Synergistic Effects of Road Closure, Climate and Vegetation Change on Elk Counts: Implications for Management

Matthew B. Mullins, Department of Wildland Resources & The Ecology Center, Utah State University, 5230 Old Main Hill, 84322 Logan UT. Email: mmullins436@gmail.com

Charles A. Schneebeck, Forest Service Volunteer, 1505 Percheron Drive, 83001 Jackson WY. Email: chuckschneebeck@gmail.com

Lise M. Aubry, Fish, Wildlife and Conservation Biology Department, Colorado State University, Fort Collins, CO 80523-1474. Email: Lise.Aubry@colostate.edu

Abstract

Increasing our understanding of the effects motor vehicles have on elk populations is vital to their management and past research has consistently shown that elk avoid roads and traffic. However, the fine-scale impact of traffic volume is rarely quantified and the environmental context experienced by elk at the time of disturbance is systematically ignored in these studies. We use an experimental design where roads are opened or closed to motorized traffic at specific times of year, and where motorized traffic has been quantified. We provide an environmental context to the study of the impacts of road closure on elk counts by accounting for climatic and vegetation changes over the course of the study. We specifically quantify the impact of road access, vegetation green-up, and snow dynamics on Rocky Mountain elk (*Cervus canadensis nelsoni*) counts along the main road in the Gros Ventre River drainage, WY, before and after two gates were sequentially opened to the public during the spring and early summer of 2010–2014. Elk counts increased with snow depth along the main road, and counts decreased as snow receded and vegetation greened over a 5-year period (p < 0.001). An increase in vehicle traffic resulted in a significant decline in elk counts (p < 0.001), which decreased at a rate of 1.42% for each unit increase in vehicle traffic. Our results indicate that gate closures in the Gros Ventre River Drainage decreased vehicle-related anthropogenic disturbance for elk, and that environmental variables affect elk counts and distribution further. Wildlife managers should consider both motorized vehicle traffic and the environmental context elk experience when managing road access in elk habitat.

Key words: Cervus canadensis, Elk, Climate, NDVI, Road, Traffic, Winter Severity Index

INTRODUCTION

Roads are important for recreational access, commerce, and firefighting activities, but can have negative effects on animal distributions and habitat use. Fahrig et al. (2009) synthesized 79 studies covering 131 species and 30 species groups, concluding that "the negative effects of roads on animal abundance outnumbered the positive effects by a factor of 5", and that effects on large mammals were predominantly negative. Motorized travel can reduce abundance of some species near travel areas by displacing them towards areas of less motorized

use – a direct impact. This could displace animals to lesser quality habitats, indirectly resulting in poorer fitness, and possibly abundance – an indirect impact. Because of the importance of elk-related recreation in the Western United States, previous studies focused on the impacts of roads and motorized-traffic on elk (Bolon 1994).

Early research assessed the effects of roads on elk distribution and habitat use, focusing on the density of fecal pellet groups and distance from roads as indicators of habitat use. A decrease in the relative density of pellets with increasing proximity to roads indicated an aversion to roads. For instance, elk (Cervus canadensis nelsoni) in the Blue Mountains of Washington reduced habitat use within 0.5 miles from roads that were open to motorized traffic and preferred habitat further from main forest roads. Perry et al. (1977) showed elk reduced habitat use near roads by up to 95% compared to similar habitat away from roads. Lyon (1979) found elk regularly preferred similar habitats further from roads. The effect was most pronounced in areas where road densities were as low as 1 mile of road per sq. mile. Subsequent studies using radiotelemetry data of collared elk supported these results, whereby elk consistently avoided habitat near open roads as opposed to similar habitat away from roads (Marcum 1975, Hershey et al. 1976, Irwin et al. 1983, Edge et al. 1987). Witmer et al. (1985) observed that elk in Oregon used habitat within 500 meters of open roads half as much as predicted for similar habitat farther away from roads. Elk telemetry data further suggested that open road densities negatively correlated with elk telemetry points (Burcham et al. 1998) and that elk avoided human disturbance, and particularly vehicle activity, preventing them from utilizing desirable habitat (Morgantini et al. 1979).

With modern quantitative tools, models became better at predicting the probability of elk using specific areas of a landscape (McCorquodale 2013). Rowland et al. (2000) used elk telemetry data to reconsider the question of how road density models predicted elk habitat effectiveness. Their work also suggests elk avoided open roads, though a distance to road approach predicted elk habitat use better than a road density approach. One of the best variables for predicting elk habitat use in northeastern Oregon was distance from high-use and medium-use roads (Johnson et al. 2000), whereby elk use probability increased as distance from roads increased. Traffic volume also affects elk distribution. For instance, the likelihood of observing western Montana elk decreased as traffic volume increased (Edge and Marcum 1991). An Arizona study of elk wearing Global Positioning System (GPS) collars correlated

with hourly traffic data revealed the probability of elk occurring near highways decreased with increased traffic volume (Gagnon et al. 2007).

Although the scientific literature indicates that motorized use of roads negatively impacts elk, an understanding of how environmental factors known to impact elk movement, habitat use, and fitness, interact with impacts of motorized use of roads is currently lacking. For example, snowpack has been shown to limit the survival and reproduction of elk in many ecosystems (Post and Stenseth 1999, Garrott et al. 2003). Plant green-up is also closely tied to elk ecology such as seasonal migration and habitat use (Hebblewhite and Merrill 2007, Parker et al. 2009, White et al. 2010), and elk populations tend to select habitat patches at peak Normalized Difference Vegetation Index (NDVI) values during spring migration (Merkle et al. 2016).

Such environmental metrics likely mediate the relationships that exist between elk, road closure/openness, and vehicle traffic. Spring distributions of elk is closely associated with greater photosynthetic activity of spring vegetation as determined using NDVI (Hebblewhite and Merrill 2007, Parker et al. 2009, Merkle 2016), and elk migrating through intact wilderness areas to summer ranges inside Yellowstone National Park have been experiencing an increasing rate and shorter duration of green-up, coinciding with warmer spring and summer temperatures, reduced spring precipitation, and an unusually severe regional drought (Middleton et al. 2013). Indeed, while comparing migratory and resident herds of elk in Yellowstone National Park, Middleton et al. found that although habitat quality was still advantageous to elk nutrition on summer range, those conditions had declined over a 21-year period as they observed a reduction in green-up duration of 27 days over that time period (Middleton et al. 2013). They further observed a lack of a similar trend on the range of resident elk, and observed that some residents appeared to gain a nutritional subsidy from agriculture. These findings suggest that elk

should be spending less time on their higher elevation summer ranges, and more time at lower elevations where nutritional subsidies are available and where the durations of green-up may be less impacted by warming; however, this is also where anthropogenic disturbances related to road access and traffic exist.

While much of this research described above supports a negative correlation between elk and roads or traffic, certain factor such as green-up and local weather conditions may complicate this relationship further. To address cause and effect between elk and traffic, we use an experimental design where roads are opened or closed to road traffic at specific times of year, where vehicle traffic has been quantified. and where environmental factors that could potentially affect elk seasonal habitat use and abundance have been accounted for. We have the unique opportunity to study the relative impacts of vehicle traffic and environmental variables (winter severity, snow depth, and green-up) on a large population of elk in the Gros Ventre Drainage, Wyoming, USA. We use climatic and vegetation indices to provide an

environmental context for the impact of road closures on elk counts and use of low elevation habitat shared with recreationists. We specifically test: i) whether elk counts increase when roads were closed to motorized traffic; ii) the relative contribution of spring vegetation quality, winter severity, and snow depth in explaining changes in elk counts, along with road closure; and iii) the relationship between increased traffic volume and elk sightings.

STUDY AREA

The Gros Ventre River Drainage is located on the Bridger-Teton National Forest in Northwestern Wyoming (Fig. 1). Elevation ranges from approximately 2,000 to 3,422 meters. Valley bottoms are dominated by sagebrush grassland (*Artemisia* spp.) and grassland steppe ecotypes. The dominate sagebrush species are the threetip sagebrush (*Artemisia tripartita*) and the big sagebrush (*Artemisia tridentata*). Other common shrub species include Douglas rabbitbrush (*Chrysothamnus viscidiflorus*) and rubber rabbitbrush (*Ericameria nauseosa*). Grass species include Idaho

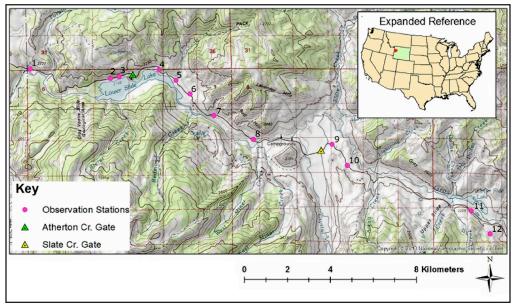


Figure 1. Locations of observation stations and gates along the main Gros Ventre road, Bridger-Teton National Forest, WY, 2010–2014.

fescue (Festuca idahoensis), Montana wheatgrass (Agropyron ulbicans), thickspike wheatgrass (Agropyron dasystachyum), Sandberg bluegrass (Poa secunda), western needlegrass (Stipu occidentalis), sedge (Carex sp.), silvery lupine (Lupinus serecius), and rose pussytoes (Antennaria rosea). Surrounding upland slopes are comprised of a mix of sagebrush grassland, grassland steppe, and forest ecotypes dominated by the quaking aspen (Populus tremuloides), Douglas fir (Pseudotsuga menziesii), lodgepole pine (Pinus contorta), Engelmann spruce (Picea engelmannii), subalpine fir (Abies laciocarpa), limber pine (Pinus flexilis), and whitebark pine (Pinus albicaulis).

Ungulate species present include mule deer (Odocoileus hemionus), pronghorn (Antilocapra americana), elk (Cervus elaphus), moose (Alces alces), bighorn sheep (Ovis canadensis), and mountain goat (Oreamnos americanus). Large carnivore species present include grey wolves (Canis lupus), coyotes (Canis latrans), black bears (Ursus americanus), grizzly bears (Ursus arctos), pine marten (Martes Americana), bobcats (Lynx rufus), lynx (Lynx Canadensis), cougars (Puma concolor), and wolverine (Gulo gulo).

Long, cold winters with considerable snowfall and short, cool summers characterize the local climate. In the nearby town of Jackson, Wyoming (elevation 1,901 meters), 22 km from our study area, temperature extremes range from -52°C during the winter to 36°C during the summer (USFWS 2007). Total average annual precipitation is 38.6 cm, with 60% coming in the form of winter snow and the remainder from rainfall. Total annual snowfall averages 228 cm.

The Jackson Elk Herd

The Gros Ventre River Drainage provides year-round habitat for a portion of the Jackson Elk Herd; including summer habitat for about 30% of that herd (Smith 2000). The population management objective, set by the Wyoming Game and Fish Department (WGFD)

for a 15-year period beginning 2007, is approximately 11,000 animals (USFWS 2007). Management of the Jackson Elk Herd includes seasonal hunting (rifle and archery) and supplemental winter feeding on the National Elk Refuge and in the Gros Ventre Drainage. The population numbered as high as 19,657 elk in the mid-1990s, but harvests have brought that number within 2,000 individuals of the 11,000 elk objective (USFWS 2007). Elk utilize lower elevations of the Gros Ventre Drainage as winter range and spring calving grounds and migrate to higher elevation summer ranges within and outside of the drainage including into the Gros Ventre Mountains, Yellowstone National Park, and Grand Teton National Park

The Gros Ventre River Drainage

As a result of the 2009 Bridger-Teton National Forest decision to designate a new motorized vehicle route system across the Forest's North Zone, many changes in motorized use occurred in the Gros Ventre drainage. This included changes to the main Gros Ventre Corridor Road referred to as the Gros Ventre road, which is a twolane gravel road that follows the drainage bottom. Prior to the 2009 Bridger-Teton National Forest motorized travel decision, the primary uses of the road include hiking, wildlife viewing, fly-fishing, hunting (elk included), OHV use, snowmobiling, cross country skiing, camping, and horseback riding as primary activities: https://www. fs.fed.us/visit/destinations. Beginning in 2010, one of the changes made in the Gros Ventre road was a seasonal closure to cars and trucks that begins on 15 December and extends through 1 June, while snowmobiling was still allowed. This seasonal road closure involved the closure of two gates: Atherton Creek Gate (open 1 May; lower Gros Ventre watershed) and Slate Creek Gate (open 1 June; middle watershed). The Bridger-Teton National Forest wanted a better understanding of wildlife distributions (including elk) and the effectiveness of seasonal travel restrictions in reducing wildlife disturbance in the Gros Ventre

drainage. This study aims to improve understanding of the effectiveness of these travel management efforts by investigating elk distribution in the Gros Ventre drainage before, during, and after road segments are opened to the public.

METHODS

Data Collection

Elk Statistics and Gate Timing – We counted elk at 12 observer stations along a 23 km stretch of the Gros Ventre road at elevations ranging from 2,073 to 2,378 meters during spring, 2010–2014 (Fig. 1). The road was divided into three sections A, B, and C by gates at Atherton Creek (open 1 May; lower Gros Ventre watershed) and Slate Creek (open 1 June; middle watershed). The sequential opening of the gates by the USFS provided progressively greater levels of public access (all types of access, including motorized) to the middle and upper portion of the watershed during spring (Fig. 2). We tested the effect of gate closure (i.e. both gates closed, Atherton gate open and Slate Cr. Closed, or both gates open) on elk counts using the statistical framework described below. The twelve observation stations were

located in "viewsheds" intentionally spaced along the road to prevent observers from counting the same elk more than once. A project crew consisting of two teams of two trained citizen-science volunteers travelling in a vehicle collected observations for approximately 10 minutes at each station (data collection at stations 9, 11 and 12 was 20 minutes each due to larger viewsheds). Observations began at station 1 at 0600 and ended at station 12. All stations were visited by observers during a survey day, weather and road conditions permitting. The crews completed twelve surveys per year, from 21 April-12 May and 20 May-11 June, between 2010 and 2014.

Winter Severity Index and Snow Depth

We obtained precipitation and temperature (TEMP) data from the Gros Ventre Summit SNOTEL site (43°39 N, 110°13 W; 2,667 m) operated by the U.S. Natural Resources Conservation Service. In addition to using daily snow depth as a variable, we created a winter severity index (WSI) described by Baccante et al. (2010). First, we calculated a monthly WSI (mWSI) for the 6 months beginning 1 November and ending 30 April by combining mean monthly air temperature in degrees Celsius (TEMP) and mean monthly

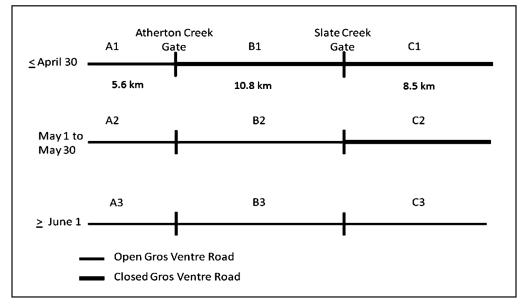


Figure 2. Road sections, travel status, and gates along the Gros Ventre Road, WY, 2010–2014.

snowfall in centimeters (SNOW) as follows: if TEMP $\leq -25^{\circ}$ C then mWSI = 4 × SNOW; if TEMP > -25° C and $\leq -15^{\circ}$ C then mWSI = 3 × SNOW; if TEMP > -15° C and $\leq -5^{\circ}$ C then mWSI = 2 × SNOW; if TEMP > -5° C then mWSI = 1 × SNOW. The total WSI for each year was calculated as the sum total of the six mWSI's for that year. Since the mWSI's began in the November of one calendar year and ended in the following calendar year, the WSI represented the year in which that winter ended. More severe winters with lower temperatures and/or increased snowfall were indicated by higher WSI values.

NDVI – NDVI has become widely used in ecological studies and measures the ratio of near infrared to red light reflected by vegetation (Pettorelli et al. 2005) and plant biomass (Muñoz et al. 2010), and is acknowledged as a good measure of green-up. We acquired Normalized Difference Vegetation Index (NDVI) data from the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD13Q1 Version 6 product provided to the public by the U.S. Geological Survey (USGS) Agency (Didan 2015). This USGS product provided a vegetation index (NDVI) which showed the relative "greenness" of vegetation produced by an algorithm that used the reflectance bands of red, blue, near infrared, and middle infrared light reflected from the Earth. The data were recorded by MODIS placed on two National Aeronautics and Space Administration (NASA) satellites. The resulting data provided pixels representing a 250m² area NDVI value for 16-day time periods. We selected the following sites to measure green-up: stations one, eight, and nine (numbered starting from West to East). Each site represented a 250m² area (one pixel) lying within each of the three sections of the Gros Ventre road. To simplify comparisons, the NDVI value of each 250m² pixel was matched to the elk count for that pixel's road section and 16day time range.

Vehicle Traffic – Using a traffic counter placed near the Atherton Creek gate by

USFS engineers, we estimated daily numbers of vehicles on the Gros Ventre road during 2010 and 2011, the only years such information was available. These data allowed a separate analysis of the impact of actual traffic on elk counts.

Data Analyses

When investigating elk count differences across gate opening scenarios, the Shapiro-Wilk test for normality of the residuals (p < 0.001) and QQ-plot, a statistical and visual way to assess normality of the residuals (Shapiro and Wilk 1965), both indicated that the residuals were not normally distributed. We thus used a nonparametric Kruskal-Wallis test, appropriate when residuals are not normally distributed (Kruskal and Wallis 1952), to determine differences in elk counts across gate opening scenarios.

We used Poisson regression analyses to evaluate changes in elk counts (response variable of interest) with respect to the timing of gate opening, NDVI, snow depth, and WSI separately and in combination. Poisson regression models are log-linear and thus appropriate in modelling positive count data as a function of both categorical and continuous explanatory variables (Kleinbaum et al. 1998). We first ensured that none of the explanatory variables were collinear by calculating variance inflation factors (VIF) using the "vif" function in R (i.e. a VIF > 10 is indicative of collinearity; Fox and Weisberg 2011). We defined Poisson regression models that tested for the singular, additive and interactive effects of non-collinear explanatory variables on elk counts (when it made biological sense) and compared these models using Akaike's Information Criterion ('AIC', Akaike 1973).

Note that due to smaller sample size and in an effort to conserve degrees of freedom, traffic data were analyzed separately using univariate Poisson regression modeling, as we only had 2 years (2010-11) of traffic data as opposed to 5 years for aforementioned analyses (2010-2015). For this analysis, we considered the impact of vehicle traffic data on elk count to test whether an increase in traffic related to a decrease in elk counts. Using AICc model selection, we compared it to a model that allowed vehicle traffic to interact with gate timing of opening to test whether the potential negative impact of vehicle traffic on elk counts augmented as gates opened.

Regression beta coefficients, 95% confidence intervals, and p-values were used to indicate the effect and relative influence of each explanatory variable on elk counts. All analyses were performed in RStudio.

RESULTS

Elk Drainage Use

The Kruscal-Wallis test indicated significant differences in elk counts as a function of gate timing (p < 0.001). Counts for 705 station visits ranged from 0 to 510 elk, totaling 12,519 elk sightings over the five-year study period. Elk counts were greatest when both Atherton and Slate Cr. Gates were closed and were lowest when both gates were open (Fig. 3).

Environmental Factors and Elk Counts

Variance inflation factors were all < 5 for all predictors tested (vif(WSI)=2.61;

vif(Timing)=1.85; vif(NDVI)=2.41; vif(Snow)=4.06) suggesting a lack of collinearity among all predictors tested. Although we had the possibility to test all explanatory variables of interest as well as interactions between them, considering snow depth and WSI in conjunction within the same Poisson regression model seemed uninformative and redundant. When excluding this possibility, the best performing model retained an effect of snow depth, NDVI, and timing of gate opening on elk count. This model largely outperformed any other model that was part of the model selection process (Table 1: AICc weight = 1) and outranked the next best performing model by 335 AICc points (Table 1). Within the best performing model, additive effects of NDVI, snow depth, and gate timing were retained, along with interactions between NDVI and gate timing, and between snow depth and gate timing. Each predictor had a significant effect (p < 0.05) on elk counts (Table 2). On their own, NDVI and snow depth both had a negative impact on elk counts, however, the negative effect of snow depth on elk counts was much subtler than that of NDVI (Table 2, Fig. 4). When considering an interaction between snow

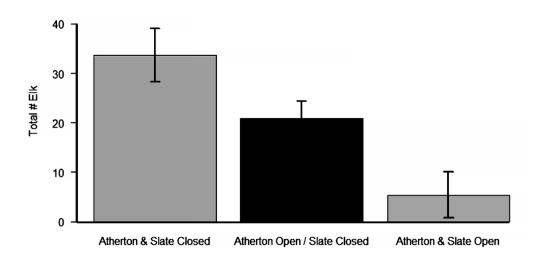


Figure 3. Differences among elk counts in response to the timing of gate opening along the Gros Ventre Road, WY. Data was collected between April 21 and June 11 for 2010-2014.

Table 1. Poisson regression models testing for the effect of Winter Severity Index (WSI), the Normalized Deviance Vegetation Index (NDVI), gate timing (Timing), snow depth (SD) and relevant interactions (':') on elk counts. K represents the number of parameters in the model. Best performing model based on AICc is presented in bold.

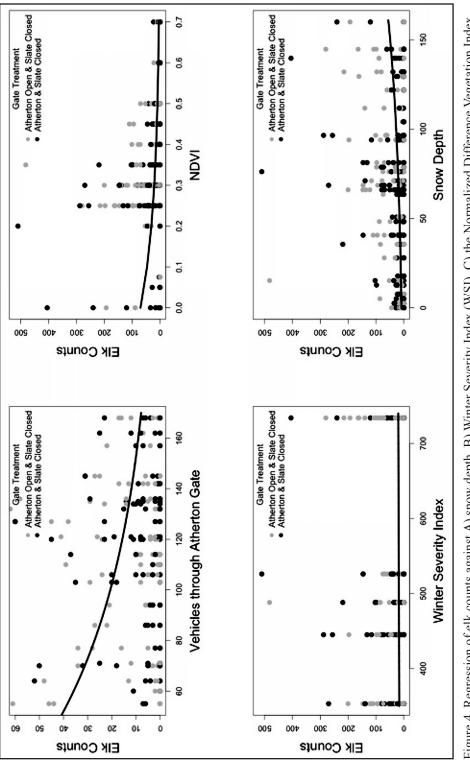
Predictors	Κ	AICc	Delta AICc	AICc weight	LogLikelihood
NDVI:Timing+SD:Timing	7	33087.97	0.00	1	-16536.91
NDVI:Timing+WSI:Timing	7	33422.80	334.83	0	-16704.32
SD:Timing	4	34137.89	1049.92	0	-17064.92
NDVI:Timing	4	36617.82	3529.84	0	-18304.88
WSI:Timing	4	37278.49	4190.52	0	-18635.22
NDVI+SD+Timing	5	34644.48	1556.51	0	-17317.20
NDVI+WSI+Timing	5	34965.26	1877.29	0	-17477.59
NDVI+SD	3	35666.12	2578.15	0	-17830.04
NDVI+WSI	3	36008.60	2920.63	0	-18001.28
SD+Timing	4	35088.20	2000.23	0	-17540.07
NDVI + Timing	4	34972.02	1884.05	0	-17481.98
Timing	3	37074.07	3986.10	0	-18534.02
SD	2	36938.24	3850.27	0	-18467.11
NDVI	2	36085.85	2997.87	0	-18040.91
WSI	2	41379.54	8291.56	0	-20687.76

Table 2. Performance of predictors from the best-fitting Poisson regression model selected in table 1 (in bold). Predictors includ: Snow Depth (SD), the Normalized Deviance Vegetation Index (NDVI), gate timing (i.e. Timing1: both gates were closed; Timing2: Atherton creek gate was open; Timing3: both Atherton and Slate creek gates were open; see Fig. 2) and relevant interactions (':') on elk counts.

		95% C.I	95% C.I		
Predictors	β	lower bound	upper bound	z-values	P-values
Intercept (Timing1)	3.7125	3.6231	3.8016	81.5180	< 0.001
NDVI	-0.4146	-0.6159	-0.2132	-4.0360	< 0.001
SD	-0.0010	-0.0017	-0.0003	-2.7870	0.005
NDVI:Timing2	-3.3349	-3.4895	-3.1801	-42.2550	< 0.001
NDVI:Timing3	-4.5911	-4.7985	-4.3865	-43.6840	< 0.001
SD:Timing2	0.0067	0.0061	0.0072	24.5150	< 0.001
SD:Timing3	0.0105	0.0090	0.0121	13.2580	< 0.001

depth and gate opening, the relationship between snow depth and elk count became more positive as gates opened (i.e. Timing1: both gates were closed; Timing2: Atherton creek gate was open; Timing3: both Atherton and Slate creek gates were open; see Table 2, Fig. 2), but remained statistically weak. When considering the interaction between NDVI and timing of gate opening, the impact of NDVI on elk count became more negative as gates opened (Table 2, Fig. 4).

Vehicle Traffic impacts on Elk Counts In a separate analysis that involved more limited data (2010-2011) on the impact of actual vehicle traffic on elk counts, we observed a negative relationship between vehicles and elk counts (Fig. 4). The Poisson



(NDVI), and D) the number of vehicles passing through Atherton Gate, WY. Data was collected between April 21 and June 11 for 2010-2014 Figure 4. Regression of elk counts against A) snow depth, B) Winter Severity Index (WSI), C) the Normalized Difference Vegetation Index or top-right and bottom panels, and between April 21 and June 11 for 2010 & 2011 for top-left panel

Synergistic Effects of Road Closure, Climate, & Vegetation Change on Elk Counts: Implications for Management 75

regression model that accounted for an interaction between traffic and timing of gate opening (AICc = 14199) outperformed the model that only accounted for vehicle traffic by 486 AICc points. Estimates from the best performing model are presented in Table 3 and indicate that, as gates opened through the spring, the impact of vehicle traffic on elk counts became increasingly negative.

DISCUSSION

Our analyses support the hypotheses that: i) elk counts increase when roads are closed to motorized travel, as suggested by previous studies; ii) The relative contribution of spring vegetation quality (NDVI) and snow depth were important in explaining changes in elk counts, and interacted with road closure; and iii) the negative impact of traffic was exacerbated when all gates were open to the general public.

Roads and Elk in Context

The novelty of this work lies in the consideration that interactions between the timing of gate opening and environmental covariates can potentially shape elk use of migration corridor, and thus elk counts in the spring and summer within such habitats. Indeed, the best performing model retained an interaction between NDVI and gate timing, and snow depth and gate timing, on elk counts. These interactions indicate that the impact of gate timing on elk counts is mitigated by environmental conditions, whereby an increase in spring green up and a decrease in snow depth lead to a progressive decline in elk counts as gates progressively open. These synergistic effects suggest that both environmental and anthropogenic factors can influence elk counts.

It is especially important to consider the impact of gate closure and traffic within the environmental context that elk are experiencing year-to-year, since failure to do so could bias management recommendations. In the Western US. an increasing frequency of spring snow storms is predicted in response to climate change (Cayan et al. 2006) and a narrower green-up window has already been observed in response to warmer springsummer temperatures and reduced spring precipitation (Middleton et al. 2013). The latter could have potential influences on elk seasonal distribution and migration (Middleton et al. 2013). Because herbivores, such as elk, time their migration phenology to that of the forage they depend on for body mass gains and fitness, one would expect elk to remain at lower elevations for a longer period of time in the spring in response to spring snowstorms while "surfing the greenwave" (Bischof et al. 2012, Aikens 2017).

Environmental impacts on elk counts

Our results suggest that elk congregate at lower elevations when snow depth was at its peak and gates were closed, and migrate up in elevation as NDVI increased. Smallidge et al. (2003) and Bischof et al. (2012) similarly observed elk migration from lower to higher elevation in association

Table 3. Estimates from Poisson regression model testing for the effect of vehicle traffic (Traffic) and timing of gate opening (Timing; i.e. Timing1: both gates were closed; Timing2: Atherton creek gate was open; Timing2: both Atherton and Slate creek gates were open; see Fig. 2) on elk counts.

Predictors	ß	95% C.I	95% C.I	z-values	P-values
i icalotoro	٣	lower bound	upper bound	2 101005	1 101005
Intercept	3.9555	3.8623	4.0484	83.3390	< 0.001
Traffic:Timing1	-0.0041	-0.0060	-0.0023	-4.3770	< 0.001
Traffic:Timing2	-0.0075	-0.0085	-0.0066	-15.6700	< 0.001
Traffic:Timing3	-0.0142	-0.0150	-0.0133	-31.7260	< 0.001

with a vegetative "greenwave". Only recently have ecologists documented the true role migration corridors, such as the Gros Ventre Drainage, play in shaping herbivore phenology and population dynamics. Although their importance in enabling animals to move between winter and summer ranges has long been understood, their actual use as key transitional habitat for herbivores such as mule deer and elk has only recently been better acknowledged. Migratory corridors are economically and ecologically important for animals which closely time their movements to track spring green-up (Aikens 2017). White et al. (2012) also found that elk numbers at lower elevations increased with greater snowpack. Counts were performed in the spring and summer, which might explain the very weak relationship between elk counts and snow depth pre-road access, as one would expect a strong and positive relationship between counts and snow depth, independently of gate closure.

Traffic Impacts on Elk Counts

Traffic volume was negatively correlated with elk counts. For every 1 vehicle increase passing through Atherton gate, there was a corresponding 1.42% decrease in elk counts when all gates were open (Table 3), suggesting that vehicle traffic had a negative impact on elk abundance in the Gros Ventre River drainage. The daily average number of vehicles through Atherton gate steadily increased from approximately 49 in April, 103 in May, 153 for June, and 233 for July during years 2010 and 2011. Our results align with findings from the literature that document the negative effects of vehicle traffic volume on elk abundance (McCorquodale 2013).

Elk counts were significantly less when roads were open, but whether this was primarily due to the negative impact of motorized traffic or natural migration behavior away from lower elevation roads is difficult to discern with the data at hand. A large number of elk were documented in the drainage well into the end of May in most years (>100 individuals, Appendix A). We were still able to observe a progressive decrease in elk counts over the spring and summer months, after the sequential opening of the gates. The impact of vehicle traffic on elk count was negative by itself (Fig. 4), which supports the hypothesis that elk avoid traffic. This adds to the literature in that past studies mostly focused on highways and their impact on elk habitat use (e.g. Edge and Marcum 1991, Gagnon et al. 2007). Here we show that motorized travel along improved gravel roads has the potential to displace elk.

Limitations, Future Work, and Management Implications

More accurate assessments of elk abundance generally follow the Capture-Mark-Recapture or Resight methods that account for imperfect detection. In this case, a point-count distance sampling approach would have been appropriate (Buckland et al. 1993) and provided a more standardized data collection approach, something to consider for future studies. Another factor that could have biased our study is the timing of survey visits. Elk are crepuscular animals most active in the evening and dawn. Stations visited later in the morning might have had less elk activity and undercounted elk compared to sites visited earlier. Another open question is whether elk would response to traffic differently if the road was open year around? Anecdotal evidence suggests that elk on feed grounds near Jackson Hole show little response to continued vehicle traffic.

Even provided such limitations, this study establishes a systematic point-count approach to estimating elk abundance in the Gros Ventre drainage, in that we have already identified environmental and anthropogenic factors that are susceptible to affect availability to detection in elk (Williams et al. 2002). Namely, the timing of gate opening, vehicle traffic, winter snow depth and spring vegetation quality have all been found to affect the probability of counting elk and thus their availability for detection. We suggest conducting point count studies pre-vegetation green-up, when elk are still utilizing the lower elevations of the Drainage, and would encourage pointcount surveys before any gate opening to maximize availability to detection.

Our research suggests that both climatic variables and vehicle traffic synergistically affect elk counts and distribution. This is important because a forecasted increase in the frequency of spring snow storms in the Western US, coupled with the general prediction that peak NDVI will intensify, but narrow in the spring (Middleton et al. 2013). This may delay spring migration to higher elevation and force elk to remain in the drainage in the spring while overlapping with recreationists and road use. If forced to migrate upwards in the spring to avoid traffic and anthropogenic disturbance before green-up, this could create a mismatch between elk migration and peak NDVI, which could ultimately affect elk fitness and persistence. If additional resources were to become available to managers, the deployment of GPS collars on elk would help inform fine-scale migration from wintering to summering grounds in response to road closure or openness, traffic volume when gates are open, and year-to year variability in environmental conditions. Our results collectively outline the importance of considering the environmental context and climatic conditions elk experience when managing for road closures and recreation. We suggest that the positive impact of road closure to elk within the Gros Ventre drainage will continue to become more pronounced in the future given the projected effects of climate change on snow dynamics and green-up in the western United States.

ACKNOWLEDGEMENTS

Our sincere gratitude goes to the following citizen scientist volunteers who labored to collect our extensive elk count data: Diane Birdsall, Franz Camenzind, Frances Clark, Morgan Graham, Gregory Griffith, Louise Lasley, Mary Lohuis, Jenny Lucchese, Susan Marsh, Jenny McCabe, Bernie McHugh, and Megan Smith. The USFS engineers, Anita Lusty and Michael Oltman, who tracked vehicle traffic through Atherton gate deserve much praise. We would also like to thank the Utah State University Master of Natural Resource Program for supporting this research, as well as Chris Luecke and Dan MacNulty for feedback on an earlier draft.

LITERATURE CITED

- Aikens, E. O., M. J Kauffman, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick and K. L. Monteith. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20: 741-750.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In Second International Symposium on Information Theory, Edited by B. N. Petrov and F. Csaki. Budapest: Akailseoniai–Kiudo. 267-281 pp.
- Baccante, D. and R. Woods. 2010. Relationship between winter severity and survival of mule deer fawns in the Peace Region of British Columbia. BC Journal of Ecosystems and Management 10(3): 145-153.
- 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? The American Naturalist 180(4): 407-424.
- Bolon, N. A. 1994. Estimates of the values of elk in the Blue Mountains of Oregon and Washington: evidence from the existing literature. U. S. Forest Service General Technical Report PNW-GTR-316. 38 pp.
- Buckland, S. T., D. R. Anderson, K. P. Burnham and J. L. Laake. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London. 446 pp.

Burcham, M. G., W. D. Edge, C. L. Marcu, and L. J. Lyon. 1998. Long-term changes in elk distributions in western Montana. Final report: Chamberlain Creek elk studies 1977-1983 and 1993-1996. School of Forestry, University of Montana, Missoula, Montana, USA. 10-48 pp.

Cayan, D. R., M. D. Dettinger, D. Pierce, T. Das, N. Knowles, F. M. Ralph and E. Sumargo. 2016. Natural variability, anthropogenic climate change, and impacts on water availability and flood extremes in the Western United States. Water Policy and Planning in a Variable and Changing Climate: 17-42.

Didan, K. 2015. MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006. NASA EOSDIS Land Processes DAAC. http://doi. org/10.5067/MODIS/MOD13Q1.006

Edge, W. D., C. L. Marcum and S. L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. Journal of Wildlife Management 51: 844-851.

Edge, W. D. and C. L. Marcum. 1991. Topography ameliorates the effects of roads and human disturbance on elk.
Edited by A. G. Christensen, L. J. Lyon, and T. N. Lonner. Proceedings of the Elk Vulnerability Symposium. Montana State University, Bozeman, Montana, USA. 132-137 pp.

Fahrig, L. and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14(1): 21.

Fox, J. and S. Weisberg. 2011. An R Companion to Applied Regression, Second Edition.

Gagnon, J. W., T. C. Theimer, S. Boe, N. L. Dodd and R. E. Schweinsburg. 2007. Traffic Volume Alters Elk Distribution and Highway Crossings in Arizona. The Journal of Wildlife Management 71: 2318-2323. Garrott, R. A., L. L., Eberhardt, P. J., White and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81(1): 33-45.

Hebblewhite, M. and E. H. Merrill. 2007. Multi-scale wolf predation risk for elk: does migration reduce risk? Oecologia 152: 377-387.

Hershey, T. J. and T. A. Leege. 1976. Influences of logging on elk summer range in north-central Idaho. Edited by S. R. Hieb. Proceedings of the Elk-Logging-Roads Symposium. University of Idaho. Moscow, ID, USA. 73-80 pp.

Irwin, L. L. and J. M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. Journal of Wildlife Management 47: 664-672.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64: 685-697.

Kleinbaum, D. G., L. L. Kupper, K.E. Muller and A. Nizam. 1998.Applied regression analysis and other multivariable methods. Duxbury Press, Pacific Grove, California.

Kruskal, W. H. and W. A. Wallis. 1952. Use of ranks in one-criterion variance analysis. Journal of the American statistical Association 47(260): 583-621.

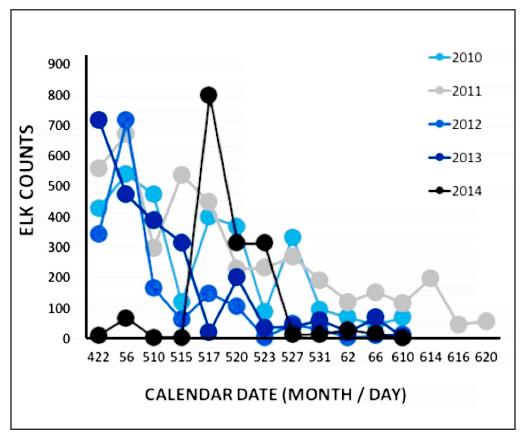
Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. Journal of Forestry 77: 658-660.

Marcum, C. L. 1975. Summer-fall habitat selection and use by a western Montana elk herd. Dissertation. University of Montana. Missoula, MT, USA. 188 pp.

McCorquodale, S. M. 2013. A Brief Review of the Scientific Literature on Elk, Roads, & Traffic. Washington Department of Fish and Wildlife Publication.

- Merkle J. A., Monteith K. L., Aikens E. O., Hayes M. M, Hersey K. H., Middleton
 A. D., Oates B. A., Sawyer H., Scurlock
 B. M. and M. J. Kauffman. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society Biology Series 283(1833): 2016-0456.
- Middleton, A. D., M. J. Kauffman, D. F. 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(6): 1245-1256.
- Morgantini, L. E. and R. J. Hudson. 1979. Human disturbance and habitat selection in elk. Edited by M.S. Boyce, and L.D. Hayden-Wing. North American elk: ecology, behavior and management. University of Wyoming. Laramie, WY, USA. 132-139 pp.
- Muñoz, P. M., M. Boadella, M. Arnal, M. J. de Miguel, M. Revilla, D. Martínez, J. Vicente et al. 2010. Spatial distribution and risk factors of Brucellosis in Iberian wild ungulates. BMC infectious diseases 10(1): 46.
- Parker, K. L., P. S. Barboza and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23: 57-69.
- Perry, C. and R. Overly. 1977. Impact of roads on big game distribution in portions of the Blue Mountains of Washington, 1972-1973. Washington Game Department Report, Olympia, WA. 38 pp.
- Pettorelli, N., J. O. Vik, A. Mysterud, J.- M. Gaillard, C. J. Tucker and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20(9): 503-10.
- Post, E. and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80(4): 1322-1339.

- 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.
- Shapiro, S. S. and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika 52(3/4): 591-611.
- Smallidge S. T., B. C. Thompson, W. R. Gould, L. E. Kantar, U. A. Rosauer and R. A. Deitner. 2003. Demographics, temporal and spatial dynamics, and resource conflict evaluation of elk wintering near San Antonio Mountain in northcentral New Mexico. Final Report Federal Aid Project W-136-R, New Mexico Department of Game and Fish, Santa Fe, NM, USA.
- Smith B. L. 2000. Jackson Hole: The Big Herds. Bugle, Fall 1991, updated 2000. Rocky Mountain Elk Foundation.
- United States Fish and Wildlife Services (USFWS). 2007. A Description of the National Elk Refuge and Grand Teton National Park.
- White, C. G., P. Zager and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. Journal of Wildlife Management 64: 355-369.
- White, P. J., K. M. Proffitt and T. O. Lemke. 2012. Changes in Elk Distribution and Group Sizes after Wolf Restoration. The American Midland Naturalist 167(1): 174-187.
- Williams, B. K., J. D. Nichols and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, CA, USA. 817 pp.
- Witmer, G. W. and D. S. Decalesta. 1985. Effect of forest roads on habitat use by Roosevelt elk. Northwest Science 59: 122-125.



Appendix A. Elk counts throughout spring, summed over 12 observatory points at each date along the Gros Ventre Road, WY. Data were collected between April 21 and June 11 for 2010-2014.

Received 16 November 2017 Accepted 18 March 2018