To the University of Wyoming:

The members of the Committee approve the Dissertation of Clay B. Buchanan presented on 2/27/2015.

Jeffrey L. Beck, Chairperson

Matthew J. Kauffman, External Department Member

Scott N. Miller

Brenda M. Alexander

Daniel F. Doak

APPROVED:

Robert O. Hall, Director, Program in Ecology

Angela L. Hild, Interim Associate Vice President for Graduate Studies

Buchanan, Clay, B., Elk response to disturbance from development of a coal bed natural gas field in northeast Wyoming, Ph.D., Department of Ecosystem Science and Management, May, 2015.

Expanding development of resources to meet growing world energy demands will inevitably increase impacts on wildlife populations. Building a greater body of knowledge on the impacts of energy resource development is thus critical for future development planning and wildlife population conservation. The elk herd (Wyoming Herd Unit 320) inhabiting the Fortification Creek Area (FCA) in northeastern Wyoming provided an ideal opportunity to isolate and study the impacts of disturbance from energy development on a wildlife population. The objectives of Chapter 2 was to identify elk resource selection and impacts of CBNG development on elk. One of the major findings of Chapter 2 was documentation of shifts in elk resource use where elk avoided areas of development, thereby reducing high use habitat by 43–50%. This chapter was published in *Rangeland Ecology and Management* (67:369–379), with co-authors Jeffrey L. Beck, Thomas E. Bills, and Scott N. Miller. The primary objective of Chapter 3 was to assess the ability of elk to mitigate disturbance impacts through spatial and temporal behavioral changes by applying a novel combination of a frequency of use sampling scheme with a mixed-effects statistical framework. One of the major findings of Chapter 3 was movement of elk into areas closer to disturbance at night to access resources when human activity was reduced. Co-authors on this manuscript include Jeffrey L. Beck, Shaun S. Wulff, and Shannon E. Albeke. The objective for Chapter 4 was to further assess disturbance impacts on the FCA elk herd by assessing population dynamics. Limitations in available demographic data drove the use of an innovative alternative analysis using a Bayesian framework. We successfully applied MCMC techniques to sample posterior distributions of simulated elk demographic traits. This application demonstrated the

applicability of Bayesian-based statistics as an analysis solution when others are inappropriate. The results of this chapter also highlight the influence of harvest on an elk population. We intend to submit this chapter for publication consideration in *Wildlife Biology*.

ELK RESPONSE TO DISTURBANCE FROM DEVELOPMENT OF A COAL BED NATURAL GAS FIELD IN NORTHEASTERN WYOMING

By

Clay B. Buchanan

A dissertation submitted to the Program in Ecology

and the University of Wyoming

in partial fulfillment of the requirements

for the degree of

DOCTORATE OF PHILOSOPHY

in

ECOLOGY

Laramie, Wyoming

May 2015

COPYRIGHT PAGE

DEDICATION PAGE

I dedicate my dissertation and the time necessary to complete this manuscript to my family. During my time as a doctoral student, the composition of my family changed considerably: added my wonderful wife and 3 children, and lost my mother. To my children, Brett, Delainey, and Rylie, I say thank you for giving me an excuse to occasionally walk away from work and for reminding me what is truly important. I give most of the credit for my achievements to my parents, Jack and Trish, who have supported me throughout all of my endeavors. I thank my mom for inspiring me to take chances. Finally, I thank my wife, Erin, for moving to Wyoming and for her continuous support, without which, I would not have completed this journey.

ACKNOWLEDGMENTS

I would like to especially thank my graduate committee for all of their assistance throughout my graduate career. Jeff Beck provided study design assistance and guided the scientific framework on which I based my research questions. As my graduate advisor, Dr. Beck was essential in finding and providing funding, equipment, and collaborative partners, and editing and providing input to multiple documents including proposals, reports, and manuscripts. Dr. Beck also encouraged cooperation among students in his lab, which created a “group think” atmosphere and benefitted all those involved. Matt Kauffman provided assistance with study design and statistical support. Dr. Kauffman also helped in refining my focus questions when there were no clear answers. Scott Miller offered expertise in obtaining and analyzing spatial data throughout my tenure at the University of Wyoming. Dr. Miller was also the co-chair of my committee for the first years of my dissertation, during which he offered general advice on graduate student life and the process of fulfilling a graduate degree. Brenda Alexander provided guidance in areas of body condition, stress hormones, and development. Dan Doak increased my understanding of population dynamics and Program R and provided great insight in developing my final dissertation chapter.

I thank the Hayden, Powder River, and Maycock Ranches for property access. Heather O’Brien, Jim Verplanke, Lynn Jahnke, James Hobbs, Troy Achterhof, Luke Driessen, Maciej Pike-Biegunski, and Jordan Ongstad provided logistical and field assistance. I particularly thank Tom Bills from the Buffalo Wyoming Field Office of the Bureau of Land Management for his insights and leadership throughout my research. Cody Molle (Ruminant Nutrition Laboratory, University of Wyoming) provided technical assistance with forage quality analysis. I thank Scott Newbold and his students from Sheridan College for their efforts in organ collection and analysis. Jim Pope and Mark Atchison (Leading Edge Aviation, LLC.) provided assistance in capture operations. My research was funded in part by the Bureau of Land Management, the School of Energy Resources, the Wyoming Reclamation and Restoration Center, and the Program in Ecology at the University of Wyoming, Anadarko Petroleum Corporation, Petro-Canada, Marathon Oil Company, and the Wyoming Game and Fish Department. I conducted our field research including capture, handling, and marking female elk according to Wyoming Game and Fish Department Chapter 33-396 permit and the University of Wyoming Institutional Animal Care and Use Committee protocol 04172008. I also thank Brenna Marsicek and Cindy Wood; without their administrative efforts my graduate career and research would not have been possible. Shaun Wulff, PhD, was particularly helpful in providing statistical assistance and offering to test my ideas for alternative analyses. Shannon Albeke, PhD, was a great resource for collaborative idea development including informal student-driven work groups. Dr. Albeke also provided numerous sessions of R coding assistance and computer capabilities to run analysis on large datasets.

TABLE OF CONTENTS

Contents

LIST OF TABLES

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

LIST OF FIGURES

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

CHAPTER ONE

Introduction

The concept that predation has non-consumptive consequences for prey populations is well supported in the peer-reviewed literature and is considered an integral component in the explanation of predator-prey interactions. In one foundational paper, red-legged grasshoppers (*Melanoplus femurrubrum*) continued to change their foraging behavior in the presence of nursery web spiders (*Pisurina mira*) even though the spiders' ability to predate grasshoppers had been compromised (Schmitz et al. 1997). After losing their tails, striped plateau lizards (*Sceloporus virgatus*) responded to increased predation risk by increasing their flight initiation distance and increasing the use of refuges (Cooper and Wilson 2008). Non-consumptive effects of predation are currently deemed a great influence on wildlife community interactions and research in this field will continue to be of increasing value in the conceptualization of wildlife population dynamics. Similarly, our understanding of wildlife responses to disturbance risk will provide great insight into the conservation of natural communities.

The concept of disturbance risk as an influence on wildlife behavior has been noted for at least 4 decades (Walther 1969); however, only relatively recently has a framework for research in this field been developed (Frid and Dill 2002). Similar to predation risk, disturbance risk is concerned with the non-consumptive effects of anthropogenic disturbance. In the wake of an ever increasing human population and gaining popularity of the disturbance risk hypothesis, the effects of numerous anthropogenic activities have become the focus of wildlife research and conservation efforts. Aircraft flights (Krausman et al. 1998), hiking (Taylor and Knight 2003), skiing (Patthey et al. 2008), terrestrial vehicle traffic (on and off road), watercraft (Burger 1998), ecotourism (Weinrich and Corbelli 2009), and energy development (Sawyer et al. 2009) are some of the activities of focus in disturbance risk research. When coping with disturbance risk, animals may alter normal resource use and behavioral patterns. The costs of these pattern changes may manifest themselves through population distribution shifts, decreased body condition, diminished reproductive output, and ultimately, population decline (Gill et al. 2001, Johnson et al. 2005).

An animal should select resources in a manner that increases its fitness, hence selecting the best available habitat. Therefore, if disturbance stimuli cause an animal to avoid an area that was previously used, then a decline in resource availability and fitness is probable. Unable to locate alternative, high quality habitat, capercaillie (*Tetrao urogallus*) in southwestern Germany were forced to use suboptimal resources during the winter ski season (Thiel et al. 2008). Though environmental factors may be a part of the increased stress on these birds during the winter months, a population decline of 65% suggests negative consequences of suboptimal resource selection as a result of disturbance risk (Thiel et al. 2008). Bottlenose dolphins (*Tursiops sp.*), a growing tourist attraction in Shark Bay, Australia, are being displaced by the very boats used to provide tourists with a dolphin watching experience (Bejder et al. 2009). Although no detrimental population effects have been measured for the Shark Bay dolphin population as a whole, the future management of marine tourism activities suggests consideration of long term viability of both ecotourism trade and marine wildlife populations (Bejder et al. 2009). The development of energy resources has caused greater sage-grouse (*Centrocercus urophasianus*) to avoid otherwise suitable habitats, thus it may be critical to employ more stringent temporal and spatial regulations on development practices (Holloran 2005, Doherty et al. 2008, Kirol et al. 2015). The subdivision of previously open areas in parts of southern Kenya decreased animal movement and increased continuous livestock grazing intensity within constrained habitat, resulting in a sharp decline in wildlife numbers (Western et al. 2009).

Growing evidence from recent research offers examples of the influence of disturbance risk on ungulate behavior. The effects of recreational activities have been measured for a number of ungulate species. Often ungulate response in the case of recreational disturbance is highly influenced by the approach of the person or vehicle (Naylor et al. 2009). Similar to the approach of a predator, speed and angle of the approaching risk are important factors in the response intensity; faster more direct approaches pose a greater threat. Counter to that fact is the elevated response elicited by humans on foot, which may pose a greater threat due to the unpredictability of the encounter (Papouchis et al. 2001). Ungulates demonstrated physiological and behavioral changes as a result of aircraft overflights (Maier et al. 1998), although their activity often returned to normal soon after the cessation of the flights (Weisenberger et al. 1996, Krausman et al. 1998). More linear infrastructures are commonly considered to act as barriers or in the least cause some temporal or spatial avoidance of the impacted area (Dyer et al. 2002, Vistnes et al. 2004). Roads and other infrastructure, such as power lines are regularly avoided (Vistnes et al 2004) especially when accompanied by increased human activity (e.g., higher traffic levels; Rowland et al. 2000). The consensus throughout most of the scientific ecological community is the measurable presence of negative disturbance effects on ungulate species. However, some have provided examples where disturbance has little or no influence on some ungulate populations (e.g., caribou [*Rangifer tarandus*] in North American oilfields; Van Dyke 1996, Cronin et al. 1998, Noel et al. 2004). Thus there are some inconsistencies in the conclusions developed from ungulate disturbance risk studies, meaning we still lack a clear understanding of the relationship between ungulate population dynamics and disturbance risk.

The aim of my dissertation research was to add to the cumulative knowledge on wildlife disturbance risk through quantitative assessment of the wildlife-disturbance relationship. The elk herd (Wyoming Game and Fish Department Herd Unit 320) inhabiting the Fortification Creek Area (FCA) in northeastern Wyoming provided an ideal opportunity to isolate and study the impacts of disturbance on a wildlife population. In Chapters 2–4 my coauthors and I document elk response to development of a natural gas field using multiple analytical tools. The objective of Chapter 2 was to identify elk behavioral and distribution response to the disturbance from development of a natural gas field. The objectives of Chapter 3 were to assess the ability of elk to mitigate disturbance impacts through spatial and temporal behavioral changes by applying a novel combination of a frequency of use sampling scheme with a mixed-effects statistical framework. Chapter 4 completes the picture of disturbance impacts on the FCA elk herd by assessing population dynamics.

LITERATURE CITED

Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Conner, M. Heithaus, J. Watson-Capps, C. Flaherty, and M. Krutzen. 2009. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20:1791–1798.

Burger, J. 1998. Effects of motorboats and personal watercraft on flight behavior over a colony of common terns. Condor 100:528–534.

Cooper, W. E., and D. S. Wilson. 2008. How to stay alive after losing your tail. Behaviour 145:1085–1099.

Cronin, M. A., S. C. Amstrup, G. M. Durner, L. E. Noel, T. L. McDonald, and W. B. Ballard. 1998. Caribou distribution during the post-calving period in relation to infrastructure in the Prudhoe Bay oil field, Alaska. Arctic 51:85–93.

Doherty, K., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 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.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11–26.

Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioral responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265–268.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocerus urophasianus*) population response to natural gas field development in western Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. Wildlife Monographs 160:1–36.

Kirol, C. P., Beck, J. L., Huzurbazar, S. V., Holloran, M. J., and S. N. Miller. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications 25:*In press*.

Krausman, P. R., M. C. Wallace, C. L. Hayes, and D. W. DeYoung. 1998. Effects of jet aircraft on mountain sheep. Journal of Wildlife Management 62:1246–1254.

Maier, J. A. K., S. M. Murphy, R. G. White, and Michael D. Smith. 1998. Responses of caribou to overflights by low-altitude jet aircraft. Journal of Wildlife Management 62:752–766.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management 73:328–338.

Noel, L. E., K. R. Parker, and A. A. Cronin. 2004. Caribou distribution near an oilfield road on Alaska’s North Slope, 1978–2001. Wildlife Society Bulletin 32:757–771.

Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. Journal of Wildlife Management 65:573–582.

Patthey, P., S. Wirthner, N. Signorell, and R. Arlettaz. 2008. Impact of outdoor winter sports on the abundance of a key indicator of alpine ecosystems. Journal of Applied Ecology 45:1704–1711.

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.

Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052–1061.

Schmitz, O. J., A. P. Beckerman, and K. M. Obrien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388–1399.

Taylor, A. R. and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications 13:951–963.

Thiel, D., S. Jenni-Eiermann, V. Braunisch, R. Palme, and L. Jenni. 2008. Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. Journal of Applied Ecology 45:845–853.

Van Dyke, F. and W. C. Klein. 1996. Response of elk to installation of oil wells. Journal of Mammalogy 77:1028–1041.

Vistnes, I., C. Nelleman, P. Jordhoy, and O. Strand. 2004. Effects of infrastructure on migration and range use of wild reindeer. Journal of Wildlife Management 68:101–108.

Walther, F. R. 1969. Flight behaviour and avoidance of predators in Thomsons gazelle – (*Gazella thomsoni guenther* 1884). Behaviour 34:184–221.

Weinrich, M. and C. Corbelli. 2009. Does whale watching in southern New England impact humpback whale (*Megaptera novaeangliae*) calf production or calf survival? Biological Conservation 142:2931–2940.

Weisenberger, M. E., P. R. Krausman , M. C. Wallace, D. W. De Young, and O. E. Maughan. 1996. Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. Journal of Wildlife Management 60:52–61.

Western, D., R. Groom, and J. Worden. 2009. The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem. Biological Conservation 142:2538–2546.

CHAPTER TWO

Seasonal Resource Selection and Distributional Response by Elk to Development of a Natural Gas Field

Clay B. Buchanan[1], Jeffrey L. Beck[1], Thomas E. Bills[2], and Scott N. Miller[3]

[1]Department of Ecosystem Science and Management, University of Wyoming, 1000 E. University Ave., Laramie, WY 82071, USA.

[2]Bureau of Land Management, Buffalo Field Office, Buffalo, WY 82834, USA.

[3]Department of Ecosystem Science and Management, University of Wyoming, 1000 E. University Ave., Laramie, WY 82071, USA; and Wyoming Center for Environmental Hydrology and Geophysics, University of Wyoming, 1000 E. University Ave., Laramie, WY 82071, USA.

Rangeland Ecology and Management 67:369–379

Abstract:

Global energy demand is predicted to increase dramatically, suggesting the need to better understand the role of disturbance from energy development and develop more efficient conservation strategies for affected wildlife populations. We evaluated elk (*Cervus elaphus*) response to disturbance associated with natural gas development in summer and winter, including shifts in resource selection and concomitant distribution. We collected elk locations prior to (1992–1995) and during (2008–2010) coal bed natural gas (CBNG) development in the ~498-km^2 Fortification Creek Area (FCA) of northeastern Wyoming, USA where approximately 700 CBNG wells and 542 km of collector, local, and resource roads were developed from 2000 through 2010. We developed resource selection functions for summer and winter using coordinate data from VHF-collared female elk prior to CBNG development and similar location data from GPS-collared female elk during CBNG development to assess spatial selection shifts. By pooling across all locations we created population level models for each time period (e.g., pre- and during-development) and incorporated individual variation through bootstrapping standard errors for parameter estimates. Comparison of elk resource selection prior to and during natural gas development demonstrated behavioral and distributional shifts whereby during-development, elk demonstrated a higher propensity to use distance and escape cover to minimize exposure to roads. Specifically, during-development elk selected areas with greater Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) cover, increased terrain ruggedness, and farther from CBNG roads than prior to development. Elk distributional changes resulting from avoidance behavior lead to a loss of high use areas by 43.1% and 50.2% in summer and winter, respectively. We suggest reducing traffic, protecting woody escape cover, and maintaining refugia within the energy development footprint to promote persistence of elk within energy fields.

INTRODUCTION

Generally, the distribution of wildlife is the result of animals selecting for or against surrounding habitat characteristics (Boyce and McDonald 1999). Animals must often balance tradeoffs between acquiring resources and reducing risk from predation or disturbance (Lima and Dill 1990; Schmitz et al. 1997; Frid and Dill 2002). Increasingly animal resource selection is influenced by human disturbance including energy extraction activities, which is a rapidly expanding source of disturbance for a variety of species across the globe (e.g., Cameron et al. 2005; Bayne and Dale 2011; Smith et al. 2014). Large populations of ungulates overlap the distribution of extensive energy resources in forest and rangeland ecosystems across western North America (Sawyer et al. 2006, 2009a,b; Hebblewhite 2008; Sorensen et al. 2008), providing scientists and natural resource managers opportunities to evaluate the influences of energy development on these populations and to identify factors that may provide options for mitigation.

Much of the Intermountain Region of western North America has low human population densities and thus wildlife experience relatively low disturbance from anthropogenic activities (Sanderson et al. 2002). However, the U.S. Energy Information Administration has predicted a 44% increase in the world consumption of energy between 2006 and 2030 (EIA 2009). In contrast to land use practices such as ranching, the development and extraction of energy resources includes substantial infrastructure and anthropogenic activity. For example, the Bureau of Land Management (BLM) has stated that 1 natural gas well is, on average, accompanied by 2 km of roads, which does not include the disturbance incurred by connecting pipelines, tanker truck transport of hydrocarbon products, or electrical power lines (BLM 2003). Copeland et al. (2011) predicted the overall influence of energy development could directly or indirectly affect up to 21% or 96 million ha of the 5 major ecosystems in western North America including grassland, boreal forest, shrubland, temperate forest, and wetland. A critical concern for wildlife conservation is the direct habitat loss resulting from energy extraction; however, the indirect impacts of energy development on ungulate species may be of greater concern than the direct loss of habitat (Van Dyke and Klein 1996; Sawyer 2006; Hebblewhite 2008; Festa-Bianchet et al. 2011). Previous work demonstrated indirect influences of energy development on ungulates. For example, mule deer (*Odocoileus hemionus*) in western Wyoming avoided natural gas wells on winter range, thus shifting their distribution, resulting in population declines across the area of development (Sawyer et al. 2006; 2009a). Cumulative influences of energy development and forestry activities have been shown to result in changes in habitat use and population growth rate on boreal caribou (*Rangifer tarandus caribou*) in northern Alberta (Sorensen et al. 2008). Elk (*Cervus elaphus*) are known to avoid roads, thus reducing habitat availability (Rowland et al. 2000; Sawyer et al. 2007; Frair et al. 2008). Documented changes in levels of human activity were thought to drive shifts in elk avoidance behavior in respect to roads in south-central Colorado (Dzialak et al. 2011). Others have examined the influences of energy extraction activities on elk populations (Hiatt 1981; Ward 1986; Van Dyke and Klein 1996); however, these studies typically lacked sufficient sample sizes or predevelopment data to provide a rigorous analysis of potential impacts of energy development on elk (Hebblewhite 2008).

The Fortification Creek Study Area (FCA), which encompassed Wyoming Game and Fish Department Elk Herd Unit 320 in northeastern Wyoming, USA, provided us an opportunity to isolate the effects of energy development on elk. The FCA elk population experienced limited human-related impacts prior to the initiation of large-scale energy development in the early 2000s because of restricted access to the area and land use dominated by livestock grazing.. Previous monitoring of elk in Elk Herd Unit 320 during the 1990s provided knowledge of elk resource selection prior to the initiation of coal-bed natural gas (CBNG) development (WGFD 1996, 2007a). Our specific objectives were to (1) identify summer and winter elk resource selection within the study area prior to CBNG development, and (2) compare two independent measures of population-level resource selection (e.g., pre- and during-development) to assess elk distributional and resource selection shifts associated with energy development. We predicted elk would alter their distribution and resource selection in response to CBNG development.

METHODS

Study Area

We conducted our study in the 498 km^2 FCA, approximately 40 km west of Gillette, Wyoming, USA. Elevation in the study area ranged from 1,130 to 1,463 m. The northern portion of the study area included a 49-km^2 BLM wilderness study area (BLM 2008). The BLM (44%), State of Wyoming (6%), and private landowners administered the FCA, which encompassed portions of Campbell, Johnson, and Sheridan counties. Cattle grazing occurred across the FCA in pre- and during development stages of CBNG development. Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp.*wyomingensis* Beetle & Young) shrubland dominated land cover with scattered patches of Rocky Mountain juniper (*Juniperus scopulorum Sarg.*; hereafter, juniper) that comprised only 11% of the landscape. Grasses common to the northern mixed-grass prairie dominated our study area including bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), cheatgrass (*Bromus tectorum* L.), little bluestem (*Schizachyrium scoparium* [Michx.] Nash*), and western wheatgrass (Pascopyrum smithii* [Rydb] Á. Löve*).* Northeast Wyoming is characterized by a semiarid climate with an average annual precipitation of about 22 cm (WRCC 2009). Annual precipitation during our study averaged 23 cm, of which >90% fell between April and October. During our study, the average temperature was 9.0 C° with an average daily maximum and minimum temperature of 15.4 and 3.4 C°, respectively (WRCC 2009).

From 2008 to 2010, the FCA provided yearlong habitat for approximately 230 non-migratory elk (WGFD 2007a). Elk population numbers have remained relatively stable since the initiation of consistent yearly harvest seasons in 2000, but ranged from 180 to 400 during the 1990s (WGFD 2007b). Over 700 CBNG wells and 542 km of roads were developed in the FCA since the early 2000s and the BLM has projected potential field development of approximately 2,000 wells with 0.32-km^2 (80 ac) well spacing (BLM 2008).

Elk Capture and Monitoring

Data used for our temporal control were collected from 1992 to 2000 by the Wyoming Game and Fish Department using VHF radio collars affixed to 17 female elk; however, we limited our analysis to data from 1992–1995 when bimonthly relocations were collected via fixed wing aircraft flights (WGFD 1996). To obtain information on elk response to CBNG development, we used helicopter net-gunning (Leading Edge Aviation, Lewiston, ID, USA) to capture 59 adult female elk in March and December 2008. Captured elk were fitted with Global Positioning System (GPS) collars (North Star Science and Technology, LLC, King George, VA, USA) programmed to collect 1 location every 5 hours over 3 years (2008–2011). Across individuals we observed GPS fix rates ranging from 58 to 98%. Habitat characteristics that block satellite transmission or random collar failure can cause fix rates of less than 100% which can result in erroneous conclusions (Moen et al. 1996; D'Eon et al. 2002; Nielson et al. 2009). We tested for differences in resource selection between animals with high (≥90%) and low (<90%) GPS fix rates using independent sample *t*-tests. Because we found no differences ($P > 0.05$) in resource selection coefficients between high and low fix rate groups we included all animals in resource selection modeling. We defined summer (1 Apr–31 Oct) and winter (1 Nov–31 Mar) seasons based on development timing stipulations and forage green up (green-up based on field observations and NDVI measurements).

Anthropogenic Predictor Variables

We digitized roads in a GIS using National Agriculture Imagery Program (USDA-FSA, Aerial Photography Field Office, Salt Lake City, UT, USA) and Landsat (USGS-EROS Center, Sioux Falls, SD, USA) imagery at 1 m and 30 m resolutions, respectively. We then developed decay distance variables as a function of Euclidean distance to roads using the form $e^{-d/\alpha}$ where d was the distance from each pixel to roads in meters and α were constant values of 100, 500, 1,000, 1,500, 2,000, 3,000, 4,000, and 5,000. The decay function scaled the distance variables between 1 and 0, with values increasing in proximity to roads. We had initially included well pads as a predictor variable, but a correlation ($|r|$) >0.60 with roads obligated removal of one of the variables. In the interest of interpretation simplicity, we kept roads and removed distance to well pads from further analysis.

Environmental Predictor Variables

We developed a suite of environmental variables to assess elk resource selection. Previous work has suggested that elevation (Sawyer et al. 2007; Gregory et al. 2009; Beck et al. 2013), terrain ruggedness (Skovlin et al. 2002; Frair et al. 2005), cover type (Beck et al. 2006; Barbknecht et al. 2011; Beck et al. 2013), and distance to water (Beck et al. 2006) are important predictors of elk resource selection. Thus we included elevation, vector ruggedness measure (VRM; Sappington et al. 2007), percent juniper cover, and north- and south-oriented sagebrush cover in our analyses. In addition to being previously used by others, we determined these variables were important for the FCA elk herd, which due to the physical nature of the landscape, provided the main sources of escape and thermoregulatory cover. We also included a viewshed metric, which measured the number of road segments from which any particular location on the FCA landscape could be observed. Landscape visibility has been demonstrated as an important variable for wildlife in response to disturbance (Ndaimani et al. 2013). The viewshed metric was driven by topography and line of sight, where locations on the landscape that could be observed from many road segments were assigned a high value and locations on the landscape that could be seen from few road segments were assigned a low value. We derived elevation from a 10 m resolution digital elevation map (National Elevation Dataset, USGS, Sioux Falls, SD, USA). We identified and classified juniper and sagebrush cover using 30 m landcover data developed at the University of Wyoming (Landcover_REGAP_2007, Wyoming Geographic Information Science Center, University of Wyoming, Laramie, USA). We separated environmental variables into cover type and terrain groups, to simplify variable and model selection.

Statistical Analyses

Our study used pre- and during-development data as two independent measures of elk resource selection and variation to assess change in selection through time. We modeled resource selection at the population level by pooling location data across all individuals. Similar to Nielson and Sawyer (2013) and Sawyer et al. (2006; 2007; 2009a), we used relative frequency of use as the response variable in a resource selection function (RSF; Manly et al. 2002) framework to model the probability of use for each elk as a function of anthropogenic and environmental predictor variables (Marzluff et al. 2004). RSF models using elk location data were developed for pre- and during-development for summer (1 Apr–31 Oct) and winter (1 Nov–31 Mar) periods. We mapped probability of elk use across the FCA using the best fit population-level models and compared elk resource selection between pre- and during-development periods. Changes in the distribution of elk selection probabilities across years provided a means to evaluate the influence of CBNG development on elk resource selection in summer and winter.

We used 3 000 randomly placed circular sampling units of 250-m radii to extract habitat variables and estimate intensity of use by elk (Sawyer et al. 2009*a*; Nielson and Sawyer 2013). Sampling unit size should reflect the scale of changes in animal concentrations and movement, but still include adequate locations to approximate a known error distribution (e.g., Poisson or negative binomial distributions; Millspaugh et al. 2006). Because a large number of sampling units contained no elk locations, we used a negative binomial distribution, which is more adapted for overdispersion than the Poisson distribution (White and Bennetts 1996; Millspaugh et al. 2006). Sampling units of a 250-m radius fit the scale of elk movement patterns (e.g., distance between consecutive GPS locations for an individual animal) in the FCA and sampling units of that size have been successfully used in another elk study with similar GPS fix rate schedules (Sawyer et al. 2007). We extracted both anthropogenic and environmental variable data, averaged across each sampling unit, and counted the number of elk locations within each sampling unit. Using this method, sampling units may overlap, therefore they are not mutually exclusive and the unit-sum constraint does not apply (Aebischer et al. 1993). The size of the sampling unit also allows for a range of expected telemetry location error without affecting model results (Nielson and Sawyer 2013). The response variable within our analyses was a count of locations in each sampling unit allowing the treatment of elk locations as a random variable. Using location frequency within each sampling unit as the response variable removed any associated time stamp other than the period of interest (e.g., summer) while, providing a measure of relative intensity of elk use with respect to predictor variables of interest. Thus, issues of sample size are less of a hindrance to analysis because we did not model resource selection based on a single point at a time (e.g., logistic regression), but rather two independent measures (e.g., pre- and during development) of relative intensity of resource use.

Prior to model development, we used multiple methods of variable screening. First, we evaluated collinearity between variables using Pearson's pairwise correlation and excluded highly correlated variables ($|r| > 0.60$) based on variable performance using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We conducted this variable screening process for anthropogenic and environmental predictor variables. There were no highly correlated environmental predictor variables in our dataset, however, we used AIC$_c$ to select the top performing or competitive environmental variables for cover type and terrain variable groups to reduce the number of variables in our candidate set. Many of the decay distance variables were highly correlated, thus we retained only 1 decay distance variable by selecting the top performing variable using AIC$_c$. Second, we did not allow competing variables to remain in a model if the sign of either variable switched upon inclusion of the other variable. Lastly, we screened remaining variables to ensure they were informative by assessing whether 85% CI's around parameter estimates for each variable included zeroes (Arnold 2010). Selected variables were carried forward to develop our list of candidate models.

We created population level RSF models for summer and winter prior to and during CBNG development. The RSF models were developed following the form:

$$\ln[E(t_i)] = \ln(T) + \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} \ldots + \beta_p x_{pi} \qquad (1)$$

where t_i is the total number of elk locations within sampling unit i, ln(T) is the offset term, β_0 is the intercept term, $\beta_1, \beta_2, \ldots, \beta_p$ are the estimated coefficient terms, $x_{1i}, \ldots, x_{pi}$ are the measured values of p covariates on sampling unit i, and E[.] represents the expected value (Sawyer et al. 2006; 2009a). The offset term rescales the response as a relative frequency of use rather than a count of locations. We bootstrapped (iterations = 1000) across individuals using the final model to estimate standard errors for model coefficients for the during-development dataset, which provided a means to account for individual variation (Nielson and Sawyer 2013). This approach addressed two major problems of resource selection functions: pooling across individuals and ignoring correlation among animal locations, by designating the individual animal as the experimental unit (Thomas and Taylor 2006). We bootstrapped (iterations = 1000) locations irrespective of individuals, to estimate standard errors for the predevelopment model coefficients,. This was necessary because of the relatively small number of locations included in the predevelopment dataset. Top performing models were selected using $\mathrm{AIC_c}$ ($\Delta\mathrm{AIC_c} < 4$; Arnold 2010) from a multi-model candidate set for the predevelopment dataset. We used model averaging to calculate mean coefficients, standard errors, and 95% confidence intervals when a single top model was not identified among candidate models (Burnham and Anderson 2002).

After identifying the top model for summer and winter predevelopment data sets, we applied these models to the during-development data sets for summer and winter, respectively. Application of the same models to both pre- and during-development data sets was necessary to make accurate comparisons of change in coefficient sign and magnitude, as inclusion of alternative or additional variables would have in itself influenced variable coefficients. Differences were identified by assessing overlap of 95% confidence intervals for each variable coefficient. We documented magnitude of change using a ratio of during-development ($_d$) coefficient estimates to predevelopment ($_b$) coefficient estimates using:

$$ratio = \frac{x_{i,d}}{x_{i,b}} \text{ ,} \tag{2}$$

and ratio standard errors were calculated using,

$$SE(ratio) = \frac{x_{i,d}}{x_{i,b}} \sqrt{\left(\frac{SE\left(x_{i,d}\right)}{x_{i,d}}\right)^2 + \left(\frac{SE\left(x_{i,b}\right)}{x_{i,b}}\right)^2 - \frac{2\operatorname{cov}\left(x_{i,d}, x_{i,b}\right)}{x_{i,d} \times x_{i,b}}} \text{ ,} \tag{3}$$

where, $x_{i,d}$ was variable coefficient i during-development and $x_{i,b}$ was variable coefficient i predevelopment. Ratios less than 1 suggested a decrease in selection magnitude, while ratios greater than 1 suggested an increase in selection magnitude. We then mapped each model back on the FCA landscape as a relative probability of elk use. All map values were verified to be between 0 and 1 so as not to fall outside of our range of inference. We then binned map pixel values into 5 quantiles: high use, 100–81%; medium-high use, 80–61%; medium use, 60–41%; medium-low use, 40–21%; and low use, 20–0%, to assist in interpretation of model probabilities.

We validated our predevelopment models by separating our probability of use maps during each season in 10 equal distribution bins. Predevelopment and validation locations were overlaid on probability distribution bin maps to assign each location with a distribution bin value. We used an independent data set of 290 elk locations recorded from 1993–2000 as a validation location dataset. The validation dataset were opportunistic locations of un-collared elk taken during relocation flights using a handheld GPS unit. We took an average distribution of 5 iterations of 100 randomly sampled locations across the 10 distribution bins to validate both summer and winter models. We used Spearman's rank correlations (r_s) to compare location frequency distributions of predevelopment data with average frequency distributions of the validation data set. All statistical analyses were conducted in R language and environment (R Development Core Team 2011; Package MASS).

RESULTS

We used 256 locations from 17 elk in our summer 1992–1995 predevelopment resource selection model and 69 307 GPS locations from 55 GPS-collared female elk to assess summer resource selection during CBNG development. Only 55 of 59 captured female elk were used in our during-development analysis due to collar failure. We used 149 locations from 17 female elk to model resource selection in winters 1992–1995 prior to CBNG development and 44 033 GPS locations from 55 GPS-collared female elk to assess winter resource selection during CBNG development.

Elk Resource Selection

Predevelopment. The top model explaining elk resource selection in summer prior to CBNG development included 3 variables and no other models were competitive with this top model (Table 1). In summer, prior to CBNG development, elk selected for areas with higher percent juniper cover, lower percent north-facing sagebrush cover, and away from roads (Table 2; Fig. 1a). High use areas in summer predevelopment averaged 32% juniper cover, 21% north-facing sagebrush cover, and 1 136 m from roads. In winter prior to CBNG development, the top 6 models were competitive in explaining elk resource selection (Table 1). Prior to CBNG development in winter, elk selected for areas with increased juniper cover, increased terrain ruggedness, increased slope, decreased viewshed exposure, and away from roads (Table 2; Fig. 1b). Model-averaged 95% confidence limits bounding the parameter estimate of the variable coefficient for decay distance to roads overlapped 1; therefore, we considered decay distance to roads as uninformative for elk resource selection in winter predevelopment. However, we retained decay distance to roads for the application of our top predevelopment model to the during-development data set to assess change in elk distribution as influenced by roads. Predevelopment, high use areas in winter averaged 34% juniper cover, 0.05 VRM, 38% slope, 7.9 viewshed measurement, and 995 m from roads.

The Spearman's rank correlation coefficient (r_s) for the summer season predevelopment model compared to validation data was 0.90 and was 0.86 for the top winter season predevelopment model compared to validation data. These correlation coefficients indicated our top models in summer and winter predevelopment were strong, positive predictors of elk resource selection.

Comparison of Pre- and During-Development Resource Selection. By applying the top-performing predevelopment model to the during-development data set we compared pre- and during-development RSF results in summer and winter (Fig. 1). In summer, pre- and during-development coefficients differed across all variables (Table 2). The coefficient for decay distance to roads (calculated with a constant value of 500 m) demonstrated the greatest change resulting in an increased avoidance behavior of elk from roads of more than 5 times (Fig. 2a,c). When we applied the top-performing predevelopment model to the during-development GIS and location data, high use areas averaged 26% juniper cover, 27% north-facing sagebrush cover, and 2 459 m from roads in summer. Comparisons of predicted high use areas indicated a change of –6% juniper cover, +6% north-facing sagebrush cover, and +1 323 m from roads in summer. In winter, pre- and during-development coefficients differed across percent juniper, viewshed, and decay distance to roads (Table 2). Again, the coefficient for decay distance to roads (calculated with a constant value of 500 m) demonstrated the greatest change resulting in an increased avoidance of 118 fold (Table 2, Fig. 2b, d). Ratios for VRM and distance to roads were not expressed graphically as 95% confidence limits overlapped 1 (Table 3). When we applied the top performing predevelopment model to the during-development GIS and location data, high use areas averaged 21% juniper cover, 0.04 VRM, 33% slope, 2.3 viewshed measurement, and 2 594 m from roads in winter. Comparisons of predicted high use areas indicated a change of –13% juniper cover, –0.1 VRM, –5% slope, –7.6 viewshed measurement, and +1 599 m from roads in winter

High use areas made up 20% of the landscape; however, these areas encompassed approximately 60.5% and 59.2% of during-development elk locations in summer and winter, respectively. Spatial comparisons between relative probabilities of elk use pre- and during-development across the FCA, identified losses of areas categorized as high use prior to CBNG development. In summer, the loss of previously identified high use areas was 43.1% (Fig. 3a). During winter, the loss of high use habitat was 50.2% (Fig. 3b).

DISCUSSION

Our results indicate that elk responded to CBNG development by avoiding roads during both summer and winter. The avoidance response was especially evident in winter where the model coefficient for distance to roads was two orders of magnitude greater during than prior to development. Predictive environmental variables differed somewhat between winter and summer selection and with the exception of VRM and slope in winter, variables demonstrated some change from the pre- to during-development datasets. In summer during-development, elk selected for areas with greater juniper cover while avoiding north-facing sagebrush in comparison to predevelopment selection. In winter during-development, elk selected for areas of decreased juniper cover and visibility than they did prior to development.

As observed in other ungulate populations (Cameron et al. 2005; Sawyer et al. 2009a), elk avoidance behavior resulted in a distribution that mirrored the distribution of development through time. In the FCA, elk distribution shifts resulted in approximately 43% and 50% loss of habitat classified as high use predevelopment in summer and winter seasons, respectively. Our results suggest the observed shifts were likely driven by elk avoidance of human activity associated with CBNG development. Others have made similar observations of a direct relationship between the level of human activity and the level of observed response in wildlife species (Nellemann et al. 2001; Vistnes et al. 2001; Gavin and Komers 2006). Human activities with varying levels of intensity (e.g., recreation or energy development) are important to consider because of their spatial and temporal unpredictability (Haskell and Ballard 2008; Neumann et al. 2010). Reducing the footprint of CBNG development and extraction should be a priority to mitigate impacts from energy development (Sorensen et al. 2008); however, it may be equally beneficial for stakeholders to focus efforts toward reducing traffic levels (Fahrig and Rytwinski 2009; Sawyer et al. 2009; but see Vistnes and Nellemann 2001).

Although ranch access and utility roads have existed in the FCA for decades, there was little change in elk distribution associated with these roads prior to CBNG development (WGFD 1996; WGFD 2007a). Consistent elk distribution across the FCA suggests conditions dictating elk resource selection were also relatively consistent prior to CBNG development. However, during-development we observed increases in the magnitude of elk avoidance behavior in relation to roads. Model comparisons between pre and during data sets revealed differences between selection coefficients, suggesting changes in behavior through time. Seasonal avoidance distances from roads increased 1.3–1.5 km during-development based on the average distance to roads in high use areas. In the time between our pre- and during-development data sets there was little change in land use practices or land cover aside from the impacts caused by CBNG development. As there were no other landscape-level changes in the FCA during this time period, we are confident that we isolated the impacts of development and therefore the driving factors behind elk distributional shifts. In addition, high correlation coefficients from our validation exercise with an independent sample of elk locations suggest strong support for the ability of our models to predict elk distribution predevelopment in summer and winter. Our models thus provided a useful tool to measure elk resource use across the FCA in response to CBNG activity.

In an ideal setting, our predevelopment dataset would have equaled our during-development dataset, however, that was not the case. The predevelopment dataset was, however, consistent with VHF samples sizes from data collected that were subsequently used to model home range and resource selection (Kochanny et al. 2009; Beck et al. 2013). There are two reasons we feel confident in making comparisons between our VHF and GPS datasets. First, by comparing the outputs of the same RSF model applied to both datasets we are assessing differences between two independent measures of the same phenomenon thus, creating sound basis for comparison. Second, our modeling is based on intensity of use, thus the response variable in both the pre- and during-development models becomes a relative frequency of use rather than sets of spatial points (e.g., use v. non-use), thus decreasing the issue of sample size. It was also anticipated that the location error for the 2 datasets was different. However, we were able to ignore the difference in error because our sampling unit size was likely larger than the expected error for both VHF and GPS collars.

Elk population numbers in the FCA remained relatively constant ($\bar{X}$ = 256, SE = 16.5, range: 220–400) from 1990–2010 with average calf:cow ratios of 40:100 in 1992–1995 and 47:100 in 2008–2010 (WGFD 2007; 2010), which suggests no detectable population response to disturbance associated with CBNG field development during our study. However, the intensity of behavioral response by elk may change as refugia become less available and density dependence begins to play a larger role in population dynamics (Vistnes et al. 2001; Nellemann et al. 2003). Longer time scales are likely needed to parse the influence of energy development on demography for the FCA elk population.

IMPLICATIONS

Our results indicate that human access facilitated by road development indirectly resulted in a 43–50% loss of high use elk habitat during CBNG development of the FCA in northeastern Wyoming. Eliminating the impacts of CBNG development on elk is unlikely; however, decreasing impacts on elk should be considered. For example, reducing daily traffic levels on high use collector and local roads from levels ranging from 70–319 vehicles per day to less than 10 could reduce indirect habitat loss for elk in the FCA (C. B. Buchanan, unpublished data). Decreasing impacts may also be possible by reducing human presence through new technologies such as directional drilling, telemetered well monitoring, and piping, rather than trucking liquid byproducts off site (Sawyer et al. 2009a); however, some human presence is necessary to monitor equipment and perform maintenance to energy field infrastructure. Our results suggest management plans that consider multiple mitigation factors including reducing traffic, maintaining visual obstruction (e.g., patches of woody vegetation and ridgelines), and retaining undeveloped refugia should be implemented to conserve elk populations within developing energy fields. An added benefit of reducing traffic volumes would likely be a reduction of the influx of exotic species into areas disturbed by energy development (Trombulak and Frissell 2000). Within the FCA, there remains a wilderness study area that is off limits to development, thus possibly providing refuge for elk during development. Although the wilderness study comprised only 10% of the FCA, it included 26 to 40% of the elk locations during CBNG development years. These same implications should also be considered in light of conserving other wildlife species impacted by energy development.

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.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management* 74:1175–1178.

Barbknecht, A. E., W. S. Fairbanks, J. D. Rogerson, E. J. Maichak, B. M. Scurlock, and L. L. Meadows. 2011. Elk parturition site selection at local and landscape scales. *Journal of Wildlife Management* 75:646–654.

Bayne, E. M., and B. C. Dale. 2011. Effects of energy development on songbirds. Pages 95–114 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, DC, USA.

Beck, J. L., J. M. Peek, and E. K. Strand. 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. *Journal of Wildlife Management* 70:283–294.

Beck, J. L., K. T. Smith, J. T. Flinders, and C. L. Clyde. 2013 Seasonal habitat selection by elk in north central Utah. *Western North American Naturalist* 73:442–456.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* 14:286–272.

Bureau of Land Management [BLM]. 2003. Final environmental impact statement and proposed plan amendment for the Powder River Basin oil and gas project. Buffalo Field Office, Buffalo, Wyoming, USA.

Bureau of Land Management [BLM]. 2008. Fortification Creek planning area resource management plan amendment/environmental assessment. Buffalo Field Office, Buffalo, Wyoming, USA.

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

Cameron, R. D., W. T. Smith, R. G. White, and B. Griffith. 2005. Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. *Arctic* 58:1–9.

Copeland, H. E., A Pocewicz, and J. M. Kiesecker. 2011. Geography of energy development in Western North America: potential impacts on terrestrial ecosystems. Pages 7–22 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, DC, USA.

D’Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430–439.

Dzialak M. R., S. M. Harju, R. G. Osborn, J. J. Wondzell, L. D. Hayden-Wing, J. B. Winstead, and S. L. Webb. 2011. Prioritizing conservation of ungulate calving resources in multiple-use landscapes. *PLoS One* 6:e14597.

Energy Information Administration [EIA]. 2009. Annual energy outlook 2009. <http://www.eia.doe.gov/oil_gas/natural_gas/info_glance/natural_gas.html>. Accessed 22 Jan 2010.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14:21.

Festa-Bianchet, M., J. C. Ray, S. Boutin, S. Cote, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20:273–287.

Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology* 45:1504–1513.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11–26.

Gavin, S. D., and P. E. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Canadian Journal of Zoology* 84:1775–1780.

Gregory, A. J., M. A. Lung, T. M. Gehring, and B. J. Swanson. 2009. The importance of sex and spatial scale when evaluating sexual segregation by elk in Yellowstone. *Journal of Mammalogy* 90:971–979.

Haskell, S. P., and W. B. Ballard. 2008. Annual re-habituation of calving caribou to oilfields in northern Alaska: implications for expanding development. *Canadian Journal of Zoology* 86:627–637.

Hiatt, G. and D. Baker. 1981. Effects of oil/gas drilling on elk and mule deer winter distributions on Crooks Mountain, Wyoming. Wyoming game and Fish Department, Cheyenne, Wyoming, USA.

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, MT.

Kochanny, C. O., G. D. Delguidice, and J. Fieberg. 2009. Comparing global positioning system and very high frequency telemetry home ranges of white-tailed deer. *Journal of Wildlife Management* 73:779–787.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, and T. L. McDonald. 2002. Resource selection by animals: statistical design and analysis for field studies. Second Edition. Kluwer Acedemic, Boston, Massachusetts, USA.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller’s Jays. *Ecology* 85:1411–1427.

Millspaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70:384–395.

Moen, R., J. Pastor, Y. Cohen, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. *Journal of Wildlife Management* 60:659–668.

Ndaimani, H., A. Murwira, and S. Kativu. 2013. Comparing terrain and vegetation-based visibility for explaining sable flight behavior in a Southern African savanna. Geocarto International 28:130–143.

Nellemann, C. I., I. Vistnes, P. Jordhoy, and O. Strand. 2001. Winter distribution of wild reindeer in relation to power lines, roads, and resorts. *Biological Conservation* 101:351–360.

Nellemann, C. I., I. Vistnes, P. Jordhoy, O. Strand, and A. Newton. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. *Biological Conservation* 113:307–317.

Nielson, R. M., B. F. Manly, L. L. McDonald, H. Sawyer, and T. L. McDonald. 2009. Estimating habitat selection when GPS fix success is less than 100%. *Ecology* 90:2956–2962.

Nielson, R. M., and H. Sawyer. 2013. Estimating resource selection with count data. *Ecology and Evolution* 3:2233-2240.

Neumann, W., G. Ericsson, and H. Dettki. 2010. Does off-trail backcountry skiing disturb moose? *European Journal of Wildlife Research* 56:513–518.

Nielson, R. M., B. F. J. Manly, L. L. Mcdonald, H. Sawyer, and T. L. McDonald. 2009. Estimating habitat selection when GPS fix success is less than 100%. *Ecology* 90:2956–2962.

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.

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* 52:891–904.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management* 71:1419–1426.

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. 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* 71:868–874.

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. 2009b. Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications* 19:2016–2025.

Schmitz, O. J., A. P. Beckerman, and K. M. Obrien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531–556 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institute Press, Washinton, D.C., USA.

Smith, K. T., C. P. Kirol, J. L. Beck, and F. C. Blomquist. 2014. Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. *Ecosphere* 5: article 15.

Sorensen, T., P. D. McLoughlin, D. Hervieux, E. Dzus, J. Nolan, B. Wynes, and S. Boutin. 2008. Determining sustainable levels of cumulative effects for boreal caribou. *Journal of Wildlife Management* 72:900–905.

Thomas, D.L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management* 49:397–405.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communites. *Conservation Biology* 14:18–30.

Van Dyke, F. and W. Klein. 1996. Response of elk to installation of oil wells. *Journal of Mammalogy* 77:1028–1041

Vistnes, I. C., and C. Nellemann. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. *Journal of Wildlife Management* 65:915–925.

Vistnes, I., C. Nellemann, P. Jordhoy, and O. Strand. 2001. Wild reindeer: impacts of progressive infrastructure development on distribution and range use. *Polar Biology* 24:531–537.

Ward, L. 1986. Displacement of elk related to seismograph activity in south-central Wyoming. Pages 246–254 *in* Anonymous. Preceedings II: Issues and technology in the management of impacted western wildlife. Thorne Ecological Institute, Glenwood Springs, CO, USA.

[WRCC] Western Regional Climate Center. 2009. Remote Automatic Weather Station, Echeta, WY, USA. Available at : http://www.wrcc.dri.edu/. Accessed October 2009.

White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* 77:2549–2557.

Wyoming Game and Fish Department [WGFD]. 1996. Fortification elk completion report, Appendix A: fortification elk study final report. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Wyoming Game and Fish Department [WGFD]. 2007a. Fortification elk study progress report. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Wyoming Game and Fish Department [WGFD]. 2007b. Job Completion Report: EL320 – Fortification. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Wyoming Game and Fish Department [WGFD]. 2010. Job Completion Report: EL320 – Fortification. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Table 1. Goodness of fit statistics for the top, second, null, and competitive models (if applicable), predicting elk resource selection at the population level within the Fortification Creek Area (FCA) of northeastern Wyoming, USA, summer and winter, predevelopment (1992–1995). Number of parameters in each model (*K*), Akaike's Information Criterion corrected for small sample sizes (AIC_c), difference in AIC_c from the top model (ΔAIC_c), Akaike's weights (w_i), and model rank are reported.

Model	K	AIC_c	ΔAIC_c	w_i	Rank
Summer Predevelopment (16 candidate models)					
Percent juniper + percent north-facing sagebrush + decay distance to roads (500 m)	4	2023.16	0.00	0.96	1
Percent sagebrush north + viewshed+dkrd3_500	4	2029.37	6.22	0.04	2
Null	1	2105.18	82.02	<0.001	16
Winter Predevelopment (32 candidate models)					
Percent juniper + slope + viewshed	4	1426.26	0.00	0.28	1
Percent juniper + slope + viewshed + VRM	5	1426.80	0.54	0.21	2
Percent juniper + viewshed + VRM	4	1426.93	0.70	0.20	3
Percent juniper + slope + viewshed + decay distance to roads (500 m)	5	1427.58	1.32	0.14	4
Percent juniper + slope + viewshed + VRM + decay distance to roads (500 m; global)	6	1428.53	2.27	0.09	5
Percent juniper + viewshed + VRM + decay distance to roads	5	1428.68	2.42	0.08	6
Percent juniper + viewshed	3	1432.15	5.89	0.01	7
Null	1	1462.24	35.98	<0.001	32

Table 2. Estimated variable coefficients (β), bootstrapped SEs (iterations = 1000), and 95% confidence intervals for population-level resource selection models for elk in the Fortification Creek Area, northeastern Wyoming, USA, summer and winter, pre- (1992–1995) and during (2008–2011) development. Coefficients for winter before development were model averaged because six competing models existed.

Variable	β	SE	95% LL	95% UL
Summer Predevelopment				
Intercept	–7.05	<0.01	–7.07	–7.03
Percent juniper	1.44	0.02	1.40	1.47
Percent north-facing sagebrush	–1.80	0.02	–1.84	–1.77
Decay distance to roads (500m)	–1.05	0.01	–1.07	–1.03
Summer During-Development Using Predevelopment Top Model				
Intercept	–7.36	<0.01	–7.38	–7.34
Percent juniper	1.88	0.03	1.83	1.93
Percent north-facing sagebrush	–1.40	0.02	–1.44	–1.37
Decay distance to roads (500m)	–5.90	0.10	–6.09	–5.72
Winter Predevelopment				
Intercept	–8.23	0.06	–8.36	–8.11

Percent juniper	1.60	0.04	1.51	1.69
VRM	4.11	1.79	0.60	7.61
Slope	<0.01	<0.01	<0.01	0.01
Viewshed	<–0.01	<0.001	–0.01	<–0.01
Decay distance to roads (500m)	–0.07	0.05	–0.16	0.02
Winter During-Development Using Predevelopment Top Model				
Intercept	–7.81	0.01	–7.84	–7.80
Percent juniper	0.35	0.03	0.29	0.42
VRM	7.44	0.15	7.15	7.72
Slope	<0.01	<0.001	<0.01	<0.01
Viewshed	<–0.01	<0.001	<–0.01	<–0.01
Decay distance to roads (500m)	–8.30	0.11	–8.52	–8.079

Table 3. Response ratios and 95% confidence limits comparing the magnitude of coefficients during-development to predevelopment for each predictive variable during the summer and winter seasons within the Fortification Creek Area of northeastern Wyoming, USA. A value greater than 1 suggests increased elk use, a value less than 1 suggest decreased use, and a value 1 represents no change in coefficient magnitude during development in comparison to before development.

Variable	Response Ratio	95% LL	95% UL
Summer			
Juniper (%)	1.31	1.26	1.35
North-facing sagebrush (%)	0.78	0.76	0.81
Distance to road	5.73	5.52	5.95
Winter			
Juniper (%)	0.22	0.18	0.26
VRM	1.81	0.27	3.35
Slope	0.59	0.24	0.93
Viewshed	0.80	0.17	1.43
Distance to road	118.71	-39.43	276.82

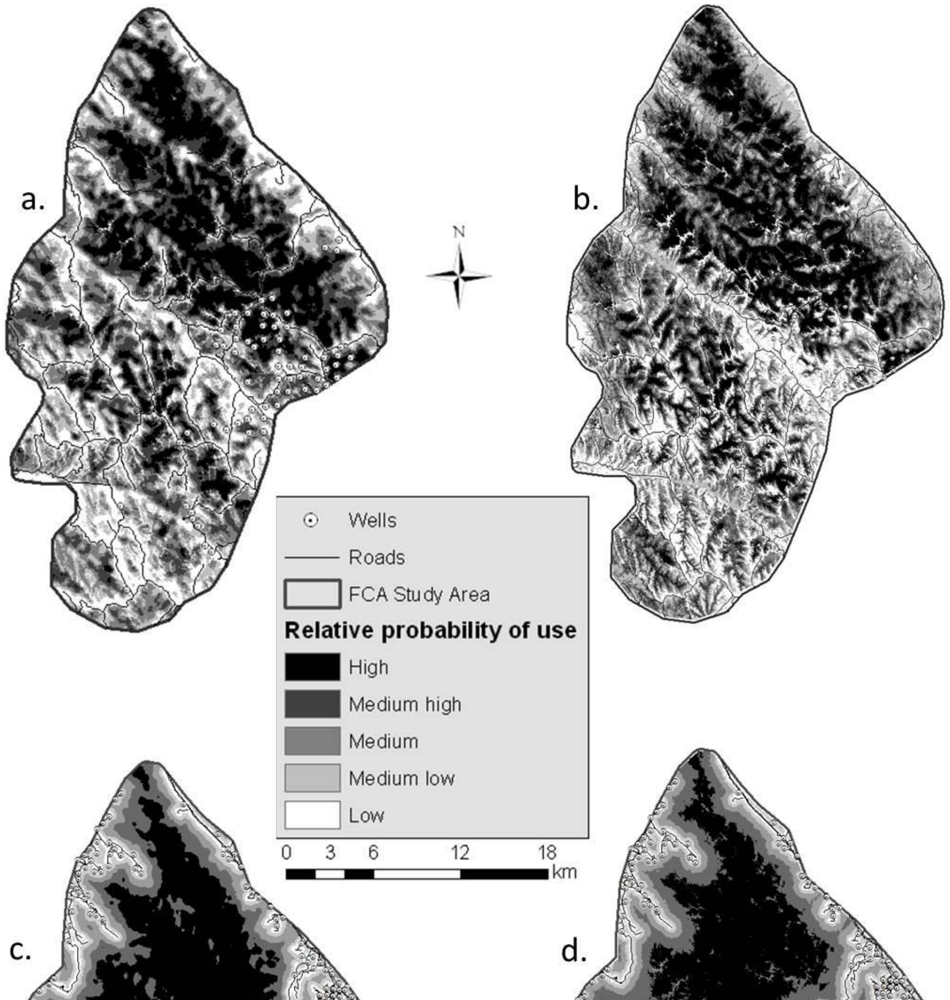

Figure 1. Population-level probability of use based on 5 quartiles of elk use in summer (a) and winter (b) pre- (1992–1995) coal bed natural gas development, and in summer (c) and winter (d) during-development (2008–2010) within the Fortification Creek Area of northeastern Wyoming, USA.

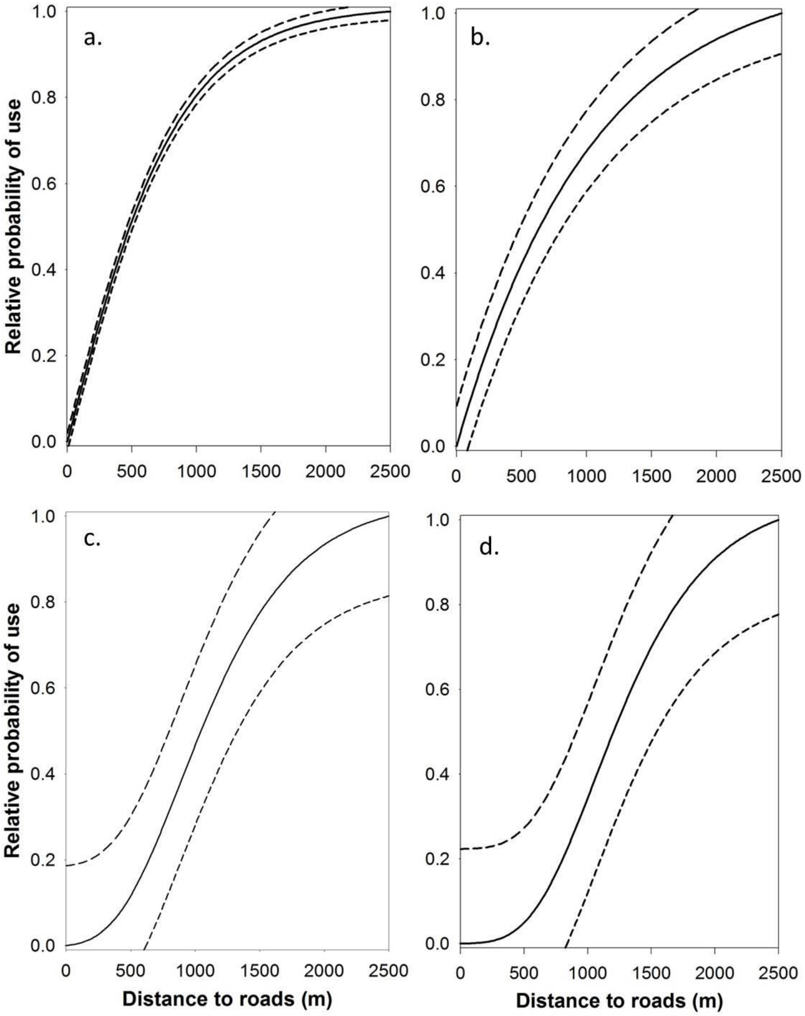

Figure 2. Probability (solid line) and 95% confidence limits (dashed lines) of elk use in summer as a function of distance to roads during different time periods; summer predevelopment (a), winter predevelopment (b), summer during-development (c), and winter during-development (d) in the Fortification Creek Area of northeastern Wyoming, USA. Predevelopment data were collected from 1992–1995 and during-development data collected 2008–2010. Probability curves were developed from the top predictive model for elk resource selection predevelopment. Variables of interest were allowed to vary, while others within the model were held at their mean values.

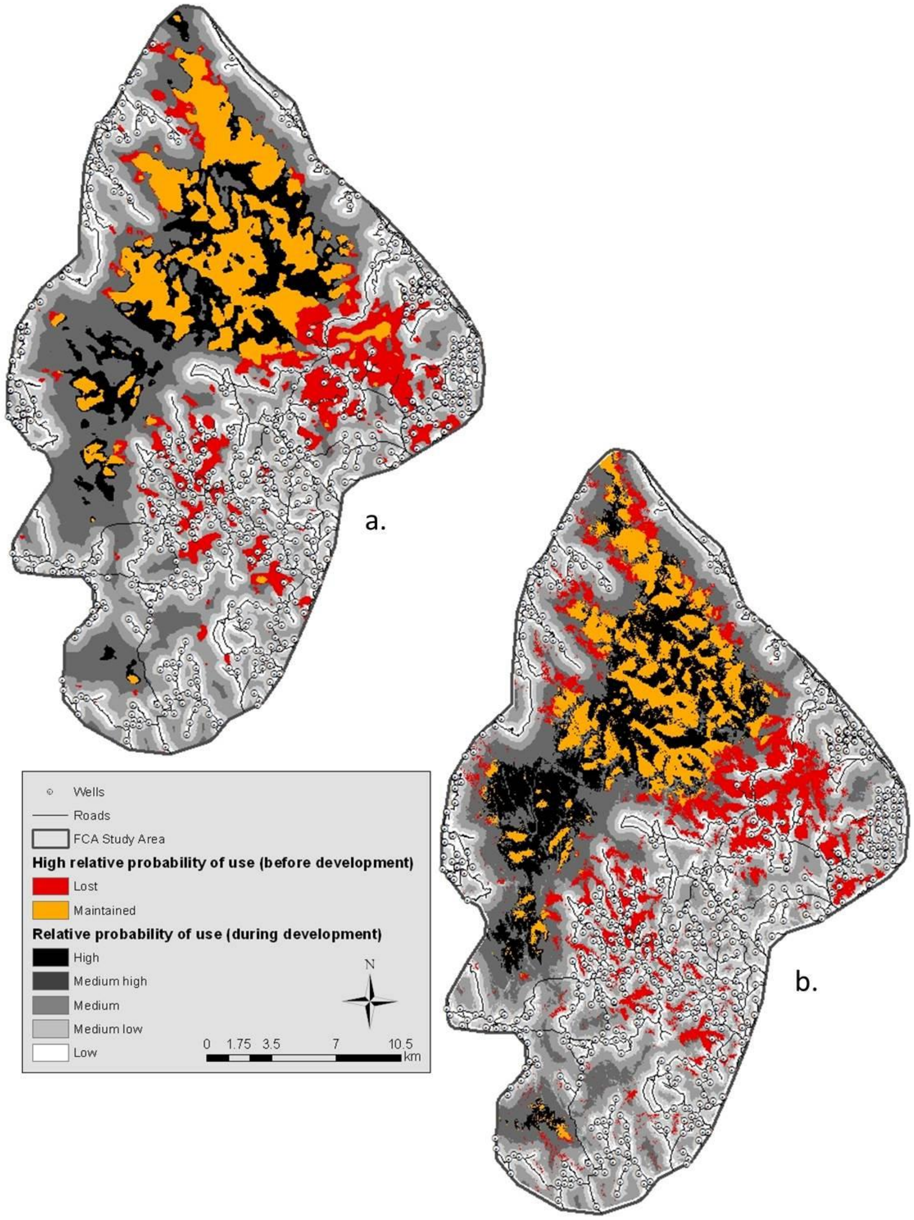

Figure 3. Population-level model and categories of elk use in summer (a) and winter (b) during coal bed natural gas development (2008–2010) overlain with areas identified as high relative probability of use predevelopment (1992–1995) within the Fortification Creek Area of northeastern Wyoming, USA. Predevelopment high use areas that were maintained during-development are in orange whereas areas lost during-development are in red. Loss of habitat previously identified as high use equaled 43.1% and 50.2% in summer (a) and winter (b), respectively.

CHAPTER THREE

Elk Shift Resource Selection Temporally to Mitigate Impacts from Natural Gas Development

CLAY B. BUCHANAN, [1]Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA

JEFFREY L. BECK, [1]Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA

SHAUN S. WULFF, [2]Department of Statistics, University of Wyoming, Laramie, WY 82071, USA

SHANNON E. ALBEKE, [3]Wyoming Geographic Information Science Center, University of Wyoming, Laramie, WY 82071, USA

In the format for manuscripts submitted to journals of the Ecological Society of America

Abstract.

Resource selection is a process in which animals maximize resource uptake through unequal use of resource heterogeneity on the landscape. In addition, shifts in resource and disturbance gradients should cause animals to correspondingly shift resource use and distribution. Although there is an increasing body of evidence of the impacts of disturbance risk on wildlife populations, there are few studies assessing fine-scale impacts of human disturbance on wildlife. The main objective of our work was to identify differences in day and night resource selection and relate those differences to population fitness parameters. Elk may be able to reduce the fitness impacts of coal bed natural gas (CBNG) development through expansion of resource use at night, thus ameliorating population impacts. To collect fine-scale temporal data, we used GPS-collar data from 55 female elk (*Cervus elaphus*) as well as habitat and human disturbance variables for a study system in northeastern Wyoming, USA. We used a novel approach to quantify shifts between day and night elk resource selection within a CBNG field, which incorporated frequency of elk use in a mixed-effects model framework. We also collected fitness-based metrics such as body condition scores from hunter-harvested animals to identify population consequences of observed resource selection shifts. This combination of resource selection and demographic data provided information on the ability of elk to mitigate the impacts of CBNG development. Elk exhibited differences in day and night resource selection, whereby they used areas with decreased escape cover and closer to roads at night. There was more variation in resource selection between individuals at night compared to day. Fitness indicators for this elk population suggested little impact on population health. Our results suggest elk are able to, at least partially, mitigate the impacts of CBNG development through diel behavioral shifts in resource selection patterns in response to human disturbance activity patterns.

Key words: Cervus elaphus; diel behavior; energy development; mitigation; mixed-effects model; population dynamics; resource selection function;

INTRODUCTION

The study of space use by animals is of fundamental interest in wildlife ecology. Animals respond to resource heterogeneity on landscapes leading to non-uniform distributions. As availability of resources shifts so must animal populations to maximize resource uptake and fitness. Recent research has documented the influence of risk of predation on animal distribution and resource selection (Luttbeg and Sih 2004, Creel et al. 2005). More specifically, predation risk has been shown to promote anti-predatory behavior in prey species (Festa-Bianchet 1988, Lima and Dill 1990). For example, prey animals, such as grasshoppers, often shift feeding time budgets in the presence of predators such as spiders (Schmitz et al. 1997). Some species use group size to deter or better detect predators (Lingle 2001). Wood frog (*Rana sylvatica*) tadpoles may even change their phenotype to address predation risk (Relyea 2003). Bison (*Bison bison*) in Canada shifted their fine scale foraging behavior at a cost to forage intake in an attempt to reduce wolf (*Canis lupus*) predation risk (Harvey and Fortin 2013). Response to predation risk varies greatly across different predator-prey systems, but can have great influence on wildlife populations and ecosystem function (Schmitz et al. 2004). Disturbance risk response is considered to be analogous to predation risk response (Walther 1969, Frid and Dill 2002). In the wake of an ever increasing human population and gaining acceptance of the disturbance risk hypothesis, the effects of numerous anthropogenic activities have become the focus of wildlife research and conservation efforts. Aircraft flights (Krausman et al. 1998), hiking (Taylor and Knight 2003), skiing (Patthey et al. 2008), terrestrial vehicle traffic (on and off road), watercraft (Burger 1998), ecotourism (Weinrich and Corbelli 2009), and energy development (Sawyer et al. 2009) are some of the activities of focus in disturbance risk research. When coping with disturbance risk, animals may alter normal resource use and behavioral patterns. The costs of these pattern changes may manifest themselves through population distribution shifts, decreased body condition, diminished reproductive output, and ultimately, population decline (Gill et al. 2001, Johnson et al. 2005).

Similar to other taxa, ungulates must make trade-offs along gradients of resources and risk. In Nepal, a combination of habitat and disturbance variables best predicted presence of three ungulate species and abundance of all three species declined with proximity to human disturbance (Paudel and Kindlmann 2012). Resource gradients can occur along different axes. Animal migration often capitalizes on increased forage occurring along temperature and water gradients. Many ungulates in mountainous regions take advantage of high quality forage by tracking green-up patterns up-slope in the spring akin to following a phenological wave (Sawyer and Kauffman 2011, Bischof et al. 2012). However, if human disturbance decouples ungulate movement pathways with timing of forage green-up, ungulates must make trade-off decisions between risk avoidance and forage intake, possibly impacting future fitness (Bischof et al. 2012). Ungulates also take advantage of resource gradients at smaller scales. Robinson et al. (2010) documented elk using human development as refuge from wolf predation more at night than during the day. Comparable to Robinson et al. (2010), Bonnot et al. (2013) recorded avoidance of human dwellings by an ungulate, whereby roe deer (*Capreolus capreolus*) used distance or protective habitat cover to reduce perceived risk from human disturbance.

The development of energy resources is a major source of disturbance that creates gradients of risk and resources for many wildlife species. In the western United States, impacts of energy development have been noted for ungulate species including elk, mule deer (*Odocoileus hemionus*; Sawyer et al. 2009a), and pronghorn (*Antilocapra americana*; Hebblewhite 2011, Beckmann et al. 2012). Our study focused on an elk population (2008–2011) in the Fortification Creek Area (FCA) of the Powder River Basin in northeastern Wyoming, USA; a region that was experiencing rapid expansion of coal bed natural gas (CBNG) extraction (BLM 2010). Previous work on elk resource selection within the FCA identified long term shifts in resource use and distribution based on avoidance of CBNG infrastructure and development activity (Buchanan et al. 2014). This work provided greater understanding of elk response at the landscape level as elk redefined their distribution as a result of perceived disturbance risk from CBNG development. One understudied aspect of disturbance risk is whether animals may make fine-scale tradeoffs to mitigate effects of energy development (Hebblewhite and Merrill 2009). We used a novel combination of sampling units to collect frequency of use and predictor variable values (Sawyer et al. 2009) with a mixed-effects modeling framework to assess shifts in elk resource selection between day and night in a CBNG development field (Gilles et al. 2006). We also collected demographic data to assess population fitness impacts of elk response to disturbance risk and resulting fine-scale resource selection tradeoffs. If anthropogenic variables were better predictors of elk resource selection than environmental variables, then we expected improvement in model fit with inclusion of anthropogenic variables into candidate models. Maintenance of elk demographic metric levels congruently with diel resource selection shifts would suggest possible self-mitigation of the impacts of CBNG development. To this end, we demonstrate the ability of elk to mitigate the impacts of CBNG development by shifting diel resource selection patterns to inversely reflect diel CBNG development activity.

METHODS

Study Area

The FCA is a 498 km^2 area approximately 40 km west of Gillette, Wyoming, USA (*sensu* Buchanan et al. 2014). Our study area included the FCA, but approximately 10% of our elk locations occurred outside of the defined FCA boundary. To include all locations, our study boundary extended outside of the FCA, which encompassed 1432 km^2 (Fig. 1). For the sake of simplicity, we continue to use FCA when referring to our study area. Our expanded FCA study area encompassed portions of Campbell, Johnson, and Sheridan Counties, Wyoming and was administered by the BLM (34%), State of Wyoming (6%), and private landowners (60%). Cattle grazing has been a consistent land use in the FCA prior to and during CBNG development. Our study area included 2,441 km of roads and 3,293 oil and gas wells. Elevation in the study area ranged from 1,095 to 1,550 m. Land cover was dominated by Wyoming big sagebrush (*Artemisia tridentate wyomingensis*) shrubland with scattered patches of Rocky Mountain juniper

(*Juniperus scopulorum*; hereafter, juniper) that comprised only 6% of the landscape. Grasses common to the northern mixed-grass prairie dominated our study area including bluebunch wheatgrass (*Pseudoroegneria spicata*), cheatgrass (*Bromus tectorum*), little bluestem (*Schizachyrium scoparium), and western wheatgrass (Pascopyrum smithii). The FCA and surrounding area* was characterized by a semiarid climate with an average annual precipitation of about 22 cm (WRCC 2009). Annual precipitation during our study averaged 23 cm, of which >90% fell between April and October. The average temperature was 9.0 C° with an average daily maximum and minimum temperature of 15.4 and 3.4 C°, respectively (WRCC 2009).

Location Data

To obtain fine-scale location data we employed helicopter net-gunning (Leading Edge Aviation, Lewiston, ID, USA) to capture n = 59 adult female elk in separate capture operations in March (n = 39) and December (n = 20) 2008. These elk were fitted with real-time Global Positioning System (GPS) collars (North Star Science and Technology, LLC, King George, VA, USA) programmed to collect 1 location every 5 hours over 3 years (2008–2011). Across all individuals we observed GPS fix rates from 58 to 98%. Fix rates of less than 100% can be caused by habitat characteristics that block satellite transmission or random collar failure (Moen et al. 1996, D'Eon et al. 2002, Nielson et al. 2009). Occurrence of habitat bias in GPS location data can result in erroneous conclusions that must be assessed. We tested for differences in resource selection between animals with high (≥90%) and low (<90%) GPS fix rates using independent sample *t*-tests. We found no differences (P >0.05) in resource selection coefficients between high and low fix rate groups (Buchanan et al., 2014). However, 4 animals were removed due to full collar failure. We did not differentially correct GPS locations due to a high percentage (99%) of 3-dimensional locations. Elk locations were separated into 4 time periods; summer day (SD;

0700—1900 hrs, April 1—October 31), summer night (SN; 0000—0700 hrs and 1900—0000 hrs, April 1—October 31), winter day (WD; 0700—1900 hrs, November 1—March 31), and winter night (WN; 0000—0700 hrs and 1900—0000 hrs, November 1—March 31). These time periods coincided with development timing stipulations (BLM 2010) and traffic patterns.

Forage Collections and Analyses

We collected forage samples to assess forage quality across the FCA, as we expected elk to select areas of greater forage quality. We collected 10 forage samples for perennial forb and perennial grass forage classes from 10 randomly-selected sites within three dominant cover types in the FCA including north-facing sagebrush, south-facing sagebrush, and juniper in early (1 June—15 June) and late summer (15 July—1 August) 2009 and 2010. Samples were clipped to ground level in 10 quadrats placed every 10 m along two 50 m transects randomly located within the three cover types. We also estimated forb and grass production in 10 quadrats every 10 m alternating with clipped quadrats along the 2 transects. Forage mass was estimated for perennial forb and grass classes using a double sampling method within 0.1-m^2 quadrats (Bonham 1989). All forage samples were dried at 60°C for 48 hours and reweighed to obtain dry mass measurements. Dried samples were ground to 1 mm particle size (Svejcar and Vavra 1985) and stored prior to further analyses. Due to small sample size, we combined all forb, and separately all grass, subsamples from each sample site prior to nutritional analyses.

Percent nitrogen of each forage sample was evaluated using McGeehan and Naylor's (1988) combustion technique and crude protein (CP) was approximated as 6.25 x [%N] (Robbins 1993). We followed techniques described by Tilley and Terry (1963) to estimate apparent *in vitro* dry-matter digestibility (IVDMD) for all forage samples. Rumen inoculum was collected from fistulated beef cows provisioned with forage available during similar phenological time periods as forage collection periods in the FCA (Beck and Peek 2005). We used 25 micron pore ANKOM filter bags (Ankom Technology, Macedon, NY, USA) during digestion trials. Samples were digested in triplicate following Tilley and Terrry (1963) to obtain average IVDMD, with additional replicates as necessary to achieve a ≤ 5% coefficient of variation computed from the average of at least 2 replicates. We used bomb calorimetry on duplicate forage samples to evaluate gross energy (GE). Digestible energy (DE) was approximated as the product of mean apparent IVDMD and mean GE for each sample (Robbins 1993). Standing CP and DE were calculated per forage class through multiplication of forage production values with the respective protein or energy values per forage class at sampling sites. We assessed differences in forage quality using analysis of variance tests.

RSF Predictor Variables

–Anthropogenic Predictors

We considered a number of anthropogenic variables related to CBNG development to predict elk resource use (Table 1). Previous work has identified elk response to roads and associated traffic volumes, where roads with greater traffic volumes result in greater avoidance distances (Buchanan et al. 2014). To quantify the influence of roads on elk resource selection, we measured vehicle traffic volumes using active infrared monitors (TrailMaster TM 1550; Goodson and Associates, Inc., Lenexa, KS, USA). Traffic volumes were monitored across 16 sites from 2 June–4 August 2009 and 24 sites from 27 May–2 August 2010. We observed 187 vehicle passes across all monitored sites to assess reliability of our monitors and found 94% (176 of 187) of our observations were correctly recorded by the infrared monitors. We digitized roads in a GIS using 2009 and 2012 National Agriculture Imagery Program (NAIP; USDA-FSA, Aerial Photography Field Office, Salt Lake City, UT, USA) and Landsat (USGS-EROS Center, Sioux Falls, SD, USA) imagery at 1 m and 30 m resolution, respectively. We then developed decay distance variables as a function of Euclidean distance for all roads using the form $e^{-d/\alpha}$ where d was the distance from each pixel to roads in meters and α were constant values of 100, 500, 1,000, 1,500, 2,000, 3,000, 4,000, and 5,000. This decay transformation scaled the distance variables between 1 and 0, with values increasing in proximity to roads. The autocorrelated nature of these distance variables necessitated the use of AIC to identify the best fitting variable, which we retained for further analyses. We also considered density of roads (km/km^2) as a predictor variable.

We included metrics in our analysis that represented the influences of well pads. Well location data was extracted from the Wyoming Oil and Gas Conservation Commission (WOGCC). Wells were included in the analyses if they had been spudded prior to or during our study period. As the WOGCC provided information on all wells, including those that had not been constructed, we assessed existence of wells through on-the-ground observations and satellite imagery including NAIP and Landsat. We developed decay distance variables following the methods used in developing road variables explained above. A well density (number/km^2) variable and well viewshed variable were also developed. The viewshed variable defined the number of wells from which a point on the landscape could be seen. Variable names and descriptions are found in Table 1.

–Environmental

We developed a suite of environmental variables to predict elk resource use (Table 1). Previous work has suggested that elevation (Sawyer et al. 2007, Gregory et al. 2009), terrain ruggedness (Skovlin et al. 2002, Frair et al. 2005), and cover type (Beck et al. 2006, Barbknecht et al. 2011) are important predictors of elk resource selection. Thus, we developed a suite of environmental variables (Table 1). We determined these variables were important for the FCA elk herd, which due to the physical nature of the landscape, provided the main sources of escape and thermoregulatory cover, in addition to being previously used by others. We derived ELEV and SLOPE from a 10 m resolution digital elevation map (National Elevation Dataset, USGS, Sioux Falls, SD, USA). We identified and classified juniper and sagebrush-grassland cover using 30 m landcover data developed at the University of Wyoming (Landcover_REGAP_2007, Wyoming Geographic Information Science Center, University of Wyoming, Laramie, USA). Landscape level forage quality layers were created by combining average standing crop of forb and grass CP (g/m^2) and forb and grass DE (kcal/m^2) values for the three cover types with the distribution of those cover types. Variable names and descriptions are found in Table 1.

Statistical Analyses

We used a negative binomial (NB2; Cameron and Trivedi 1998) mixed-effects resource selection function (RSF; Manly et al. 2010, Hilbe 2011) to assess day and night elk resource selection seasonally (e.g., SD). A mixed modeling approach is advantageous for, minimally, two reasons. First, it allows for unbalanced data, where one individual may have more relocations than another. Second, random intercepts and coefficients can be used to account for variation between individual elk in their resource selection and functional response (Gilles et al. 2006). We applied this RSF model in a relative frequency of use design at the individual home-range level (Thomas and Taylor 2006, Nielson and Sawyer 2013), while assessing population-level response to CBNG development.

Resources were considered available to an elk if they were within the animal's home range. Individual animal home ranges were developed using a 90% fixed kernel estimator. We used a 90% kernel estimator rather than 95% because kernel estimators often overestimate home range sizes (Ryan et al. 2006, Boyle et al. 2009). We used random 250 m radii sampling units to extract predictive variable values from the landscape as well as the number of elk locations, or frequency of use (Sawyer et al. 2007, 2009*a*). The size of our sampling units was larger than the expected GPS location error (<20 m), thereby removing concern of error influencing model results. The quantity of sampling units was based on the absolute value of sampling unit area that approximated 60% coverage of the target home range. Sampling unit area of 60% coverage was used because it best characterized the variation in resource use without over sampling elk locations. Representative values for each predictive variable and the number of elk locations were extracted from each sampling unit. This method removed temporal relationships between locations beyond the seasonal or time of day classifications (e.g., summer, night; Nielson and Sawyer 2013).

Prior to model selection, we tested for collinearity among variables using a Pearson correlation matrix. We omitted one variable from analyses from all correlated variable pairs where correlation coefficients (r) were $\geq |0.6|$. We examined collinearity further using a collinearity-tolerance statistic, which provided a measure of interdependence that may not be detected by the correlation matrix (Allison 2009, Kirol et al. 2012). Variables were subject to removal based on low tolerance scores (t) ≤ 0.40. Removal of variables in response of both correlation and tolerance statistics was based on individual variable importance in accordance with published literature and biological relevance in reference to elk natural history.

The negative binomial distribution was used to model the counts, t_{ij}, representing the total number of locations within sampling unit i for individual j. The use of negative binomial distribution allows for the variance to be greater than the mean which is common for count data

(Cameron and Trivedi 1998, Hilbe 2011). Using the log link, the linear predictor conditional on the random effects is given by:

$$\ln[E(t_{ij})] = \ln(T) + \beta_0 + \gamma_{0j} + \gamma_{ij}x_{ij} + \beta_1 x_{1ij} + \cdots + \beta_n x_{nij} \qquad (1)$$

where t_{ij} was the total number of locations within sampling unit *i* for individual *j*, as a function of $x_1...n$ covariates measured in sampling unit *i*, $\beta_1...n$ and γ_{ij} were the fixed and random selection coefficients, and β_0 and $\gamma_{0\mathrm{i}}$ were the fixed and random intercepts from the mixed-effects regression, respectively. The term ln(*T*) is the offset where *T* was the total number of locations during the time period of interest which, scaled the response to model relative frequency of use rather than integer counts (Nielson and Sawyer 2013) and was constant across *i* and *j*. Frequency of use per sampling unit can be regressed against predictor variables (Nielson and Sawyer 2013) in contrast to a traditional binary approach (1 = used; 0 = available) where the actual state of available locations is unknown (Keating and Cherry 2004). Use of the negative binomial distribution allows for the variance to be greater than the mean, which is common in observed count data (Cameron and Trivedi 1998, Hilbe 2011). We carried out sequential model selection using AIC (ΔAIC < 4; Arnold 2010) to select the top performing model in two tiers. The first tier selection identified predictive environmental models. The second tier added anthropogenic models and assessed improvement of model fit to test the hypothesis that anthropogenic variables had greater impact on elk resource selection.

We then mapped each model back onto the FCA landscape as a relative probability of use to assist in interpretation and visualization of model probabilities. All map values were verified to be between 0 and 1 so as not to fall outside of our range of inference. We compared mapped, raw RSF value distributions between day and night to assess changes in use, where elk may have shifted daily use patterns to offset the impacts of CBNG development. Comparisons of day and night probability of use distributions during summer and winter were conducted using Kolmogorov-Smirnov tests (Massey 1951). Separate generalized linear mixed models were developed for day and night RSFs with respect to environment al and anthropogenic variables in order to identify possible drivers of diel variation in selection. In addition to including road metrics in resource selection modeling, we also measured the distance from each elk location to the nearest road and found the average distance to road by individual elk. We used a paired t-test to compare day and night distance to roads by individual elk.

An independent sample of 35 cow elk was captured in March 2011 to continue monitoring the FCA elk herd. Because 9 individuals were recaptured from our first sample of collared elk, we used location data from 26 of these elk to form an independent sample for model validation. Locations from these animals in summer 2011 (validation summer day, 5630; validation summer night, 6099) and winter 2011–2012 (validation winter day, 2807; validation winter night, 2591) were used to validate our models. We separated locations during each season and time of day (e.g., summer, night) into 10 equal distribution bins. We then applied the respective models from the development data (2008–2010) to the 2011 summer and 2011–2012 winter landscapes and overlaid probability maps from these models with 2011 summer or 2011–2012 winter elk locations, which we binned as previously described. We used Spearman's rank correlations (r_s) to evaluate location frequency distributions during 2008–2010 with location frequency distributions of the validation data set (e.g., binned summer elk distribution compared to the summer 2011 binned elk distribution) to test the ability of each model to measure elk resource selection for each season. All statistical analyses were conducted in the R language and environment (R Development Core Team 2011; Packages MASS, glmmadmb).

Population Fitness

To evaluate the influence of anthropogenic disturbance on elk population fitness, we used four metrics including estimated populations numbers, calf:cow ratios, pregnancy rates, and approximate body condition. Collar failure limited our ability to estimate survival for female elk in the FCA elk herd. Elk population numbers and calf:cow ratio data were collected by the Wyoming Game and Fish Department during multiple annual aerial surveys. We assessed pregnancy rate though blood samples collected during elk capture events in 2008, 2011, and 2014. Pregnancy was tested by measuring the presence of pregnancy-specific protein B in blood serum (BioTracking LLC, Moscow, Idaho, USA). We also collected organs during the fall hunt season to assess fat content. Organ collections occurred within the FCA and an independent hunt area: Rochelle Hills Area (RHA). The RHA was located approximately 60 km southeast of the FCA and consisted of similar landcover and climatic regimes, although the RHA elk herd was estimated to be larger than the FCA herd. We collected the heart, kidneys, and pericardium from elk donated by cooperating hunters within the FCA and RHA from 2009–2011 and 2013. Organ fat content was visually judged using a modified Kistner score developed for elk at the Starkey Experimental Forest and Range in southeastern Oregon (R. C. Cook, National Council for Air and Stream Improvement, LaGrande, OR, personal communication). We did not often receive the pericardium in our collections, so, we present comparisons between the FCA and RHA using heart and kidney scores. We pooled organ fat scores across years and used Mann-Whitney *U* tests to make comparisons between areas due to small yearly sample sizes.

RESULTS

We used 37092 and 38502 GPS elk locations from 55 elk to model resource selection during SD and SN, respectively. We used 22587 and 21766 GPS elk locations from 55 elk to model resource selection during WD and WN, respectively.

Forage Analyses

We collected 2400 forb and grass subsamples from 3 cover types in the FCA and an equal number of forage estimates from double sampling efforts. After pooling of samples by site we used 240 samples in forage quality analyses. There were greater differences in standing DE (g/m^2; $F = 595.2$, $P < 0.01$) than standing CP (kcal/m^2; $F = 27.6$, $P < 0.01$; Table 2) between cover types. Post-hoc Tukey tests suggested that all groups differed significantly ($P < 0.05$) in DE except juniper grass and forb and north-facing sagebrush grass and forb. All significant differences in standing CP occurred between functional groups (e.g., forbs and grasses) across cover types with no differences in CP across cover types within the same functional group according to post-hoc Tukey tests.

Resource Selection

–*Summer*

There were differences between SD and SN elk resource selection (Fig 2A). The top environmental model predicting elk selection during SD included 3 variables and no other models were competitive (Table 3). During SD, elk selected for areas with greater grass digestible energy, percent juniper, and terrain ruggedness (Table 4). Addition of the top disturbance model, decay distance to road ($\alpha = 100$ m) and well viewshed, improved model fit by 229 AIC points (Table 3). High use areas averaged 371.9 kcal/m^2 grass digestible energy, 23.1% percent juniper, 0.03 terrain ruggedness, 561.4 m from roads, and were visible from 18.2 wells.

The top environmental model predicting elk selection during SN included 3 variables and no other models were competitive (Table 3). During SN, elk selected for areas with greater percent juniper and elevation, and distance to juniper (Table 4). Addition of the top disturbance model, decay distance to roads ($\alpha = 500$ m) and well viewshed, improved AIC model fit by 242 AIC units. High use areas averaged 25.2% percent juniper 1330.7 m elevation, 57.6 m from juniper cover, 536.7 m from roads, and were visible from 17.3 wells. The Spearman's rank correlation coefficient (r_s) for the summer models evaluated against our validation data were 0.94 and 0.94 for SD and SN, respectively, where our RSF models predicted location distribution of an independent dataset. These correlation coefficients indicated our top SD and SN models were strong, positive predictors of elk resource selection.

Probability of use distributions between day and night RSFs during summer were significantly different (Kolmogorov-Smirnov $D = 0.027$, $P < 0.001$) where night probabilities were more broadly distributed (Fig 3). In summer, differences in day and night selection were best predicted by distance to juniper cover and roads. At night, elk used areas farther from juniper cover and closer to roads than during the day. Average distance (± SE) to roads available within FCA elk home range before (1992–1995) development was 734.0 ± 0.2 m. Average distance to roads available within FCA elk home range during development (black bar) was 284.3 ± 0.2 m (Fig. 4). Within the original 498-km^2 study area, before development average distance to roads for elk locations in summer was 836.4 ± 132.7 m. We detected a difference in the average distance to roads for elk between SD 582.1± 50.9 m) and SN (510.8 ± 52.7 m; $t_{51} = 8.11$, $P < 0.01$; Fig 4).

–Winter

There were differences between WD and WN elk resource selection (Fig. 2B). The top model predicting elk selection during WD included 4 variables and no other models were competitive (Table 3). During WD, elk selected for areas with greater grass digestible energy, percent juniper, terrain ruggedness, and elevation (Table 4). Addition of the top disturbance model, decay distance to roads ($\alpha = 500$ m) and well viewshed, improved model fit by 231 AIC points. High use areas averaged 375.0 kcal/m^2 grass digestible energy, 20.3% percent juniper, 0.03 terrain ruggedness, 1322.7 m elevation, 641.4 m from roads, and visible from 16.6 wells. The top model predicting elk selection during WN included 6 variables and no other models were competitive (Table 3). During WN, elk selected for areas with greater grass digestible energy, terrain ruggedness, elevation, and distance to juniper cover (Table 4). Addition of the top disturbance model, decay distance to roads ($\alpha = 1000$ m) and well viewshed, improved model fit by 160 AIC points. High use areas averaged 397.7 kcal/m^2 grass digestible energy, 0.02 terrain ruggedness, 1352.3 m elevation, 749.4 m from juniper cover, 555.6 m from roads, and visible from 31.3 wells. The Spearman's rank correlation coefficient (r_s) for the winter models against our validation data were 0.99 and 1.00 for WD and WN, respectively, where our RSF models predicted location distribution of an independent dataset. These correlation coefficients indicated our top WD and WN models were strong, positive predictors of elk resource selection.

Probability of use distributions between day and night RSFs during winter were significantly different (Kolmogorov-Smirnov $D = 0.018$, $P < 0.001$) where night probabilities were more broadly distributed (Fig. 3). In winter, differences in day and night selection were best predicted by distance to juniper cover and roads, where, at night, elk were using areas farther from juniper cover and closer to roads than during the day. Within the original 498-km^2 study area, before development average distance (± SE) to roads for elk locations in winter was

874.6 ± 156.2 m. We detected a difference in the average distance to roads for elk between WD (592.4 ± 44.4 m) and WN (573.8 ± 46.9 m; t_{50} = 1.52, P = 0.07; Fig 4).

Population Fitness

Elk population numbers in the FCA remained relatively constant ($\bar{X}$ = 256, SE = 16.5, range: 220–400) from 1990–2010 with average calf:cow ratios of 40:100 in 1992–1995 and 47:100 in 2008–2010 (WGFD 2007, 2010). Pregnancy rates of 91.6% (*n* = 36), 86.3% (*n* = 36), 97.1% (*n* = 35) in 2008, 2011, and 2014, respectively, were assessed from 3 separate capture events. Heart fat content was lower in the FCA than RHA (*n* = 80, *U* = 328, *P* < 0.01), but kidney fat content did not statistically differ between areas (*n* = 54, *U* = 321, *P* = 0.13; Fig. 5). Using the modified Kistner score on organ samples where we received all three components (e.g., kidney, heart, and pericardium), the data suggested that elk in the FCA (*n* = 15) and RHA (*n* = 8) had relatively low average ingesta-free body fat at 5.9% (± 0.8%) and 10.4% (±1.2%), respectively, which were significantly different (*n* = 23, *U* = 20.5, *P* = 0.01).

DISCUSSION

Previous work in the FCA documented impacts of CBNG development on elk resulting in changes in elk resource selection and distribution compared to patterns observed before development (Buchanan et al. 2014). Our study documented shifts in resource selection as a behavioral response to the effects of CBNG development; however those shifts did not translate into population fitness consequences, although some fat scores were lower in the FCA than in an off-site, non-impacted reference area. These findings support the conclusions that elk are able to alter day and night resource selection to mitigate some of the impacts of development.

It is not unusual to observe differences in animal resource selection across time and space (Hopcraft et al. 2012). Many species often take advantage of gradients in resources and risk to obtain forage whereby reducing exposure disturbance or predation (Gill et al. 1996, Sawyer et al. 2009, Middleton et al. 2013). A prime example of animals using resource gradients is the phenomena of migration (Sawyer and Kauffman 2011). However, our study evaluated a non-migratory elk population, thus animal movement and use of resource or risk gradients were more subtle in comparison too many other resource use studies (but see Neumann et al. 2013). Resource and perceived risk gradients operated on a smaller time scale in our study system where elk use shifted on a diel cycle in response to levels of CBNG development activity (also see Burkepile et al. 2013); however, because disturbance occurred throughout the year, elk avoidance response also occurred throughout the year. Our results suggest distance metrics from cover and roads were the important variables driving differences in diel resource selection in summer and winter. We argue that the difference in selection represented a release of CBNG development impacts on elk at night, although, there was greater variation among individual resource selection at night compared to day (Table 3). This selection pattern corresponded with the broader selection distributions observed at night (Fig. 3) and greater average distance to roads during day than at night in summer and winter (Fig. 4). In summer, approximately 82% of vehicle traffic in the FCA occurred during the day thus our results suggest elk were moving from escape cover to areas closer to roads where human activity was reduced during night time hours (Fig. 6). Similarly, zebra (*Equus quagga*) used burns with greater visibility when the risk of predation was higher (Burkepile et al 2013). Brown bears (*Ursus acrtos*) were documented increasing movement at night after day-time encounters with humans (Ordiz et al. 2013), resulting in a long-term response similar to FCA elk. These daily resource selection shifts likely allowed access to resources at night that were deemed unavailable or risky during the day.

We observed little change in population fitness across our study. Pregnancy did decline slightly during a portion of our study, but would still be considered in the expected range for Rocky Mountain elk (Raithel et al. 2007). We also report the pregnancy rate for 2014, which is outside of our spatial data collection time period, however, we contend that this extra measurement of pregnancy provided a better long-term population assessment. Heart fat content was also lower when compared to the RHA reference population. However, fat deposition was highly variable within both populations and we did not estimate forage nutritional quality in the RHA so we could not compare forage quality between the two areas. We are skeptical of low levels of ingesta-free body fat that we estimated based on potential bias in hunter-contributed samples. Because our three samples of pregnancy rates for the FCA elk herd included some of the highest recorded for Rocky Mountain elk (Raithel et al. 2007), we would expect greater body fat in accompaniment of such high pregnancy rates (Middleton et al. 2013), thus it is possible that fat was inadvertently removed during field collection. However, if we assume similar error through loss of organ fat for both the FCA and RHA, we should still be able to make relative comparisons of organ fat content, which suggests lower body condition in FCA elk. Despite possible decreased body condition, population numbers and calf:cow ratios have remained consistent and above Wyoming Game and Fish Department (WGFD 2010) herd objectives of 150 elk throughout the period of CBNG development. These mixed signals in population health may provide evidence for a possible disturbance threshold where continued development may increase the impacts of development on elk fitness.

Selection shifts as a result of avoidance behavior and concurrently lacking observed population fitness consequences suggests elk are able to achieve some level of self-mitigation of the impacts of CBNG development. Animals should select and forage in areas that provide the greatest energy gain (MacArthur and Pianka 1966), however, perceived risk (e.g., predation or disturbance) should force animals to make trade-offs between maximizing fitness and minimizing risk (Lima and Dill 1990, Frid and Dill 2002). The pattern of resource selection exhibited by FCA elk exemplifies a trade-off of risk avoidance during the day for expanded resource availability at night. During the day elk used distance and escape cover to avoid the large proportion of daily human activity and then moved from escape cover to take advantage of resources, (grass DE in 3 of 4 RSF models) closer to roads at night. In balancing this trade-off, FCA elk were able to maintain population productivity, thus mitigating some level of CBNG development impacts. Similarly, Guertin et al. (2012) found otters were able to mitigate the effects of chronic contaminants in their environment by altering their habitat use. Our findings suggest a behavioral response where elk were reducing CBNG impacts by using areas closer to infrastructure at night when development activity was reduced.

Just as others have suggested that behavioral responses need not represent population consequences (Gill et al. 2001), lack of population consequences in the face of behavioral changes may not represent a form of mitigation. There are other factors that may have reduced the impact of development on population dynamics. First, elk are rather long lived animals, thus our study time frame may have been too short to truly measure population declines. However, population numbers and calf:cow ratios were collected over a time period representative of an elk life span and showed no consistent declines (WGFD 2010). Second, there was a decrease in CBNG development as our study progressed. While the development footprint was not reduced, the amount of human activity likely declined post construction, thus possibly reducing the perceived risk. If decreased development were the driver allowing continued population success we would expect probability of use to return to patterns more similar to predevelopment, however, that has not occurred (Buchanan et al. 2014).

Although we argue in support of possible self-mitigation as a beneficial adaptation of FCA elk in response to human disturbance, we caution possible downplaying of the impacts of CBNG development on elk. Changes in resource use and distribution have been demonstrated for the FCA elk herd in response to development (Buchanan et al. 2014), and while severe population fitness consequences have not been documented, we have yet to fully understand disturbance effects on population dynamics. External to possible mitigation, elk, in general, are rather robust, mobile animals, thus development in the FCA may not have reached a point where population dynamics have been greatly influenced. Continued development may increase density dependent effects as areas available as refugia will likely decline. Areas of high use may become depleted of resources, or at least reduced in quality, possibly leading to reduced resistance to stochastic climate events (Owen-Smith et al. 2011). To compensate, individual elk may use areas of higher risk to obtain necessary resources or move to other habitat patches if available similar to behavior observed in moose (*Alces alces*; Eldegard et al. 2012). Some combination of these processes could provide some relief of development impacts. Continued monitoring and study of this elk population may provide crucial information on density dependent effects and thresholds of energy development impacts on elk and other ungulate populations experiencing expansion of energy resource extraction.

Although our results suggest elk may be able to mitigate disturbance impacts, that ability likely functions inversely to the intensity of development. To maintain elk populations it should be a priority to retain escape cover. Retention of conifer patches within rugged terrain may be especially critical in areas like the FCA, where the landscape was dominated by sagebrush steppe with little available concealment. Development protocols often avoid rugged terrain due to erosion issues, thus, creating greater buffers around these areas may provide greater concealment opportunities for elk and offer greater refugia to avoid development activity during the day.

Finally, our methodology successfully combined the benefits of using frequency of use as the response variable and a mixed effects model framework. This method removed some of the issues common when using other resource selection study methods (i.e., binary response). For example, the correlative issues of sequential location data were addressed by removing time stamps from each location (Nielson and Sawyer 2013) and resource availability was defined for each animal at the home range level. Using a mixed-effects model we were able to account for unequal location sample sizes between individuals and variation in resource selection between individuals (Gilles et al. 2006). Our statistical method did require a large dataset and greater computing power than traditional resource selection methods, however, these restrictions were outweighed by the ability to meet or remove assumptions limiting other methods. Increased availability of large datasets through the use of GPS and other innovative technologies promotes the need for sampling and statistical methods such as those used in our study. These methods offered the capacity to accurately assess small scale shifts in elk resource selection and elk ability to mitigate the impacts of CBNG development.

ACKNOWLEDGMENTS

We thank the Hayden, Powder River, and Maycock Ranches for property access. H. O’Brien, J. Verplanke, L. Jahnke, J. Hobbs, T. Achterhof, L. Driessen, M. Pike-Biegunski, and J. Ongstad provided logistical and field assistance. We particularly thank T. Bills from the Buffalo Wyoming Field Office of the Bureau of Land Management for his insights and leadership throughout our study. C. Molle (Ruminant Nutrition Laboratory, University of Wyoming) provided technical assistance with forage quality analysis. We thank S. Newbold and his students from Sheridan College for their efforts in organ collection and analysis. M. Kauffman provided assistance with study design and statistical support. J. Pope and M. Atchison (Leading Edge Aviation, LLC.) provided assistance in capture operations. Our research was funded in part by the Bureau of Land Management, the School of Energy Resources and the Wyoming Reclamation and Restoration Center at the University of Wyoming, Anadarko Petroleum Corporation, Petro-Canada, Marathon Oil Company, and the Wyoming Game and Fish Department. We conducted our field research including capture, handling, and marking female elk according to Wyoming Game and Fish Department Chapter 33-396 permit and the University of Wyoming Institutional Animal Care and Use Committee protocol 04172008.

LITERATURE CITED

Allison, P. D. 2009. Logistic regression using SAS: theory and application, 8th edition. SAS Institute, Cary, NC.

Arnold, T. W. 2010. Uniformative parameters and model selection using Akaike’s information criterion. Journal of Wildlife Management 74:1175–1178.

Barbknecht, A. E., W. S. Fairbanks, J. D. Rogerson, E. J. Maichak, B. M. Scurlock, and L. L. Meadows. 2011. Elk parturition site selection at local and landscape scales. Journal of Wildlife Management 75:646–654.

Beck, J. L., and J. M. Peek. 2005. Great Basin summer range forage quality: do plant nutrients meet elk requirements? Western North American Naturalist 65:516–527.

Beck, J. L., J. M. Peek, and E. K. Strand. 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. Journal of Wildlife Management 70:283–294.

Beckmann, J. P., K. Murry, R. G. Seilder, and J. Berger. 2012. Human-mediated shifts in animal habitat use: sequential changes in pronghorn use of a natural gas field in Greater Yellowstone. Biological Conservation 147:222–233.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? American Naturalist 180:407–424.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons, Incorporated, New York, USA.

Bonnot, N., N. Morellet, H. Herheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. J. M. Hewison. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research 59:185–193.

Boyle, S. A., W. C. Lourenco, L. R. da Silva, and A. T. Smith. 2009. Home range estimates vary with sample size and methods. Folia Primatol 80:33–42.

Buchanan, C. B., J. L. Beck, T. E. Bills, and S. N. Miller. 2014. Seasonal resource selection and distributional response by elk to development of a natural gas field. *Rangeland Ecology and Management* 67:369–379.

Bureau of Land Management [BLM]. 2010. Fortification creek area draft resource management plan amendment/environmental assessment. U.S. Department of Interior, Bureau of Land Management, Buffalo Field Office, Buffalo, Wyoming, USA.

Burkepile, D. E., C. E. Burns, C. J. Tambling, E. Amendola, G. M. Buis, N. Govender, V. Nelson, D. I. Thompson, A. D. Zinn, and M. D. Smith. 2013. Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. Ecosphere 4:article 139.

Burger, J. 1998. Effects of motorboats and personal watercraft on flight behavior over a colony of common terns. The Condor. 100:528–534.

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

Cameron, A. C., and P. K. Trividi. 1998. Regression analysis of count data. Cambridge University Press, New York, NY.

Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an anitpredator response to wolves. Ecology 86:3387–3397.

D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin 30:430–439.

Eldegard, K., J. T. Lyngved, and O. Hjeljord. 2012. Coping in a human-dominated landscape: trade-off between foraging and keeping away from roads by moose (*Alces alces*). European Journal of Wildlife Research 58:969–979.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between foragequality, forage quantity, and predatory avoidance. Oecologia 75:580–586.

Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. Landscape Ecology 20:273–287.

Frid, A., and L M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11–26.

Gill, J. A., W. J. Sutherland, and A. R. Watkinson. 1996. A method to quantify the effects of human disturbance on animal populations. Journal of Applied Ecology 33:786–792.

Gill, J. A., K. Norris, W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation. 97:265–268.

Gilles, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gregory, A. J., M. A. Lung, T. M. Gehring, and B. J. Swanson. 2009. The importance of sex and spatial scale when evaluating sexual segregation by elk in Yellowstone. Journal of Mammalogy 90:971–979.

Guertin, D. A., M. Ben-David, A. S. Harestad, and J. E. Elliot. 2012. Fecal genotyping reveals demographic variation in river otters inhabiting a contaminated environment. Journal of Wildlife Management 76:1540–1550.

Harvey, L. and D. Fortin. 2013. Spatial heterogeneity in the strength of plant-herbivore interactions under predation risk: the tale of bison foraging in wolf country. PLoS ONE 8:e73324. Doi:10.1371/journal.pone.0073324.

Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

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, DC, USA.

Hilbe, J. M. 2008. Negative binomial regression. Cambridge University Press, Cambridge, U. K.

Hopcraft J. G. C., T. M. Anderson, S. Perez-Vila, E. Mayemba, and H. Olff. 2012. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. Journal of Animal Ecology 81:201–213.

Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. Wildlife Monographs 160:1–36.

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 70:347–357.

Kirol, C. P., J. L. Beck, J. B. Dinkins, and M. R. Conover. 2012. Microhabitat selection for nesting and brood-rearing by the greater sage-grouse in xeric big sagebrush. The Condor 114:75–89.

Krausman, P. R., M. C. Wallace, C. L. Hayes, and D. W. DeYoung. 1998. Effects of jet aircraft on mountain sheep. Journal of Wildlife Management 62:1246–1254.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lingle, S. 2001. Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. Ethology 107:295–314.

Luttbeg, B., and A. Sih. 2004. Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk. Israel Journal of Zoology 50:233–254.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. The American Naturalist 100:603–609.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, and T. L. McDonald. 2002. Resource selection by animals: statistical design and analysis for field studies. Second Edition. Kluwer Acedemic, Boston, Massachusetts, USA.

Massey, Jr., F, J. 1951. The Kolmogorov-Smirnov test for goodness of fit. Journal of the American Statistical Association 46:68–78.

McGeehan, S. L., and D. V. Naylor. 1988. Automated instrumental analysis of carbon and nitrogen in plant and soil samples. Communications in Soil Science and Plant Analysis 19:493–505.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.

Moen, R., J. Pastor, Y. Cohen, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60:659–668.

Neumann, W., G. Ericsson, H. Dettki, and V. C. Radeloff. 2013. Behavioural response to infrastructure of wildlife adapted to natural disturbances. Landscape and Urban Planning 114:9–27.

Nielson, R. M., and H. Sawyer. 2013. Estimating resource selection with count data. Ecology and Evolution 3:2233-2240

Ordiz, A., O. Støén, S. Saebø, V. Sahlén, B. E. Pedersen, J. Kindberg, J. E. Swenson. 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. Journal of Applied Ecology 50:306–314.

Owen-Smith, N. G. J. Chirima, V. Macendza, and E. Le Roux. 2011. Shrinking sable antelope number in Kruger National Park: what is suppressing population recovery? Animal Conservation 15:195–204.

Patthey, P., S. Wirthner, N. Signorell, and R. Arlettaz. 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of Applied Ecology. 45:1704–1711.

Paudel, P. K., and P. Kindlmann. 2012. Human disturbance is a major determinant of wildlife disturbance in Himalayan midhill landscapes of Nepal. Animal Conservation 15:283–293.

Ryan, S. J., C. U. Knechtel, and W. M. Getz. 2006. Range and habitat selection of African buffalo in South Africa. Journal of Wildlife Management 70:764–776.

Relyea, R. A. 2003. How prey respond to combined predators: a review and empirical test. Ecology 84:1827–1839.

Robinson, B. G., M. Hebblewhite, and E. H. Merrill. 2010. Are migrant and resident elk (Cervus elaphus) exposure to similar forage and predation risk on their sympatric winter range? Oecologia 164:265–275.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419–1426

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 71:868–874.

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. 2009b. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.

Sawyer, H., and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078–1087.

Schmitz, O. J., A. P. Beckerman, K. M. O’Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology. 78:1388–1399.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters. 7:153–163.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531–556 *in* D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institute Press, Washinton, D.C., USA

Svejcar, T., and M. Vavra, 1985. The influence of several range improvements on estimated carrying capacity and potential beef production. Journal of Range Management 38:395–399.

Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications. 13:951–963.

Thomas, D.L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 49:397–405.

Tilley, J. M. A., and R. A. Terry. 1963. A two-stage technique for the in vitro digestion of forage crops. Journal of the British Grassland Society 18:104–111.

Walther, F. R. 1969. Flight behaviour and avoidance of predators in Thompson’s gazelle (Gazella thomsoni guenther 1884). Behaviour. 3:184–221.

Weinrich, M., and C. Corbelli. 2009. Does whale watching in Southern New England impact humpback whale (Megaptera novaengliae) calf production or calf survival? Biological Conservation 142:2931–2940.

Western Regional Climate Center [WRCC]. 2009. Remote Automatic Weather Station, Echeta, WY, USA. Available at: http://www.wrcc.dri.edu/. Accessed October 2009.

Wyoming Game and Fish Department [WGFD]. 2007b. Job Completion Report: EL320 – Fortification. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Wyoming Game and Fish Department [WGFD]. 2010. Job Completion Report: EL320 – Fortification. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Table 1. Resource variables measured within sampling units across the Fortification Creek Area of northeastern Wyoming, USA.

Variable	Description
Environmental	
AFDE	Average forb digestible energy (kcal/m^2)
AGDE	Average grass digestible energy (kcal/m^2)
AFP	Average forb protein (g/m^2)
AGP	Average grass protein (g/m^2)
ELEV	Elevation (m)
DWAT	Distance to water (m)
DJUN	Distance to juniper patch (m)
PERJUN	Percent juniper cover
PNS	Percent north-facing aspect
PSS	Percent south-facing aspect
SLOPE	Slope
VRM	Vector ruggedness metric (Sappington 2007)
Anthropogenic	
DKRD	Decay distance to road (m; α = 100–5000 m)
DKWL	Decay distance to well (m; α = 100–5000 m)
KRD	Kernel road density (km/km^2)
KWD	Kernel well density (number/km^2)
VROAD	Road viewshed
VWELL	Well viewshed

Table 2. Mean (± 95% CI) standing CP (g/m^2) and DE (kcal/m^2) for north-facing sagebrush, south-facing sagebrush, and juniper cover types, Fortification Creek, northeastern Wyoming, USA. These estimates were averaged over early and late summer 2009 and 2010.

	CP (g/m^2)			DE (kcal/m^2)		
	North-facing sagebrush	South-facing sagebrush	Juniper	North-facing sagebrush	South-facing sagebrush	Juniper
Forb	13.3 ± 2.2	7.6 ± 1.4	10.4 ± 1.7	210.3 ± 7.2	124.1 ± 4.9	159.7 ± 5.3
Grass	8.3 ± 1.3	16.3 ± 2.4	7.1 ± 0.8	259.2 ± 3.5	534.4 ± 2.3	220.5 ± 2.8

Table 3. Top-ranked environmental models with random intercept and environmental plus anthropogenic models with random coefficients demonstrating elk resource selection in the Fortification Creek Area, northeastern Wyoming, USA from 2008–2010. No models were competitive with the top model during any time period, thus we do not report Akaike weights.

Model	AIC	ΔAIC	Intercept	Coefficient
Summer Day				
Environmental + Anthropogenic Model AGDE + PERJUN + VRM + DKRD (100 m) + VWELL + random coefficient for DKRD(100 m) by animal	34977.8		1.3	0.8
Environmental Model AGDE + PERJUN + VRM + random intercept by animal	35207.2	229.4	1.2	
Summer Night				
Environmental + Anthropogenic Model PERJUN + ELEV + DJUN + DKRD (500 m) + VWELL + random coefficient for DKRD (500 m) by animal	39754.8		1.1	0.9
Environmental Model PERJUN + ELEV + DJUN + random intercept by animal	39997.0	242.2	1.0	
Winter Day				
Environmental + Anthropogenic Model AGDE + PERJUN + VRM + ELEV + DKRD (500 m) + VWELL+ random coefficient for DKRD (500 m) by animal	23664.2		3.2	1.0
Environmental Model AGDE + PERJUN + VRM + ELEV+ random intercept by animal	23895.4	231.2	3.2	
Winter Night				
Environmental + Anthropogenic Model				

AGDE + VRM + ELEV + DJUN + DKRD (1000 m) + VWELL+ random coefficient for DKRD (1000 m) by animal	24492.0		2.2	2.0
Environmental Model				
AGDE + VRM + ELEV + DJUN+ random intercept by animal	24652.0	160.0	3.1	

Table 4. Top model variables for each time period with variable coefficients (β), standard errors (SE) and *P*-values, Fortification Creek Area, northeastern Wyoming, USA, 2008–2010.

Variable	β	SE	*P*
Summer Day			
Intercept	-12.200	0.223	<0.001
Grass DE	0.001	0.0004	<0.001
Percent juniper	0.042	0.001	<0.001
VRM	25.600	2.110	<0.001
Distance to road (100 m)	-0.870	0.170	<0.001
Well viewshed	-0.006	0.0008	<0.001
Summer Night			
Intercept	-10.200	0.524	<0.001
Percent juniper	0.014	0.0014	<0.001
Elevation	0.0006	0.0004	0.137
Distance to juniper	-0.00009	0.00002	<0.001
Distance to road (500 m)	-0.067	0.148	0.646
Well viewshed	-0.003	0.0007	0.001
Winter Day			
Intercept	-16.200	0.759	<0.001
Grass DE	0.003	0.0004	<0.001
Percent juniper	0.024	0.002	<0.001
VRM	36.700	2.330	<0.001
Elevation	0.003	0.0005	<0.001
Distance to road (500 m)	-1.010	0.191	<0.001
Well viewshed	-0.005	0.0010	<0.001
Winter Night			
Intercept	-22.700	0.768	<0.001
Grass DE	0.007	0.0004	<0.001
VRM	17.400	2.430	<0.001
Elevation	0.008	0.0005	<0.001
Distance to juniper	-0.00010	0.00002	<0.001
Distance to road (500 m)	-1.130	0.267	<0.001
Well viewshed	-0.003	0.001	<0.001

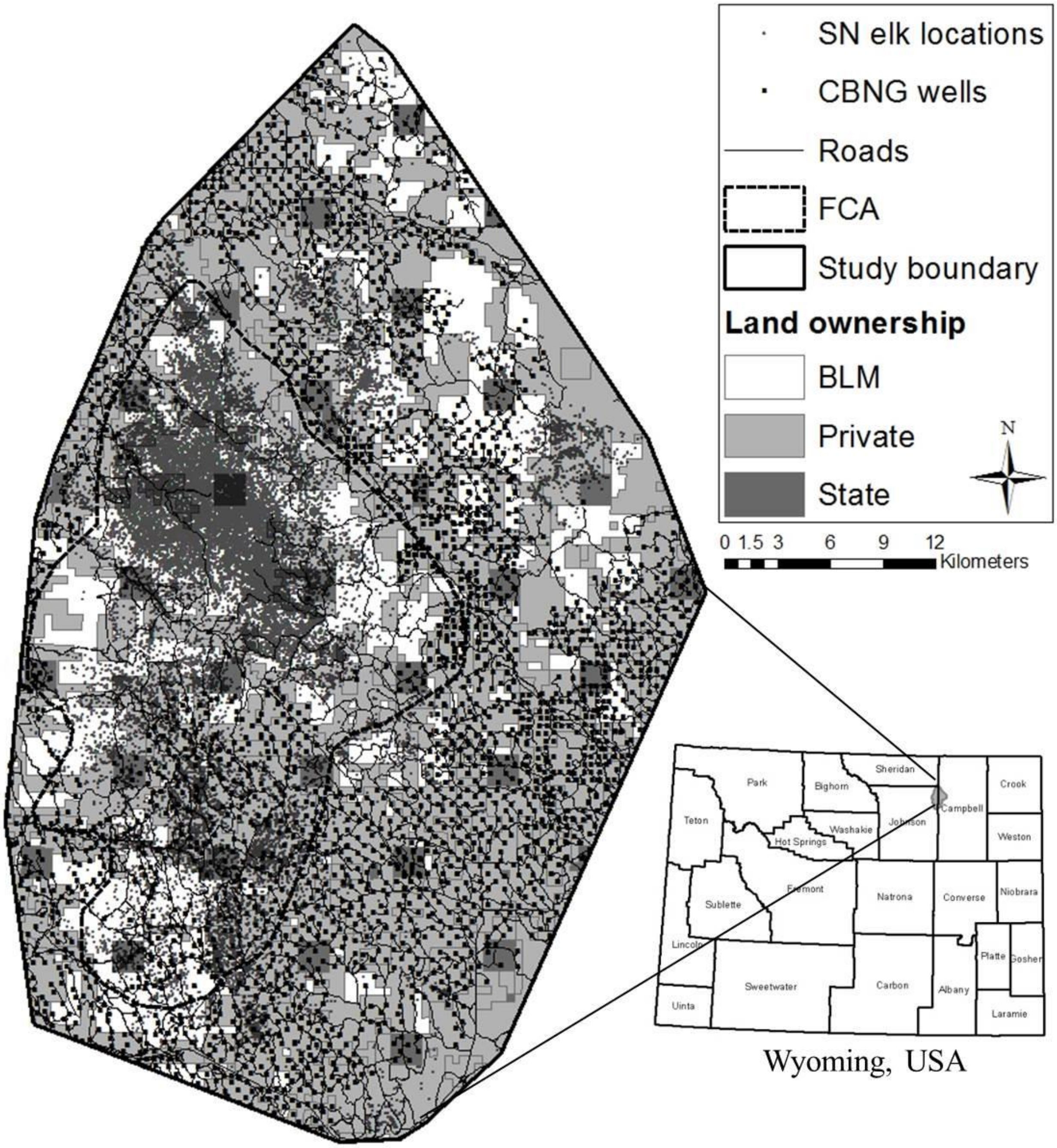

Figure 1. The Fortification Creek Area (FCA) and the study area boundary, depicting original ($498\ km^2$) and expanded study area ($1432\ km^2$), respectively. For simplicity, we term the entire $1432\ km^2$ area as the FCA. The FCA is located in northeastern Wyoming, USA and is home to a resident elk (*Cervus elaphus*) herd as well as a site for natural gas development.

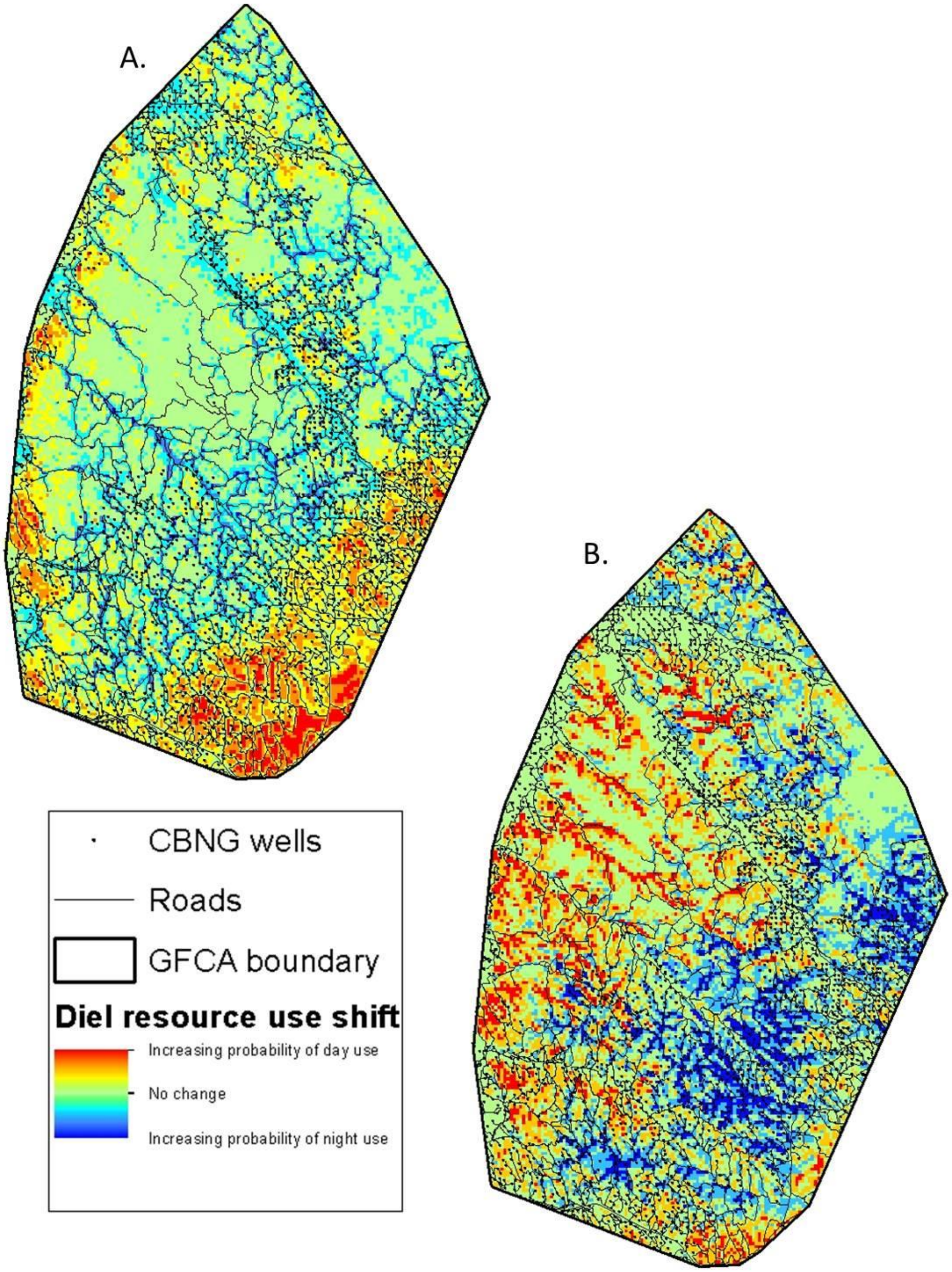

Figure 2. The difference in day and night elk resource selection across the Fortification Creek Area in northeastern Wyoming during summer (A) and winter (B), 2008–2010. Cooler colors (light blue to dark blue) represent areas of higher probability of use during the night and warmer colors (yellow to red) represent areas of higher probability of use during the day.

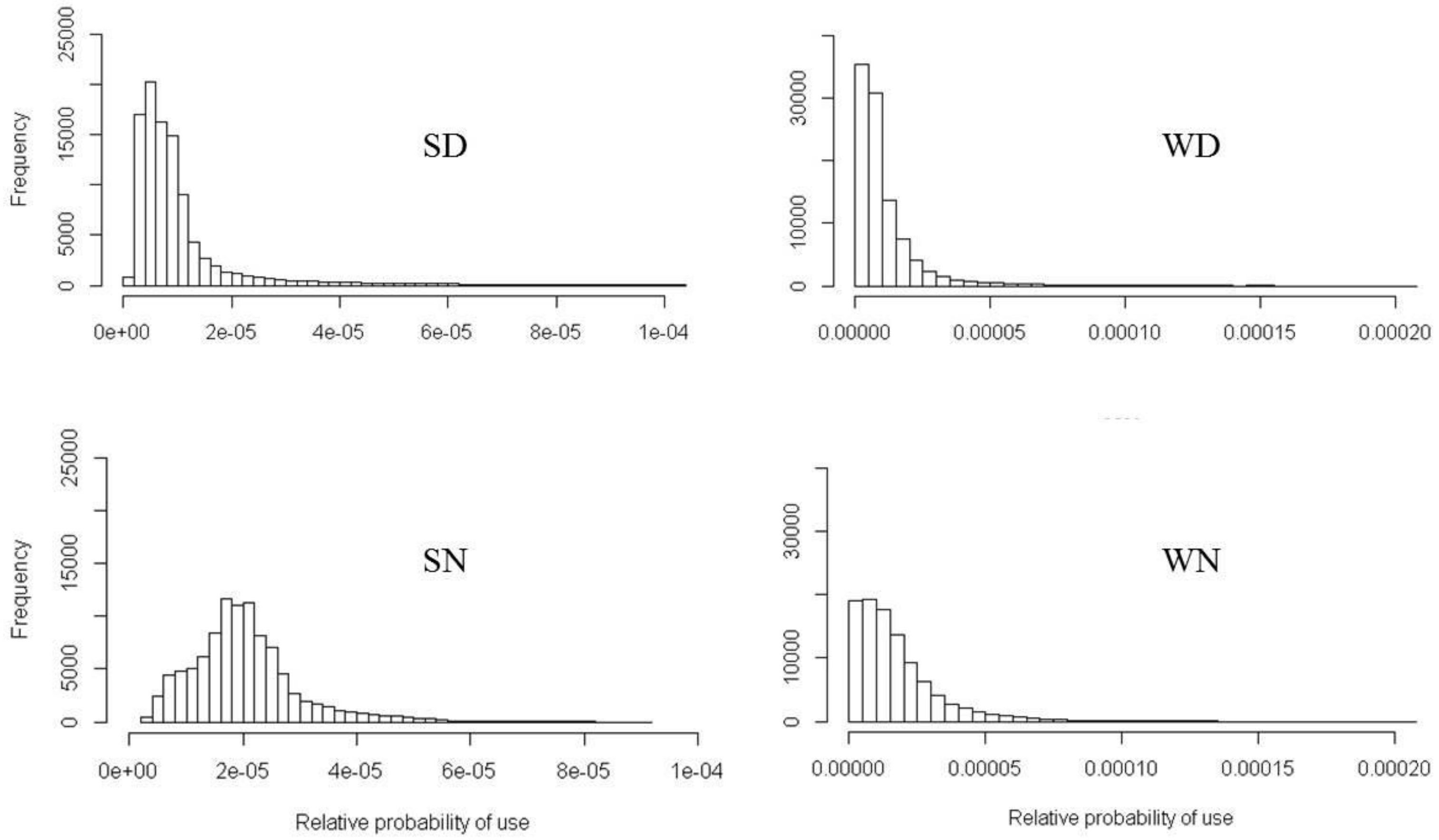

Figure 3. Distributions of relative probability of use during summer day (SD), summer night (SN), winter day (WD), and winter night (WN) across the Fortification Creek Area in northeastern Wyoming, 2008–2010. Kolmogorov-Smirnov tests confirmed differences ($P < 0.01$) in distribution between day and night during summer and winter, where distribution of relative probability of use was broader at night.

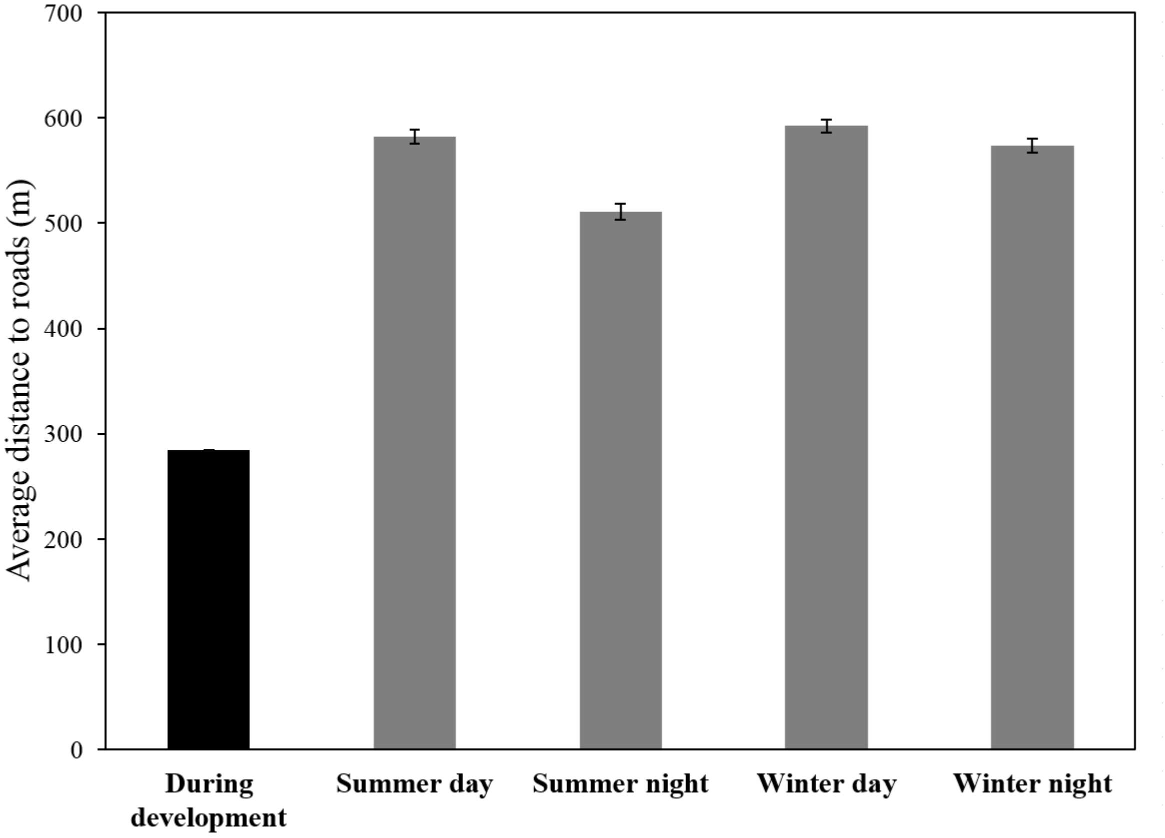

Figure 4. Average distance (m) to roads (± SE) for elk locations in the Fortification Creek Area for elk locations during day and night in summer and winter during development, 2008–2010.

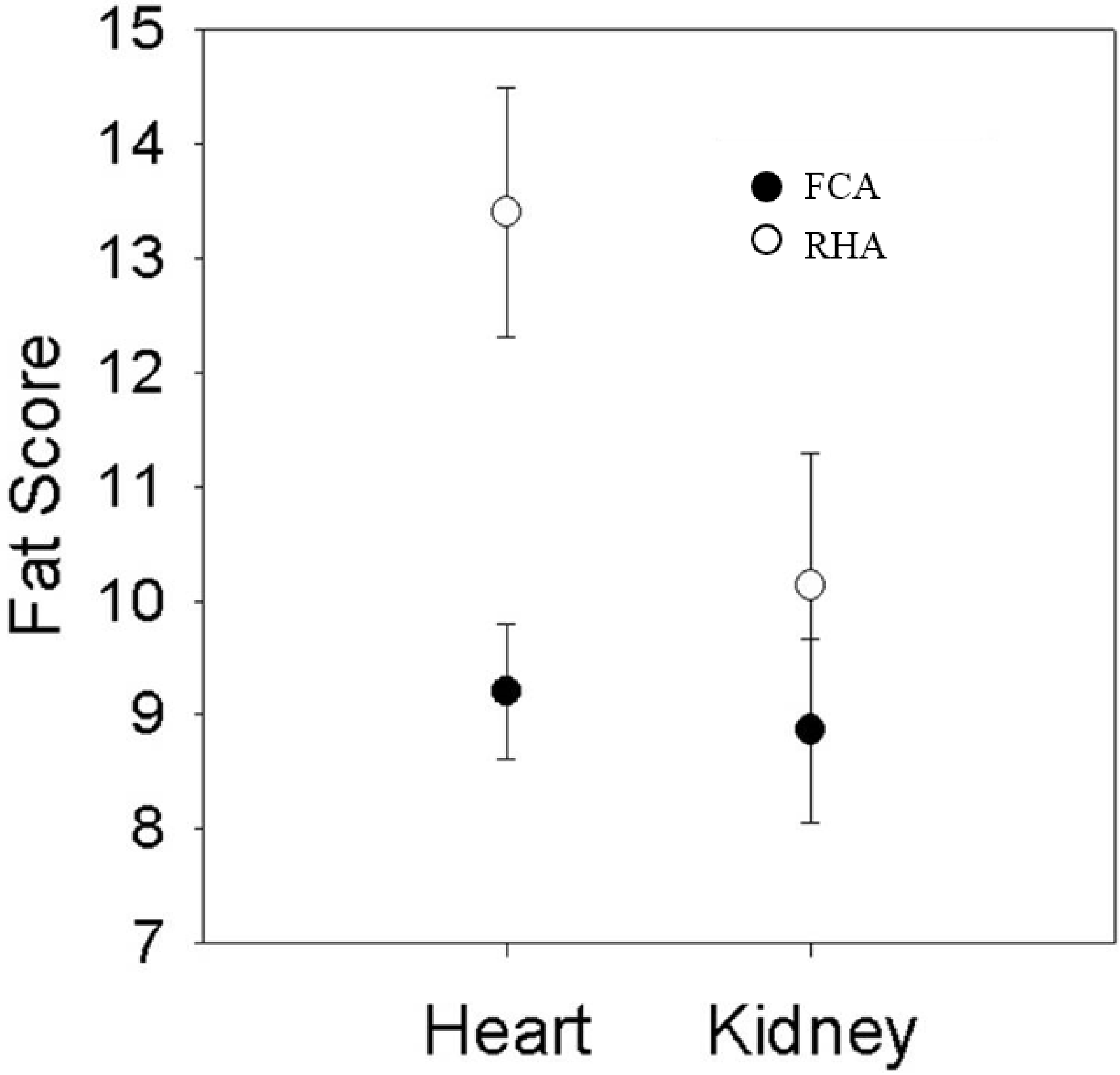

Figure 5. Organ fat score comparisons between the Fortification Creek Area (FCA) and the Rochelle Hills Area (RHA) of northeastern Wyoming. A modified Kistner score was used to assess fat deposition around hearts and kidneys of harvested elk in the FCA and RHA in 2009–2011 and 2013.

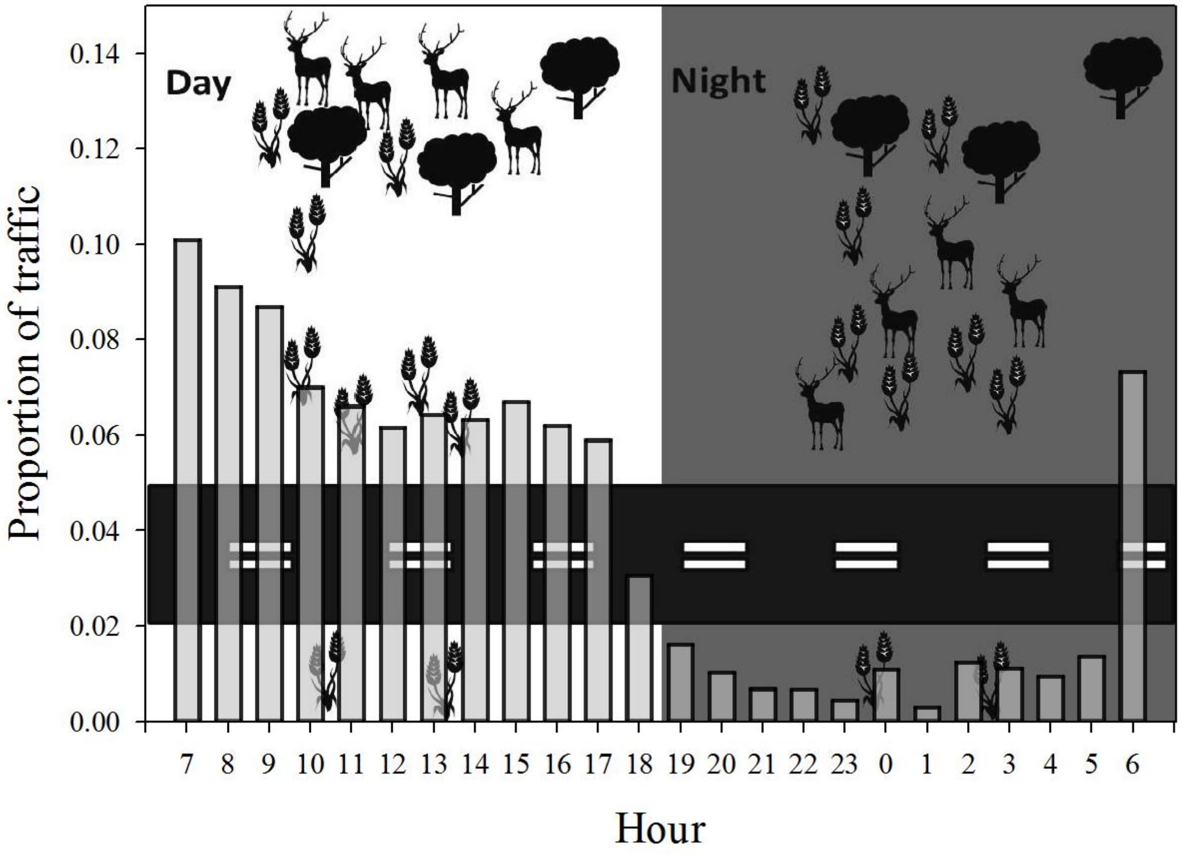

Figure 6. Proportion of traffic events during each hour period of a 24-hour day in Fortification Creek, northeastern Wyoming, USA. The graph begins at 07:00 hrs so all day and night hours are grouped together for visualization. The distribution of traffic in this figure summarizes over 64,000 individual traffic events collected by infrared monitors. In the background of the figure, Fortification Creek Area elk are moving closer to roads at night and away from juniper cover when traffic levels are relatively lower than levels during day time hours. This shift in resource selection may allow elk to mitigate some of the impacts of coal bed natural gas development. As suggested by our mixed model results, there is also more variation in night elk resource selection than observed during the day.

CHAPTER FOUR

The Influence of Harvest and Natural Gas Development on the Demography and Dynamics of an Isolated Elk Population

Clay B. Buchanan, Daniel F. Doak, and Jeffrey L. Beck

Key words: Cervus elaphus, hunt, Markov Chain Monte Carlo

Clay B. Buchanan and Jeffrey L. Beck, Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82070, USA – email addresses: ecology.clay@gmail.com (Clay B. Buchanan); jlbeck@uwyo.edu (Jeffrey L. Beck)

Daniel F. Doak, Environmental Studies Program, University of Colorado, Boulder, CO 80309, USA – email address: daniel.doak@colorado.edu

Corresponding author: Clay B. Buchanan

In the format for manuscripts submitted to *Wildlife Biology*

Abstract

It is critical to consider demography in the study of population dynamics and their responses in the face of changing management interventions and disturbance regimes. However, data limitations often hamper the ability to clearly judge these effects on wildlife populations. Collection of individual-based survival data is often intensive and expensive, while population and harvest surveys may not provide sufficient detail to assess population dynamics. Here, we estimate the importance of intensifying energy development and fluctuating harvest levels on the Fortification Creek Area (FCA) elk (*Cervus elaphus*) herd in northeast Wyoming. Improvements in computing power and Bayesian analysis methods makes it possible to incorporate often incomplete or imperfectly-matched data types to help inform understanding population dynamics. Our study used averaged elk population vital rates from previously studied populations and population and harvest estimates from the FCA within a Markov Chain Monte Carlo modeling framework to estimate effects of development and harvesting in altering demographic rates and hence population dynamics. Use of Bayesian methods was successful in fitting observed population numbers, and our results suggest that shifting harvest rates are the main forces driving substantial shifts in population numbers of the FCA elk herd with much weaker effects from any other effect on demographic rates. Models with no other temporal effect other than harvest numbers accounted for 39% of the variation (R^2) in estimated elk numbers, and models that allowed other changes increased R^2 to only 48%. However, we caution that other mechanisms may have increasing influence on elk population dynamics if the natural gas development footprint in this area continues to increase.

INTRODUCTION

Identification of behavioral and population-level responses to disturbance can provide a partial measure of the total impacts of disturbance on a wildlife population. In particular, assessment of disturbance impacts on wildlife species ideally includes analysis of behavior and demography (Christianson and Creel 2014). Two factors influencing wildlife populations across North America are the development of energy resources and regulated harvest. The Fortification Creek Area (FCA) elk herd, in northeast Wyoming, USA, experienced both of these influences and little else with respect to human influence. Previous work in the FCA identified shifts in elk resource selection resulting in losses of high quality habitat (Buchanan et al. 2014). In addition, these two factors—rapidly increasing petroleum or other energy development and harvesting—are likely to be among the most important factors driving the dynamics of many other ungulate populations in western North America in the coming decades (Copeland et al. 2011).

Collection of individual survival data, however, often includes intense, expensive sampling. Short study timeframes and reduced budgets often hamper the ability of researchers to collect suitable data needed to make such assessments of the impacts of disturbance on many wildlife populations. Another common problem in wildlife studies is the generation time of focal species in comparison of radio telemetry collar battery life. The difference in species generation time and collar life can limit researchers' ability to assess survival. Collar reliability can also be an issue (Jiang et al. 2008) where the case of partial or total collar failure greatly hinders the ability to adequately estimate survival.

In contrast to demographic data obtained from marked individuals in telemetry studies, data collected at the level of a wildlife population may be relatively easy and inexpensive to gather and are recorded for many populations. Management agencies and researchers often conduct counts and demographic surveys providing an alternative data source to individual survival and reproduction estimates (WGFD 2007b, 2010). Another possible source of information on population dynamics is harvest data, such as the annual number of animals harvested from a population. Many large mammal populations are harvested, sometimes intensively, which serves as a recreational hunting draw and population management tool (Vucetich et al. 2005, Parker and Rosell 2014). These data, which document a major source of mortality for some populations, serve as a readily available, though only partial, source of demography that can in combination with changes in numbers be used to improve understanding of wildlife dynamics. However, population numbers and harvest rates, or other coarse demographics, may not always provide sufficient information to accurately assess disturbance impacts on population dynamics (Hebblewhite 2011).

Rather than using demographic data from telemetry studies and population surveys separately, combinations of known vital rates and coarse population data can offer a way to bridge data gaps to answer population impact questions. Elk populations have been studied and monitored across North America, thus data for this type of analysis should be available (e.g., Moran 1973, Unsworth et al. 1993, Lubow et al. 2002, Cook et al. 2004). Methods for an analysis of these combined data have been less available; however advancement in Bayesian analysis methods and computing power offers a platform to conduct such an analysis (Marion et al. 2012). Bayesian methods permit estimation of population metrics through Markov Chain Monte Carlo (MCMC) sampling of posterior distributions (Gilks et al. 1996) and thus the ability to simulate population demographic scenarios or test alternative mechanisms that may drive population dynamics. Combining measured vital rates from numerous elk populations with estimates of harvest and population numbers of elk from the FCA provided an opportunity to assess the applicability of this general approach while congruently assessing the influence of harvest on the FCA elk population. In particular, we sought to test two questions about this population: 1) To what extent can the large fluctuations in elk numbers seen over a 23-year period (1989–2011) be explained solely as a simple response to harvest rates? and 2) Is there support for the hypothesis that increasing energy development in the area has altered elk demographic rates?

We addressed these two questions by building a suite of alternative models and asking how well each could predict observed changes in elk numbers over 23 years. In particular, models that allowed no dynamic changes in demographic rates, other than the observed mortality from harvest, address the question of how well harvest alone can explain shifting population sizes over time. Support for models that also fit other changes in survival rates over this time provided a test of whether increasing energy development in this area has left a clear imprint on demography, and hence dynamics, and how much such changes improve the predictive power of the model.

METHODS

Study area

Our study was conducted in the 498 km^2 FCA, approximately 40 km west of Gillette, Wyoming, USA. The FCA encompassed portions of Campbell, Johnson, and Sheridan counties and was administered by the BLM (44%), State of Wyoming (6%), and private landowners (50%). Cattle ranching was the dominant land use prior to CBNG development. Elevation in the study area ranged from 1,095 to 1,550 m. Over 700 CBNG wells and 542 km of roads were developed in the FCA since the early 2000s (BLM 2008). Land cover was dominated by Wyoming big sagebrush *Artemisia tridentata* shrubland with scattered patches of Rocky Mountain juniper *Juniperus scopulorum* that comprised only 11% of the landscape. Grasses common to the northern mixed-grass prairie dominated our study area including bluebunch wheatgrass P*seudoroegneria spicata*, cheatgrass *Bromus tectorum,* little bluestem *Schizachyrium scoparium*, and western wheatgrass *Pascopyrum smithii*. The FCA and surrounding area of northeast Wyoming were characterized by a semiarid climate with an average annual precipitation of about 22 cm (WRCC 2011).

Annual population and harvest estimates

Aerial surveys for elk in the FCA (Wyoming Elk Herd Unit 123) were conducted by Wyoming Game and Fish Department (WGFD) using fixed wing and helicopter aircraft. Surveys were conducted prior to and post-harvest, which occurred annually over the last 10 days of October, 1989–2011. Opportunistic flights were also conducted when funding and personnel were available during other times of the year. These data were used by WGFD to annually estimate the size of the elk population (WGFD 1996, 2007a, 2007b, 2010). These estimates were for the entire population including both sexes and all age groups. While not specified in the reports, preliminary analyses showed that elk numbers appeared to correspond to late fall (post-harvest) population sizes. Hunter surveys and field observations were collected during the harvest season by WGFD to assess harvest numbers and hunter success. Harvest was permitted on males and females, and all ages, however no data were available on the age and sex distribution of harvested elk from this population. We used population estimates and harvest estimates from 1989–2011 to represent our observed annual population sizes, and annual harvest numbers, respectively (Fig. 1). No estimates of uncertainty were available for either harvest or population sizes. In our analyses we assumed that harvest numbers were completely accurate, but that population size was estimated with uncertainty.

Population model

We developed multiple models to assess the influence of increasing energy development impacts and fluctuating harvest numbers on the FCA elk herd. To test for either static or changing demographic rates for the FCA herd, we began with a base demographic model for average elk demography. As described below, in alternative model structures, the survival and fecundities in the base model were modified to allow either static or time-varying changes in rates. The relative support for these different models by allowing variation in vital rates provides a test of the support for the importance of energy development and of harvest in driving elk numbers in the FCA population.

Our base model was an age-structured 16 x 16 population pre-reproduction matrix using elk vital rates from Raithel et al. (2007). We used the grand mean values for survival and fecundity of calf and female elk as reported by Raithel et al. (2007) from analysis of 37 studies conducted across the western United States. Yearling age and prime-age classes included individuals 1 year old and 2–9 years of age, respectively. Old-age individuals included animals that were 10–14 years of age, with senescence occurring at 15 years of age. We assigned equal survival and fecundity values across all elk within each age class (Table 1). We assumed a 50:50 sex ratio of new calves for analysis to match Raithel et al. (2007). Our model was implicitly two-sex: only half the reproductive individuals produced offspring (accounting for male and female numbers), but we did not distinguish between the vital rates of males and females. While it would be informative to build in greater information on male and female vital rates, with no sex or age breakdowns of numbers or harvest rates, we needed to employ a simple modeling framework.

MCMC model-fitting

Our 16 x 16 population matrix was the base model for the simulation of population numbers through time. In particular, for elk aged 2-16, the model estimates the number of elk of age j in year i, $Nest_{j,i}$ as:

$$Nest(j,i) = \left(\left(1 - m_{j-1} * mod_i\right) * Nest_{j-1,i-1}\right) - H_i * \left(\frac{1}{15}\right)$$

While the number of one year olds is:

$$Nest(j,1) = \sum_j Nest_{j,i-1} * f_j * mod_f * (1 - m_0 * mod_i)$$

Here, H_i is the number of harvested elk in year i, $m_{j,}$is the base model mortality rate (1 minus survival) for age j animals, $f_{j,}$ is the base fecundity rate for age j animals, and mod_i and mod_f are year-specific mortality and time-independent fecundity modifier functions, respectively. The total elk population number for each year was calculated as:

$$Ntot_i = \sum Nest_{j,i}.$$

We ran six alternative models that used one of three modification functions for mortality and had either no fecundity modification, or included a simple one parameter modification, modf, applied to all years. The three mortality modifiers were:

Model 1: a single time-invariant modifier, mod1. This model allowed alteration of the mortality rates for the FCA herd away from the averages reported in Raithel et al. (2007) but did not include any shifts in these rates over time. This model tested the ability of changing annual harvest levels alone to predict the annual dynamics of the population.

Model 2: a single modifier value for years 1989–2000 and a separate modifier for years 2001–2011. This model fit different modifiers of baseline mortality rates for the years prior to and during intensive energy development; therefore, disturbances from energy development should have been measurable, if they occurred. This model therefore tested whether the simplest possible model of energy development effects on survival substantially improved the model predictions of annual dynamics of the population.

Model 3: A smooth and flexible time-varying mortality modifier, based on a logistic function and including both linear (in logistic transform) and quadratic temporal effects:

$\left(\frac{1}{1+\exp(-mod1-mod2*i-mod3*i*i}\right)$. With three fitted parameters, this was the most complex modifier function used. As with Model 2, this model tested whether energy development effects could improve model predictions, but did so with a more flexible framework. Also, like Model 2, this model was capable of showing whether predicted survival rate changes were consistent with a negative effect of energy development.

We refer to the three models that only alter mortality rates as Models 1, 2, and 3. And those that also modify fecundities as 1F, 2F, and 3F.

We fit our models using rjags software (R Development Team 2013). It is typical in Markov models to split the model into a process model and observation model (Marion et al. 2012). The process model incorporates biological assumptions and represents the unobserved population dynamic states of interest. In the MCMC framework, the parameters in a model are estimated by fitting an observable set of predictions (here, population sizes in each year) to independent data from the field (here, estimated total numbers in each year). The observation model described the observed population numbers as estimated by WGFD personnel. As is typical of MCMC models, we assume that observed numbers are not perfect, and thus include observation uncertainty in the model fitting. The fitting of all unknown parameters in the model was based on maximizing the likelihood of predicting the observed numbers, across all years. Table 2 summarizes all the fitted parameters in the model, as well as the prior distributions used to initiate the Markov chains. While it is possible to use informative priors in MCMC modeling, we used flat priors for all fitted parameters.

The MCMC technique allows posterior sampling of population parameters and observations, where the posterior distribution is the equilibrium distribution. Estimates of parameters and observations improve as the number of samples is increased. We developed an MCMC model to estimate elk population dynamics incorporating harvest numbers. The model included 3 chains and an adaptation period of length 1,500. We examined trace plots to assess chain behavior, which represented model convergence and mixing. We used an update or burn-in phase of 1,000 to approximate dynamic equilibrium. The entire model included 150,000 iterations with a thin rate of 3 to best sample modeling results while reducing computation memory. The Gelman test was also used to test for model convergence (Gelman et al. 2004). We employed Deviance Information Criteria (DIC) to assess the fit of alternative models, and present the mean and uncertainty (standard deviations [SD]) for key estimated parameters. To assess the predictive power of each model, we also regressed observed annual numbers on the mean predicted numbers from each model and report R^2 values from these fits. All modeling and statistical analyses were conducted using R language and environment (Packages: rjags, coda [Plummer et al. 2012]; R Development Team 2013). Example model code of the top model is reported in Appendix B.

RESULTS

Elk harvest numbers showed very similar fluctuations with observed elk population numbers (Fig. 1a). Changes in elk harvest numbers also corresponded with changing estimated annual population growth rates (Fig. 1), with low growth rates following years of high harvest.

Model convergence was supported by Gelman test results for all six models, and visual assessment of trace plots suggested good mixing across chains. All six models resulted in significant fits to the observed population numbers, with R^2 values ranging from 0.39 to 0.48 (Table 3). Model 3F (Table 2) had the lowest DIC and highest R^2 values, and was thus the best supported predictor of the population dynamics of this population (Table 3). However, the improvement in explanatory power of this time-varying model over the time-invariant Models 1 and M1F was not impressive, suggesting that fluctuating harvest numbers alone did an excellent job of explaining the dynamics of this population (Fig. 2).

All models predicted that demographic performance of this population was better than that reported by Raithel et al. (2007) for average populations (Tables 3 and 4); data that was collected across 37 Rocky Mountain and northwestern region elk populations. Different models predicted that mortality rates were only 11% to 57% of average values, while fecundity was predicted to be from 30% to 110% higher than average (Table 3).

DISCUSSION

Our modeling approach was successful in making reasonable predictions of yearly population estimates that approximated observed numbers of elk in our study area. The simulation was able to reach acceptable model convergence for all models, and appeared to reflect the major aspects of the FCA herd dynamics. Our model results support the hypothesis that harvest was the most important factor driving the population dynamics of FCA elk. The importance of harvest has been demonstrated for other elk populations, where harvest of prime-age individuals was the major driver of female elk survival (Brodie et al. 2013). As the FCA elk population was harvested at an average rate of approximately 20% of the population, harvest should take a major role in population dynamics. Other ungulate populations have experienced a range of harvest rates such as moose (*Alces alces*) in northern Norway where harvest (~25% of autumn population) also added complexity to population dynamics and influenced fecundity (Solberg et al. 1999), red deer (*Cervus elaphus*) in Scotland where populations continue to increase despite a ~15% harvest rate (Milner et al. 2006), and the Jackson elk herd in Wyoming that experienced a harvest rate of ~12% (Lubow and Smith 2004), Elk in Yellowstone National Park were also influenced by harvest which explained nearly half of the observed variation in population growth rate of the northern Yellowstone elk herd (Vucetich et al. 2005).

In Model 2 and 2F, the addition of a modification term to separately alter survival rates before and during natural gas development decreased DIC scores, however the modification terms did not differ in any substantial way between the two time periods, indicating natural gas development was not influencing population numbers. The best model (Model 3F) also allowed shifting survival rates through time. However, the trends predicted by this model showed a general increase in survival over years, which does not correspond to increasing negative impacts of energy development. This suggests that population dynamics were influenced far more by harvest than by natural gas development. However, we caution that changes in the spatial pattern or disturbance intensity could alter this relationship in the future, potentially resulting in larger impacts of natural gas development would have on the FCA elk population.

At current levels of natural gas development, all available data support the influence of harvest as the main driver of FCA elk population dynamics (Figs. 1 and 2). Population numbers declined with increased harvest and rebounded when harvest was decreased or zero. The FCA population was heavily harvested in many years, thus we might have predicted declines in population numbers, however numbers stabilized towards the end of our simulation. Krofel et al. (2014) noted a similar pattern with a brown bear (*Ursus arctos*) population that demonstrated an increase in population despite experiencing high human harvest. A potential explanation for this result is that the FCA herd had relatively high reproduction or survival. Our predicted modifier values support this hypothesis, with mortality rates predicted to be substantially lower than the mean for North American elk, and the fecundities substantially higher (Table 1). These high survival and low mortality rates may be due to good forage conditions, low densities of natural predators, or maintenance of the population well below carrying capacity by harvest. While we do not have the data to discriminate between these hypotheses, high reproductive and survival rates do appear to be important in compensating for high harvest rates and provided a mechanism for maintaining elk numbers in the FCA (Table 3). Increased fecundity is important for populations to recover following a reduction in population density (Sinclair et al. 2006) and there is evidence that other mammals, such as beaver (*Castor fiber),* exhibit the ability to rebound from high harvest rates by increasing fecundity (Parker and Rosell 2014).

While our models did approximate observed elk population numbers, they were not perfect. One reason for the difference between observed and modeled elk numbers could be the inability of the simple modifier functions we used to reflect the actual suite of age- and sex-specific vital rates of the actual population. The basic vital rates used in our simulation were averaged across 37 elk populations (Raithel et al. 2008) that likely experienced varying levels of disturbance, range quality, predation, and other influencing factors. Simple multiplicative modifiers may not have been able to alter these average vital rates to accurately represent this elk population, especially if there were age or sex-specific differences between this population and the average rates. The FCA elk herd was a reintroduced population that was growing in numbers steadily prior to implementation of more consistent harvest in 1989 to reduce population growth in the area (WGFD 1996, 2007a), thus vital rates averaged across multiple populations did not best describe FCA elk. Alternatively there may have been some inaccuracy in the observed population numbers or harvest rates. The FCA was a sagebrush dominated landscape, which should lend to efficient population surveys. However, the terrain was rather rugged and interspersed with dense juniper patches that made surveys difficult. We also investigated weather patterns during the study period to identify any weather events that could have influenced elk numbers. Using data from the Western Regional Climate Center (WRCC 2011) in linear regressions on the annual counts of the FCA herd, we found no weather variables that significantly explained population trends of the FCA elk population (results not shown). While it would be ideal to test considerably more complex models that alter survival and reproductive rates in more complex ways, the available data on numbers and harvest do not provide any statistical power to fit such models. Only if harvest and number data were broken down by sex and age class could such models be informative.

Our results provide support for the hypothesis that harvest was the mechanism driving the pattern in population dynamics observed in the FCA elk herd and regulating its numbers. The carrying capacity for the FCA is likely greater than any population numbers observed based on forage availability and remaining areas void of human development (C. B. Buchanan, unpublished data). Our simulation effort thus provided insight into the factors driving population numbers in the FCA, a possible secondary assessment of population numbers, and a method to check population survey estimates. Our results also provide an example of how MCMC modeling approaches can be used in combination with partial data on a population of interest to test alternative mechanisms of population dynamics. Using basic population data collected by wildlife management agencies we were able to effectively identify the importance of harvest on population dynamics. Ideally, population studies should use directly measured vital rates, but when unavailable our methods could provide an alternative method of population assessment. Given how many important questions in wildlife ecology are left unaddressed due to imperfect data sources, analyses like those we use here have an important place in the set of analysis tools used to address management issues.

LITERATURE CITED

Brodie, J., H. Johnson, M. Mitchell, P. Zager, K. Proffitt, M. Hebblewhite, M. Kauffman, B. Johnson, J. Bissonette, C. Bishop, J. Gude, J. Herbert, K, Hersey, M. Hurley, P. M. Lukacs, S. McCorquodale, E. McIntire, J. Nowak, H. Sawyer, D. Smith, and P. J. White. 2013. Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America. Journal of Applied Ecology 50:295–305.

Buchanan, C. B., J. L. Beck, T. E. Bills, and S. N. Miller. 2014. Seasonal resource selection and distributional response by elk to development of a natural gas field. Rangeland Ecology and Management 67:369–379.

Bureau of Land Management [BLM]. 2008. Fortification Creek planning area resource management plan amendment/environmental assessment. Buffalo Field Office, Buffalo, Wyoming, USA.

Christianson, D., and S. Creel. 2014. Ecosystem scale declines in elk recruitment and population growth with wolf colonization: a before-after-control-impact approach. PLoS ONE 9: e102330. doi:10.1371/journal.pone.0102330.

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.

Copeland, H. E., A Pocewicz, and J. M. Kiesecker. 2011. Geography of energy development in Western North America: potential impacts on terrestrial ecosystems. Pages 7–22 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, DC, USA.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian Data Analysis, second edition. Chapman & Hall/CRC Press, Boca Raton, FL, USA.

Gilks, W. R., S. Richardson, and D. J. Spiegelhalter. 1996. Markov Chain Monte Carlo in practice. Chapman & Hall/CRC Press, London, UK.

Hebblewhite. 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, DC, USA.

Jiang, Z., M. Sugita, M. Kitahara, S. Takatsuki, T. Goto, and Y. Yoshida. 2008. Effects of habitat feature, antenna position, movement, and fix interval on GPS radio collar performance in Mount Fuji, central Japan. Ecological Research 23:581–588.

Krofel, M., M. Jonozovic, and K. Jerina. 2012. Demography and mortality patterns of removed bears in a heavily exploited population. International Association for Bear Research and Management 23:91–103

Lubow, B. C., F. J. Singer, T. L. Johnson, and D. C. Bowden. 2002. Dynamics of interacting elk populations within and adjacent to Rocky Mountain National Park. Journal of Wildlife Management 66:757–775.

Lubow, B. C., and B. L. Smith. 2004. Population dynamics of the Jackson elk herd. Journal of Wildlife Management 68:810–829.

Marion G., G. J. McInerny, J. Pagel, S. Catterall, A. R. Cook, F. Hartig, and R. B. O’Hara. 2012. Parameter and uncertainty estimation for process-oriented population and distribution models: data, statistics and the niche. Journal of Biogeography 39:2225–2239.

Milner, J. M., C. Bonenfant, A. Mysterud, J. Gaillard, S. Csanyi, and N. C. Stenseth. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. Journal of Applied Ecology 43:721–734.

Moran, R. J. 1973. The Rocky Mountain elk in Michigan. Michigan Department of Natural Resources. Wildlife Division and Development report 267, Lansing, MI, USA.

Parker, H., and F. Rosell. 2006. Rapid rebound in colony number of an over-hunted population of Eurasian beaver *Castor fiber*. Wildlife Biology 20:267–269.

Plummer, M., N. Best, K. Cowles, K. Vines, D. Sarkar, and R. Almond. 2012. Output analysis and diagnostics for MCMC CODA. http://cran.r-project.org/web/packages/coda/index.html. accessed August 2013.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/. accessed July 2014.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795–803.

Sinclair, A.R.E., J. M. Fryxell, and G. Caughley. 2006. Wildlife ecology, conservation, and management, 2nd edition. Blackwell Publishing, Victoria, Australia.

Solbert, E. J., B. Saether, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. Journal of Animal Ecology 68:186–204.

Stankowich, T. 2008. Ungulate flight response to human disturbance: a review and meta-analysis. Biological Conservation 141:2159–2173.

Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of north-central Idaho. Journal of Wildlife Management 57:495–502.

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. Oikos 111:259–270.

Western Regional Climate Center [WRCC]. 2011. Remote Automatic Weather Station, Echeta, WY, USA. Available at : http://www.wrcc.dri.edu/. Accessed March 2015.

Wyoming Game and Fish Department [WGFD]. 1996. Fortification elk completion report, Appendix A: Fortification elk study final report. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Wyoming Game and Fish Department [WGFD]. 2007a. Fortification elk study progress report. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Wyoming Game and Fish Department [WGFD]. 2007b. Job Completion Report: EL320 – Fortification. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Wyoming Game and Fish Department [WGFD]. 2010. Job Completion Report: EL320 – Fortification. Wyoming Game and Fish Department, Gillette, Wyoming, USA.

Table 1. Survival and fecundity rates used in a 16 x 16 vital rate population matrix to simulate elk population numbers from 1989–2011. Vital rates in matrix model were adapted from Raithel et al. (2007).

Life stage	Survival Rate	Fecundity Rate
Calf	0.354	0
Yearling	0.883	0.099
Prime-age	0.894	0.464
Old-age	0.868	0.432
Senescent	0.724	0.265

Table 2. Summary of fitted parameters and prior distributions assumed for each in the MCMC models. Upper limits on the modifier parameters distributed as uniform variables was set to insure that no values were picked outside a range that would result in biologically possible survival or fecundity rates. The mean for the first year population estimate was determined by the first year population estimate, corrected for that year's harvest.

Parameter: symbol and description	**Prior Distribution**
Survival Modifier parameters in Models 1 and 2	Uniform distribution (0, 1.5)
Survival Modifier parameters in Model 3	Normal (mean = 0, SD = 1/0.0001)
Fecundity Modifier parameter	Uniform distribution (1,2.15)
Variance in population estimates, SigmaNi	Uniform distribution (0,10)
Variance in first year population estimates,SigmaN1	Uniform distribution (0,10)
Ntoti	Normal (mean = 303, SD = SigmaNi)
Ntot1	Normal (mean = Ntot[i], SD = SigmaN1)

Table 3. Population model modification terms used to simulate elk population numbers for the Fortification Creek Area elk herd. Modification terms allowed each model to vary the vital rate matrix adapted from Raithel et al. (2007) to match observed elk population numbers. We provide modification term averages, 1 standard deviation (SD), the model DIC score and the coefficient of determination (R^2) for observed population numbers in relation to simulated population numbers. Model 1 includes one static mortality modification term, so that predicted dynamics rely only on changing harvest rates. Model 2 includes a separate mortality modification term for before and during development, and thus includes effects of harvest rates and energy development on elk numbers. Model 3 includes a continuous modification of mortality rates over time, using two parameters. Models that include a single modifier for fecundity are labels with F. As with AIC, lower DIC scores indicate higher model support.

Model	**Modification Terms**	**Modification Term Average**	**Modification Term SD**	**Model DIC**	**R^2**
Model 1				4817	0.39
	Mod1	0.413	0.002		
Model 1F				4129	0.40
	Mod1	0.114	0.155		
	ModF	1.316	0.331		
Model 2				3572	0.45
	Mod1	0.330	0.004		
	Mod2	0.547	0.004		
Model 2F				3567	0.46
	Mod1	0.358	0.016		
	Mod2	0.573	0.014		
	ModF	2.097	0.051		
Model 3				3472	0.41
	Mod1	0.696	0.405		
	Mod2	-0.291	0.085		

	Mod3	0.015	0.004		
Model 3F				3456	0.48
	Mod1	0.820	0.369		
	Mod2	-0.291	0.073		
	Mod3	0.015	0.003		
	ModF	2.099	0.055		

Table 4. Estimated fecundity and survival rates from the top model, Model 3F, for elk in the Fortification Creek Area in northeastern Wyoming. Average values for the modification terms, mod1, mod2, mod3, and modF, were used in calculating these rates.

Estimated fecundity rates

	Calf	Yearling	Prime-age	Old-age	Senescent
	0.0	0.21	0.97	0.91	0.56

Estimated survival rates

Year	Calf	Yearling	Prime-age	Old-age	Senescent
1989	0.59	0.92	0.93	0.92	0.83
1990	0.62	0.93	0.94	0.92	0.85
1991	0.66	0.94	0.94	0.93	0.86
1992	0.70	0.94	0.95	0.94	0.88
1993	0.73	0.95	0.95	0.94	0.88
1994	0.74	0.95	0.96	0.95	0.89
1995	0.76	0.96	0.96	0.95	0.90
1996	0.77	0.96	0.96	0.95	0.90
1997	0.77	0.96	0.96	0.95	0.91
1998	0.77	0.96	0.96	0.95	0.91
1999	0.77	0.96	0.96	0.95	0.91
2000	0.76	0.96	0.96	0.95	0.90
2001	0.75	0.95	0.96	0.95	0.90
2002	0.73	0.95	0.96	0.95	0.89
2003	0.71	0.95	0.95	0.94	0.88
2004	0.68	0.94	0.95	0.93	0.87
2005	0.65	0.94	0.94	0.93	0.86
2006	0.61	0.93	0.94	0.92	0.85
2007	0.57	0.92	0.93	0.91	0.83
2008	0.53	0.92	0.92	0.90	0.81
2009	0.49	0.91	0.92	0.90	0.80
2010	0.46	0.90	0.91	0.89	0.78
2011	0.43	0.90	0.91	0.88	0.77

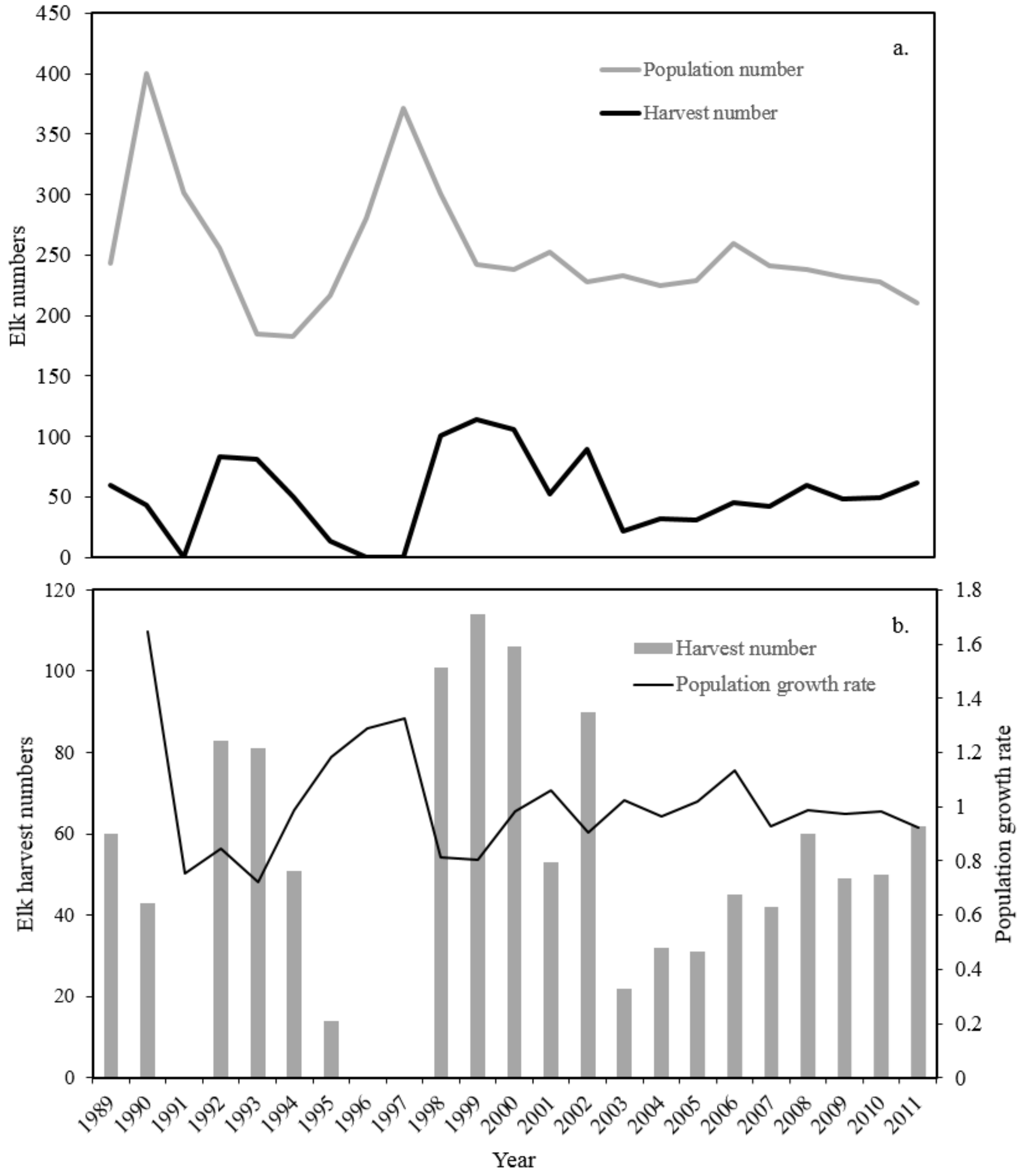

Figure 1. Observed elk population numbers and harvest numbers (a.) for the Fortification Creek Area elk herd in northeastern Wyoming, USA. Elk population growth rate (lambda values) with respect to elk harvest number (b.). The patterns in both a. and b. suggest a strong influence of harvest on the FCA elk population. Data from 1989–2011.

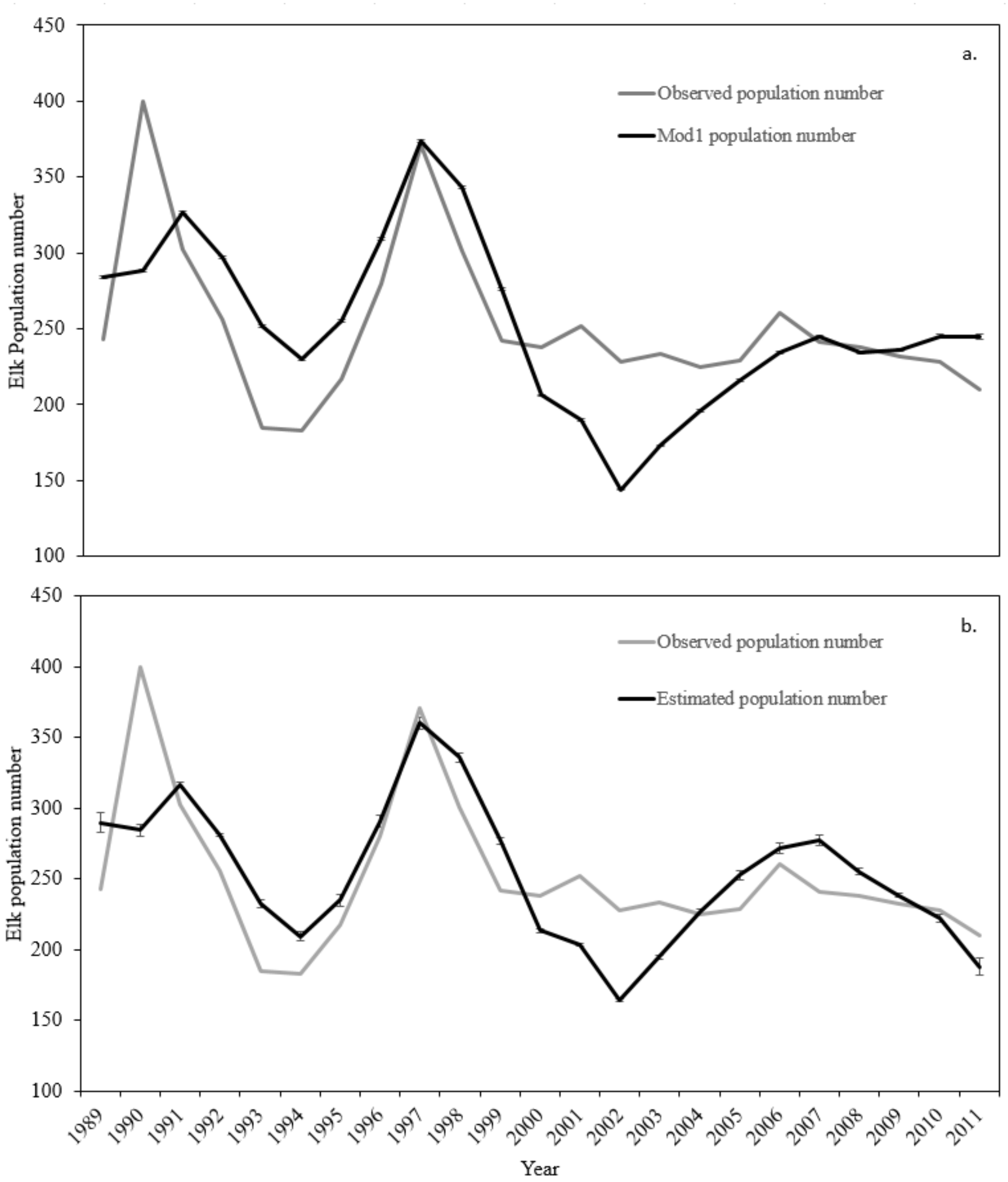

Figure 2. Observed and estimated elk population numbers (± 1 SD) for the Fortification Creek Area elk herd in northeastern Wyoming, USA for Model 1 (a) and the top model, Model 3F (b). Observed numbers were provided by the Wyoming Game and Fish Department, 1989–2011. Estimated population numbers were developed using vital rates adapted from Raithel et al. (2007) and in an MCMC simulation using Model 1 and Model 3F (code detailed in Appendix B).

APPENDIX A

Monitoring CBNG Development Noise Influence on Elk

As part of my assessment of elk resource selection I measured noise levels from energy development activity across the FCA. The goal of the noise monitoring efforts was to use those data as a predictive variable in elk resource selection models. My purpose was to evaluate whether elk were using anthropogenic sound to assist in making resource use decisions—more specifically, were elk avoiding areas of increased noise associated with CBNG development? Similar assessment of noise impacts is becoming a greater priority in current wildlife research (Barber et al. 2010, Blickley et al. 2012). I predicted that elk would avoid areas of higher noise levels especially those areas where noise levels were more unpredictable.

I was interested in using noise levels as a variable in RSF models and thus wanted to include this information at the scale of the entire study area (i.e., landscape-level variable). Use of large-scale noise data required an understanding of sound propagation across the landscape, which in turn required measurement of noise levels at numerous locations within the FCA. I used two different methods to measure noise levels. The first incorporated readily available sound recording devices, ZoomH2 (Zoom Corporation, Tokyo, Japan), which were commonly used for recording music. I modified the Zoom battery source and memory card to increase the recording capacity. I also developed a tripod mount with a weather cover and wind screen. The tripod was anchored to the ground and also used the weight of the battery box to hold the entire unit securely on the ground in high Wyoming winds. The second method of noise measurement was a sound level meter. I used a Larson Davis 620 sound level meter (LD620, Larson Davis, PCB Piezotronics Division, Depew, New York, USA) to make acute sound amplitude measurements in A weighted decibels (dB). The LD620 provided accurate measures of sound levels that could be used in modeling and could also provide a method of calibrating the level of noise in the Zoom recordings. These two methods not only provided accurate measures of noise at specific sites on the landscape, but these noise measurements could also be used to predict noise propagation across the FCA.

I developed a noise propagation layer in ArcGIS (ESRI, Redlands, California, USA) using the SPreAD-GIS toolbox (Reed et al. 2010). The SPreAD-GIS toolbox incorporates readily available datasets such as topology, elevation, land cover, and weather conditions (i.e., humidity, wind direction, temperature) in combination with measurements of noise to model sound propagation on the landscape. My sound propagation model used point source sound measurements to inform the SPreAD-GIS tool. At the time of this work, point sound source information seemed to function better within the SPreAD-GIS tool than using linear sources of sound (i.e., roads), thus I used well pad sites for the point sound source locations within the propagation model. This model provided a GIS layer depicting areas on the landscape predicted to have greater than ambient sound levels resulting from CBNG development activities, which could then be related to elk GPS location data.

Intuitively anthropogenic sound is related to anthropogenic activity: in this case CBNG development. To isolate the sound effects on elk from the simple presence of humans on the landscape, I attempted to use the noise from CBNG compressor stations as a control. Because compressor stations run nearly nonstop, with or without human presence, these locations should have provided a sufficient separation of noise and human impacts on elk. I planned to measure sound propagation from 3 compressor stations within the FCA: 1 old and 2 newly constructed. Unfortunately, the 2 new stations were not activated during my study period. During my field work in 2009 and 2010, natural gas prices began to drop resulting in decreased production, which reduced the need to run more compressor stations. Without the constant noise produced by these compressor stations I was unable to separate the influence of noise from simple human presence, thus reducing my ability to make strong inferences regarding the impacts of development noise on elk. In hindsight, I should have had a backup plan to use large speakers to project anthropogenic sounds across the landscape and measure elk response; however that was not included in my project planning and budget and would have been impractical given the large landscape these elk inhabited.

The sound propagation modeling that I was able to accomplish does suggest that elk were using areas where noise was closer to ambient levels. Areas with ambient noise levels included over 70% of elk locations, which could be interpreted as a population response to noise from CBNG development, however, these areas were also highly correlated with distance to roads and well pad locations, thus making any direct causative inferences inaccurate. I chose to remove noise level variables from elk resource selection modeling as a result of the correlative relationships with other disturbance variables, which were more reliable and interpretable. Understanding noise propagation on the landscape and its impacts on wildlife species is a difficult, yet important issue and one that should include extensive planning and development of baseline knowledge in future investigations.

LITERATURE CITED

Barber, J. R., K. R. Crooks, and K. M. Fistrup. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends in Ecology and Evolution 25:180–189.

Blickley, J. L., D. Blackwood, and G. L. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology 26:461–471.

Reed. S. E., J. L. Boggs, and J. P. Mann. 2010. SPreAD-GIS: an ArcGIS toolbox for modeling the propagation of engine noise in a wildland setting. User's guide, version 2.0. The Wilderness Society, San Francisco, CA.

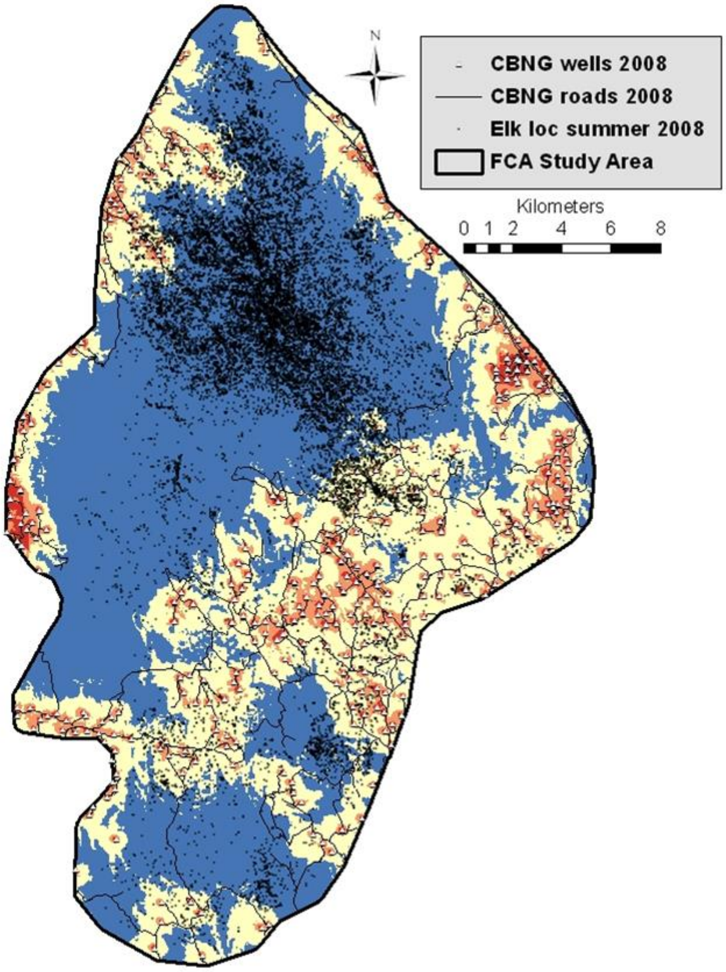

Figure 1. Sound propagation map where areas in blue were ambient sound levels with increasing sound levels from light brown to dark brown. Over 70% of the elk locations during summer 2008 were found within areas of ambient sound levels.

APPENDIX B

Code for analysis of elk population dynamics using a vital rate matrix population model, observed elk population and harvest numbers and MCMC simulation sampling.

```
#Model R script file
#Set priors and define model
model{
  tauN <- pow(sigmaN, -1)
  sigmaN ~ dunif(0,10)


  taustart <- pow(sigmastart, -1)
  sigmastart ~ dunif(0,10)


  Ntot[1] ~ dnorm(243+60,taustart)
  mod1 ~ dnorm(0,0.0001)
  mod2 ~ dnorm(0,0.0001)
 mod3 ~ dnorm(0,0.0001)
 modF ~ dunif(1,2.15)

    Nest[1,1] <- ssd[1]*Ntot[1]

for (ii in 2:16) {
  Nest[ii,1] <- ssd[ii]*Ntot[1]} #-elkharv[1]*(1/15)}


  #process:
  for(i in 2:nn){

      Nest[1,i]<- sum((1-morts*(1/(1+exp(-mod1-mod2*i-mod3*i*i))))*fecs* modF*Nest[,i-1]/2)

    for (jj in 2:15) {Nest[jj,i]<- (1-morts[jj-1]*(1/(1+exp(-mod1-mod2*i-mod3*i*i))))*Nest[jj-1,i-1] -
elkharv[i]*(1/15)  }

     Nest[16,i]<- (1-morts[15]*(1/(1+exp(-mod1-mod2*i-mod3*i*i))))*Nest[15-1,i-1] +(1-
morts[16]*(1/(1+exp(-mod1-mod2*i-mod3*i*i))))*Nest[16,i-1] -elkharv[i]*(2/15)

    Ntot[i] <- sum(Nest[,i])
  }

  #observation process:
  for(i in 1:nn){
    popobs[i] ~ dnorm(Ntot[i],tauN)
  }

}
```

```
#Run the MCMC simulation
jags <- jags.model('testelkmodel.bug.R', data = list('mx'=mx,'ssd'=ssd,
        'nn'=nn,'elkharv'=elkharv,'popobs'=popobs), n.chains = 3, n.adapt = 1500)


#Burn in
update(jags,5000)

#Compile the MCMC samples and monitor all parameters of interest
K <- coda.samples(jags, c('Ntot[1:23]', 'mod'),n.iter=150000, thin=3)

#Simple test for model convergence
gelman.diag(K)

#Create density plots for population numbers each year
densityplot(K[,1:23])

#Get summary statistics for the rjags simulation
nestis=summary(K)$stat[1:23,1]

#Plot observed and estimated population numbers for all years
matplot(1:nn,cbind(popobs,nestis),type='l', ylab = "Population number", xlab = "Time period
        (1-23)")
```