A Mechanistic Examination of Interspecific Competition Between Wild and Domestic Herbivores

Courtney Check
Utah State University

Follow this and additional works at: https://digitalcommons.usu.edu/etd

Part of the Animal Sciences Commons, and the Environmental Sciences Commons

Recommended Citation
Check, Courtney, "A Mechanistic Examination of Interspecific Competition Between Wild and Domestic Herbivores" (2023). All Graduate Theses and Dissertations, Spring 1920 to Summer 2023. 8863.
https://digitalcommons.usu.edu/etd/8863

This Thesis is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations, Spring 1920 to Summer 2023 by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.
A MECHANISTIC EXAMINATION OF INTERSPECIFIC COMPETITION

BETWEEN WILD AND DOMESTIC HERBIVORES

by

Courtney Check

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Simona Picardi, Ph.D.
Major Professor

Tal Avgar, Ph.D.
Committee Member

Garrett Street, Ph.D.
Committee Member

Kari Veblen, Ph.D.
Committee Member

D. Richard Cutler, Ph.D.
Vice Provost of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2023
ABSTRACT

A Mechanistic Examination of Interspecific Competition Between Wild and Domestic Herbivores

by

Courtney Check, Master of Science

Utah State University, 2023

Major Professor: Dr. Simona Picardi
Department: Wildland Resources

Competition plays a key role in ecological processes, including individual fitness, population dynamics, community composition, and species evolution. However, competition can be challenging to study in the field, and the mechanism of competition is often assumed a priori without examination of alternative hypotheses. My research compares two hypotheses for competition between mule deer (*Odocoileus hemionus*) and domestic cattle (*Bos taurus*) (forage and shade competition), and one noncompetitive mechanism of cattle effects on deer space use and behavior. Using a remote camera grid, I explored how deer abundance changes in response to forage, shade, and predation risk, and whether cattle abundance influences these responses. Using GPS location data from over 300 collared deer, I also explored how deer foraging, resting, and commuting behavior changes in response to cattle density across several hundred grazed pastures. I found that, whereas cattle abundance and deer abundance are positively related, cattle abundance had a negative effect on deer abundance in forage-rich areas, indicating that these species likely compete for vegetation. Supporting this, cattle density had a positive
effect on the probability of deer to be in a foraging state. This may be because deer must spend more time foraging to meet their nutritional needs on cattle pastures, or because cattle abundance and forage availability are correlated. I also found that deer are less likely to be in a commuting state when cattle are present, though the reasons for this change are unclear. I found no indication of shade competition between deer and cattle, or any evidence that cattle impact predation risk in deer. Overall, my findings indicate that forage competition occurs between deer and cattle, and that the presence of competitors can alter space use and behavior in large herbivores. My work also demonstrates the importance of using multiple data streams and evaluating alternative hypotheses when assessing competition in the field. Managers should take forage competition into account when balancing their goals for livestock, deer population size, and rangeland health.

(98 pages)
A Mechanistic Examination of Interspecific Competition Between Wild and Domestic Herbivores

Courtney Check

Large herbivores, such as mule deer and cattle have similar life histories and likely compete for resources. However, quantifying the extent to which these species compete and the specific resources they compete for has proved challenging. My research examines if cattle influence deer abundance and behavior due to competition for forage, competition for shade, and/or by affecting the predation risk of deer. Using a grid of autonomous trail cameras, I was able to determine if cattle abundance influences local deer abundance in relation to specific resources and habitat features. Using GPS data from collared deer, I was also able to examine if cattle density affects the probability that a deer was in a foraging, resting, or commuting state. I found evidence that cattle abundance reduces deer abundance in forage-rich areas, indicating that these species are likely competing for forage. Likewise, I found that cattle density increases the probability that a deer is foraging, and reduces the probability that a deer is commuting. Behavioral data is difficult to interpret, but this may suggest that deer must compensate for having less forage available due to competitors by spending more time foraging. However, it is also possible that cattle are merely an indicator of good habitat, so deer are more likely to forage in areas where cows are present. I did not find any compelling evidence of shade competition or predation risk effects between deer and cattle. My work demonstrates that it is important to examine many different data sources when trying to assess competition
between large herbivores, and to not just assume what resources are driving competition. Additionally, my work demonstrated that forage competition occurs between mule deer and cattle, so managers should take this into account when balancing their goals for livestock, mule deer, and rangeland health.
ACKNOWLEDGMENTS

This research was conducted on the territories of the eight tribes of Utah: the Confederated Tribes of the Goshute Indians, Navajo Nation, Ute Indian Tribe, Northwestern Band of Shoshone, Paiute Indian Tribe of Utah, San Juan Southern Paiute, Skull Valley Band of Goshute, and White Mesa Band of the Ute Mountain Ute. These Nations have been living and caring for these lands since time immemorial, and it carries the stories of their struggles for survival and identity.

It feels weird to submit a thesis that only has my name on it, because I don’t believe any scientific endeavor has truly been completed by just one person. And in the case of this thesis, there are so many people who made it possible.

I owe the biggest thank-yous to my advisors, Dr. Simona Picardi and Dr. Tal Avgar for guiding me through this whole process. Simona, I am so grateful that you always pushed me to think about the bigger picture of my research and stay focused on what was important without getting bogged down in frivolous details. Thank you for stepping in to support me when I needed it. Tal, I appreciate that you never let me settle for ‘good enough’ and always encouraged me to questions my assumptions. Thank you for taking a chance on me and finding space in your lab for me three years ago. Both of you have made me a better scientist and I will try to carry what I’ve learned from you forward in everything I do. I also cannot thank you both enough for all the encouragement over the years – it has helped me find confidence in myself and have the courage to continue pursuing research, even when I felt out of place or inadequate.
are both phenomenal scientists and, more importantly, genuinely kind and generous humans.

I would also like to thank my co-advisor Dr. Garrett Street and my committee member Dr. Kari Veblen for their insight and guidance with this work. Garrett, you were extremely helpful for honing the focus of this study and determining the best course of analysis. Kari, your edits to my proposal and thesis were amazingly thoughtful and helpful, and you also provided the impetus for me to create some of the best conceptual figures I have ever made. Thank you both for your time and expertise.

Thank you to my funding sources, primarily the USDA Advancing Agricultural Research through High-Performance Computing (AAR-HPC) initiative, a collaborative agreement between Mississippi State and the USDA-Agriculture Research Service. I would also like to thank the Utah State University Department of Wildland Resources, the Ecology Center, and the Utah Agricultural Experiment Station for providing me with grants for travel and field work. I am also extremely grateful to the Utah Department of Natural Resources and the Utah Migration Initiative for allowing me access to their impressive database of mule deer GPS locations, and to the United States Forest Service for their assistance in collecting cattle stocking data.

I owe a huge thank you to all of my lab mates in the Space-Use Ecology lab, (in no particular order) Brian Smith, Ronan Hart, Veronica Winter, Dani Berger, John Huang, and Megan Whetzel, who provided input and assistance over the entire course for this project. Thank you for the many hours spent troubleshooting code, giving writing feedback, redesigning data management protocols, and just having fun. I owe a particular thank you to Megan Whetzel, who has been my partner in the field and lab since day one,
and whose camaraderie is the only thing that made clipping 400 quadrats of vegetation bearable. Thank you for showing me that aspen are pretty neat. I also want to give a special thank you to Ronan Hart, forever my roommate in my heart, who I owe for never failing to answer my Google Earth Engine questions at 9pm at night and for letting me co-parent his cat Milo for the last few years. I also would like to thank Brian Smith for near singlehandedly improving my coding skills by ten-fold, always having the time to explain a statistics concept or give advice on my project, and teaching me mysterious the ways of “networking.” And lastly, a big thank you to Dani Berger for providing incredible writing advice and also being a wonderful colleague the last few years. I feel so lucky to have been a part of this lab group, and can’t wait to see all of the incredible things you all do.

Thank you to all of my field technicians over the years, in particular Emily Bonebrake and Emily Onderbeke, who together tagged almost all of the 325,000 trail camera photos used in this study. In no particular order, Christian Knudson, Kate Huffman, Kevin Check, Quinn Herbine, Shannon Whetzel, Emily Lane, Reggie Ekorus, Brooklyn Harris, Sierra Campbell, Dylan Lipscomb, Daralyn James, Mike Clark, and Giulia Mantero also contributed invaluable time and energy to data collection for this project. No field study would be possible without technicians, and I would not have completed this degree without your assistance.

Lastly, I would be remiss to not sincerely thank all of the friends who have helped me along the way with their encouragement and support, and for (occasionally) providing a welcome distraction from work. To everyone who I have hiked, skied, birded, swam, built, cooked, laughed with over the last few years: you will always have a special place
in my heart. Thank you to Aimee Van Tatenhove for always being up for an adventure. Thanks to Caroline Kittle for always picking up the phone when I needed it. Thanks to my oldest friends, Megan Massa and Erin Eichenberger for being a steady presence in my life. And thanks to Soren Struckman for always getting me where I needed to go.

Courtney Check
CONTENTS

Abstract ............................................................................................................................ iii
Public Abstract ................................................................................................................ v
Acknowledgments ........................................................................................................... v
List of Tables ..................................................................................................................... xii
List of Figures .................................................................................................................. xiii
Chapter I Introduction ..................................................................................................... 1
  References ...................................................................................................................... 5
Chapter II Abundance Response of Mule Deer to Interspecific Competition with Cattle . 8
  Abstract ......................................................................................................................... 8
  Introduction ..................................................................................................................... 9
  Methods .......................................................................................................................... 16
    Study Area .................................................................................................................. 16
    Data Collection .......................................................................................................... 17
    Density Estimation ..................................................................................................... 19
    Statistical Analysis ................................................................................................... 19
  Results ........................................................................................................................... 24
  Discussion ..................................................................................................................... 30
  References ...................................................................................................................... 34
Chapter III Behavior Response of Mule Deer to Interspecific Competition with Cattle.. 40
  Abstract ......................................................................................................................... 40
  Introduction ..................................................................................................................... 41
  Methods .......................................................................................................................... 47
    Data Collection .......................................................................................................... 47
    Behavioral Segmentation ............................................................................................ 49
    Post-hoc Analysis of Behavioral Segmentation ........................................................... 50
    Bootstrapping ............................................................................................................. 51
  Results ........................................................................................................................... 24
  Discussion ..................................................................................................................... 30
  References ...................................................................................................................... 34
Chapter 4 Conclusion ....................................................................................................... 66
Management Implications .......................................................................................... 68
References .............................................................................................................. 69

Appendices .............................................................................................................. 70

Appendix A. Chapter 2 Tables and Figures .............................................................. 71
Appendix B. Chapter 3 Tables and Figures .............................................................. 83
LIST OF TABLES

Table A.1. Null Model Output ................................................................. 71
Table A.2. Instantaneous Cattle Abundance Only Model Output .................. 72
Table A.3. Cumulative Cattle Footprint Only Model Output ............................ 73
Table A.4. Forage Competition Model Output ............................................. 74
Table A.5. Shade Competition Model Output ................................................. 75
Table B.1. Indirect Predation Risk Model Output .......................................... 83
Table B.2. Indirect Predation Risk Model Output .......................................... 83
**LIST OF FIGURES**

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 1</td>
<td>Conceptual Diagram of Potential Deer Abundance Responses to Cattle</td>
<td>16</td>
</tr>
<tr>
<td>Figure 2</td>
<td>Deer Abundance Response to Cattle Abundance</td>
<td>25</td>
</tr>
<tr>
<td>Figure 3</td>
<td>Deer Abundance Response to Forage Competition (Instantaneous Cattle)</td>
<td>26</td>
</tr>
<tr>
<td>Figure 4</td>
<td>Deer Abundance Response to Forage Competition (Cumulative Cattle)</td>
<td>27</td>
</tr>
<tr>
<td>Figure 5</td>
<td>Deer Abundance Response to Shade Competition</td>
<td>28</td>
</tr>
<tr>
<td>Figure 6</td>
<td>Deer Abundance Response to Indirect Predation Risk</td>
<td>29</td>
</tr>
<tr>
<td>Figure 7</td>
<td>Conceptual Diagram of Potential Deer Behavior Responses to Cattle</td>
<td>47</td>
</tr>
<tr>
<td>Figure 8</td>
<td>Fitted HMM Step Length and Turning Angle Distribution</td>
<td>53</td>
</tr>
<tr>
<td>Figure 9</td>
<td>Dirichlet Coefficients (Bootstrapped)</td>
<td>55</td>
</tr>
<tr>
<td>Figure 10</td>
<td>Deer Foraging Response to Forage Competition</td>
<td>56</td>
</tr>
<tr>
<td>Figure 11</td>
<td>Deer Resting Response to Shade Competition</td>
<td>57</td>
</tr>
<tr>
<td>Figure 12</td>
<td>Deer Commuting Response to Indirect Predation Risk</td>
<td>58</td>
</tr>
<tr>
<td>Figure A.1</td>
<td>Deer Abundance to Terrain Features</td>
<td>77</td>
</tr>
<tr>
<td>Figure A.2</td>
<td>Deer Abundance to Vegetation Features</td>
<td>78</td>
</tr>
<tr>
<td>Figure A.3</td>
<td>Deer Abundance to Shade</td>
<td>79</td>
</tr>
<tr>
<td>Figure A.4</td>
<td>Deer Abundance to Predation Risk</td>
<td>80</td>
</tr>
<tr>
<td>Figure A.5</td>
<td>Map of Trail Cameras</td>
<td>81</td>
</tr>
<tr>
<td>Figure A.6</td>
<td>Trail Camera Setup Diagram</td>
<td>82</td>
</tr>
<tr>
<td>Figure B.1</td>
<td>Map of Deer GPS Locations</td>
<td>84</td>
</tr>
</tbody>
</table>
CHAPTER 1
INTRODUCTION

Competition is a type of species interaction that may have cascading effects on individual fitness, population dynamics, species distribution, community composition, and biodiversity. Historically, the existence and strength of competition between species has been assessed by quantifying negative demographic effects of one species on another. However, the difficulty of evaluating competition in the field and a lack of consideration for alternative hypotheses about the drivers of species’ population changes has led to debate over the importance of interspecific competition in structuring ecological communities (Connell et al. 1983, Grace et al. 1991, Schoener 1983, Wiens 1977, Betini et al. 2017). Simply establishing that species negatively affect one another’s fitness does not identify the mechanisms driving competition, and even detecting competitive interactions can be dependent on species’ relative abundances. Furthermore, focusing solely on population-level increases and decreases in abundance may obscure the fine-scale nuances in how competitive pressures shape behavior and space use. While decades of research on plant communities have now provided insight on plant responses to competitive pressures, studies of competition in animal communities have proven to be much scarcer, and are often limited to taxa that can be easily manipulated in experimental settings such as rodents and insects, rather than characterization of a natural field environment.

In large herbivores competition is believed to shape species coexistence, with cascading consequences on community structure. Because forage is commonly a shared, limited resource among large herbivores, many species have evolved dietary
specializations as a way of circumventing potential competitive conflict, with sympatric species often existing along a continuum of grazers and browsers (Kartzinel et al. 2015). However, there can still be considerable overlap among mixed-strategy species. Furthermore, competitive interactions are not uniform through space and time, and can vary based on environmental factors or population density (Kimuyu et al. 2017). For instance, seasonality can lead to periods of resource scarcity, when competition has more pronounced effects on the behavior and fitness of competing species (Chaikina and Ruckstuhl 2006, Odadi et al. 2011, Raborn et al. 2004, Stears and Shrader 2020). Likewise, resource depletion and its consequences on individual fitness will be greater with increasing competitor density (Carrete et al. 2006, Stewart et al. 2011). However, individuals may adjust their behavior and space use at high competitor densities to compensate for reduced per-capita resource availability (Ferretti and Fattorini 2020, Mobæk et al. 2009, van Beest et al. 2014, van Beest et al. 2016). Indeed, observational reports suggest that large ungulates rarely engage in direct behavioral interference, and more commonly simply adjust their space-use in response to competitors by temporally dividing resource use, or ranging into suboptimal habitats in search of resources (Ferretti and Mori, 2020, Valeix et al. 2007). Therefore, at least among large herbivores, it is important to not only consider the overall fitness effects of competition, but also the spatial and behavioral effects. For example, the negative fitness effects of interspecific competition may be weakened if one species is able to move into and utilize alternative habitats when a competitor is present, though the species’ spatial distribution and resource use would look drastically different than if it had no competitors. Space use is
therefore an easier method of quantifying competition in some ways, since fitness effects may take generations to manifest, can be weakened via behavioral modification, and can be difficult to tie explicitly to competition.

Livestock grazing is a pervasive form of land use across the globe that, in addition to reshaping vegetation structure through direct consumption and trampling, can introduce a potential competitor to wild large herbivores inhabiting these rangelands (Filazzola et al. 2020, Kohler et al. 2004, Riginos et al. 2012). In recent decades, competition between mule deer (*Odocoileus hemionus*) and domestic cattle (*Bos taurus*) has received substantial interest due to the economic importance of both species (cattle as livestock, deer as game species). However, there remain many lingering questions about its existence, the mechanisms that drive it, and its strength in natural settings. Competition between these species is usually quantified based on dietary or habitat overlap, but there are inherent issues with these metrics. Dietary overlap can fluctuate greatly based on seasonal and regional factors and may be misleading if competitive exclusion forces one species to consume less preferred forage. For example, some studies of mule deer and domestic cattle diets calculate forage overlap to be as low as 15%, while others estimate it to be as high as 51% (Campbell and Johnson 1983, Faber 2017, Hansen and Reid 1975). Studies examining the seasonal diet overlap between these species also vary wildly in their assessments; winter, fall, and/or spring have all been identified as the period of greatest overlap depending on the study (Beck et al. 2005, Frisinia et al. 2008, Mackie et al. 1970, Tortenson et al. 2006, Wagoner et al. 2013). Likewise, habitat overlap is often quantified on the basis of co-occurrence, which is an inherently
problematic metric for assessing ecological interactions due to confounding variables (Blanchet et al. 2020). Because both diet and habitat overlap are commonly assessed through observational data (fecal samples, habitat use, etc.) they also capture only what resources animals are able to use (i.e. realized niche) rather than the full set of potential resources available to them (i.e. fundamental niche) (Behmer and Joern 2008). If the realized niche is indeed constrained by competition, its interspecific overlap should be a poor indicator of competition.

To accurately understand and quantify potential competitive relationships between wild and introduced herbivore species, it is essential to examine space use in addition to dietary and habitat overlap metrics. Quantifying competition based only on diet and habitat overlap necessarily requires an assumption that these two species compete for forage, and does not account for reduced niche capacity in the presence of competitors. Furthermore, it fails to account for alternative avenues of competition between these species and ignores non-competitive explanations for species responses. Understanding how an organism’s space use changes in the presence of competitors may also provide a deeper insight for how competition shapes communities, beyond just demographic effects. Space use is a critical tool for mobile organisms to manage stressors and acquire resources, and changes in individual space use can result in large-scale changes to the distribution of populations and the resources consumed and/or provided by competing species (Nathan et al. 2008). My thesis research will improve upon previous studies of competition in large herbivores by identifying specific, localized spatial and behavioral responses of mule deer to competitors and evaluating multiple possible
avenues for competition (e.g. forage and thermal refuges) as well as alternative drivers of space-use change (e.g. cattle reducing the effectiveness of deer anti-predator response).

References


Ferretti, F., and Mori, E. 2020. Displacement interference between wild ungulate


Riginos, C., Porensky, L.M., Veblen, K.E., Odadi, W.O., Sensenig, R.L., Kimuyu, D.,


CHAPTER 2

ABUNDANCE RESPONSE OF MULE DEER TO INTERSPECIFIC COMPETITION WITH CATTLE

Abstract

Livestock grazing has altered ecosystems globally and introduced a new potential competitor for large herbivores. In the western United States, competition between cattle (Bos taurus) and mule deer (Odocoileus hemionus) has been a source of interest to managers for decades, but previous research has provided inconclusive evidence. Using a grid of 108 autonomous trail cameras, I examined deer abundance relationship with cattle abundance in the context of three specific hypotheses that may drive potential negative relationships: competition for forage, competition for shade, and indirect increase predation risk. I found that deer abundance in forage-rich areas declined as cattle abundance increased, indicating that forage competition occurs in these species. I found no evidence that cattle abundance modified deer abundance as it relates to shade or predation risk. Interestingly, I found that in the absence of specific limiting resources, deer and cattle abundances are significantly positively correlated, demonstrating that they likely rely on similar habitats. My findings therefore provide a rare field example of why co-occurrence data cannot be relied upon for assessing ecological interactions, and clarify the existence and mechanism of interspecific competition in these species.
Introduction

Ecosystems globally have undergone widespread perturbations due to anthropogenic influences, with introduced competitors being one such form of disturbance (David 2017, Mollot 2017). Introduced species may outcompete their native counterparts for resources such as food or space, and can alter ecosystem balance by worsening environmental stressors, such as predation risk (Bennett et al. 2011, Dangremond et al. 2010, Shinen and Morgan 2009). While invasive exotic species are the most commonly examined form of biotic disturbance to ecosystems, domestic species such as livestock are another potentially damaging form of introduced competitor. Livestock grazing is pervasive across rangelands worldwide, and there is a growing interest in understanding how the presence of domestic grazers affects native species, particularly other large herbivores (Pozo et al. 2021). Domesticated and wild herbivores are particularly likely to have competitive effects on one another, as these species have not had the chance to evolve distinct dietary specializations like other sympatrically evolved herbivores (Kartiznel et al. 2015). Introduced livestock can alter vegetation communities through plant removal, trampling, and deposition of feces (Filazzola et al. 2020, Kohler et al. 2004, Riginos et al. 2012). In systems that evolved with intense grazing, these effects can bolster plant species richness by creating landscape heterogeneity and promoting nutritious forage regrowth (Clark et al. 2000, Humphrey et al. 2000, Liu et al. 2015). However in some cases, livestock grazing has also been shown to reduce biodiversity, encourage the growth of invasive plant species, and reduce the
amount of forage available to wild herbivores (Kimball et al. 2003, Leege et al. 1981). The direction and magnitude of cattle grazing effects likely has to do with a variety of contextual factors such as timing, intensity, and historical grazing regime (Davies and Boyd 2020). While many studies have attempted to quantify the impact of forage competition from livestock, few have examined the spatial effects of interspecific competition between domestic and wild herbivores.

Cattle grazing is ubiquitous in the American West, and potential competition between cattle and mule deer has been a source of interest to managers for decades. State and federal agencies operate under the principles of multiple-use management, and must balance the many competing uses of western rangelands such as ranching, hunting, forestry, recreation, and wildlife habitat (Carter et al. 2019, Danvir et al. 2018). Mule deer are a highly valued game species throughout much of the western United States, and their population sizes are carefully monitored by many state agencies. In recent years, there have been concerns regarding migratory barriers and loss in this species, as well as population declines in some regions (Sawyer et al. 2009). Similarly, cattle are an important economic resource in the West and many state and federal agencies are charged with ensuring the stability of this resource, while also maintaining rangeland health. Because mule deer and cattle have similar habitat requirements, understanding if and how these two large ungulates compete is essential to guiding management goals.

Previous research has attempted to elucidate competitive interactions in these species through diet and habitat overlap. As is thought to be common among large grazers, there is evidence suggesting deer and cattle utilize different vegetation types to
avoid competing. Several studies have found that deer tend to eat a higher proportion of forbs and a lower proportion of grasses than cattle (Campbell and Johnson 1981, Faber 2017, Findholt et al. 2004). However, estimates of dietary overlap vary greatly, and do not account for competitive exclusion reducing the realized niche of either species in the first place (Campbell and Johnson 1983, Findholt et al. 2004, Hansen and Reid 1975). Competitive exclusion is particularly likely in the case of mule deer, which are forage generalists and can take advantage of subpar foods when necessary (Staudenmaier et al. 2022). Studies of habitat overlap have found that mule deer generally use areas where cattle are present less; however, simply using co-occurrence data to infer species interactions is problematic, as it may obscure species interactions when there is very strong competition (i.e. exclusion occurs before interactions can be observed) or when two species rely heavily on the same resource (i.e. species appear to have a positive relationship when in fact their abundance is related to a shared factor) (Loft et al. 1991, Stewart et al. 2002). Additionally, simply observing general changes in species abundance due to competitor presence or density does not clarify the mechanism of competition between these species, though it is often a priori assumed to be forage-related. To truly understand if and how competitive interactions between cattle and mule deer affect their spatial distribution, specific hypotheses regarding the mechanism of competition between these species must be identified and tested in relation to their space use.

In the first chapter of my thesis research, I will explore whether the presence of a competitor (cattle) causes changes in the local abundance of another large herbivore
(mule deer) and whether competition is driving these changes. If mule deer and cattle do compete, it is likely the deer are the weaker competitor and change their space use in response to cattle. Previous research has shown that larger ungulates tend to have a competitive advantage over smaller species, and adult cattle are considerably larger than even the largest mule deer (Ferretti and Mori, 2019). Livestock have also previously been shown to have a displacement effect on other large herbivores such as elk (Chaikina and Ruckstuhl 2006, Fritz et al. 1996, Stewart et al. 2002). Furthermore, cattle are anthropogenically distributed, and therefore cannot undergo distribution and/or demographic shifts even in a highly competitive environment. Quantifying if and to what extent mule deer are displaced by cattle may aid managers in understanding localized mule deer population declines and how they can bolster local deer abundances. Additionally, it can provide insight on how competition among large herbivores shapes the spatial structure of their communities.

I propose three alternative hypotheses for why cattle may alter the local abundances of mule deer (Figure 1):

**H1 (Forage Competition Hypothesis):** *Cattle are dominant competitors for forage, forcing deer to utilize otherwise suboptimal forage patches.*

As ruminants, deer and cattle primarily consume herbaceous forage throughout the year. Some studies have found diet overlap to be weak between these species; a fecal analysis by Findholt et al (2004) found 19% overlap between deer and cattle, and Campbell and
Johnson (1983) found cattle and mule deer diets overlap by 15%. However, Hansen and Reid (1975) found up to 38% overlap between deer and cattle, and a recent study using DNA metabarcoding to identify plant species in fecal samples estimated 51% overlap between deer and cattle (Faber, 2017). In general, differences in diet between these two ungulates are attributed to variation in forb and grass selection. Cattle generally eat a higher proportion of grasses than mule deer, which eat a higher proportion of forbs (Cambell and Johnson 1981, Faber 2017, Findholt et al. 2004). However, competition for herbaceous vegetation can increase when areas are overgrazed, or in seasons when plant growth is limited (Chaikina and Ruckstuhl 2006, Lucich and Hansen 1981, Olsen and Hansen 1977). If these species are substantially competing for forage, then I would expect to see fewer deer than expected in forage-rich areas when cattle are present (P1a), with this effect becoming greater as cumulative cattle presence over the last month increases (P1b).

**H2 (Shade Competition Hypothesis):** Cattle are dominant competitors for shade, forcing mule deer to alter their space use patterns to find shade in suboptimal habitats.

Multiple studies have demonstrated that ungulates, including mule deer, and cattle will seek out habitats that provide thermal cover from extreme temperatures (Cain et al. 2006, Mysterud and Østbye 1999). As solar radiation increases, both of these species select habitats with greater canopy cover, often bedding down while they dissipate body heat (Bennett et al. 1985, Cain et al. 2006, Millspaugh et al. 1998, Sargeant et al. 1994).
Seeking cover during periods of intense solar radiation allows these species to maximize convective heat loss and better regulate their body temperatures (Parker and Robbins 1983, Sargeant et al. 1994). In arid regions, where vegetative cover can be scarce, ungulates may compete for a small number of shaded patches on the landscape. Previous research has shown that deer may select areas with low-to-moderate tree cover to avoid heat stress (Ager et al. 2003, Morano et al. 2019). As with forage, competition for this resource may also vary temporally, with competition occurring primarily during periods of greatest thermal stress. If deer and cattle are competing for shade, then I would expect to see fewer deer than expected in shaded areas during hours of thermal stress when cattle are present (P2).

**H3 (Indirect Predation Risk Hypothesis):** Cattle are noisy and/or smelly and inhibit the ability of mule deer to detect predators, causing deer to avoid them to reduce mortality risk.

Mule deer may also avoid cattle for reasons other than direct competition. In Utah, mule deer face predation pressure from cougars, and may select habitats where it is easier to avoid or detect predators to lessen predation risk (Lowrey et al. 2019). Vegetation height and complexity influence the ability of both prey and predators to conceal themselves, and cervids have been shown to select for vegetative characteristics that minimize predation risk (Altendorf et al. 2001, Atwood et al. 2009, Frair et al. 2005, Lowrey et al. 2019, Pierce et al. 2004). Mule deer have even demonstrated avoidance of areas with
abundant forage when predation risk is very high (Lowrey et al. 2019). However, reducing predation risk involves not just avoiding encounters with predators, but also being able to detect predators when they are present. As cervids, mule deer rely heavily on scent and sound for threat detection, and the presence of loud, pungent livestock may inhibit their ability to do so (Lynch et al. 2014). Consequently, cattle may indirectly serve as interference competitors to mule deer by forcing them out of areas they would otherwise occupy, due to a heightened predation risk. If cattle heighten predation risk for deer, then I would expect fewer deer to be present when cattle are around, with the strongest effect in risky habitats and times of day ($P_3$).
Figure 1: A conceptual diagram displaying potential mule deer responses to cattle, and their ecological implications

**Methods**

**Study Area**

I conducted this research in Spanish Fork Canyon in central Utah. This is a mountainous region with an elevational gradient of 5,000-9,000 feet. Lower elevations are characterized by sagebrush steppe, with intermittent juniper and Gambel’s oak (*Quercus gambelii*) stands. At higher elevation, the landscape transitions into aspen...
(Populus tremuloides) and conifer forests. The area is characterized by a continental climate, with hot, dry summers and cold, snowy winters. Critical water availability in this area is provided by the Diamond Fork river, which flows through a majority of the study region, along with supplemental drinking ponds maintained by cattle ranchers in the summer. In addition to supporting populations of migratory mule deer, the land is also managed as working rangeland by the USFS under a rest-rotation grazing system. My study area encompasses the entirety of the Diamond Fork grazing allotment, which is subdivided into three pastures (“Diamond Fork” Pasture: 124,567,487 m², “Hollows” Pasture: 128,005,524 m², “Waters” Pasture: 116,882,134 m²). Between 1600-2100 cattle are present on the allotment from early June to mid-October, though approximately 20 or fewer cattle escape round up each year and remain on the allotment year-round. Cougars are also present throughout the study area, allowing me to assess interactions between predation risk and cattle abundance.

Data Collection

Camera traps can be used to discern local population density without identifying specific individuals (Gilbert et al. 2020, Schaus et al. 2020, Triguero-Ocaña et al. 2020). I used a grid of 108, autonomous, continually active trail cameras (Cuddeback H20 MP IR – Model H-1453) that were stratified over a range of elevations and across three cattle pastures in a rest-rotation grazing system to capture photos of both deer and cattle over a two-year period. All cameras were mounted at a standard height and at least 250 m away from one another so that they would occupy a unique NDVI pixel. Each site was visited
3-4 times per year to collect data and perform general maintenance. Photos from these cameras were then filtered through Megadetector, a publicly available algorithm that identifies blank photos (Beery et al. 2019). Photos that were determined to have animals in them were then uploaded to the Camelot photo tagging software and manually reviewed by technicians. Although Megadetector provides a level of confidence for each of the photos it determines as containing an animal, I took the conservative approach of manually reviewing all photos with a confidence > 0 (A confidence level of 1 indicated that an animal was definitely present, while a confidence level of 0 indicated an animal was probably not present. Photos that the algorithm deemed to be blank were not given a confidence rating). Several technicians then recorded species, number, and estimated age and sex of mule deer and cattle in all photos. Technicians also noted whether animals occurred within 21.2 m² from the camera (demarcated by three conduits placed in front of each camera), which I consider my effective detection area, within which the probability of detection is uniformly high.

Environmental attributes characterizing each camera site across space and time were obtained from a variety of sources through Google Earth Engine (Gorelick et al. 2017). Terrain characteristics, including elevation, slope, and aspect, and roughness were calculated from the U.S. Geological Survey, 3D Elevation Program 10-Meter Resolution Digital Elevation Model (2019). Vegetation was estimated using a combination of MODIS NDVI data (250m/8day resolution, Didan 2021b, 2021a) and vegetation cover metrics from the Rangeland Analysis Platform (RAP) (30m/annual resolution, v3; Allred et al. 2021). Hourly temperature and snow depth data were acquired from the ERA5-
Land Hourly dataset from the ECMWF Climate Reanalysis (11,132m resolution, Muñoz-Sabater et al. 2021).

**Density Estimation**

Deer counts from trail cameras were used as an estimate of localized deer density using the Random Encounter and Staying Time model (REST; Nakashima et al. 2018). REST is based on the simple notion that the cumulative time spent by animals within a given detection area is linearly related to animal density, the size of the area, and the monitoring time. Hence, if we know the detection area, the time the camera has been active and ready to be triggered by animals within the detection area, the duration of a single photo (how long it takes from the camera being triggered until it can be triggered again), and the overall number of animals observed in photos during the camera’s active time, we can estimate density. I defined the detection area as the 21.2 m$^2$ delineated by the three conduits in front of the camera. Only deer and cattle with at least 50% of their body mass within the detection area were counted as within the sample area. I considered a single photo duration to be 3 seconds, and used a temporal grain (the time over which we sum animal presence) of one hour.

**Statistical Analysis**

I used zero-inflated negative binomial generalized linear mixed models to model how deer abundance changed in response to cattle. My response variable was the cumulative number of deer observed within the detection area of a given camera during a
given hour, which is linearly proportional to density. Abundance was used as the response variable rather than density since abundance is more easily interpretable and the two are linearly related. Because cattle are only present in the study area during the growing season, and resource availability varies widely between the growing season and the non-growing season, I limited my study to the months of April-November. This time window encompasses roughly a month before and a month after cattle are present on the allotment. Both the zero-inflated portion of the model and the count (negative binomial) portion of the model also included a random effect of the interaction between site and year, allowing the intensity of the process to vary randomly among sites and years (and hence accounting for unobserved predictors).

In the zero-inflated portion of the model, I included variables that influenced whether or not deer were likely to be present at a given site, including time until dawn and dusk (both log-transformed) and a series of metrics designed to account for seasonal change (julian date, julian date squared, the interaction of julian date and elevation, and the interaction of julian date squared and elevation). Time until dawn and dusk were used because these variables influence daily deer activity and movement. Likewise, seasonal metrics were included to account for changes in deer density that result from elevational migrations, which are a common occurrence across my study area. Thus, the seasonal change metrics were chosen to account for both time of year and differences in seasonal change that may occur between high and low elevation sites. This series of seasonal metrics has previously been demonstrated to accurately capture deer movement in my study area (Del Bosco, 2021). All variables in the zero-inflated model were scaled and
centered, except for julian date and julian date squared. The julian date variables were only scaled and not centered.

My null model for the spatiotemporal dynamics of localized deer density included all non-competition variables that might affect deer abundance. There are generally three primary factors that are thought to derive animal distribution and abundance: conditions, resources, risks (Matthiopoulos et al. 2015). To account for conditions, I included topographic ruggedness, the cosine of aspect (northness), and thermal refugia variables. Areas with greater topographic ruggedness are more strenuous for deer to travel through, while more north-facing slopes may attract more deer because they are typically more productive than the more arid south facing slopes. Thermal refugia were defined as the product of heat stress and green tree canopy cover (the product of NDVI and RAP tree cover), since shade would be most valuable to deer when heat stress was high. Heat stress was defined as the product of temperature and whether or not it was daylight, since both temperature and solar radiation are known contributors to thermal stress in mule deer (Parker and Robbins 1983, Sargeant et al. 1994). To quantify resources, I included variables for shrub and herbaceous vegetation cover, as these represent potential categories of forage for mule deer. These metrics were estimated by multiplying the respective RAP categories by NDVI to account for both plant abundance on an annual basis and greenness at a specific time of the year. Although RAP separates annual and perennial herbaceous growth, I used their sum for my herbaceous forage metric, since both vegetation types are potential forage for ungulates. I did not include water as a resource in any model, since water does not seem to be a limiting resource in my study
area (Bonebrake et al. in prep). Lastly, I quantified predation risk as the interaction of ruggedness and tree cover, which has previously been demonstrated to be a good proxy for cougar habitat (Kohl et al. 2019).

To account for competitive pressure from cattle, I used two metrics, one that quantifies the instantaneous competitive pressure at a given point in time, and another that quantifies the cumulative competitive pressure over a longer interval preceding that point in time. To measure instantaneous competitive pressure, I created an “instantaneous cattle abundance” metric that accounted for both the number of cattle present at a camera site and the amount of time that had passed since their presence within the previous 24 hours. Let $n(t)$ be the number of cows observed at time $t$, and $\tau$ the time elapsed since the previous time cows were detected at the camera, $n(t)>0$; the 24-hour ‘cattle abundance’ is given by:

$$m(t) = \beta * \left( \frac{n(t - \tau) + 1}{\tau + 1} \right)$$

**Equation 1:** Let $n(t)$ be the number of cows observed at time $t$, and $\tau$ the time elapsed since the last time $n(t)>0$. As long as $\tau \leq T_1$ (where $T_1$ is at least 24 hours), then ‘instantaneous cattle abundance’ $m(t)$ at time $t+\tau$ can be quantified as the equation above. If no cows were detected within $T_1$ ($\tau>T_1$), set $[\tau+1]=ln(T_1+1)$, and $[n(t-\tau)+1]=0$. If the camera was only continuously active for time $T<T_1$, and no cows were detected within $T$, set $[\tau+1]=[T+1]$, and $[n(t-\tau)+1]=0$.

Because forage competition may also be a function of the cumulative number of competitors, I also created a 30-day “cumulative cattle footprint” to quantify the cumulative amount of competitive pressure over a 30-day period. I elected to use a 30-day period because this is the average amount of time cattle spent on each of the three
pastures in my study area during the growing season.

$$m(t) = \delta \sum_{\tau=0}^{T_2} \left( \frac{n(t - \tau) + 1}{(\tau + 1)} \right)$$

**Equation 2:** The ‘cumulative cattle footprint’ over time horizon $T_2$ (where $T_2$ is at least 30 days) can be quantified as the equation above. If no cows were detected within $T_2$ ($\tau>T_2$ for all $\tau$’s), set $ln(\sum_{\tau=0}^{T_2}(\tau + 1)) = [T_2+1]$ and $\sum_{\tau=0}^{T_2} n(t - \tau) = 0$. If the camera was only continuously active for time $T<T_2$, and no cows were detected within $T$, set $\sum_{\tau=0}^{T_2}(\tau + 1) = [T+1]$ and $\sum_{\tau=0}^{T_2} n(t - \tau) = 0$.

To quantify the general association between cattle and deer abundance over both the short and the long term, I fit two models that included the baseline model formulation plus the ‘instantaneous cattle abundance’ and the ‘cumulative cattle footprint’, respectively. To test my three hypotheses regarding mechanisms underlying competitive effects, I fit a set of models that each included the baseline null model formulation plus an interaction between a metric of competitive pressure and the relevant predictor for each hypothesis. In the case of **H1**, I created two models to test for competition for forage over the short and long term by interacting herbaceous forage with the instantaneous and the cumulative cattle footprint, respectively. To test **H2** and **H3**, I interacted the instantaneous cattle abundance with shade availability and predation risk, respectively.
Results

Between March 2019 and December 2020, the trail camera grid collected 325,986 photos of animals, including 22,522 mule deer photos and 43,401 cattle photos that qualified for our abundance calculations. Of these, 19,627 deer photos and 43,314 cattle photos fell within my April-November study period.

In the zero-inflated portion of the model, I found that time until dusk, and the interaction between squared julian date and elevation both had negative relationships with mule deer abundance. In contrast, time until dawn and julian date all had positive relationships with mule deer abundance. I did not detect a significant effect of squared julian date or the interaction between julian date and elevation, although they both had a negative relationship with mule deer abundance.

In the null model, neither ruggedness nor the cosine of aspect had an effect. I also did not detect a significant effect of tree cover or shade availability in this model. Conversely, herbaceous forage and shrub cover both had positive relationships with deer abundance. Both risk during the day and risk at night had positive relationships with deer abundance, though these effects were not significant. I also did not detect an effect of risk at twilight, though this variable had an overall negative relationship with deer abundance.

When included without interaction terms, both the instantaneous cattle abundance and the cumulative cattle footprint had positive effects on mule deer abundance (Figure 2). However, the interaction between herbaceous forage and the instantaneous cattle abundance and the interaction between herbaceous forage and cumulative cattle footprint both had negative relationships with mule deer abundance (Figures 3 & 4). The
interaction between herbaceous forage and the cumulative cattle footprint appeared to have a slightly more negative effect than the interaction between herbaceous forage and the instantaneous cattle abundance (Figures 3 & 4). I did not detect an effect of the interactions between the instantaneous cattle abundance and shade, nor between instantaneous cattle abundance and risk during the day, night and twilight (Figures 5 & 6).

Figure 2: Prediction plot demonstrating mule deer abundance response to instantaneous cattle abundance and cumulative cattle footprint. Shaded region represents 95% confidence intervals.
Figure 3: Prediction plot demonstrating how the instantaneous cattle abundance modifies mule deer response to herbaceous forage. Shaded region represents 95% confidence intervals.
Figure 4: Prediction plot demonstrating how the cumulative cattle abundance modifies mule deer response to herbaceous forage. Shaded region represents 95% confidence intervals.
Figure 5: Prediction plot demonstrating how cattle abundance modifies mule deer abundance response to shade at three different levels of heat stress. Shaded region represents 95% confidence intervals.
My findings demonstrate not only that mule deer alter their space use in the presence of cattle, but that these changes can be directly linked to forage competition.

Figure 6: Prediction plot demonstrating how cattle abundance modifies mule deer abundance response to trees at three different levels of ruggedness, during the day, night, and twilight. Shaded region represents 95% confidence intervals.
with cattle apparently acting as the dominant competitor in this system. This conclusion is supported by the fact that deer abundance declines in proportion to cattle abundance in areas with high herbaceous forage, and that the cumulative cattle footprint had a greater effect than instantaneous cattle abundance. This suggests that exploitative competition is likely occurring, with cattle removing available vegetation and forcing deer to seek food in other areas.

Although I cannot make inference as to the strength of fitness effects resulting from dynamics, my work does provide evidence that species will alter their space use in response to competitive pressures, even when those pressures are exploitative rather than direct. Many animals are known to alter their behavior in the presence of heterospecifics, often via heightened aggression and territoriality (Drury et al. 2020, Harrington et al. 2011). However, few studies have demonstrated a similar outcome in cases of exploitative competition. Female mule deer have previously been shown to have larger home ranges as cattle stocking rate increases, though this dynamic could not be explicitly linked to forage competition (Loft et al. 1988, Loft et al. 1991). Therefore, my findings provide evidence that, at least in large herbivores, competition can have effects on an individual’s behavior and distribution. This matters because although competition must result in some form of fitness decline, the strength of these effects likely varies widely depending on the amount of alternative resources available and the degree to which species can behaviorally adapt. Therefore, to truly understand the magnitude of competition’s effects on interspecies dynamics, it is necessary to discern how it alters flexible characteristics such as space use and behavior.

Another key insight of my research is that co-occurrence data is insufficient for
assessing competition in the field. Among many of the potential confounding correlations of co-occurrence data, competitive interactions in particular can be masked when habitat similarity produces an apparently strong positive relationship between two species, and because effects that are very strong at a fine scale disappear when measured at a coarse scale (Blanchet et al. 2020). Indeed, when simply comparing deer and cattle abundances, I found that the two species seem to have a net positive effect on one another. However, by examining the specific effect of cattle with regards to limiting resources, it is clear that competition between these species does occur. Co-occurrence has previously been shown to be inadequate for identifying species interactions in theory, but my research provides one of the only examples of this phenomena in a natural setting, and among large, mobile animals (Blanchet et al. 2020). Tying competition to a specific limiting resource, rather than relying on competitor abundance alone, may make it easier to separate abiotic and biotic effects when modeling species spatial distributions, which has previously been difficult (Godsoe et al. 2016). Although field studies of ecological interactions are challenging, it is still necessary to carefully examine specific competitive mechanisms in the field to avoid spurious conclusions about interspecies relationships.

Critics have previously called attention to the lack of hypothesis testing in ecology, particularly in competition research, as it can lead to false assumptions about the causes of observed phenomena (Schoener et al. 1983, Betini et al. 2017). In addition to avoiding spurious signals regarding co-occurrence, testing alternative hypotheses was important for allowing me to firmly identify forage as the limiting resource driving competition, rather than shade or predation risk. I found that cattle abundance did not appear to modify deer use of shade, indicating that there is likely not strong competition
for this resource. Although, a large portion of my study site is forested riparian area or high elevation mixed conifer-aspen forest, so it is possible that shade is not a truly limiting resource. Likewise, cattle did not appear to have a detectable effect on deer selection for risky habitat. This indicates that deer are not avoiding cattle due to an indirect effect on their ability to avoid predators. However, because risky habitat does not appear to have a strong effect on deer abundance in this system, it is also possible that deer are simply not selecting habitat based on risk posed by cattle. By examining multiple potential drivers of negative relationships, I was able to rule out alternatives and have confidence that forage competition was truly driving the responses I observed.

Outside of competitive dynamics, the effects of habitat and seasonal variables across all models were largely consistent with current understanding of mule deer. Deer are crepuscular, explaining why their detections are higher around dawn and dusk (Morano et al. 2019). Mule deer in this region also undergo elevational migrations, explaining why their presence at high elevation sites fluctuates depending on the time of year (McClure et al. 2005). Because deer will consume both herbaceous forage and shrubs, it is also unsurprising that their abundance tracks these resources. However, shrubs in this area largely consist of sagebrush, and therefore may be correlated with flatter, more open habitats, so it is possible deer merely appear to be selecting for shrubs when in fact they are selecting a specific terrain type.

Previous work on interspecific competition in mule deer and cattle has not provided clear answers, and these contradictions may partially be explained by a reliance on co-occurrence data and a lack of consideration for behavioral flexibility. Several studies have identified spatial separation between deer and cattle, with deer using steeper
slopes than cattle (Stewart et al. 2002, Yeo et al. 1993). But this cannot rule out the possibility of competition if one species is completely excluding another. I found that deer will leave a localized area to seek forage elsewhere when cattle are present, which lends evidence to the possibility that exclusion could result in deer retreating to steep slopes to find forage. Likewise, behavioral flexibility in diet may explain why studies of diet overlap in these species have varied drastically. If forage competition drives space-use change in mule deer, it is reasonable that it may also drive changes in diet, either directly via broadened forage selection or indirectly via deer relocation into areas with different vegetation availability. Our current understanding of interspecific competition has largely focused on fitness responses between species, but by prioritizing coarse population-level changes we miss the complex mechanisms driving the observed fitness responses. In the case of mule deer and cattle, it has obscured changes in space use behavior that result from forage competition. Displacement from ideal habitat and into suboptimal habitats has already been demonstrated at an intraspecific level among many species, including mule deer (Hurley et al. 2020, Murphy et al. 2023). Future research is needed to determine how interspecific competition may create a similar hierarchy of habitat preferences, and to what extent intra- and inter-specific competition determines the distribution of deer across a range of habitat types.

References


2271.


Leege, T.A., Herman, D.J., and Zamora, B. 1981. Effects of cattle grazing on mountain


CHAPTER 3

BEHAVIOR RESPONSE OF MULE DEER TO INTERSPECIFIC COMPETITION WITH CATTLE

Abstract

Behavior is an essential tool used by animals to accommodate stressors and respond to change. However, behavioral change resulting from interspecific competition, particularly when it is exploitative in nature, is often overlooked in favor of focusing solely on fitness effects. I examined whether mule deer change their behavior in response to interspecific competition from cattle. To avoid making assumptions about the presence and mechanism of competition, I examined behavior in the context of three alternative hypotheses for how cattle may influence deer behavior: competition for forage, competition for shade, and indirect predation risk effects. I classified remotely obtained deer locations into three behavioral states (‘resting’, ‘foraging’, and ‘commuting’) using a Hidden Markov Model, and then quantified the effects of covariates on all three states simultaneously using a Dirichlet regression model. As cattle density increased, deer were more likely to be in a foraging state and less likely to be in a commuting state. The probability that a deer was in a resting state did not change with cattle density. This indicates that deer may be forced to spend more time foraging when in the presence of cattle. This finding may support the idea that forage competition occurs between these species and induces behavioral responses. Using multiple sources of data, including spatial and behavioral data, can improve our understanding of competition in field settings.
Introduction

Behavior is a critical tool used by animals to improve resource acquisition, attract mates, and/or avoid predators (Beckerman et al. 1997, Haave-Audet et al. 2022). Because behavior is often a response to environmental stimuli, it can also be context-dependent, changing depending on the stressors an individual faces (Killen et al. 2013, Potts et al. 2013). For example, roe deer will display different movement rates when hunters are on the landscape (Picardi et al. 2019). Likewise, wild dogs have demonstrated behavior-specific habitat selection, using roads specifically when they are traveling over long distances (Abrahms et al. 2015). Although the degree to which behavioral changes such as these improve fitness is not always clear, it is apparent that behavior can be an important mechanism by which animals accommodate stressors and adapt to changing environments.

Despite this, behavioral changes resulting from interspecific competition are rarely examined, even though competition can be a major environmental stressor. Intraspecific competition has widely been shown to increase aggression in many species, presumably as a result of heightened territory and/or resource defense (Vander Wal et al. 2013). Several species also display changes in resource acquisition to mitigate competitive effects, though these activities often come with an energetic cost. For example, it is well documented that intraspecific competition can lead to higher rates of migration in partial migrant species (Mysterud et al. 2011). If such behavioral changes can occur at the intraspecific level, then it is likely that interspecific competition can also drive changes in species’ behavior. And, if these behavior changes are adaptive, they may even weaken some of the negative fitness effects of interspecific competition. For
example, Wauters et al. (2019) found that red squirrels (*Sciurus vulgaris*) became more sociable in the presence of invasive gray squirrel (*Sciurus carolinensis*) competitors, which the authors speculate may reduce the physiological stress of territory disputes when an invader is present. Similarly, some species appear to undergo temporal shifts in activity when competitors are around to reduce the chance of conflict (Harrington et al. 2009). Adaptive behavioral responses to competitors such as these may even partially explain why negative fitness effects are often difficult to identify in field settings. Therefore, to accurately understand the magnitude of the effect of interspecific competition on a species in natural settings, it is essential to quantify behavioral responses.

Quantifying interspecific competition is particularly important when managing non-native species. Non-native species have become highly prolific competitors in ecosystems around the world, and successful conservation requires understanding how they alter the dynamics of species around them (Mollot et al. 2017). Until recently, studies of non-native species have focused on population- or community-level effects, but there is a growing understanding that these outcomes are likely driven by individual-level changes in the physiology and behavior of native species in response to non-natives and greater focus is needed in these areas (Crystal-Ornelas and Lockwood, 2020). Behaviorally-mediated management has even been proposed as a conservation planning tool to assist species with adapting to novel anthropogenic and environmental risks such as invasive species (Berger-Tal et al. 2011). While livestock do not undergo uncontrolled spread, as is the case with traditionally invasive species, they have been introduced to ecosystems globally and in recent decades there has been interest in understanding how
they compete with native herbivores. This is particularly true in the western United States, where managers must balance both the needs of economically important livestock such as cattle, and the population sizes of game species such as mule deer.

In my second chapter, I will examine whether competitor (cattle) density drives changes in mule deer behavioral allocation. Previous research quantifying the strength of competition between cattle and mule deer has produced mixed results, which may in part be due to a lack of simultaneous consideration of behavioral adjustment in the face of competition (Chaikina and Ruckstuhl 2006, Schieltz et al. 2016). In my first chapter, I found that deer and cattle appear to compete for forage, with deer abundance lower in foraging habitat when cattle are present. However, it is not clear if these observed changes in space use are accompanied by fine-scale behavioral changes, which may or may not entail additional energetic cost. Cattle also provide an ideal competitor to study the effects of behavioral change, since unlike most non-native species they are anthropogenically distributed and their population sizes are carefully managed to remain at carrying capacity. Therefore, their spatial distribution and population size will not change in response to other, potentially confounding non-anthropogenic factors. Additionally, most cattle in the western US are managed under a rest-rotation grazing system which means that pastures are only grazed for part of the growing season and/or may go ungrazed every few years. Understanding how mule deer behavior changes in the presence of competitors will provide valuable insight regarding the fine-scale mechanisms that drive population responses.

I propose three potential hypotheses for how cattle may impact deer behavior within pastures (Figure 7). Importantly, because I will exclusively be using behavioral
data from deer that are residing on grazed pastures, these hypotheses reflect potential behavioral changes that may occur given that competitors are present:

**H1 (Foraging Hypothesis):** Because competition for herbaceous forage is higher on cattle pastures, mule deer will spend more time foraging on cattle pastures.

I predict that mule deer will spend more of their time foraging as cattle density increases ($P_1$), due to a decrease in forage availability on pastures. If cattle act as forage competitors to mule deer, then shared resources will be scarcer and/or more difficult for mule deer to obtain in the presence of cattle. Therefore, deer in areas with high cattle density would have different resource acquisition patterns compared to deer without high competition pressures. Previous research has shown that female mule deer have larger home ranges in the presence of cattle, possibly indicating that they must cover more ground to obtain sufficient resources (Kie 1996). Some studies have also found that mule deer spend more time feeding and less time resting when forage is scarce, including in areas where cattle are grazed (Kie et al. 1991, Kie 1996).

**H2 (Resting Hypothesis):** Because competition for shade is higher on cattle pastures, mule deer will spend less time resting because they must spend more time seeking shade.

As solar radiation increases, both mule deer and cattle bed down to dissipate body heat and better regulate their body temperatures (Bennett et al. 1985, Cain et al. 2006,
Millspaugh et al. 1998, Parker and Robbins. 1983, Sargeant et al. 1994). If cattle compete with mule deer for shade, then there will be fewer shaded refuges available to mule deer in a given area when cattle are present. Therefore, deer would have to spend less time resting and more time locating available shaded areas when cattle are present, or go without shade completely. Little research has been conducted on shade competition in large ungulates, but thermoregulation has been shown to be a factor influencing mule deer habitat selection during hours of the day with the most intense solar radiation (Ager et al. 2003, Morano et al. 2019). I predict that mule deer will spend less time resting during times of intense heat stress as cattle density increases (P2), as there will be fewer available thermal refugia on pastures.

**H3 (Commuting Hypothesis):** Because cattle place mule deer at a greater predation risk, deer will spend less time moving through cattle occupied areas to reduce their risk of predation.

Previous research has demonstrated that mule deer will avoid landscape features that they perceive as risky, such as hydrocarbon development, roads, and/or other human infrastructure, by up to several hundred meters (Dwinell et al. 2019, Northrup et al. 2015, Sawyer et al. 2017). Additionally, encounter rates between predators and prey are generally lower when both species have reduced movement speeds and encounter radii (Gerritsen and Strickler 1977, Suraci et al. 2022). Therefore, I predict that mule deer will spend less time commuting as cattle density increases (P3), since cattle represent a risk factor that deer will attempt to avoid, thus restricting their movement to a smaller, safer
core area.

Alternatively, it is possible that cattle provide a form of additional vigilance, and deer intentionally inhabit areas where they are present because they reduce the risk of predation. The “many eyes” effect is well documented as reducing the risk of predation in ungulates (Rieucau and Martin 2008). However, it is not clear how this effect would impact the probability of commuting.
Methods

Data Collection

I obtained GPS points for collared mule deer from the Utah Division of Wildlife Resources, which was collected as part of their Migration Initiative. Deer data spanned 2011-2022 across 4015 individuals, for a total of 18,291,338 GPS points. All duplicate
points, points with suspiciously fast travel times, and points within 1 day of a mortality event were removed. I limited my analysis to only points that occurred in areas of known cattle density. Additionally, because I also wanted to stratify my sampling by individual, season, and year, I also limited my sample size to only individual-season-year combinations that had 100 or more points per season-year. For example, if an individual had 100 points in fall 2019, but only 10 points in winter 2019, then only that individual’s fall 2019 points would be included in my analysis. I classified each point as being within one of four seasons, which I delineated based on mule deer life history. These four seasons included fawning (April-May), summer (June-August), rut (September-November), and winter (December-March). After imposing these limitations, I had a usable sample size of 769,746 points spanning 375 individuals across the years 2018-2021.

Environmental attributes for each usable GPS point were obtained through Google Earth Engine (Gorelick et al. 2017). Terrain ruggedness was calculated from the U.S. Geological Survey, 3D Elevation Program 10-Meter Resolution Digital Elevation Model (2019), vegetation was estimated using a combination of MODIS NDVI data (250m/8day resolution) (Didan 2021b, 2021a) and vegetation cover metrics from the Rangeland Analysis Platform (RAP) (30m/annual resolution, v3; Allred et al, 2021). Hourly temperature and snow depth were acquired from the ERA5-Land Hourly dataset from the ECMWF Climate Reanalysis (11,132m resolution) (Muñoz-Sabater et al. 2021).

Cattle stocking rates obtained for the years 2018-2021 for all pastures within eleven different USFS districts in northern and central Utah. I focused only on northern
and central Utah for this study because the region contains and is ecologically similar to the landscape where my cameras in Chapter 1 were placed. My usable data spanned 323 pastures across 119 allotments in 10 different USFS districts, all with variable levels of stocking rates and rotation regimes. I included only pastures that were grazed by cattle, and no other kind of livestock.

**Behavioral Segmentation**

For each step containing two consecutive GPS points, I assigned the probability of that step belonging to each of 3 behavioral states (‘resting’, ‘foraging’, and ‘commuting’) estimated via a Hidden Markov Models (HMM) using the momentuHMM package in program R (McClintock and Michelot 2018). All available deer data was used to fit the HMM, not just my usable sample size that overlapped with pastures. Before fitting the HMM, I standardized the data such that only steps that were exactly 2 hours apart were used, and any missing timestamps were given coordinates of NA. GPS points were always collected on the hour, however occasionally some collars would skip data collection at their predetermined timestamp and pick up again on the following hour. This resulted in one set of two hour-spaced points collected on “even” time stamps, and another set of two hour-spaced points collected on “odd” timestamps. When this occurred, I split the individual’s points into two “bursts,” each with a unique ID in an effort to utilize all available data. Ultimately, I fitted the HMM using only steps from individuals that had at least 1000 GPS points per year, as these individuals were most likely to represent the true distribution of behavioral states. After fitting the HMM on these high-quality individuals, I then estimated the behavioral states off all other steps in my dataset using the Viterbi algorithm and my fitted HMM (Zucchini et al. 2016).
Post-hoc Analysis of Behavioral Allocation

I used a Dirichlet regression model to examine the effect of cattle density on the probabilities of deer resting, foraging, and commuting. To account for circadian patterns of behavior patterns of activity, I included time to dawn and time to dusk (both log transformed), where twilight is defined as being within 2 hours of dawn or dusk. I also included topographical ruggedness as a variable that may affect deer resting, foraging, and commuting behavior outside of competition.

To account for effects on foraging behavior, I included snow depth and forage availability in the model. Deer are more likely to be foraging when and where forage availability is high, and likewise may spend less time foraging when snow depth has buried available vegetation. Forage availability was represented as the product of NDVI and the sum of RAP herbaceous and shrub cover. Herbaceous forage is important to deer in the growing season, however, shrubs are important forage in the winter when herbaceous forage is scarce. Because my data for this chapter encompasses the entire seasonal cycle, I summed these vegetation types into one category representing important forage. The sum of RAP herbaceous and shrub cover was multiplied by NDVI to account for seasonal changes in vegetation greenness.

To account for effects on resting behavior, I included hourly temperature, shady tree cover, and shade availability in the model, since deer are known to bed down in shade during periods of high heat stress. Shady tree cover is defined as the product of NDVI and RAP tree cover. Shade availability was defined as the interaction of the product of NDVI and tree cover, hourly temperature, and a categorical variable indicating that it is day, as shade is only valuable to deer when the sun is present.
To account for effects on commuting behavior, I included features associated with heightened predation risk, as deer are expected to reduce commuting to lower encounter rate with predators. The main predator of deer in my study area, cougars, tend to hunt on rugged, forested terrain at night (Kohl et al. 2019, Mitchell. 2013). Thus, predation risk was represented by the interaction of ruggedness, RAP tree cover, and time of day (day, night, or twilight). Thus, predation risk was represented by the interaction of ruggedness, RAP tree cover, and time of day (day, night, or twilight). However, it is also possible that rugged terrain is more difficult for deer to move through, slowing them down and causing their behavior to be classified as “commuting” less often.

To test my three hypotheses regarding specific competitive mechanisms for how cattle may affect deer behavior, I fit three separate models, each of which interacted cattle density with the relevant predictor for each hypothesis. To test $H_1$, I interacted cattle density with herbaceous-shrub forage availability. To test $H_2$, I interacted cattle density with shade availability. To test $H_3$, I interacted cattle density with predation risk during the day, night, and twilight. I also included cattle density alone as a term in all three models, to isolate the effect of cattle outside of competitive contexts.

**Bootstrapping**

Because it is not possible to include random effects in Dirichlet models outside of a Bayesian framework, I stratified the data going into my model by individual, season, and year to control for variation due to these factors. I then bootstrapped my model over 1000 runs, using a random sample of 27 individuals for every season-year for every run. I selected 27 individuals since this was the minimum number of individuals present in a
given season-year. I also randomly sampled with replacement only 100 steps per individual per season-year, to remove temporal autocorrelation among steps. In total, each run of the model contained 43,200 total steps, evenly distributed across individuals, seasons and years. This bootstrapping approach allowed me to equalize representation of individuals in each season-year sample, so that individuals who were overrepresented in the data would not dominate the estimation of model parameters.

**Results**

After selecting only high-quality individuals, I fit my HMM on 589,868 GPS points that were distributed across 103 individuals over the years 2018-2021. The mean step length for the resting state was 40.594 m (SD: 36.582 m, Zeromass: $5 \times 10^{-3}$), the mean step length for the foraging state was 193.407 m (SD: 191.956 m, Zeromass: $1 \times 10^{-8}$), and the mean step length for the commuting state was 525.276 m (SD: 622.822 m, Zeromass: $1 \times 10^{-8}$). The mean turning angle for the resting state was $-3.113$ (Concentration: 0.321), the mean turning angle for the foraging state was $-0.001$ (Concentration: 0.249), and the mean turning angle for the commuting state was $-0.008$ (Concentration: 0.593). The distribution of behavioral states across step lengths and turning angles for data used in the fitted HMM can be found in Figure 8.
Within the data that was on cattle pastures and therefore useable to me, 203,172 points (26%) were classified as resting, 506,820 points (66%) were classified as foraging, and 58,825 points (8%) were classified as commuting.

The mean coefficients for each covariate can be found in Figure 9. Snow depth appeared to have the greatest effect on behavior, increasing resting and foraging probabilities and reducing commuting probability. Similarly, hourly temperature and ruggedness increased resting and commuting, while not affecting and slightly reducing foraging, respectively. Shady tree cover reduced both commuting and foraging probabilities. Time until dawn increased commuting and foraging probabilities and reduced resting. Conversely, time until dusk had a slight positive effect on resting. Herbaceous forage slightly increased the probability of foraging and reduced resting. Shade increased foraging and resting probabilities. During the day, predation risk

Figure 8: Distribution of behavioral states across step lengths and turning angles from points used to fit HMM.
positively affected commuting and foraging. At night, predation risk had a negative effect on foraging, and a positive effect on resting. At twilight, predation risk had a positive effect on resting and foraging, and a slightly positive effect on commuting.

Cattle density had a positive effect on foraging and commuting probabilities. Forage competition had positive effects on foraging and resting and negative effects on commuting. The probability that a deer was in a foraging state increased as herbaceous forage increased, with this effect becoming stronger at higher cattle densities (Figure 10). Shade competition did not affect any behavioral state. Deer were more likely to be in a resting state as heat stress increased, though there was no effect of cattle density on this behavior (Figure 11). The effect of the interaction of cattle density and predation risk varied by time of day. During both the day and night, cattle-predation risk interactions had negative effects on resting and foraging. At twilight, cattle-predation risk interactions had negative effects on foraging and a positive effect on resting. The probability that a deer was in a commuting state decreased as ruggedness increased, though the effect of tree cover varied with the degree of ruggedness (Figure 12). At low ruggedness deer responded negatively to increasing tree cover, while at high ruggedness this relationship became positive, with consistent responses across all times of day. Consequently, at mean levels of ruggedness there was no response to tree cover. However, overall the probability of commuting decreased as cattle density increased (Figure 12).
Figure 9: Plot of mean coefficient values for all Dirichlet runs with mean standard errors.
Figure 10: Plot demonstrating how the probability of foraging changes in response to herbaceous forage availability and cattle density. Each line represents one individual model, with the darkened lines representing the average values of all models.
Figure 11: Plot demonstrating how the probability of resting changes in response to shade availability and cattle density. Each line represents one individual model, with the darkened lines representing the average values of all models.
Figure 12: Plot demonstrating how the probability of commuting changes in response to herbaceous predation risk, time of day and cattle density. Each line represents one individual model, with the darkened lines representing the average values of all models.
Discussion

My research found that deer modify their behavioral allocation as competitor density increases, spending more time foraging and less time commuting. If forage becomes scarcer when cattle are present, deer residing on pastures may have to spend more time feeding to acquire sufficient nutrition. Kie et al. (1991) found that deer have a greater number of feeding bouts and spend more time feeding as herbaceous forage availability decreases and as cattle stocking rate increases, indicating that foraging time has a negative relationship with forage abundance. This negative relationship also makes sense in the context of deer physiology, as deer are ruminants that must stop feeding once their rumen is at capacity (Searle et al. 2007). Although it is difficult to pinpoint the exact reason for my observed change in foraging response, it appears probable that the presence of cattle creates energetic trade-offs for deer.

However, grazing has been shown to improve forage quality in certain systems by increasing the nutritional value of plants and maintaining a certain vegetation community, and therefore deer could also be spending more time foraging more in cattle pastures because the forage quality is higher (Clark et al. 2000, Humphrey et al. 2000, Liu et al. 2015). However, when viewed in the context of my first chapter, which demonstrated that increasing cattle abundance had a negative effect on deer abundance in forage-rich areas, it seems more likely that in this system cattle are depleting forage rather than jumpstarting nutritious regrowth. Instead, the observed positive relationship could suggest that cattle are an indicator of forage availability. The USFS adjusts grazing plans on an annual basis, allowing more cows on the landscape when vegetation is abundant and removing cows prematurely during drought years. Therefore, cattle density could
simply be strongly correlated with forage abundance in a given year. If this is the case, then deer and cattle likely still compete to some degree due to their overlap forage resource selection.

In addition to an effect on foraging, cattle also seemed to decrease the probability of commuting by deer, though the driver of this phenomenon is murky. Although deer responded as would be predicted if cattle increased prediction risk, it is notable that deer did not display the expected response to tree cover across ruggedness levels or times of day. This may indicate that tree cover and ruggedness are a poor metric of predation risk in my system, or that predation risk is not a major driver of deer commuting behavior. Commuting itself is a catch-all category that likely encompasses several different behaviors beyond just predation risk response, which further complicates interpretation. In either case, this makes it impossible to truly determine if and how cattle have an impact on deer predation. Ruggedness did appear to decrease the probability of commuting in deer across all times of day, though this is potentially because rugged terrain is more simply difficult to move through, causing deer to slow down and their movements to be classified as “commuting” under the HMM less often. Furthermore, because all behavior probabilities must sum to one, it is also entirely possible that the decrease in commuting is simply a side effect of the simultaneous increase in foraging that occurs at high cattle densities, rather than the result of any specific behavioral process. The multiple possible interpretations of this finding reinforce the need for context when assigning drivers to behavioral responses.

Overall, the array of possible explanations for the observed changes in deer behavior demonstrates the importance of context when interpreting behavioral data. In
my first chapter, I was able to carefully examine multiple specific avenues of competition between mule deer and cattle, including forage, and conclude that deer and cattle likely competed for forage. This prior knowledge then provided context for understanding deer behavior, allowing me to make informed interpretations of observed behavioral patterns. Animal behavior can vary depending on a variety of factors and without context it is exceedingly difficult, if not impossible, to understand the true drivers of behavior. Therefore, my results indicate that care should be taken when using behavior alone to assess ecological responses, particularly with regards to competition. Conversely, using multiple data streams can make inference much stronger. Both my first and second chapter results indicate cattle modify deer response to forage, providing strong evidence that forage resources drive competitive effects in this species. As when examining the drivers of competition, studies of behavior should examine multiple competing causes for the drivers of behavioral change to avoid making assumptions about their causes.

Lastly, these findings provide evidence that animal behavior can differ in the presence of competitors, and reinforces the importance of considering spatial and behavioral change when exploring the effects of competition. Competition and its effects are notoriously difficult to isolate in field settings, particularly among animals, and behavioral adjustment may be one contributing factor. When faced with competitive pressure, the behaviors that animals displayed in non-competitive environments may no longer be fitness-maximizing. However, while the overall achievable fitness maximum is likely still reduced when competitors are present, animals could adopt new behaviors that potentially reduce the strength of negative fitness effects. For example, in this study, it appears that cattle introduce a stressor to deer by reducing the amount of available forage,
but deer compensate by devoting more time and energy to foraging. Behavioral modification to improve fitness outcomes in cases such as this can make it exceedingly difficult to identify the true fitness costs associated with competition in field settings where the absolute fitness maximum isn’t known. However, if we observe a behavioral change that can be directly linked to competitor presence, then it is reasonable to indirectly infer a fitness cost associated with competition.

References


Kohl, M.T., Ruth, T.K., Metz, M.C., Stahler, D.R., Smith, D.W., White, P.J., and MacNulty, D.R. 2019. Do prey select for vacant hunting domains to minimize a multi-


CHAPTER 4
CONCLUSION

Interspecific competition is notoriously difficult to study in the field, but inference can be improved by comparing multiple hypotheses and methods. I compared three alternative hypotheses that could explain negative relationships between deer and cattle, including competition for forage, competition for shade, and indirect predation risk effects. Both deer spatial and behavioral responses appeared to change in the presence of cattle, while neither shade or predation risk appeared to be influenced, indicating that forage competition occurs between these species. Deer abundance in forage-rich areas declined as cattle abundance increased, suggesting that vegetation in these areas was removed by cattle and deer had to seek resources elsewhere. Likewise, the probability that a deer was in a foraging state increased as cattle density increased. This suggests that deer have to spend more time foraging to make up for reduced vegetation availability, or that deer and cattle overlap in terms of their resource use. Notably, when just looking at co-occurrence, these species were positively related to each other, supporting the need to examine competition in the context of specific limiting resources. Furthermore, exploring all three hypotheses in terms of two different responses (spatial and behavioral) I was able to reinforce my findings that forage was the true driver of the observed relationships.

Spatial and behavioral traits are often overlooked in studies of competition, though my research demonstrates that they do change in the presence of competitors. Although I cannot quantify the extent to which cattle induce fitness declines in mule deer,
it is clear that mule deer are utilizing their environment differently because of interspecific competition. Some of these changes may be compensatory. For example, spatial redistribution could allow deer to access additional or alternative forage resources, letting them survive and reproduce successfully even with abundant competitors on the landscape. Likewise, spending more time foraging when cattle are present may help deer maintain sufficient nutrition under competitive conditions. However, it is likely that both of these observed responses still force deer to incur additional stressors such as heightened energetic costs or subpar vegetation quality, otherwise they would be performing such behaviors all the time. Additionally, redistributing into new un-preferred environments in search of food may expose deer to threats they would not otherwise face such as predators or human infrastructure. All this is to say, large-scale fitness responses are likely inextricably tied to, and potentially driven by, fine-scale changes in space use and behavior, particularly in large mobile animals. Therefore, identifying competition solely through population viability may be inadequate for understanding how it works in natural systems. Instead, it may be worth reconsidering our definition of competition and instead viewing it as a context-dependent phenomenon, where the strength of negative fitness effects is dependent on environmental and behavioral factors.

A lack of consideration for the aforementioned factors may explain why quantifying interspecific competition between mule deer and cattle has been difficult for decades. Studies of competition in these species range across a variety of ecosystems, years, seasons, and stocking rates, and have historically relied on spatial and diet overlap metrics. However, by specifically testing hypotheses related to limiting resources and examining a variety of responses, I was able to demonstrate that forage competition does
occur. This finding adds to a growing body of literature on competitive dynamics in large herbivores by providing insight as to how competition between species that did not coevolve can manifest in a natural system. It also may provide guidance for managers hoping to balance livestock and wild game population objectives in the face of a changing climate, where competitive pressures may be exacerbated by drought. Although studying competition among animals in the field is difficult, my work may be able to provide the scaffolding for future studies to successfully understand its effects in other systems.

Management Implications

Central Utah is an arid region with a short growing season and has been suffering from a prolonged drought for several years, so care should be taken when extrapolating these results to a particular area. However, at least for the arid Intermountain West, my research indicates that forage competition should be taken into account when devising management plans. Importantly, because cattle appear to drive decreases in local deer abundance in prime foraging habitat, it can be inferred that they are the dominant competitor in this system. Therefore, reducing deer abundances should not result in substantial increases in the overall forage available to cattle. Although grazing by cattle has been shown to increase forage quality later in the season, this effect is likely negated in this region due to the aridity of the late summer and negligible forage regrowth (Clark et al. 2000). Careful monitoring of forage conditions before and during the growing season could ensure that enough vegetation is present to meet management objectives for both species.
Additionally, because my work indicates that deer may locally abandon an area when forage has been depleted, consideration should be given to where deer may relocate. Road edges or human population centers may provide resource-rich havens with few competitors for deer to move into. Therefore, high deer populations in these areas increase the potential for human-wildlife conflict.

Lastly, as climate change exacerbates drought in the western United States, it is possible that forage competition will increase between these species in the coming decades. Increased water stress will reduce the amount of available forage and shorten the length of the growing season, creating a smaller pool of resources to draw from (Emadodin et al. 2021). Although deer and cattle do not have complete diet overlap, my work indicates that cattle are consuming at least some portion of the forage that may have otherwise been eaten by deer. As available forage decreases and both species are forced to consume less preferred vegetation, this diet overlap will likely continue to narrow and it will be increasingly difficult for deer to behaviorally compensate. Depending on region and the desired management outcomes, practitioners may seek to increase the use of rest-rotation grazing, or supplemental feeding to meet their goals.

References


APPENDICES
### Table A.1: Model Output from Null Model (no cattle covariates)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.61580</td>
<td>0.10810</td>
<td>-24.199</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>-0.39969</td>
<td>0.21782</td>
<td>-1.835</td>
<td>0.0665</td>
</tr>
<tr>
<td>Cosine Aspect</td>
<td>-0.22273</td>
<td>0.12343</td>
<td>-1.804</td>
<td>0.0712</td>
</tr>
<tr>
<td>NDVI * RAP Herbaceous Forage Cover</td>
<td>0.35346</td>
<td>0.09046</td>
<td>3.907</td>
<td>9.33e-05</td>
</tr>
<tr>
<td>NDVI * RAP Shrub Cover</td>
<td>0.16611</td>
<td>0.07720</td>
<td>2.152</td>
<td>0.0314</td>
</tr>
<tr>
<td>NDVI * RAP Tree Cover</td>
<td>0.10993</td>
<td>0.11298</td>
<td>0.973</td>
<td>0.3306</td>
</tr>
<tr>
<td>Shade Availability (Hourly Temperature * NDVI * RAP Tree Cover * is_Day)</td>
<td>0.12969</td>
<td>0.11868</td>
<td>1.093</td>
<td>0.2745</td>
</tr>
<tr>
<td>Predation Risk – Day (Ruggedness * RAP Tree Cover * is_Day)</td>
<td>2.62159</td>
<td>1.92086</td>
<td>1.365</td>
<td>0.1723</td>
</tr>
<tr>
<td>Predation Risk – Night (Ruggedness * RAP Tree Cover * is_Night)</td>
<td>0.62235</td>
<td>2.15917</td>
<td>-0.347</td>
<td>0.7287</td>
</tr>
<tr>
<td>Predation Risk - (Ruggedness * RAP Tree Cover * is_Twilight)</td>
<td>-0.74097</td>
<td>2.13597</td>
<td>1.093</td>
<td>0.2745</td>
</tr>
<tr>
<td><strong>Zero-Inflated Terms</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Intercept)</td>
<td>-8.981</td>
<td>0.08165</td>
<td>-10.999</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dawn)</td>
<td>0.7813</td>
<td>0.8165</td>
<td>11.872</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dusk)</td>
<td>-0.7370</td>
<td>0.06581</td>
<td>-11.446</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Julian Date</td>
<td>0.1330</td>
<td>0.06438</td>
<td>6.865</td>
<td>6.67e-12</td>
</tr>
<tr>
<td>Julian Date Squared</td>
<td>-8.385e-05</td>
<td>4.858e-05</td>
<td>-1.726</td>
<td>0.084353</td>
</tr>
<tr>
<td>Julian Date * Elevation</td>
<td>-0.02656</td>
<td>0.01995</td>
<td>-1.331</td>
<td>0.183060</td>
</tr>
<tr>
<td>Julian Date Squared * Elevation</td>
<td>-1.790e-04</td>
<td>5.201e-05</td>
<td>-3.443</td>
<td>0.000576</td>
</tr>
</tbody>
</table>
Table A.2: Model Output from Instantaneous Cattle Abundance Only Model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-3.03529</td>
<td>0.15441</td>
<td>-19.657</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>-0.39990</td>
<td>0.21652</td>
<td>-1.847</td>
<td>0.0648</td>
</tr>
<tr>
<td>Cosine Aspect</td>
<td>-0.23267</td>
<td>0.12059</td>
<td>-1.929</td>
<td>0.0537</td>
</tr>
<tr>
<td>NDVI * RAP Herbaceous Forage Cover</td>
<td>0.39797</td>
<td>0.09073</td>
<td>4.386</td>
<td>1.15e-05</td>
</tr>
<tr>
<td>NDVI * RAP Shrub Cover</td>
<td>0.16492</td>
<td>0.07514</td>
<td>2.195</td>
<td>0.0282</td>
</tr>
<tr>
<td>NDVI * RAP Tree Cover</td>
<td>0.11389</td>
<td>0.11100</td>
<td>1.026</td>
<td>0.3049</td>
</tr>
<tr>
<td>Shade Availability (Hourly Temperature * NDVI * RAP Tree Cover * is_Day)</td>
<td>0.14798</td>
<td>0.11865</td>
<td>1.247</td>
<td>0.2124</td>
</tr>
<tr>
<td>Predation Risk – Day (Ruggedness * RAP Tree Cover * is_Day)</td>
<td>3.03089</td>
<td>1.93960</td>
<td>1.563</td>
<td>0.1181</td>
</tr>
<tr>
<td>Predation Risk – Night (Ruggedness * RAP Tree Cover * is_Night)</td>
<td>1.19447</td>
<td>2.17000</td>
<td>0.550</td>
<td>0.5820</td>
</tr>
<tr>
<td>Predation Risk - (Ruggedness * RAP Tree Cover * is_Twilight)</td>
<td>-0.44181</td>
<td>2.15443</td>
<td>-0.205</td>
<td>0.8375</td>
</tr>
<tr>
<td>Instantaneous Cattle Abundance</td>
<td>2.14833</td>
<td>0.38408</td>
<td>5.593</td>
<td>2.23e-08</td>
</tr>
</tbody>
</table>

Zero-Inflated Terms

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-8.693</td>
<td>0.9146</td>
<td>-9.505</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dawn)</td>
<td>0.7757</td>
<td>0.06557</td>
<td>11.830</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dusk)</td>
<td>-7.332e-01</td>
<td>6.359e-02</td>
<td>-11.529</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Julian Date</td>
<td>0.1305</td>
<td>0.01892</td>
<td>6.894</td>
<td>5.42e-12</td>
</tr>
<tr>
<td>Julian Date Squared</td>
<td>-8.538e-05</td>
<td>4.775e-05</td>
<td>-1.788</td>
<td>0.073774</td>
</tr>
<tr>
<td>Julian Date * Elevation</td>
<td>-0.02631</td>
<td>0.01936</td>
<td>-1.359</td>
<td>0.174189</td>
</tr>
<tr>
<td>Julian Date Squared * Elevation</td>
<td>-1.710e-04</td>
<td>5.067e-05</td>
<td>-3.375</td>
<td>0.000739</td>
</tr>
<tr>
<td>Parameter</td>
<td>Estimate</td>
<td>SE</td>
<td>t-value</td>
<td>p-value</td>
</tr>
<tr>
<td>-----------------------------------------------</td>
<td>----------</td>
<td>--------</td>
<td>---------</td>
<td>-----------</td>
</tr>
<tr>
<td>(Intercept)</td>
<td>-2.69427</td>
<td>0.11588</td>
<td>-23.251</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>-0.40875</td>
<td>0.21722</td>
<td>-1.882</td>
<td>0.0599</td>
</tr>
<tr>
<td>Cosine Aspect</td>
<td>-0.22831</td>
<td>0.12255</td>
<td>-1.863</td>
<td>0.0625</td>
</tr>
<tr>
<td>NDVI * RAP Herbaceous Forage Cover</td>
<td>0.37869</td>
<td>0.09040</td>
<td>4.189</td>
<td>2.80e-05</td>
</tr>
<tr>
<td>NDVI * RAP Shrub Cover</td>
<td>0.17281</td>
<td>0.07622</td>
<td>2.267</td>
<td>0.0234</td>
</tr>
<tr>
<td>NDVI * RAP Tree Cover</td>
<td>0.11512</td>
<td>0.11254</td>
<td>1.023</td>
<td>0.3063</td>
</tr>
<tr>
<td>Shade Availability (Hourly Temperature * NDVI * RAP Tree Cover * is_Day)</td>
<td>0.15030</td>
<td>0.11925</td>
<td>1.260</td>
<td>0.2076</td>
</tr>
<tr>
<td>Predation Risk – Day (Ruggedness * RAP Tree Cover * is_Day)</td>
<td>2.85703</td>
<td>1.92473</td>
<td>1.484</td>
<td>0.1377</td>
</tr>
<tr>
<td>Predation Risk – Night (Ruggedness * RAP Tree Cover * is_Night)</td>
<td>0.94981</td>
<td>2.15550</td>
<td>0.441</td>
<td>0.6595</td>
</tr>
<tr>
<td>Predation Risk - (Ruggedness * RAP Tree Cover * is_Twilight)</td>
<td>-0.61774</td>
<td>2.14139</td>
<td>-0.288</td>
<td>0.7730</td>
</tr>
<tr>
<td>Cumulative Cattle Footprint</td>
<td>1.18351</td>
<td>0.26626</td>
<td>4.445</td>
<td>8.79e-06</td>
</tr>
</tbody>
</table>

**Zero-Inflated Terms**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-8.921</td>
<td>0.7689</td>
<td>-11.602</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dawn)</td>
<td>0.7667</td>
<td>0.06440</td>
<td>11.905</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dusk)</td>
<td>-0.7248</td>
<td>0.06300</td>
<td>-11.505</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Julian Date</td>
<td>0.1330</td>
<td>0.01869</td>
<td>7.116</td>
<td>1.11e-12</td>
</tr>
<tr>
<td>Julian Date Squared</td>
<td>-8.933e-05</td>
<td>4.759e-05</td>
<td>-1.877</td>
<td>0.060517</td>
</tr>
<tr>
<td>Julian Date * Elevation</td>
<td>-0.02662</td>
<td>0.01957</td>
<td>-1.360</td>
<td>0.173745</td>
</tr>
<tr>
<td>Julian Date Squared * Elevation</td>
<td>-1.720e-04</td>
<td>5.107e-05</td>
<td>-3.368</td>
<td>0.000758</td>
</tr>
</tbody>
</table>
Table A.4: Model Output from Forage Competition Model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.59621</td>
<td>0.20562</td>
<td>-12.626</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>-0.35643</td>
<td>0.23908</td>
<td>-1.491</td>
<td>0.1360</td>
</tr>
<tr>
<td>Cosine Aspect</td>
<td>-0.22686</td>
<td>0.12192</td>
<td>-1.861</td>
<td>0.0628</td>
</tr>
<tr>
<td>NDVI * RAP Herbaceous Forage Cover</td>
<td>0.43926</td>
<td>0.09459</td>
<td>4.644</td>
<td>3.42e-06</td>
</tr>
<tr>
<td>NDVI * RAP Shrub Cover</td>
<td>0.18010</td>
<td>0.07590</td>
<td>2.373</td>
<td>0.0177</td>
</tr>
<tr>
<td>NDVI * RAP Tree Cover</td>
<td>0.08656</td>
<td>0.11443</td>
<td>0.756</td>
<td>0.4494</td>
</tr>
<tr>
<td>Shade Availability (Hourly Temperature * NDVI * RAP Tree Cover * is_Day)</td>
<td>0.15229</td>
<td>0.11748</td>
<td>1.296</td>
<td>0.1949</td>
</tr>
<tr>
<td>Predation Risk – Day (Ruggedness * RAP Tree Cover * is_Day)</td>
<td>2.76986</td>
<td>2.17727</td>
<td>1.272</td>
<td>0.2033</td>
</tr>
<tr>
<td>Predation Risk – Night (Ruggedness * RAP Tree Cover * is_Night)</td>
<td>0.90899</td>
<td>2.40718</td>
<td>0.378</td>
<td>0.7057</td>
</tr>
<tr>
<td>Predation Risk - (Ruggedness * RAP Tree Cover * is_Twilight)</td>
<td>-0.81036</td>
<td>2.41084</td>
<td>-0.336</td>
<td>0.7368</td>
</tr>
<tr>
<td>Cumulative Cattle Footprint</td>
<td>0.56442</td>
<td>0.28025</td>
<td>2.014</td>
<td>0.0440</td>
</tr>
<tr>
<td>Cumulative Cattle Footprint * (NDVI * RAP Herbaceous Forage Cover)</td>
<td>-1.76944</td>
<td>0.30439</td>
<td>-5.813</td>
<td>6.14e-09</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Zero-Inflated Terms</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-8.008</td>
<td>1.607</td>
<td>-4.982</td>
<td>6.30e-07</td>
</tr>
<tr>
<td>Log(Time Until Dawn)</td>
<td>0.7518</td>
<td>0.06668</td>
<td>11.275</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dusk)</td>
<td>-0.7174</td>
<td>0.06290</td>
<td>-11.406</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Julian Date</td>
<td>0.1269</td>
<td>0.02190</td>
<td>5.793</td>
<td>6.93e-09</td>
</tr>
<tr>
<td>Julian Date Squared</td>
<td>-7.770e-05</td>
<td>4.897e-05</td>
<td>-1.587</td>
<td>0.11256</td>
</tr>
<tr>
<td>Julian Date * Elevation</td>
<td>-0.02988</td>
<td>0.01881</td>
<td>-1.589</td>
<td>0.11212</td>
</tr>
<tr>
<td>Julian Date Squared * Elevation</td>
<td>-1.619e-04</td>
<td>5.021e-05</td>
<td>-3.225</td>
<td>0.00126</td>
</tr>
</tbody>
</table>
Table A.5: Model Output from Shade Competition Model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-3.03383</td>
<td>0.15220</td>
<td>-19.934</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>-0.39101</td>
<td>0.21618</td>
<td>-1.809</td>
<td>0.0705</td>
</tr>
<tr>
<td>Cosine Aspect</td>
<td>-0.23583</td>
<td>0.12038</td>
<td>-1.959</td>
<td>0.0501</td>
</tr>
<tr>
<td>NDVI * RAP Herbaceous Forage Cover</td>
<td>0.39784</td>
<td>0.09046</td>
<td>4.398</td>
<td>1.09e-05</td>
</tr>
<tr>
<td>NDVI * RAP Shrub Cover</td>
<td>0.16574</td>
<td>0.07502</td>
<td>2.209</td>
<td>0.0271</td>
</tr>
<tr>
<td>NDVI * RAP Tree Cover</td>
<td>0.11621</td>
<td>0.11100</td>
<td>1.047</td>
<td>0.2951</td>
</tr>
<tr>
<td>Shade Availability (Hourly Temperature * NDVI * RAP Tree Cover * is_Day)</td>
<td>0.04470</td>
<td>0.23204</td>
<td>0.193</td>
<td>0.8472</td>
</tr>
<tr>
<td>Predation Risk – Day (Ruggedness * RAP Tree Cover * is_Day)</td>
<td>2.91517</td>
<td>1.93752</td>
<td>1.505</td>
<td>0.1324</td>
</tr>
<tr>
<td>Predation Risk – Night (Ruggedness * RAP Tree Cover * is_Night)</td>
<td>1.07244</td>
<td>2.16933</td>
<td>0.494</td>
<td>0.6210</td>
</tr>
<tr>
<td>Predation Risk - (Ruggedness * RAP Tree Cover * is_Twilight)</td>
<td>-0.55966</td>
<td>2.15213</td>
<td>-0.260</td>
<td>0.7948</td>
</tr>
<tr>
<td>Instantaneous Cattle Abundance</td>
<td>2.14827</td>
<td>0.38351</td>
<td>5.602</td>
<td>2.12e-08</td>
</tr>
<tr>
<td>Instantaneous Cattle Abundance * Shade Availability</td>
<td>0.52421</td>
<td>1.01409</td>
<td>0.517</td>
<td>0.6052</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Zero-Inflated Terms</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-8.706e</td>
<td>0.9052</td>
<td>-9.618</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dawn)</td>
<td>0.7761e</td>
<td>0.06554</td>
<td>11.841</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dusk)</td>
<td>-0.7335</td>
<td>0.06361</td>
<td>-11.531</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Julian Date</td>
<td>0.1307</td>
<td>0.01892</td>
<td>6.908</td>
<td>4.91e-12</td>
</tr>
<tr>
<td>Julian Date Squared</td>
<td>-8.564e-05</td>
<td>4.772e-05</td>
<td>-1.795</td>
<td>0.072680</td>
</tr>
<tr>
<td>Julian Date * Elevation</td>
<td>-0.02640</td>
<td>0.01938</td>
<td>-1.363</td>
<td>0.173003</td>
</tr>
<tr>
<td>Julian Date Squared * Elevation</td>
<td>-1.710e-04</td>
<td>5.068e-05</td>
<td>-3.375</td>
<td>0.000739</td>
</tr>
</tbody>
</table>
Table A.6: Model Output from Indirect Predation Risk Effects Model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-3.05375</td>
<td>0.18088</td>
<td>-16.883</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Ruggedness</td>
<td>-0.40865</td>
<td>0.21813</td>
<td>-1.873</td>
<td>0.0610</td>
</tr>
<tr>
<td>Cosine Aspect</td>
<td>-0.22909</td>
<td>0.12258</td>
<td>-1.869</td>
<td>0.0616</td>
</tr>
<tr>
<td>NDVI * RAP Herbaceous Forage Cover</td>
<td>0.40058</td>
<td>0.09289</td>
<td>4.312</td>
<td>1.61e-05</td>
</tr>
<tr>
<td>NDVI * RAP Shrub Cover</td>
<td>0.17643</td>
<td>0.07646</td>
<td>2.308</td>
<td>0.0210</td>
</tr>
<tr>
<td>NDVI * RAP Tree Cover</td>
<td>0.10256</td>
<td>0.11131</td>
<td>0.921</td>
<td>0.3569</td>
</tr>
<tr>
<td>Shade Availability (Hourly Temperature * NDVI * RAP Tree Cover * is_Day)</td>
<td>0.16978</td>
<td>0.11909</td>
<td>1.426</td>
<td>0.1540</td>
</tr>
<tr>
<td>Predation Risk – Day (Ruggedness * RAP Tree Cover * is_Day)</td>
<td>4.64417</td>
<td>2.24210</td>
<td>2.071</td>
<td>0.0383</td>
</tr>
<tr>
<td>Predation Risk – Night (Ruggedness * RAP Tree Cover * is_Night)</td>
<td>1.80776</td>
<td>2.68687</td>
<td>0.673</td>
<td>0.5011</td>
</tr>
<tr>
<td>Predation Risk - (Ruggedness * RAP Tree Cover * is_Twilight)</td>
<td>1.65842</td>
<td>2.52242</td>
<td>0.657</td>
<td>0.5109</td>
</tr>
<tr>
<td>Instantaneous Cattle Abundance</td>
<td>2.05343</td>
<td>0.39687</td>
<td>5.174</td>
<td>2.29e-07</td>
</tr>
<tr>
<td>Instantaneous Cattle Abundance *Predation Risk (Day)</td>
<td>-11.52275</td>
<td>8.24061</td>
<td>-1.398</td>
<td>0.1620</td>
</tr>
<tr>
<td>Instantaneous Cattle Abundance *Predation Risk (Night)</td>
<td>-3.60367</td>
<td>12.09548</td>
<td>-0.298</td>
<td>0.7658</td>
</tr>
<tr>
<td>Instantaneous Cattle Abundance *Predation Risk (Twilight)</td>
<td>-14.51459</td>
<td>9.24231</td>
<td>-1.570</td>
<td>0.1163</td>
</tr>
</tbody>
</table>

Zero-Inflated Terms

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-8.839</td>
<td>1.148</td>
<td>-7.697</td>
<td>1.39e-14</td>
</tr>
<tr>
<td>Log(Time Until Dawn)</td>
<td>0.7818</td>
<td>0.06748</td>
<td>11.585</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Log(Time Until Dusk)</td>
<td>-0.7352</td>
<td>0.06459</td>
<td>-11.382</td>
<td>&lt; 2e-16</td>
</tr>
<tr>
<td>Julian Date</td>
<td>0.1325</td>
<td>0.02009</td>
<td>6.595</td>
<td>4.25e-11</td>
</tr>
<tr>
<td>Julian Date Squared</td>
<td>-9.068e-05</td>
<td>4.973e-05</td>
<td>-1.824</td>
<td>0.06821</td>
</tr>
<tr>
<td>Julian Date * Elevation</td>
<td>-0.02727</td>
<td>0.01946</td>
<td>-1.401</td>
<td>0.16114</td>
</tr>
<tr>
<td>Julian Date Squared * Elevation</td>
<td>-1.680e-04</td>
<td>5.109e-05</td>
<td>-3.288</td>
<td>0.00101</td>
</tr>
</tbody>
</table>
Figure A.1: Prediction plots demonstrating mule deer abundance in response to terrain habitat features. Predictions made using the null model. Shaded region represents 95% confidence intervals.
Figure A.2: Prediction plots demonstrating mule deer abundance response to vegetation features. Predictions based on the null model. Shaded region represents 95% confidence intervals.
Figure A.3: Prediction plots demonstrating mule deer abundance response to trees at three different values of heat stress. Predictions based on the null model. Shaded region represents 95% confidence intervals.
Figure A.4: Prediction plot demonstrating mule deer response to tree cover at three different values of ruggedness during the day, night, and twilight. Prediction plots based on the null model. Shaded region represents 95% confidence intervals.
Figure A.5: Map of camera locations spread across all three pastures of the Diamond Fork grazing allotment in Spanish Fork, UT.
Figure A.6: Conceptual diagram of trail camera setup.
Appendix B.  CHAPTER 3 TABLES AND FIGURES

Table B.1: Maximum likelihood estimates of step length from fitted HMM.

<table>
<thead>
<tr>
<th></th>
<th>Resting</th>
<th>Foraging</th>
<th>Commuting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>40.593724425</td>
<td>193.4068</td>
<td>525.2745</td>
</tr>
<tr>
<td>SD</td>
<td>36.581702004</td>
<td>191.9564</td>
<td>622.8221</td>
</tr>
<tr>
<td>Zeromass</td>
<td>0.005062629</td>
<td>1.000054e-08</td>
<td>1.000050e-08</td>
</tr>
</tbody>
</table>

Table B.2: Maximum likelihood estimates of turning angle from fitted HMM.

<table>
<thead>
<tr>
<th></th>
<th>Resting</th>
<th>Foraging</th>
<th>Commuting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>-3.1129670</td>
<td>-0.001231667</td>
<td>-0.007806699</td>
</tr>
<tr>
<td>Concentration</td>
<td>0.3215653</td>
<td>0.249230059</td>
<td>0.593348739</td>
</tr>
</tbody>
</table>
Figure B.1: Map of mule deer locations distributed across USFS pastures. Star represents the Spanish Fork study site from Chapter 1 where cameras are located.