and M. C. Fowler. 1986.** Responses of mule deer to disturbance by persons afoot and snowmobiles. Wildlife Society Bulletin 14:63-68.

**Frid, A., and L. Dill. 2002.** Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

**Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003.** Road ecology: science and solutions. Island Press, Washington, D.C., USA.

**Gainer, R. S. 1995.** Range extension of white-tailed deer. Alberta Naturalist 25:34-36.

**Gamo, R. S., and S. H. Anderson. 2002.** Use of reclaimed minelands by pronghorn and mule deer. Intermountain Journal of Sciences 8:213-222.

**Gill, J. A., W. J. Sutherland, and A. R. Watkins. 1996.** A method to quantify the effects of human disturbance for animal populations. Journal of Applied Ecology 33:786-792.

**Hebblewhite, M. 2008.** A literature review of the effects of energy development on ungulates: implications for central and eastern Montana. Report prepared for Montana Fish, Wildlife and Parks, Miles City, USA.

**Hebblewhite, M. 2011.** Effects of energy development on ungulates. Pages 71–94 in D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington D.C., USA

**Heffelfinger, J. R., and T. A. Messmer.** Introduction. Pages 1-11 in J. C. deVos, Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.

**Holm, A., L. Blodgett, D. Jennejohn, and K. Gawell. 2010.** Geothermal energy: international market update. Geothermal Energy Association, Washington, D.C., USA.

**Kuvlesky, W. P., Jr., L. A. Brennan, M. L. Morrison, K. K. Boydston, B. M. Ballard, and F. C. Bryant. 2007.** Wind energy development and wildlife conservation: challenges and opportunities. Journal of Wildlife Management 71:2487-2498.

**Lutz, D. W., M. Cox, B. F. Wakeling, D. McWhirter, L. H. Carpenter, S. Rosenstock, D. Stroud, L. C. Bender, and A. F. Reeve. 2003.** Impacts to changes to mule deer habitat. Pages 13-61 in J. C. deVos, Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Utah State University, Logan, USA.

**Medcraft, J. R., and W. R. Clark. 1986.** Big game habitat use and diets on a surface mine in northeastern Wyoming. Journal of Wildlife Management 50:135-142.

**Merrill, E. H., T. P. Hemker, K. P. Woodruff, and L. Kuck. 1994.** Impacts of mining facilities on fall migration of mule deer. Wildlife Society Bulletin 22:68-73.

**National Energy Policy. 2001.** Reliable, affordable, and environmentally sound energy for America's future. Report of the National Energy Policy Development Group. U.S. Government Printing Office, Washington, D.C.

**Naugle, D. E., B. L. Walker, and K. E. Doherty. 2006.** Sage-grouse population response to coal-bed natural gas development in the Powder River Basin: interim progress report on region-wide lek-count analysis. Unpublished report, University of Montana, Missoula, USA.

**New Mexico Department of Game and Fish (NMDGF). 2007.** Oil and gas development guidelines: conserving New Mexico's wildlife habitats and wildlife. <http://www.wildlife.state.nm.us/documents/oilandgasguidelines.pdf> Accessed 8 July 2010.

**Noss, R. F., and A. Y. Cooperrider. 1994.** Saving nature's legacy. Island Press, Washington, D.C., USA.

**Pojar, T. M., and D. C. Bowden. 2004.** Neonatal mule deer survival in westcentral Colorado. Journal of Wildlife Management 68:550–560.

**Rost, G. R., and J. A. Bailey. 1979.** Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43:634-641.

**Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009a.** Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052-1061.

**Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009c.** Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016-2025.

**Sawyer, H., F. Lindzey, D. McWhirter, and K. Andrews. 2002.** Potential effects of oil and gas development on mule deer and pronghorn populations in western Wyoming. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:350-365.

**Sawyer, H., F. Lindzey, and D. McWhirter. 2005.** Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin 33:1266-1273.

**Sawyer, H., and R. Nielson. 2010.** Mule deer monitoring in the Pinedale Anticline project area: 2010 annual report. Western Ecosystems Technology, Inc. Cheyenne, Wyoming, USA.

**Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006.** Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396-403.

**Sawyer, H., R. Nielson, and D. Strickland. 2009b.** Sublette mule deer study (phase II): final report 2007 - long-term monitoring plan to assess potential impacts of energy development on mule deer in the Pinedale Anticline project area. Western Ecosystems Technology, Inc. Cheyenne, Wyoming, USA.

**Stalling, D. 2003.** Gas and oil development on western public lands; impacts on fish, wildlife, hunting, and angling. A report produced by Trout Unlimited's Public Lands Initiative.

**The Wildlife Society. 2008a.** Impacts of wind energy development on wildlife and wildlife habitat, final position statement. The Wildlife Society, Bethesda, Maryland, USA.

**The Wildlife Society. 2008b.** Oil and gas development in the Rocky Mountain West, final position statement. The Wildlife Society, Bethesda, Maryland, USA.

**Trombulak, S. C., and C. A. Frissell. 2000.** Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.

**U.S. Department of Energy (DOE). 2007.** Concentrating Solar Power commercial application study: reducing water consumption of Concentrating Solar Power electricity generation. Report to Congress. U.S. Department of Energy, Washington, DC, USA.

**U.S. Department of Energy (DOE). 2010.** Wind and water power program: wind power today 2010. USDOE, DOE/GO-102010-3011 May 2010. http://www1.eere.energy.gov/windandhydro/wind_pubs.html. Accessed 17 May 2011.

**U.S. Department of the Interior, Bureau of Land Management (USDI). 1999.** Glenwood Springs Resource Area; oil and gas leasing and development: final supplemental environmental impact statement, Bureau of Land Management. Glenwood Springs Field Office, Colorado, USA.

**U.S. Department of the Interior, Bureau of Land Management (USDI). 2005.** Record of decision: implementation of a wind energy development program and associated land use plan amendments. Washington, D.C., USA.

**U.S. Department of the Interior, Bureau of Land Management (USDI) and U.S. Department of Agriculture, U.S. Forest Service (USDA). 2008.** Programmatic Environmental Impact Statement for geothermal leasing in the Western United States. FES 08-44, U.S. Government Printing Office. Washington, D.C., USA.

**U.S. Fish and Wildlife Service (USFWS). 2007.** 2006 national survey of fishing, hunting, and wildlife-associated recreation. <http://library.fws.gov/Pubs/nat_survey2006_final.pdf>. Accessed 7 Dec 2009.

**U.S. Fish and Wildlife Service (USFWS). 2010.** Wind Turbine Guidelines Advisory Committee recommendations. <http://www.fws.gov/habitatconservation/windpower/wind_turbine advisory_committee.html>. Accessed 29 Oct. 2010.

**U.S. Fish and Wildlife Service (USFWS). 2011.** U.S. Fish and Wildlife Service draft land-based wind energy guidelines: recommendations on measures to avoid, minimize, and compensate for effects to fish, wildlife, and their habitats. <http://www.fws.gov/habitatconservation/wind.html>. Accessed 17 May 2011.

**Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977.** Evaluation of deer habitat on a nutritional basis. Journal of Range Management 30:122 – 127.

**Watkins, B. E., C. J. Bishop, E. J. Bergman, B. Hale, B. F. Wakeling, A. Bronson, L. H. Carpenter, and D.W. Lutz. 2007.** Habitat guidelines for mule deer: Colorado Plateau shrubland and forest ecoregion. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies, USA.

**Western Association of Fish and Wildlife Agencies (WAFWA). 2010.** Resolution on energy development, Western Association of Fish and Wildlife Agencies, USA.

**Western Governor's Association. 2008.** Wildlife corridors initiative. < http://www.westgov.org > . Accessed 17 Dec 2010.

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

**Winward, A. H. 1991.** A renewed commitment to management of sagebrush grasslands. Pages 2-7 in Management in the sagebrush steppe. Oregon Agricultural Experiment Station Special Report 880. < oregonstate.edu/dept/eoarc/sites/default/files/researchhome/documents/360a.pdf > . Accessed 17 May 2011.

**Wyoming Game and Fish Department (WGFD). 2010a.** Recommendations for development of oil and gas resources within important wildlife habitats. Wyoming Game and Fish Department, Cheyenne, USA.

**Wyoming Game and Fish Department (WGFD). 2010b.** Wildlife protection recommendations for wind energy development in Wyoming. Wyoming Game and Fish Department, Cheyenne, USA.

**Young, J. A., and R. A. Evans. 1981.** Demography and fire history of a western juniper stand. Journal of Range Management 34:501-506.

# ACKNOWLEDGEMENTS

*This document was written by the Mule Deer Working Group of the Western Association of Fish and Wildlife Agencies (WAFWA). Authors thank the member agencies of WAFWA for their support and guidance. Additional thanks go out to Nevada Department of Wildlife (NDOW), Wyoming Game and Fish Department (WGFD), Arizona Game and Fish Department (AGFD), South Dakota Game, Fish, and Parks (SDGFP), Idaho Department of Fish and Game (IDFG), Utah Division of Wildlife Resources (UDWR), Nebraska Game and Parks Commission (NGPC), Oregon Department of Fish and Wildlife (ODFW), and California Department of Fish and Game (CDFG) for allowing their representatives time to participate in the development of this document.*

*Others who assisted with the development of this document include T. Keegan, A. Wang, J. Moore, K. Aune, H. Sawyer, M. Rodriguez, D. Chi, E. Tomlinson, R. Kahn, G. Buckner, T. Thompson, M. Richards, S. Belinda, C. Anderson, L. Carpenter, B. Trindle, L. Fox, G. Ritter, J. Scott, A. Wilheim, B. Cook, B. Knowles, C. D. Carter, D. E. Nelson, D. Weedman, R. Springer, D. D. Grandmaison, J. Stroud, J. M. Francis, J. Mikolajczyk, K. Wolff, L. Canaca, L. Lambert, M. Stewart, N. Brown, R. Schweinsburg, R. Peck, R. Teran, T. Grosch, T. Hughes, T. Cadden, T. Buhr, T. Hoover, T. Smith, V. Boyarski, and J. Short. Their written contributions, review, critical comments, and insights strengthened the document immeasurably.*

# Western Association of Fish and Wildlife Agencies Member Organizations

Alaska Department of Fish and Game
Alberta Department of Sustainable Resource Development, Fish and Wildlife Division
Arizona Game and Fish Department
British Columbia Ministry of Forests, Lands and Natural Resource Operations
California Department of Fish and Game
Colorado Division of Parks and Wildlife
Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife
Idaho Department of Fish and Game
Kansas Department of Wildlife and Parks
Montana Department of Fish, Wildlife and Parks
Nebraska Game and Parks Commission
Nevada Department of Wildlife
New Mexico Department of Game and Fish
North Dakota Game and Fish Department
Oklahoma Department of Wildlife Conservation
Oregon Department of Fish and Wildlife
Saskatchewan Department of Environment and Resource Management
South Dakota Department of Game, Fish and Parks
Texas Parks and Wildlife Department
Utah Division of Wildlife Resources
Washington Department of Fish and Wildlife
Wyoming Game and Fish Department
Yukon Department of Environment

*"Delivering conservation through*
*information exchange and working partnerships"*

THE WILDERNESS SOCIETY

ECOLOGY AND
ECONOMICS
RESEARCH
DEPARTMENT

# ANALYSIS OF HABITAT FRAGMENTATION FROM OIL AND GAS DEVELOPMENT AND ITS IMPACT ON WILDLIFE:

## A FRAMEWORK FOR PUBLIC LAND MANAGEMENT PLANNING

Report By:
Mark Wilbert
Janice Thomson, Ph.D.
Nada Wolff Culver

May 20, 2008

**PURPOSE**

This brief is submitted as part of the NEPA process for this land management proposal. It is intended to:

- Identify habitat and wildlife impacts that must be analyzed in the plan,
- Demonstrate the potential impacts on wildlife of habitat fragmentation from oil and gas development at various well-pad densities, and
- Offer methodologies to assist the Bureau of Land Management (BLM) to fulfill its responsibility to analyze the direct, indirect, and cumulative impacts on wildlife of proposed oil and gas development in the management plan.

Our mission:

To protect wilderness and to inspire Americans to care for our wild places.

# TABLE OF CONTENTS

## CONTENTS

## FIGURES AND TABLES

# INTRODUCTION

This document is structured around the following topics:

- **Legislative and Administrative Requirements for Scientific Analysis.**
  We review the legislative and administrative obligations the BLM has to assess the environmental consequences of proposed oil and gas development activities.

- **The Science of Habitat Fragmentation and Wildlife Impacts from Oil and Gas Development.**
  We describe the current state of knowledge of the direct, indirect, and cumulative impacts of roads and similar development on wildlife and their habitats. We also describe easily computed spatial metrics that can be used to meaningfully assess the degree and impact of habitat fragmentation.

- **A Methodology for Analyzing Habitat Fragmentation and Wildlife Impacts.**
  We describe an analytical framework that uses geographic information systems (GIS) to aid in examining the direct, indirect, and cumulative impacts of proposed oil and gas development alternatives.

- **Results of an Analysis Applying our Methodology to a Hypothetical Landscape.**
  We discuss the results of a habitat fragmentation analysis simulating the development of an oil and gas field to progressively higher well-pad densities over time.

- **Conclusions and Recommendations for Oil and Gas Management Planning.**
  We draw conclusions from the results of our hypothetical analysis and make specific recommendations regarding the analyses the BLM should conduct and the consideration that should be given to the effects that different levels of oil and gas development have on wildlife.

The methodology presented here provides a necessary, but by no means sufficient, framework for the evaluation of proposed land management decisions regarding oil and gas development. Fragmentation impacts are only one facet of the total ecological impact of such decisions. In order to fully evaluate the merits of different land management alternatives a complete set of ecological and socioeconomic analyses must be conducted and interpreted.

While we present both an analytical framework and results from a hypothetical analysis using that framework, we emphasize the importance of the BLM using the framework to conduct site-specific analyses wherever planning is taking place. The charts and numeric results of our sample analysis (including the charts in Appendix A) can give a preliminary estimate of the minimum potential fragmentation impacts of development on wildlife and their habitats. In this sense, these sample results may be useful in the early stages of planning to help focus the BLM's own analyses, but they are not intended to be a substitute for those site-specific analyses.

# LEGISLATIVE AND ADMINISTRATIVE REQUIREMENTS FOR SCIENTIFIC ANALYSIS

The BLM has a responsibility to manage the landscape for wildlife, energy development, and many other purposes. The Federal Land Policy and Management Act (FLPMA) requires the BLM to “manage the public lands under principles of multiple use and sustained yield,” in a manner that will “minimize adverse impacts on the natural, environmental, scientific, cultural, and other resources and values (including fish and wildlife habitat) of the public lands involved.”[1] FLPMA also requires the BLM to inventory its lands and their resources and values, and then take this inventory into account when preparing land use plans.[2] Through management plans, the BLM can and should protect wildlife (as well as scenic values, recreation opportunities, and wilderness character) on the public lands by prescribing various management actions, including the exclusion or limitation of certain uses of the public lands.[3] This is necessary and consistent with FLPMA’s definition of multiple use, which identifies the importance of wildlife (in addition to other values) and requires the BLM to consider the relative values of these resources but "not necessarily to [choose] the combination of uses that will give the greatest economic return."[4]

The National Environmental Policy Act (NEPA) requires the BLM to take a “hard look” at the potential environmental consequences of a proposed action, such as a resource management plan or oil and gas development project, so that the BLM must assess impacts and effects that include: “ecological (such as the effects on natural resources and on the components, structures, and functioning of affected ecosystems), aesthetic, historic, cultural, economic, social, or health, whether direct, indirect, or cumulative.”[5] NEPA’s hard look at environmental consequences must be based on “accurate scientific information” of “high quality.”[6] Essentially, NEPA “ensures that the agency, in reaching its decision, will have available and will carefully consider detailed information concerning significant environmental impacts.”[7] The Data Quality Act and the BLM’s interpreting guidance expand on this obligation, requiring that “influential information” (information that is expected to lead to a “clear and substantial” change or effect on important public policies and private sector decisions as they relate to federal public lands and resources issues, such as that information contained in or used to develop a resource management or major oil and gas development project) use the “best available science and supporting studies conducted in accordance with sound and objective scientific practices.”[8]

---

[1] 43 U.S.C. §1732.

[2] 43 U.S.C. §§ 1711(a), 1712(a).

[3] *See* 43 U.S.C. § 1712(e).

[4] 43 U.S.C. § 1702(c).

[5] 40 C.F.R. § 1508.8.

[6] 40 C.F.R. § 1502.15.

[7] Robertson v. Methow Valley Citizens Council, 490 U.S. 332, 349 (1989).

[8] Treasury and General Government Appropriations Act for Fiscal Year 2001, Pub.L.No. 106-554, § 515. *See also*, Bureau of Land Management “Information Quality Guidelines,” available at http://www.blm.gov/nhp/efoia/data_quality/guidelines.pdf.

NEPA also requires that the BLM conduct its environmental impact analysis based upon an adequate and accurate description of the environment that will be affected by the proposed action under consideration—the "affected environment."[9] The affected environment represents the baseline conditions against which impacts are assessed. The importance of accurate baseline data has been emphasized by courts, which have found that "a baseline against which to compare predictions of the effects of the proposed action and reasonable alternatives is critical to the NEPA process."[10]

It is important that the BLM continue to update data on the distribution and quality of wildlife habitat, in order to establish an accurate baseline and determine necessary management actions to preserve and enhance habitat. In the context of managing oil and gas development, the agency can best fulfill its obligation to evaluate the impacts of potential management decisions, then select a course of action based on the best available science, by using both field monitoring and spatial analysis to make the assessments called for under NEPA, FLPMA, and the Data Quality Act. Specifically, the BLM should evaluate the effects on wildlife (and natural and cultural resources) of habitat fragmentation from the existing and proposed network of roads and well pads, and only permit development in a manner that will not cause significant damage to wildlife habitat, using the techniques discussed below.

## THE SCIENCE OF HABITAT FRAGMENTATION AND WILDLIFE IMPACTS FROM OIL AND GAS DEVELOPMENT

### Impacts of Habitat Fragmentation

Oil and gas development creates a complex network of roads, well pads, pipelines, pumping stations, and other infrastructure across a landscape. Roads are widely recognized by the scientific community as having a range of direct, indirect, and cumulative effects on wildlife and their habitats (Trombulak and Frissell 2000, Gucinski et al. 2001, Gaines et al. 2003, Wisdom et al. 2004a, Wisdom et al. 2004b, New Mexico Department of Game and Fish 2005). Increasingly, studies are demonstrating many of the negative effects on wildlife specific to oil and gas development (Colorado Department of Wildlife et al. 2008, Wyoming Game and Fish Department 2004, Confluence Consulting 2005, Holloran 2005, Sawyer et al. 2006, Berger et al. 2006). These negative effects range from direct removal of habitat to long-term displacement of species from preferred habitat. Direct effects can be measured by calculating the physical dimensions of the development feature (e.g., roads or well pads). Indirect and cumulative effects on wildlife are often assessed through analysis of habitat fragmentation.

---

[9] 40 C.F.R. § 1502.15.

[10] Half Moon Bay Fisherman's Marketing Ass'n v. Carlucci, 857 F.2d 505, 510 (9th Cir. 1988) ("without establishing . . . baseline conditions . . . there is simply no way to determine what effect [an action] will have on the environment, and consequently, no way to comply with NEPA.").

Habitat fragmentation has been defined as the "creation of a complex mosaic of spatial and successional habitats from formerly contiguous habitat" (Lehmkuhl and Ruggiero 1991). Habitat fragmentation alters the distribution of wildlife species across the landscape and affects many of their life functions such as feeding, courtship, breeding, and migration. Transportation networks and similar infrastructure are one of the most significant causes of habitat fragmentation, and negatively impact wildlife well beyond the surface area disturbed by an actual road or oil/gas well pad (Wyoming Game and Fish Department 2004). The hundreds of scientific papers covered in the literature reviews cited in the previous paragraph illustrate the preponderance of evidence that routes ranging from narrow dirt tracks to paved roads can and do have adverse affects on wildlife. In fact, habitat fragmentation from roads and other human infrastructure has been identified as one of the greatest threats to biological diversity worldwide (Wilcove 1987). This volume of science simply cannot be ignored in a major land management planning effort.

## Measures of Habitat Fragmentation

To quantitatively assess the impacts of habitat fragmentation on wildlife, we need two things: a way to measure fragmentation, and a way to tie various degrees of fragmentation to their impacts on wildlife. Many measures of fragmentation are available—McGarigal and Marks (1995) present dozens—and each has its advantages and disadvantages. Other publications illustrate the importance of such metrics for landscape-level planning (Leitao and Ahern 2002) and measuring the indirect and cumulative impacts of development on wildlife (Theobald et al. 1997, Thomson et al. 2005). In federal land management planning, where transparency and public involvement are important, metrics that are easily computed and easily understood are desirable. The ability to tie these metrics to wildlife impacts comes from the biological literature, which contains an increasing number of references to easily computed fragmentation metrics and values for those metrics at which various wildlife impacts have been recorded. Table 1 contains examples of these indicator values for a few important wildlife species present in oil and gas development areas across the West. This is only a sample, and BLM staff should search the scientific literature for the latest and most appropriate values associated with species of local importance whenever land management planning is undertaken.

| Species | Indicator Value | Impact/Observation/Recommendation | Reference |
|---|---|---|---|
| Sagebrush-obligate birds | 328 foot distance to nearest road | Within this distance the density of sagebrush-obligate birds drops by 50 percent regardless of the amount of activity on the road. | Ingelfinger 2001 |
| Greater Sage-Grouse | < 5 producing wells within 1.9 miles of a lek | No impact on lek attendance by males was observed. | Holloran 2005 |
| | 5-15 producing wells within 1.9 miles of a lek | Medium impact on lek attendance by males was observed. | |
| | > 15 producing wells within 1.9 miles radius of a lek | Heavy impact on lek attendance by males was observed. | |
| | 2 mile radius around a lek | Well density within this distance of a lek was observed to be one-third lower for active leks than for inactive leks. | Naugle et al. 2006 |
| | 3.4 mile radius around a lek | No surface occupancy (NSO), no new road construction, and seasonal closure of existing roads are recommended within this distance of a lek. | Braun 2006 |
| | 4 mile radius around a lek | Minimum disturbance is recommended within this distance of a lek. | Northwest Colorado Greater Sage-Grouse Working Group 2006 |
| | 4 mile radius around a lek | NSO designation for areas within this distance of leks is scientifically supported when nesting and brood rearing maps are not available. | Colorado Department of Wildlife 2008 |
| | 1 well pad/mi$^2$ pad density | Measurable negative impacts on breeding populations are observed at this density. | |
| Elk | 1 mi/mi$^2$ road density | Road density above which habitat effectiveness is eliminated in non-forested landscapes | Lyon 1979 |
| Mule Deer | 328 foot distance to nearest road | Distance from a road at which deer are observed to exhibit avoidance in shrub landscape. | Rost and Bailey 1979 |
| | 436 foot distance to nearest road | Female deer on winter range move away from humans on snowmobiles. | Freddy et al. 1986 |
| | 627 foot distance to nearest road | Female deer on winter range move away from humans on foot. | |
| | 1,096 foot distance to nearest road | Female deer on winter range alert to humans on foot. | |
| | 1,542 foot distance to nearest road | Female deer on winter range alert to humans on snowmobiles. | |
| | 1.6, 1.9, and 2.3 miles from well pads | Minimum distances from well pads at which deer are most likely to occur over three years of progressive oil and gas development. | Sawyer et al. 2006 |
| Pronghorn | 0.6 mile distance to nearest road | Distance from a maintained road at which pronghorn exhibit avoidance. | Ockenfels et al. 1994 |
| | 1 mi/mi$^2$ road density | Road density at which negative impacts were acknowledged to occur. | BLM 1999 |
| Bighorn Sheep | 433 foot distance to nearest road | Sheep flee from human activity on roads at this distance. | Papouchis et al. 2001 |
| | 1,191 foot distance to nearest road | Sheep alert to human activity on roads at this distance. | |

Table 1. Fragmentation Indicator Values for Selected Wildlife Species.

A sampling of road density, distance-to-nearest-road-or-well-pad, or related values at which indirect and cumulative impacts on wildlife occur.

We recommend the use of two fragmentation metrics that are both easy to compute and easy to understand: road density and distance to nearest road or well pad.

**Road density** is the total length of road per unit area (e.g., miles per square mile). It can be computed by dividing the entire study area into a grid of areas (cells) appropriately sized[11] for the total size of the study area, and assigning to each cell the total length of road in the surrounding circular one-square-mile area. Figure 1 is an illustration of this concept. Feature dimensions, especially cell size, are exaggerated for clarity.

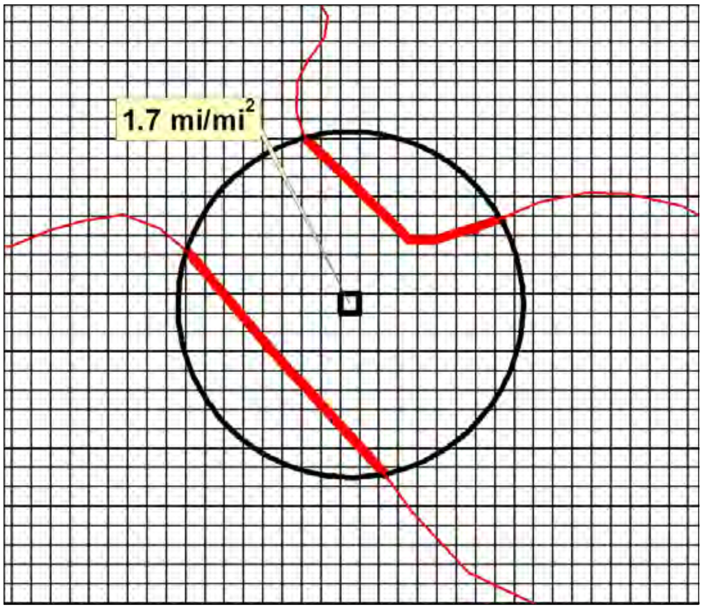


Figure 1. Illustration of Road Density Metric.

Road density is computed for each grid cell in the study area using a GIS tool that totals the length of road in the circular one square mile area surrounding the cell and assigns that value to the cell. With total road length measured in miles, road density has units of miles per square mile. This figure illustrates the one-square-mile circle, the central cell being processed, and the roads (red/bold within the circle) whose lengths are being summed to give the cell's road-density value.

**Distance to nearest road** is the distance from any place in the study area to the nearest road (or other fragmenting feature—in this document we also include the distance to the nearest well pad in this metric). It can be computed by dividing the entire study area into a grid of areas (cells), again appropriately sized for the total size of the study area, and assigning to each cell the distance between the center of that cell and the center of the nearest cell with a road in it. Figure 2 illustrates this concept—again, with feature dimensions exaggerated for clarity.

---

[11] There are no hard and fast rules for selecting an appropriate cell size. Analysts must balance the desire for a small cell that gives fine resolution and smooth visual display against the desire for a larger cell that reduces computer processing time.

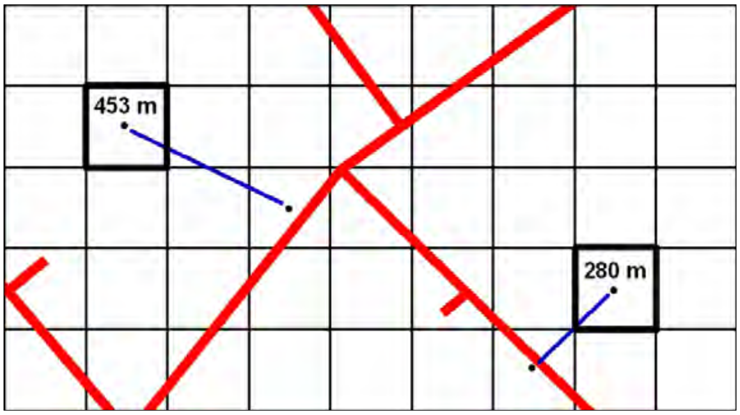


Figure 2. Illustration of Distance-to-Nearest-Road Metric.

Distance to nearest road is computed for each grid cell in the study area using a GIS tool that measures the distance from the cell's center to the center of the nearest roaded cell and assigns that value to the cell. This figure shows cell centers for two sample cells as points, roads as bold red lines, and the distance between cell centers as thinner blue lines.

## A METHODOLOGY FOR ANALYZING HABITAT FRAGMENTATION AND WILDLIFE IMPACTS

Authorization of oil and gas development on federal land requires the BLM to examine the direct, indirect, and cumulative impacts of the proposed development and a range of management alternatives. This assessment necessarily includes looking at levels of reasonably foreseeable development under the alternatives (see e.g., Instruction Memorandum 2004-089). In order to evaluate likely effects and select the appropriate alternative in terms of both development and impacts to other resources such as wildlife habitat, the agency should assess a range of well-pad densities and specifically determine acceptable levels. In the absence of such comprehensive analyses, fields can develop faster than originally expected without the agency having considered the potential effects of, for instance, full-field development with infill, and put in place specific limitations. The result is development density, and destruction of wildlife habitat, exceeding anything considered during the plan approval process.

For example, in the Jonah Field in Wyoming, original predictions in 1998 were for drilling of 500 wells over 15 to 20 years with a maximum well density[12] of one well per 80 acres. Within five years, however, an additional 500 wells

---

[12] The BLM sometimes uses the term *spacing* to describe the distribution of well pads on the surface of the land. This term can be confusing—both because it was originally developed to describe the number of drill holes needed to drain a certain reservoir (this is downhole spacing) and because terms like *increasing spacing* may be interpreted either as placing pads farther apart or as increasing the number of pads per square mile. For these reasons, we use the term *well-pad density* to describe the surface distribution of well pads.

were drilled and a well density of one well per 40 acres had been approved. Most recently, the infill project for this field resulted in the approval of 3,100 more wells, with a well density averaging one well per 10 acres and ranging as high as one well per 5 acres in some parts of the field. While all of these step-wise increases were approved by BLM, the agency's decision-making would have been better informed by an analysis made at the outset that examined the degree of habitat fragmentation likely to result from different levels of development. This would have assisted in setting limits on acceptable development, and would also have limited industry expectations. Performing such an analysis and putting limitations on the degree of habitat fragmentation that will be allowed is important for responsible land management.

The BLM is already recognizing the potential for using GIS analysis to evaluate development impacts. For instance, the Record of Decision (ROD) for the Resource Management Plan Amendment for Federal Fluids Mineral Leasing and Development in Sierra and Otero Counties (New Mexico) sets out two limitations to protect Chihuahuan Desert Grasslands: restricting surface disturbance to 5 percent of a leasehold at one time and limiting total surface disturbance to 1,589 acres over the life of the RMP Amendment. The ROD states that both limitations will be monitored and enforced using GIS technology. (See ROD, p. 12, available at http://www.blm.gov/pgdata/etc/medialib/blm/nm/field_offices/las_cruces/las_cruces_planning/white_sands___otero0/docs_white_sands_.Par.82039.File.dat/PRINTABLEROD-LCFO-FINAL_text.pdf.)

To demonstrate an analytical framework for the analysis of fragmentation, and to provide estimates of the fragmentation effects of oil and gas development on wildlife, we have simulated the incremental development of an oil and gas field, from low well-pad density to high, on a hypothetical 28,120-acre site. The seven well-pad densities analyzed were chosen to match densities commonly discussed in BLM management plans: one pad per 640 acres, 320 acres, 160 acres, 80 acres, 40 acres, 20 acres, and 10 acres. These densities, respectively, are equivalent to 1 pad per square mile (mi$^2$), 2 pads/mi$^2$, 4 pads/mi$^2$, 8 pads/mi$^2$, 16 pads/mi$^2$, 32 pads/mi$^2$, and 64 pads/mi$^2$ (the BLM and others sometimes use pads/mi$^2$ in reference to what they call well-pad spacing). Throughout this analysis we express well-pad density using one or the other of these units, choosing the most appropriate for the context. We refer to each simulation of a stage of incremental development as a development scenario.

## Scenario Development and Assumptions

The first step in creating development scenarios for analysis was to define the set of roads we assumed to be present before any oil and gas development. The number of roads in the pre-development landscape has an effect on the magnitude of change in fragmentation metrics from the pre-development condition to the first stage (and a few subsequent stages) of oil and gas development. The change in fragmentation between the pre-development condition and the first few development stages is smaller when pre-development roadedness is higher because the landscape is already relatively fragmented before well pads and connecting roads are added. The impact of pre-development roadedness decreases as development continues, because the number of well pads on the landscape becomes the driver in the total number and distribution of roads. We chose to create a relatively small initial road system in an effort to remain conservative in our depiction of fragmentation effects.

The pre-development road centerline dataset was digitized on-screen using ArcGIS (ArcInfo) 9.2[13]. Road centerlines were converted to a new dataset representing the actual width of road rights-of-way (the assumed area of direct disturbance) by buffering the centerlines by 20 feet on each side—giving a total width of 40 feet[14].

Development of the oil and gas field was simulated through an iterative process, involving three steps for each stage of development:

1) **Randomly place the number of well pads necessary to achieve the desired well-pad density.** We did this using tools available in CommunityViz 3.2 (Scenario 360),[15] software designed to work as an extension of ArcGIS. We chose to represent well pads as 4-acre squares[16] and to restrict placement of new well pads so that they not overlap with existing well pads and/or roads present in the preceding stage of development. For the first stage of oil and gas development, this exclusion area is the dataset representing the set of 40-foot-wide roads defined for the pre-development landscape.

2) **Manually create road centerline segments, through on-screen digitizing, to connect the newly placed well pads to the existing road system**. We maintained a single roads dataset, with new road segments being added at each stage of simulated oil and gas development. Dataset attributes were maintained to allow identification of the complete road network associated with each development stage. When digitizing road segments, we assumed no restrictions on road routing (e.g., no topographic limitations). As new road centerlines were added, they were often routed along the edge of existing well pads in an effort to minimize fragmentation as measured by the distance-to-nearest-road-or-well-pad metric. However, this practice may slightly increase fragmentation as measured by the road-density metric because a road segment can be slightly longer than the shortest distance between its end points. No effort was made to quantify these effects.

3) **Convert road centerlines to a dataset representing road width, and combine this with the well-pad dataset associated with the current development stage.** This created a dataset representing the area directly disturbed by roads and well pads. As for the pre-development road system, road width was set to 40 feet. For the next stage of development, the combined road/pad dataset was fed back into step 1 above, as the area which the next set of well pads must not overlap.

---

[13] Manufactured by ESRI (Environmental Systems Research Institute), Redlands, CA.

[14] The 40-foot width is based on the average initial width of direct disturbance used in the Draft Environmental Impact Statement for the Pinedale Resource Management Plan from the BLM's Pinedale Resource Area in Wyoming. We selected this width as a representative example of the way that the agency measures impacts in an area where the BLM is regularly addressing oil and gas development.

[15] Manufactured by Placeways, LLC, Boulder, CO.

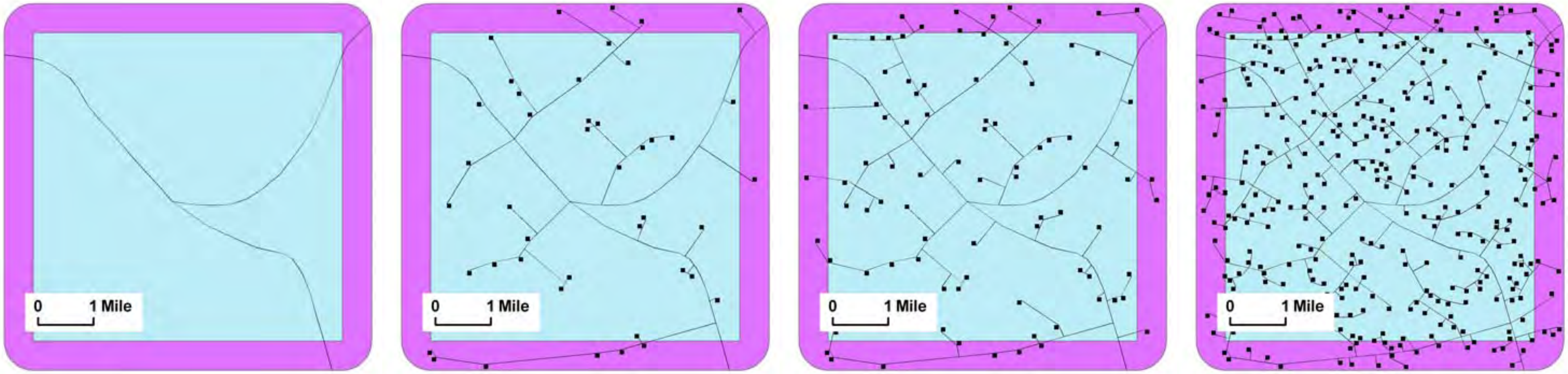
[16] The 4-acre well pad size is the area of direct disturbance projected for one well pad with a single well in the Reasonably Foreseeable Development document for the Little Snake Resource Area Management Plan in Colorado.

This process was repeated seven times to create representations of the road and well-pad infrastructure associated with a pre-development condition and seven hypothetical stages of oil and gas development. Figure 3 presents a pictorial view of these eight development scenarios.

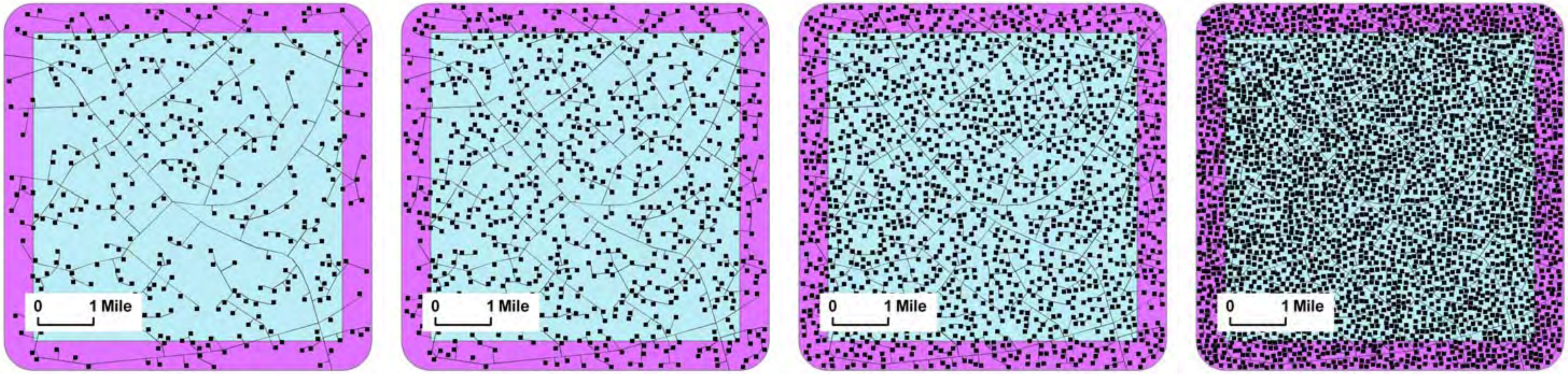
For the pre-development condition and each of the development stages, measurements were made of the area of direct disturbance, road density, and distance to nearest road or well pad using the techniques described in the previous section of this document. The grid cell size chosen was 33 feet—providing good resolution as well as good GIS processing times. Fragmentation metrics were calculated for the entire 28,120-acre study area, but the results presented below are those associated with only the center 20,000-acre analysis area (the lighter shaded interior area in Figure 3). This was done in order to avoid including erroneous results that may naturally arise when processing data near the edge of the full 28,120-acre area.

## Conservative Estimates

The results presented here are conservative estimates of the actual degree of habitat fragmentation and its impacts on wildlife for several reasons. First, these hypothetical scenarios consider the effects of roads and well pads but not of pipelines, pumping stations, and other infrastructure associated with oil and gas development. Second, our road networks do not include closed loops, which commonly occur in real oil and gas developments and increase the overall miles of road and degree of fragmentation. Third, our assumption of no topographic influences on road construction yields a shorter road network than in most real landscapes. Fourth, we assume few roads in the pre-development scenario, but in real landscapes throughout the West the number of roads existing prior to oil and gas development varies greatly, and many areas have pre-development road networks significantly larger than that used in this analysis. Where pre-development road networks are larger, the total degree of fragmentation will be greater, particularly in the early stages of development. Fifth, we assumed a well-pad size of only 4 acres, which is substantially smaller than frequently proposed sizes ranging from 4 to 160 acres depending on the number of wells per pad. Sixth and finally, our analysis of the effect of well pads on Greater Sage-Grouse leks, in which we assume one well per pad, underestimates the impact resulting when more than one well occupies a single pad. Taken together, these factors suggest that the degree of habitat fragmentation and the associated impacts on wildlife from oil and gas development in real landscapes will be even greater than those presented in this document.



Pre-development  One pad per 640 acres  One pad per 320 acres  One pad per 160 acres



One pad per 80 acres  One pad per 40 acres  One pad per 20 acres  One pad per 10 acres

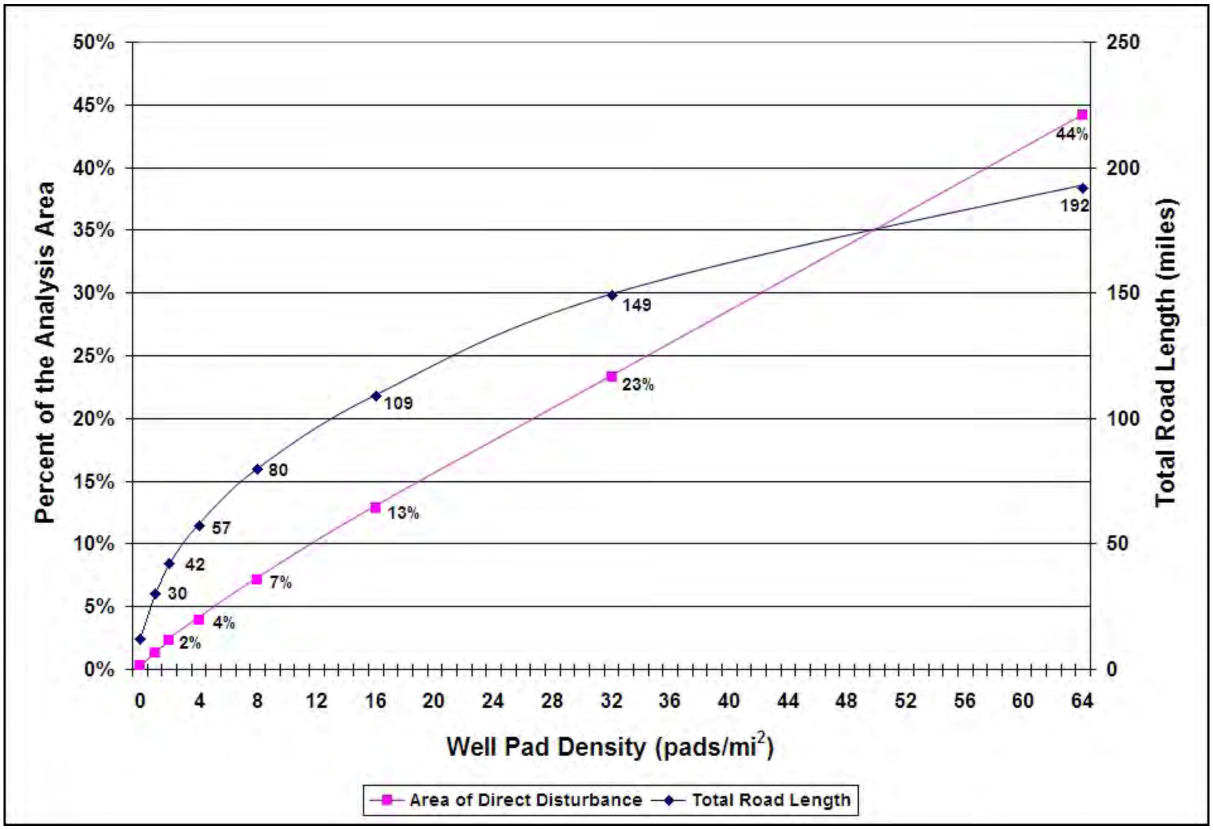
Figure 3. Eight Stages of Simulated Oil and Gas Development.

This series of maps shows the area of direct disturbance from well pads and roads for eight development scenarios. With the pre-development scenario serving as the base condition, each new scenario is created by randomly adding square 4-acre well pads to the previous scenario and connecting them to the growing network of 40-foot-wide roads. Fragmentation metrics are reported for the center 20,000-acre analysis area (blue/lighter shaded) in order to avoid errors that naturally occur as a result of data processing near the edge of the study area.

# RESULTS OF AN ANALYSIS APPLYING OUR METHODOLOGY TO A HYPOTHETICAL LANDSCAPE

## Measuring Direct Disturbance

Simple measures of direct disturbance from oil and gas development include total miles of road and total combined road and well-pad area. The graph and table in Figure 4 summarize these measures of direct disturbance for our eight oil and gas field development scenarios. The total area of direct disturbance increases approximately linearly as well-pad density increases. This is expected since the number of well pads (and hence, total well-pad area) doubles as well-pad density doubles. Total road length behaves differently, increasing more rapidly in the early stages of development. Again, though, this is expected, since, in the earlier stages of development, the random placement of a few well pads in our relatively unroaded area will likely require the construction of long roads to connect the well pads to the existing road system. In the later stages of field development, new well pads are likely to be placed near existing roads, and even the larger number of roads needed does not offset the significantly shorter length of each road. This relatively more rapid increase in total road length in the early stages of field development has implications for the indirect impacts of habitat fragmentation, as measured by road density and distance to nearest road or well pad (as shown in the next section).



| Well-Pad Density (acres/pad) | Well-Pad Density (pads/mi²) | Total Road System Length (miles) | Total Area Directly Impacted (acres) | Percent of Study Area Directly Impacted |
|---|---|---|---|---|
| Pre-development | 0 | 12 | 59 | <1% |
| 640 | 1 | 30 | 271 | 1% |
| 320 | 2 | 42 | 459 | 2% |
| 160 | 4 | 57 | 793 | 4% |
| 80 | 8 | 80 | 1,429 | 7% |
| 40 | 16 | 109 | 2,579 | 13% |
| 20 | 32 | 149 | 4,661 | 23% |
| 10 | 64 | 192 | 8,830 | 44% |

Figure 4. Measures of Direct Disturbance for Eight Development Scenarios.

This table and graph show the growth of the area of direct disturbance in our oil and gas field development simulation. While the area of direct disturbance, driven by the increasing well-pad area, increases linearly, total road system length increases more rapidly in the earlier stages of field development.

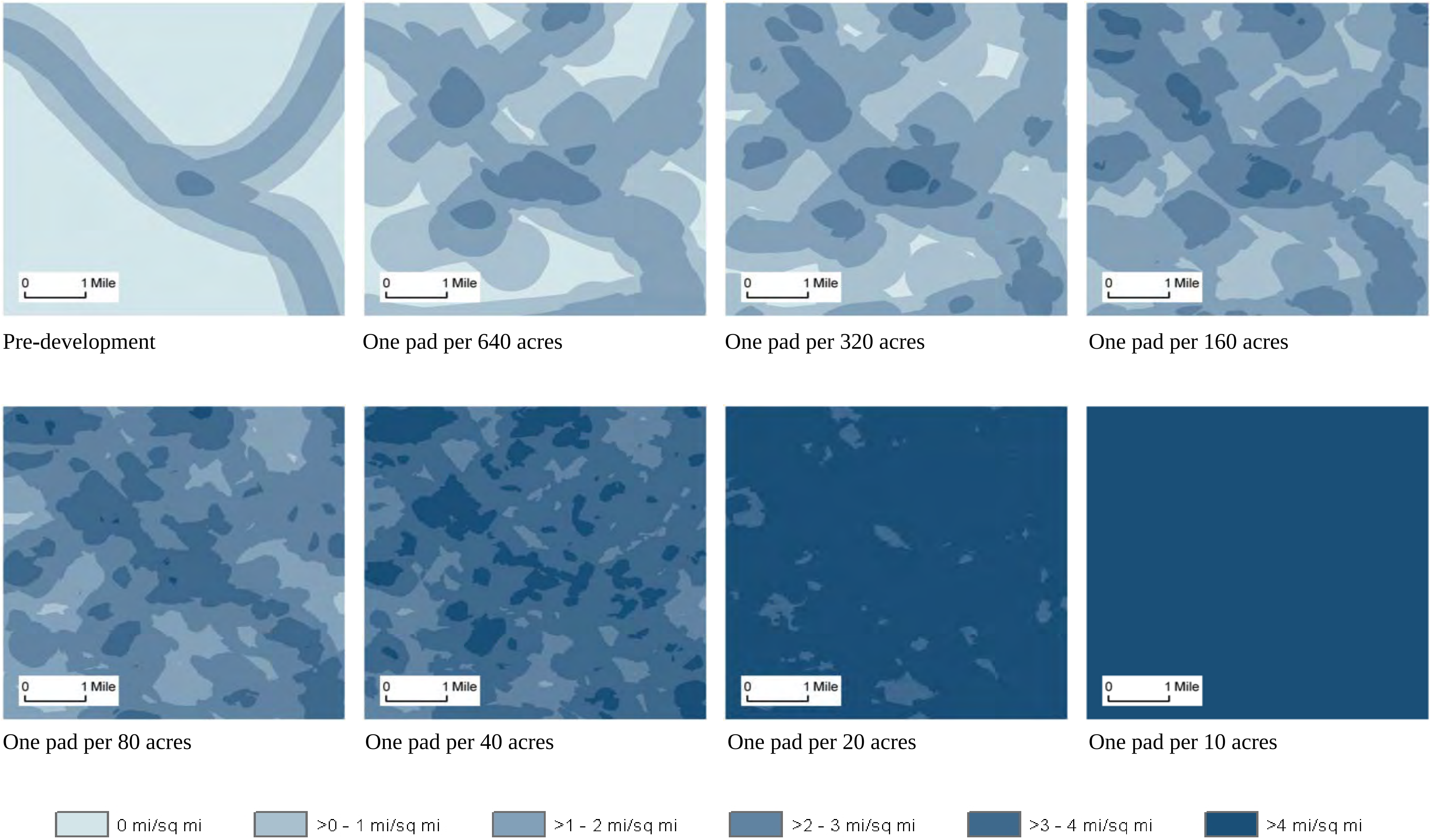
## Measuring Indirect and Cumulative Impacts

### Road Density

Road density, when calculated spatially, may be assessed visually by mapping. Figure 5 shows the patterns of road density across the landscape at the different well-pad densities used in our simulation. Using GIS, these data can be displayed with wildlife habitat boundaries such as seasonal range, breeding and rearing habitat, migration paths, and other data for individual species to give a visual sense of road density specifically within these habitats. GIS technology can also combine the road-density and habitat information to give quantitative results within key habitats.

Mean road density—the area-weighted average of individual road-density grid values for the analysis area—can be measured and plotted against well-pad density for each development scenario as shown in Figure 6. This graph shows that the *rate* of increase in road density is higher at earlier stages of development than at later stages. This is consistent with the rate of growth in total road system length and suggests the high relative impact of initial development and the importance of maintaining undeveloped areas.

The utility of spatial road-density computations is increased by tying them to the biological literature on wildlife impacts of fragmentation. To make this connection we plotted the cumulative area distribution of road density for each development scenario (Figure 7). This yielded a series of curves showing the percentage of the landscape at or below any given road density, which can indicate how much of the landscape will likely remain as viable habitat (i.e., below some road-density indicator value obtained from wildlife field research). For instance, Lyon (1979) found that a road density of 1 mi/mi$^2$ will eliminate elk habitat effectiveness in non-forested landscapes. To help us understand how the percentage of the landscape with road density below this value changes with increasing oil and gas development, we can superimpose a line corresponding to a road density value of 1 mi/mi$^2$ (the vertical dashed line in Figure 7) and read the proportion of unimpacted area directly from the chart for each development density (dashed horizontal lines). This reveals that even at the lowest development density—one well pad per 640 acres—just 50 percent of the landscape has a road density less than Lyon's (1979) indicator for loss of habitat effectiveness. At the 320- and 160-acre densities, this proportion falls to 36 percent and 15 percent respectively. At even higher well-pad densities, virtually none of the landscape meets Lyon's criterion. Wherever oil and gas development is planned, assessments of this type should be done for all potentially impacted local species for which road-density indicator values are available in the biological literature.


Pre-development

One pad per 640 acres

One pad per 320 acres

One pad per 160 acres

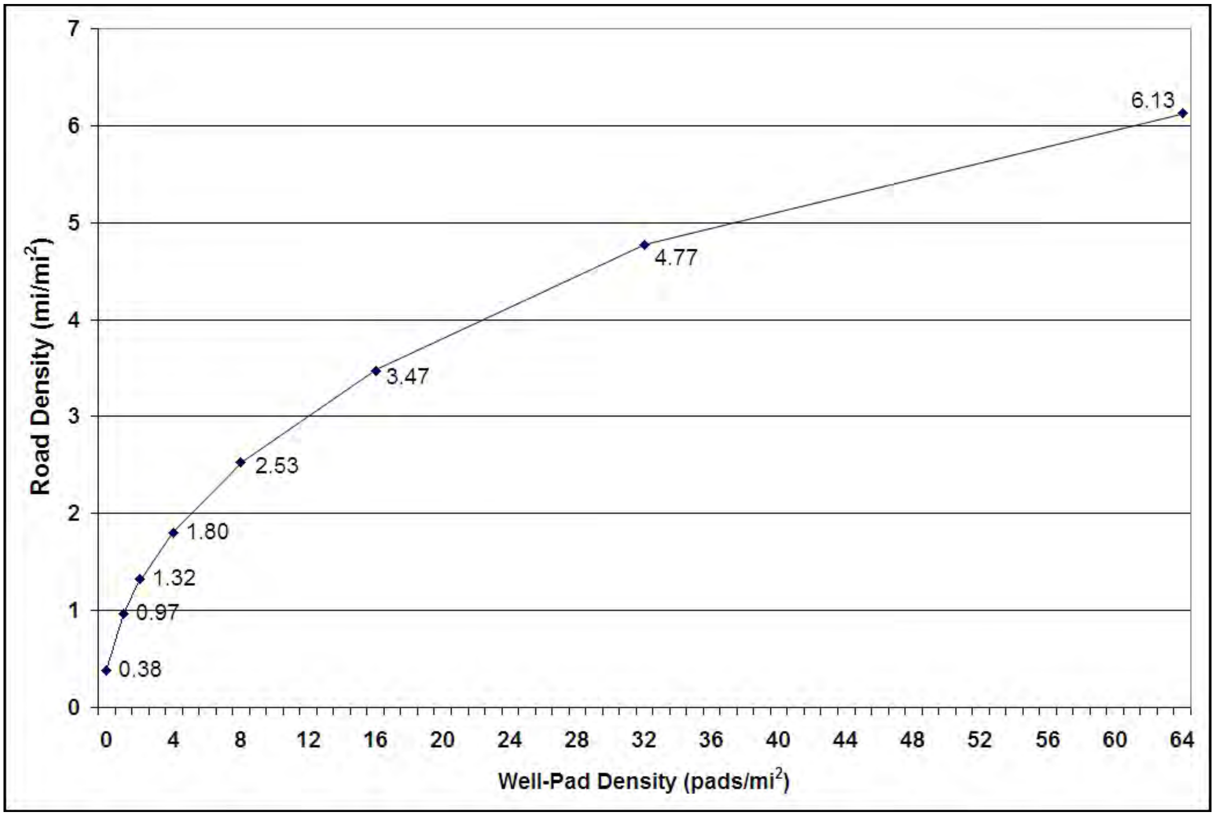
One pad per 80 acres

One pad per 40 acres

One pad per 20 acres

One pad per 10 acres

Figure 5. Maps of Road Density for Eight Oil and Gas Development Scenarios.



| Well-Pad Density (acres per pad) | Well-Pad Density (pads/mi$^2$) | Mean Road Density (mi/mi$^2$) | Change in Mean Road Density | Rate of Change in Road Density |
|---|---|---|---|---|
| Pre-development | 0 | 0.38 | -- | -- |
| 640 | 1 | 0.97 | 0.59[17] | 0.59[17] |
| 320 | 2 | 1.32 | 0.35 | 0.35 |
| 160 | 4 | 1.80 | 0.48 | 0.24 |
| 80 | 8 | 2.53 | 0.73 | 0.18 |
| 40 | 16 | 3.47 | 0.94 | 0.12 |
| 20 | 32 | 4.77 | 1.30 | 0.08 |
| 10 | 64 | 6.13 | 1.36 | 0.04 |

Figure 6. Mean Road Density for Eight Development Scenarios.

This graph and table show that the rate of change in road density (computed as the change in mean road density divided by the change in pad density) occurs most rapidly at lower development densities. This indicates the high relative impact of initial development, and emphasizes the importance of maintaining undeveloped areas.

---

[17] Note that the magnitude of the change in road density from the pre-development condition to a well-pad density of 1 pad/mi$^2$ is dependent on our assumption of a relatively small pre-development road system. With a more extensive pre-development road system this change in mean road density would be smaller. The size of the pre-development road system has an effect on the magnitude of change between subsequent development stages as well, but the effect decreases as development density increases.

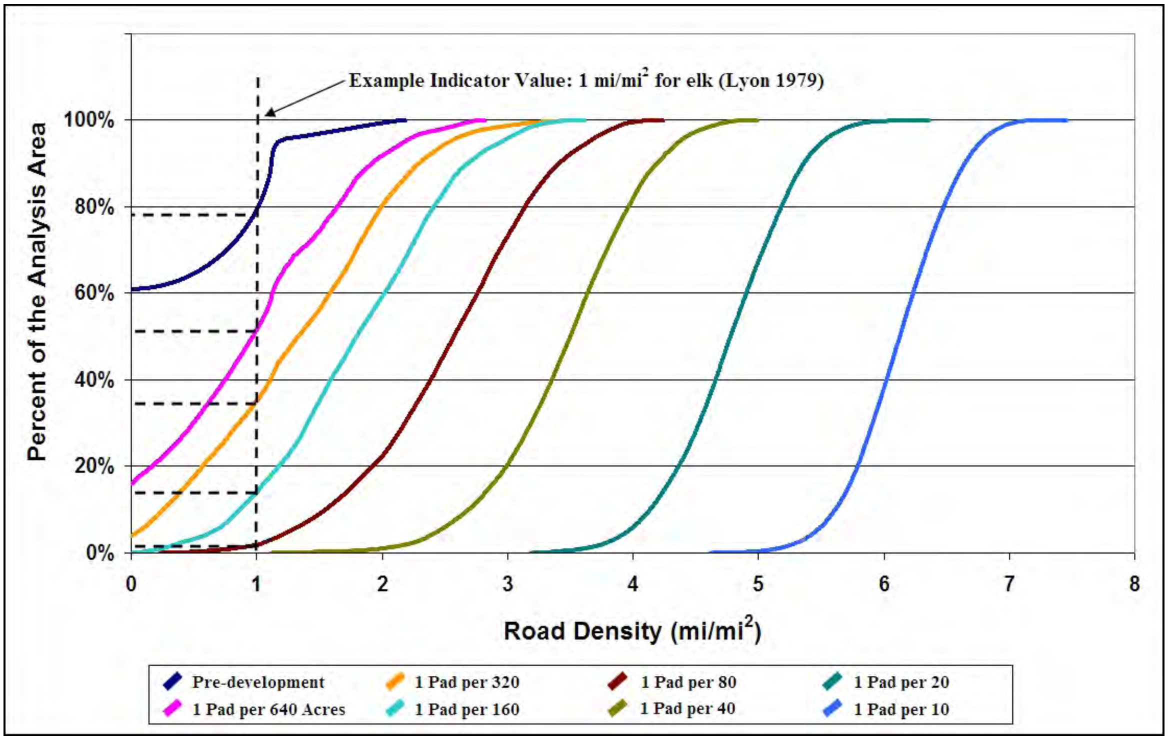
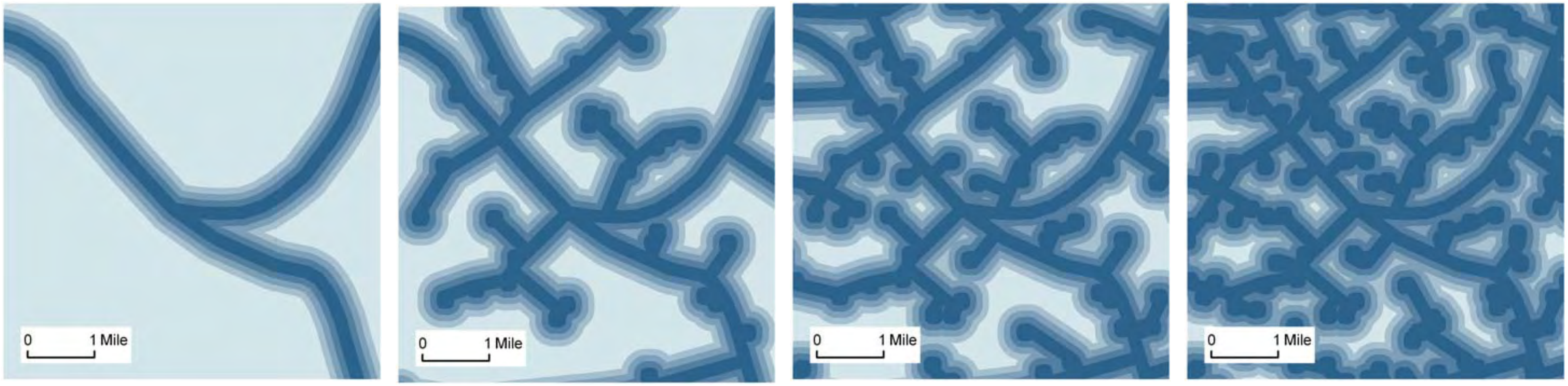


Figure 7. Proportion of Analysis Area at or Below a Road Density for Eight Development Scenarios. These curves show the proportion of the analysis area at or below a given road density for each development scenario. The curves can be examined in relation to wildlife indicator values found in the scientific literature (such as in Table 1) to assess the likely impact of different oil and gas development densities on wildlife species. This example shows that, even at the lowest oil and gas development densities, relatively high percentages of the landscape exceed Lyon's (1979) indicator value for loss of elk habitat effectiveness in open landscapes.

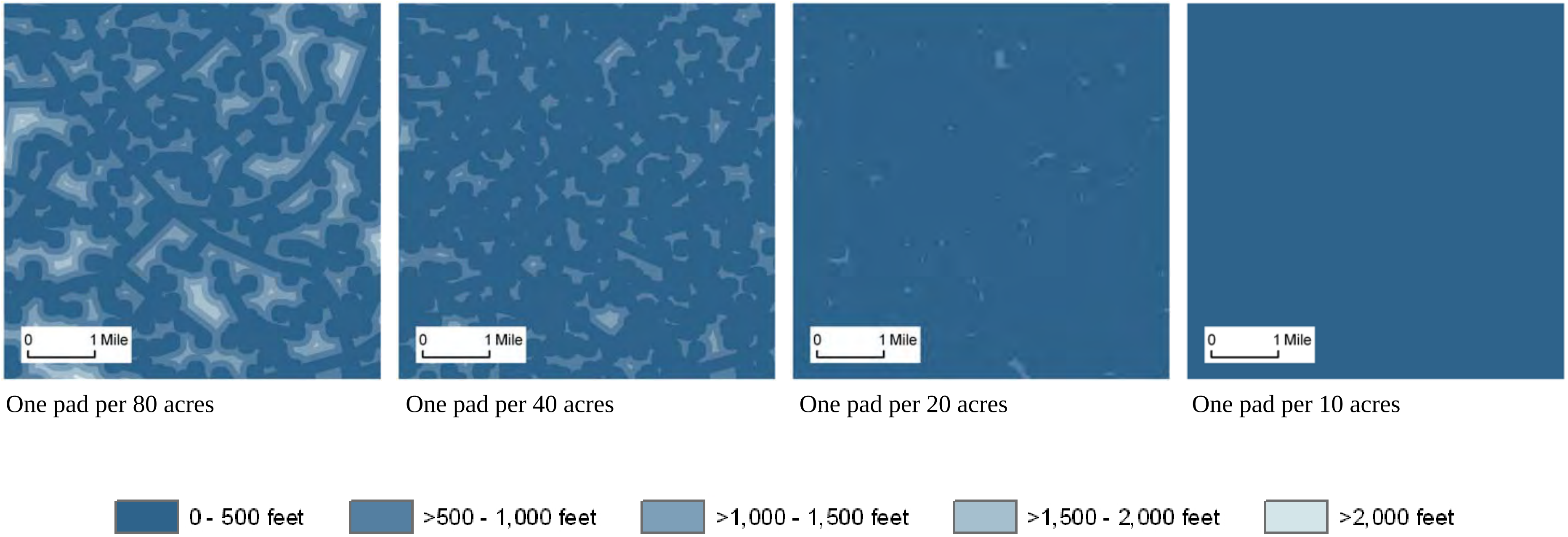
### Distance to Nearest Road or Well Pad

Distance to nearest road or well pad, when calculated spatially, may also be assessed visually by mapping. Figure 8 shows the patterns of proximity to roads and well pads across the landscape at the different well-pad densities analyzed in our simulation. The treatment and use of the distance-to-nearest-road-or-well-pad metric is similar to that described for road density above. Using GIS, the distance-to-nearest-road-or-well-pad data can be displayed with wildlife habitat boundaries such as seasonal range, breeding and rearing habitat, migration paths, and other data for individual species to give a visual sense of road and well-pad proximity specifically within these habitats. GIS analysis can also combine the distance-to-nearest-road-or-well-pad and habitat data to give quantitative results within sensitive habitats.

The mean distance to nearest road or well pad—the area-weighted average of the values of individual grid cells for the analysis area—can be measured and plotted against the density of well pads across the landscape for each development scenario (Figure 9). As was the case with road density, the *rate* of decrease in distance-to-nearest-road-or-well-pad values is higher at earlier stages of development than at later stages, implying that the relative rate of impact from development is higher at lower development densities and suggesting the importance of maintaining undeveloped areas.

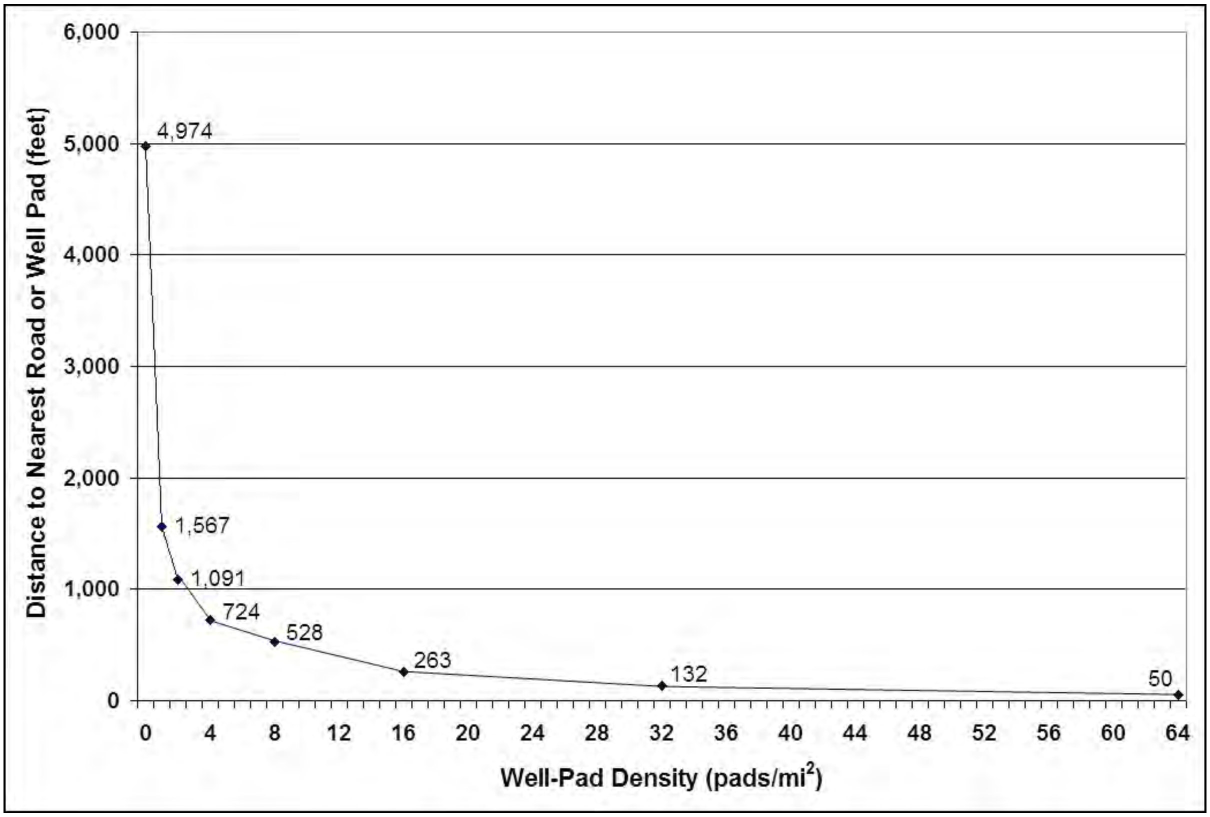


Pre-development One pad per 640 acres One pad per 320 acres One pad per 160 acres



One pad per 80 acres One pad per 40 acres One pad per 20 acres One pad per 10 acres

Figure 8. Maps of Distance to Nearest Road or Well Pad for Eight Oil and Gas Development Scenarios.



| Well-Pad Density (acres per pad) | Well-Pad Density (pads/mi$^2$) | Mean Distance to Nearest Road or Pad (feet) | Change in Mean Distance to Nearest Road or Pad | Rate of Change in Distance to Nearest Road or Pad |
|---|---|---|---|---|
| Pre-development | | 4,974 | -- | -- |
| 640 | 1 | 1,567 | 3,407[18] | 3,407[18] |
| 320 | 2 | 1,091 | 476 | 476 |
| 160 | 4 | 724 | 367 | 184 |
| 80 | 8 | 528 | 196 | 49 |
| 40 | 16 | 263 | 265 | 33 |
| 20 | 32 | 132 | 131 | 8 |
| 10 | 64 | 50 | 82 | 3 |

Figure 9. Mean Distance to Nearest Road or Well Pad for Eight Development Scenarios.

This graph and table show that the rate of change in the distance to nearest road or well pad (computed as the change in mean distance to nearest road or well pad divided by the change in pad density) occurs most rapidly at lower development densities. This indicates the high relative impact of initial development, and emphasizes the importance of maintaining undeveloped areas.

Just as was the case with road density, the utility of spatial distance-to-nearest-road-or-well-pad computations is increased by tying them to the biological literature on wildlife impacts of fragmentation. To make this connection we

---

[18] As noted above for road density, the magnitude of the change in distance to nearest road or well pad from the pre-development condition to a well-pad density of 1 pad/mi$^2$ is dependent on our assumption of a relatively small pre-development road system. With a more extensive pre-development road system this change in mean distance would be smaller. The size of the pre-development road system has an effect on the magnitude of change between subsequent development stages as well, but the effect decreases as development density increases.

plotted the cumulative area distribution of distance to nearest road or well pad for each development scenario (Figure 10). This yielded a series of curves showing the percentage of the landscape beyond any given distance to a road or well pad, which can indicate how much of the landscape will likely remain as viable habitat (i.e., beyond some distance-to-nearest-road indicator value obtained from wildlife field research) at any given development density. For example, Ingelfinger (2001) found that the density of sagebrush-obligate birds drops by 50 percent within 328 feet of a road, regardless of the amount of activity on the road. To help us understand how the percentage of the landscape beyond this distance from the nearest road or well pad changes with increasing oil and gas development, we can superimpose a line representing this indicator value (the dashed vertical line in Figure 10) and read the proportion of unimpacted area directly from the chart for each development density (horizontal dashed lines). This exercise shows that at a well-pad density of just one pad per 80 acres, less than 55 percent of the landscape is beyond Ingelfinger's distance. The proportion of unimpacted area drops rapidly from there as development continues. Wherever oil and gas development is planned, assessments of this type should be done for all the potentially impacted local species for which distance-to-nearest-road-or-well-pad indicator values are available in the biological literature.

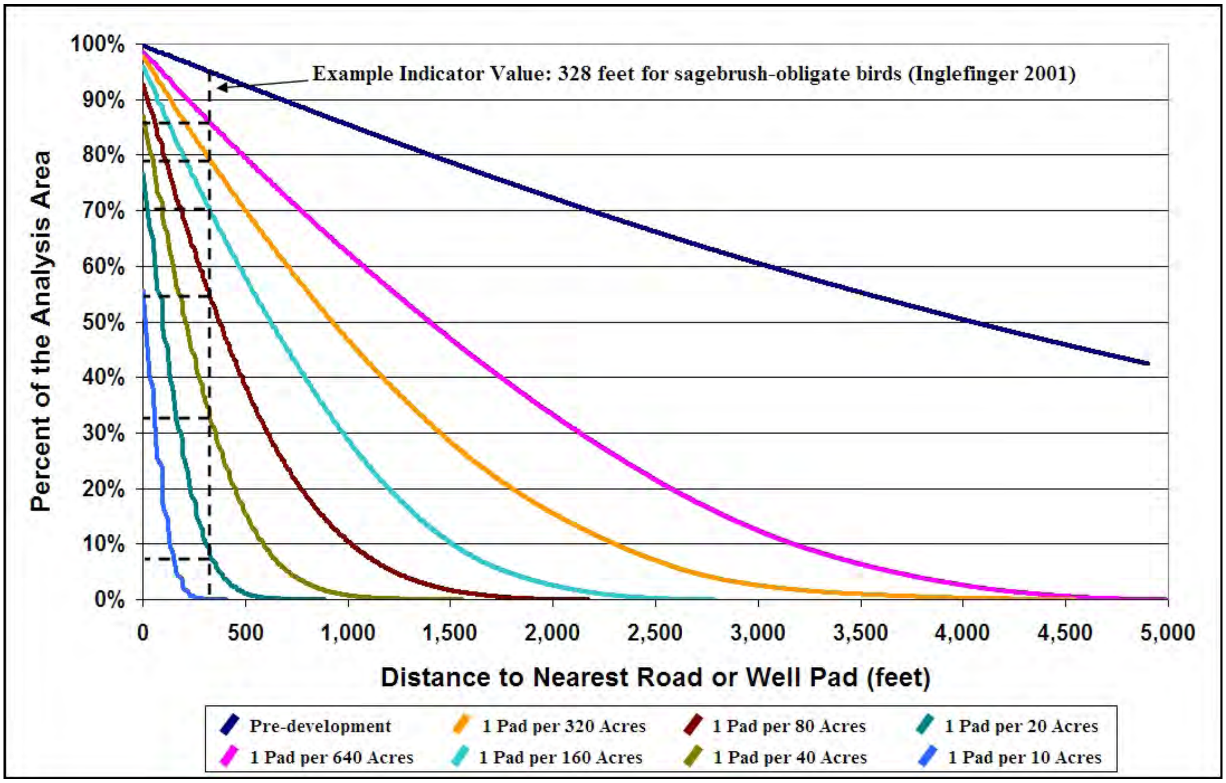


Figure 10. Proportion of Analysis Area Beyond a Distance of a Road or Well Pad for Eight Development Scenarios. These curves show the proportion of the analysis area beyond a given distance to the nearest road or well pad for each development scenario. The curves can be examined in relation to wildlife indicator values found in the scientific literature (such as in Table 1) to assess the likely impact of different oil and gas development densities on wildlife species. This example shows that, even at relatively low well-pad densities, significant percentages of the study area are close enough to roads or well pads to show the 50 percent reduction in the density of sagebrush-obligate birds reported by Ingelfinger (2001).

### Special Case: Greater Sage-Grouse

A variety of fragmentation indicator values for different wildlife species may be found in the scientific literature, and these will necessitate application of different GIS processes to properly assess and represent them. We mention a special case of indicator values for Greater Sage-Grouse because of the presence of this species in so many oil and gas development areas across the West, its at-risk status, and the many state and federal agency efforts underway to protect it. Such efforts include the Greater Sage-Grouse Comprehensive Conservation Strategy from the Western Association of Wildlife Agencies (Stiver et al. 2006), a review of the latest science on Greater Sage-Grouse by the wildlife agencies of Colorado, Montana, North Dakota, Utah, and Wyoming (Colorado Department of Wildlife et al. 2008), and the Colorado Greater Sage-Grouse Conservation Plan (Colorado Greater Sage-Grouse Conservation Plan Steering Committee 2008).

Several studies have examined Greater Sage-Grouse lek use in relation to the proximity of those leks to oil and gas wells, and recommended corresponding management actions. Braun (2006) recommends no surface occupancy (NSO), no new road construction, and seasonal closure of existing roads within 3.4 miles of Greater Sage-Grouse leks. Holloran (2005) considered lek attendance by males in relation to the number of producing wells within 1.9 miles of a lek, finding no measurable impact for fewer than 5 wells, moderate decline in male attendance for 5 to 15 wells, and significant decline for more than 15 wells within 1.9 miles of a lek. GIS buffer tools can identify the area within any radius of each lek, while GIS neighborhood analysis can be used to compute the number of wells within a specified distance for each lek. The BLM will likely have lek location data with which to perform these analyses, yielding the site-specific information needed for planning.

In the hypothetical landscape we used in our analysis, where lek locations cannot be known, we can only perform the neighborhood analysis for all grid cells in the analysis area and provide a general sense of the likelihood of development impacts on Greater Sage-Grouse lek use: the higher the proportion of the landscape exceeding the indicator values, the higher the proportion of leks likely to be impacted. The results of this analysis are summarized in Figure 11, which shows that only the one-pad-per-square-mile development scenario yielded even as much as 10 percent of the analysis area in Holloran’s no-impact class (fewer than 5 wells within 1.9 miles). In the two-pads-per-square-mile development scenario, 35 percent of the analysis area was in the medium-impact class. For all other development scenarios virtually no portion of the analysis area fell outside of the high-impact class. These results suggest that substantial impacts on Greater Sage-Grouse must be acknowledged for oil and gas development in or near the bird’s breeding habitat, a conclusion that is supported by the findings of a report recently released by the wildlife agencies of five western states (Colorado Department of Wildlife et al. 2008).

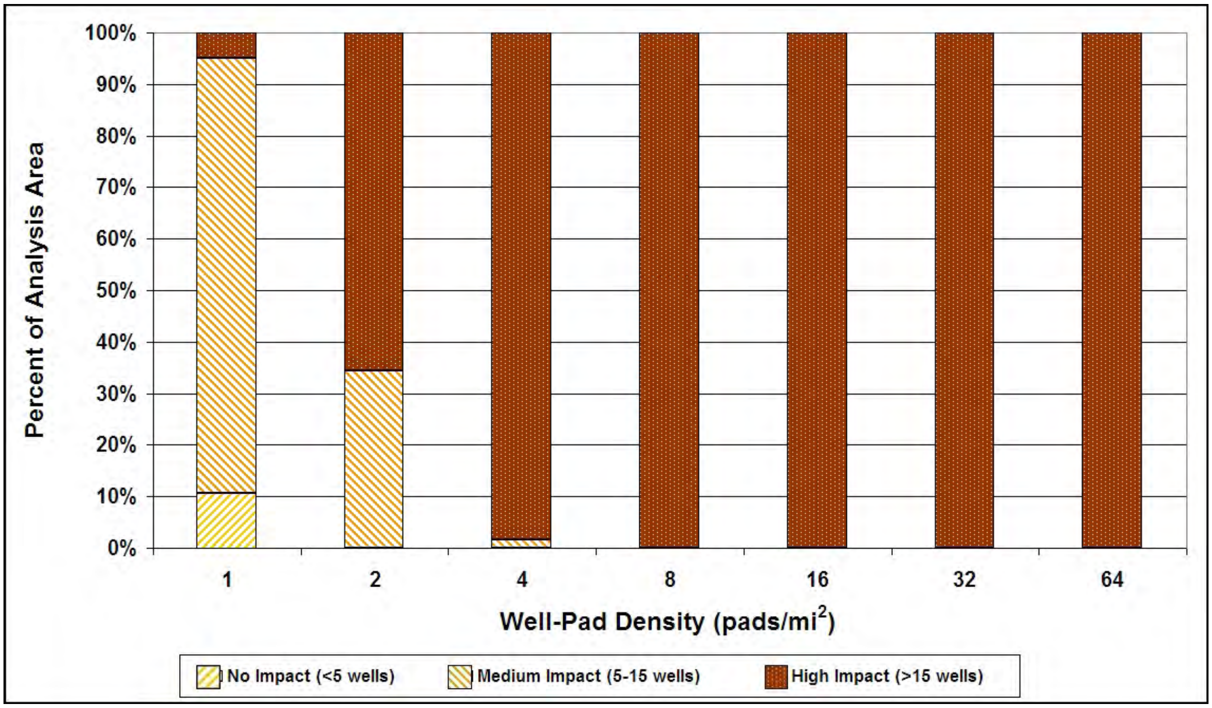


Figure 11. Distribution of Analysis Area Among Three Sage-Grouse Lek Impact Classes Identified by Holloran (2005) This analysis (based on Holloran 2005) of the number of well pads within 1.9 miles of a possible Greater Sage-Grouse lek shows that even the lowest oil and gas development densities are likely to have significant impact on lek attendance. It is important to note that, because Holloran's study considered the number of actual wells, and our analysis considers well pads, our measure of impact will be an underestimate when pads contain more than one well.

## CONCLUSIONS AND RECOMMENDATIONS FOR OIL AND GAS MANAGEMENT PLANNING

### Conclusions

The following conclusions arising from our analysis have direct implications for management planning for oil and gas development:

1. **Substantial scientific research is available indicating that the roads, well pads, and associated activities cause direct, indirect, and cumulative impacts on wildlife.**
   Indicators of indirect and cumulative impacts of development on wildlife and habitat can and should be collected from a survey of scientific literature relevant to species found in the resource planning area. There is abundant evidence in peer reviewed literature of negative impacts from roads and well pads, including reductions in particular wildlife functions (e.g., breeding, foraging), reductions in overall habitat use or effectiveness, and complete abandonment of habitat. Sufficient research may not yet be available to provide detailed wildlife response models for all species for different road densities or distance-to-nearest-road-or-well-pad values. However, there are adequate indicator values for specific metrics for many wildlife species, including key species of concern for the BLM, to allow the agency to assess threats from oil and gas development.

2. **Landscape analysis using GIS is necessary to take advantage of the best science regarding indicators of direct, indirect, and cumulative impacts.**

   Because the discussion of indirect and cumulative impacts due to roads and well pads is by its very nature spatial, it requires a means of analysis that can incorporate spatial measures such as (but not limited to) road density or distance to nearest road or well pad. Because GIS technology is readily available and is not costly to use, GIS analysis is an accessible way of meeting this requirement.

3. **Habitat fragmentation and negative impacts on wildlife occur at low well-pad densities and increase most rapidly at low well-pad densities.**

   Based on scientific literature, road density and distance-to-nearest-road-or-well-pad values indicating potential negative impacts on wildlife can be reached quickly, at relatively low oil and gas development densities. Looking at the wildlife indicator values presented in this document (Table 1) and many others in the biological literature, along with the graphs in Figures 7 and 10, it is apparent that significant negative effects on wildlife occur over a substantial portion of a landscape even at the lower well-pad densities characteristic of the early stages of development in a gas or oil field. Further, the rate at which road density increases and distance to nearest road or well pad decreases is higher at lower well-pad densities than at higher densities (Figures 6 and 9). This suggests that landscape-level planning for infrastructure development and analysis of wildlife impacts need to be done prior to initial development of a field. Where development has already occurred, the existing impacts on local wildlife species must be measured and acknowledged, and the cumulative impacts from additional development must be assessed.

   The fact that wildlife impacts for some species occur over a substantial portion of a landscape at low well-pad densities suggests that portions of a landscape that contain habitat for threatened and endangered species, unique habitats, species valued for hunting and recreational pursuits, and other species of concern should remain free from oil and gas development.

4. **The charts and numeric results of our sample analysis, together with relevant indicator values in the biological literature, can help guide the BLM, but they are no substitute for site-specific analyses.**

   The graphs in Figures 7, 10, and 11 may be used to estimate the minimum percent of a landscape reaching a given indicator value from the biological literature at a given level of development. The cumulative area distribution curves in Figure 7 give the percent of a landscape at or below any given road-density value for each well-pad density. The cumulative area distribution curves in Figure 10 give the percent of a landscape beyond any given distance-to-nearest-road-or-well-pad value for each well-pad density.

   For a view of how these curves might be used in management planning, consider a situation where a BLM planning alternative proposes a well-pad density of one pad per 160 acres and the latest biological literature suggests that habitat use by a species of concern in the development area declines by 50 percent at road densities above one mile per square mile. Placing a vertical line at one mile per square mile on the graph in Figure 7 allows

BLM staff to estimate that under this alternative no more than 15 percent of the development area will provide habitat exhibiting less than a 50 percent decline in use by that species. If Greater Sage-Grouse are present in the planning area, Figure 11 suggests (based on research by Holloran 2005) that the one pad per 160 acres alternative will result in highly detrimental impacts for this species over 98 percent of the planning area. These same figures can also be used to estimate habitat fragmentation impacts for other indicator values reported in the scientific literature. Their value lies in their ability to provide a quick, preliminary estimate of the magnitude of habitat fragmentation impacts for potential development alternatives. Complete spatial analyses of the specific landscape for which oil and gas development plans are being made must still be done using techniques such as those we suggest above in order to help develop and evaluate the alternatives finally proposed.

## Recommendations

By applying the methodology and assessing the fragmentation metrics we have described here, the BLM can better fulfill its obligations to evaluate the direct, indirect, and cumulative impacts of various management alternatives. Therefore, we formally request that the following actions be taken for any NEPA analysis of impacts from proposed oil and gas development:

1. **Conduct a spatial analysis of the direct, indirect, and cumulative impacts on wildlife of all proposed oil and gas development alternatives.**

   This step is necessary to demonstrate the use of the best available science and fulfill the BLM's legal obligations in evaluating alternatives in a draft resource management plan and draft EIS. The best available GIS data layers for wildlife habitat boundaries and status information for species potentially threatened by oil and gas development should be assembled. The latest biological literature on the impacts of road networks, oil and gas infrastructure, and related activities on local species should be collected. All infrastructure elements proposed or reasonably anticipated under each management alternative should be considered, and their combined impact on wildlife and habitat assessed. A spatial development simulation should be generated for the entire planning unit for each development alternative. These should incorporate, spatially and quantitatively, all existing and proposed infrastructure to accurately represent the construction of elements from the Reasonably Foreseeable Development Scenario (RFD) and the particular plan alternative. The analysis should yield the location and acreage or percent area where selected species of concern could be adversely affected by oil and gas development (with maps if possible). The results of this analysis should be reflected in each management alternative in the draft management plan and draft EIS, and reflect indirect and cumulative impacts in addition to direct surface disturbance. Efforts should be made to craft and select management plan alternatives that minimize the acreage of the planning area likely to experience direct, indirect, and cumulative impacts based on these results. The graphs and charts in this document (and included in Appendix A) can be used to help shape proposed alternatives and focus the analysis of them, but they cannot take the place of those analyses.

2. **Assess the habitat fragmentation effects of oil and gas development for maximum well-pad development densities.**

It is not uncommon for oil and gas field development to proceed much faster than the BLM anticipates, and for well and/or pad densities to quickly exceed those assessed during planning processes. A full range of development densities should be included in the EIS so that fragmentation effects are fully anticipated, understood, and controlled.

3. **Include oil and gas field development options that leave areas of threatened habitats undeveloped.**
   Because our results indicate that substantial impacts occur even at lower levels of oil and gas development, the BLM needs to consider means for leaving important wildlife habitat undeveloped. Clearly one option is to prescribe no surface occupancy (NSO) in particularly rare or sensitive habitat areas. Other management options available to the BLM include directional drilling to allow access to areas of NSO from adjacent lands. Phased development and cluster development, singly or in combination, can be implemented to allow some areas to be developed intensely while other areas are temporarily left undeveloped. This requires strict guidelines that prevent additional development until after the original development area has been reclaimed, keeping a specific portion of the landscape in large undeveloped patches and development clustered in limited areas.
4. **Conduct landscape-scale analyses to evaluate impacts and provide sound ecological protection for a landscape's wildlife, habitat, and other ecological resources.**
   The importance and complexity of using the best available science to plan at the landscape scale is increasingly recognized by scientists (Leitao and Ahern 2002, Szaro et al. 2005, Noss 2007). Many ecological functions such as the seasonal migrations of wildlife, connectivity required to prevent genetic isolation, and natural disturbances affecting wildlife habitat occur across broad landscapes. Indicators of wildlife impacts are spatial in nature and should be considered in a landscape context. Consequently, decision-making about oil and gas development and conservation of natural resources must be made at the landscape scale using spatial analysis of projected well-pad densities and other field development infrastructure.
5. **Use GIS technology to evaluate the impacts of oil and gas development on wildlife.**
   GIS is the best approach for this analysis because it is readily available and not costly. The analyses of direct, indirect, and cumulative impacts described above can be done with ArcGIS software that is already standard within the BLM and with its contractors. As mentioned earlier in this document, GIS is, in fact, already being used by the BLM for impact assessment in some locations (e.g., Las Cruces District, New Mexico). The automated placement of well pads (or other structures) in the simulation of step-wise development of oil and gas fields requires an ArcGIS software extension (CommunityViz) that is beginning to be used in some BLM offices. The GIS analyses suggested in this document are straightforward and do not require advanced modeling or scripting skills; further, the GIS data required for these analyses are already in the possession of most BLM offices. A modest investment of time (a tiny fraction of the total resources invested in BLM resource management plans) in carrying out these GIS analyses could substantially improve the NEPA compliance of resource management plans involving oil and gas development.
6. **Use landscape analysis techniques to improve public engagement.**
   In addition to helping the BLM meet its legal requirements under FLPMA, NEPA, and the Data Quality Act to use

the best available data and science, landscape analysis improves the ability of many constituencies and stakeholders to understand and engage in the land management planning process. The GIS inputs and results can be mapped to graphically illustrate an area's existing resources and threats to those resources under different management alternatives. For instance, maps can be made that display data on the location of elk critical winter range overlaying data showing where road density thresholds for significant impacts on elk will be exceeded under different management alternatives.

7. **Encourage research on habitat fragmentation indicators for wildlife of local importance.**
   Because of its authority over oil and gas management actions and the need for increased scientific understanding of wildlife responses to roads, well pads, and related infrastructure, the BLM should encourage field research monitoring the impacts of these on wildlife by wildlife agencies and research institutions.

## REFERENCES

Berger, J., K.M. Berger, and J.P. Beckmann. 2006. *Wildlife and Energy Development: Pronghorn of the Upper Green River Basin – Year 1 Summary*. Wildlife Conservation Society, Bronx, NY. Available at: http://www.wcs.org/media/file/Shell%20Year%201%20Progress%20REVISED%20III.pdf.

Braun, C.E. 2006. *Sage-grouse Habitat Conservation Strategies: A Blueprint for Conservation and Recovery*. Grouse Inc., Tucson, AZ.

Bureau of Land Management. 1999. *Draft EIS for the Pinedale Anticline Oil and Gas Exploration and Development Project, Sublette County, WY.* U.S. Department of the Interior, Bureau of Land Management, Pinedale Field Office, Pinedale, WY.

Colorado Department of Wildlife, Montana Department of Fish, Wildlife and Parks, North Dakota Game and Fish, Utah Division of Wildlife Resources, and Wyoming Game and Fish Department. 2008. *Using the Best Available Science to Coordinate Conservation Actions that Benefit Greater Sage-Grouse Across States Affected by Oil & Gas Development in Management Zones I-II (Colorado, Montana, North Dakota, South Dakota, Utah, and Wyoming)*. (Unpublished report, available at http://www.ourpubliclands.org/files/upload/BestScience_2008_sagegrouse_energy.pdf.)

Colorado Greater Sage-Grouse Conservation Plan Steering Committee. 2008. *Colorado Greater Sage-grouse Conservation Plan*. Colorado Division of Wildlife, Denver, Colorado. (Unpublished report.)

Confluence Consulting. 2005. *Annotated Bibliography of Potential Impacts of Gas and Oil Exploration and Development on Coldwater Fisheries*. Prepared by Confluence Consulting, Inc., for Trout Unlimited, Bozeman, MT.

Freddy, D.J., W.M. Bronaugh, and M.C. Fowler. 1986. Responses of mule deer to disturbance by persons afoot and snowmobiles. *Wildlife Society Bulletin* 14:63-68.

Gaines, W., P. Singleton, and R. Ross. 2003. *Assessing the Cumulative Effects of Linear Recreation Routes on Wildlife Habitats on the Okanogan and Wenatchee National Forests*. General Technical Report PNW-GTR-586. U.S. Department of Agriculture, U.S. Forest Service, Pacific Northwest Research Station, Portland, OR.

Gucinski, H., J.J. Furniss, R.R. Ziemer, and M.H. Brookes. 2001. *Forest Roads: A Synthesis of Scientific Information*. General Technical Report PNW-GTR-509. U.S. Department of Agriculture, U.S. Forest Service, Pacific Northwest Research Station, Portland, OR.

Holloran, M.J. 2005. *Greater Sage-Grouse (*Centrocercus urophasianus*) Population Response to Natural Gas Field Development in Western Wyoming*. Doctoral Dissertation, University of Wyoming, Laramie, WY.

Ingelfinger, F. 2001. *The Effects of Natural Gas Development on Sagebrush Steppe Passerines in Sublette County, Wyoming*. M.Sc. Thesis, University of Wyoming, Laramie, WY.

Lehmkuhl, J.F., and L.F. Ruggiero. 1991. Forest fragmentation in the Pacific Northwest and its potential effects on wildlife. Pages 35-46 in: Ruggiero, L.F., K.B. Aubry, A.B. Carey, and M.H. Huff, Tech. Coords. *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. General Technical Report PNW-GTR-285. U.S. Department of Agriculture, U.S. Forest Service, Pacific Northwest Research Station, Portland, OR.

Leitao, A.B., and J. Ahern. 2002. Applying landscape ecological concepts and metrics in sustainable landscape planning. *Landscape and Urban Planning* 59:65-93.

Lyon, L.J. 1979. Habitat effectiveness for elk as influenced by roads and cover. *Journal of Forestry* 77:658-660.

McGarigal, K., and B. J. Marks. 1995. *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure*. General Technical Report PNW-351. U.S. Department of Agriculture, U.S. Forest Service, Pacific Northwest Research Station, Portland, OR.

Naugle, D.E., B.L. Walker, and K.E. Doherty. 2006. *Sage-Grouse Population Response to Coal-Bed Natural Gas Development in the Powder River Basin: Interim Progress Report on Region-wide Lek-Count Analysis*. University of Montana, Bozeman, MT.

New Mexico Department of Game and Fish. 2005. *Habitat Fragmentation and the Effects of Roads on Wildlife and Habitats*. Available at http://www.wildlife.state.nm.us/conservation/habitat_handbook/documents/2004EffectsofRoadsonWildlifeandHabitats.pdf.

Northwest Colorado Greater Sage-Grouse Working Group. 2006. *Northwest Colorado Greater Sage-Grouse Conservation Plan*.

Noss, R.G. 2007. Conservation thresholds: Overview and commentary. Pages 1-12 in: R. Kihslinger and J. Wilkinson, eds. *Lasting Landscapes: Reflections on the Role of Conservation Science in Lands Use Planning*. Environmental Law Institute, Washington, D.C.

Ockenfels, R.A., A. Alexander, C.L. Dorothy Ticer, and W.K. Carrel. 1994. *Home Range Movement Patterns and Habitat Selection of Pronghorn in Central Arizona*. Technical Report 13. Arizona Game and Fish Department, Phoenix, AZ.

Papouchis, C.M., F.J. Singer, and W.B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. *Journal of Wildlife Management* 65(3):573-582.

Rost, G.R., and J.A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management* 43(3):634-641.

Sawyer, H., R. Nielson, F. Lindzey, and L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396-403.

Stiver, S.J., A.D. Apa, J.R. Bohne, S.D. Bunnell, P.A. Deibert, S.C. Gardner, M.A. Hilliard, C.W. McCarthy, and M.A. Schroeder. 2006. *Greater Sage-Grouse Comprehensive Conservation Strategy*. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming. (Unpublished report.)

Szaro, R.C., D.A. Boyce, and T. Puchlerz. 2005. The challenges associated with developing science-based landscape scale management plans. *Landscape and Urban Planning* 72:3-12.

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

Thomson, J.L., N.W. Culver, P.C. Aengst, and T.S. Schaub, 2005. *Wildlife at a Crossroads: Energy Development in Western Wyoming.* The Wilderness Society, Washington, D.C. Trombulak, S.C., and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18-30.

Wilcove, D.S. 1987. From fragmentation to extinction. *Natural Areas Journal* 7:23-29.

Wisdom, M.J., N.J. Cimon, B.K. Johnson, E.O. Garton, and J.W. Thomas. 2004a. Spatial partitioning by mule deer and elk in relation to traffic. *Transactions of the North American Wildlife and Natural Resources Conference* 69:509-530.

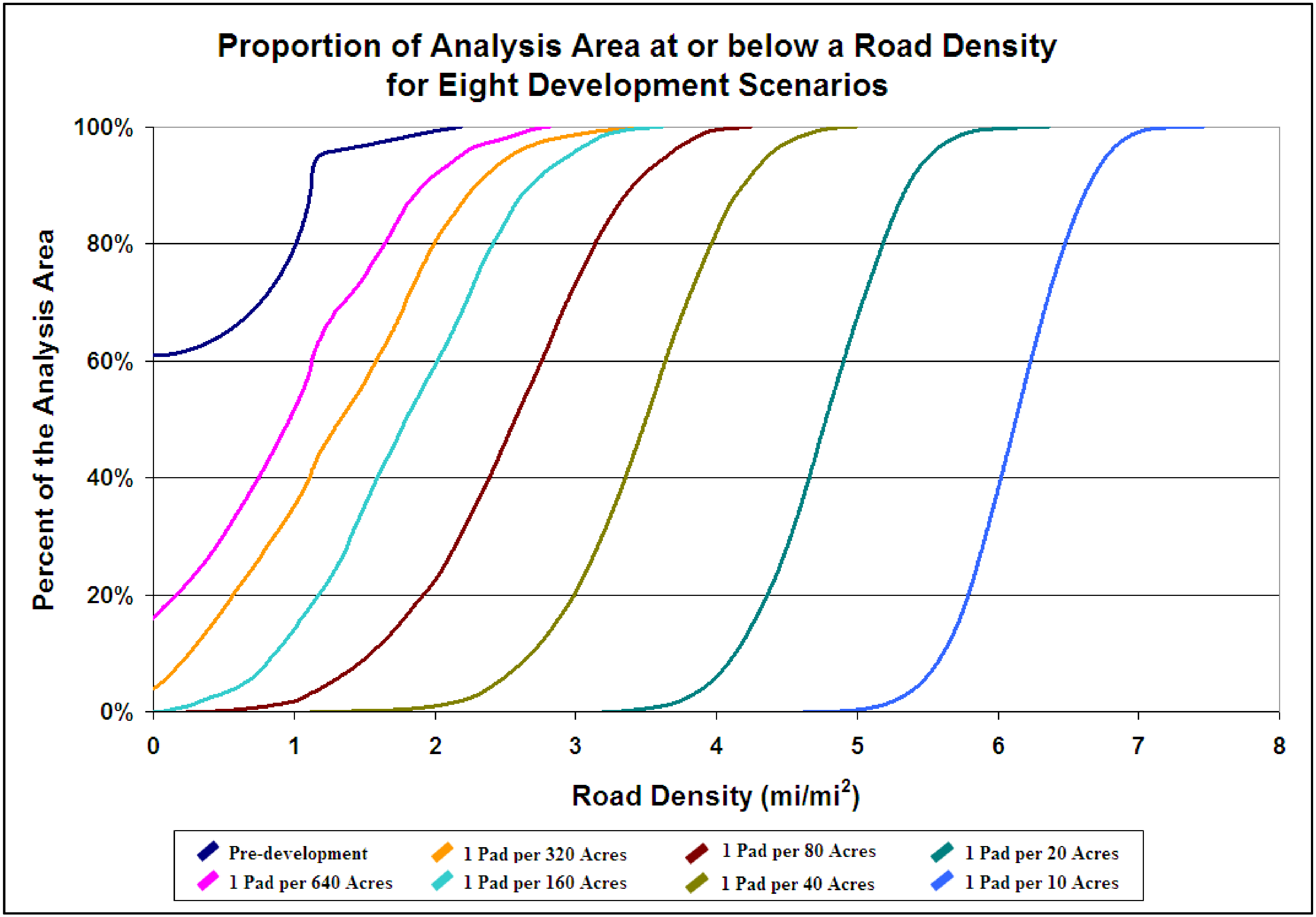
Wisdom, M.J., A.A. Ager, H.K. Preisler, N.Cimon, and B.K. Johnson. 2004b. Effects of offroad recreation on mule deer and elk. *Transactions of the North American Wildlife and Natural Resources Conference* 69:531-550.

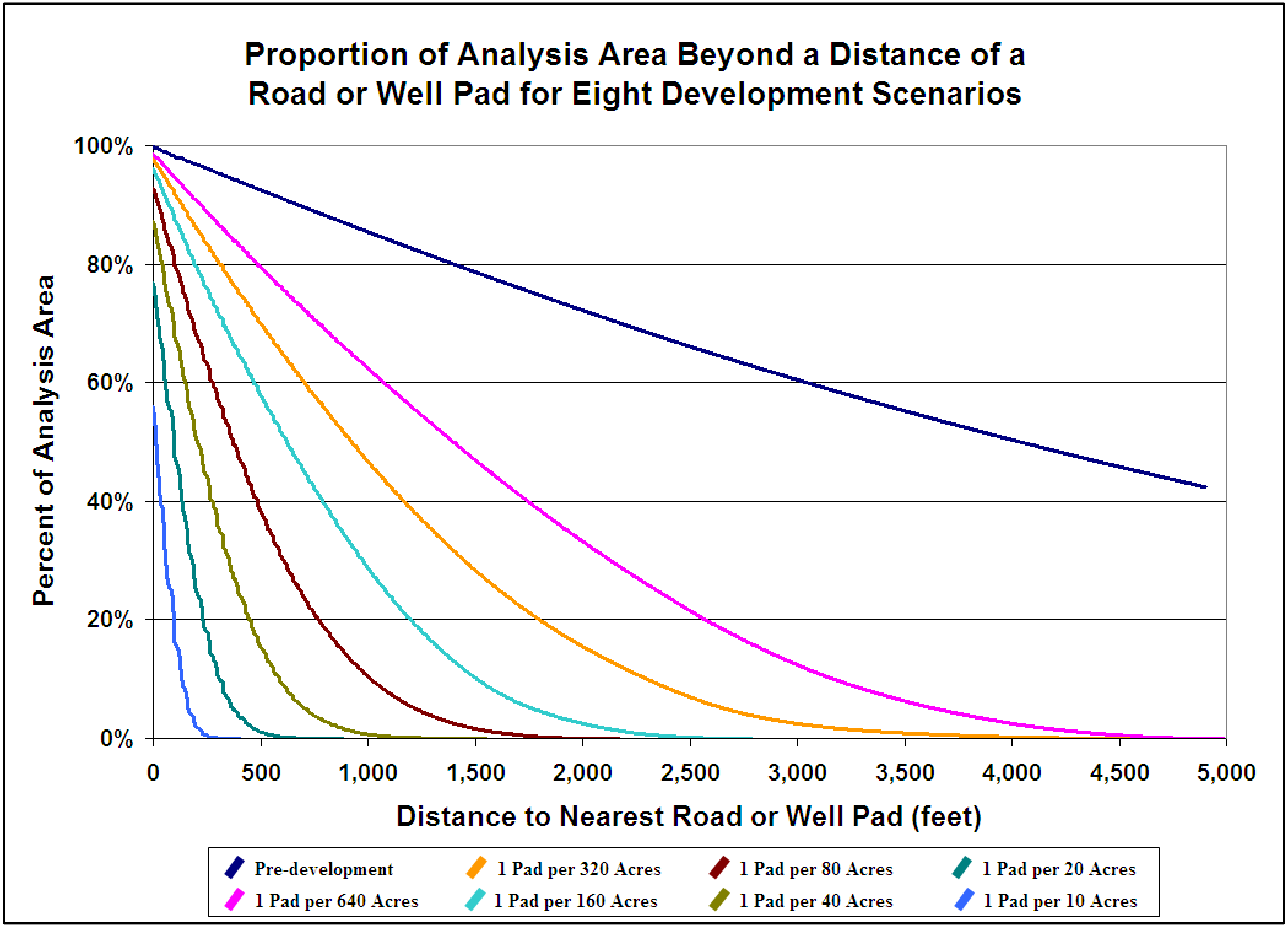
Wyoming Game and Fish Department. 2004. *Recommendations for Development of Oil and Gas Resources within Crucial and Important Wildlife Habitat: A Strategy for Managing Energy Development Consistently with the FLPMA Principles of Multiple Use and Sustained Yield.* Available at http://gf.state.wy.us/downloads/pdf/og.pdf.

# APPENDIX A: GRAPHICAL TOOLS FOR PRELIMINARY LANDSCAPE ANALYSIS

This appendix provides copies of the cumulative area distribution graphs for road density and distance to nearest road or well pad for eight common oil and gas development densities (originally presented in Figures 7 and 10 respectively). These graphs are intended to be used to plot indicator values found through a literature review for wildlife species in a planned oil and gas development area. The first graph allows the user to estimate what percent of the landscape has road density lower than a road-density indicator value found in the biological literature—the portion of the landscape likely to remain unaffected (or less affected) by a given level of development. The second graph allows the user to determine what percent of the landscape is farther from the nearest road or well pad than a distance-to-nearest-road indicator value—the portion of the landscape likely to remain unaffected (or less affected) by a given level of development.

As stated in the main body of this document, the value of these graphs lies in their utility as a coarse screen that can give a quick sense of the magnitude of habitat fragmentation impacts for potential development alternatives. Complete spatial analyses of the specific landscape for which oil and gas development plans are being made must still be done using techniques such as those we suggest in the main text in order to help develop and evaluate the alternatives finally proposed.


Proportion of Analysis Area at or below a Road Density
for Eight Development Scenarios
Percent of the Analysis Area
100%
80%
60%
40%
20%
0%
0
1
2
3
4
5
6
7
8
Road Density (mi/mi$^2$)
Pre-development
1 Pad per 640 Acres
1 Pad per 320 Acres
1 Pad per 160 Acres
1 Pad per 80 Acres
1 Pad per 40 Acres
1 Pad per 20 Acres
1 Pad per 10 Acres


Proportion of Analysis Area Beyond a Distance of a Road or Well Pad for Eight Development Scenarios
Percent of Analysis Area
100%
80%
60%
40%
20%
0%
0
500
1,000
1,500
2,000
2,500
3,000
3,500
4,000
4,500
5,000
Distance to Nearest Road or Well Pad (feet)
Pre-development
1 Pad per 640 Acres
1 Pad per 320 Acres
1 Pad per 160 Acres
1 Pad per 80 Acres
1 Pad per 40 Acres
1 Pad per 20 Acres
1 Pad per 10 Acres

Forest Ecology and Management 411 (2018) 223–233

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Elk responses to trail-based recreation on public forests

Michael J. Wisdom[a,*], Haiganoush K. Preisler[b], Leslie M. Naylor[c,1], Robert G. Anthony[d,2], Bruce K. Johnson[e], Mary M. Rowland[a]

[a] *USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, OR 97850, USA*
[b] *USDA Forest Service, Pacific Southwest Research Station, 800 Buchanan Street West Annex, Albany, CA 94710, USA*
[c] *Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA*
[d] *Oregon Cooperative Fish & Wildlife Research Unit, Department of Fisheries & Wildlife, Oregon State University, Corvallis, OR 97331, USA*
[e] *Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA*

## ARTICLE INFO

*Keywords:*
All-terrain vehicles
ATV riding
Elk
Forest roads
Hiking
Horseback riding
Mountain biking
Motorized traffic
Off-highway vehicles
Public forests
Recreation
Recreation trails
Road avoidance
Roads

## ABSTRACT

Trail-based recreation is a popular use of public forests in the United States, and four types are common: all-terrain vehicle (ATV) riding, mountain biking, hiking, and horseback riding. Effects on wildlife, however, are controversial and often a topic of land use debates. Accordingly, we studied trail-based recreation effects on elk (*Cervus canadensis*), a wide-ranging North American ungulate highly sought for hunting and viewing on public forests, but that is sensitive to human activities, particularly to motorized traffic on forest roads. We hypothesized that elk would respond to trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. We evaluated elk responses using a manipulative landscape experiment in a 1453-ha enclosure on public forest in northeast Oregon. A given type of recreation was randomly selected and implemented twice daily along 32 km of designated recreation trails over a five-day period, followed by a nine-day control period of no human activity. Paired treatment and control replicates were repeated three times per year for each recreation type during spring-fall, 2003–2004. During treatments, locations of elk and recreationists were simultaneously collected with telemetry units. Elk locations also were collected during control periods. Elk avoided the trails during recreation treatments, shifting distribution farther out of view and to areas farthest from trails. Elk shifted distribution back toward trails during control periods of no human activity. Elk avoided recreationists in real time, with mean minimum separation distances from humans that varied from 558 to 879 m among the four treatments, 2–4 times farther than elk distances from trails during recreation. Separation distances maintained by elk from recreationists also were 3–5 times farther than mean distances at which elk could be viewed from trails. Distances between elk and recreationists were highest during ATV riding, lowest and similar during hiking and horseback riding, and intermediate during mountain biking. Our results support the hypothesis that elk avoid trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. Forest managers can use results to help optimize trade-offs between competing objectives for trail-based recreation and wildlife species like elk that are sensitive to human activities on public forests.

## 1. Introduction

Trail-based recreation is common on public forests in the United States, and four types are especially popular: all-terrain vehicle (ATV) riding, mountain biking, hiking, and horseback riding (Cordell, 2012). ATV riding, in particular, has increased rapidly. The number of off-highway vehicle (OHV) riders reached 36 million in the early 2000s (Cordell, 2012), and is projected to increase ~30–60% (to 62–75 million participants) by 2060 (Bowker et al., 2012). Increasing ATV use has prompted concerns about effects on wildlife (Proescholdt, 2007; Tarr et al., 2010; Webb and Wilshire, 2012), which include distribution shifts of populations away from trails; increased flight responses, movement rates and energetic costs; reduced foraging times; and reduced carrying capacity from cumulative effects (Havlick, 2002; Brillinger et al., 2004, 2011; Wisdom et al., 2004a; Preisler et al., 2006, 2013; Naylor et al., 2009; Ciuti et al., 2012).

---

* Corresponding author.

*E-mail addresses:* mwisdom@fs.fed.us (M.J. Wisdom), hpreisler@fs.fed.us (H.K. Preisler), lesnaylor@ctuir.org (L.M. Naylor), bruce.k.johnson1@state.or.us (B.K. Johnson), mrowland@fs.fed.us (M.M. Rowland).

[1] Current address: Confederated Tribes of the Umatilla Indian Reservation, Department of Natural Resources, Agricultural Service Center, Room 2, 10507 North McAlister Road, Island City, OR 97850, USA.

[2] Deceased.

https://doi.org/10.1016/j.foreco.2018.01.032
Received 29 November 2017; Received in revised form 19 January 2018; Accepted 19 January 2018
0378-1127/ Published by Elsevier B.V.

Mountain biking, hiking, and horseback riding also are popular uses of public lands in the United States (Cordell, 2012), and all three activities are among those projected to increase most in per capita participation by 2060 (Bowker et al., 2012). Mountain biking, in particular, is growing rapidly, with an increase in users of 22% from 2006 to 2015 (The Outdoor Foundation, 2016). In 2006, cycling (road and mountain biking) was the fourth-most popular recreational activity in the United States, behind fishing, camping, and running (Cordell, 2012); mountain biking had > 820 million user days in 2008 (Cordell, 2012).

In contrast to ATV riding, non-motorized forms of trail-based recreation often are considered benign by recreationists (Taylor and Knight, 2003a; Larson et al., 2016), but current knowledge indicates otherwise (Green and Higginbottom, 2000; Leung and Marion, 2000; Newsome and Moore, 2008; Naylor et al., 2009; Ciuti et al., 2012; Larson et al., 2016; Hennings and Soll, 2017). Effects on wildlife are similar to those of ATV riding (e.g., population displacement away from trails, Larson et al., 2016), but ATVs likely have more pronounced negative effects because of high levels of speed and noise and thus affect more area per unit time (Lovich and Bainbridge, 1999; Wisdom et al., 2004a; Proescholdt, 2007; Naylor et al., 2009; Ciuti et al., 2012; Preisler et al., 2013). Motorized uses like ATV riding thus are more likely to have a greater impact than non-motorized recreation on wide-ranging mammals whose large home ranges put them in more frequent contact with the larger ranges and spatial influence of motorized riders (Wisdom et al., 2004a; Ciuti et al., 2012; Beyer et al., 2013).

Concerns about ATV use and the more general effects of motorized traffic on wildlife and other natural resources prompted the USDA Forest Service to revise its policy regarding motorized travel management on National Forests in 2005. A new regulation that year required that all roads, trails, and areas open to motorized use be formally designated to better manage vehicle traffic and prevent resource damage (USDA Forest Service, 2004; Federal Register, 2005; Adams and McCool, 2009). This change in policy acknowledged a variety of negative effects from unmanaged motorized uses, especially OHVs, whose numbers had been increasing steadily on National Forests (Cordell, 2005; Federal Register, 2005). Similar changes in policy have occurred on state-managed forests in response to negative effects of OHVs (Asah et al., 2012a, 2012b).

Despite the changes in public forest policy that occurred over a decade ago, current knowledge of both motorized and non-motorized recreation is not well-developed regarding the extent and intensity of effects at most spatial and temporal scales meaningful to wildlife populations (Gutzwiller et al., 2017). Wisdom et al. (2004a), Preisler et al. (2006, 2013), and Naylor et al. (2009) addressed some of these knowledge voids with their ungulate research in northeast Oregon, United States, and Ciuti et al. (2012) conducted a similar study in Alberta, Canada. Replication elsewhere and for many wildlife species, however, is lacking. Knowledge voids have likely contributed to ongoing public debate about recreational uses on public forests, particularly ATV riding (Asah et al., 2012a, 2012b). Public comments on National Forest travel management plans have been diverse and contentious (Yankoviak, 2005; Thompson, 2007), reflecting strong societal views in the face of limited knowledge and perceptions of overly restrictive federal policies (Adams and McCool, 2009).

In response to these issues, we studied effects of trail-based recreation on elk (*Cervus canadensis*), a wide-ranging North American ungulate highly sought for hunting and viewing on public forests, but that is sensitive to human activities, particularly to motorized traffic on forest roads (e.g., Lyon, 1983; Cole et al., 1997, 2004; Rowland et al., 2000, 2004; Frair et al., 2008; Montgomery et al., 2012, 2013; Prokopenko et al., 2016). We hypothesized that populations of elk would avoid trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests during non-hunting periods of late spring through early fall. We further hypothesized that avoidance would occur at distances that allow elk to stay out of view of recreationists, and that avoidance would be strongest in response to motorized recreation (ATV riding).

We tested our hypotheses by evaluating behavioral responses of elk to trail-based recreation using a manipulative landscape experiment in a 1453-ha enclosure on public forest in northeast Oregon. We had 2 objectives: (1) to document the degree of elk avoidance of trails during each recreation activity, compared to control periods of no activity; and (2) to evaluate direct, real-time responses of elk to recreationists during each type of recreation. We estimated distances between elk and the trails during recreation activities, and in real time between elk and recreationists based on simultaneous collection of telemetry locations of animals and humans. We provided context for interpreting results by estimating the distances at which elk could be viewed from the trails, per our hypothesis that avoidance occurs at distances that allow elk to hide from view. We also characterized differences in spatial distributions of elk during each type of recreation treatment versus paired control periods when no humans were present.

Research was conducted with approval and guidance by the Starkey Institutional Animal Care and Use Committee (IACUC 92-F-0004), as required by the United States Animal Welfare Act of 1985. We followed protocols established by the IACUC for conducting ungulate research at the Starkey Experimental Forest and Range (Wisdom et al., 1993).

## 2. Materials and methods

### 2.1. Study area

Research was conducted from April-October 2003–2004 at the USDA Forest Service Starkey Experimental Forest and Range (Starkey), 35 km southwest of La Grande in northeast Oregon, USA (Fig. 1A). In 1987, approximately 10,125 ha of elk summer range within Starkey were enclosed with a 2.4 m (8-foot) elk-proof fence for long-term ungulate research (Rowland et al., 1997; Wisdom, 2005). Our study was conducted in the 1453-ha Northeast Study Area (Fig. 1A), which is separated from Starkey's other study areas by elk-proof fence (Wisdom et al., 2005). The Northeast Study Area is further subdivided by elk-proof fence into 2 pastures, East (842 ha) and West (610 ha) (Stewart et al., 2005). Approximately 98 elk occupied the East Pasture (69 adult females, 16 calves, and 13 adult males) and 25 occupied the West Pasture (18 adult females, 2 calves, and 5 adult males). Elk were last hunted in the study area in 1996 as part of a rifle hunt of males to evaluate their responses to motorized versus non-motorized hunting access (Wisdom et al., 2004b). Our research did not include hunting and focused on the non-hunting periods of late spring through early fall.

Approximately 70% of the area was forested, arranged in a mosaic of patches interspersed with thin-soiled grasslands. Forested areas were composed of dry or mixed conifer types common to the interior western United States (Wisdom et al., 2005). Dominant tree species included Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*). Approximately 50% of the forest types underwent commercial timber harvest from 1992 to 1994 that included clearcutting, seed tree, and shelterwood prescriptions applied as small (1–22 ha) harvest units interspersed with untreated stands (Wisdom et al., 2004b). Regeneration cuts established a mosaic of open and closed forest structural conditions, interspersed with the less common open grasslands (Wisdom, 2004b). Rowland et al.,(1997), Stewart et al. (2005), Wisdom (2005), and Naylor et al. (2009) provide details about the study area and past research.

### 2.2. Data collection

#### 2.2.1. Recreation treatments and locations of recreationists

We implemented ATV riding, mountain biking, hiking, and horseback riding as four separate types of recreation treatments to which elk responses were evaluated during spring-fall, 2003–2004. A given

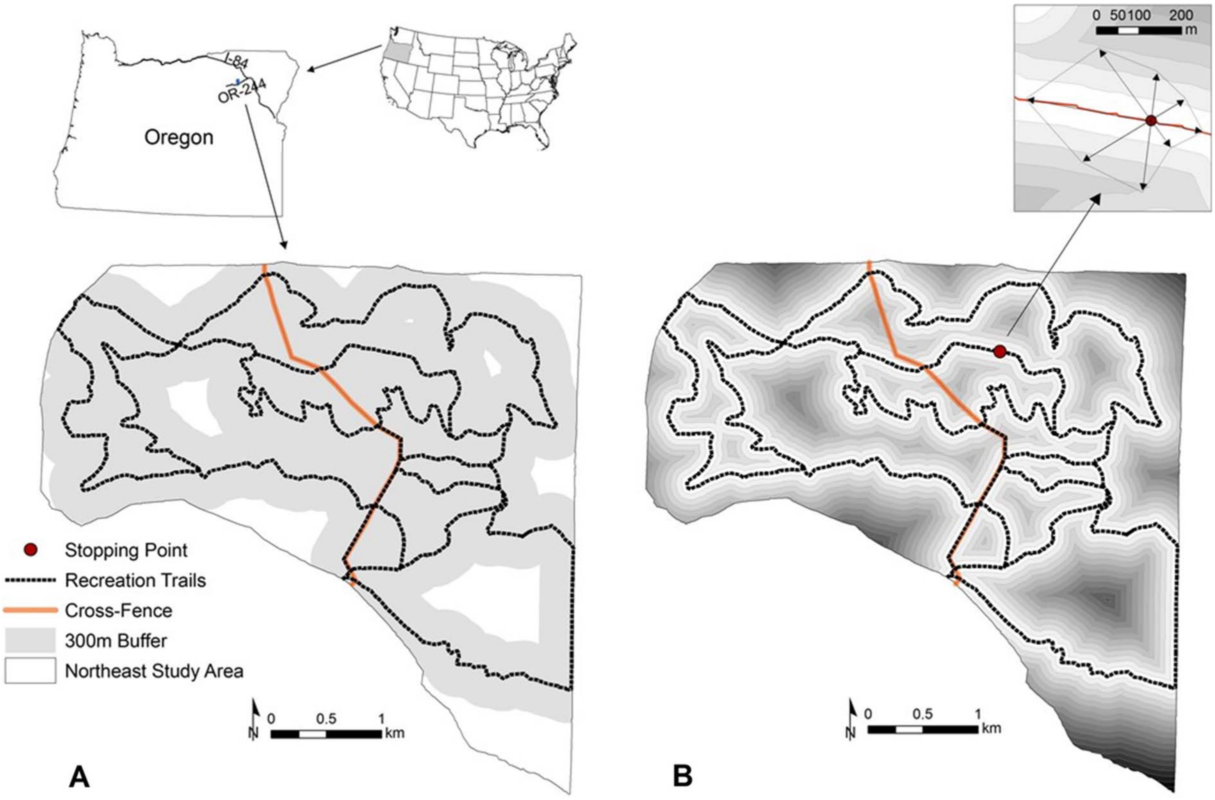


**Fig. 1.** Location of the 1453-ha Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA, with 32 km of recreation trails on which four recreation treatments were evaluated during 2003–2004 (A). Viewing distances were estimated in eight cardinal directions at sampling points every 0.2 km along trails (upper right, B), and 50-m distance intervals from the trails were mapped to estimate the percentage of study area in relation to viewing distances and elk locations (B).

treatment type was implemented over a five-day period, followed by nine days of control, during which no human activity occurred in the study area. Each pair of treatment and control replicates was applied three times/year for each of the four types of recreation (12 total treatment–control periods annually, 24 for the two years), with the order of treatment type randomly assigned. During each five-day period, the assigned treatment was implemented along 32 km of recreation trails that followed old road beds and trails typically used by recreationists on public forests (Fig. 1A) (Wisdom et al. 2004a). An initial two-week control period was implemented each year before treatments began.

Treatments were implemented by recreationists who traveled the trails once each morning (0800–1159 h local time) and afternoon (1200–1600 h local time) while carrying global positioning system (GPS) units to record their locations. Coverage of the 32 km of trails on a given morning or afternoon required one group of ATV riders or mountain bikers, two groups of hikers, and three groups of horseback riders because of differences in recreation speeds (Wisdom, unpublished data; see Section 4). Each of the two groups of hikers traversed one-half of the trails, and each of the three groups of horseback riders rode one-third. This design resulted in the same spatial coverage of recreationists on trails, and exposure of elk to recreationists, each morning and afternoon, but with different rates of speed (Naylor, 2006; see Section 4).

Each treatment followed a “tangential” experimental approach in which recreationists did not directly target or pursue elk, but remained along the pre-determined trails (Taylor and Knight, 2003b). Recreationists followed explicit instructions regarding these methods of implementing the treatments. See Naylor et al. (2009) for additional details about design and implementation of the treatments.

GPS units (Trimble 3C, Trimble, Inc.) worn by recreationists collected human locations continuously (every second). Mean spatial error of GPS locations was < 10 m, based on distances measured in ArcGIS (ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, CA) between the plotted locations of recreationists and the geo-referenced location of the recreation trails (Wisdom, unpublished data).

### 2.2.2. *Telemetry locations of elk*

We used long-range aid to navigation (LORAN-C) and GPS telemetry (Johnson et al., 1998; Hansen and Riggs, 2008) to evaluate responses of 35 telemetered adult female elk to the four types of recreation. Telemetry locations were collected throughout each five-day treatment and paired nine-day control.

Telemetry collars were programmed to obtain one location/telemetered elk every 10 and 30 min under the LORAN-C and GPS systems, respectively, during recreation treatments. The higher relocation schedule of LORAN-C collars was designed to analyze the real-time responses of telemetered elk to the telemetered recreationists. Similar data were collected in 2002 and published earlier (Wisdom et al., 2004a), but with different response variables than considered here. All collars were programmed at 30-min relocation schedules during control periods. Limited battery life of GPS collars and sampling restrictions on the total number of LORAN-C locations that could be collected among all collars at Starkey study areas (Johnson et al., 1998) dictated the 30-min relocation schedule during control periods.

Spatial error of the elk telemetry locations was < 50 m and < 20 m for LORAN-C and GPS telemetry, respectively (Johnson et al., 1998; Hansen and Riggs, 2008). Fix success, defined as the percentage of programmed locations successfully obtained from collars, exceeded 98% for GPS data, indicating no need for bias correction (Frair et al., 2004; Nielson et al., 2009). Fix success for LORAN-C data averaged 65% and was largely associated with unbiased sources of random variation (Johnson et al., 1998). LORAN-C fix success varied slightly by location, however, and was corrected with a spatially-explicit algorithm developed for the study area (Johnson et al., 1998, 2000).

### 2.2.3. Viewing distances

At the conclusion of the study, we measured the distances at which we estimated an elk could be viewed from the recreation trails (Fig. 1B). Viewing distances provided context for interpreting the distances that elk maintained from the recreation trails and from recreationists during treatments, and for evaluating support for our hypothesis that elk would stay hidden from view of recreationists.

We sampled viewing distances approximately every 0.2 km along the trails, for a total of 231 sampling points. At each sampling point, we used a GPS unit (Trimble Unit TSCe, Trimble, Inc.) to spatially reference the point and used a laser rangefinder (Bushnell™ Yardage Pro 1000) to measure the distance at which we estimated an elk could be viewed. Because elk could be viewed at any possible angle from the trails, we measured distances in the eight cardinal compass directions, with 0 degrees set as straight ahead on the trail at a given sampling point (Fig. 1B).

Viewing distances can be interrupted by topography or vegetation, such that elk can be viewed at closer and farther distances but not in between. Consequently, for each of the eight angles, we measured the distance at which an elk could be viewed to the first point of visual obstruction, referred to as the "near" distance. We also measured the subsequent distance at which an elk could be viewed, beyond the first point of visual obstruction, referred to as the "far" distance. The far distance thus represented the distance at which elk could be viewed without consideration of the near distance obstruction. For a given viewing angle in which there were no obstructed areas between near and far distances, the near and far distances were identical and recorded as the same for both distances. By contrast, near and far distances could be substantially different where dense vegetation or topography obstructed views close to the trails, but open areas could be viewed farther from the trails. Rangefinder estimation errors generally were < 5% of the true distance (Wisdom, unpublished data), similar to published estimates of these technologies as tested in forest environments (Sicking, 1998).

## 2.3. Data analysis

### 2.3.1. Viewing distances from trails

We calculated the mean and 95% confidence interval (CI) of the near and the far viewing distances to which elk could be viewed from the recreation trails, considering all distances measured at the sampling points. We used each sampling point as a sample unit and the eight distance measurements/sampling point as subsamples. We averaged the values of the eight near viewing distances measured at each sampling point, and did the same for the eight far viewing distances, to estimate the mean values and 95% CIs.

We also calculated the percentage of near and far viewing distances by 50-m distance intervals away from the recreation trails (Fig. 1B), and the percentage of the study area within these distance categories. We did the same for the percentage of the study area from trails within the maximum viewing distance, estimated to be 300 m. Analyses provided insight about the percentage of the study area in which elk could be viewed from the recreation trails.

### 2.3.2. Avoidance of trails

We used analysis of variance (ANOVA) with random elk effects (i.e., each telemetered elk as a sample unit) to evaluate differences in mean distances ( ± 95% CIs) of elk from the nearest trail among the four recreation treatments and paired controls, and further summarized these distances in parallel boxplots with median notches (Chambers et al., 1983; Benjamini, 1988). Mean distances and boxplots of elk from the nearest trail were summarized for each telemetered elk/day/treatment type and control, pooled across like replicates, using observations that were averaged for each morning (0800–1159 h local time) and each afternoon (1200–1600 h local time). This analysis evaluated average responses to treatments across seasons and years, but accounting for diurnal effects (Wisdom et al., 2004a; Naylor et al., 2009). Prior analyses (Wisdom et al., 2004a; Wisdom, unpublished data) also indicated that elk in a given pasture responded to recreation treatments in both pastures, given the adjacency of trails and long distances of elk responses. Calculation of distances thus considered trails in both pastures. Results were further related to the mean near and far viewing distances ( ± 95% CIs) from trails.

We analyzed the spatial distribution of elk in relation to trails in two additional ways. First, we calculated the percentage of elk locations by 50-m distance intervals from the nearest trail during each treatment type and control, and percentage of near and far viewing distances by the 50-m intervals. Locations were pooled across animals. And second, we estimated and mapped kernel densities of elk locations during each treatment type and control. Kernel densities (Venables and Ripple, 1997) were based on the pooled locations among telemetered elk as an estimate of the stationary distribution of the population (Preisler et al., 2013) during each treatment type and control. We used a random subsample of locations from the recreation treatments equal to the number of locations during the corresponding control periods to estimate kernel densities and produce comparable maps.

Analyses of elk distances and distributions in relation to trails documented the degree of trail avoidance and whether the elk population shifted beyond viewing distances during the recreation treatments, and shifted back toward trails during control periods. If elk were farther from trails than they could be viewed during recreation, this would support our hypothesis that avoidance was related to elk staying hidden from view. Moreover, a shift in elk distributions closer to the trails during control periods, with more locations in view during these periods of no human activity, would further support this hypothesis as a potential cause-effect process.

### 2.3.3. Avoidance of recreationists

We analyzed the minimum separation distances that elk maintained from recreationists as a measure of how tolerant elk were to the proximity of humans. We first matched the locations of recreationists in time with the LORAN-C telemetry locations of elk (Preisler et al., 2006). LORAN-C elk locations were used because of the higher relocation frequency (every 10 min) compared to the GPS telemetry locations (every 30 min), thus providing a larger set of close matches in time. Each LORAN-C elk location was matched with the location of the nearest group of recreationists closest in time to the elk location, considering all locations of recreationists within a five-minute time window before each elk location. Time-matched locations of elk and recreationists were measured as the shortest Euclidean distance between each (ArcGIS 9.2, Environmental Systems Research Institute, Inc., Redlands, CA).

To calculate the mean and 95% CI for the minimum separation distance/treatment type, we identified the distance of each LORAN-C elk to the nearest group of recreationists during each morning and each afternoon for each of the five days of a treatment replicate. This provided two observations of minimum distance/elk/day/treatment replicate, spanning the three seasons and two years. Minimum separation distances/elk for each morning and afternoon were used as subsamples, and a mean minimum distance of these values calculated for each animal among replicates of each treatment type. We then calculated the mean minimum distance and 95% CI among all LORAN-C telemetered elk (n = 19) across like replicates in the same manner as done for calculating mean distances from trails. We further analyzed the distribution of minimum separation distances of elk with boxplots and median notches by treatment type.

We considered minimum separation distance to be the most direct indicator of the spatial tolerance of elk to recreationists, particularly their tolerance to remain in view. Elk often seek edges close to cover or in cover, presumably for hiding from humans or predators, even during non-hunting periods of spring-fall (Witmer et al., 1985; Johnson et al., 2000; Coe et al., 2011; Harju et al., 2011; Buchanan et al., 2014).

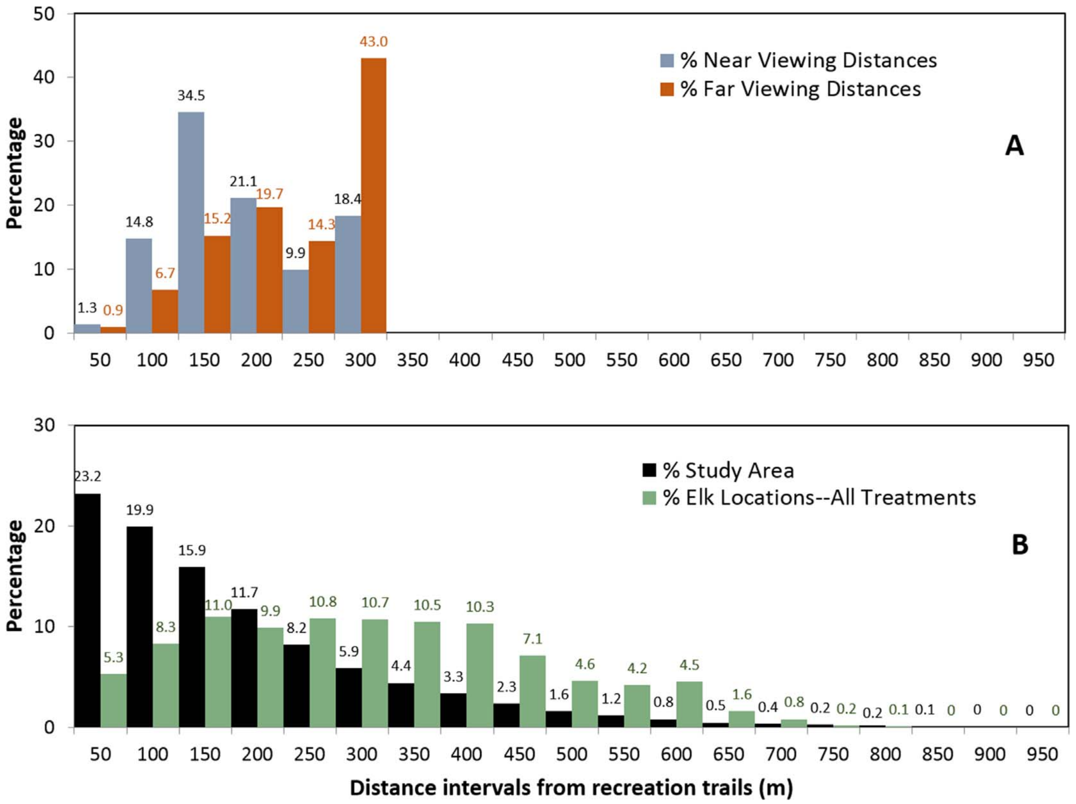


**Fig. 2.** Percentage of near and far viewing distance values by 50-m distance intervals from the recreation trails (A) in relation to the percentage of the study area and percentage of elk locations by intervals (B), Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Elk locations were from 35 telemetered elk monitored during all-terrain vehicle riding, mountain biking, hiking, and horseback riding, 2003–2004 combined.

Evaluation of separation distances in relation to viewing distances considered elk use of visual obstructions of cover and topography to hide from view as part of avoidance responses.

## 3. Results

### 3.1. Viewing distances from trails and area available for elk use

Mean near and far distances to which elk could be viewed from the recreation trails were 172 m and 222 m, respectively (Fig. 2A; Table 1). Over 50% of the study area was within the mean near viewing distance of 172 m, and > 70% was within the mean far viewing distance of 222 m, based on study area percentage by distance intervals from trails (Fig. 2A). Just 15% of the study area exceeded the maximum viewing distance of 300 m that was estimated for near and far viewing distances at 18% and 43% of the sampling points, respectively (Fig. 2A). The percentage of the study area available for elk use by 50-m distance intervals from trails (Fig. 1B, 2A) directly followed the patterns of study area percentage by viewing distance (Fig. 2A).

### 3.2. Elk avoidance of trails

We found significant differences in elk avoidance of trails among the four recreation treatments and paired controls (ANOVA, P < .01). Mean distances of elk from the recreation trails ranged from 239 to 310 m during the four recreation activities (Fig. 3; Table 1). Mean and median distances were significantly farther (non-overlapping 95% CIs and median notches) during ATV riding, mountain biking, and horseback riding than distances of these same telemetered elk during the paired control periods (Fig. 3; Table 1), indicating that elk moved away from the trails during recreation and back toward trails when no humans were present. During hiking, mean and median distances of elk from trails were similar to those during horseback riding, but elk movement back toward trails during the hiking control period was less distinct (Fig. 3), and CIs for the hiking treatment and control periods slightly overlapped (5-m overlap, Table 1).

Shifts of elk away from and back toward trails in the presence versus absence of recreationists were evident in the boxplot distributions (Fig. 3). Shifts also were evident spatially in the kernel densities of elk locations of paired treatment and control periods, shown in Fig. 4 for ATV and horseback riding. Similar spatial differences in kernel densities between treatment and control periods were found during mountain

**Table 1**
Mean ( ± 95% CI) near and far distances at which elk could be viewed from recreation trails, and mean distances ( ± 95% CIs) that elk maintained from nearest trail during all-terrain vehicle riding (ATV), mountain biking (BIKE), hiking (HIKE), and horseback riding (HORSE) treatments (T) and control periods (C), 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA.

| Mean viewing distance (m) (N = 231) | | Mean distance (m) of elk from nearest trail (N = 35) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Near | Far | ATV | | BIKE | | HIKE | | HORSE | |
| | | T | C | T | C | T | C | T | C |
| 172 ( ± 5) | 222 ( ± 5) | 311 ( ± 28) | 237 ( ± 15) | 286 ( ± 26) | 197 ( ± 8) | 276 ( ± 18) | 248 ( ± 15) | 240 ( ± 13) | 172 ( ± 9) |

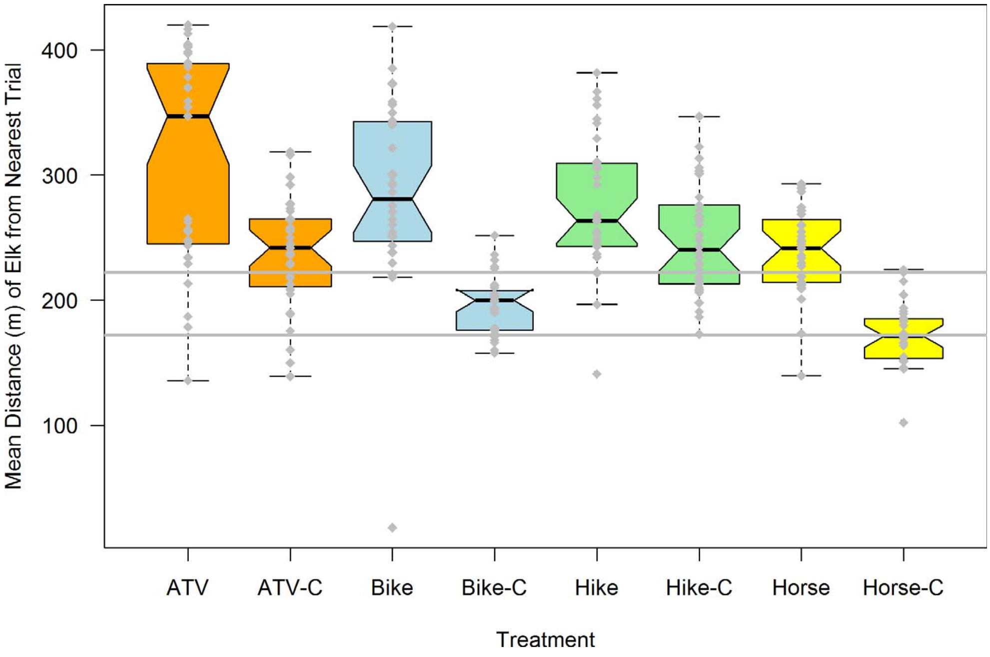


**Fig. 3.** Parallel boxplots showing the variability among elk (variability within each box) and among treatments (variability between boxes) in mean distances of telemetered elk (n = 35) from the nearest recreation trail during four types of recreation (all-terrain vehicle riding [ATV], mountain biking [Bike], hiking [Hike], horseback riding [Horse]) and corresponding control (C) periods, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Non-overlapping notches provide 'strong evidence' that the two medians differ (Chambers et al. 1983, p. 62; Benjamini, 1988). Silver dots show mean distances of individual elk. The two horizontal grey lines indicate the mean near (172 m) and mean far (222 m) viewing distances from trails.

biking. Shifts away from and back toward trails during the hiking treatment versus control periods were more subtle, as reflected in the small overlap of CIs of mean values (Table 1) and overlapping median notches (Fig. 3).

Mean and median distances of elk from the recreation trails were farther during ATV riding than during the three non-motorized types of recreation (non-overlapping CIs and notches); these distances were not different between mountain biking, hiking, and horseback riding (overlapping CIs and notches, Fig. 3; Table 1). Boxplot distributions, however, indicated an overall trend of strongest avoidance during ATV riding, followed by mountain biking, hiking, and horseback riding (Fig. 3). These trends were supported by the rank order of both mean and median values among the four treatments (Fig. 3; Table 1).

Variability in mean distances among individual elk, however, was highest (least precise) during ATV riding. Lower precision of elk response to ATV riding was evident in the longer boxplot below the median, and high number of individual mean distances farther below the median, compared to other types of recreation (Fig. 3), suggesting that ATV riding elicited either a hiding (stationary) or a flight (active) response (see Section 4). Higher precision was associated with elk responses to horseback riding and hiking, and during all control periods except hiking.

Mean distances of elk from the trails also were farther (non-overlapping CIs) during all four recreation activities than the mean near and far viewing distances (Table 1). The large majority of elk locations were well beyond the mean near and far viewing distances from trails, and 44% of all elk locations during the recreation treatments were beyond the maximum viewing distance of 300 m (Fig. 2B). This pattern was stronger during ATV riding and mountain biking, when 52% and 50% of all elk locations occurred > 300 m from the trails. The pattern was weaker during hiking and horseback riding, when 37% and 25% of elk locations were beyond the maximum viewing distance (Fig. 2B).

Almost one-half (44%) of elk locations occurred on just 15% of the study area farthest from trails and out of view (Fig. 2B). The large majority (85%) of the study area was within the maximum viewing distance of 300 m from the recreation trails, but only 56% of elk locations occurred in these distance intervals (Fig. 2B). These patterns were evident in the kernel densities of treatment versus control periods (Fig. 4).

### 3.3. Elk avoidance of recreationists

Mean minimum separation distances that elk maintained from recreationists were highest during ATV riding (879 m, ± 68 m), lowest and similar during hiking (547 m, ± 44 m) and horseback riding (558 m, ± 45 m), and intermediate during mountain biking (662 m, ± 53 m). Boxplot distributions and median notches followed this same pattern (Fig. 5): median distances were highest during ATV riding, followed by mountain biking, both of which had non-overlapping notches with each other and with the overlapping notches of hiking and horseback riding. The taller height of the boxplot above the median during ATV riding compared to other types of recreation (Fig. 5) further illustrated the stronger but less precise elk response to motorized recreation.

Separation distances from recreationists were significantly farther than elk distances from trails (non-overlapping CIs with those in Table 1), illustrating the difference in real-time responses of elk to recreationists (five-minute time windows each morning and afternoon) versus the more static responses to trails (8-h time window each day). Specifically, mean minimum distances of elk from recreationists (558–879 m) were 2–4 times farther than mean distances from trails (239–310 m, Table 1) during the same recreation periods. Differences in elk distances from recreationists also were more distinct and consistent (more precise) between the four treatments than those for distances from trails (boxplot variability across treatments in Fig. 3 versus 5), suggesting that the direct responses of elk to recreationists was more predictable than their indirect responses to trails.

Minimum separation distances also were 3–5 times farther than the mean near and far distances of 172 and 222 m at which elk could be viewed from the trails (non-overlapping CIs with those in Table 1), and 2–3 times farther than the maximum viewing distance of 300 m. Over 75% of the minimum distances between elk and recreationists exceeded the maximum viewing distance of 300 m (see boxplot portions above 300 m, Fig. 5), indicating a strong tendency of elk to be hidden from view of recreationists. This percentage of elk distances from recreationists beyond 300 m, estimated for a 5-min time window (Fig. 5), was higher than the estimate of 44% of elk locations beyond 300 m based on the more generic 8-h time window (Fig. 2B). The long "tails" of elk distances extremely far from recreationists (e.g., 1500–4000 m distances, per dotted lines in uppermost part of each boxplot, Fig. 5) were evident during all four recreation activities, indicating avoidance

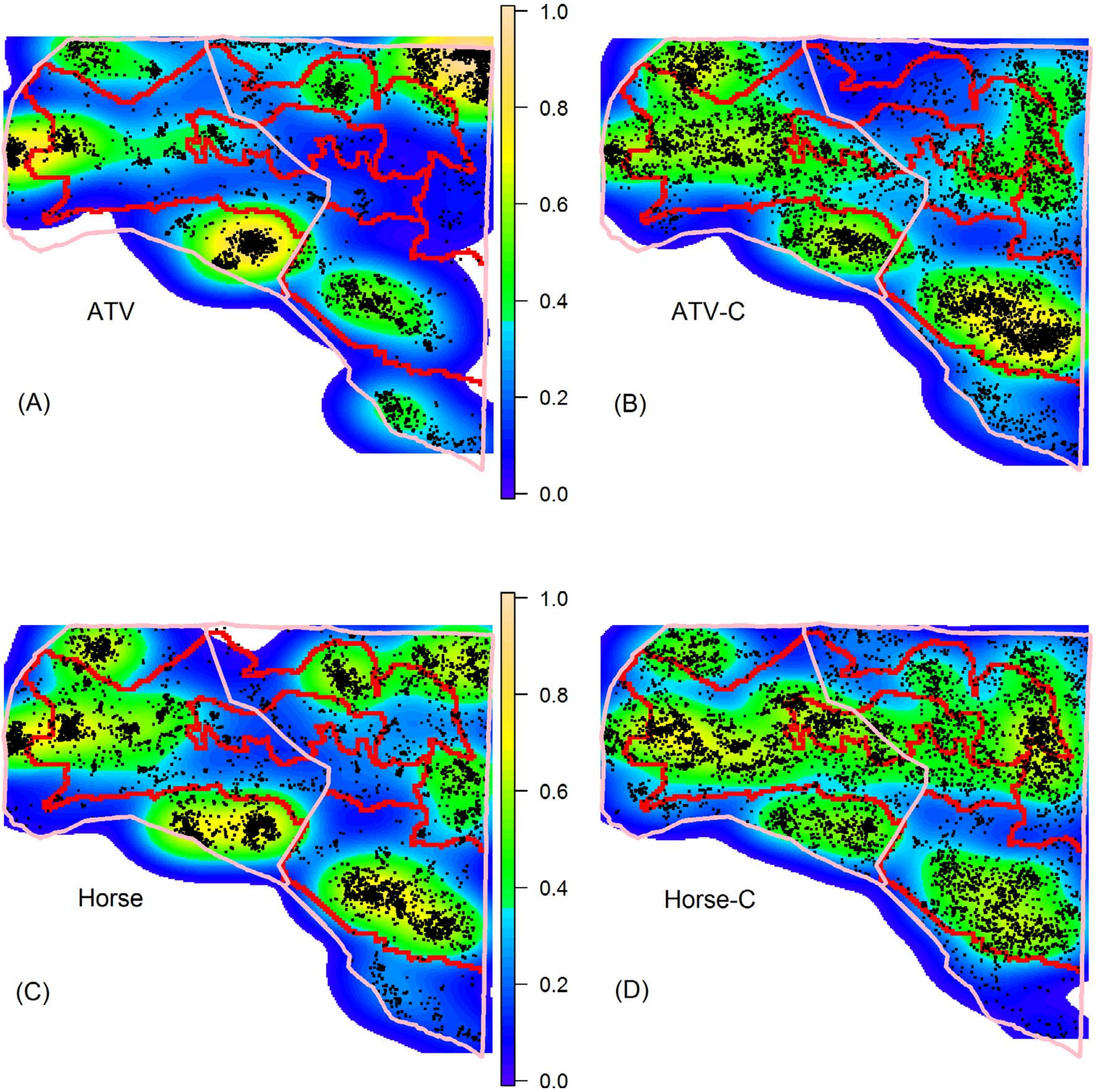


**Fig. 4.** Locations of 35 elk during ATV riding (ATV, A) and horseback riding (Horse, C) versus corresponding control periods (B and D), superimposed on estimates of the spatial probability distribution of elk locations, estimated as kernel densities, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Probability of use is scaled from 0 to 1, with higher use shown by warmer colors (yellow, then green) and lower use by cooler colors (light blue, then dark blue). Red lines are the recreation trails and pink lines fences. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

responses at distances as far as possible from recreationists.

## 4. Discussion

### *4.1. Elk avoidance of recreation trails and recreationists*

Our results showed strong avoidance by elk to the recreation trails during each of the four types of recreation. Almost one-half of all elk telemetry locations during the recreation activities occurred on just 15% of the study area farthest from trails. Elk avoidance of recreation trails was strongest during ATV riding. Elk avoidance of trails during mountain biking, hiking and horseback riding was statistically similar but the distribution of elk locations during these three types of recreation indicated that elk shifted farther from trails during mountain biking.

Elk avoidance of trails was calculated as the mean distance of telemetered elk to trails, using data pooled for each animal across treatment and control replicates of each recreation type. Estimates thus represented the "average" distribution of elk in relation to trails during each recreation treatment, and did not account for finer temporal responses, such as potential population shifts away from and back toward trails as recreationists passed by a given area. By contrast, the minimum separation distances that elk maintained from recreationists in real time documented the direct effect of human movement on the species' behavior at five-minute time windows during each recreation treatment. Results showed that elk were quite sensitive to human presence, shifting distributions away from recreationists and farther out of view as the activities moved along the trails. The minimum daily distances maintained by elk from recreationists were notably large (averaging 558–879 m among treatments), indicating a strong spatial intolerance of elk to recreationists and well beyond areas visible from trails. Direct responses of elk to recreationists were stronger and more precise across treatments than their indirect responses to trails.

The pattern of long-distance avoidance by elk to recreationists was supported by real-time documentation of elk fleeing from approaching recreationists that was documented in earlier publications from data collected in our study area (Preisler et al., 2006, 2013). Flight responses of elk to the recreation activities in our study area showed substantially higher probabilities of flight than expected at distances of 500–1000 m (Wisdom et al., 2004a). Minimum separation distances in our study

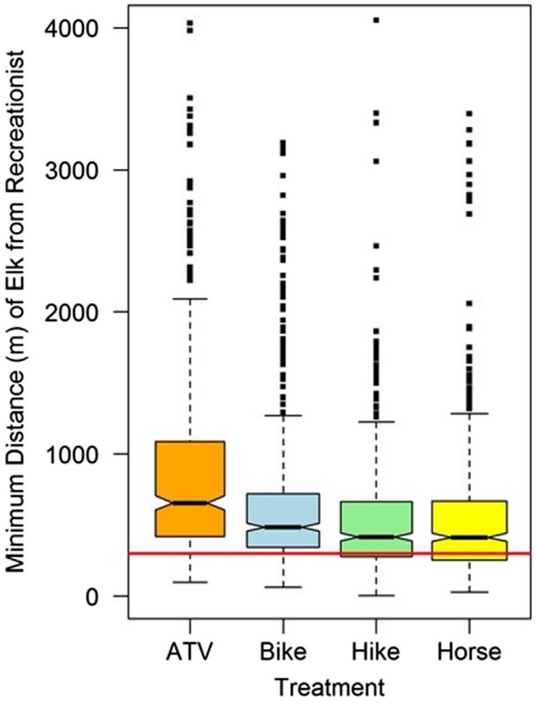


**Fig. 5.** Parallel boxplots showing the variability among elk (variability within each box) and among treatments (variability between boxes) in minimum separation distances of LORAN-C telemetered elk (n = 19) from recreationists during all-terrain vehicle riding (ATV), mountain biking (Bike), hiking (Hike), and horseback riding Horse, 2003–2004, Northeast Study Area, Starkey Experimental Forest and Range, northeast Oregon, USA. Minimum distances were evaluated per elk/day, with two values per day (morning and afternoon) per elk. Horizontal red line shows the maximum viewing distance of 300 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

followed a similar pattern to these flight responses, with the latter modeled with 2002 elk telemetry data not used in our analysis (Wisdom et al., 2004a).

Separation distances maintained by elk from recreationists appear to represent a cause-effect process that we cannot attribute to other factors. We controlled for human access with our design of randomly selecting and implementing one type of recreation activity for a given five-day period, followed by a paired nine-day control period of no human activity. We further controlled for effects of season and year by replicating this design during spring, summer, and fall, and across years. Other factors influencing elk movements may have involved the two main predators of elk in our study area, cougars (*Puma concolor*) and black bears (*Ursus americanus*); however, these predators were constant background factors operating during both treatment and control periods (Wisdom et al., 2005). We know of no other factors beyond the recreation activities that would help explain our results.

### 4.2. Sensory cues used by elk to avoid recreationists

Long separation distances maintained by elk from recreationists beg the question: what types of sensory cues are elk using to react to humans? Large mammals and many other vertebrates have keen senses of smell, hearing, and sight that have evolved to detect predators (Hunter and Skinner, 1998; Lima and Dill, 1990; Bennett et al., 2009; Wikenros et al., 2015). Elk moved largely out of view during the recreation activities, suggesting visibility was a strong factor in avoidance of trails. However, viewing distances were based on human capacity to see elk, not vice versa. Moreover, ungulates such as elk can easily hear and smell humans at the distances that elk maintained from recreationists (see citations above), suggesting that any combination of sensory cues could have been used.

In addition, visual detection of humans can be impaired by obstructions of vegetation and topography, and auditory and olfactory cues to human presence are affected by wind speed and direction. Olfactory cues also were likely different for each recreation activity: ATVs emit a distinct gasoline odor and horses provide an additional olfactory cue beyond that of humans.

Each recreation activity also was associated with a different level of noise, which clearly affects wildlife (Barber et al., 2009). ATV riding is the loudest of the four recreation activities, with levels as high as 110 dB (Lovich and Bainbridge, 1999), and thus has high noise impact on wildlife (Bowles, 1995, Lovich and Bainbridge, 1999). It is unclear whether any of the other three recreation activities were louder than the others. We are not aware of any comparative research on noise associated with non-motorized forms of trail-based recreation.

Differences in speed of the recreation activities may also have provided additional cues for elk detection of recreationists. The speed of ATVs was > 2 times faster than mountain bikes, and > 4–5 times faster than hikers and horseback riders, respectively, during our study (Wisdom, unpublished data). Our treatment design ensured equal spatial coverage of the trail system by all four recreation treatments, but ATVs covered the trails at a faster rate each morning and afternoon. The higher speed of ATVs, combined with their substantially higher noise, may help explain the stronger avoidance response of elk to ATVs. The higher speed of ATVs might also have limited the reaction time of elk, as shown by some elk maintaining closer distances to trails and possibly hiding during this activity (see Wisdom et al. (2004a) for a related discussion of elk hiding versus flight responses to ATV riding). Given the wide variety of visual, auditory, and olfactory stimuli, different combinations of sensory cues were likely used by elk under varying conditions to detect and respond to recreationists.

### 4.3. Support for hypotheses on viewing, ATV effects, and forest roads

We identified three hypotheses for our analyses: (1) that elk avoidance would occur at distances that allow animals to stay out of view of recreationists; (2) that avoidance would be strongest in response to motorized recreation (ATV riding); and (3) that elk would respond to trail-based recreation similarly to their avoidance of roads open to motorized traffic on public forests. We found support for all three hypotheses. Elk avoided trails and recreationists at distances largely beyond human view (hypothesis 1). This result agrees with past studies showing elk use of areas obstructed from view (e.g., Montgomery et al., 2012), sometimes referred to as “hiding cover” for elk (Thomas et al., 1979; Canfield et al., 1986; Lyon, 1987). Elk also use areas of steeper slopes, complex topography, or areas closer to cover-forage edges, presumably as a means of remaining hidden from humans or predators (e.g., Witmer et al., 1985; Thomas et al., 1988; Johnson et al., 2000; Coe et al., 2011; Harju et al., 2011; Buchanan et al., 2014).

Extensive timber harvest occurred on 35% of our study area during the 1990s, which uniformly increased openness of the landscape due to the even distribution of harvested vs. unharvested stand mosaics (Wisdom et al., 2004b). Viewing distances in our study increased in response to the extensive timber harvest and may have increased the distances that elk maintained from recreationists. The influence of silviculture and forest topography on viewing, and the subsequent recreation effects on wildlife sensitive to human presence, agrees with Lyon’s (1987) modeling of forest structure and topography to characterize hiding cover for elk.

Elk avoidance of ATVs also was stronger than to the three types of non-motorized recreation (hypothesis 2). Ciuti et al. (2012) found similar results in a comparative study of ATV riding, mountain biking, hiking, and horseback riding in Alberta, Canada. Other authors have inferred that ATV riding has a stronger effect on wildlife than non-motorized recreation because of higher noise and faster speeds, which influences more area per unit time (Lovich and Bainbridge, 1999; Wisdom et al., 2004a; Proescholdt, 2007; Ciuti et al., 2012; Preisler et al., 2013). However, Larson et al.'s (2016) meta-analysis of recreation effects on wildlife suggested that non-motorized recreation had stronger effects than motorized (but differences were not statistically significant). Additional research is needed to address inconsistencies among studies and to investigate effects of trail-based recreation on fitness of different wildlife species and taxa.

Avoidance responses by elk to the recreation activities also were similar to those documented in relation to forest roads open to motorized traffic (hypothesis 3). Our review of the literature revealed displacement of elk from forest roads open to motorized traffic that often exceeded 0.5–1.5 km. Avoidance responses by elk distance to open roads, or to open road density, have been documented consistently and overwhelmingly by > 30 studies conducted during the past 5 decades in forested areas of western North America. Examples from each decade are Perry and Overly (1977), Lyon (1983), Cole et al. (1997), Rowland et al. (2000), and Prokopenko et al. (2016).

Distance responses by elk to recreationists during our study mirrored the general avoidance distances of 0.5–1.5 km or farther that were documented in many roads studies during non-hunting seasons. Elk sometimes move much longer distances (e.g., > 25 km) from public to private lands during hunting seasons when public forests are highly roaded and lack adequate security for elk to hide from hunters (Proffitt et al., 2013). We did not evaluate the effects of hunting, nor could we evaluate the potential for such longer-distance landscape responses by elk because of the study area enclosure.

Similarities between elk responses to trail-based recreation and forest roads also depend on the specific response variables evaluated and the spatial and temporal scales at which responses are measured. Different studies evaluated elk avoidance over different time periods (seasonal or multiple seasons in a year or multiple years) and spatial extents. Results will vary by sample size and the degree of "averaging" of avoidance effects by time of day, seasons, and years. This variation was obvious in our results. Analysis of elk distances to trails represented an average response over the eight-hour period of all days among all replicates of each treatment type. These avoidance distances were substantially less than the minimum separation distances maintained by elk from recreationists, as measured in five-minute time windows over the same eight-hour days and replicates. Minimum separation distances of elk from recreationists are a more direct measure of elk responses; we consider these results comparable to contemporary finer-scale distance responses of elk to open roads (e.g., Buchanan et al., 2014; Morris et al., 2016; Prokopenko et al., 2016; Ranglack et al., 2017).

### 4.4. Bias in visual observations of elk

Elk are widely distributed and occupy summer ranges on nearly every National Forest in the western United States (O'Gara and Dundas, 2002). Consequently, the species has been a topic of public comments as part of travel management planning on National Forests. Motorized recreationists often have commented that elk populations do not avoid OHVs because elk are observed while riding. We heard this comment numerous times during meetings we held with recreation stakeholders about our research. Of direct relevance to these public comments was the research by Naylor (2006), who summarized the distances at which elk were directly observed by recreationists during implementation of the recreation treatments in our study area. Elk were observed by recreationists at mean distances of 116–161 m among the four types of treatments (Naylor, 2006). These distances are shorter than or similar to the average near viewing distance of 172 m at which elk could be viewed without visual obstruction.

Telemetered elk, representing a random sample of female elk in our study area, maintained minimum separation distances that were 4–8 times farther from recreationists than the distances estimated by visual observation. Thus, a large percentage of telemetered elk were present beyond the distances at which visual observations were possible, and elk consistently maintained these longer distances during each type of recreation.

Recreationists in our study were able to observe a small portion of the elk population in view of trails, but unable to see the large majority of the elk population that remained hidden from view during recreation activities. Visual observations of elk during recreation thus could not detect the strong avoidance by elk that occurred out of view. This pattern explains the differences between motorized recreationists' comments about elk as part of travel management planning and the responses that we documented with telemetered elk in our study.

Stankowich (2008) summarized results from > 50 studies that reported results of flight distance of wild ungulate species in response to human activities. The majority of reported studies were based on visual observations, but no mention was given in Stankowich (2008) about the potential for bias with the use of visual observations in environments where viewing was substantially limited, or for ungulate species whose response to human presence is to remain out of view. Automated and remotely-sensed technologies are now available that document a variety of animal behaviors and responses to human activities without dependence on human observations (e.g., Cooke et al., 2004; Coulombe et al., 2006; Shepard et al., 2008; Naylor et al., 2009; Suraci et al., 2017).

### 4.5. Implications

Avoidance by elk to recreation trails and recreationists represents a form of "habitat compression," similar to that described for effects of forest roads open to traffic (Wisdom et al., 2000, Rowland et al., 2004, Buchanan et al., 2014, Prokopenko et al., 2016). Habitat compression in response to human activities is a form of habitat loss for species like elk (Rowland et al., 2004, Frair et al., 2008, Buchanan et al., 2014), considering the potentially large areas not used or used less in the presence of humans, and that otherwise might be selected by a species in the absence of humans. Habitat compression can ultimately lead to large-scale population shifts by elk from public forests to private lands, thus eliminating hunting and viewing opportunities on public lands (Proffitt et al., 2013).

To address these types of effects, forest managers could use our results to evaluate trade-offs between competing objectives for trail-based recreation and wildlife species like elk that are sensitive to human activities on public forests. Although public forests are governed by laws and policies of multiple use, not all areas can be simultaneously co-managed for recreation and recreation-sensitive wildlife. Different land allocations can accommodate such competing uses, but often on different landscapes with clear objectives about which resources are featured. Optimizing land allocations through spatial analyses of trade-offs between competing forest uses (Wang et al., 2004), with the inclusion of human ecology mapping (McLain et al., 2013a, 2013b) and stakeholder engagement (Asah et al., 2012a, 2012b) is a forest planning approach that holds promise in helping address recreation and wildlife conflicts. We suggest that such an approach be considered in co-managing trail-based recreation and sensitive wildlife like elk on public forests.

## Author contributions

BJ, LN, RA, and MW conceived, designed, and implemented the research; BJ, HP, LN, MR, and MW analyzed the data and wrote and edited the manuscript.

## Acknowledgments

Funding was provided by the Oregon Department of Parks and Recreation, Oregon Department of Fish and Wildlife, and USDA Forest Service Pacific Northwest Region and Pacific Northwest Research Station. Additional support was provided by the USDA Forest Service Pacific Southwest Research Station. Jennifer Hafer and Bridgett Naylor helped prepare figures and summarize results. The authors wish to thank > 50 individuals, particularly Kristen Munday, who implemented the recreation activities for this study.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.01.032.

## References

Adams, J.C., McCool, S.F., 2009. Finite recreation opportunities: the Forest Service, the Bureau of Land Management, and off-road vehicle management. Nat. Res. J. 49, 45–116.

Asah, S.T., Bengston, D.N., Wendt, K., DeVaney, L., 2012a. Prognostic framing of stakeholders' subjectivities: a case of all-terrain vehicle management on state public lands. Environ. Manage. 49, 192–206.

Asah, S.T., Bengston, D.N., Wendt, K., Nelson, K.C., 2012b. Diagnostic reframing of intractable environmental problems: case of a contested multiparty public land-use conflict. Environ. Manage. 108, 108–119.

Barber, J.R., Crooks, K.R., Fristrup, K.M., 2009. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25, 180–189.

Benjamini, Y., 1988. Opening the box of a boxplot. Am. Statist. 42, 257–262.

Bennett, V.J., Beard, M., Zollner, P.A., Fernández-Juricic, E., Westphal, L., LeBlanc, C.L., 2009. Understanding wildlife responses to human disturbance through simulation modeling: a management tool. Ecol. Complex. 6, 113–134.

Beyer, H.L., Ung, R., Murray, D.L., Fortin, M.J., 2013. Functional responses, seasonal variation and thresholds in behavioural responses of moose to road density. J. Appl. Ecol. 50, 286–294.

Bowker, J.M., Askew, A.E., Cordell, H.K., Betz, C.J., Zarnoch, S.J., Seymour, L., 2012. Outdoor recreation participation in the United States – projections to 2060. U.S. Forest Service Gen. Tech. Rep. SRS-GTR-160, Asheville, NC, USA.

Bowles, E., 1995. Responses of wildlife to noise. In: Knight, L., Gutzwiller, J. (Eds.), Wildlife and Recreationists. Island Press, Washington DC, USA, pp. 108–156.

Brillinger, D.R., Preisler, H.K., Ager, A.A., Wisdom, M.J., 2004. Stochastic differential equations in the analysis of wildlife motion. 2004 Proceedings, American Statistical Association, Section on Statistics and the Environment, Alexandria, VA, USA: American Statistical Association < https://www.stat.berkeley.edu/users/brill/Papers/jsm2004j.pdf > .

Brillinger, D.R., Preisler, H.K., Wisdom, M.J., 2011. Modelling particles moving in a potential field with pairwise interactions and an application. Brazil. J. Prob. and Stat. 25, 421–436.

Buchanan, C.B., Beck, J.L., Bills, T.E., Miller, S.N., 2014. Seasonal resource selection and distributional response by elk to development of a natural gas field. Rangeland Ecol. Manage. 67, 369–379.

Canfield, J.E., Lyon, L.J., Hillis, J.M., 1986. The influence of viewing angle on elk hiding cover in young timber stands. U.S. Forest Service Research Paper INT-371, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.

Chambers, J.M., Cleveland, W.S., Kleiner, B., Tukey, P.A., 1983. Graphical Methods for Data Analysis. Wadsworth International Group, Belmont, CA, USA.

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7, e50611. http://dx.doi.org/10.1371/journal.pone.0050611.

Coe, P.K., Johnson, B.K., Wisdom, M.J., Cook, J.G., Vavra, M., Nielson, R.M., 2011. Validation of elk resource selection models with spatially independent data. J. Wildl. Manage. 75, 159–170.

Cole, E.K., Pope, M.D., Anthony, R.G., 1997. Effects of road management on movement and survival of Roosevelt elk. J. Wildl. Manage. 61, 1115–1126.

Cole, E.K., Pope, M.D., Anthony, R.G., 2004. Influence of road management on diurnal habitat use of Roosevelt elk. Northwest Sci. 78, 313–321.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: a mechanistic approach to ecology. Trends Ecol. Evol. 19, 334–343.

Cordell, K., Betz, J., Green, G., Owens, M., 2005. Off-highway vehicle recreation in the United States, regions and states: A national report from the National Survey on Recreation and the Environment (NSRE). USDA Forest Service Southern Research Station, Athens, GA, USA.

Cordell, H.K., 2012. Outdoor recreation trends and futures: a technical document supporting the Forest Service 2010 RPA Assessment. U.S. Forest Service Gen. Tech. Rep. SRS-GTR-150, Asheville, NC, USA.

Coulombe, M.L., Massé, A., Côté, S.D., 2006. Quantification and accuracy of activity data measured with VHF and GPS telemetry. Wildl. Soc. Bull. 34, 81–92.

Federal Register, 2005. Part IV. Department of Agriculture, Forest Service. 36 CFR Parts 212, 251, and 295. Travel management; designated routes and areas for motor vehicle use; Final Rule, vol. 70. Federal Register, Washington, DC, USA0, pp. 68264–68291.

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B., Beyer, H.L., 2004. Removing GPS collar bias in habitat selection studies. J. Appl. Ecol. 41, 201–212.

Frair, J.L., Merrill, E.H., Beyer, H.L., Morales, J.M., 2008. Thresholds in landscape connectivity and mortality risks in response to growing roads networks. J. Appl. Ecol. 45, 1504–1513.

Green, R.J., Higginbottom, K., 2000. The effects of non-consumptive wildlife tourism on free-ranging wildlife: a review. Pacific Cons. Biol 6, 183–197.

Gutzwiller, K.J., D'Antonio, A.L., Monz, C.A., 2017. Wildland recreation disturbance: broad-scale spatial analysis and management. Front. Ecol. Environ. http://dx.doi.org/10.1002/fee.1631.

Hansen, M.C., Riggs, R.A., 2008. Accuracy, precision, and observation rates of global positioning system telemetry collars. J. Wildl. Manage. 72, 518–526.

Harju, S.M., Dzialak, M.R., Osborn, R.G., Hayden-Wing, L.D., Winstead, J.B., 2011. Conservation planning using resource selection models: altered selection in the presence of human activity changes spatial prediction of resource use. Animal Cons. 14, 502–511.

Havlick, D., 2002. No Place Distant: Roads and Motorized Recreation on America's Public Lands. Island Press, Washington D, C., USA.

Hennings, L., Soll, J., 2017. Hiking, mountain biking and equestrian use in natural areas: A recreation ecology literature review. Portland Metro Parks and Nature, 600 NE Grand Avenue, Portland, OR, USA.

Hunter, L.T.B., Skinner, J.D., 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour 135, 195–211.

Johnson, B.K., Ager, A.A., Findholt, S.L., Wisdom, M.J., Marx, D., Kern, J., Bryant, L.D., 1998. Mitigating spatial differences in observation rate of automated telemetry systems. J. Wildl. Manage. 62, 958–967.

Johnson, B.K., Kern, J.W., Wisdom, M.J., Findholt, S.L., Kie, J.G., 2000. Resource selection and spatial separation of mule deer and elk in spring. J. Wildl. Manage. 64, 685–697.

Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PLoS ONE 11 (12), e0167259. http://dx.doi.org/10.1371/journal.pone.0167259.

Leung, Y.F., Marion, J.L., 2000. Recreation impacts and management in wilderness: a state-of-knowledge review, in: Cole, N.D., McCool, S.F., Borrie, W.T. O'Loughlin, J. (Comps.), Wilderness science in a time of change conference, Volume 5: Wilderness ecosystems, threats, and management; U.S. Forest Service Rocky Mountain Research Station RMRS-P-15-VOL-5, Ogden, UT, USA, pp 23–48.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640.

Lovich, J.E., Bainbridge, D., 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. Environ. Manage. 24, 309–326.

Lyon, L.J., 1983. Road density models describing habitat effectiveness for elk. J. Forestry 81, 592–613.

Lyon, L.J., 1987. HIDE2: Evaluation of elk hiding cover using a personal computer. U.S. Forest Service, Intermountain Research Station, INT-365, Odgen, UT, USA.

McLain, R., Cerveny, L., Besser, D., Banis, D., Biedenweg, K., Todd, A., Kimball-Brown, C., Rohdy, S., 2013a. Mapping human-environment connections on the Olympic Peninsula: an atlas of landscape values. Occas. Pap. Geogr. 7.

McLain, R., Poe, M., Biedenweg, K., Cerveny, K.L., Besser, D., Blahna, D., 2013b. Making sense of human ecology mapping: an overview of approaches to integrating socio-spatial data into environmental planning. Hum. Ecol. 41, 651.

Montgomery, R.A., Roloff, G.J., Millspaugh, J.J., 2012. The importance of visibility when evaluating animal response to roads. Wildl. Biol. 18, 393–405.

Montgomery, R.A., Roloff, G.J., Millspaugh, J.J., 2013. Variation in elk response to roads by season, sex, and road type. J. Wildl. Manage. 77, 313–325.

Morris, L.R., Proffitt, K.M., Asher, V., Blackburn, J.K., 2016. Elk resource selection and implications for anthrax management in Montana. J. Wildl. Manage. 80, 235–244.

Naylor, M., 2006. Behavioral Responses of Rocky Mountain Elk (Cervus elaphus) to Recreational Disturbance. Oregon State University, Corvallis, Oregon, USA M.S. Thesis.

Naylor, L.M., Wisdom, M.J., Anthony, R.G., 2009. Behavioral responses of North American elk to recreational activity. J. Wildl. Manage. 37, 328–338.

Newsome, D., Smith, A., Moore, S.A., 2008. Horse riding in protected areas: a critical review and implications for research and management. Curr. Iss. Tourism 11, 144–166.

Nielson, R.M., Manly, B.F.J., McDonald, L.L., Sawyer, H., McDonald, T.L., 2009. Estimating habitat selection when GPS fix success is less than 100%. Ecol. 90, 2956–2962.

O'Gara, B.W., Dundas, R.G., 2002. Distribution: past and present. In: Toweill, D.E., Thomas, J.W. (Eds.), North American Elk: Ecology and Management. Smithsonian Institution Press, Washington, D.C., USA, pp. 67–119.

Perry, C., Overly, R., 1977. Impact of roads on big game distribution in portions of the Blue Mountains of Washington, 1972–1973. Washington Game Department Technical Bulletin, Olympia, WA, USA.

Preisler, H.K., Ager, A.A., Wisdom, M.J., 2006. Statistical methods for analyzing responses of wildlife to human disturbance. J. Appl. Ecol. 43, 164–172.

Preisler, H.K., Ager, A.A., Wisdom, M.J., 2013. Analyzing animal movement patterns using potential functions. Ecosphere 43, 32. https://doi.org/10.1890./ES12-00286.1.

Proescholdt, K., 2007. Collision Course? Off-Road Vehicle Impacts on Hunting and Fishing. Izaak Walton League of America, Gaithersburg, MD, USA < http://www.iwla.org/docs/default-source/Outdoor-America-articles/off-track-by-kevin-proescholdt.pdf?sfvrsn=2 > (accessed 17.08.03).

Prokopenko, C.M., Boyce, M.S., Avgar, T., 2016. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. J. Appl. Ecol. 54, 470–479.

Proffitt, K.M., Gude, J.A., Hamlin, K.L., Messer, M.A., 2013. Effects of hunter access and habitat security on elk habitat selection in landscapes with a public and private land matrix. J. Wildl. Manage. 77, 514–524.

Ranglack, D.H., Proffitt, K.M., Canfield, J.M., Gude, J.A., Rotella, J., Garrott, R.A., 2017. Security areas for elk during archery and rifle hunting seasons. J. Wildl. Manage. 81, 778–791.

Rowland, M.M., Bryant, L., Johnson, B., Noyes, J., Wisdom, M.J., Thomas, J.W., 1997. The Starkey Project: History, Facility and Data Collection Methods for Ungulate Research. U.S. Forest Service Gen. Tech. Rep. PNW-GTR-396, Portland, OR, USA.

Rowland, M.M., Wisdom, M.J., Johnson, B.K., Kie, J.G., 2000. Elk distribution and modeling in relation to roads. J. Wildl. Manage. 64, 672–684.

Rowland, M.M., Wisdom, M.J., Johnson, B.K., Penninger, M.A., 2004. Effects of roads on elk: implications for management in forested ecosystems. Trans. N. Amer. Wildl. Nat. Res. Conf. 69, 491–508.

Shepard, E.L.C., Wilson, R.P., Quintana, F., Laich, A.G., Liebsch, N., Albareda, D.A., Halsey, L.G., Gleiss, A., Morgan, D.T., Myers, A.E., Newman, C., Macdonald, D.W., 2008. Identification of animal movement patterns using tri-axial accelerometry. Endang. Species Res. 10, 47–60.

Sicking, L. P. 1998. Rangefinder comparison. USDA Forest Service Technology Development Center Bulletin 9824 1307-SDTDC, San Dimas Technology and Development Center, San Dimas CA, USA < https://www.fs.fed.us/eng/pubs/html/98241307/98241307.html > (accessed 10 November 2017).

Stankowich, T., 2008. Ungulate flight responses to human disturbances: a review and meta-analysis. Biol. Cons. 141, 2159–2173.

Stewart, K.M., Bowyer, R.T., Dick, B.L., Johnson, B.K., Kie, J.G., 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143, 85–93.

Suraci, J.P., Clinchy, M., Mugerwa, B., Delsey, M., Macdonald, D.W., Smith, J.A., Wilmers, C.C., Zanette, L.Y., 2017. A new automated behavioural response system to integrate playback experiments into camera trap studies. Meth. Ecol. Evol. 8, 957–964.

Tarr, N.M., Simons, T.R., Pollock, K.H., 2010. An experimental assessment of vehicle disturbance effects on migratory shorebirds. J. Wildl. Manage. 74, 1176–1183.

Taylor, A.R., Knight, R.L., 2003a. Wildlife responses to recreation and associated visitor perceptions. Ecol. Appl. 13, 951–963.

Taylor, A.R., Knight, R.L., 2003b. Behavioral responses of wildlife to human activity: terminology and methods. Wildl. Soc. Bull. 31, 1263–1271.

Thomas, J. W., Black Jr., H., Scherzinger, R.J., Pedersen, R.J., 1979. Deer and elk. In: Thomas, J.W. (Ed.), Wildlife habitats in the managed forests, the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture Handbook 553, U.S. Government Printing Office, Washington, D.C., USA, pp 104–125.

Thomas, J.W., Leckenby, D.A., Henjum, M., Pedersen, R.J., Bryant, L.D., 1988. Habitat-effetiveness index for elk on Blue Mountain winter ranges. U.S. Forest Service Pacific Northwest Research Station Gen. Tech. Rep. PNW-GTR-218, Portland, OR, USA.

The Outdoor Foundation, 2016. Outdoor Recreation Participation. The Outdoor Foundation, Washington, DC, USA.

Thompson, A., 2007. Management perceptions of off-highway vehicle use on National Forest System lands in Appalachia. West Virginia University, Morgantown WV M.S. Thesis.

USDA Forest Service, 2004. Managing the National Forest System: Great Issues and Great Divisions. U.S. Department of Agriculture, Forest Service report, January 21, 2004, on file, Pacific Northwest Research Station, La Grande, OR, USA.

Venables, W.N., Ripley, B.D., 1997. Modern Applied Statistics with S-PLUS, Second Edition with 1999 Updates. Springer, New York.

Wang, X., Yu, S., Huang, G.H., 2004. Land allocation based on integrated GIS-optimization modeling at a watershed level. Landsc. Urban Plan. 66, 61–74.

Webb, R.H., Wilshire, H.G., 2012. Environmental Effects of Off-Road Vehicles: Impacts and Management in Arid Regions. Springer Science and Business Media, New York, New York.

Wikenros, C., Dries, D.P.J., Kuijper, P.J., Behnke, R., Schmidt, K., 2015. Behavioural responses of ungulates to indirect cues of an ambush predator. Behaviour 152, 1019–1040.

Wisdom M.J., Cook, J.G., Rowland, M.M., Noyes, J.H., 1993. Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range. U.S. Forest Service Gen. Tech. Rep. PNW-GTR-311, Portland, Oregon, USA.

Wisdom, M.J., Holthausen, R.S., Wales, B.C., Hargis, C.D., Saab, V.A., Lee, D.C., Hann, W. J., Rich, T.D., Rowland, M.M., Murphy, W.J., Eames, M.A., 2000. Source habitats for terrestrial vertebrates of focus in the Interior Columbia Basin: broad-scale trends and management implications. U.S. Forest Service Pacific Northwest Research Station Gen. Tech. Rep. PNW-GTR-485, Portland, OR. USA.

Wisdom, M.J., Ager, A.A., Preisler, H.K., Cimon, N.J., Johnson, B.K., 2004a. Effects of off-road recreation on mule deer and elk. Trans. N. Amer. Wildl. Nat. Res. Conf. 69, 531–550.

Wisdom, M.J., Johnson, B.K., Vavra, M., Boyd, J.M., Coe, P.K., Kie, J.G., Ager, A.A., Cimon, N.J., 2004b. Cattle and elk responses to intensive timber harvest. Trans. N. Amer. Wildl. Nat. Res. Conf. 69, 727–758.

Wisdom, M.J. (Ed.), 2005. The Starkey Project: A Synthesis of Long-Term Studies of Elk and Mule Deer. Alliance Communications Group Allen Press, Lawrence, KS, USA.

Witmer, G.W., Wisdom, M.J., Harshman, E.P., Anderson, R.J., Carey, C., Kuttel, M.P., Luman, I.D., Rochelle, J.A., Scharpf, R.W., Smithey, D.A., 1985. Deer and elk. In: Brown, E.R. (Ed.), Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington, part 1-chapter narratives. USDA Forest Service Publication R6-F&WL-192-1985. U.S. Government Printing Office, Washington, DC, USA, pp 41–55.

Yankoviak, M., 2005. Off-Road Vehicle Policy on USDA National Forests: Evaluating User Conflicts and Travel Management. University of Montana, Missoula, MT, USA M.S. Thesis.