

FROM *ALCELAPHUS* TO *ZAPUS*: CONSERVATION OF MODERN MAMMALIAN  
POPULATIONS

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**Title**

From *Alcelaphus* to *Zapus*: Conservation of Modern Mammalian Populations

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North Dakota State University's regulations and meets the accepted standards  
for the degree of

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## ABSTRACT

Conservation priorities are increasingly important in the face of modern human activities. Anthropogenic activities such as deforestation, pollution, and climate change have negative impacts on all vertebrates. In chapter 1, I examine whether there are relationships among density dependence, population size variability, and extinction risk in mammals to see whether these parameters are indicative of population health. Also included were analyses of how body mass and age to maturity affect those three measures. On a smaller, more local scale, I asked questions regarding biodiversity of small mammals in a highly fragmented environment, the tallgrass prairie. In chapter 2, I examined how cattle grazing impacts small mammal biodiversity in the Sheyenne National Grassland on a short term, season-long scale. By understanding the interaction of large herbivores, vegetation height, and small mammals, appropriate measures can be taken to conserve this rare habitat properly, without sacrificing biodiversity.

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## PREFACE

Conservation priorities are increasingly important in the face of modern human activities. Anthropogenic activities such as deforestation, pollution, and climate change have negative impacts on all vertebrates (Purvis et al. 2000a, Anderson et al. 2011). Especially concerning is that the current extinction rate for birds and mammals of 0.5 species per year is considerably higher than background rates of 0.015-0.0015/year (Mills 2012). While about 33% of all mammal species are listed as being of conservation concern (IUCN 2015), in order to prevent more loss and to dampen the risks to these species, understanding how species respond to anthropogenic changes is increasingly necessary.

In looking at conservation broadly, population viability analysis (PVA) has been utilized in creating management plans and aiding in the legislative listing of species, such as via the Endangered Species Act (Boyce 1992). While PVAs have practical and inferential limitations (Brook et al. 2000, Coulson et al. 2001), they provide the potential to compare multiple aspects of population dynamics and biology with extinction vulnerability. In chapter 1, I examine whether there are relationships among density dependence, population size variability, and extinction risk in mammals. Also included were analyses of how body mass and age to maturity affect those three measures. In looking at these aspects of population dynamics, we may be able to draw inferences about population health and general patterns of population vulnerability.

On a smaller, more local scale, we can also ask how anthropogenic activities and management work together. The tallgrass prairie is one of the most endangered ecosystems in North America (Noss et al. 1995). The Sheyenne National Grasslands is one of the few protected preserves for this habitat. Historically, grasslands experienced fire and bison grazing but human development has altered that system (Axelrod 1985, Collins 2000) resulting in habitat

fragmentation and problems invasive species. Contemporary management plans for tallgrass prairie include prescribed burning and grazing of domestic cattle to increase and maintain high plant biodiversity (Hartnett et al. 1996), with plant community responses having been well studied. In contrast, the response of small mammal communities is less well understood. In chapter 2, I examine how cattle grazing impacts small mammal biodiversity in the Sheyenne National Grasslands on a short term, season-long scale. By understanding the interaction of large herbivores, vegetation height, and small mammals, appropriate measures can be taken to conserve this rare habitat properly, without sacrificing biodiversity.

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THE INTERPLAY OF POPULATION SIZE VARIABILITY, DENSITY DEPENDENCE,  
AND EXTINCTION RISK IN MAMMALS

**Abstract**

Rapid declines in mammalian populations necessitate the identification of potential relationships among population dynamic parameters and extinction risk, allowing for a better understanding of population and species vulnerability. Here we used the Global Population Dynamics Database's mammalian records to look for among-species and among-population relationships within density dependence, population size variability, and extinction risk using a mixed modeling approach. We also estimated relationships among age to sexual maturity and mass at adulthood with population dynamics and extinction risk. We found that at the among-population level, there was only a significant relationship between population size variability and extinction risk, which was likely due to mathematical dependencies rather than biology. There was also a lack of relationships among-species across density-dependence, population size variability, and extinction risk. When analyzing life history traits we found that as age to maturity increased population size variability decreased, suggesting greater population stability in mammals that have delayed development. There was also a positive relationship between age to maturity with extinction risk and as mass increased mean time to extinction decreased. Importantly, when looking at the variation explained, considerable variation remains at the among-species level. This suggests that other life history or ecological traits (aside from mass and age to maturity) are playing a role in determining density dependence, population size variability, and mean time to extinction.

## **Introduction**

Given the pervasive declines in mammalian populations globally, identifying common relationships among population dynamic parameters across taxa could allow for better understanding of extinction vulnerability and could be useful in determining conservation priorities (Anderson et al. 2011). As anthropogenic impacts on the environment increase, extinction vulnerability increases and should be reflected in population dynamics (Soule 1991). Among mammals, and other taxa, factors such as pollution, competition with invasive species, and habitat loss have all been identified as key factors in population declines and are ongoing and prevalent problems (Kerr and Currie 1995). Vulnerability caused by environmental changes may also influence otherwise intrinsic aspects of population dynamics such as reproductive rates (Cardillo et al. 2005). By comparing density dependence, population size variability, and mean time to extinction across species and populations, we may be able to draw inferences on how extrinsic and intrinsic factors play into mammalian population viability.

The availability of population data for numerous (~1400) species within the Global Population Dynamics Database (GPDD) allows population dynamics to be quantitatively compared (Inchausti and Halley 2001). It offers an abundance of time series data, ecological data collected over time from various geographical locations including published and gray literature data. The GPDD includes a variety of taxa and can be used to test hypotheses about population vulnerability, cyclic patterns, and responses to climate change (Kendall et al. 1998, Fagan et al. 2001, Knape and de Valpine 2011). The GPDD data also allows us to explore patterns across higher levels of taxonomic organization, rather than just on a species by species or population by population basis, for example by analyzing temporal variability and reviewing stability (Inchausti and Halley 2001, Sibly et al. 2005). Time series data (i.e. measures of abundance over

some period of time) allows for analysis of large scale population dynamics and testing of hypotheses related to density dependence and population size variability. For example, historical debates within ecology, such as the role of population resilience and population stability (Holling 1973, Connell and Sousa 1983), can be quantitatively assessed across taxa using the large sample sizes provided by the GPDD.

Additional topics that can be addressed using data from the GPDD are (i) whether populations that exhibit strong density dependence also exhibit decreased population size variability (Connell and Sousa 1983, Schoener 1985) (Figure 1.1); (ii) since high variability is associated with high extinction risk, it would also be expected that populations with greater stability would be less vulnerable to extinction (Bengtsson and Milbrink 1995); and (iii), following from (i) and (ii), increased strength of density-dependence should correspond to decreased extinction risk (Table 1.1). Using taxonomic mixed-effects models (Nakagawa and Santos 2012), these hypotheses can also be addressed at both the among-population and among species levels. Analyses at the among-population level allow us to make inferences about population dynamics regardless of species and will capture intrinsic connections among population dynamic parameters. Among-species effects capture differences in population dynamics due to differences in life history, biogeography, evolutionary history, and other species level characteristics.

In addition to the benefits afforded by the quantity of time series data within the GPDD, the diversity of mammalian species available therein allows for analysis of how population parameters are related to life history. For example, large body size in mammals has been associated with increased extinction risk due to the need for large range sizes and, frequently, exhibiting low densities (Cardillo et al. 2005, Liow et al. 2008, Wang et al. 2013). Further, as age

to sexual maturity increase, time lags between reproductive events can have impacts on fecundity rates (Purvis et al. 2000b) and mammals that take a longer time to develop to maturity, have fewer offspring, and gestate for longer periods of time are predicted to be more sensitive to extinction than species that have opposing life history strategies (MacArthur and Wilson 1967, Purvis et al. 2000b, Cardillo 2003, Davidson et al. 2009). These relationships can be evaluated using data from the GPDD.

Here we sought to better understand the relationships among density dependence, population size variability, and mean time to extinction at among-population and among-species levels using GPDD time series data (Table 1.1). In addition, we analyzed how body mass and age to sexual maturity affect those three parameters (Table 1.1). We expected strong density dependence to be linked to greater mean time to extinction and to exhibit a negative relationship with population size variability (Table 1.1, Figure 1.1). As adult body size of mammals increases, we also expected a positive relationship to density dependence and a negative relationship with population size variability (Table 1.1). Since body mass and age to maturity are related measures, we expected that as age to sexual maturity increases, population size variability would decrease and there would be a positive relationship with density dependence and negative relationship with mean time to extinction (Table 1.1).

Table 1.1. Predicted direction of relationships at the among species and among population levels across density dependence (DD), population size variability (PV), mean time to extinction (MTE), adult body size, and age to maturity. “+” indicates positive predicted relationships, “—” indicates negative relationships, “|” indicates no *a priori* expectation, “NA” indicates a relationship could not be estimated.

	Density Dependence	Population Size Variability	Mean Time to Extinction
Adult Body Size	Among Species: +	Among Species: +	Among Species: — (risk increases)
	Among Population: NA	Among Population: NA	Among Population: NA
Age to Maturity	Among Species: +	Among Species: +	Among Species: — (risk increases)
	Among Population: NA	Among Population: NA	Among Population: NA
Density Dependence		Among Species:	Among Species:
		Among Population: —	Among Population: — (risk increases)
Population Size Variability			Among Species:
			Among Population: intrinsically correlated

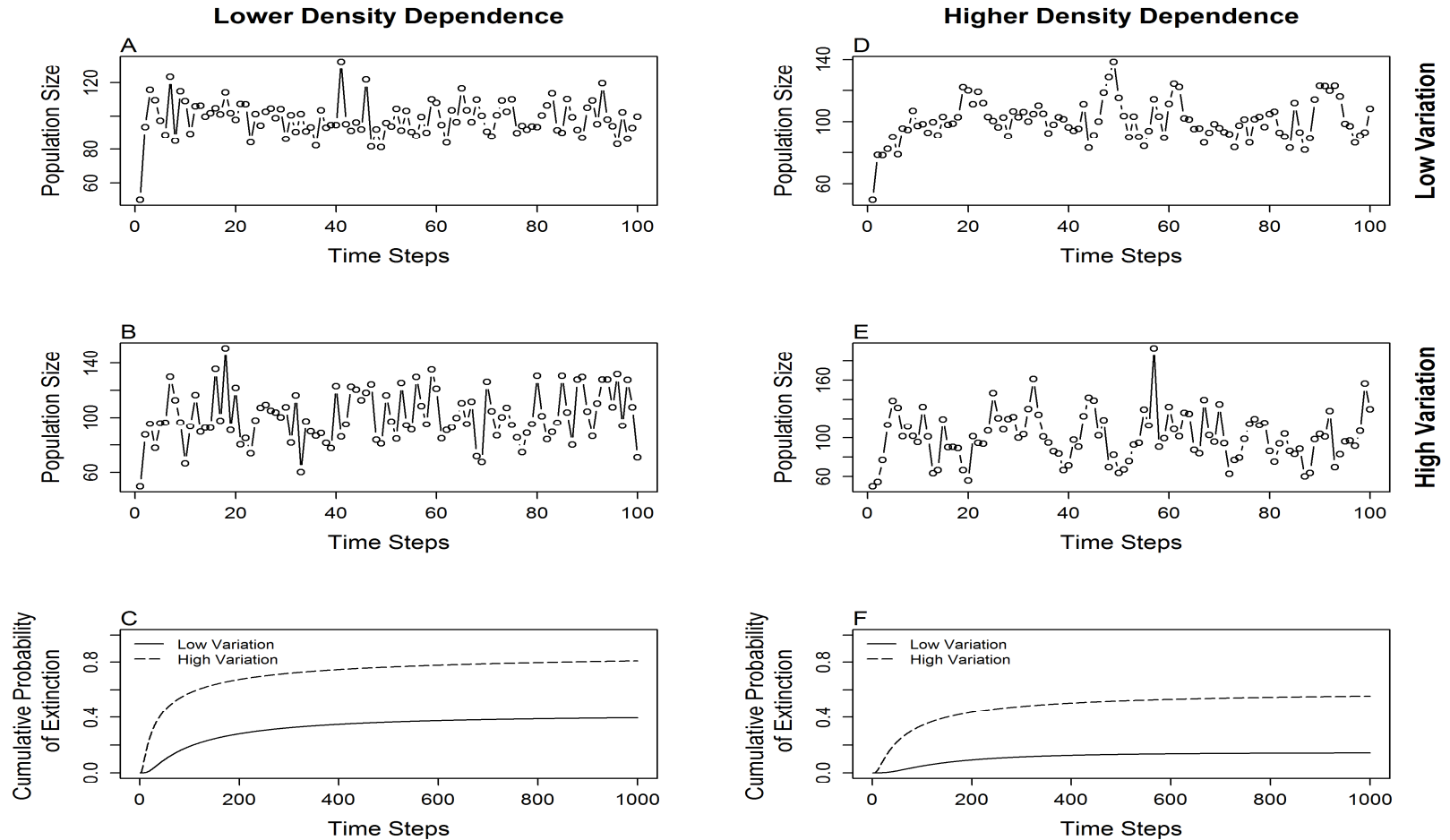


Figure 1.1. Simulated example of the expected relationships among density-dependence, population size variation, and extinction risk. A, B, D and E show simulated population sizes over time while C and F show cumulative probabilities of extinction over time for these simulated populations. As population size variability increases (A & D versus B & E) extinction risk is expected to increase (solid versus dashed lines in C & F) and as the strength of density-dependence increases (D & E versus A & B) extinction risk is expected to decrease (C versus F). Populations were simulated according to a theta-logistic model of population growth and cumulative probability of extinction was calculated according to Morris and Doak (2004). Additional simulation details and parameter values are given in the Appendix.

## Methods

To estimate density dependence, population variability, and extinction risk, mammalian population data were obtained from the Global Population Dynamics Database (GPDD) (NERC Centre for Population Biology). We only included records that contained continuous data over ten years or longer, records without apparent extinctions, and records with actual animal counts. We also excluded records with reliability scores of zero, the lowest rating in the database (Inchausti and Halley 2001). Based on the inclusion criteria, the total number of records analyzed was 144, spanning 9 orders, 22 families, 54 genera, and 69 species.

### *Population Parameters*

Density dependence (DD) was estimated by using the Gompertz model of population growth:

$$N_t = N_{t-1} \exp(a + b \ln N_{t-1} + \varepsilon_t) \quad (1)$$

where  $a$  and  $b$  are constants and estimated via maximum likelihood,  $N_t$  and  $N_{t-1}$  are population abundance at time  $t$  and  $t-1$ , and  $\varepsilon_t$  is residual error (Gompertz 1825, Dennis and Taper 1994, Dennis et al. 2006). We fit the Gompertz model using a state-space approach (Dennis et al. 2010), which reduces estimation bias in the strength of density dependence:  $b$ . Estimates of  $b$  were used in subsequent analyses. Negative estimates of  $b$  correlate to strong density dependence which becomes weaker as  $b$  increases. This model was chosen as its modeled *shape* of population growth is similar to that observed in natural populations (Sibly et al. 2005, Brook and Bradshaw 2006, Dennis et al. 2010).

Population variability (PV) was estimated for the time-series records using Heath's measure of population variability (Heath 2006). This metric was chosen because it is strongly correlated to classic measures of population variability (e.g., the coefficient of variation in



population sizes and the standard deviation of log transformed species abundances (Dochtermann and Peacock 2010)) but is less affected by large stochastic population size changes. Larger estimates of Heath's PV correspond to greater population variability (Heath 2006).

Extinction risk was estimated as mean time to extinction within a population viability analysis framework (Foley 1994, Lotts et al. 2004):

$$MTE = \frac{2n_0}{v_{re}} \left( k - \frac{n_0}{2} \right) \quad (2)$$

where  $n_0$  is the initial population size,  $v_{re}$  is the variance in growth rate after accounting for autocorrelation, and  $k$  is the carrying capacity (included as two-times the maximum population size observed).

Estimates of age to sexual maturity (weeks) and adult body mass (grams) were collected from the American Society of Mammologist's Mammalian Species publications and the Human Ageing Genomics Resources website.

### *Data Analysis*

To estimate the relationships among density dependence, population variability, and mean time to extinction, as well as the effect of age at first reproduction and adult mass on each, we used multi-response mixed-effects models (Dingemanse and Dochtermann 2013). We treated the three population parameters—density dependence, population variability, and mean time to extinction—as response variables, with age at first reproduction and adult mass as fixed effects which independently influenced the average value of each population parameter. We included species as a random factor to account for taxonomic structure in the data (Hadfield and Nakagawa 2010, Nakagawa and Santos 2012, Dochtermann and Peacock 2013). Because we

lacked variation within most orders and families and thus could not fit higher order taxonomic structures we assumed independence above the level of species.

The multi-response mixed-model was fit using a Bayesian approach with the MCMCglmm library in R 2.14.1 (Hadfield 2010). We used a prior that was flat (i.e. uniform) for correlations and generally uninformative for variances from zero to the total observed variance. Five independent chains were run for a total of  $1.3 \times 10^6$  iterations with a  $3.0 \times 10^5$  burn-in, and a sampling interval of 1000. The five chains were then pooled. This number of iterations and length of burn-in maintained low levels of autocorrelation and high levels of mixing and should also have further weakened any effects of the prior.

The relationships among the population parameters were determined by using the among-species and among-population variances and covariances to calculate the among-species and among-population correlations and the posterior probability that a correlation differed from zero (values closer to one indicate greater support, posterior probabilities greater than 0.95 were interpreted as “significant”).

The “significance” of effects of mass and age on each of the population parameters was assessed based on posterior modal coefficient estimates and the posterior probability that this estimate differed from zero (values closer to one indicate greater support). To improve interpretation, we also calculated a standardized effect size estimates ( $r_{pseudo}$ ) based on the coefficient’s modal estimate and the standard deviation of the posterior (3).

$$(t_{pseudo} = \frac{mode(posterior)}{sd(posterior)}; r_{pseudo} = \frac{t_{pseudo}}{\sqrt{t_{pseudo}^2 + 65}}) \quad (3)$$

We also calculated the relative contribution (and credibility intervals) of among-species variation to the total variation in density dependence, population variability, and mean time to extinction. These relative contributions were calculated as  $F^2$  (4; Nakagawa and Santos 2012):

$$I^2 = \frac{V_{species_0}}{V_{species_0} + V_{e_0}} \quad (4)$$

where  $V_{species_0}$  and  $V_{e_0}$  correspond to among- and within-species variances for density-dependence, population size variability, or mean time to extinction.  $I^2$  ranges from 0 to 1 and indicates how much of the variation in a parameter is due to differences among species. A value of 1 would indicate that observed differences not explained by adult mass or age at maturity in density dependence, population variability, or mean time to extinction are due entirely to species differences and a value of 0 would indicate that differences are among populations regardless of species.

This overall approach allowed us to determine the levels at which mammals exhibit variation in each of the three population parameters, to distinguish how these parameters were related to each other, and how each was affected by age at first reproduction and adult mass.

## **Results**

### *Among-population and among-species correlations*

There were no strong relationships present at the among-population level for density dependence  $\times$  population size variability or density dependence  $\times$  mean time to extinction ( $r = -0.16, -0.15$ , respectively; Figure 1.2A & 1.2B). There was, however, a significant relationship between mean time to extinction and population size variability ( $r = -0.53, p > 0.99$ ; Figure 1.2C). This correlation is likely due to the fact that both parameters include population size variance estimates. There were no significant relationships at the among-species level for the three population parameters (Figure 1.2D-1.2F).

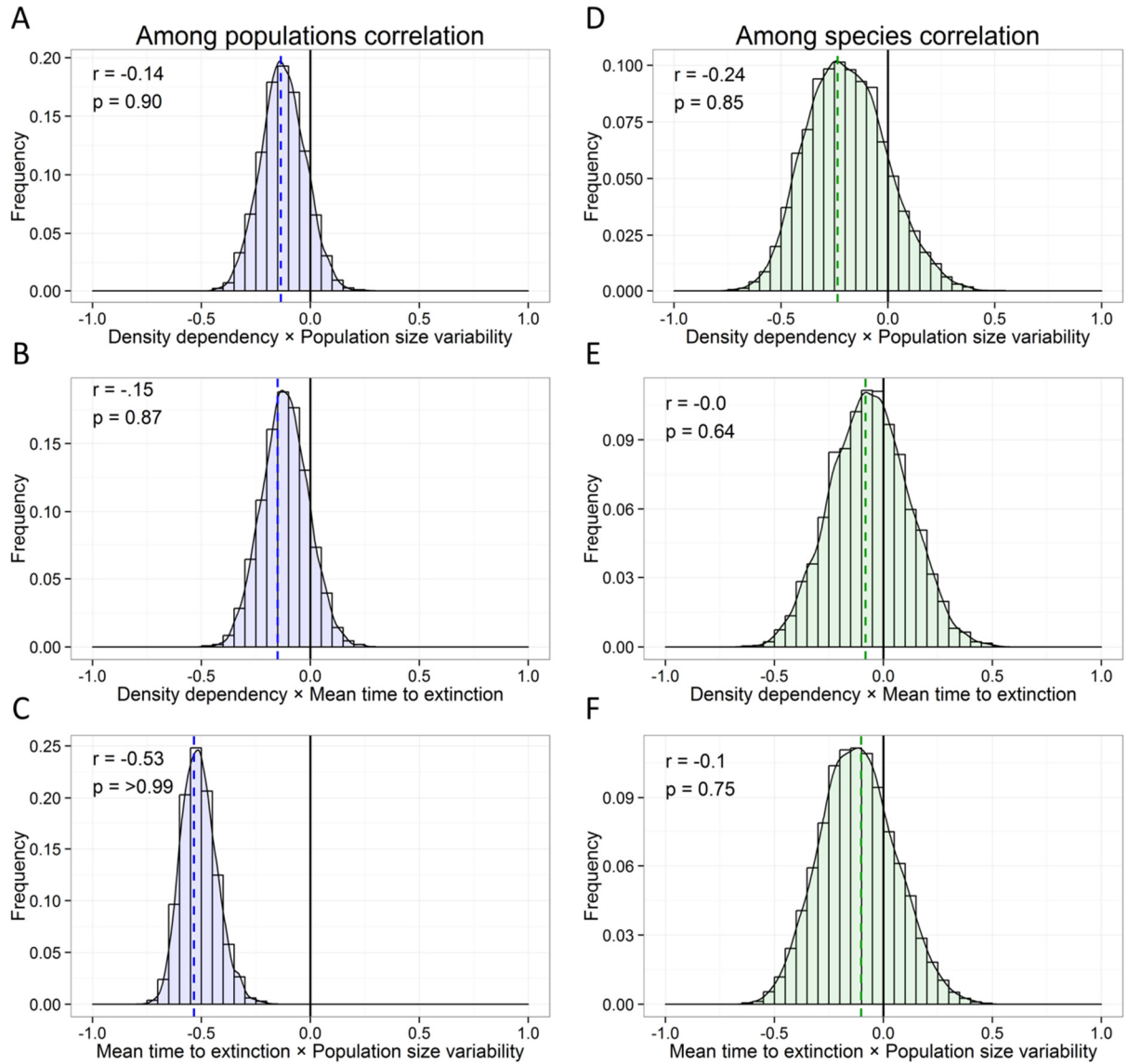


Figure 1.2. Posterior probability histograms of the among-population and among-species correlations between density dependence, population size variability, and mean time to extinction. Within pane  $r$ -values are the modal estimates for the relevant Pearson's correlation. Within pane  $p$ -values are based on the posterior distribution of correlation estimates and the overlap of these distributions with zero.

*Effects of age to maturity and adult mass*

There were two significant outcomes in analyzing age to maturity and the three population parameters. Age to maturity negatively affected population size variability such that as age to maturity increased, population size variability decreased ( $r = -0.23$ ,  $p = 0.97$ ; Table 1.2). Further, as age to maturity increased, so too did mean time to extinction ( $r = 0.31$ ,  $p = 0.99$ ; Table 1.2). Mass at maturity was only significantly related to mean time to extinction. As mass increased, mean time to extinction decreased ( $r = -0.31$ ,  $p = 0.99$ ; Table 1.2). Density dependence was not significantly related to either of the fixed effects (Table 1.2).

Table 1.2. Parameter estimates relating density dependence (DD), population size variability (PV), and extinction risk (MTE) to adult body mass or age to sexual maturity. Standard effect size ( $r$ ) was used for interpretation. Whether an effect differed from zero, i.e. was “significant”, was based on the posterior distribution of parameter estimates and the overlap of these distributions with zero.

Relationship	Standardized Effect Size ( $r$ )	Modal Estimate (parameter coefficient)	Probability different than zero (parameter coefficient)	95% Credibility Interval (parameter coefficient)	
				Lower	Upper
DD ~ Mass	0.15	2.16E-04	0.90	-1.82E-04	7.20E-04
DD ~ Age	-0.05	-6.83E-04	0.65	-3.64E-03	2.52E-03
PV ~ Mass	0.02	1.72E-04	0.44	-6.15E-04	7.22E-04
<b>PV ~ Age</b>	<b>-0.23</b>	<b>-4.56E-03</b>	<b>0.97</b>	<b>-8.91E-03</b>	<b>2.40E-04</b>
<b>MTE ~ Mass</b>	<b>-0.31</b>	<b>-9.10E-04</b>	<b>0.99</b>	<b>-1.46E-03</b>	<b>-1.93E-04</b>
<b>MTE ~ Age</b>	<b>0.31</b>	<b>5.30E-03</b>	<b>0.99</b>	<b>1.50E-03</b>	<b>1.03E-02</b>

*Among-species variability in density dependence, population size variability, and mean time to extinction*

To evaluate among-species variation across the data, individual species variation was analyzed over total variation across species (equation 4). The relationships of variation in density dependence, population size variability, and mean time to extinction across these levels demonstrated that there was considerable among-species variation present across all three

variables even after controlling for the effects of age to maturity and adult mass (Figure 1.3). Of the three population parameters, mean time to extinction exhibited the greatest relative remaining among-species variation.

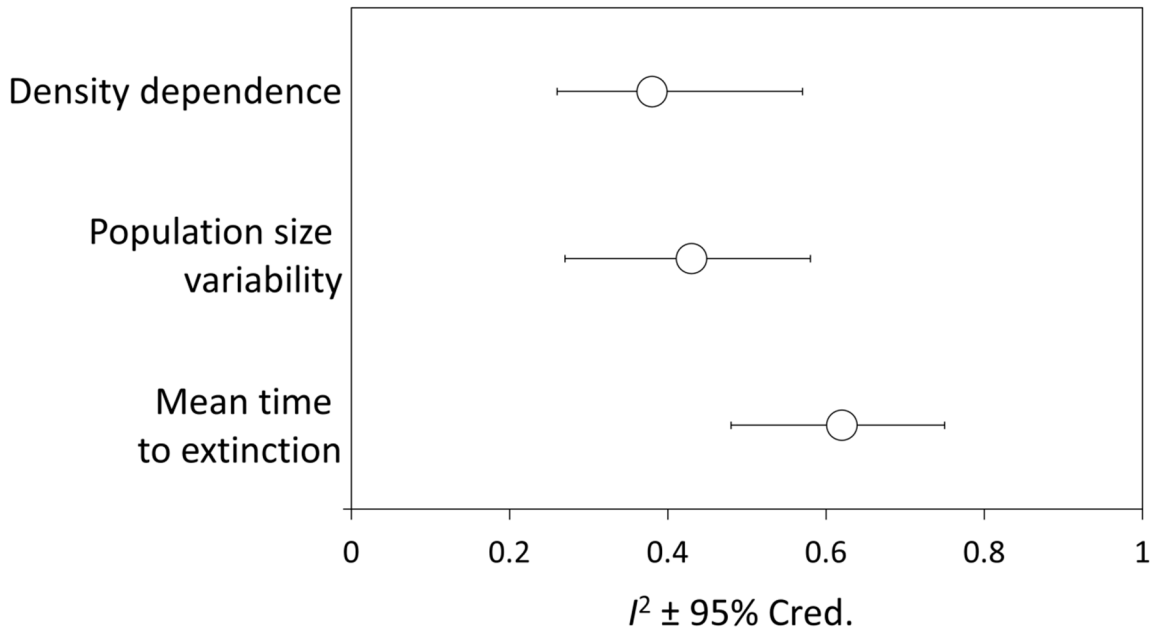


Figure 1.3.  $I^2$  estimates at the among-species level for density dependence, population size variability, and mean time to extinction. Open circles represent posterior modal estimates with error bars corresponding to an estimate's 95% credibility interval.

## Discussion

There are several interesting conclusions regarding the interactions among population parameters for mammalian taxa. While existing literature supports positive correlations among measures of density dependence with population size variability and mean time to extinction (Holling 1973, Connell and Sousa 1983, Bengtsson and Milbrink 1995; Table 1.1), our analyses did not detect any strong relationships at either the among-population or among-species level between these parameters. This suggests these aspects of population dynamics—at least as

estimated and modeled here—are not intrinsically linked to one another and that assumptions about population size variability and extinction risk cannot be made when looking strictly at the presence or absence of density dependence. Previous research has exhibited that these factors should covary with each other, with density dependence acting to dampen population size variability (Holling 1973, Brook and Bradshaw 2006, Dochtermann and Peacock 2013). Since populations tend to experience density dependent and independent effects at the same time, our results might suggest that density independent or extrinsic effects have a greater influence on extinction vulnerability. Mean time to extinction and population size variability, on the other hand, were found to be significantly related to one another among-populations, where high population variability was related to decreased future persistence. This idea has been frequently supported (Pimm et al. 1988, Vucetich and Waite 1998, Fagan et al. 2001) wherein populations that tend to greatly increase and decrease in size over time have greater sensitivity to extinction events. However, here this relationship is likely due to the fact that both of our measures included estimates of population size variance and that the relationship is not biologically meaningful.

Relationships between age to maturity and mass with population parameters were similarly complicated. As age to maturity increased, population size variability decreased, suggesting greater population stability occurs in mammals that require more time to reach sexual maturity. In addition, there was a positive relationship between age to maturity and mean time to extinction. Since our estimate for mean time to extinction is in years, this may be a function of longer lived species persisting further into the future than those with shorter life spans. However, longer development times are associated negatively with population growth rates and inflate extinction risk (Purvis et al. 2000b). We also found as body mass increases mean time to

extinction decreases. While body mass has been linked to an increased extinction risk (Cardillo et al. 2005, González-Suárez and Revilla 2013), this result conflicts with the relationship between age to maturity and mean time to extinction. Large mammals have been shown to exhibit delayed development to sexual maturity (Stearns 1983, Bielby et al. 2007) and are associated with greater longevity (Lindstedt and Calder 1981, Healy et al. 2014). One caveat to these interpretations is that the relatively short length of time series data may result in extinction risk being underestimated (Lotts et al. 2004).

Our most intriguing finding is at the among-species level for each population dynamic measure. Across density dependence, population size variability, and mean time to extinction, we observed considerable variation at the species level that was unexplained by the included fixed effects of age to maturity and mass. Mean time to extinction in particular exhibited the greatest relative among-species variation remaining to be explained. From this we can infer that differences in life history and natural history traits among species have a greater effect on extinction vulnerability than do differences among populations. These results also suggest that age to maturity and mass are not necessarily the main forces driving among species variation. Instead, other aspects of ecology, life history, and evolution produce among species variation in population dynamics. This conclusion is consistent with the observations of other researchers (Purvis et al. 2000a, Davidson et al. 2009) and provides support for the recommendation that management planning requires looking at species on an individual level.

Although our analyses were dependent on the GPDD, the database was somewhat limited. A particular issue was the taxonomic coverage available. While there were 144 records that met our inclusion criteria, this only included 69 species. Some major mammalian orders, such as *Chiroptera*, were not represented at all. Sampling bias might also have been present, as



our dataset included species for which data collection might be easier (e.g., species that persist in high numbers, are charismatic, easy to find). While a factor of our inclusion criteria was having at least ten years of data, it is suggested that to see appropriate population dynamic effects, several decades might be necessary (Vucetich and Waite 1998, Lotts et al. 2004, Brook and Bradshaw 2006), which would have prevented us from asking any of our questions. These issues could be solved by more biologists proactively submitting their data to the database, especially those in possession of large and lengthy time series data that are as yet unpublished.

Identifying tools to utilize in the face of large biodiversity losses becomes increasingly important as we gain more insight into how anthropogenic activities are intertwined with population dynamics and extinction risk. Based on our findings, density dependence and population size variability are not, on their own or in relation to each other, reliable for making conservation decisions regarding mammals. Despite this, our analyses did highlight topics of interest in regards to how to evaluate population dynamics. For example, while a relationship between population size variability and mean time to extinction was present, it was likely not biologically significant, which raises questions of how to appropriately compare these two measures. Our results also convey that there are aspects of mammalian life histories beyond age to maturity and mass that play into increased extinction risk, and may be more important factors to look into in regards to conservation planning.

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# IMPACTS OF CATTLE GRAZING ON SMALL MAMMAL DIVERSITY IN THE SHEYENNE NATIONAL GRASSLAND

## **Abstract**

Tallgrass prairie was once the most abundant habitat type in North America, and presently most of its historic distribution has been converted or is highly fragmented. To maintain plant heterogeneity, management plans include prescribed burning and grazing by domesticated herbivores. While plant communities respond positively to this management, less is understood about the impacts of management on small mammals. The Sheyenne National Grassland, located in Richland and Ransom counties in North Dakota (USA), allows for the analysis of the short term response of small mammals to cattle grazing. Twelve sites were evaluated with a paired trapping grid design. 30m × 30m electric fence exclosures were established at each site which prevented domestic grazing but did not impede small mammal movement. To assess diversity, Simpson's Index of Diversity, Shannon-Weiner Index, Evenness, and Richness were calculated. Capture rates were not significantly different between treatments, but plant height was significantly higher in ungrazed (fenced) grids. There were no significant relationships between the diversity indices and treatment. Despite this, Simpson's Index of Diversity appeared to increase in unfenced (grazed) grids as plant height also increased. Richness also appeared to increase in fenced grids than unfenced. Since there were no strong relationships found, this suggests cattle grazing does not have an impact on small mammal diversity in the Sheyenne National Grassland on a short term scale. While no recommendation for management can be made based on this data, conserving the heterogeneity of all communities in the grassland should be priority in an ever rare ecosystem.



## **Introduction**

Tallgrass prairie was once the most dominant habitat type in the continental United States spanning from Canada to the Mexican border as well as extending west towards the Rocky Mountains and east into Wisconsin and Indiana (Samson and Knopf 1994). The rise of agriculture and urban development has decreased the amount of grassland still in existence, leaving it one of the most endangered major ecosystems (Noss et al. 1995, Howe and Brown 1999). Despite this vulnerability, tallgrass prairie is generally characterized by high levels of biodiversity which may be due to the amount of disturbance common in grassland ecosystems. Historically, tallgrass prairie experienced fire events, both natural and human induced, and considerable disturbance due to bison grazing (Axelrod 1985, Collins 2000). As the grasslands were developed by Euro-American settlers, a regime of fire suppression began which, combined with the near extinction of bison, drastically altered the structure of the grasslands (Knapp et al. 1999). By incorporating management plans that include disturbances such as prescribed burning and grazing by domestic species, there is potential to appropriately increase the heterogeneity of native plant species and the other communities associated with them (DeKeyser et al. 2009).

While effects of major disturbances (fire and large herbivores) are well-studied in plant communities, there is also potential for impacts on other species, especially small herbivores or “cryptic consumers” (Howe et al. 2006, Rebollo et al. 2013). Fire and grazing decrease aboveground biomass while promoting new growth and suppressing non-native species intolerant to grazing and fire (Symstad 2000, DeKeyser et al. 2009). Different stages of grassland can host different small mammals temporally and spatially. For example, ungrazed grasslands with high cover tend to have increased seed sets and are composed of high but variable small mammal biomass (Grant et al. 1982). Small mammals play an important role as seed predators,

seed dispersal agents, prey, and a source of energy transfer (French et al. 1976, Lambert et al. 2006) and understanding their community structure in response to management may be indicative of habitat quality (Vellend 2010). Large scale, long term studies have shown that rodents can have large effects on plant composition, even going as far as significantly altering habitats (Batzli and Pitelka 1970, Brown and Heske 1990). The presence of large herbivores may dampen such large impacts as grazing directly impacts plant biomass. This decrease in biomass can change aspects of food availability for small mammals and also decreases cover from predation. Since cattle do not graze uniformly, there is potential for microhabitats to form and alter distributions of species (Schmidt et al. 2005).

The Sheyenne National Grassland in North Dakota provides a unique setting for analyzing the relationship of management in a rare, remnant tallgrass prairie and the responses of small mammal communities to this management. More specifically, we pose the question of how cattle grazing impacts small mammal community structure in the short term. Also, do communities within different microhabitats respond differently to the presence of grazing?

## **Methods**

### *Study Site*

The Sheyenne National Grassland (46.4270, -97.2950), which is publicly owned and managed by U.S. Forest Service, spans 28,500 hectares in the southeastern portion of North Dakota within Ransom and Richland Counties. This is the only national grassland present in the tallgrass region of the Great Plains. The Sheyenne National Grassland consists of remnant sandhill, tallgrass prairies, and oak savanna, mixed with riparian forests and wetlands. Also present within the Grasslands are former croplands that have been restored to grassland. The Grassland supports many threatened species including greater prairie chickens (*Tympanuchus*

*cupido*) and western fringed prairie orchids (*Platanthera praeclara*). Varying degrees of management are utilized to maintain habitat integrity, such as prescribed fire, mowing, and grazing. A majority of the grassland is fenced off into 62 total grazing allotments. Many of these allotments are currently on a cattle grazing schedule where cattle are either at pasture season-long or are rotated on or off partway through the grazing season. Sheep grazing also occurs but is less common. High average annual temperature for the area is 12.7°C and low annual temperature is 0°C, with annual precipitation of 56.9 centimeters (National Climate Data Center 1981-2010).

### *Trapping*

Twelve trapping sites were identified based on habitat type and accessibility and to ensure a majority of the grasslands were covered (Figure 2.1, Table 2.1). We selected a diverse set of sites to analyze grazing pressure including two sites that were identified in the 2013 field season and two sites were previously assessed by Sweitzer (2003). We expected to trap up to 19 different small mammal species, based on the size of the traps and home ranges of these animals (Table 2.2).

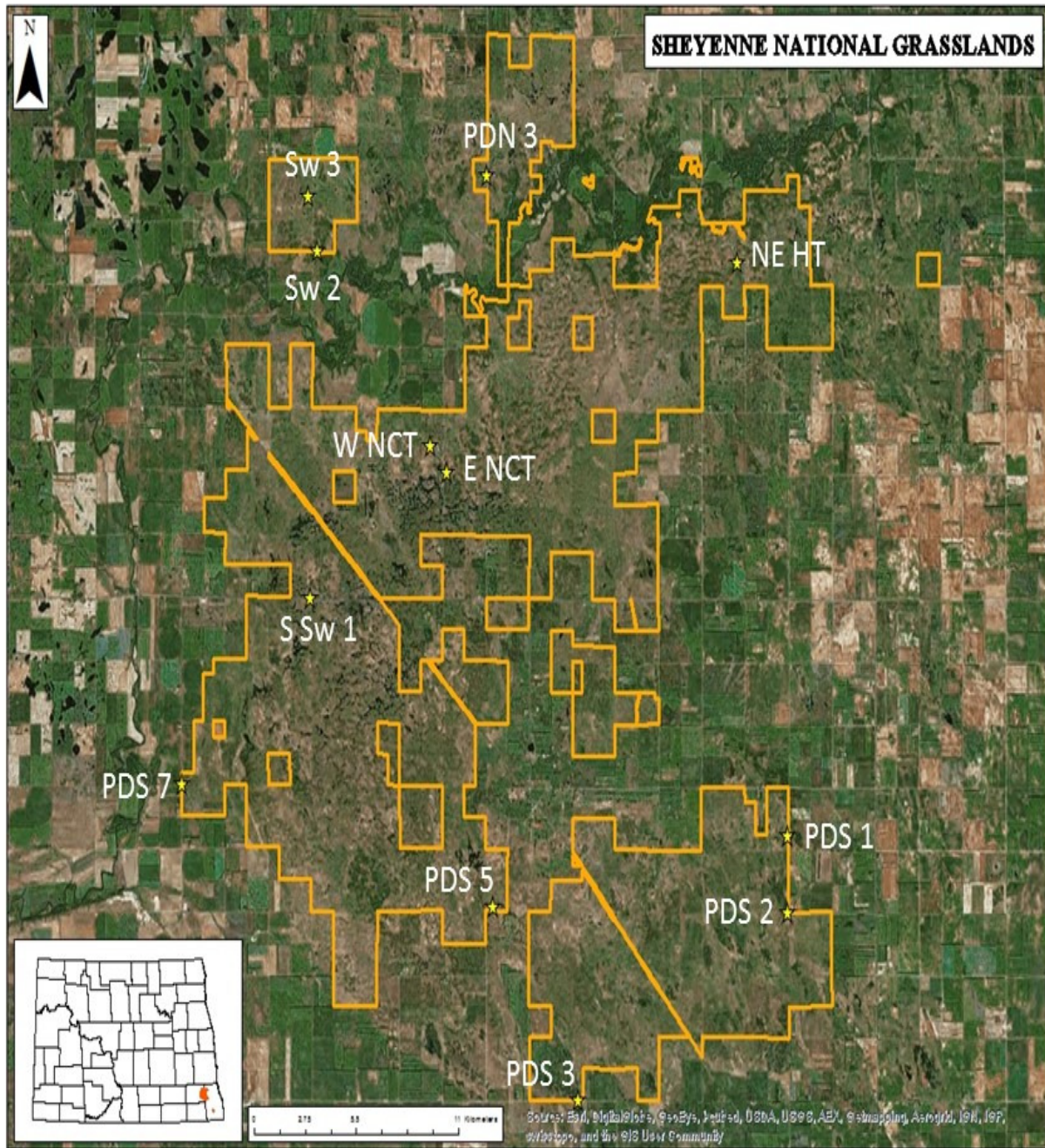


Figure 2.1. A map of the Sheyenne National Grassland. The smaller map is representative of the state of North Dakota, the grassland location identified with a red marker. On the map of the grassland, trapping sites are marked with a yellow star.

Table 2.1. Site descriptions for all twelve trapping sites in the Sheyenne National Grassland. Names of sites correlate to names located on map in Figure 2.1.

Site Name	Location	Site Description
PDS 1	46.38689 -97.1764	Paired unfenced grid located to the south of the fenced grid. ~10m from road, ~20m from windbreak trees, and just east of a wetland. Dominant plant species: Big Bluestem, Nodding Wild Onion, Prairie Rose, Leadplant, Kentucky Bluegrass, Sage, Purple Prairie Clover, Blazing Star, Indian Grass, Leafy Spurge, Switch Grass
PDS 2	46.36902 -97.1766	Paired unfenced grid located west of fenced grid. ~20m from road, heavy graze season-long in unfenced area. Sandier soil than PDS 1, fenced area had slight elevation. Stand of oak trees ~30m north of grids. Dominant plant species: Willow saplings, Leafy Spurge, Cord Grass, Kentucky Bluegrass, Marigold, Big Bluestem, Sweet clover, Scurf pea, Sage, Switch Grass, Panic Grass
PDS 3	46.32593 -97.2773	Paired unfenced grid located south of fenced grid. Wet meadow habitat with a few oaks and berm to the east. Dominant plant species: sedges, Blue Bluestem, Canada Milk Vetch, Cordgrass, Anemone, Willow saplings, Marigold, Little bluestem.
PDS 5	46.36613 -97.3225	Paired unfenced grid location north of fenced grid. Slope to the north in both grids. Wetland ~50m northeast. Patch of dogwood in the middle of fenced grid. Heavy graze. Dominant plant species: Kentucky Bluegrass, Sage, Ragweed, Leafy Spurge, Marigold, Wild Strawberry, Red clover, Brome, Leadplant, Little Bluestem, Foxglove Beardtongue.
S Sw 1	46.44177 -97.4066	Paired unfenced grid located west of fenced grid. Large slope starting at eastern portion of fenced area going west. Slope is drier and more upland whereas bottom of slope it more of a wetland. Fence was removed between periods 1 & 2 so fenced area experienced grazing. Dominant plant species: Cordgrass, Blue Vervain, Willow saplings, dogwood saplings, Prairie Rose, Common Milkweed, Canadian Thistle, Wild Strawberry, Little Bluestem, Blazing Star, Brome, Leafy Spurge, Leadplant, sedges.

Table 2.1. Site descriptions for all twelve trapping sites in the Sheyenne National Grassland (continued). Names of sites correlate to names located on map in Figure 2.1.

Site Name	Location	Site Description
PDS 7	46.39891 -97.4688	Paired unfenced grid located east of fenced grid. Heavy graze, fenced area separated by Forest Service fence to a mowed parking lot. Dominant plant species: Little Bluestem, Kentucky Bluegrass, Big Bluestem, Marigold, Scurfpea, Canada Thistle, Prairie Rose, Switchgrass, Common Milkweed.
W NCT	46.47708 -97.3487	Paired unfenced grid located to the north of the fenced grid. ~25m from road and ditch. Sandier soils with more bare patches, heavy graze. Dominant plant species: Big Bluestem, Little Bluestem, Switchgrass.
E NCT	46.47088 -97.3409	Paired unfenced grid located south of fenced grid. ~30m from gravel parking lot, ~15m from small woodland, oak tree in between fenced and unfenced grids. Dominant species: Big Bluestem, Little Bluestem, Leadplant, Foxglove, Switchgrass.
Sw 2	46.53481 -97.4078	Paired unfenced grid located west of fenced grid. ~10m from road, many invasives, soil dries out headed west from road. Denser vegetation in fenced grid, heavy graze outside of grid. Dominant plant species: Canada Thistle, Red clover, Sweet clover, Reed Canary Grass, Leafy Spurge, Scurfpea.
Sw 3	46.52198 -97.406	Paired unfenced grid location east of fenced grid. More inland site from road in oak savanna area separated by woodland. Sandy soils. Nearest oak ~ 10m from grids. Dominant plant species: Leadplant, Big Bluestem, Blazing Star, Little Bluestem.
PDN 3	46.5396 -97.3218	Paired unfenced grid located south of fenced grid. Grassland habitat, heavy graze, grids roughly ~10m from road. Dominant plant species: Kentucky Bluegrass, Little Bluestem, Big Bluestem, Leadplant, Horsetail.

Table 2.1. Site descriptions for all twelve trapping sites in the Sheyenne National Grassland (continued). Names of sites correlate to names located on map in Figure 2.1.

Site Name	Location	Site Description
NE HT	46.51947 -97.2006	Paired unfenced grid located south of fenced grid. Fenced area seems to be wetter than unfenced. ~20m from road, wet ditch in-between. More dense vegetation located on the western half of grids. Dominant plant species: sedges, Switchgrass, Willow saplings, Blue Vervain, Horsetail, Big Bluestem, Brome, Marigold.

Table 2.2. List of trappable species in the Sheyenne National Grassland. The species in this list are of the size that would be able to fit into the Sherman traps used and whose range overlaps the Sheyenne National Grassland. Not all species on this list were captured (Seabloom et al. 2011).

<b>Species Latin Name</b>	<b>Species Common Name</b>	<b>Species Habitat Characteristics</b>	<b>Species Range</b>
<i>Blarina brevicauda</i>	Northern Short-tailed Shrew	In the Great Plains, prefers heavy vegetation. Tallgrass prairie, bushy areas, forests. Establishes burrows and runways in ground and leaf cover.	Occurs over most of the northeastern and Midwest U.S. Primarily east of the Missouri river in N.D.
<i>Sorex cinerus</i>	Masked Shrew	Prefers mesic areas in forest and prairie habitats. Utilizes areas of heavy leaf litter and ground cover.	Spread throughout the northern portion of the U.S. Found in nearly all counties in N.D., though occurring less in the southwestern part of the state.
<i>Sciurus carolinensis</i>	Eastern Grey Squirrel	Hardwood forest with sparse understory. In N.D., occur in oak woodlands.	Throughout northeastern U.S., southern Saskatchewan and Manitoba.
<i>Sciurus niger</i>	Fox Squirrel	Small strands of mature forest with sparse understory.	Similar distribution to the Grey Squirrel but extends west into Montana and other plains states. Found in all counties in N.D.
<i>Poliocitellus franklinii</i>	Franklin's Ground Squirrel	Prefers dense grassy vegetation with forest edges. Utilize unmowed roadsides and railroad right of ways. Avoid mowed, burned, grazed areas.	Occurs in the eastern Dakotas, Nebraska, Kansas, Minnesota, and Iowa. In all counties east of the Missouri River in N.D.



Table 2.2. List of trappable species in the Sheyenne National Grassland (continued). The species in this list are of the size that would be able to fit into the Sherman traps used and whose range overlaps the Sheyenne National Grassland. Not all species on this list were captured (Seabloom et al. 2011).

<b>Species Latin Name</b>	<b>Species Common Name</b>	<b>Species Habitat Characteristics</b>	<b>Species Range</b>
<i>Urocitellus richardsonii</i>	Richardson's Ground Squirrel	Prefers open grasslands and croplands. Common in grazed and mowed areas.	Its range is exclusively in the Great Plains. Occurs north and east of the Missouri River in N.D.
<i>Ictidomys tridecemlineatus</i>	Thirteen-lined Ground Squirrel	Grassland species with preferences similar to Richardson's Ground Squirrels.	Found throughout most of the Midwest and in Texas. Found in all counties in N.D.
<i>Tamias striatus</i>	Eastern Chipmunk	Continuous strands of deciduous forest, especially with logs and brush for cover.	Occurs over most of the northeastern U.S., the eastern Dakotas being the most west of their range. Restricted in areas and tributaries associate with the Red River.
<i>Tamiasciurus hudsonicus</i>	Red Squirrel	Utilize mature, deciduous trees with cavities, including riparian woodland and urban areas	Mostly located in boreal forests in the U.S. Are found in the eastern and northern portion of N.D.
<i>Perognathus flavescens</i>	Plains Pocket Mouse	Associated with sandy soils in grasslands and mixed-grasslands. Found in disturbed sites and cultivated land.	North Dakota is the northern limit of the species in the U.S and is found as south as Mexico. Are found patchily in N.D., in refuges including the Sheyenne Grassland.

Table 2.2. List of trappable species in the Sheyenne National Grassland (continued). The species in this list are of the size that would be able to fit into the Sherman traps used and whose range overlaps the Sheyenne National Grassland. Not all species on this list were captured (Seabloom et al. 2011).

<b>Species Latin Name</b>	<b>Species Common Name</b>	<b>Species Habitat Characteristics</b>	<b>Species Range</b>
<i>Zapus hudsonius</i>	Meadow Jumping Mouse	Ranges from prairie to deciduous forests. Prefers non-forested, moist areas.	Found throughout the Great Plains and the Midwest. Is distributed state-wide in N.D.
<i>Zapus princeps</i>	Western Jumping Mouse	Shares habitat with Meadow Jumping Mouse, but prefers denser and drier communities.	Occur in the Rocky Mountains from southern Yukon to Arizona. Reported in the southeastern counties in N.D.
<i>Microtus ochrogaster</i>	Prairie Vole	Upland prairie but may be found in riparian and cropland areas.	Found in a majority of the Great Plains states and the Midwest.
<i>Microtus pennsylvanicus</i>	Meadow Vole	Wide variety of grassland types but are found in more mesic areas with dense cover. Also prefer prairie-forest transition areas.	The widest distribution of any <i>Microtus</i> species. Found throughout the state of N.D.
<i>Clethrionomys gapperi</i>	Southern Red-backed Vole	Prefer forest habitats with understory litter and logs.	Located across mountain ranges from east to west in the U.S. Are found north and east of the Missouri river in N.D.
<i>Onychomys leucogaster</i>	Northern Grasshopper Mouse	Primarily found in semi-arid grasslands and shrub lands. Prefer sandy soils with areas of mixed grasses and forbs.	From southern Canada to Mexico. Found in grasslands and deserts in M.N., N.D., and I.A.

Table 2.2. List of trappable species in the Sheyenne National Grassland (continued). The species in this list are of the size that would be able to fit into the Sherman traps used and whose range overlaps the Sheyenne National Grassland. Not all species on this list were captured (Seabloom et al. 2011).

<b>Species Latin Name</b>	<b>Species Common Name</b>	<b>Species Habitat Characteristics</b>	<b>Species Range</b>
<i>Peromyscus maniculatus</i> <i>Peromyscus leucopus</i>	Deer Mouse/ White-footed Mouse	Wide variety of habitats, from forests to grasslands, and prefer successional stage grasslands.	Found throughout the U.S. and in all counties in N.D.
<i>Reithrodontomys megalotis</i>	Western Harvest Mouse	Live in densely vegetative habitats and avoid forests and uplands. Prefer ungrazed, undisturbed habitats.	Located throughout the Midwest in the U.S. as south as Mexico. Is found in southern counties across N.D.

In order to address questions regarding cattle grazing, electric fence exclosures (30 m × 30 m) were installed at each of the twelve sites. We used a paired grid design, where one 25 m × 25 m trapping grid was placed within a fence, and a second 25 m × 25 m grid was placed 10 m outside the exclosure (Figure 2.2). Traps were set 5 m apart from each other. Fences were installed in June, 2014 and were taken down in November 2014. Sherman live traps (10 cm × 11 cm × 38 cm) baited with wild bird seed, rolled oats, and peanut oil were used to census small mammal populations. Traps were set mid to late afternoon and closed after checking in the morning. Each site experienced four trap nights per period and three periods were completed consisting of four weeks. There were a total of 600 trap nights per site over the three periods for a total of 7200 trap nights during 2014. When animals were captured in traps, they were identified, sexed, weighed, and given a numbered ear tag for mark-recapture purposes. Total captures amounted to 269 individuals, 31 individuals were recaptured in a different period.

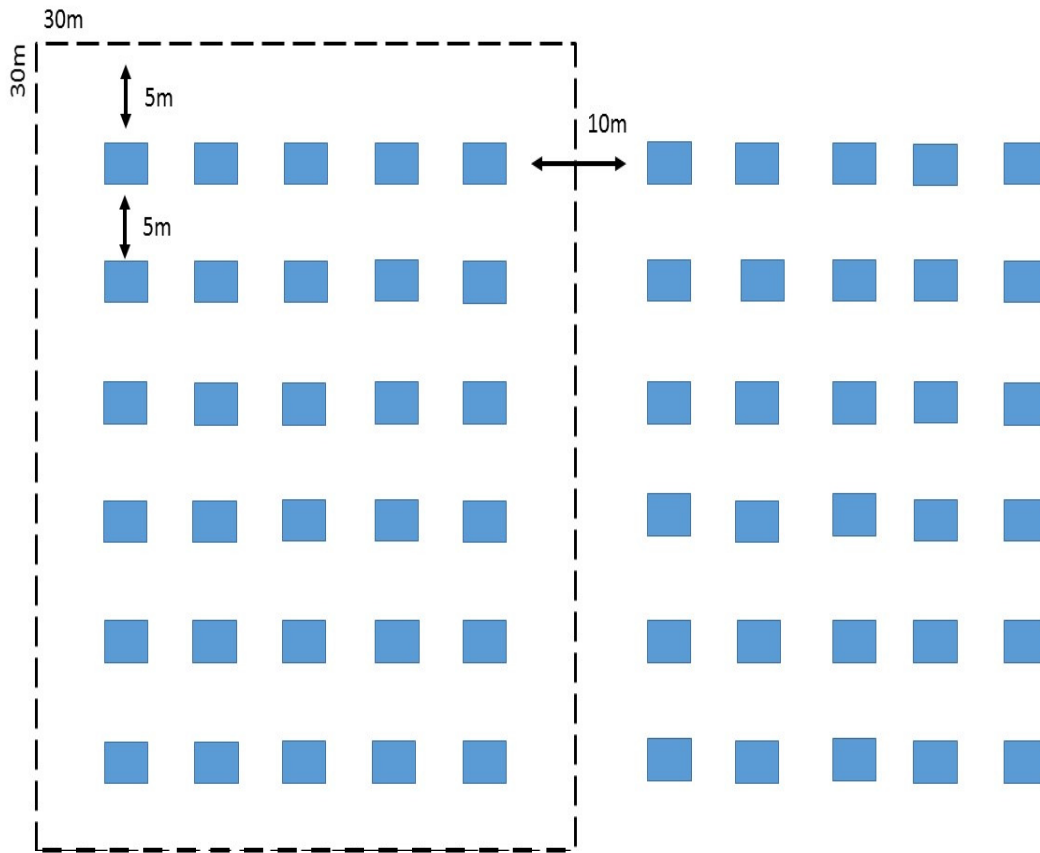


Figure 2.2. Schematic of trapping grids. 30 m  $\times$  30 m electric fence enclosures (dashed line) were set up at each of the twelve sites. 25 m  $\times$  25 m trapping grids were set up in enclosures. A paired site was located 10 m away from enclosure. (trap locations represented by blue rectangles)

### *Diversity Indices*

Four measures of species diversity were used to evaluate the effects of grazing on community composition: Simpson's Index of Diversity (SID), Shannon-Wiener Index (SWI), Evenness (E), and Richness (R). While these indices all incorporate some aspect of diversity, they account for different components of diversity. SID calculates the probabilities of capturing a species over the total number of species captured. SWI incorporates the same probabilities but is more influenced by density of captures (Miller 1990). E is used to understand distributions of

species captures where *R* gives an output of how much diversity is present. We used minimum known alive counts to calculate these measures as capture and recapture rates were low.

### *Vegetation Sampling*

Vegetation was characterized at each site in three ways: First, dominant plant species per site were identified. Second, within each trapping grid, we used a 1 m × 1 m square subdivided into a 10 cm × 10 cm increments grid and identified what type of vegetation (grass, forb, tree, shrub, bare) was present at 10 randomly selected points within the square. Third, at each of the 10 points, plant height was measured in centimeters. These measures were taken once per site during the end of the second or beginning of the third trapping periods.

### *Data Analysis*

Paired t-tests were used to compare response of vegetation and capture rates between treatments. Nested ANOVAs were performed for each of the four measures of diversity as well as minimum known alive counts in program *R* using the *lme4* package. Site was used as a nesting variable (i.e. random intercept) due to the design of the study to control for pseudoreplication (Hurlbert 1984). Treatment, average plant height at a site, and the interaction between the two were included as fixed effects.

## Results

Seven mammalian species were trapped during the 2014 field season: *Ictidomys tridecemlineatus*, *Peromyscus maniculatus*, *Blarina brevicauda*, *Microtus pennsylvanicus*, *Perognathus flavescens*, *Poliocitellus franklinii*, and *Sorex cinerus*. *Ictidomys tridecemlineatus* was found at all sites but other species were more sporadically distributed (Figure 2.3). There was no statistical difference in the number of captures per treatment ( $t_{11} = 1.5994$ ,  $p = 0.138$ ) though there were more individuals captured in fenced areas than unfenced ( $N_{\text{fenced}} = 151$ ,  $N_{\text{unfenced}} = 118$ ). Vegetation height was averaged per site between fenced and unfenced treatments. Fenced treatments had significantly taller plant heights than unfenced treatments ( $t_{21.6} = 3.4975$ ,  $p = 0.002$ , Figure 2.4).

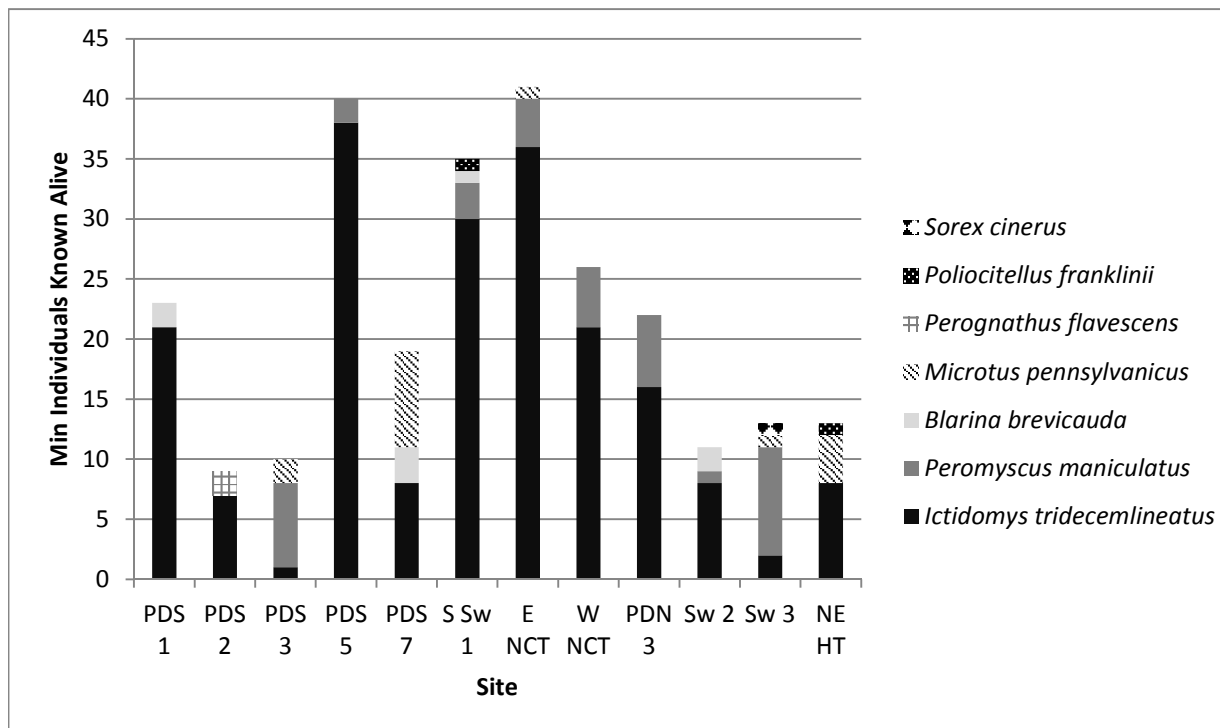


Figure 2.3. Minimum known alive counts of small mammals per site in the Sheyenne National Grassland. The number captured is on the y-axis and each species is labeled according to the legend. *Ictidomys tridecemlineatus* was the most captured species across all sites.

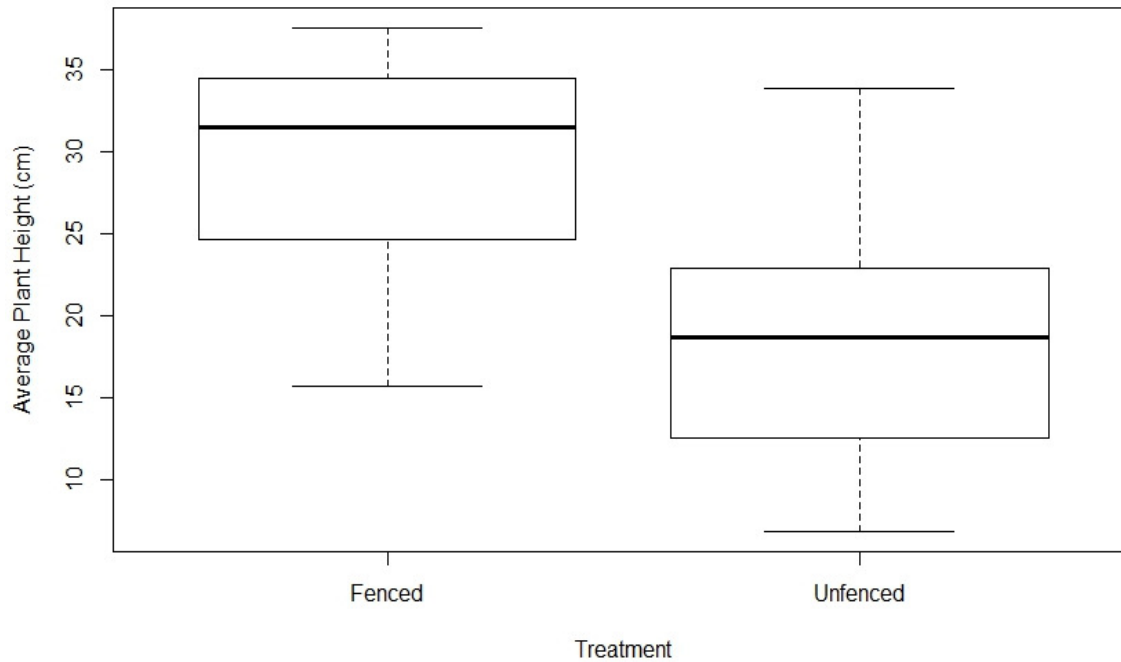


Figure 2.4. Boxplot representing the difference in average plant height (cm) between the treatments of fenced (ungrazed) and unfenced (grazed) plots. Fenced treatments had significantly higher plant heights than unfenced treatments.

To test for community level differences between treatments, four indices of diversity were used: Simpson's Index of Diversity, Shannon-Wiener Index, Evenness, and Richness. SID was not influenced by treatment or plant height alone ( $F_{1,14.532} = 1.6963$ ,  $p = 0.213$ ,  $F_{1,18.755} = 3.3685$ ,  $p = 0.082$  respectively). Despite a lack of statistical significance, there was some indication of an interaction effect between plant height and treatment on SID ( $F_{1,14.447} = 3.1446$ ,  $p = 0.097$ ): as plant height increased, diversity increased in unfenced plots (Figure 2.5).

SWI was likewise not influenced by treatment or average plant height ( $F_{1,14.425} = 1.4957$ ,  $p = 0.241$ ,  $F_{1,18.747} = 1.2078$ ,  $p = 0.286$  respectively) and there was no difference between the slopes by treatment ( $F_{1,14.339} = 1.3901$ ,  $p = 0.258$ ). Treatment and average plant height had no



effect on E ( $F_{1,20} = 0.002$ ,  $p = 0.967$ ,  $F_{1,20} = 2.735$ ,  $p = 0.114$  respectively). There was also no significant interaction between treatment and plant height ( $F_{1,20} = 0.038$ ,  $p = 0.847$ ). Average plant height did not significantly affect R ( $F_{1,19.939} = 0.009$ ,  $p = 0.923$ ) nor did the slopes of R's response to average plant height differ between the treatments ( $F_{1,17.008} = 2.8797$ ,  $p = 0.108$ ). While not significant, there was a trend toward an increase in R in fenced plots compared to unfenced ( $F_{1,16.874} = 3.796$ ,  $p = 0.068$ ).

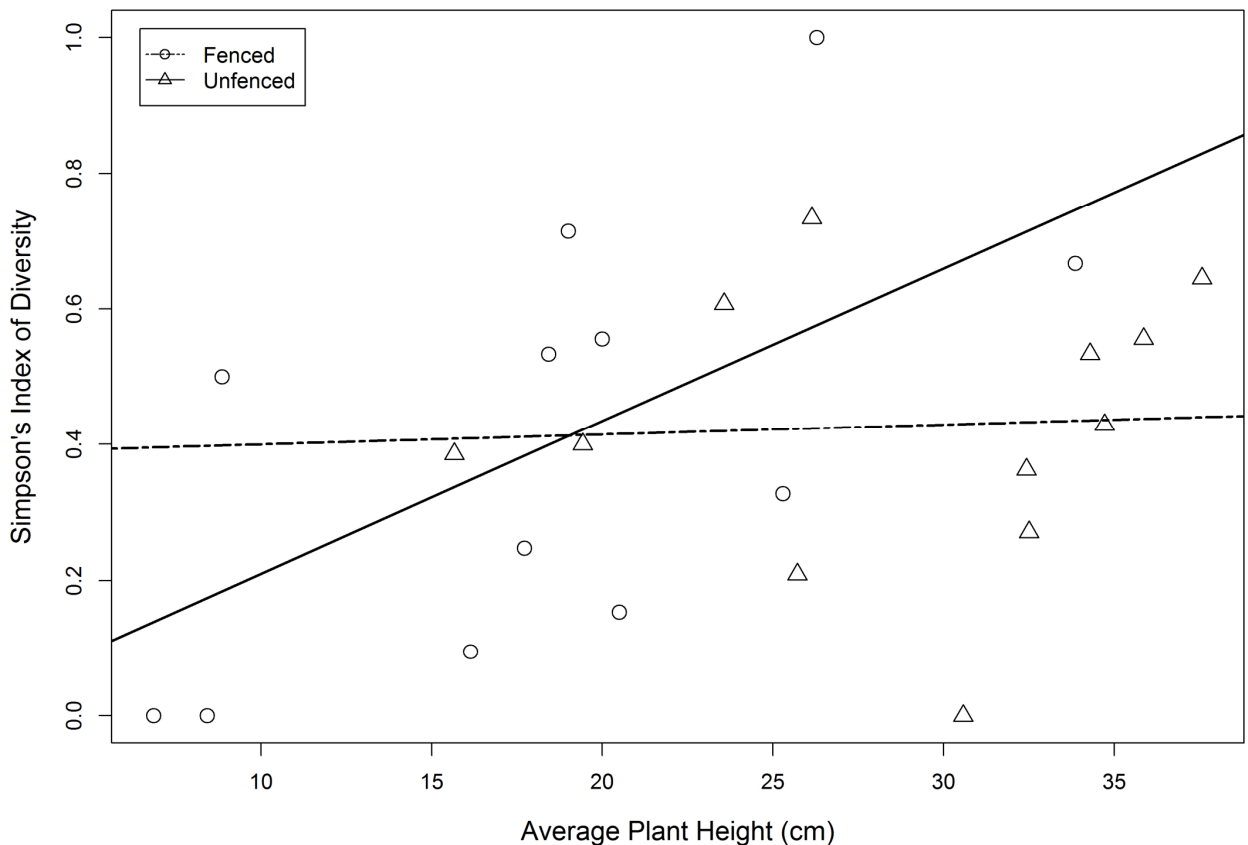


Figure 2.5. The relationship between Simpson's Diversity Index and average plant height. Circles indicate fenced (ungrazed) grids and triangles indicate unfenced (grazed) grids. The dotted slope is the relationship of the fenced (ungrazed) grids and the solid line is in reference to the unfenced (grazed) grids. While the relationship was not significant, a positive trend of greater diversity as plant height increases in unfenced grids was suggested.

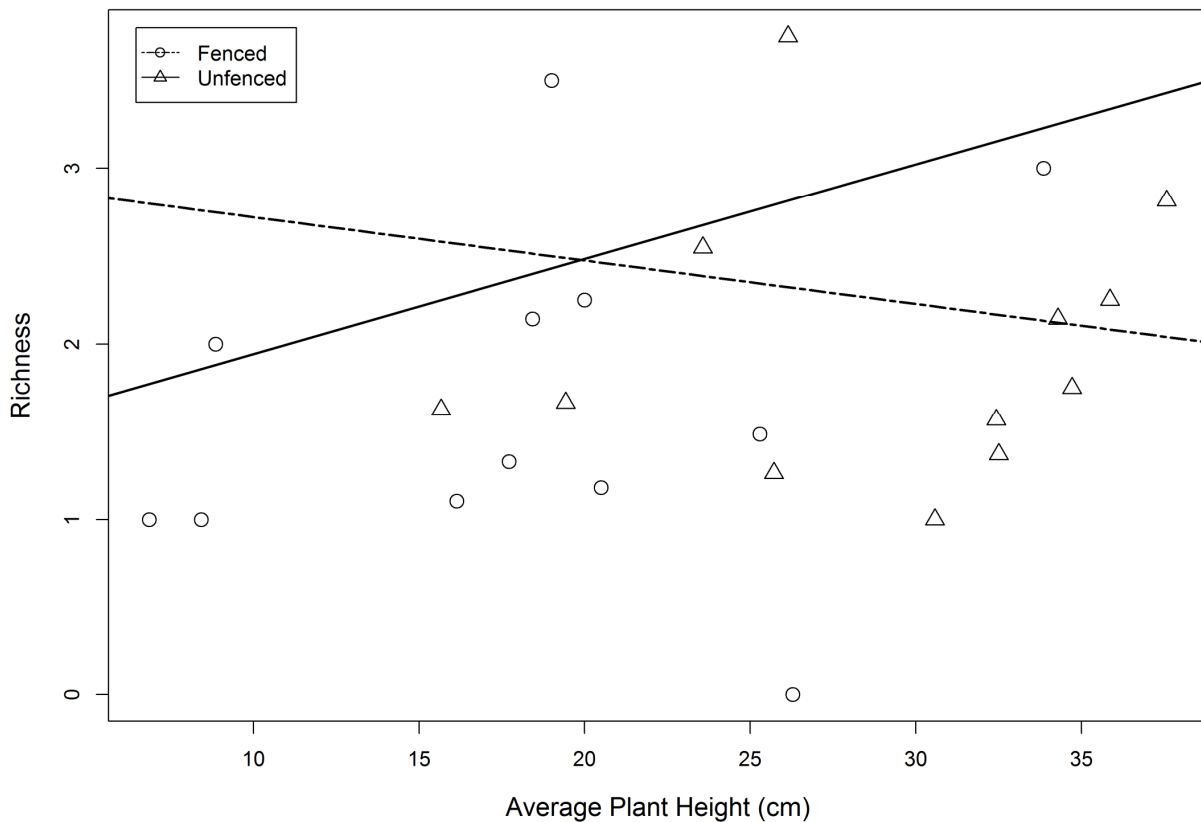


Figure 2.6 The relationship between R and average plant height. Circles indicate fenced (ungrazed) grids and triangles indicate unfenced (grazed) grids. The dotted slope is the relationship of the fenced (ungrazed) grids and the solid line is in reference to the unfenced (grazed) grids. Increasing numbers on the y-axis are related to higher richness. While not significant, there appears to be a positive trend of greater richness as plant height increases in unfenced grids.

## Discussion

Despite the fact that fenced sites had significantly taller plant heights (Figure 2.4), there were no statistically significant relationships between diversity of small mammal species and grazing treatment. This may suggest that grazing does not have major impacts on small mammal biodiversity in the Shenyenne National grasslands in the short term, i.e., within a single summer. Due to low capture rates and relatively low number of species captured, this is not unexpected (Schmidt et al. 2005). The lack of significance in regards to Evenness is also not surprising, and

may be a function of different plant composition at each of the sites (Table 2.1; Grant and Birney 1979).

Although not statistically significant, the data do suggest some potentially biologically relevant inferences. For example, as plant height increased, SID also increased in unfenced grids. While this relationship was absent in fenced plots, it may suggest that taller plant height averages in general result in greater small mammal abundances. R also tended to increase between the two treatments, where R was higher in ungrazed grids than grazed. This suggests that a higher variety of species are utilizing areas with taller plant height.

The presences of the significant plant height differences between the two treatments and the lack of relationship in other aspects of diversity suggest potential effects of habitat fragmentation and edge effects. Ungrazed treatment grids could be considered one of a number of small patches than can only provide for certain abundances of individuals. The lack of continuous habitat increases the number of individuals that may immigrate and emigrate from a patch (Fahrig 2003). Because the fences did not exclude small mammals from leaving or entering they may utilize areas of taller plant height for foraging due to increased biomass and also added protection from predators by increased cover. This usage may not, however, result in individuals avoiding grazed areas. For example, ground squirrels tend to forage in areas of dense vegetation, but prefer areas with short vegetation for burrow creation due to increased predator detectability (Downey et al. 2006, Bylo et al. 2014).

While no strong statistical effects were found, this may have been due to several ways in which this study might have lacked power. Relative to plant diversity, small mammal diversity is low in tallgrass prairie, totaling just nineteen trappable species in the Sheyenne National Grassland (Table 2.2). Additionally, capture and recapture rates were low, with only 269

individuals being captured and only 31 being captured more than once. This could be attributed to the boom and bust cycles that many rodents exhibit (Krebs 1996). Weather related events could also be attributed to the decline. While December of 2013 had high precipitation (2.3cm), January and February of 2014 were dry in comparison to years prior (1cm, and 0.5cm respectively) (Mullins 2014). Litter dwelling species such as *Peromyscus maniculatus* and *Microtus pennsylvanicus* may have higher mortality than average due to a lack of snowfall, as there was less insulation and protection from predation and low temperatures. Logistically, only twelve sites were surveyed, which may not be enough to detect community responses in the short-term. The treatment grids were also set up 10m away from each other, which potentially allows for animals to move easily between treatments and utilize sites differently, such as preferring one treatment for better forage or protection.

Significant effects of domesticated cattle on small mammal communities were not strongly apparent but requires further study. Regardless, North American grasslands are still highly endangered, and conserving species in this rare environment is biologically relevant. While no directional recommendations can be proposed in reference to grazing of the Sheyenne National Grassland, mindful management practices should be promoted. Rotational grazing and patch/burn grazing techniques are becoming highly regarded in terms of maintaining plant heterogeneity (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Cummings et al. 2007), which in turn should have positive effects on small mammal, bird, and invertebrate communities. Employing multiple management strategies to combat invasive plants and to make up for the lack of corridors present could secure the future of the Sheyenne National Grassland.

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## APPENDIX

Figure 1.1. includes a simulated example of the hypotheses regarding the relationships between density dependence, population size variability, and extinction risk. Populations were simulated according to a theta-logistic model of population growth:

$$N_{t+1} = N_t e^{r \left( 1 - \left( \frac{N_t}{K} \right)^\theta \right) + \varepsilon(0, \sigma^2)}$$

where  $N$  corresponds to population size at time  $t$  or  $t+1$ ,  $K$  corresponds to carrying capacity,  $r$  corresponds to the population growth rate,  $\theta$  is the shape of density-dependence, and  $\varepsilon$  is random variation in population size changes with a mean of 0 and variance of  $\sigma^2$ . All populations were simulated with starting population sizes of 50,  $r = 1$ , and  $K = 100$  (A, B, D, F). “Lower Density Dependence” (A & B) populations were generated with a  $\theta$  of 1 while “Higher Density Dependence” (D & E) populations were generated with a  $\theta$  of 0.5. These different  $\theta$ 's had the effect of increasing the strength of density dependence below  $K$  for D & E relative to A & B.  $\sigma^2$  was set to 0.1 and 0.2 for the low and high variation populations respectively. Cumulative probability of extinction was calculated according to Morris and Doak (2004) (C & F). Populations with a lower strength of density-dependence below  $K$  had a higher probability of extinction than those with a higher strength of density-dependence and populations with higher population size variability also experienced greater extinction risk.