

Evaluating Landscape Connectivity and Habitat Fragmentation Effects on Elk in the Roaring Fork and Eagle Valleys

August 2019

Prepared by Paul Millhouser

Rocky Mountain Wild



ROCKY MOUNTAIN WILD

Acknowledgements

This project was made possible by a generous grant from Patagonia. I would like to thank several individuals who took the time to provide their insight: Erica Smithwick of Penn State and Tehri Parker, Paige Singer, Alison Gallensky, and Megan Mueller of Rocky Mountain Wild. I would also like to thank Julia Mao and Brad Petch of Colorado Parks and Wildlife, who were instrumental in providing elk population and hunting data as well as valuable historical information about management practices.

Disclaimer

The contents of this report reflect the views of the author, who is solely responsible for the content herein. Rocky Mountain Wild assumes no liability relating to the completeness, correctness, or fitness for use of this data. The contents do not necessarily reflect the official views or policies of any of the aforementioned individuals, agencies, organizations or groups.

Citation

The document should be cited as:

Millhouser, Paul. *Evaluating Landscape Connectivity and Habitat Fragmentation Effects on Elk in the Roaring Fork and Eagle Valleys*. Rocky Mountain Wild, 2019.

Additional Information

For more information or access to the GIS data please contact:

Paul Millhouser
paul@rockymountainwild.org

Rocky Mountain Wild
1536 Wynkoop Street, Suite 900
Denver, CO 80202
303-546-0214

www.rockymountainwild.org

Abstract

Recent studies conducted by Colorado Parks and Wildlife have identified an alarming decline in elk populations in the Eagle and Roaring Fork valleys of Colorado (Boyd 2018). Based on elk censuses for the area conducted by Colorado Parks and Wildlife, the population decline was more than 50% from 1999 to 2015, exacerbated by an increase in hunting pressure in 2003-4, followed by a failure to recover as expected when that pressure was reduced. Even more alarming, the rate of elk calf production per cow has decreased to a level that suggests populations may not recover, and may decline still further. This paper applies measures of human influence on the landscape, including habitat fragmentation and landscape connectivity, to the study area in a time series from 1981 to 2017, to identify possible correlations with elk population changes during that period. Additional variables thought likely to contribute to elk population change, including hunting pressure, phenological patterns, and human population change, were also analyzed using linear regression. Because elk utilize different habitats seasonally and these habitats may not be uniformly affected by human or phenological processes, I differentiated among these seasonal habitats in my analysis where possible. Because data required to measure habitat fragmentation and loss of connectivity were not available for the entire 1981 to 2017 period, I explored the use of a recently published building development index as a proxy. It proved to correlate strongly (R-squared value 0.76 to 1.00 depending on measure) with the direct measures of habitat fragmentation and connectivity loss, and thus served as useful proxy for those measures. This study finds that, when a threshold of accumulated landscape influence is reached, the relationship among predictor variables and elk population growth rate changes. I conclude that human influence on the landscape has reduced the equilibrium calf to cow ratio, and thus increased the effect of hunting and other human activities on the growth rate of the elk population in the Roaring Fork and Eagle valleys, lessening the population's resilience and possibly establishing a new equilibrium population. In order to manage this elk population to prevent further decrease, wildlife managers will need to account for the effect of these landscape level changes in the study area when setting hunting targets and evaluating other human uses of public lands.

Introduction

Over the last twenty years, research on the effects of human changes to the landscape has increasingly emphasized the impacts of habitat fragmentation and loss of landscape connectivity on the continued viability of wildlife populations. Development, in the form of roads, trails and other infrastructure, can have negative effects on habitat suitability and wildlife more generally. Impacts include changes in wildlife behavior and activity due to an increase in human presence; reduced species abundance; loss of habitat and spread of invasive species; increased forms of pollution, including noise and light; species' loss of access to crucial habitat and resources due to road and human avoidance; decreased population viability; and, increased potential for human-wildlife conflicts; and direct wildlife mortality (for example, Benítez-López et al. 2010; Bennett et al. 2011; Gelbard and Belnap 2003; Jaeger et al. 2005; Jones et al. 2015; Mortensen et al. 2009; Trombulak et al. 2000).

Landscape connectivity and habitat fragmentation, while distinct concepts, both affect wildlife access to critical habitat. *Habitat fragmentation* occurs when a large, contiguous area of uniform habitat “is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original” (Wilcove et al. 1986, p. 237). Wilcove’s definition “implies four effects of the process of fragmentation on habitat pattern: (a) reduction in habitat amount, (b) increase in number of habitat patches, (c) decrease in sizes of habitat patches, and (d) increase in isolation of patches” (Fahrig 2003, p. 491). While fragmentation is not always driven by human activity, development and resource extraction are important causes, in addition to “natural” factors such as fire and insect activity. While reducing the amount and connectivity of habitat, fragmentation has the effect of altering the relative proportions of edge and core habitat, which results in disproportionate effects on different species (Bennett and Saunders 2010). Ever-smaller habitat patches are less resilient in the face of drought, fire, disease, and other unpredictable events that are likely to increase as a result of global climate change.

Landscape connectivity most commonly refers to permeability of the landscape to the movement of terrestrial vertebrates (Bissonette and Cramer 2008; Theobald et al. 2012). Connectivity permits animals to disperse into new territories, access seasonal resources and breeding habitat, and maintain the flow of individuals and genes across the landscape (Manel et al. 2003; Rudnick et al. 2012). Much as in the case of fragmentation, impediments to connectivity may be natural, but increasingly come in the form of human-caused change to the landscape. Continued landscape connectivity is critical to sustaining species richness and populations, and becomes increasingly important as fragmentation grows and climate change alters habitat distribution (Heller and Zavaleta 2009).

This study evaluates changes over time in measures of habitat fragmentation and landscape connectivity as predictors of changes in elk population in a single landscape, whereas prior studies of habitat fragmentation and landscape connectivity have most commonly characterized a single landscape (or collection of landscapes) at a moment in time or compared two otherwise similar landscapes differing in those variables (see, for example, Dickson et al. 2016; Fernandez et al. 2018; Jaeger et al. 2005; McClure et al. 2017; Watson et al. 2005; but, see Haddad et al. 2015). While in some cases a time series analysis has been applied to habitat fragmentation or landscape connectivity, the analysis has not generally focused on evaluating the correlation between these variables and empirically-measured species population (see, for example, Bishop-Taylor et al. 2018; Jaeger et al. 2007; Santini et al. 2019).

Elk populations in the Roaring Fork and Eagle valleys of Colorado from 1981 to 2017 have failed to recover from substantial population declines in the last two decades, despite efforts by the Colorado Department of Parks and Wildlife to manage for population growth. This decline in population may be correlated with reduced connectivity and increased habitat fragmentation in the region, suggesting that human influence may have altered the resilience and/or stability of this population. To address this possibility, I tested the following hypothesis:

Failures of elk populations in the Roaring Fork and Eagle valleys of Colorado to recover from substantial population declines are correlated with, and possibly a result of, changes to connectivity and habitat fragmentation over recent decades, after accounting for other possibly contributing variables (e.g., hunting pressure, precipitation, and vegetative health).

Methods

Study Area

The Roaring Fork and Eagle Rivers are tributaries of the Colorado River located in the Rocky Mountains in the west central region of Colorado (see Figure 1). Both flow through public and private lands around the White River National Forest, and their watersheds include the resort towns of Vail and Aspen as well as wilderness areas. The rivers' valleys and surrounding watersheds provide habitat for a variety of wildlife, and in particular are home to elk herds totaling more than 10,000 individuals. My study area consists of two "Data Analysis Units" (DAUs) designated by Colorado Parks and Wildlife as E-15 and E-16, totaling 576,633 hectares. Each DAU corresponds to the entire range of a single elk herd, and these two roughly correspond to the Roaring Fork and Eagle Valleys. My habitat fragmentation and connectivity analyses included a 25-kilometer buffer around the DAUs, for a total analysis area of 1,602,080 hectares. In addition to considering the study area in terms of elk herd DAUs, my analysis considered the landscape in terms of (1) seasonal elk habitat and (2) land ownership. The Roaring Fork and Eagle valleys are dominated by federally-owned lands; 432,510 hectares (75.00%) of the study area falls within the White River National Forest, and an additional 48,186 hectares (8.35%) is managed by the Bureau of Land Management.

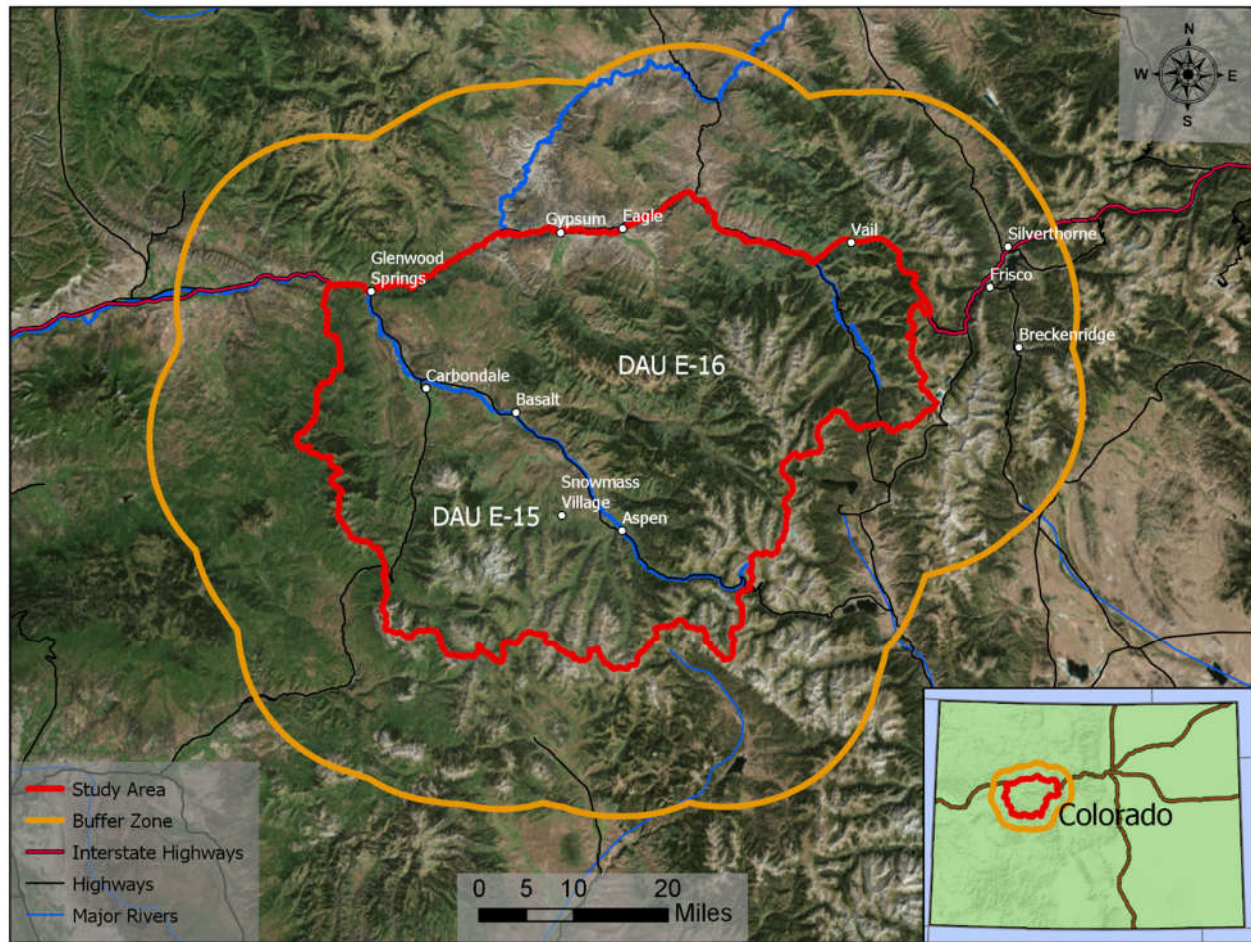


Figure 1: Map of the study area, with study area delineated in red and the buffer zone in orange. Data Analysis Units E-15 and E-16 are contained within the southwestern and northeastern parts, respectively, of the study area and are separated by the Roaring Fork River. Map data: ESRI; United States Geological Survey.

The herds in each of these DAUs increased in population from the late 1980s into the 1990s, peaking in 1995 at an estimated 20,036 elk in the combined DAUs. Concerned that these population levels might result in starvation events or habitat degradation, CPW issued larger numbers of hunting licenses, particularly for cow elk, in response (Petch 2019). The reduction in population exceeded what CPW intended, so it subsequently—and indeed, to this day—issued fewer hunting licenses; based on models and past population trends, CPW anticipated that population would trend upward toward prior levels. From 2010 to the present, the total elk population has fluctuated between 9,000 and 11,500.

During the study period, human population and human infrastructure have increased substantially in the study area. Human population of the study area, as estimated from U.S. Census Bureau figures, increased by more than 150% between 1990 and 2018. From 1990 to 2000, the period of most rapid growth, the increase exceeded 55%. Statistics measuring habitat

fragmentation, building construction, and landscape connectivity all showed increasing human influence over the landscape during the 1981-2017 period; given that 75% of the study area is within the White River National Forest, where human population is very small and new construction has been greatly limited, the increase on the remaining 25% of the landscape is of higher intensity than the overall statistics suggest.

Overview of Approach

To understand the causes of elk population decline in the study area, I used two tools of landscape ecology to understand changes in habitat fragmentation and loss of connectivity in the study area from 1990 to present. To understand habitat fragmentation, I used FRAGSTATS software (McGarigal et al. 2012); to understand changes in connectivity, I used Circuitscape software (McRae et al. 2008, 2013; www.circuitscape.org). Both of these tools are described in detail below. In addition to the data required for these tools, I considered data regarding hunting pressure, precipitation, and vegetative health to evaluate the contribution of other variables.

To evaluate the effect of human influence on elk population across different seasonal habitats as well as on the entire landscape, I used polygon shapefiles published by the Colorado Department of Parks and Wildlife (CPW) that classify the study area into seasonal elk habitat types (Colorado Department of Parks and Wildlife 2018). Reflecting the tendency of elk to use some areas during more than one season and prefer certain areas within seasonal habitat, these polygons overlap substantially. To create a raster permitting analysis with other datasets, I classified each 30 meter by 30 meter cell based on the perceived highest value seasonal use. For example, if a location fell within both the “Production Area” (used for calving and calf-rearing) and general summer range, I classified it as “Production Area.” CPW also provided elk population data, including estimated annual population, and the hunting data, including number of hunting licenses, and kills by bull, cow and calf (see Appendix 1 for complete data).

My analysis of habitat fragmentation considered seasonal elk habitat as delineated by CPW, and focused on roads, motorized trails, and nonmotorized trails as the basis for evaluating human contribution to habitat fragmentation. To characterize landscape connectivity, I constructed a surface approximating resistance to movement by elk based on the inverse of an existing habitat model based on land cover type and proximity to roads (Colorado Division of Wildlife 2006), with further resistance provided by slope, major rivers, and road crossings. I considered both mean resistance by each elk seasonal habitat type and the results of a Circuitscape analysis of this surface.

Fragmentation Analysis

FRAGSTATS is the most widely used software tool for calculating fragmentation-related metrics (McGarigal et al. 2012). It is capable of producing dozens of metrics of fragmentation, but many of them are largely duplicative. In addition, landscape level metrics may not be able to differentiate among within-landscape patterns—for example, the mean habitat patch size of a

landscape with numerous equal-sized patches might be similar to that of a landscape with a broad range of patch sizes. Riitters et al. (1995), sought to distill these measures to a few key categories, each represented by a single metric. Despite considerable research in the field since 1995, their approach remains relevant, although some of the metrics they recommend have since been further refined and recategorized (see McGarigal 2015).

Fragmentation analysis using FRAGSTATS requires a land cover dataset as its primary input. I used the GAP/LANDFIRE National Terrestrial Ecosystems 2011 dataset from the U.S. Geological Survey (GAP 2011), which characterizes vegetation cover/habitat type at a spatial resolution of 30 meters, which is well suited to the scale of analysis. The land cover categories can be evaluated at 7 different levels of increasing specificity, ranging, for example, from “Shrub & Herb Vegetation” to “Western Great Plains Foothill and Piedmont Grassland” or from “Forest & Woodland” to “Rocky Mountain Lodgepole Pine Forest.” To consider the fragmenting effect of roads and trails, which are not included in GAP 2011, I used current and historic data regarding their locations. For state and municipal roads, I used 1990-2017 TIGER data from the US Census Bureau and Colorado Department of Transportation data. Reliable data on road construction dates from earlier time periods were not available, and so my fragmentation and connectivity analyses were limited to the 1990 to 2018 period. TIGER data may not be complete for roads without human habitation and is of inconsistent positional accuracy in earlier periods. Because I used a buffered area around road centerlines as the zone of fragmenting effect, small discrepancies in positional accuracy are unlikely to be significant. Roads and trails in the National Forest were identified from the United States Forest Service (USFS) Transportation Line dataset, which is derived from USFS and USGS data that is supplemented with local, county, and state data to create the best available dataset of transportation feature in National Forests (USFS 2018). Because the latter dataset is compiled from multiple sources of different vintages, my analysis was unable to track some changes within the National Forest. As new construction of roads and trails within the National Forest, particularly in designated Wilderness Areas, have been restricted throughout the study period, this may not be a major limitation. Figure 2 shows the uneven distribution of fragmentation among different seasonal habitats as of 2018. Fragmentation is most notable in winter habitat areas, which tend to be at lower altitudes along valley floors. Appendix 5, Figure 1 and Appendix 5, Figure 2 show closeup views of the fragmentation of the Roaring Fork and Eagle valleys, respectively, and further highlight the degree of fragmentation along the valley floors.

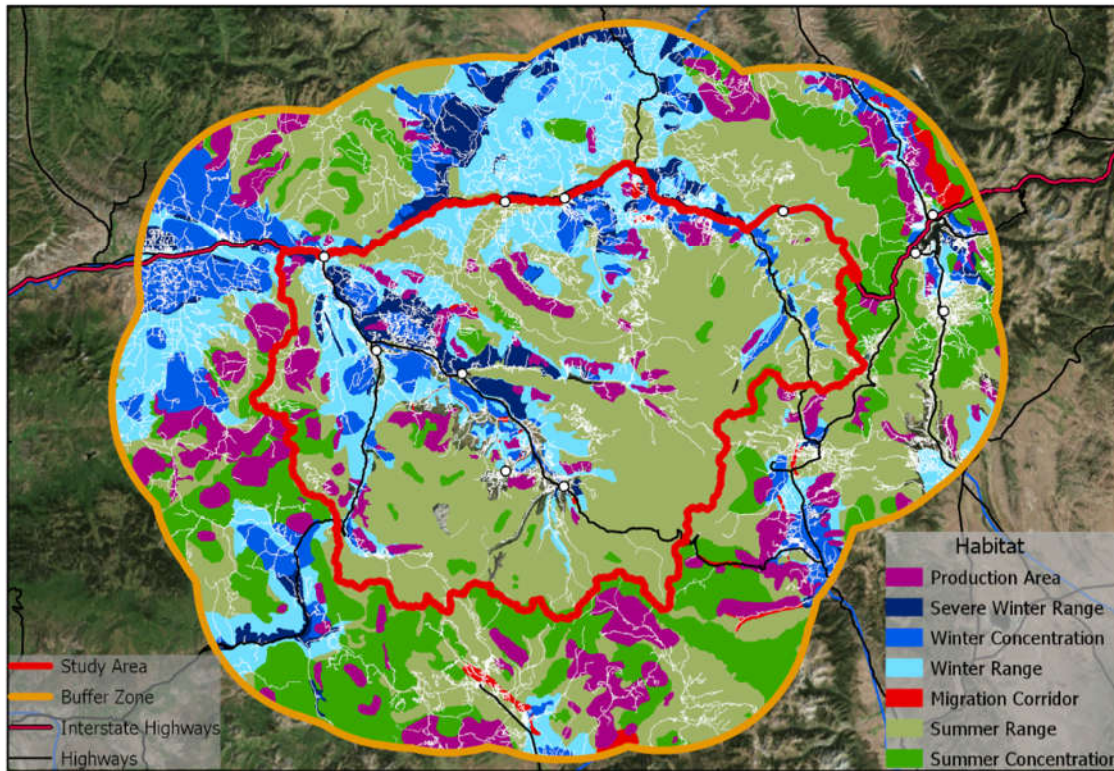


Figure 2: Fragmentation by elk habitat type as of 2018. Fragmenting roads and trails depicted in white. Elk Data: Colorado Parks and Wildlife.

To provide a broad view of the effects of fragmentation and to allow fragmentation to be distinguished from habitat loss, I chose measures provided by FRAGSTATS that reflected both changes in the total amount of different habitat classes and changes in the structure of that habitat. I analyzed the data based on the elk seasonal habitat classes discussed above, as well as at a landscape level. No single measure combines a complete characterization of fragmentation, but together they describe both the degree and kind of fragmentation that has occurred. For a complete description of the metrics considered in this study, see Appendix 2. To avoid edge effects, I included a 25-kilometer buffer zone around the study area in my analysis; habitat within the buffer zone was included for purposes of considering adjacency and similar factors regarding the study area itself. I selected Core Area Index and Proximity Index for summer concentration and migration areas as candidate predictor variables for modeling because they displayed the greatest change over the study period, perhaps because winter habitat areas had already become highly fragmented in earlier periods.

Connectivity Analysis

Most connectivity research involves creating a “resistance surface” raster in which each cell is assigned a value based on the ease or difficulty of wildlife movement across it. Typical parameters for constructing a resistance surface might include, for example, human-built

infrastructure, vegetation type, distance to water, slope, etc. Some researchers have successfully employed a landscape integrity approach that posits that landscape suitable for residence and for movement are not necessarily the same, and that human alteration to the landscape is the largest factor in resistance to movement. (see, e.g., Belote et al. 2016; Theobald 2013; Krosby et al. 2015). Given the smaller area of landscape to be considered in my capstone project, the more limited range of human activities occurring there, and the focus on a single species, I based my resistance surface on an inverse of an elk habitat suitability model, then applied various penalty factors.

The Colorado State Wildlife Action Plan's "Making Connections for Wildlife" program was an interagency effort that assembled a team of biologists and GIS experts to model wildlife movement corridors based on habitat suitability parameters for a variety of species, including elk, that are specifically applicable to the Colorado portion of the Rocky Mountains (Colorado Division of Wildlife 2006). The resulting habitat suitability model, based on vegetation cover type and distance to nearest road, was created through expert consultation and has the advantage of having been used successfully in prior research. The data required to transform this habitat suitability model into my final resistance surface included the GAP 2011 and road/trails data discussed above under Fragmentation Analysis. In addition, I used USGS NHD Plus datasets for hydrographic data to assign resistance to major rivers (USEPA/USGS 2012). I also used USGS 3DEP digital elevation data, at a spatial resolution of 1/3 arc seconds (~10 meters), downsampled to 30 meter resolution, to create a slope resistance layer (USGS 2017).

I modeled connectivity using the open source software Circuitscape, which simulates running electric current across the resistance surface, based on the premise that wildlife movement will flow across the landscape in the same fashion (McRae et al. 2008). In particular, I used a relatively novel approach to Circuitscape, known as Omniscape, that measures overall flow across the landscape, rather than simply between predetermined locations (McRae et al. 2016; McClure et al. 2017). By avoiding arbitrary selection of movement start and end points required by other approaches to evaluating connectivity, Omniscape presents a broader view of the possibilities of movement available to wildlife.

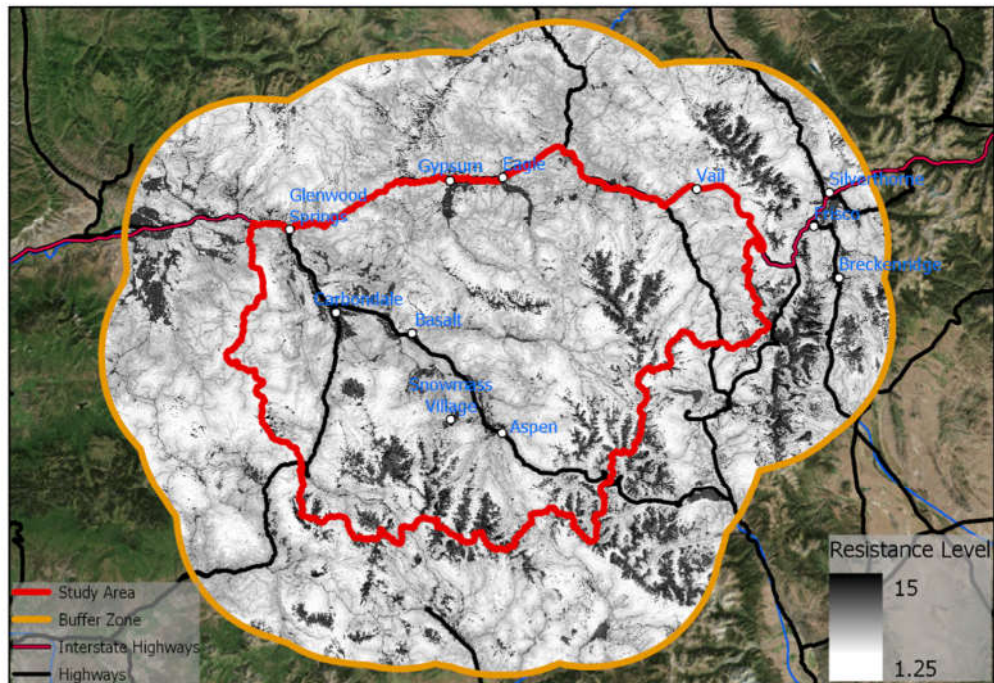


Figure 3: Resistance layer as of 2018 for the study area and buffer zone.

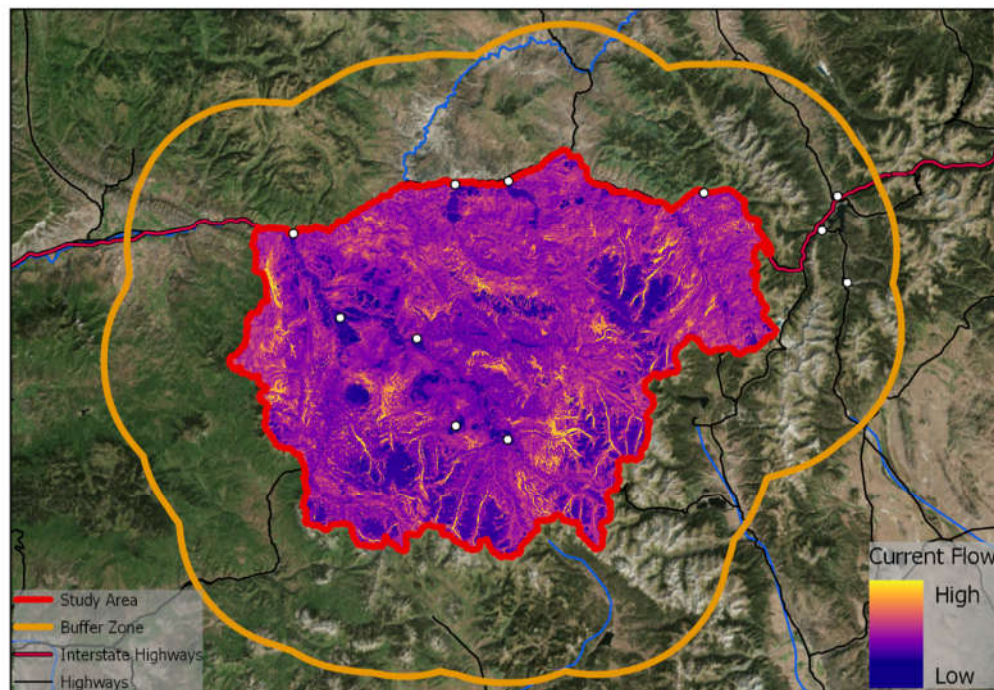


Figure 4: Results of Circuitscape/Omniscap analysis of the study area for 2018.

Figure 3 shows the resistance layer created for 2018; Figure 4 shows the results of Omniscape analysis of that layer. As expected, areas of high resistance correspond to areas of rugged terrain, rivers, roads, and other human developments. While the Omniscape analysis provided a visual depiction of movement potential that can also be compared to empirical wildlife movement data where available and can also be used to identify critical connectivity areas, it is not well-suited to comparing connectivity changes over time, as it does not produce meaningful numeric data. My analyses evaluating connectivity against other variables contributing to elk population thus used resistance surface data, in the form of a mean value for each year for the study area, rather than Circuitscape output.

Fragmentation and Connectivity Data Limitations

While the elk population for the entire 1981 to 2017 study period was available annually, measures of habitat fragmentation and landscape connectivity were subject to limitations: (1) all measures were available less frequently than annually; (2) FRAGSTATS and connectivity metrics were available for only a portion of the study period; (3) human population was an indirect proxy for landscape changes; (4) measures varied in degree of spatial resolution from census block group to 30 meters; and (5) FRAGSTATS and connectivity measures metrics were constructed from data that did not capture all change over time. Appendix highlights these characteristics for the habitat fragmentation and landscape connectivity measures used in this study. In addition to these limitations, resistance value did not display substantial variability among habitat classes; I therefore used the mean value across the study area for analysis. U.S. Census population data was not available at adequate spatial resolution to permit analysis based on habitat class or indeed to include only areas within the precise study area boundaries, so I used best estimate values for the study area based on evaluation of census block groups.

To address the unavailability of direct measures of habitat fragmentation and landscape connectivity prior to 1990, I used the recently-developed Built-up Intensity measure as a proxy (Leyk and Uhl 2018). Built-up Intensity is reported on a 1 to 15 scale for the conterminous United States at five year intervals for the period 1810 to 2015. Higher scaled scores are assigned to each 250 meter pixel based on the number of square feet of human construction within the pixel. To permit analysis of the dependent variables relating to habitat fragmentation and landscape connectivity with the annual elk data, I used linear interpolation between measurement dates for each independent variable to provide annual values. In the case of the Built-up Intensity, which was last produced for 2015, I used linear extrapolation based on the slope from 2010 to 2015 to produce values for 2016-18.

Other Variables and Data Sources

I considered other datasets that measured variables with the potential to affect elk population, including hunting pressure, phenology, precipitation, and human presence in the study area:

- 1) Elk Data: Colorado Parks and Wildlife provided records of annual elk population and herd structure estimates from 1981 to 2018, and also annual hunting license and

harvest data from 1996 to 2018. Elk population and herd structure estimates were based on data collected annually, but years prior to 2018 were re-modeled by Colorado Parks and Wildlife staff using their most current modeling approach, ensuring comparability of data.

- 2) Phenology: To evaluate possible effects relating to forage quality, I used data from the United States Geological Survey's Remote Sensing Phenology (RSP) collection, which includes a variety of NDVI-based metrics based on data from the Advanced Very High Resolution Radiometer (AVHRR) and the Moderate Resolution Imaging Spectroradiometer (MODIS) (USGS 2001-17). This dataset (or comparable data) is not available for years prior to 2001, but as it was not included in any of the preferred models for the 2001 to 2017 period, I did not seek to evaluate phenology for earlier periods.
- 3) Precipitation: In addition to its effect on phenology, precipitation may directly affect elk population based on the amount of snow and other precipitation occurring during the year. Snowfall may affect access to preferred habitat areas and may restrict access to food even in reachable areas. These effects are dependent on both the total snowfall and its timing. Total precipitation, regardless of form, may affect availability of drinking water and may, through the impact of runoff on stream flows, limit connectivity. The Colorado Climate Center provides historic weather data from several stations in the study area, but only the Aspen 1SW station provides consistent data for the entire study period of 1981 to 2018 (Colorado State University, 1981-2018).

Results

Prior to statistical analysis, I reviewed the elk population and other data to review trends that might inform model selection. As an initial matter, I considered the pattern of elk population and population growth rate over time (Figure 5). Consistent with anecdotal reports, the elk population more than doubled from the late 1980s through the late 1990s, then declined rapidly from 2000 through 2015. An increase in growth rate commenced in 2013, leading to a climb in population from 2016 to the present. To understand these trends, I identified possible predictor variables from the datasets described above.

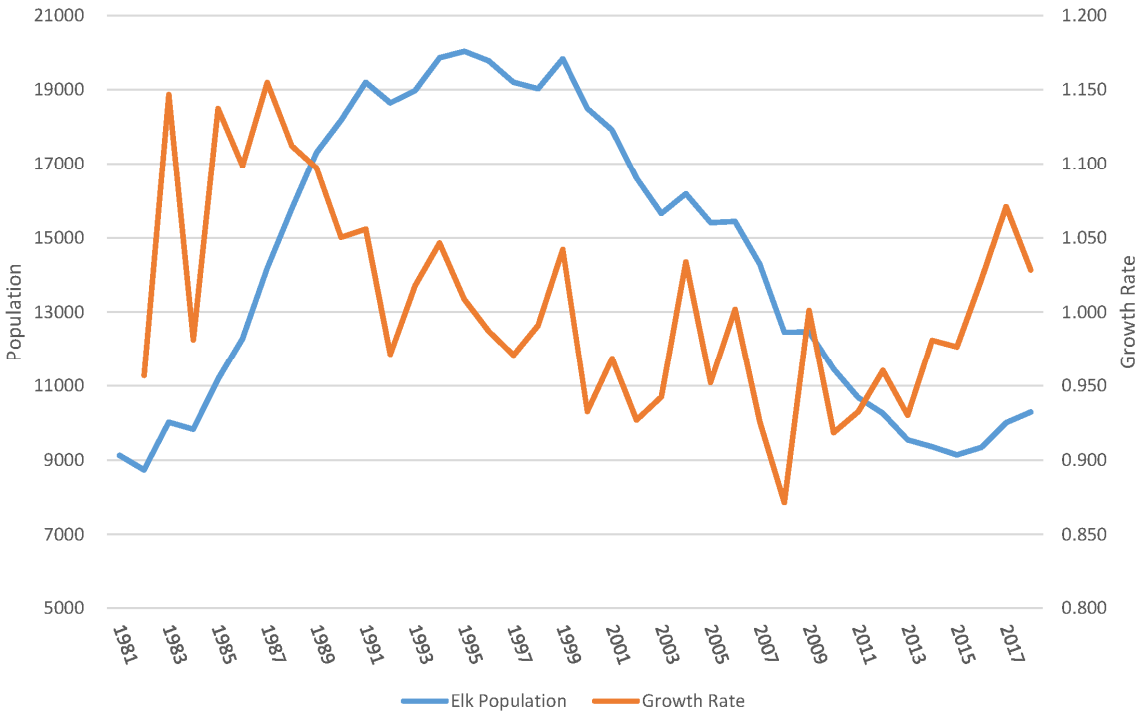


Figure 5: Elk population and population growth rate from 1981 to 2018. Note that the growth rate was less than one (declining population) for most of the period 2000 to 2015. Data: Colorado Parks and Wildlife.

Correlation among Human Influence Variables

To understand the covariance of these habitat fragmentation and landscape connectivity variables and their abilities to serve as proxies for one another, I constructed a Pearson correlation matrix (see Table 1) covering the period for which all measures were available, 1990 to 2018. As Table 1 shows, there is a high degree of correlation between these variables, suggesting that they are suitable proxies for one another, most importantly in the case of Built-up Intensity when considering periods prior to 1990.

	Population	Built-up Intensity (Mean)	Resistance (Mean)	Core Area Index (Migration)	Proximity Index (Migration)	Core Area Index (Summer)	Proximity Index (Summer)
Population	1						
Built-up Intensity (Mean)	0.97	1					
Resistance (Mean)	0.94	0.99	1				
Core Area Index (Mean Migration Corridors)	-0.96	-1	-0.99	1			
Proximity Index (Mean Migration Corridor)	-0.96	-1	-0.99	1	1		
Core Area Index (Mean Summer Concentration)	-0.76	-0.80	-0.89	0.79	0.81	1	
Proximity Index (Mean Summer Concentration)	-0.85	-0.89	-0.95	0.89	0.90	0.99	1

Table 1: Pearson matrix showing correlation among direct and indirect measures of habitat fragmentation and landscape connectivity.

Predictor Variable Selection by Evaluating Correlation

Based on these results, I chose to include Built-up Intensity in my modeling, as it serves as a useful proxy for habitat fragmentation and landscape connectivity loss and covers the entire study period. BUI does show an inverse correlation with the following year's growth rate (see Figure 6, although that correlation weakens at higher levels of BUI—which also correspond with more recent years. I also included measures of hunting pressure in my model, as control of hunting licenses and resulting deaths is the management technique perhaps most widely used by wildlife agencies. While elk deaths due to hunting ("harvest") have an obvious direct effect on population, its correlation with the following year's growth rate (and also when lagged to second and third years) proved negligible. To the extent that population and harvest are correlated, the causation may run in both directions; harvest does reduce population, but

Colorado Parks and Wildlife may issue fewer licenses in response to reduced population (see Appendix 5, Figure 3). On the other hand, the proportion of the harvest comprised of cow elk showed a clear inverse correlation with the following year growth rate (see Appendix 5, Figure 4).

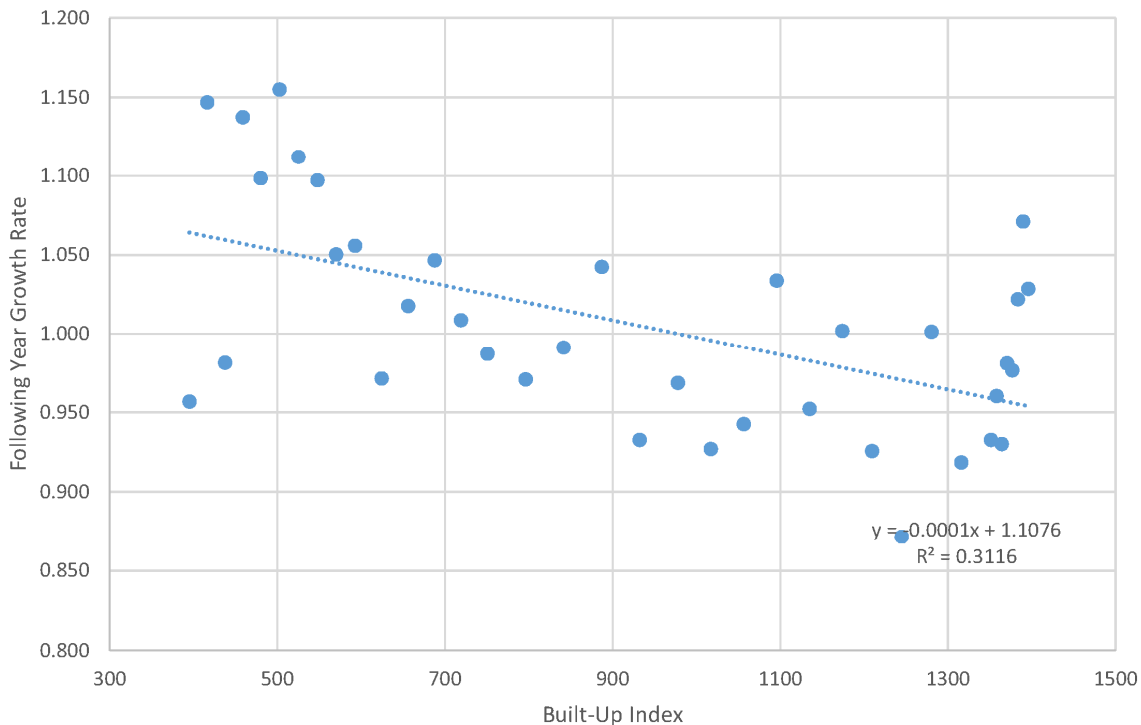


Figure 6: Chart showing the correlation of the Built-up Intensity with the following year growth rate for 1981 through 2017. Data: Colorado Parks and Wildlife; Leyk and Uhl 2018.

Due to the complexity of the relationships among these and other possible predictor variables, I used R to construct a Pearson correlation matrix to evaluate the correlations of more than thirty variables regarding elk population structure, hunting pressure, human influence on the landscape, weather, and phenology among one another and with following year population growth rate (R Core Team 2019). Using the *rcorr* function from the Hmisc package allowed this matrix to include p-values for each correlation coefficient (Harrell et al. 2019). Figure 7 shows a correlogram produced using this process. I then selected a subset of these predictor variables to use in modeling based on their degree of correlation with following year growth rate, the p-value of that correlation, and consistency with factors believed to influence elk population growth.

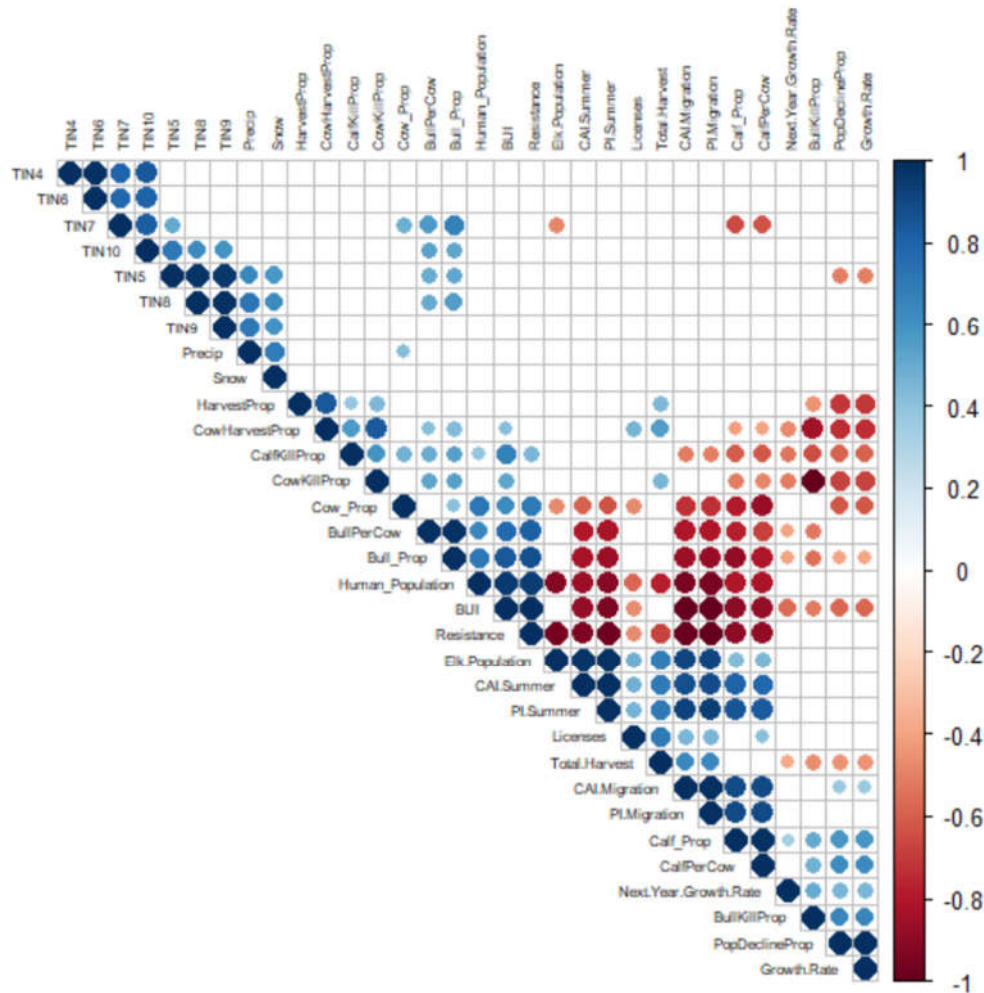


Figure 7: Correlogram showing candidate predictor variables. Color and size of circles indicate the strength and direction of correlation. Blank squares indicate correlations with a p-value of greater than 0.05.

Built-up Intensity and Elk Population as Key Model Variables for 1981 to 2017

I used the stepAIC function from the MASS R package, which allows for simultaneous consideration of multiple models using a stepwise process, to identify candidate linear regression models to explain following year elk population growth rate (Venables and Ripley 2002). This function constructs models from all submitted predictor variables and tests them against the designated dependent variable, then returns the models with the best Akaike information criterion (AIC) values. Because of the differing availability of predictor variables for different time periods and in order to explore the possibility of models performing differently over different time periods, I applied this approach to different chronological subsets of my data. To address AIC's tendency to overfit models with small sample sizes, as is the case in this study, I also performed exploratory linear regression with the identified models to determine if models with similar r-squared and multiple r-squared values could be obtained when omitting

one or more predictor variables (Bedrick and Tsai 1994). Although this study's goal is not to predict future growth rates, I applied the predictive r-squared value to further limit the possibility of overfitting. The predictive r-squared is based on iteratively removing an observation from the dataset, determining the regression equation from the remaining observations, then applying it to the removed observation (Minitab Blog 2013).

The model for 1981 to 2017 (the last year for which the following year's growth rate is available) with best fit (Model A) resulted from applying linear regression to the following baseline year variables: calf to cow ratio, total precipitation, the third degree polynomial of the total elk population, and the third degree polynomial of the Built-up Intensity. This model returned a multiple R-squared value of 0.7727, an adjusted R-squared value of 0.697, and a predictive R-squared value of 0.551 (see Appendix 5, Table 1). Note that annual license numbers and phenology data, as well as direct measures of resistance and fragmentation, were not available for the entirety of this time period; the Built-up Intensity stood in for the human influence variables, but license numbers and phenology were omitted. Both the plot of actual versus predicted following year growth rate (Appendix 5, Figure 5) and absolute residual value versus predicted next year growth rate (Appendix 5, Figure 6) show that the model as a whole lacks a systematic error relating to growth rate, suggesting it does not suffer from serious heteroskedastic errors. There is a tendency toward more variability for growth rate values closer to one, however.

Considering that the effects of the population structure variables in the preceding models have high p-values and are in one case inconsistent with anticipated ecological processes, I applied the model omitting those variables (Model B). I also eliminated precipitation as a predictor variable, as it was both low in significance and of limited contribution to the goodness of fit. The only two remaining variables were the third degree polynomials of elk population and of Built-up Intensity. The resulting model returned a multiple R-squared value of 0.7264, an adjusted R-squared value of 0.6716, and a predictive R-squared value of 0.5534 (see Appendix 5, Table 2).

Variables Subject to Threshold Effects

Statistical models of ecological phenomena are of limited value unless the predictor variables can be persuasively associated with ecological processes. In the case of the models described above, population structure variables such as calf per cow ratio and proportion of cows harvested were expected to influence population growth rate; adding other such variables to the model, including the ratio of bulls to cows, unexpectedly did not improve fit. Indeed, the population structure variables used in the models above have p-values high enough to suggest their exclusion, as shown by Model B. The negative effects of a higher cow harvest, shown in Appendix 5, Figure 4, obviously reduce the following year's potential calf population (and thus growth rate), but the *negative* effect of a higher calf to cow ratio (whether lagged or not) is less straightforward to explain. Given that female calves have long been thought to typically begin breeding in their third year, the lagged calf to cow ratio would seem more likely to predict an *increased* growth rate (see, *e.g.*, Kittams 1953 regarding age of first breeding for elk). The small

number of observations in the underlying dataset, the low significance of this variable, nonlinearity, and covariance with other variables may explain this unexpected result. More broadly, the strong influence of elk population and human influence on the landscape may render the effect of other variables difficult to distinguish from noise.

To understand the variation in, and influence of, the calf to cow ratio, I applied the R package “segmented” to find breakpoints for the ratio that might better explain its possible nonlinear effect (Muggeo 2008). Analysis showed that when the calf per cow ratio was less than 0.4808, the mean following year growth rate was 0.971483; when the calf per cow ratio was greater than or equal to 0.4808, the mean following year growth rate was 1.034469 (see Figure 8).

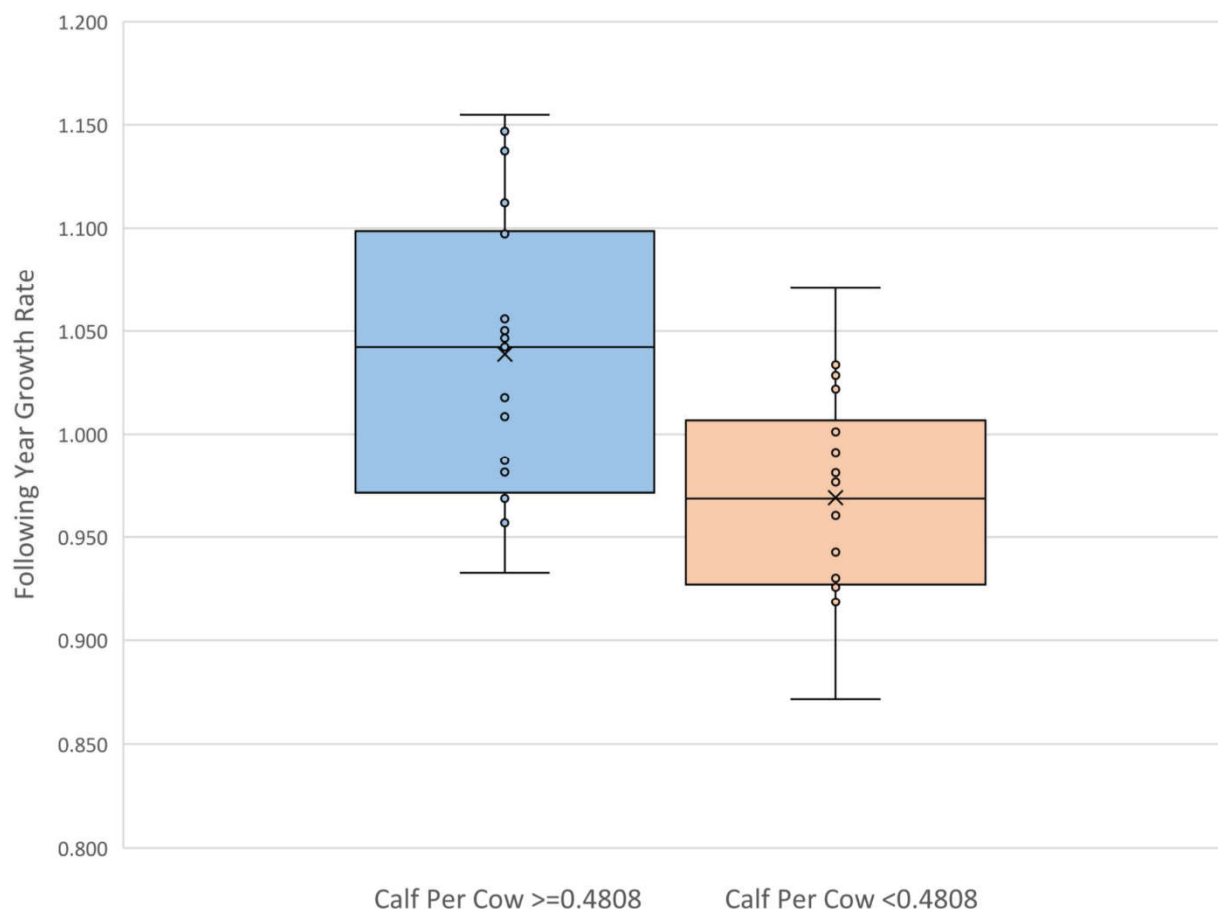


Figure 8: Whisker plot showing range of following year growth rates assuming a calf per cow ratio breakpoint of 0.4808. Elk Data: Colorado Parks and Wildlife.

Most notably, this breakpoint marks the difference between a declining and increasing population, and suggests an important positive relationship between calf to cow ratio and growth rate not evident in a linear regression analysis. All of the years of lower calf to cow ratio (and lower growth rate) except 1997 occur between 2001 and 2017 (excluding 2004), suggesting a temporal aspect to its variance, and possible covariance with a variable that also varies temporally. Figure 9 illustrates the strong negative correlation between the calf to cow

ratio and the Built-up Intensity, which has a consistent temporal trend. One possible interpretation of this covariance is that the range of variation of the calf to cow ratio becomes depressed when the Built-up Intensity crosses a threshold value. Based on the calf to cow ratio dipping below the breakpoint of 0.4808 between 2000 and 2001, this BUI value would be in the range of roughly 978 to 1017; at higher BUI values, other variable(s) would presumably explain variance within the lower range of calf to cow ratios and following year growth rates.

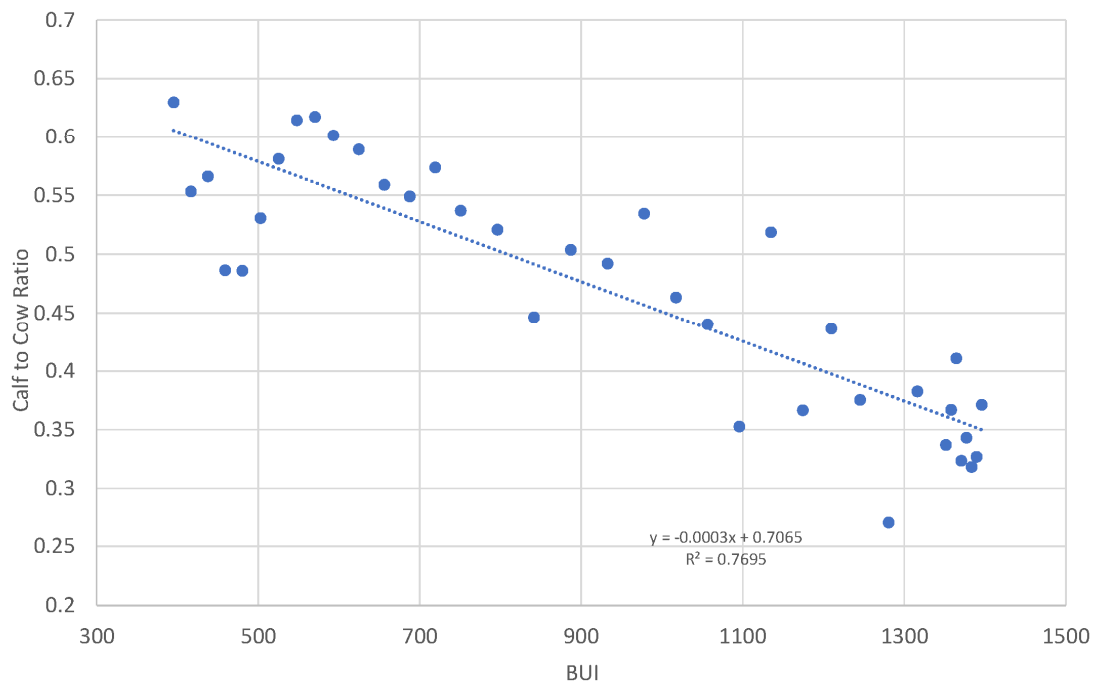


Figure 9: Scatterplot showing the correlation between calf to cow ratio and Built-up Intensity for 1981 to 2017. Note the increased variability of the calf to cow ratio at higher BUI values, which corresponds to more recent years. Data: Colorado Parks and Wildlife; Leyk and Uhl 2018.

The negative effect of the total elk population on following year growth rate in Models A and B is consistent with the finding by Taper and Gogan (2002) that Yellowstone elk growth rate was negatively affected by increased population density. Figure 10 suggests that the correlation is relatively weak at lower population levels, but that the mean growth rate is depressed when population approaches 20,000. In the case of this variable, it may be that the negative effect is negligible until a threshold value is reached.

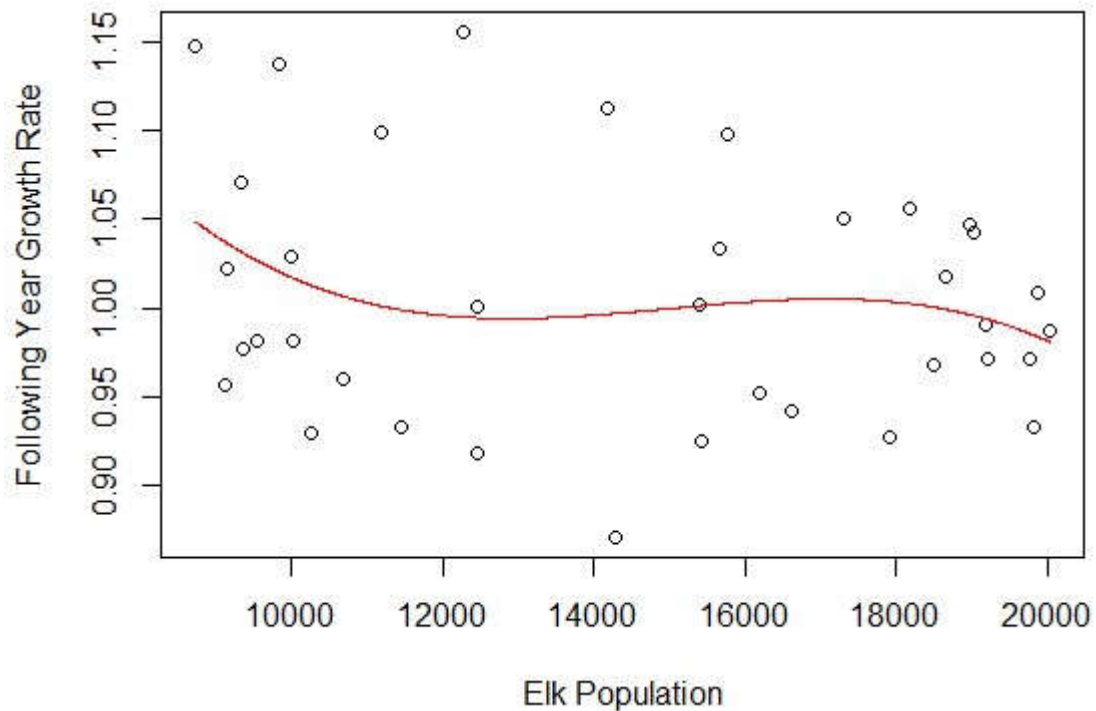


Figure 10: Scatterplot showing the third order polynomial model of the effect of total elk population on the following year growth rate. Elk Data: Colorado Parks and Wildlife.

To understand the variation in the relationship between the elk population and following year growth rate, I again performed breakpoint analysis using the “segmented” R package (Muggeo 2008); none of the generated breakpoints operated consistently throughout the study period. Reviewing the suggested breakpoints did, however, reveal that the relationship had a strong temporal element, and that applying different coefficients for different time periods provided a better explanation of the variation in correlation. High degrees of correlation exist between elk population and following year growth rate when considered separately for the periods 1993 to 2008 (mean following year growth rate 1.014) and 2009 to 2017 (0.9800) (see Appendix 5, Figure 7 and Appendix 5, Figure 8). The latter period’s negative correlation is 50% stronger, suggesting that the limiting effect of population may have increased over time.

Increased Influence of Hunting Variables: Modeling 2001 to 2017

To better understand more recent trends in elk population, I applied both Model A and Model B as devised for 1981-2017 to observations from 2001 to 2017 only. While the multiple R-squared score of 0.84 and the adjusted R-squared score of 0.8074 suggest even better fit of Model A for this time period, the predictive R-squared value of -0.1805 implies some weaknesses in the model; the simpler Model B produced similar results. While a good compromise fit for the entire period, changes over time in the relationship between predictor variables (including the threshold effects discussed above) may reduce the overall model’s usefulness when analyzing shorter and, particularly, more recent time frames. Given my findings regarding the changes over time in the behavior of calf per cow ratio and elk population, I used the broader array of

predictor variables available for more recent years to construct a new model, again using the stepAIC function in R and exploratory linear regression.

Eliminating years prior to 1990 allowed adding direct resistance and fragmentation measures to the model, while eliminating years prior to 1996 allowed adding hunting licenses. Finally, eliminating years prior to 2001 allowed the use of phenology data from the United States Geological Survey's Remote Sensing Phenology (RSP) collection. In this case, the use of the stepAIC function was not useful, as the models it rated highest based on AIC were inconsistent with any reasonable ecological interpretation (e.g., increased resistance led to increased following year growth rate). Exploratory linear regression yielded a model with strong R-squared and p values that resulted from applying linear regression to the preceding year elk population, the proportion of cows (vs. bulls and calves) in the total harvest in the preceding year, the mean resistance in the preceding year, the Core Area Index for summer concentration areas in the preceding year, and the number of hunting licenses issued in the preceding year (Model C). This model resulted in a multiple R-squared value of 0.871, an adjusted R-squared value of 0.8124 and a predictive R-squared value of 0.6952579 (see Appendix 5, Table 3). Appendix 5, Figure 9 and Appendix 5, Figure 10 confirm that the model fit is good, although with a wide range of residuals at lower predicted values of following year growth rate.

Discussion

Examination of elk population trends in the study area from 1980 to 2018 shows substantial variation that is not fully explained by the expected predictor variables of elk population structure or hunting pressure (see Monello et al. 2014; Raithel et al. 2007; Hebblewhite 2000). Rather, as hypothesized, variables relating to human influence on the landscape and to elk population structure explain a substantial portion of the variability in elk population growth in the Eagle and Roaring Fork valleys, either directly or through their apparent effect on the behavior of other variables, particularly calf to cow ratio. Models A, B, and C all incorporated one or more variables measuring some aspect of human influence on the landscape: habitat fragmentation, resistance, or Built-up Intensity. Given the substantial number of available predictor variables, the parsimony and goodness of fit of Model B—which considered only elk population and Built-up Intensity—was surprising.

Analysis over the period 1990 to 2015 further demonstrates that four measures of human influence—total population, resistance, habitat fragmentation, and Built-up Intensity—are also highly correlated with one another. This correlation permitted modeling the effect of human influence on elk population growth as far back as 1981, whereas reliance on other measures would have limited the analysis to periods after 1990, missing important trends during a period of rapid elk and human population growth.

The degree of variability over time of various habitat fragmentation metrics differed when applied to different seasonal habitat classes (Appendix 4). All seasonal habitat classes showed increased fragmentation during the study period, but summer concentration areas and

migration corridors displayed the largest changes overall. While the negative effect of winter disturbance of elk population has been stressed historically (see, e.g., Kittams 1953), there is increasing concern over the effect of summer disturbance (Canfield et al. 1999). This study suggests this concern is warranted, as the changes in summer concentration areas and migration corridors evidenced higher correlation with variation in growth rate than did other seasonal habitats. These metrics were not available prior to 1990, so it is possible that severe winter, winter concentration, and production areas had been disproportionately fragmented in earlier periods, limiting the potential for their further fragmentation.

As mentioned above, breakpoint analysis showed a segmentation in the relationship between calf to cow ratio and following year growth rate, with calf to cow ratios below 0.48 showing a substantially lower growth rate. This breakpoint is largely temporal, with most ratio values above it occurring prior to 2001 and most values below it occurring thereafter. This result, when combined with the high degree of correlation ($R^2 = 0.7695$) between calf per cow ratio and Built-up Intensity, strongly suggests that human influence on the landscape may have a depressing effect on elk population growth. With the exception of proportion of cows in harvests, harvest data was not strongly correlated with population growth rate. For years after 2000, however, the number of hunting licenses issued did show correlation, suggesting that mere human presence during hunting season may play a larger role than the number of elk killed in at least some circumstances.

Phenology and precipitation are also widely considered to be predictive of elk population growth (Lubow and Smith 2004; Hebblewhite 2000). However, none of the evaluated models that included one or more phenology variables produced a p value of 0.05 or better for those variables, and the explanatory value of variables relating to precipitation was also weak. Data regarding overall precipitation, snowfall, and phenology, were not prerequisites for modeling population growth rate during the study period; it is possible that these variables take on importance only at (i) levels of elk population not reached during the study period or (ii) in the case of phenological variables, for elk population levels not reached during the period of data availability.

The changes over time in the relationships between expected predictor variables such as calf to cow ratio and elk population and the dependent variable of population growth rate point toward possible changes in the stability and resilience of elk populations in the Roaring Fork and Eagle valleys. Holling (1973) formalized the understanding of resilience and stability as distinct, but related, concepts. He proposed that “resilience determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes . . . and still persist” rather than move toward extinction, while stability describes “the ability of a system to return to an equilibrium state after a temporary disturbance” (Holling 1973, p. 17). In the present case, the elk population seems unstable, as it has fluctuated substantially in response to changes in the ecosystem; whether it is resilient remains to be seen, but the changes in the behavior of predictor variables over the last two decades suggest otherwise. It instead seems likely that changes in the landscape have resulted in a change to the equilibrium

population of elk in the study area that may be sustainable, or that may be below the extinction threshold (Hanski and Ovaskainen 2002; Levins 1969).

Certainly, close monitoring of population trends is warranted by this possibility. While this study found changes in the behavior of calf per cow ratio and elk population occurring during the period 2000 to 2008 that seems correlated with human influence on the landscape, it is not clear whether the relevant threshold for this effect was crossed at that time or earlier.

Elaborating on the concept of extinction thresholds, Tilman et al. (1994) coined the term “extinction debt” to refer to the cumulative effect of habitat destruction that sets a species on an inexorable path to extinction over the course of multiple generations. In the case of the elk of the Roaring Fork and Eagle valleys, it is not clear if such an extinction threshold has been crossed, but the cumulative debt of connectivity loss and habitat fragmentation seems to have reached a level that has increased the limiting effect of other factors on elk populations.

The increased predictive value after 2000 of variables related to hunting pressure suggests that the elk population in the region may no longer support levels of hunting that were previously thought to be sustainable; as noted above, the fact that number of hunting licenses issued each year seems to have an effect independent of harvest level implies a negative effect on growth rate relating to human presence outside of developed areas. This effect begs the question of whether other forms of recreational activity have a similar negative effect on growth rate. Unfortunately, the majority of elk habitat in the study area is located on National Forest land for which no systematic data on recreational use is collected. The lack of information on the construction date of trails may also understate the degree of change in habitat fragmentation and loss of connectivity from 1980 to 2018. Recreational use of these lands on a year-round basis is anecdotally reported to have increased in recent years, but in the absence of data it is unclear to what extent this growth is correlated with other measures of human influence—and thus at least partially accounted for in the models above—or if it has an independent trend not accounted for by these models.

Conclusion

Understanding the effects on elk population of increasing human influence on the landscape over time presents practical and methodological challenges. Perhaps the largest practical challenge is finding temporally accurate data on the construction of human infrastructure that has been collected in a consistent fashion over the relevant time period and with sufficient frequency to require minimal interpolation. The Built-up Intensity index covers a broad range of time with a shorter sampling frequency than other data sources; this study demonstrates its strong correlation with measures of habitat fragmentation and connectivity, and its potential as a valuable resource for time-based studies. From a methodological standpoint, this study shows that the relationship between human influence on the landscape and elk population growth rate in the study area cannot be adequately described through purely linear modeling. This study instead suggests that, when a threshold of accumulated landscape influence is reached, the relationship among various predictor variables and elk population growth rate changes.

Further study using other modeling techniques may allow for a better understanding of this relationship.

This study has shown that habitat fragmentation, loss of landscape connectivity, and related human impacts on the landscape have played a major role in the variation of elk population growth rate in the Roaring Fork and Eagle valleys from 1981 to 2017. To the degree that these human impacts are less directly predictive for the most recent periods, that may be because their accumulated effects are expressed in a new equilibrium state in which other variables play a larger role in explaining variation. In addition, the region's elk population may have lost resilience in the face of other variables, including long-studied ones like hunting pressure and others, like recreational pressure, that have not yet been accounted for. Future management of elk populations in the Roaring Fork and Eagle valleys by the Forest Service and the Colorado Department of Parks and Wildlife should be based on an understanding that previously valid assumptions about the anticipated population growth rate of elk herds in response to changes in hunting and other variables may no longer hold true.

References

- Bedrick, Edward J., and Chih-Ling Tsai. 1994. "Model Selection for Multivariate Regression in Small Samples." *Biometrics* 50, no. 1 (March 1994): 226.
<https://doi.org/10.2307/2533213>.
- Belote, R. Travis, Matthew S. Dietz, Brad H. McRae, David M. Theobald, Meredith L. McClure, G. Hugh Irwin, Peter S. McKinley, Josh A. Gage, and Gregory H. Aplet. 2016. "Identifying Corridors among Large Protected Areas in the United States." *PLOS ONE* 11 (4): e0154223.
- Benítez-López, A., R. Alkemade, and P. A. Verweij. 2010. The Impacts of Roads and Other Infrastructure on Mammal and Bird Populations: A Meta-Analysis. *Biological Conservation* 143 (6): 1307–1316.
- Bennett, A. F., & Saunders, D. A. 2010. Habitat fragmentation and landscape change. In *Conservation Biology for All* (pp. 1544–1550). Oxford University Press. Retrieved from http://www.smithfellows.org/images/content_publications/Chapter5.pdf.
- Bennett, V. J., W. P. Smith, and M. G. Betts. 2011. Toward Understanding the Ecological Impact of Transportation Corridors. Gen. Tech. Rep. PNW-GTR-846. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland, OR. 40 pp.
- Beyer, H. L., R. Ung, D. L. Murray, and M. Fortin. 2013. Functional Responses, Seasonal Variation and Thresholds in Behavioural Responses of Moose to Road Density. *Journal of Applied Ecology* 50 (2): 286–294.

- Bishop-Taylor, Robbi, Mirela G. Tulbure, and Mark Broich. "Evaluating Static and Dynamic Landscape Connectivity Modelling Using a 25-Year Remote Sensing Time Series." *Landscape Ecology* 33, no. 4 (April 2018): 625–40. <https://doi.org/10.1007/s10980-018-0624-1>.
- Bissonette, J. A. and P. C. Cramer. 2008. Evaluation of the use and effectiveness of wildlife crossings. NCHRP Report 615. National Cooperative Highway Research Program, Transportation Research Board, National Academies, Washington, DC.
- Boyd, Pam. "Where Has All the Wildlife Gone: CPW Officials Cite 50 Percent Drop in Eagle Valley's Elk Population." *Vail Daily*, June 16, 2018. <https://www.vaildaily.com/news/where-has-all-the-wildlife-gone-cpw-officials-cite-50-percent-drop-in-eagle-valleys-elk-population/>.
- Colorado Division of Wildlife. 2006. Colorado Wildlife Action Plan. Colorado Division of Wildlife, Denver, Colorado.
- Colorado Department of Parks and Wildlife. 2018. "Species Activity Mapping: Elk." Data files downloaded from <http://www.arcgis.com/home/item.html?id=804abf2794b346828eeff285bffe9259>, December 1, 2018.
- Colorado State University, Colorado Climate Center. 1981-2018. Precipitation data downloaded from https://climate.colostate.edu/data_access.html, February 12, 2019.
- Fernandez, Corina, James Spayd, and Robert P. Brooks. "Landscape Indicators and Ecological Condition for Mapped Wetlands in Pennsylvania, USA." *Wetlands*, November 28, 2018. <https://doi.org/10.1007/s13157-018-1116-4>.
- Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17 (2): 420-432.
- Haddad, Nick M., Lars A. Brudvig, Jean Clobert, Kendi F. Davies, Andrew Gonzalez, Robert D. Holt, Thomas E. Lovejoy, et al. "Habitat Fragmentation and Its Lasting Impact on Earth's Ecosystems." *Science Advances* 1, no. 2 (March 2015): e1500052. <https://doi.org/10.1126/sciadv.1500052>.
- Hanski, Ilkka and Otso Ovaskainen. 2002. "Extinction Debt at Extinction Threshold." *Conservation Biology* 16, no. 3 (June 2002): 666–73.
- Harrell, Frank Jr, with contributions from Charles Dupont and many others. 2019. Hmisc: Harrell Miscellaneous. R package version 4.2-0. <https://CRAN.R-project.org/package=Hmisc>

- Hebblewhite, Mark. "Wolf and Elk Predator-Prey Dynamics in Banff National Park." Master's Thesis, University of Montana, 2000.
- Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Conservation Biology* 142 (1): 14-32.
- Holling, C. S. 1973. "Resilience and stability of ecological systems." *Annual Review of Ecological Systems* 4:1–23.
- Jaeger, J. A. G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. T. von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. *Ecological Modeling* 185 (2-4): 329-348.
- Jaeger, Jochen A. G., Hans-Georg Schwarz-von Raumer, Heide Esswein, Manfred Müller, and Manfred Schmidt-Lüttmann. "Time Series of Landscape Fragmentation Caused by Transportation Infrastructure and Urban Development: A Case Study from Baden-Württemberg, Germany." *Ecology and Society* 12, no. 1 (2007). <https://doi.org/10.5751/ES-01983-120122>.
- Jones, N. F., L. Pejchar, and J. M. Kiesecker. 2015. The Energy Footprint: How Oil, Natural Gas, and Wind Energy Affect Land for Biodiversity and the Flow of Ecosystem Services. *BioScience* 65 (3): 290-301.
- Kittams, Walter H. "Reproduction of Yellowstone Elk." *The Journal of Wildlife Management* 17, no. 2 (April 1953): 177. <https://doi.org/10.2307/3796713>.
- Krosby, Meade, Ian Breckheimer, D. John Pierce, Peter H. Singleton, Sonia A. Hall, Karl C. Halupka, William L. Gaines, et al. 2015. "Focal Species and Landscape 'naturalness' Corridor Models Offer Complementary Approaches for Connectivity Conservation Planning." *Landscape Ecology* 30 (10): 2121–32.
- Leyk, Stefan, and Johannes H. Uhl. "HISDAC-US, Historical Settlement Data Compilation for the Conterminous United States over 200 Years." *Scientific Data* 5 (September 4, 2018): 180175. <https://doi.org/10.1038/sdata.2018.175>. Data downloaded: "Historical built-up intensity layer series for the U.S. 1810 – 2015, contained in the dataverse "HISDAC-US: Historical Settlement Data Compilation for the United States" <https://dataverse.harvard.edu/dataverse/hisdacus>).
- Levins, R. 1969. "Some demographic and genetic consequences of environmental heterogeneity for biological control." *Bulletin of the Entomological Society of America* 15:237–240.

Lubow, Bruce C., and Bruce L. Smith. "Population Dynamics of the Jackson Elk Herd." Edited by McCorquodale. *Journal of Wildlife Management* 68, no. 4 (October 2004): 810–29. [https://doi.org/10.2193/0022-541X\(2004\)068\[0810:PDOTJE\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[0810:PDOTJE]2.0.CO;2).

McGarigal, Kevin. 2015. "FRAGSTATS Help." https://www.umass.edu/landeco/research/fragstats/documents/fragstats_documents.html.

McGarigal, K., SA Cushman, and E Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>

McClure, Meredith L., Brett G. Dickson, and Kerry L. Nicholson. 2017. "Modeling Connectivity to Identify Current and Future Anthropogenic Barriers to Movement of Large Carnivores: A Case Study in the American Southwest." *Ecology and Evolution* 7 (11): 3762–72. <https://doi.org/10.1002/ece3.2939>.

McRae, Brad H., Brett G. Dickson, Timothy H. Keitt, and Viral B. Shah. 2008. "Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation." *Ecology* 89 (10): 2712–24.

McRae, Brad, Ken Popper, Aaron Jones, Michael Schindel, Steve Buttrick, Kimberly Hall, Bob Unnasch, and Jim Platt. 2016. "Conserving Nature's Stage: Pacific Mapping Omnidirectional Connectivity for Resilient Terrestrial Landscapes in the Pacific Northwest." Pacific Northwest and Northern California Final Report to the Doris Duke Charitable Foundation. The Nature Conservancy. https://www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/oregon/science/Documents/McRae_et_al_2016_PNW_CNS_Connectivity.pdf.

Manel, Stéphanie, Michael K. Schwartz, Gordon Luikart, and Pierre Taberlet. "Landscape Genetics: Combining Landscape Ecology and Population Genetics." *Trends in Ecology & Evolution* 18, no. 4 (April 2003): 189–97. [https://doi.org/10.1016/S0169-5347\(03\)00008-9](https://doi.org/10.1016/S0169-5347(03)00008-9).

Millhouser, Paul and Paige Singer, "Report on Habitat Fragmentation in Boulder County, Colorado." Rocky Mountain Wild, 2018.

Minitab Blog. 2013. "Multiple Regression Analysis: Use Adjusted R-Squared and Predicted Squared to Include the Correct Number of Variables." Accessed May 24, 2019. <https://blog.minitab.com/blog/adventures-in-statistics-2/multiple-regression-analysis-use-adjusted-r-squared-and-predicted-r-squared-to-include-the-correct-number-of-variables>.

- Monello, Ryan J., Jenny G. Powers, N. Thompson Hobbs, Terry R. Spraker, Mary Kay Watry, and Margaret A. Wild. "Survival and Population Growth of a Free-Ranging Elk Population with a Long History of Exposure to Chronic Wasting Disease." *The Journal of Wildlife Management* 78, no. 2 (2014): 214–23. <https://doi.org/10.1002/jwmg.665>.
- Mortensen, D. A., E. S. J. Rauschert, A. N. Nord, and B. P. Jones. 2009. Forest Roads Facilitate the Spread of Invasive Plants. *Invasive Plant Science and Management* 2 (3): 191-199.
- Muggeo, Vito M. R. 2008. segmented: an R Package to Fit Regression Models with Broken-Line Relationships. *R News*, 8/1, 20-25. URL <https://cran.r-project.org/doc/Rnews/>.
- Brad Petch, Colorado Parks and Wildlife. Personal communications, January-May 2019.
- Pratim Roy, Partha, Somnath Paul, Indrani Mitra, and Kunal Roy. 2009. "On Two Novel Parameters for Validation of Predictive QSAR Models." *Molecules* 14, no. 5 (April 29, 2009): 1660–1701. <https://doi.org/10.3390/molecules14051660>.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Raithel, Jarod D., Matthew J. Kauffman, and Daniel H. Pletscher. "Impact of Spatial and Temporal Variation in Calf Survival on the Growth of Elk Populations." *Journal of Wildlife Management* 71, no. 3 (May 2007): 795–803. <https://doi.org/10.2193/2005-608>.
- Riitters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. "A Factor Analysis of Landscape Pattern and Structure Metrics." *Landscape Ecology* 10 (1): 23–39. <https://doi.org/10.1007/BF00158551>.
- Rudnick D. A., P. Beier, S. Cushman, F. Dieffenbach, C. W. Epps, L. Gerber, J. Hartter, J. Jenness, J. Kintsch, A. M. Merenlender, R. M. Perkl, D. V. Preziosi, S. J. Ryan, and Trombulak, S. C. 2012. The Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities. *Issues in Ecology*. Report No. 16. Ecological Society of America. Washington, DC.
- Santini, Luca, Stuart H. M. Butchart, Carlo Rondinini, Ana Benítez-López, Jelle P. Hilbers, Aafke M. Schipper, Mirza Cengic, Joseph A. Tobias, and Mark A. J. Huijbregts. "Applying Habitat and Population-density Models to Land-cover Time Series to Inform IUCN Red List Assessments." *Conservation Biology*, February 25, 2019. <https://doi.org/10.1111/cobi.13279>.
- Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. "Identifying and prioritizing ungulate migration routes for landscape-level conservation." *Ecological Applications* 19 (8): 2016-2025.

- Singer, Paige, and Paul Millhouser. "Assessment of Wildlife Connectivity on Federal Lands in Colorado: A Report to The Wilderness Society." Rocky Mountain Wild, 2018.
- Taper, Mark L., and Peter J. P. Gogan. "The Northern Yellowstone Elk: Density Dependence and Climatic Conditions." *The Journal of Wildlife Management* 66, no. 1 (January 2002): 106. <https://doi.org/10.2307/3802877>.
- Theobald, David M. 2013. "A General Model to Quantify Ecological Integrity for Landscape Assessments and US Application." *Landscape Ecology* 28 (10): 1859–74.
- Theobald, David M., Sarah E. Reed, Kenyon Fields, and Michael Soulé. "Connecting Natural Landscapes Using a Landscape Permeability Model to Prioritize Conservation Activities in the United States: Connecting Natural Landscapes." *Conservation Letters* 5, no. 2 (April 2012): 123–33. <https://doi.org/10.1111/j.1755-263X.2011.00218.x>.
- Tilman, D., May, R. M., Lehman, C., & Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature*, 371(6492), 65-66. <https://doi.org/10.1038/371065a0>.
- Trombulak, S. C., and C. A. Frissell. 2000. "Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities." *Conservation Biology* 14 (1): 18–30.
- U.S. Environmental Protection Agency (USEPA) and the U.S. Geological Survey (USGS). 2012. National Hydrography Dataset Plus – NHDPlus. <https://www.usgs.gov/core-science-systems/ngp/national-hydrography/nhdplus-high-resolution>.
- U.S. Geological Survey (USGS), Earth Resources Observation and Science Center. 2001-17. C6 Western CONUS 250 m eMODIS RSP data. <https://doi.org/10.5066/F7PC30G1>.
- U.S. Geological Survey (USGS). 2017. 1/3rd arc-second Digital Elevation Models (DEMs). <https://www.sciencebase.gov/catalog/folder/4f70aa9fe4b058caae3f8de5>.
- U.S. Forest Service (USFS). 2018. FSTopo Transportation Line feature class. <https://data.fs.usda.gov/geodata/edw/datasets.php>
- Venables, W. N. & Ripley, B. D. 2002. *Modern Applied Statistics with S*. Fourth Edition. Springer, New York.
- Watson, James E. M., Robert J. Whittaker, and David Freudenberger. "Bird Community Responses to Habitat Fragmentation: How Consistent Are They across Landscapes?: Avifaunal Responses to Habitat Fragmentation." *Journal of Biogeography* 32, no. 8 (June 2, 2005): 1353–70. <https://doi.org/10.1111/j.1365-2699.2005.01256.x>.

White, Gary C., David J. Freddy, R. Bruce Gill, and John H. Ellenberger. "Effect of Adult Sex Ratio on Mule Deer and Elk Productivity in Colorado." *The Journal of Wildlife Management* 65, no. 3 (July 2001): 543. <https://doi.org/10.2307/3803107>.

Appendix 1

Elk Population and Hunting Data, 1981 to 2018

Year	Calves	Cows	Bulls	Elk Population	Licenses	Calves Harvested	Bulls Harvested	Cows Harvested	Total Harvest
1981	3,186	5,060	884	9,130	-	48	1,088	540	1,676
1982	2,895	5,233	608	8,736	-	73	1,093	546	1,712
1983	3,290	5,812	916	10,018	-	64	827	433	1,324
1984	2,919	6,002	910	9,832	-	108	978	625	1,711
1985	3,168	6,519	1,496	11,183	-	62	663	543	1,268
1986	3,723	7,014	1,549	12,285	-	61	760	290	1,111
1987	4,534	7,802	1,852	14,188	-	45	734	287	1,066
1988	5,180	8,431	2,169	15,780	-	86	1,015	709	1,810
1989	5,656	9,163	2,496	17,314	-	105	1,161	782	2,048
1990	5,933	9,870	2,382	18,185	-	108	1,621	874	2,603
1991	6,240	10,591	2,369	19,200	-	133	1,591	903	2,627
1992	6,000	10,734	1,917	18,651	-	146	1,819	1,186	3,151
1993	5,905	10,753	2,324	18,981	-	154	954	1,147	2,255
1994	6,390	11,139	2,336	19,865	-	92	1,258	823	2,173
1995	6,099	11,360	2,577	20,036	-	84	1,148	1,039	2,271
1996	6,058	11,630	2,087	19,775	4,468	148	1,688	901	2,737
1997	5,231	11,715	2,253	19,199	4,507	74	1,057	965	2,096
1998	5,574	11,066	2,388	19,029	4,362	159	973	1,440	2,572
1999	5,758	11,701	2,374	19,833	3,788	108	1,297	634	2,039
2000	5,683	10,628	2,186	18,497	4,452	115	1,168	1,693	2,976
2001	4,892	10,556	2,468	17,916	3,625	83	751	904	1,738
2002	4,318	9,809	2,480	16,607	4,189	240	1,291	1,771	3,302
2003	3,379	9,581	2,695	15,654	5,193	118	1,088	1,348	2,554
2004	4,667	8,998	2,516	16,182	5,333	132	1,110	1,308	2,550
2005	3,357	9,160	2,893	15,410	4,524	174	1,068	1,182	2,424
2006	3,885	8,905	2,647	15,437	3,959	114	1,131	1,022	2,267
2007	3,193	8,509	2,588	14,290	3,747	113	898	1,061	2,072
2008	2,142	7,930	2,383	12,455	3,881	95	915	1,099	2,109
2009	2,840	7,422	2,208	12,470	3,665	120	844	1,005	1,969
2010	2,340	6,947	2,166	11,453	4,330	116	852	1,115	2,083
2011	2,356	6,421	1,904	10,682	4,203	73	903	1,018	1,994
2012	2,448	5,959	1,852	10,259	4,428	160	755	1,010	1,925
2013	1,886	5,830	1,826	9,542	3,983	50	846	871	1,767
2014	1,943	5,659	1,759	9,361	3,352	91	603	616	1,310
2015	1,803	5,664	1,675	9,141	3,213	56	716	581	1,353
2016	1,896	5,800	1,645	9,341	3,402	52	620	422	1,094
2017	2,264	6,100	1,641	10,004	3,496	38	630	320	988
2018	2,599	6,255	1,435	10,289	3,713	32	697	316	1,045

Appendix 2

Fragmentation Metrics

Measures of Overall Habitat Loss and Structural Change

Total Class Area: While this metric does not strictly measure fragmentation, it does illustrate the habitat loss caused by roads and trails. Because of their surrounding zones of disturbance, roads and trails have a particular harsh effect on classes composed of small patches, many of which may be rendered uninhabitable.

Percent Landscape: This metric, which is simply the percentage of the total landscape comprised by each habitat class, highlights the structural changes in landscape composition caused by road/trail-based habitat loss. While all habitat classes will experience reduction as the road/trail disturbance zones reduce available habitat, the classes are differentially affected depending on the size and distribution of their patches.

Fragmentation Metrics

Many of these metrics are reported as means over the entire landscape or on a per habitat class basis, as these are the levels of analysis considered for this study. Large patches have a disproportionate effect on fragmentation at the landscape and habitat class level, so I evaluate the area-weighted mean, which gives more weight to larger patches, as well as the simple mean. Most metrics, other than those involving means, can be considered at the individual patch, class, or landscape level, as indicated with each description.

1. Patch Size and Shape Metrics

Mean Patch Area: This metric is simply the mean of the size of all patches, and can be measured for the entire landscape or by habitat class. Decreased patch size has a negative effect on both species richness and population and is thus useful despite its simplicity. In addition, it is used in the calculation of a number of other metrics (McGarigal 2015). (class and landscape)

Shape Index (area-weighted mean): This metric addresses the complexity and compactness of patch shape and uses the ratio of patch perimeter to area. Higher values indicate more complex, less compact shapes. Geometry dictates that, regardless of shape, this ratio is lower for patches of greater area. Shape Index normalizes that ratio against the ratio of a perfect square of equal area, so the metric is comparable across different patch sizes (McGarigal et al. 2012; see also Riitters et al. 1995). (class and landscape)

2. Core Habitat Metrics

Total Core Area/Core Area Percent of Landscape: For purpose of this measure, core habitat includes that portion of a habitat patch that is at least 100 meters from the patch edge, including edges with other habitat classes or with roads or trails. While this distance is somewhat arbitrary, using a single distance avoids attempting to make more nuanced, species-specific, and debatable distinctions between different habitat borders. Because fragmentation has the effect of introducing more edges into the landscape, core habitat is more severely reduced by roads and trails than overall habitat. (class and landscape)

Mean Core Area/Mean Core Area (area-weighted): These metrics are calculated for each habitat class. The first metric is simply the mean core area per patch (including patches too small to have any core area), while the second weights the mean based on patch area. Distinguishing core areas by habitat class allows a better understanding of which species may be affected by fragmentation (McGarigal et al. 2012). (class and landscape)

Core Area Index: This metric simply provides the percentage of each habitat class that is composed of core habitat, calculated on an area-weighted basis. (class)

3. Isolation Metric

Proximity Index/Proximity Index (area-weighted): This metric aims to measure the isolation of patches of a habitat class—that is, the extent to which it consists of scattered small patches versus patches of mixed sizes that tend to clump together. For each patch of a habitat class, this metric identifies all patches of the same habitat class with edges that are within a user-designated distance; the area of each such patch is then divided by the square of the distance to the target patch. Finally, these values are summed over the entire habitat class. This approach is intended to highlight the greater ecological contribution of neighboring patches that are large and nearby versus smaller and more distant patches (McGarigal et al. 2012). (class)

Appendix 3

Measures of Habitat Fragmentation and Landscape Connectivity

Variable	Measure	Interval	Time Period	Direct Measure	Spatial Resolution	Other Limitations
Habitat Fragmentation	FRAGSTATS analysis	~10 years	1990-2018	Yes	30 meters	Based primarily on TIGER road data
Connectivity	Resistance surface	~10 years	1990-2018	No	30 meters	Based primarily on TIGER road data
Fragmentation and Connectivity	U.S. Census Population	5 to 10 years	1980-2015	No	Census block group	Poor spatial resolution
Fragmentation and Connectivity	Built-up Intensity	5 years	1980-2015	No	250 meters	Untested measure

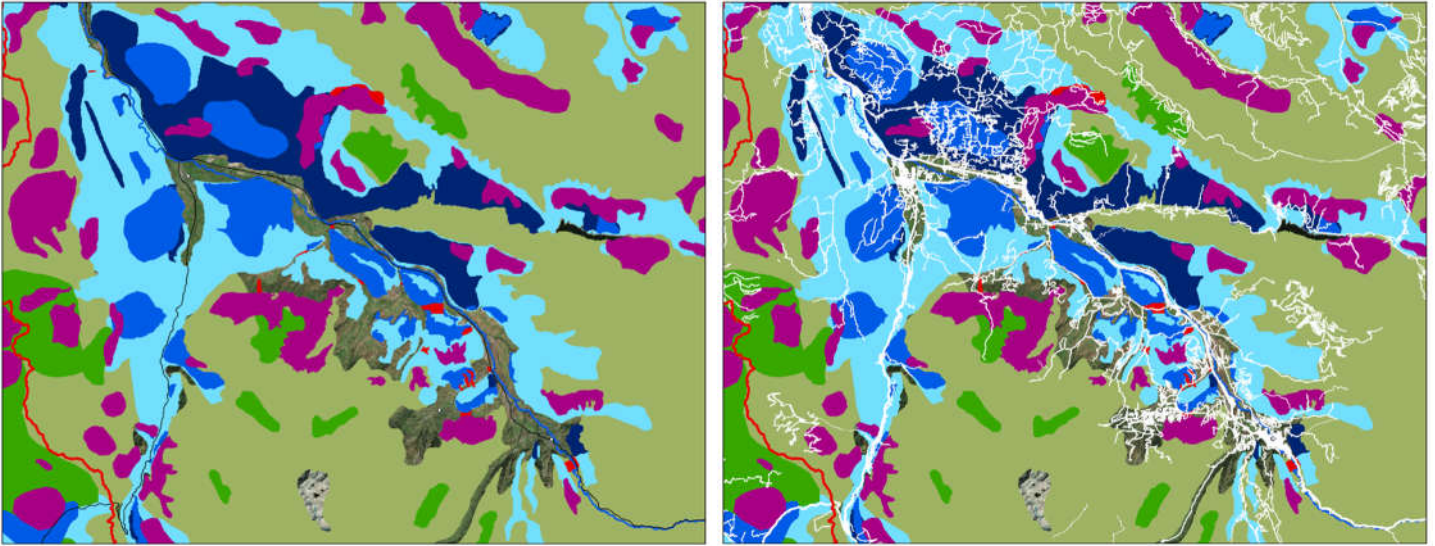
Appendix 4

Selected FRAGSTATS results, 1990 to 2018

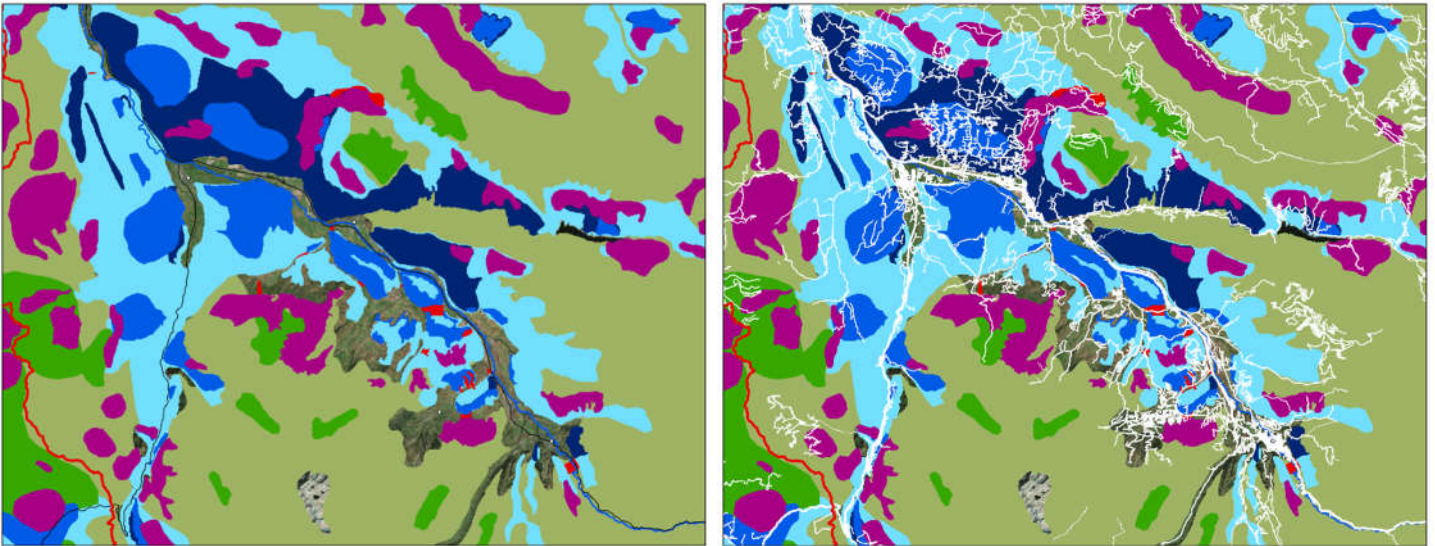
Year	Habitat Class	Total Class Area (hectares)	Percent Landscape	Landscape Index	Mean Patch Area (hectares)	Mean Shape Index	Shape Index-area weighted	Total Core Area (hectares)	Core Area Percent Landscape	Mean Core Area (hectares)	Mean Core Area-area weighted	Mean Core Area Index	Mean Core Area Index-area weighted	Mean Proximity Index	Mean Proximity Index-area weighted	Division	Mesh
1990	Summer Range	304,456.9500	54.1829	37.4773	154.2335	1.4149	3.2242	281,001.2400	50.0085	142.3512	7,511.5701	19.6261	92.2959	5,540.5919	34,685.3328	0.9924	4,259.2816
	Winter Range	79,614.4500	14.1686	41.8507	48.7834	1.4705	2.4157	66,623.3100	11.8567	40.8231	793.8009	22.4983	83.6824	498.0387	1,731.9943	0.9998	123.5211
	Summer Concentration	19,290.4200	3.4330	13.6469	58.9921	1.2667	2.2475	17,189.1000	3.0591	52.5661	793.5831	13.2802	89.1069	395.8659	1,727.3179	0.9999	30.0167
	Migration Corridor	1,288.3500	0.2293	11.9958	13.5616	1.4884	1.7456	839.7000	0.1494	8.8389	42.2069	29.3548	65.1764	50.7212	77.5298	1.0000	0.1302
	Severe Winter Range	21,418.3800	3.8117	25.2285	35.7569	1.4343	2.5905	17,402.6700	3.0971	29.0529	712.1100	19.6629	81.2511	301.4474	861.6425	0.9999	30.1454
	Winter Concentration	26,990.7900	5.3742	26.9905	45.7542	1.4352	2.1989	24,991.2000	4.4476	37.8655	374.3821	23.4733	82.7584	337.6222	791.3993	1.0000	22.8636
	Production Area	38,739.6900	6.8943	24.0769	70.0537	1.4343	2.0371	33,406.4700	5.9452	60.4095	619.2223	29.5312	86.2332	525.2816	1,058.9898	0.9999	46.8109
	MEAN	70,715.1471	12.5849	25.8952	61.0193	1.4206	2.3514	63,064.8129	11.2234	53.1296	1,549.5536	22.4895	82.9292	1,092.7956	5,847.7438	0.9988	644.6814
2000	Summer Range	305,853.2100	52.2976	38.4196	153.0031	1.4348	3.3383	281,826.3600	48.1893	140.9837	7,786.1311	19.0779	92.1443	4,943.5824	35,714.0880	0.9927	4,265.2585
	Winter Range	79,986.3300	13.6768	43.0095	45.9692	1.4801	2.4387	66,694.3200	11.4040	38.3301	798.6360	21.1696	83.3821	474.9201	1,834.9182	0.9998	120.0226
	Summer Concentration	19,228.9500	3.2879	13.1470	68.9210	1.2418	2.2482	17,175.8700	2.9369	61.5623	800.5185	15.3372	89.3230	405.2090	1,675.9634	1.0000	28.9954
	Migration Corridor	1,255.3200	0.2146	12.5865	10.3745	1.4600	1.6920	805.6800	0.1378	6.6585	42.6235	22.6470	64.1812	37.9638	81.5804	1.0000	0.1215
	Severe Winter Range	21,515.7600	3.6790	26.1595	32.2575	1.4206	2.9666	17,375.8500	2.9711	26.0507	1,029.1763	17.2359	80.7587	458.5560	727.9934	0.9999	42.1193
	Winter Concentration	30,068.4600	5.1414	28.9741	38.3526	1.4359	2.2647	24,586.5600	4.2040	31.3604	355.7797	20.5125	81.7686	299.2214	826.6163	1.0000	20.9072
	Production Area	38,691.5400	6.6158	24.4764	64.2717	1.4223	2.0442	33,301.7100	5.6942	55.3185	618.4116	27.0126	86.0697	493.5014	1,081.6251	0.9999	44.8590
	MEAN	70,942.7957	12.1304	26.6818	59.0214	1.4136	2.4275	63,109.4786	10.7910	51.4663	1,633.0395	20.4275	82.5182	1,016.1363	5,991.8264	0.9989	646.0405
2010	Summer Range	302,382.9900	51.7479	38.7559	157.0005	1.4782	3.2979	278,311.9500	47.6286	144.5026	7,645.0536	20.6839	92.0396	4,821.2004	34,196.7362	0.9929	4,142.7996
	Winter Range	78,057.4500	13.3583	42.8712	46.6293	1.4902	2.4433	64,953.6300	11.1158	38.8015	768.6569	21.8955	83.2126	423.5161	1,624.1054	0.9998	113.0827
	Summer Concentration	19,112.1300	3.2707	14.2169	33.2964	1.1612	2.3033	17,002.8000	2.9098	29.6216	794.7064	7.3094	88.9634	190.6172	1,673.3531	1.0000	28.7396
	Migration Corridor	1,211.7600	0.2074	12.7940	7.4341	1.3354	1.6994	775.4400	0.1327	4.7573	41.9080	16.1548	63.9929	24.0017	74.3254	1.0000	0.1157
	Severe Winter Range	20,993.1300	3.5926	26.1242	32.2971	1.4354	2.5935	16,915.7700	2.8949	26.0243	656.4152	17.9497	80.5776	352.7385	723.6791	1.0000	26.2228
	Winter Concentration	29,150.8200	4.9887	29.2054	37.9074	1.4520	2.2637	23,711.1300	4.0578	30.8337	345.6354	21.1954	81.3395	290.4765	682.8405	1.0000	19.7476
	Production Area	38,109.0600	6.5217	24.6759	61.2686	1.4325	1.9900	32,742.6300	5.6034	52.6409	585.4903	27.1478	85.9182	416.1360	1,021.7820	0.9999	41.8606
	MEAN	69,859.6200	11.9553	26.9491	53.6905	1.3978	2.3702	62,059.0500	10.6204	46.7403	1,548.2665	18.9052	82.2920	931.2409	5,713.8317	0.9989	624.6527
2018	Summer Range	302,337.8100	51.7372	38.7400	157.2220	1.4776	3.2979	278,275.2300	47.6195	144.7089	7,645.6910	20.6939	92.0412	4,835.5919	34,181.1026	0.9929	4,142.2758
	Winter Range	78,022.8000	13.3516	42.8202	46.6923	1.4897	2.4430	64,931.9400	11.1114	38.8581	768.9073	21.9114	83.2218	422.8574	1,623.7451	0.9998	113.0615
	Summer Concentration	19,110.9600	3.2703	14.2158	33.2944	1.1612	2.3033	17,001.8100	2.9094	29.6199	794.7385	7.3030	88.9637	190.5344	1,673.2783	1.0000	28.7373
	Migration Corridor	1,207.8900	0.2067	12.8190	7.4104	1.3377	1.7032	773.1000	0.1323	4.7429	41.9586	16.0632	64.0042	23.8868	74.2429	1.0000	0.1155
	Severe Winter Range	20,985.5700	3.5911	26.0911	32.4854	1.4380	2.5928	16,912.2600	2.8941	26.1800	656.5744	18.0603	80.5899	352.4299	723.5415	1.0000	26.2172
	Winter Concentration	29,138.1300	4.9862	29.2276	37.6949	1.4503	2.2631	23,700.6000	4.0557	30.6605	345.5365	21.0554	81.3388	289.2793	682.3555	1.0000	19.7325
	Production Area	38,102.2200	6.5202	24.6820	61.1593	1.4320	1.9899	32,734.8900	5.6017	52.5440	585.5415	27.1477	85.9133	415.7668	1,021.8097	0.9999	41.8540
	MEAN	69,843.6257	11.9519	26.9422	53.7084	1.3981	2.3705	62,047.1186	10.6177	46.7592	1,548.4211	18.8907	82.2961	932.9066	5,711.4394	0.9989	624.5705
Percent Change 1990 to 2018																	
	Summer Range	-0.70%	-4.51%	3.37%	1.94%	4.43%	2.29%	-0.97%	-4.78%	1.66%	1.79%	5.44%	-0.28%	-12.72%	-1.45%	0.05%	-2.75%
	Winter Range	-2.00%	-5.77%	2.32%	-4.29%	1.31%	1.13%	-2.54%	-6.29%	-4.81%	-3.14%	-2.61%	-0.55%	-15.10%	-6.25%	0.00%	-8.47%
	Summer Concentration	-0.93%	-4.74%	4.17%	-43.56%	-8.33%	2.48%	-1.09%	-4.89%	-43.65%	0.15%	-45.01%	-0.16%	-51.87%	-3.13%	0.01%	-4.26%
	Migration Corridor	-6.25%	-9.86%	6.86%	-45.36%	-10.12%	-2.43%	-7.93%	-11.45%	-46.34%	-0.59%	-45.28%	-1.80%	-52.91%	-4.24%	0.00%	-11.29%
	Severe Winter Range	-2.02%	-5.79%	3.42%	-9.15%	0.26%	0.09%	-2.82%	-6.55%	-9.89%	-7.80%	-8.15%	-0.81%	16.91%	-16.03%	0.01%	-13.03%
	Winter Concentration	-3.51%	-7.22%	8.29%	-17.61%	1.05%	2.92%	-5.16%	-8.81%	-19.03%	-7.70%	-10.30%	-1.72%	-14.32%	-13.78%	0.00%	-13.69%
	Production Area	-1.65%	-5.43%	2.51%	-12.70%	-0.16%	-2.32%	-2.01%	-5.78%	-13.02%	-5.44%	-8.07%	-0.37%	-20.85%	-3.51%	0.00%	-10.59%

Appendix 5

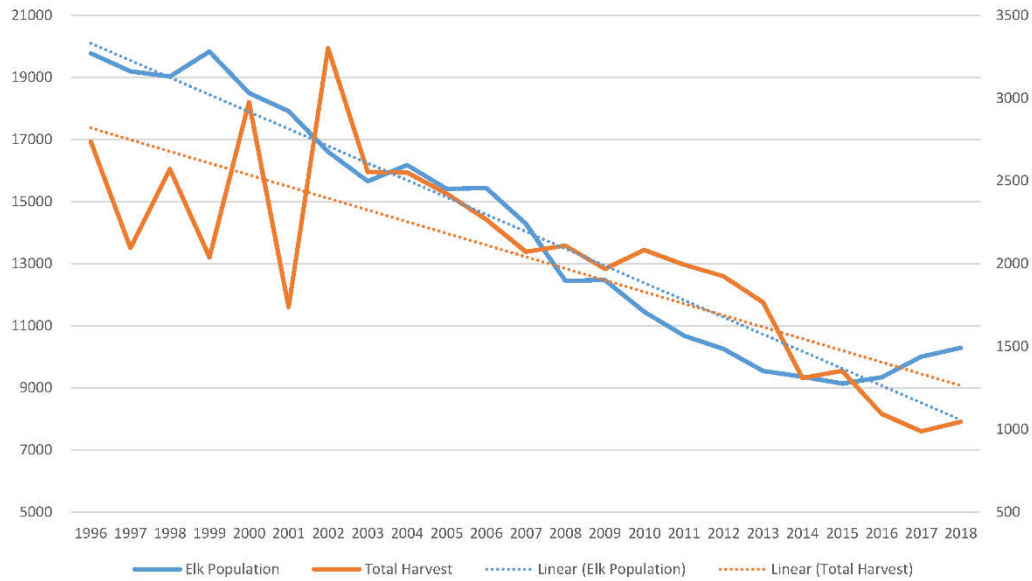
Additional Figures and Tables



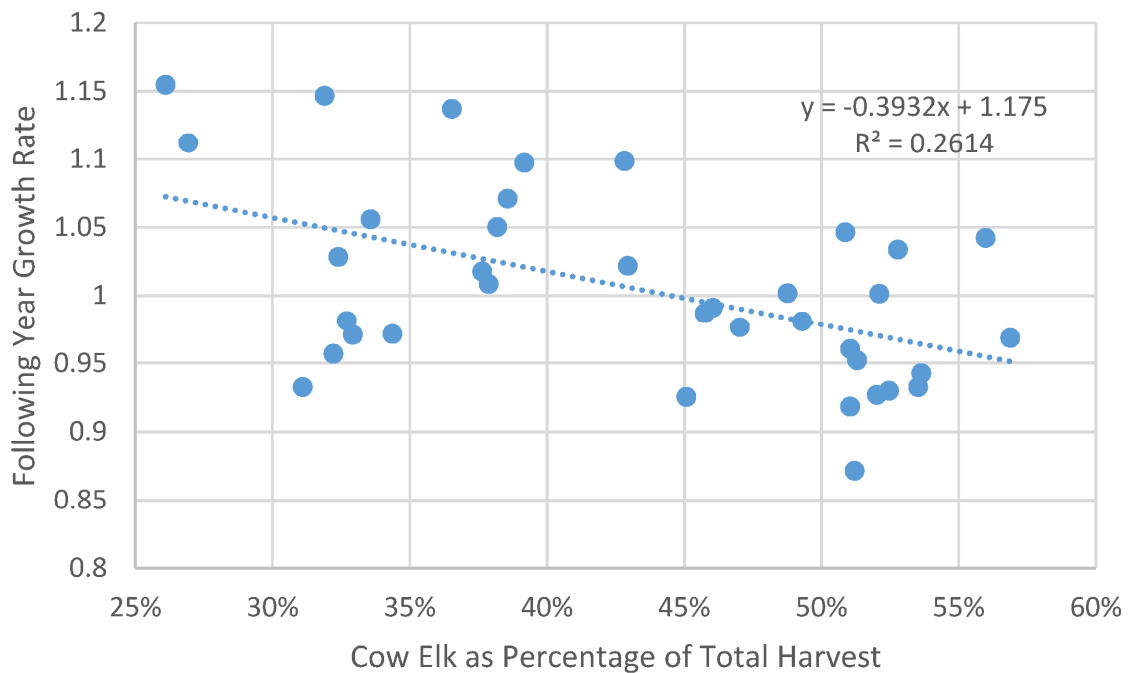
Appendix 5, Figure 1: Left: Elk seasonal habitat areas in the Roaring Fork Valley. Right: Fragmenting roads and trails as of 2018 are depicted in white. Elk Data: Colorado Parks and Wildlife.



Appendix 5, Figure 2: Left: Elk seasonal habitat areas in the Eagle Valley. Right: Fragmenting roads and trails as of 2018 are depicted in white. Elk Data: Colorado Parks and Wildlife.



Appendix 5, Figure 3: Trends in elk population and total harvest for the period 1996 to 2018. While correlation is apparent, the causal relationship is less clear. Data: Colorado Parks and Wildlife.



Appendix 5, Figure 4: Chart showing the correlation of proportion of the harvest comprised of cow elk with the following year growth rate for 1981 through 2017. Data: Colorado Parks and Wildlife.

**Following Year Growth Rate ~ poly(ElkPop, 3) + poly(BUI, 3) + Calf per Cow + Cow Harvest
Proportion + Precipitation**

Residuals:

Min	1Q	Median	3Q	Max
-0.068243	-0.025881	0.004741	0.025926	0.063760

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	1.276936	0.138301	9.233	7.64E-10	***
poly(Elk Pop 1)	-0.671383	0.258130	-2.601	0.014901	*
poly(Elk Pop 2)	-0.076085	0.048013	-1.585	0.124682	
poly(Elk Pop 3)	-0.095656	0.043873	-2.180	0.038124	*
poly(BUI 1)	-0.584709	0.102428	-5.708	4.58E-06	***
poly(BUI 2)	-0.522123	0.227218	-2.298	0.029544	*
poly(BUI 3)	0.288485	0.066710	4.324	0.000187	***
Calf per Cow	-0.396354	0.226833	-1.747	0.091946	.
Cow Harvest Prop	-0.279545	0.231219	-1.209	0.237142	
Precipitation	-0.002316	0.002144	-1.081	0.289454	

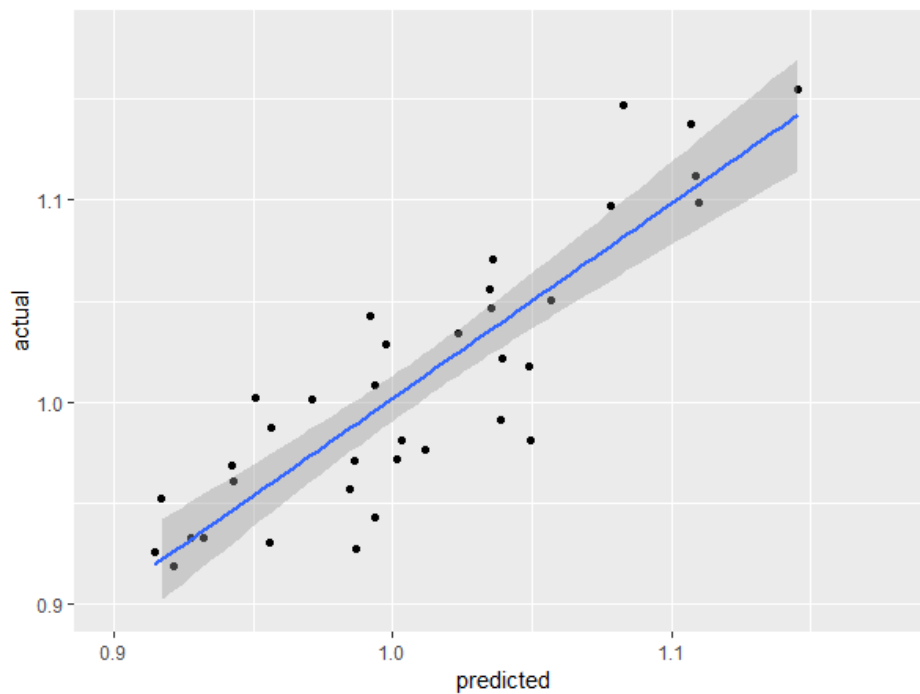
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.03823 on 27 degrees of freedom

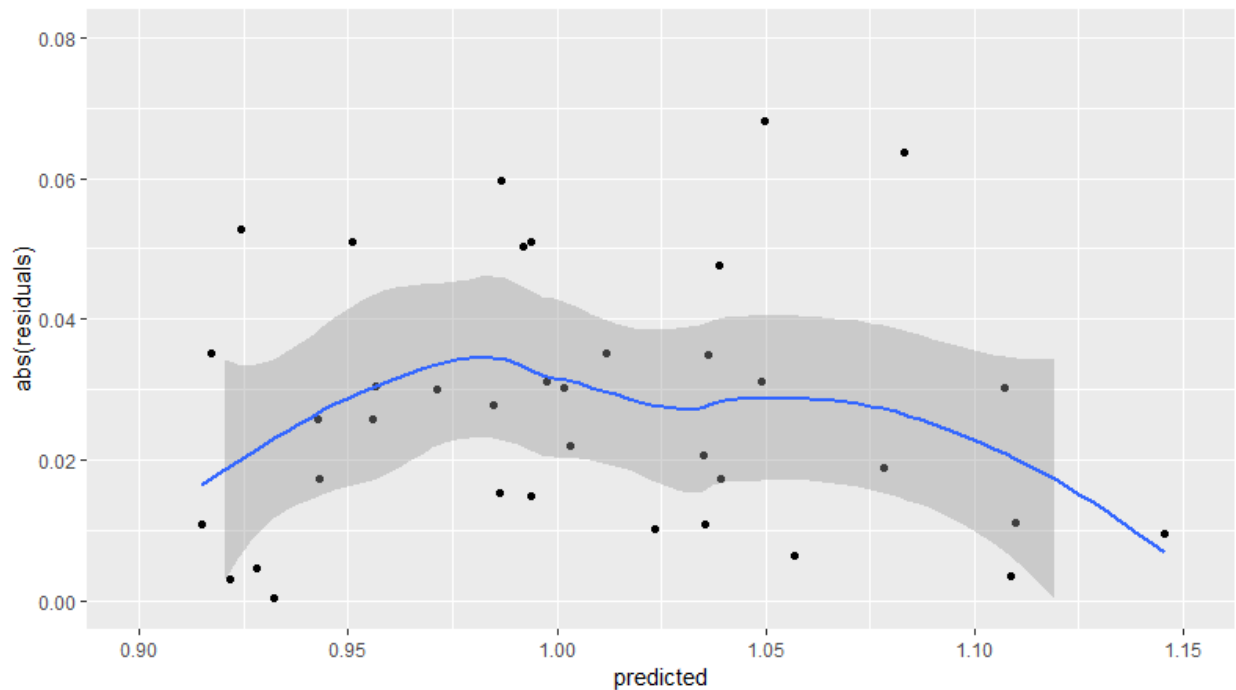
Multiple R-squared: 0.7727 Adjusted R-squared: 0.697 Predictive R-squared: 0.5510011

F-statistic: 10.2 on 9 and 27 DF, p-value: 1.186e-06

Appendix 5, Table 1: Table showing results of the linear regression of Model A, the best fit model for 1981 - 2017. Elk Data: Colorado Parks and Wildlife.



Appendix 5, Figure 5: Actual and predicted next year growth rates using Model A for 1981-2017 show relatively high goodness of fit. The gray band represents the 95% confidence interval. Elk Data: Colorado Parks and Wildlife.



Appendix 5, Figure 6: Absolute value of residuals by predicted next year growth rates using Model A for 1981-2017 show a slight increase in variability for central values of the predicted next year growth rate. The gray band represents the 95% confidence interval.

Following Year Growth Rate ~ poly(Elk Pop, 3) + poly(BUI, 3)

Residuals:

Min	1Q	Median	3Q	Max
-0.08006	-0.02598	-0.00350	0.02409	0.07762

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	1.00553	0.006542	153.693	2.00E-16	***
poly(Elk Pop 1)	-0.965148	0.19807	-4.873	3.34E-05	***
poly(Elk Pop 2)	-0.101419	0.044148	-2.297	0.028757	*
poly(Elk Pop 3)	-0.078271	0.041545	-1.884	0.06929	.
poly(BUI 1)	-0.487703	0.065311	-7.467	2.53E-08	***
poly(BUI 2)	-0.749764	0.186469	-4.021	0.000361	***
poly(BUI 3)	0.355254	0.062217	5.71	3.14E-06	***

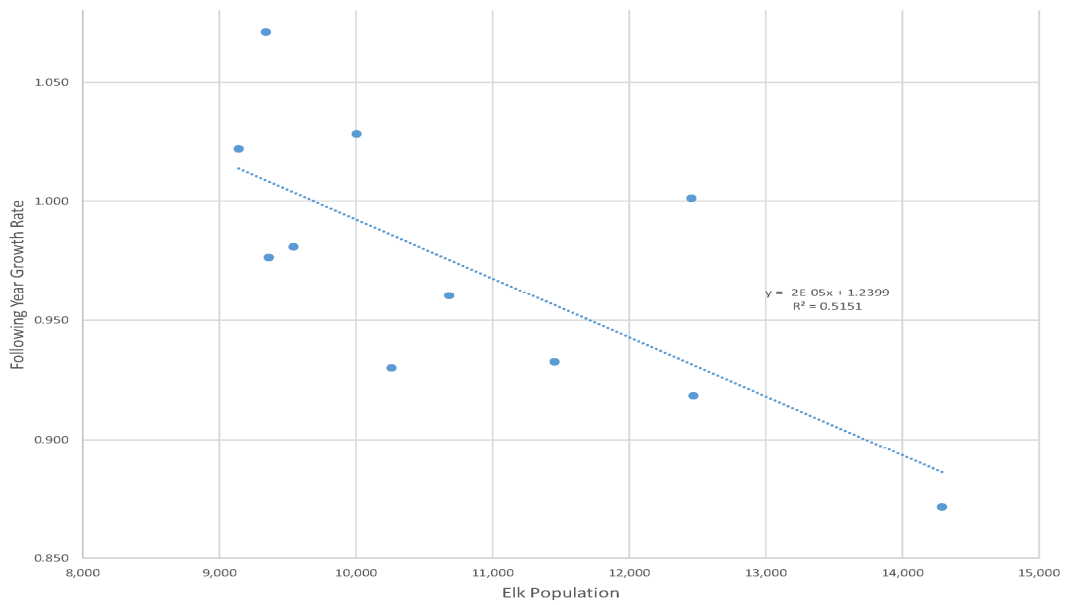
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.0398 on 30 degrees of freedom

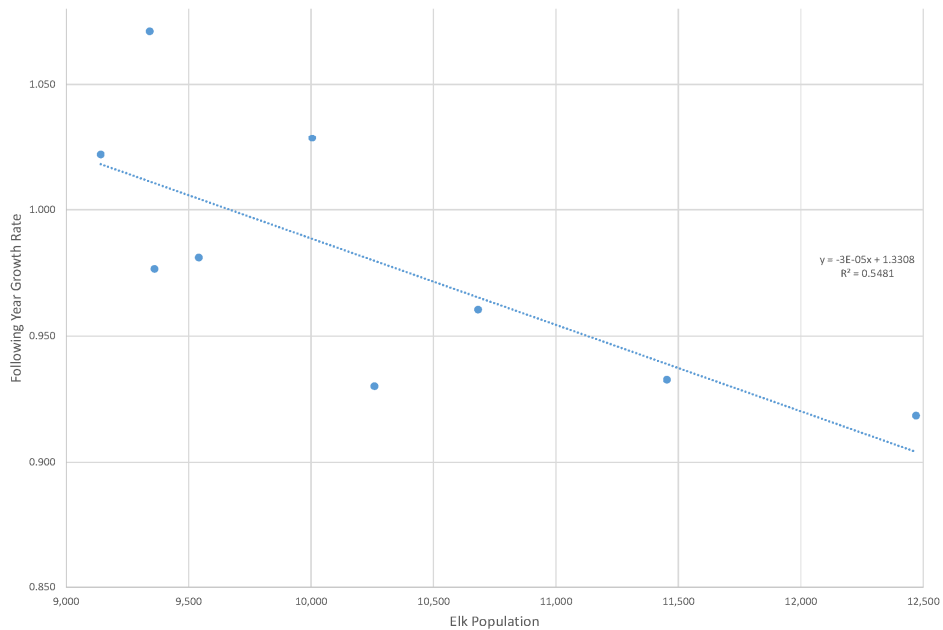
Multiple R-squared: 0.7264, Adjusted R-squared: 0.6716 Predictive R-squared: 0.5533755

F-statistic: 13.27 on 6 and 30 DF, p-value: 2.716e-07

Appendix 5, Table 2: Table showing results of the linear regression of Model B, the final model for 1981-2017.



Appendix 5, Figure 7: Scatterplot showing correlation between elk population and following year growth rate for 1993 to 2008. Elk Data: Colorado Parks and Wildlife.



Appendix 5, Figure 8: Scatterplot showing correlation between elk population and following year growth rate for 2009 to 2017. Elk Data: Colorado Parks and Wildlife.

**Following Year Growth Rate ~ Elk Pop + Cow Kill Proportion + Resistance + Core Area Index
Summer Conc + Licenses**

Residuals:

Min	1Q	Median	3Q	Max
-0.034280	-0.009275	-0.002074	0.009536	0.033757

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	1133.000000	295.600000	3.832000	0.002785	**
Elk Pop	-0.000100	0.000019	-5.302000	0.000252	***
Cow Kill Proportion	-2.016000	0.409800	-4.920000	0.000457	***
Resistance	-224.100000	58.560000	-3.828000	0.002805	**
Core Area Index	-3.182000	0.839800	-3.789000	0.003001	**
Summer Conc					
Licenses	0.000031	0.000012	2.660000	0.022198	*

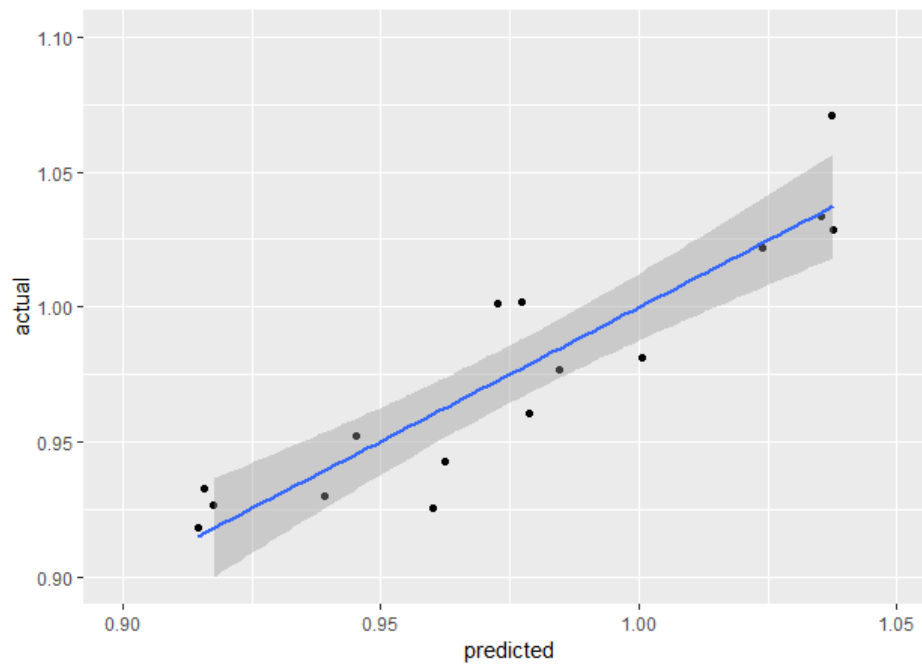
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.02241 on 11 degrees of freedom

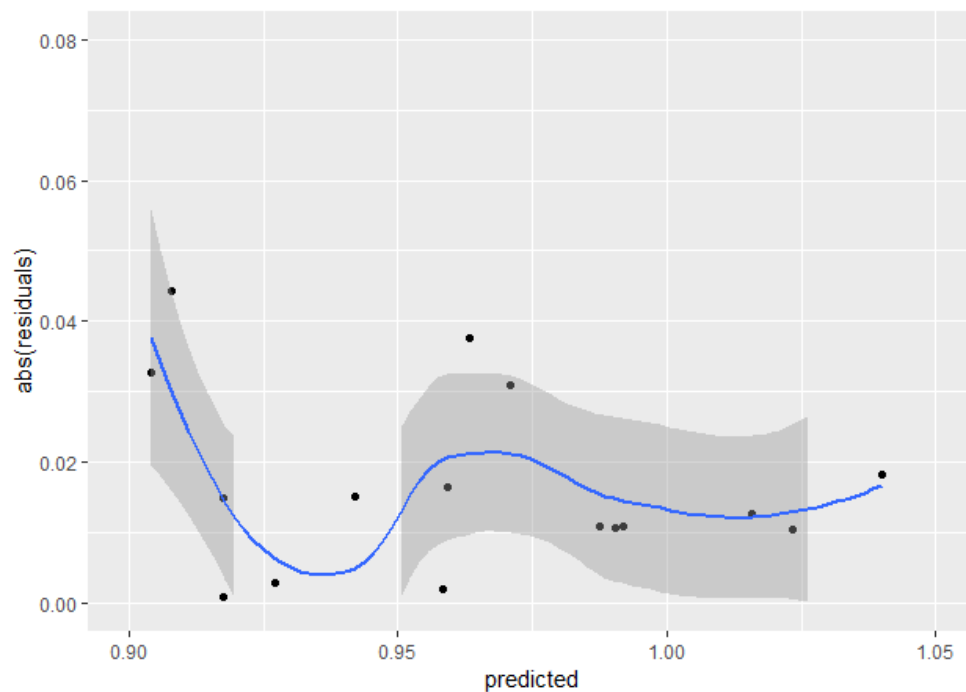
Multiple R-squared: 0.871, Adjusted R-squared: 0.8124 Predictive R-squared: 0.6952579

F-statistic: 14.86 on 5 and 11 DF, p-value: 0.000142

Appendix 5, Table 3: Table showing results of the linear regression of the model selected for 2001-2017 (Model C).



Appendix 5, Figure 9: Actual and predicted next year growth rates of the model selected for 2001-2017 show relatively high goodness of fit. The gray band represents the 95% confidence interval. Elk Data: Colorado Parks and Wildlife.



Appendix 5, Figure 10: Absolute value of residuals by predicted next year growth rates using of the model selected for 2001-2017 show a slightly improved accuracy for higher values of the predicted next year growth rate. The gray band represents the 95% confidence interval.