

LINKING PATTERNS IN ELK AGGREGATION AND BRUCELLOSIS TO
VARIATION IN GROUP SIZE, LAND USE,
CLIMATE AND WOLVES

by

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

of

Doctor of Philosophy

in

Fish and Wildlife Biology

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2014

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ACKNOWLEDGEMENTS

I would like to thank my advisors Paul Cross and Scott Creel for giving me the opportunity to work on my PhD and for inspiring and supporting me through these years. I would also like to thank Megan Higgs for her continued support, advice and patience. Many thanks to my technicians Andrea Barbknecht, Carson Butler and Andy Roosa who helped log many hours on foot or by plane, and to the many biologists of the Wyoming Game and Fish Department for their assistance on various aspects of my work. Specifically, I would like to thank Brandon Scurlock, Hank Edwards, and Tim Woolley. I will also always be grateful to Dave Stinson and Steve Ard, who kept me safe in the air.

I would like to thank my graduate committee and the many coauthors on each of these chapters. I have learned an incredible amount from these people and I am grateful for their effort and contributions. I am thankful for everyone associated with the Cross and Creel lab groups, as they helped me become a better scientist in one way or another. I am also grateful for the funding that made this work possible, provided by the National Science Foundation and National Institutes of Health Ecology of Infectious Disease (grant number DEB-1067129) and the United States Geological Survey.

I would not be here if it was not for my family and friends. So thank you Schuler's and Brennan's for your love and support. Finally, I would like to thank my best friend and husband, Scott Brennan. I would not have moved past "Go" without your loving and dedicated patience, encouragement, and confidence. You deserve a whole dissertation of thanks.

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ABSTRACT

Recent data suggest that elk were the source of brucellosis outbreaks in cattle and that the disease is on the rise in elk across the Greater Yellowstone Area. As the distribution of elk group sizes is often right-skewed and spans several orders of magnitude, the largest elk groups may be driving brucellosis dynamics. To investigate whether the increases in brucellosis could be explained by elk grouping patterns, we examined 21 years of serologic data and three years of aerial surveys to record group sizes across 10 wintering elk populations, and we evaluated the relationships between rates of increase in brucellosis and seven measures of elk aggregation. We also examined the relationships between large elk groups and land use, habitat conditions, levels of predation risk, and snow accumulation. To do this, we used quantile regression to focus on group sizes in the tail of the distribution. We found that brucellosis increased over time in eight of the 10 populations, and that these increases were positively related to all measures of aggregation. We also found that group sizes were larger on irrigated land and as the habitat got more open. Because we were interested in the effects of snow on elk grouping behavior, we also examined the consequences of using snow model predictions in place of direct measurements. We found substantial model prediction uncertainty could directly impact our inferences. Lastly, we tested a noninvasive tool for conducting wolf surveys and found the method was a poor substitute for other techniques currently used during the winter, particularly in areas where pack territories overlap. Overall, our findings suggest that (i) most measures of elk aggregation had similar utility to predict changes in brucellosis over time, (ii) there may be more than one way to be dense and spread disease in populations that are structured by grouping (iii) it may be important to focus on more than one metric of the group size distribution to inform management, and (iv) it is important to consider the implications of prediction uncertainty on inferences when using model predictions as explanatory variables.

CHAPTER ONE

INTRODUCTION TO DISSERTATION

Overview of Dissertation

The Greater Yellowstone Area (GYA) is a vast network of protected areas and other public lands stretching across much of western Wyoming, eastern Idaho, and southwestern Montana, all the while scraping its edges against growing human settlements. Many of the animals in the region live along these boundaries, moving across the public-private land matrix to fulfill their energy requirements or reproductive needs, sometimes sparking controversy as they interact with humans, livestock, or agricultural lands. Such controversies exist because the consequences of these interactions such as livestock depredation (Bradley and Pletscher 2005), disease transmission (Beja-Pereira et al. 2009) or destruction of food crops (Haggerty and Travis 2006), can be felt on both sides of the fence – affecting wild animals and human livelihoods, often resulting in challenging strategies for coexistence (*e.g.*, Bangs et al. 2006, Bienen and Tabor 2006). Without question, similar issues and challenges occur wherever human settlements and wildlife overlap, and are therefore a focus of research across the globe (*e.g.*, Cozza et al. 1996, Naughton-Treves 1999, Donnelly et al. 2003, Mishra et al. 2003, Randall et al. 2006, Marshall et al. 2007). In this dissertation, I focus on the issue of brucellosis in the GYA: an economically and politically important bacterial disease spreading among the region's elk, bison, and cattle.

Brucellosis came to the United States via European cattle, and was first discovered in the elk and bison around the GYA in the early 1900s (Meagher and Meyer 1994). In 1934, the country engaged in an ambitious campaign to eradicate the disease in cattle, and was largely successful, except among the elk and bison (Ragan et al. 2002). These populations are now the last stronghold of the disease in the US and continue to be a risk to cattle that are grazed in the region (Cheville et al. 1998). Because eradication is still the goal, when brucellosis is detected in a cattle herd, the rancher is required to lethally remove all cattle and the state must engage in expensive testing and limit cattle export to prevent spreading the disease (US Department of Agriculture 2003). Given these consequences, some people in the ranching communities and general public have strong negative reactions to any wild elk or bison wandering too close to grazing cattle. Usually, the bison of Yellowstone receive most of this attention, because they have the highest brucellosis seroprevalence (Cheville et al. 1998) and they often leave Yellowstone during the winter to access forage at lower elevations where cattle ranches also occur. However, bison that leave the park are strictly managed, either by hazing or slaughter, and there has been no evidence of transmission between bison and cattle (Bienen and Tabor 2006). Moreover, recent data suggest that elk are the most likely source of spill over infections into cattle (Beja-Pereira et al. 2009).

Elk are a widely roaming and social herbivore that often winter in areas near human settlements and livestock (Haggerty and Travis 2006). In addition, high levels of brucellosis have been detected among elk populations that are supplementally fed during the winter on Wyoming's elk feeding grounds, and recent studies suggest that brucellosis

is also increasing in elk that do not use these feeding grounds (Scurlock and Edwards 2010, Cross et al. 2010b). Though transmission of *Brucella abortus* among fed elk probably occurs because they form large, dense aggregations on the feed lines (Maichak et al. 2009, Creech et al. 2012), increasing brucellosis among unfed elk has remained largely unexplained. Several probable causes of these increases have been examined, including increased elk-elk transmission associated with increased density, dispersal of infectious elk from feedgrounds, and changes to an older-age structure (Cross et al. 2010b). Only elk density, however, explained observed rates of increasing brucellosis, but it was not clear whether the relationship was linear or nonlinear, and only annual population density was examined (Cross et al. 2010a, Cross et al. 2010b). Because elk populations are structured by social behaviors, rates of increasing brucellosis may be better explained by how elk group at local scales than by broad measures of population density.

Identifying a strong positive relationship between elk group size and brucellosis increases could be valuable information for brucellosis management efforts, but evidence for relationships between group size and transmission rates in other systems have been mixed (Rifkin et al. 2012). Moreover, elk and other social ungulate grouping can be fluid over space and time (i.e., group sizes can change frequently; Cross et al. 2013, Gerard et al. 2002). Therefore, in Chapter Two, I examined elk density and group size across multiple spatial and temporal scales using three years of aerial flights over 10 regions where brucellosis seroprevalence ranged from 0 to 30%. I used Bayesian hierarchical models and 21 years of serologic data to estimate rates of increase in brucellosis

seroprevalence among the 10 regions, and I examined the linear relationships between these estimated rates of increase and seven measures of elk aggregation.

Elk group size distributions are often right skewed, with group sizes ranging several orders of magnitude (Cross et al. 2010b). Under these circumstances, the largest groups may be driving brucellosis dynamics in the region, but also disproportionately contributing to other conflicts along the wildlife-livestock interface. Therefore, understanding factors related to large groups may be important to elk and brucellosis management. As many birds and mammals also have right-skewed group size distributions (Reiczigel et al. 2008), it is important to understand how large groups (*i.e.*, upper quantiles of the group size distribution) differ from mean or median group sizes (*i.e.*, center of the distribution) in their relationships to environmental conditions. Therefore, in Chapter Three, I demonstrated the use of quantile regression to examine relationships between explanatory variables (such as land use, habitat, snow and predation risk) and 0.10, 0.20, ..., 0.90 quantiles of the elk group size distribution.

Other studies have also examined the effects of snow accumulation (Gower 2008, Proffitt et al. 2012, White et al. 2012) and wolf predation risk (Gower 2008, Creel and Winnie 2005) on elk behavior and grouping patterns. However, in the case of snow, measuring depth or density repeatedly in remote locations can be logistically and financially challenging. As a result, many studies have relied on snow models when direct measurements of snow accumulation could not be collected, but without quantifying or accounting for the uncertainty in these model predictions before they are used as explanatory variables in ecological models. In Chapter Four, I examined the

potential levels of model prediction error at wildlife relevant scales and the practical effects of using model predictions in place of direct measurements in a typical wildlife application.

For measuring predation risk on the other hand, the challenges are largely due to the expense of survey tools and techniques, logistical difficulty of frequently accessing the animal's territory, and the animal's elusive behavior (Long et al. 2008). Therefore, researchers may seek out automated, noninvasive survey techniques to reduce monitoring costs and effort, while also increasing precision and spatial coverage. For this purpose, I tested an automated howling device in Chapter Five for measuring wolf presence and absence in a wintertime wolf survey, and I discuss the factors that may affect successful application of the tool.

Finally, in Chapter Six I provide general conclusions and discuss how these projects can inform elk and brucellosis management in the GYA.

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CHAPTER TWO

MULTIPLE WAYS TO BE DENSE AND TRANSMIT DISEASE: PATTERNS IN
ELK AGGREGATION AND INCREASING BRUCELLOSISContribution of Authors and Co-Authors

Manuscript in Chapter 2

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Contributions: Conceived, developed, and implemented hypotheses and study design. Collected and analyzed data. Wrote first draft and subsequent revisions of the manuscript.

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Contributions: Helped conceive hypotheses and study design. Provided funding and feedback on statistical analyses, presentation of findings, and all drafts of the manuscript.

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Contributions: Contributed information regarding population dynamics and behavior of elk in western Wyoming. Provided comments on final draft of the manuscript.

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Contributions: Helped develop hypotheses and study design. Provided funding, feedback on statistical analyses, and comments on all drafts of the manuscript.

Manuscript Information Page

Angela Brennan, Paul C. Cross, Megan D. Higgs, W. Henry Edwards, Brandon M. Scurlock, and Scott Creel

Status of Manuscript

☒ Prepared for submission to a peer-reviewed journal

☐ Officially submitted to a peer-review journal

☐ Accepted by a peer-reviewed journal

☐ Published in a peer-reviewed journal

Abstract

The relationship between host density and parasite transmission is critical to our understanding of disease dynamics and effective disease control strategies. In order to learn about this relationship it is important to measure host density at a scale relevant to transmission, but this is not straightforward or well-studied for social species whose group sizes range several orders of magnitude or whose aggregation patterns vary across space and time. To address these issues we studied elk (*Cervus canadensis*) aggregation patterns and brucellosis in the Greater Yellowstone Area, where previous studies suggest the disease may be increasing. We hypothesized that rates of increasing brucellosis would be more associated with the frequency of large groups than mean group size or population density, because large groups are likely to play a disproportionate role in disease dynamics. We measured elk density and group size across multiple spatial and temporal scales using aerial flights over 10 regions. All of these measures were positively related with one another, but we observed some high density populations with small group sizes and vice versa. We used Bayesian hierarchical models and 21 years of serologic data to estimate rates of increase in brucellosis seroprevalence among the 10 regions, and we examined the linear relationships between these estimated rates of increase and seven measures of elk aggregation. Brucellosis seroprevalence increased over time in eight regions (e.g., one region showed an estimated increase from 0.015 in 1991 to 0.26 in 2011), and these rates of increase were positively related to all measures of aggregation. The relationships between aggregation and rates of increase in seroprevalence were weaker when the analysis was restricted to only areas where

brucellosis was present for at least two years. Our findings suggest that (i) most measures of host aggregation had similar utility to predict changes in seroprevalence over time, (ii) these patterns may have been influenced by the effects of aggregation on disease-establishment within a population, and (iii) group size did not explain brucellosis increases any better than density, even though elk populations were structured by grouping throughout the transmission period.

Keywords: Aerial survey, *Brucella abortus*, density-dependent transmission, elk feedgrounds, group living, group size distribution, Lloyd's crowding, parasite transmission, seasonal grouping, wildlife disease.

Introduction

There is considerable evidence for a positive relationship between host density and parasite transmission rates in studies of disease ecology (Freeland 1976, Brown and Brown 1986, Davies et al. 1991, Côté and Poulin 1995, Arneberg 2002, Altizer et al. 2003), and this relationship is at the root of disease management strategies aimed at reducing the density of susceptible individuals (*e.g.*, Caley et al. 1999, Smith et al. 2001, Wobeser 2002, Lloyd-Smith et al. 2005). Measuring host density at a scale relevant to transmission, however, may not be straightforward for populations that are spatially structured by social behaviors such as territoriality or grouping. For these social species, transmission may be more related to fine scale measures of aggregation (*e.g.*, group size) than broad measures such as population density that assume individuals mix completely

at the population level. In this case, using population density as a proxy for the rate of contact among individuals could fail to explain disease dynamics driven by within-group transmission (Cross et al. 2010b, Ferrari et al. 2011). Animal aggregations can also vary over space and time (*e.g.*, Gerard et al. 2002, Focardi and Pecchioli 2005, Fortin et al. 2009, Pays et al. 2007), and therefore understanding the density-transmission relationship may also require evaluating aggregation patterns at multiple spatial and temporal scales. However, such data are rare among studies of animal disease. To address these issues, we examined the relationship between measures of aggregation and rates of increasing brucellosis seroprevalence in elk (*Cervus canadensis*) in the Greater Yellowstone Area (GYA).

Brucellosis, caused by *Brucella abortus*, has largely been eradicated in the United States, but has persisted in wildlife around the GYA for about a century (Mohler 1917, Meagher and Meyer 1994). Over this time, brucellosis prevalence has been highest in bison in Yellowstone National Park (Cheville et al. 1998) and in elk that are supplementally fed on feedgrounds during the winter in western Wyoming (Scurlock and Edwards 2010). However, recent surveillance efforts have documented increasing brucellosis in some elk populations that previously maintained the disease at lower levels (estimated seroprevalence increased from 0–7% in 1991 to 10–25% in 2010; Scurlock & Edwards 2010, Cross et al. 2010b). Several probable causes of these increases have been examined, including increased elk-elk transmission associated with increased density, dispersal of infectious elk from feedgrounds, and changes to an older-age structure. Only elk density, however, explained observed rates of increasing brucellosis seroprevalence,

but the data could not differentiate between linear or nonlinear relationships with density and only annual population density was examined (Cross et al. 2010a, Cross et al. 2010b). Rates of increasing brucellosis may be better explained by how elk aggregate during the transmission period than by broad measures of density.

Transmission of *Brucella* occurs during the months of February through June when elk aggregate on lower elevation winter range to avoid deep snowfall (Thorne et al. 1991, Roffe et al. 2004). During this period, brucellosis causes roughly half of infected females to abort their first pregnancy post-infection and roughly 10% to also abort their second calf (Thorne et al. 1978). From these abortion events, transmission occurs via uptake of the bacteria through contact with or feeding near the fetus or birthing materials (Cheville et al. 1998) and evidence suggests the duration of exposure may be limited because scavengers typically consume aborted materials within 24 to 48 hours (Cook et al. 2004, Maichak et al. 2009). However, fetuses may remain in the environment for weeks or months in areas with lower scavenger densities (Aune et al. 2012) and the effects of such long-term contamination on transmission are not known. Other modes of directly transmitting bacteria such as vertical or sexual transmission are not considered important in the spread of *Brucella* (Thorne et al. 1978).

On the winter range in western Wyoming, elk aggregate into groups ranging in size from one to thousands of individuals and, as with most species that aggregate, the group size distribution is right skewed, whereby a majority of groups are small but a majority of the individuals occur in large groups (Reiczigel et al. 2008). With this distribution, disease dynamics may be driven by the transmission occurring within groups

that are much larger than the mean. Therefore, we hypothesized that the estimated rate of increase in brucellosis seroprevalence will be more related to group sizes in the tail of the distribution than population density or mean group size. In addition, previous work on feedground elk showed brucellosis seroprevalence was higher in feedgrounds that operated later into the spring and for longer periods (Cross et al. 2007). Therefore, we also hypothesized that the estimated rate of increase in brucellosis would be related to the tail of the group size distribution observed during the end of the transmission period and the sum of monthly elk densities across the transmission period.

To test our hypotheses, we used Bayesian hierarchical models to (1) estimate the rates of increase in brucellosis seroprevalence from 21 years of serologic data across 10 elk populations, and (2) evaluate how these estimated rates of increase in brucellosis were related to fine (*e.g.*, group size) and broad scale (*e.g.*, annual population density) measures of aggregation. We included broad measures such as annual population density in order to compare our results to previous studies that assumed elk are well mixed at the population level, but we also hypothesized that estimated rates of increase in brucellosis would be more related to the density of elk on the winter range (where elk are located during the transmission period) than density measured from both winter and summer range. Therefore, by examining the relationship between multiple measures of aggregation and estimated rates of increase in brucellosis, our study expands upon previous work that focused only on broad measures of population density (Cross et al. 2010a). Furthermore, we re-tested our hypotheses using only those elk populations having brucellosis seropositive animals for at least two years to investigate the potential

importance of aggregation on increasing seroprevalence within places where the pathogen was known to be present (*i.e.*, a lack of increase in seroprevalence may be due to the absence of the pathogen). Assessing these relationships can help identify where to focus disease management efforts and improve our understanding of how a variable social structure may affect disease dynamics.

Methods

Broad Scale Density

We studied elk aggregation patterns and brucellosis seroprevalence among Wyoming elk populations in the GYA. We used the following broad scale measures: (1) herd unit density, (2) hunt area density, and (3) winter range density. The herd unit and hunt area were two sizes of elk management units delineated by the Wyoming Game and Fish Department (WGFD), where multiple hunt areas were nested within a larger herd unit (Figure 2.1). Hunt area boundaries tended to be substantial terrain features (*e.g.*, hydrographic divides and highways) and movement between hunt areas during the winter was possible, but thought to be minor for most hunt areas in our study (WGFD 2011). Each elk herd unit included multiple hunt areas and was more likely to encompass a closed elk population (less than 10% interchange with adjacent herd units throughout the year; WGFD 2011). Therefore, if any movement occurred between hunt areas, most of it did not affect density estimates at the herd unit scale. Our study examined five herd units where brucellosis was endemic in elk, but without supplemental feedgrounds (herd units 217, 216, 214, 635 and 637), and then focused on ten hunt areas within those herd units

(Figure 2.1) that represented the range of elk densities (from roughly 0.2 to 3.0 elk/km²) and estimated brucellosis seroprevalence (from roughly 0 to 0.25) in the study area (Cross et al. 2010a; Scurlock and Edwards 2010; WGFD 2011).

Herd unit density (annual population density) and hunt area density (annual sub-population density) were calculated as described in Cross et al. 2010a and b, using aerial elk trend counts collected in 2011. The area used to calculate these densities included the winter range where elk are located during the transmission period, the summer range, and other high elevation areas elk avoid in snow (WGFD 2011). To better reflect elk density during the transmission period, each hunt area was refined to only the winter range. To do this, winter ranges were delineated using all elk sightings recorded by the WGFD during the months of January through May, 2005–2009 (Figure 2.1). These sightings included elk counted during trend and classification surveys, and any opportunistic sightings made by WGFD biologists or game wardens from the air or ground. Winter range elk density was then calculated by dividing each hunt area's 2011 trend count by its winter range area.

Cumulative Winter Density and Group Size

In addition to the three broad scales measures of density, four finer scale measures of elk aggregation were calculated, including: (1) cumulative winter density, (2) mean group size, (3) Lloyd's crowding (*i.e.*, a weighted average of group size that is the expected group size of a randomly chosen individual; Lloyd 1967), and (4) Lloyd's crowding in May. To obtain these fine scale measures of aggregation, elk group sizes were recorded from a fixed wing aircraft over the winter range of each hunt area once a

month from January through May for three years (2010–2012). These aerial surveys were conducted using transects that were set 2 km apart, for 1-km viewing widths from one side of the plane. Transects were assigned to be non-overlapping, to cover the full extent of each winter range, and to follow a north-south orientation, though in several cases transects were set to follow major landscape features such as a ridgeline or narrow valley. To increase our chances of seeing elk, four to seven transects were deliberately selected (non-random) per winter range in order to cover areas with a high probability of elk occurrence, as determined by the WGFD elk sightings (*i.e.*, areas with the highest number of elk sightings were high probability areas for elk occurrence). Three additional transects were randomly selected per winter range, and the viewing direction (east or west) for all transects was also randomly selected. The number of transects selected and length of transects varied by winter range, but consistently these transects covered approximately 35% of each winter range area. The same transects and viewing directions selected at the beginning of the study were used for all subsequent monthly flights.

Transects covered a range of elevations (roughly 1230 to 2800 m), topography (e.g., mountain ridges, valleys, small drainages, and mesas), and habitat (e.g., dense and open forests, grassland, sagebrush steppe, and badlands). On average, we conducted flights at 240 m above ground level and at 150 km per hour. The timing and order of our flights differed each month, as they depended on clear or overcast (high clouds) mornings (before noon), when winds at 2700 and 3600 m above sea level were less than 32 km per hour. From the airplane, we used a camera (D5000 [with 16 megapixels], Nikon, Tokyo, Japan), zoom lens (NIKKOR 70-300 mm, Nikon, Tokyo, Japan), and camera-GPS unit

(GP-1, Nikon, Tokyo, Japan) to record elk group size and the GPS coordinates of our location (in Universal Transverse Mercator [UTM]). We examined the photos and coordinates, overlaid on 1-m resolution National Agriculture Imagery Program (NAIP) 2009 imagery data¹ in a GIS to determine precise locations of elk groups (rather than using the location of the camera when the photo was taken). Using these precise locations, we summed all elk groups within 500 m of one another so that one elk “group” was actually a collection of sub-groups and was defined by distance rather than behavior, which may be subjective or temporary (sub-groups were observed splitting and merging).

For our first fine scale measure of elk aggregation, we calculated cumulative density by dividing the total number of elk sighted over the whole survey by the total transect area of each hunt area. We used cumulative density because a winter range with more elk present consistently throughout the transmission period (January–May) may have a higher likelihood of infectious contacts than a winter range where elk are not present consistently because they migrate to the winter range late or depart for summer range early (Cross et al. 2007).

We constructed the empirical elk group size distribution for each hunt area, and calculated mean group size, Lloyd’s crowding ($c = m + ([s^2/m] - 1)$; where m is the average group size and s is the standard deviation of the empirical group size distribution), and Lloyd’s crowding in May (Lloyd 1967). We used Lloyd’s crowding because it may be a better measure of force of infection than mean group size (Cross et al. 2010a). We used Lloyd’s crowding in May was used because recent studies have

¹ To obtain NAIP imagery see <http://datagateway.nrcs.usda.gov/>

shown that elk populations remaining on supplemental feedgrounds into May may have higher brucellosis seroprevalence than feedgrounds where elk depart the feedgrounds earlier (Cross et al. 2007).

We used a double observer method to assess sightability bias (Pollock and Kendall 1987). To do this, two observers flew in separate airplanes in tandem over three winter ranges (one winter range in March 2012 and two winter ranges in April 2012) and recorded elk group sizes as described above. We determined the difference in total number of groups and total elk seen between the two observers, and estimated the difference in our group size measures of interest.

Brucellosis Datasets

We used a dataset of elk brucellosis status (0 = negative, 1 = positive), consisting of serologic test results from elk blood samples collected by hunters and researchers from 1991 to 2011 within the five herd units. We restricted these data to adult female elk to reduce the potential for confounding effects of age on time trends in brucellosis seroprevalence (*i.e.*, log odds of testing positive over time may be higher for adults than for calves or yearlings), and because male elk are not considered important to the spread of *Brucella* (Cheville et al. 1998).

Serologic test methods have been detailed elsewhere (Scurlock and Edwards 2010). To summarize, seropositivity was determined following current National Veterinary Services Laboratories protocols for the card test, plate agglutination, rivanol precipitation–plate agglutination, fluorescence polarization assay, and complement fixation. Serologic profiles were categorized using the U.S. Department of Agriculture

brucellosis eradication uniform methods and rules for cervids (Animal Plant Health Inspection Service 2003), with the exception that all suspect reactors were considered positive. These tests were used to determine brucellosis exposure, not current infection, and they do not address the possibility of titer loss.

Statistical Analysis

We used a Bayesian hierarchical model with a logit link function, serologic status as the binomially distributed response variable, and year (rescaled so that 1991 was year zero) as the explanatory variable. We did not allow the intercept to vary by herd unit or hunt area, because seroprevalence was low in the beginning of the time series for all herd units and hunt areas in our study. We assigned this intercept a normal prior distribution with a mean of zero and a precision of 0.0001. The slope term measured the log odds of testing seropositive for each one-year increase in time, and was therefore used to describe the rate of increase in brucellosis (on the logit scale). We allowed this slope to vary by herd unit or hunt area in order to understand how the rates of increase in brucellosis varied among elk populations and sub-populations. To understand how these rates of increase in brucellosis were related to elk aggregation, we assumed the herd unit or hunt area-specific slopes came from a normal distribution with a mean described by a linear relationship with an aggregation measure and a standard deviation that was uniformly distributed from 0 to 20 on the prior distribution. We assigned the intercept and slope parameters of this linear relationship (between elk aggregation and herd unit or hunt area specific slopes) normally distributed priors with means of zero and precisions of 0.0001. For a detailed description of this model, see Appendix A. We repeated these steps for

each measure of elk aggregation, and in a separate analysis we examined the relationships among all aggregation measures using simple linear regression.

Because a lack of increase in brucellosis seroprevalence may be due to the absence of *Brucella*, we conducted a post hoc analysis to understand the relationship between elk aggregation and rates of increase in brucellosis among only those areas where the pathogen was known to be present. To do this, we excluded data from the beginning of the time series for years in which seropositivity was zero; in these cases there was no evidence that the disease was present within a herd. Therefore, for each hunt area we included only the first year a seropositive sample was detected and all subsequent years. If a hunt area never had a seropositive sample, we removed it from the analysis. We also removed hunt areas having only one year with seropositive samples, because though there was evidence that *Brucella* was present once, it may not have become established. We fit models to this truncated dataset following the same framework described previously and shown in Appendix A.

While the main goal of the analysis was inference about the regression coefficients, we also compared models using the deviance information criterion (DIC) as a rough indices to assess whether measures of group size were better supported by the data than measures of density at broader scales. All models were fit using the R2WinBUGS package (Sturtz et al. 2005) to call WinBUGS version 1.4.3 (Lunn et al. 2000) from R version 2.13 (R Core Development Team 2011). For each model, three chains of 100,000 iterations were run and a burn-in period of 10,000 iterations was used before summarizing the posterior distributions. We checked convergence visually by

assessing sample trace plots and by calculating the potential scale reduction factor, $\hat{R}$ (Gelman et al. 2013), to compare within- and among-chain variance, where values of 1 to 1.1 typically indicate convergence (Gelman and Hill 2007).

Results

Elk Density

Across all three years of aerial surveys, we recorded 800 groups ranging in size from 1 to 1952 elk and group size distributions were generally right skewed (Appendix A, Figure A1). Our flights to and from each hunt area's winter range consistently revealed few elk outside the areas we delineated as winter range. Therefore, elk groups that were missed because they were outside the winter range were likely to be rare and small, and would therefore have little effect on estimates of mean group size or Lloyd's crowding. In the double observer flights used to test the repeatability of our methods, the two observers recorded 33 and 32 elk groups, and 3084 and 3067 total elk, respectively. Observer one missed three of the groups recorded by observer two, and observer two missed four of the groups recorded by observer one. These missed groups were all small, ranging in size from three to 24 elk with an average of 11 elk. The mean group size recorded by the two observers was 138 and 123, respectively, and the Lloyd's crowding determined by each observer was 651 and 648, respectively.

All measures of aggregation varied by herd unit (Appendix A, Table A1) and hunt area (Appendix A, Table A2) and were positively related with one another (Appendix A, Figure A2). However, the ranking of hunt areas varied under different measures of

aggregation. Hunt area 63, for example, had larger groups in the tail of the distribution (Lloyd's crowding = 554) but low density at the hunt area scale (hunt area density = 1.0 elk/km²), whereas hunt area 52 had moderately sized groups in the tail of the distribution (Lloyd's crowding = 261) and higher densities (hunt area density = 2.9 elk/km²) (Figure 2.2).

Brucellosis Increases Over Time

The 21-year brucellosis datasets for the five herd units and 10 hunt areas contained serologic results for 4448 and 2765 cow elk, respectively. Brucellosis increased over time in a majority of the herd units (Figure 2.3) and hunt areas (Figure 2.4). Therefore, a majority of the posterior means of the rates of increase in brucellosis were positive, but the posterior mean was negative for hunt area 25 and the 95% credible intervals extended below zero for hunt area 121 (Figure 2.5). These two hunt areas contained only one seropositive out of 253 samples, and therefore were excluded from the *post hoc* analysis that we used to estimate the rate of increase in brucellosis only where the disease was known to be present. For this analysis, we also excluded years at the beginning of the time series when brucellosis seroprevalence was zero. The resulting truncated dataset contained serologic results for 2245 cow elk among eight hunt areas, and the number of inclusive years ranged from 5 years for hunt area 54 to 15 years for hunt areas 52 and 67. The posterior means and 95% credible intervals for the rates of increase in brucellosis estimated from the truncated dataset were similar to the rates of increase in brucellosis estimated from the full dataset (Appendix A, Figure A3).

Relationship Between Brucellosis Increases and Aggregation

The rates of increase in brucellosis tended to increase with increasing aggregation for all measures of aggregation (Figure 2.6 and Appendix A, Figure A4). As measured from the posterior distribution, the probability that aggregation was positively related to rates of increase in brucellosis was estimated at greater than 0.90 for winter range density, cumulative density and Lloyd's crowding in May (Appendix A, Figure A5). For herd unit density, mean group size, Lloyd's crowding, and hunt area density, the probability that aggregation was positively related to rates of increase in brucellosis was estimated at 0.60, 0.77, 0.78, and 0.87, respectively (Appendix A, Figure A5). After truncating the data and removing hunt areas 121 and 25, the magnitude of the relationships between aggregation and rates of increase in brucellosis decreased compared to the analysis on the full hunt area dataset (Table 2.1 and Appendix A, Figure A6). Contrary to our expectation, DIC scores showed that no measure of aggregation was substantially better than any other at predicting changes in seroprevalence (Appendix A, Table A3).

Discussion

In social species it is unclear which metrics of aggregation and density may be most relevant to disease transmission. In our study, rates of increase in brucellosis seroprevalence were positively related to all the measures of aggregation we considered, and all models were equally supported by the data. Therefore, measures of group size did not explain rates of increase in brucellosis any better than broad scale measures of

density, even though elk populations were structured by grouping throughout the transmission period. These results suggest that patterns of aggregation related to both within- and between-group transmission may be increasing the spread of *Brucella* among elk. Similar complex transmission mechanisms have been suggested for other wildlife-disease systems where the prevalence of disease was not explained well by a linear relationship with host density (*e.g.*, Smith et al. 2009, Storm et al. 2013), but few studies have evaluated and compared the effects of multiple measures of density and group size and few studies examine the relationship between density and rate of increase in disease prevalence. For elk in the GYA, group size and population density may be equally important to *Brucella* transmission if individuals move frequently among groups and encounter infected material. Such movement among groups is common among social species (*e.g.*, Franklin et al. 1975, Clutton-Brock et al. 1982, Houston 1982, Gerard et al. 2002, Focardi and Pecchioli 2005, Fortin et al. 2009, Pays et al. 2007), and for elk in our study, group sizes may change during the transmission period in response to snow conditions (Proffitt et al. 2012), human disturbance (Proffitt et al. 2009), foraging opportunities, and predation risk (Creel and Winnie 2005).

The similarity in fit among models was not surprising after assessing the relationships among density and group size measures. For example, 56% of the variation in Lloyd's crowding and 43% of the variation in May Lloyd's crowding was explained by the variation in winter range density (Appendix A, Figure A2). Therefore, larger elk groups were found more often in higher density winter ranges, but much of the variation in mean group size was not explained by winter range density. Among hunt areas with

similar rates of increase in brucellosis, for example, there were some areas with high densities and large groups, some areas with high densities and smaller groups, and some areas with low densities and larger groups. Moreover, another study of elk in the GYA also found that the tail of the group size distribution was only weakly related to population density (Proffitt et al. 2012), and comparisons of mean group size and population density have produced mixed results (Hebblewhite and Pletscher 2002, Proffitt et al. 2012). This suggests there may be more than one way for elk to be “dense” and spread diseases such as brucellosis. For example, large groups are likely to increase within-group transmission but between-group transmission may be less frequent if those large groups are distributed across a large area. On the other hand, many small groups in a small area may facilitate between-group transmission via fetuses that persist on the landscape for several days to weeks.

A weak relationship between density and group size could limit the efficacy of disease management strategies aimed at reducing the total population size. In our study area for example, elk group sizes of greater than 500 elk occurred both in populations with relatively high (3.0 elk/km^2) hunt area densities and in populations relatively low (0.3 elk/km^2) hunt area densities. Therefore, large groups and within-group transmission could potentially occur even when high density populations are reduced by tenfold. Specifically, our results suggest that substantial and unrealistic decreases in densities or group size would be needed to stem the tide of increasing brucellosis. For example, based on our results winter range densities of 7.7 elk/km^2 would need to be reduced to about 0.5 elk/km^2 in order to reduce the odds of testing positive over one year from 1.17 (*i.e.*, a

17% increase in the odds of testing positive with each additional year) to only 1.07 (*i.e.*, a 7% increase in the odds of testing positive with each additional year), and this level of offtake would not be practical given other management priorities (WGFD 2011).

By examining multiple measures of aggregation, our study builds upon previous work that examined the relationship between hunt area density and the rate of increase in brucellosis (Cross et al. 2010a). We compared our analysis to the results of this other study, which used 6458 serological tests from 1991 to 2008 across 34 hunt areas and a similar Bayesian hierarchical logistic regression model, and found that the magnitude of the relationship between hunt area density and logit-scale rate of increase in brucellosis seroprevalence was similar across the two studies (the posterior mean was 0.028 in our study vs. a posterior mean of 0.027 in the previous study). However, uncertainty in the estimated posterior mean was greater in our study (the posterior standard deviation was 0.027 in our study vs. a posterior standard deviation of 0.015 in the previous study), probably due to the smaller sample size (2765 serological tests in our study vs. 6458 in previous study).

Our study also differs from previous work in that we refined the analysis to include only the hunt areas where brucellosis was known to be present. We found that when including only these eight hunt areas, the relationship between aggregation and rates of increase in brucellosis was much weaker (posterior mean decreased by roughly half) compared to the relationship estimated across all 10 hunt areas. A possible explanation is that higher elk densities have greater movement among populations and a higher probability that *Brucella* is repeatedly introduced, leading to disease establishment

within a population. Once the disease is established, however, it is likely to spread at similar rates under a wide range of densities and group sizes. In support of this explanation, even the estimated intercept values (where aggregation would be equal to zero) were positive for the relationships between aggregation and rates of increase in brucellosis (Figure 2.6).

Another explanation for the weak relationship between aggregation and rates of increase in brucellosis may be due to the effect of environmental contamination on *Brucella*-transmission dynamics. For pathogens that are transmitted by a vector or by contaminated environment, it is often assumed that transmission rates will be more related to the proportion of infected individuals (frequency-dependent transmission) than population density (density-dependent transmission) (May and Anderson 1978, Getz and Pickering 1983). However, for diseases such as chronic wasting disease (CWD) that are both directly transmitted among individuals and indirectly transmitted by contact with contaminated soil or water, transmission dynamics may be better represented by models intermediate to classic frequency- or density-dependent transmission models (Schauber and Woolf 2003, Storm et al. 2013). This may also be the case for *Brucella*-transmission, as it is possible for infected fetal materials to last for months in cold, wet environments with low scavenger densities (Aune et al. 2012). If elk are contacting infected material weeks after the abortion event, transmission of *Brucella* may only be weakly related to density or group size and disease management strategies aimed at reducing the number of susceptible elk could have little effect on reducing the spread of brucellosis.

We found that winter range density and hunt area density were similarly related to rates of increase in brucellosis, which was not unexpected due to the relationship between the two density measures (Appendix A, Figure A2). In other studies it may be important to relate disease prevalence to host density at particular places and times, particularly where seasonal differences in habitat use (*i.e.*, resulting in differences in area occupied) cause densities to change within a year even though population totals remain relatively constant (Altizer et al. 2006, Cross et al. 2007). It may also be important in social species to describe the group size distribution and how it relates to population density (or abundance) and disease prevalence. If the group size distribution remains constant even as abundance changes (*e.g.*, Cross et al. 2009, Cross et al. 2013), for example, disease control strategies aimed at reducing the total number of individuals may not reduce transmission.

We also used cumulative winter density in order to account for the duration of time spent on the winter range during the transmission period and we used Lloyd's crowding in May to account for large elk groups occurring later on the winter range. Evaluating the relationship between these measures and brucellosis increases was an important test because previous work found that feedgrounds operating longer and later have higher brucellosis seroprevalence than feedgrounds operating for shorter periods and ending operation sooner (Cross et al. 2007). In our study, however, we found both cumulative density and May Lloyd's crowding were related to broader measures of density, and both predicted rates of increase in brucellosis similar to other measures of aggregation. On the feedgrounds, total days that elk are fed may be an important

predictor of brucellosis seroprevalence because it measures the time elk spend being densely aggregated more specifically than cumulative density or May Lloyd's crowding.

In conclusion, social behaviors can affect how individuals contact one another and spread disease. We provide evidence that the spread of disease may be driven by both within- and between-group transmission in species with complex aggregation patterns. If these patterns were influenced by the effects of aggregation on disease-establishment within a population, preventing brucellosis from reaching other disease-free populations may require understanding the drivers of dispersing infectious animals and the factors promoting high densities of elk. *Brucella*-transmission dynamics may also be affected by exposure to prolonged environmental contamination, but we do not know how the probability of contacts changes with the time since abortion event on native winter range. The variability in density, group size, and rates of increase in brucellosis among hunt areas highlights the importance of evaluating spatial differences in disease prevalence and aggregation patterns. As many avian and mammalian species have complex aggregation patterns, considering the multiple spatial and temporal scales that animals aggregate could lead to a better understanding of pathogen transmission dynamics in social species.

Acknowledgements

We thank the Wyoming Game and Fish Department for collecting, analyzing, and compiling the serologic data. We thank Dave Stinson for his flying around the mountains of Wyoming and for keeping us safe in the air. We also thank Ken Overfield and Steve

Ard for their dedicated flying, and Carson Butler for his hard work as an observer. We are grateful to Teton and Cody Interagency Dispatch for keeping up with our progress in flight. This work was supported by the National Science Foundation and National Institutes of Health Ecology of Infectious Disease (grant number DEB-1067129) and the U.S. Geological Survey. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Table 2.1. Estimated posterior means (and standard deviations) for the relationship between aggregation and rates of increase in brucellosis seroprevalence (measuring the log odds of testing seropositive for each one-year increase in time). The full datasets include all years and herd units (4448 serologic results across 21 years and five herd units) or hunt areas (2765 serologic results across 21 years and 10 hunt areas), while the truncated dataset includes only the eight hunt areas with at least two years of seropositive test results and excludes early years in the time series where brucellosis seroprevalence was zero (2245 serologic results across a number of years that vary by hunt area). HU = herd unit, HA = hunt area, WR = winter range. Cumulative Density is the total number of elk sighted over the whole survey divided by the total transect area of each hunt area. Lloyd's Crowding is the group size that the average elk experiences. The units of all density measures are elk/km².

Measure of Elk Aggregation	Full Datasets	Truncated Dataset
HU Density	0.036 (0.16)	
HA Density	0.028 (0.026)	0.011 (0.013)
WR Density	0.017 (0.011)	0.0079 (0.0049)
Cumulative Density	0.00086 (0.00053)	0.00043 (0.00026)
Mean Group Size	0.00033 (0.00051)	0.00023 (0.00020)
Lloyd's Crowding	0.00010 (0.00012)	0.000060 (0.000055)
May Lloyd's Crowding	0.00031 (0.00023)	0.00015 (0.00011)

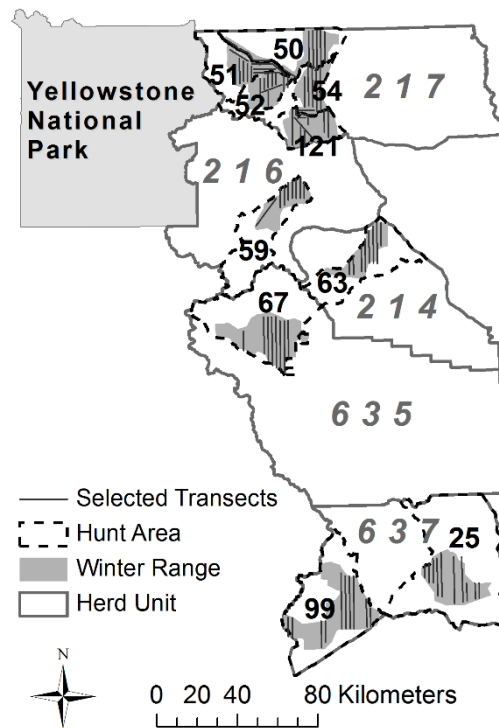


Figure 2.1. Map of the study area in the Greater Yellowstone Area , including the five herd units of interest (217, 216, 214, 635 and 637), the 10 focal hunt areas (50, 51, 52, 54, 121, 59, 63, 67, 25, and 99), winter ranges, and aerial transects selected to record elk group location and size.

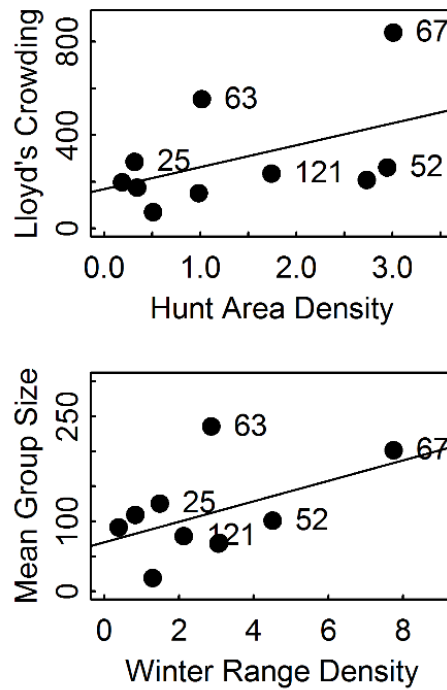


Figure 2.2. Example of relationships among all measures of aggregation. The left panel is hunt area density versus Lloyd's crowding and the right panel is winter range density versus mean group size. Lloyd's crowding and mean group size were estimated from empirical group size distributions. The solid line is the fitted relationships estimated from linear regression models. Data labels are shown for five of the hunt areas for reference. See Figure 2.1 for geographic distribution of hunt areas. The units of Hunt Area and Winter Range density are elk/km².

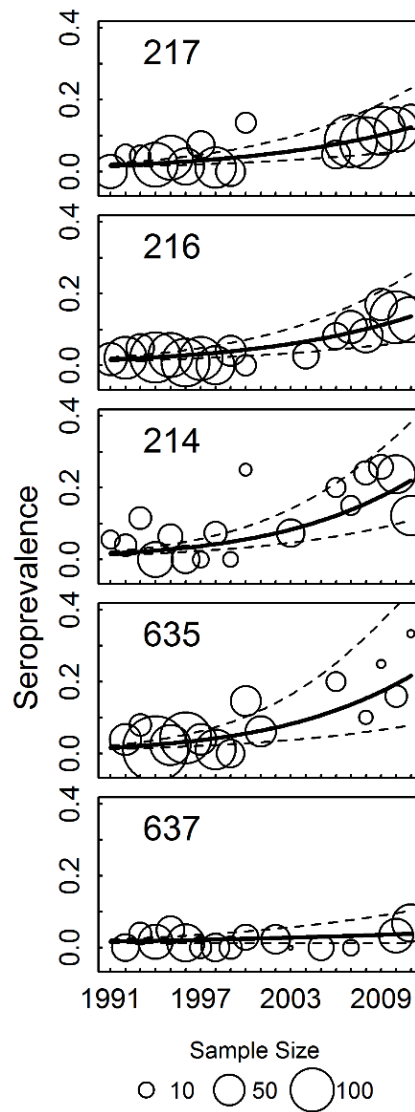


Figure 2.3. Increases in brucellosis seroprevalence from 1991 to 2011 by herd unit as estimated by a Bayesian hierarchical logistic regression model. Herd unit numbers are shown in upper left corner of each graph. See Figure 2.1 for geographical distribution of hunt areas. Size of circles is proportional to sample size, solid black lines are the posterior means of the relationships, and dotted lines display the 95% credible intervals.

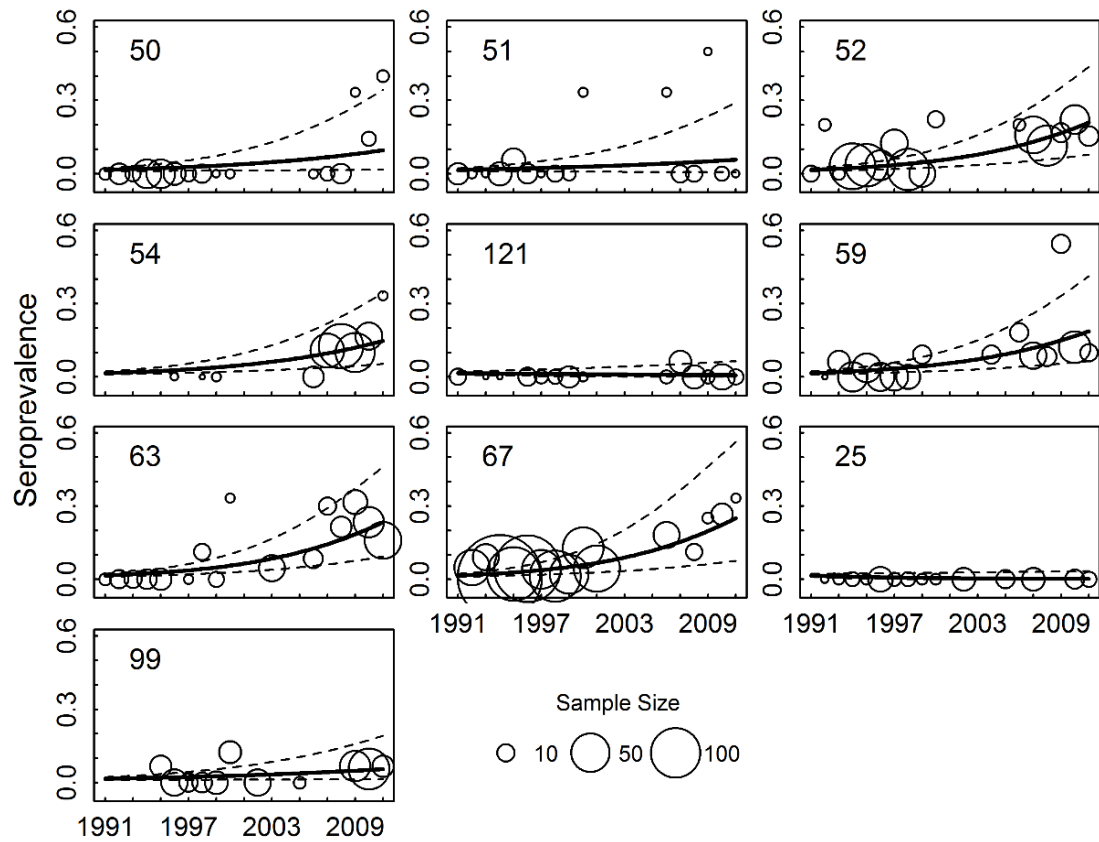


Figure 2.4. Increases in brucellosis seroprevalence from 1991 to 2011 by hunt area as estimated by a Bayesian hierarchical logistical regression model. Hunt area numbers are shown in upper left corner of each graph. See Figure 2.1 for geographical distribution of hunt areas. Size of circles is proportional to sample size, solid black lines are the posterior means of the relationships, and dotted lines display the 95% credible intervals.

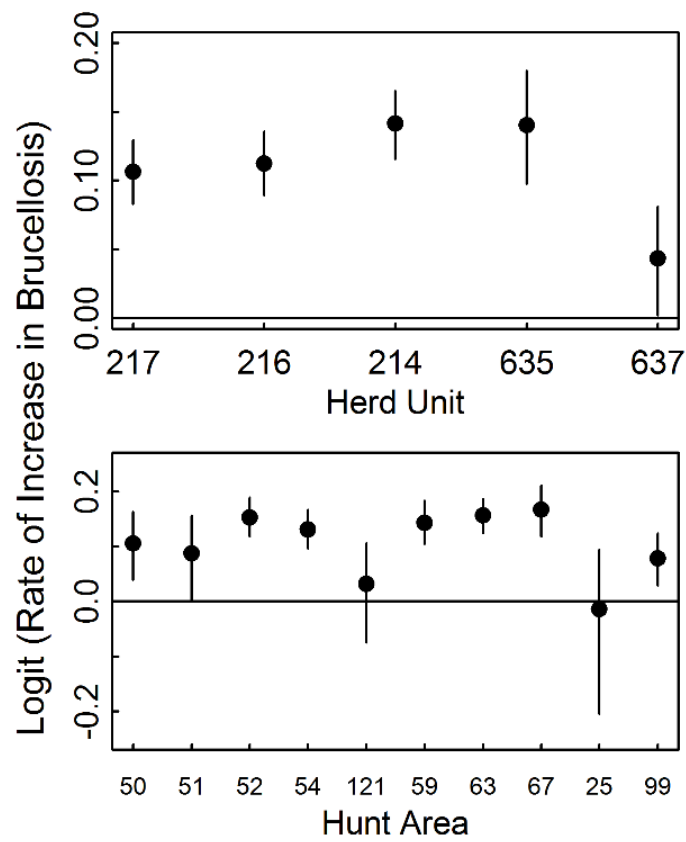


Figure 2.5. Comparison of estimated posterior means and 95% credible intervals of the rates of increase in brucellosis seroprevalence (measuring the log odds of testing seropositive for each one-year increase in time) by herd unit (top panel) or hunt area (bottom panel).

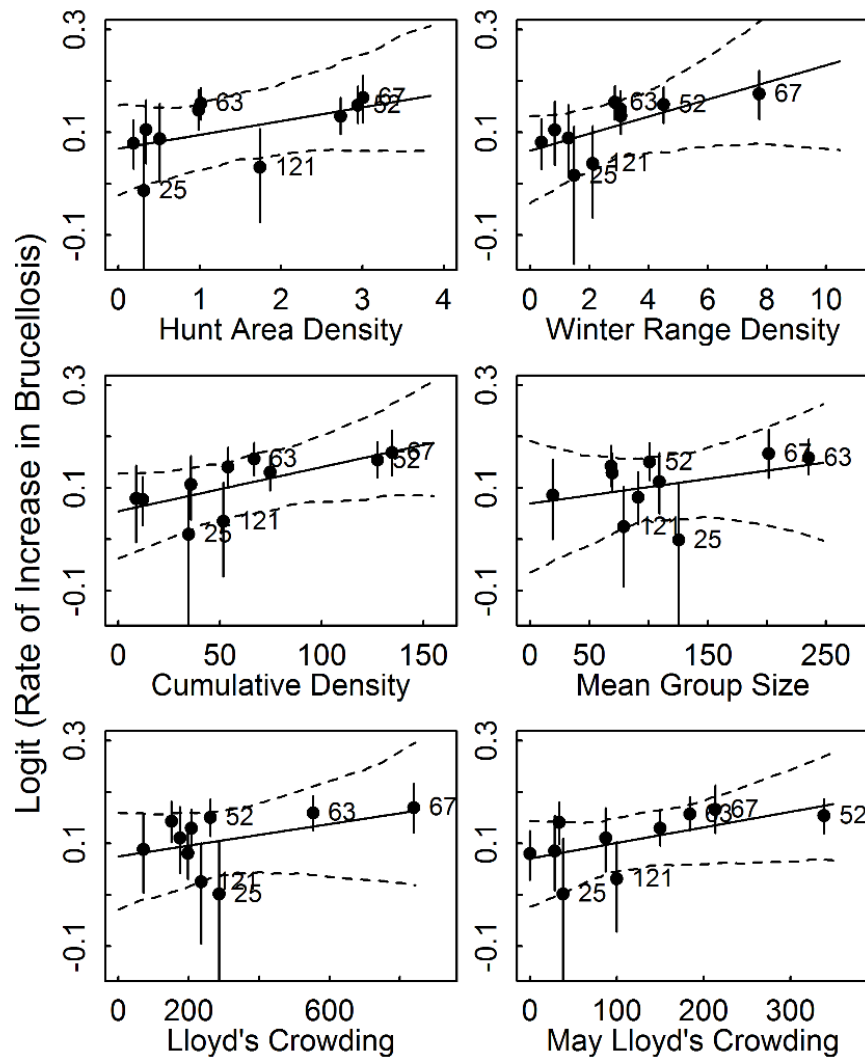


Figure 2.6. Linear relationships between elk aggregation and rates of increase in brucellosis seroprevalence (measuring the log odds of testing seropositive for each one-year increase in time), as estimated by Bayesian hierarchical models. Data labels are shown for five of the hunt areas for reference. See Figure 2.1 for geographic distribution of hunt areas. Solid black lines are the posterior means of the relationship, and dotted lines display the 95% credible intervals. Cumulative Density is the total number of elk sighted over the whole survey divided by the total transect area of each hunt area. Lloyd's Crowding is the group size that the average elk experiences. The units of all density measures are elk/km².

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CHAPTER THREE

WHERE LARGE GROUPS GET LARGER: RELATING ELK GROUP SIZE
DISTRIBUTIONS TO IRRIGATION, OPENNESS AND WOLVES

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

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Manuscript Information Page

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Status of Manuscript

☒ Prepared for submission to a peer-reviewed journal

☐ Officially submitted to a peer-review journal

☐ Accepted by a peer-reviewed journal

☐ Published in a peer-reviewed journal

Abstract

Many studies relate mean group size to environmental variables, but few take a more complete look at other aspects of the group size distribution to identify how large or small groups may respond differently to environmental covariates. Group size distributions of many bird and mammal species are right-skewed and span several orders of magnitude. In addition, large group sizes may have disproportionate effects on ecological dynamics, and management interventions may be more effective if they target the upper quantiles of the group size distribution. We studied elk aggregation patterns for three years across this region, where wintering elk group sizes reached into the thousands, and we used quantile regression models to examine variables related to upper and lower quantiles of the group size distribution. For large elk groups in the Greater Yellowstone Area, issues regarding disease transmission and impacts to private property are particularly important during the wintertime when elk move onto developed or cultivated land. Upper quantile group sizes were larger on irrigated land (0.90 quantile group sizes were larger by 121 elk [95% confidence intervals = 10, 231] compared to non-irrigated land). Predation risk by wolves had little effect on large groups, but large groups were estimated to increase in size in habitats that were flatter, more open, and less diverse. This dynamic could increase conflicts with private landowners, increase risk of interaction with cattle, and facilitate disease transmission. We also document differences in relationships with environmental variables depending on what quantile of the distribution is examined. Therefore, our results emphasize the importance of focusing on

more than one metric of the group size distribution to inform the management of many social species.

Keywords: *Cervus canadensis*, group size distribution, group living, group size effects, group size trade-offs, habitat openness, predation risk, quantile regression, wolves.

Introduction

Variation in animal group sizes occurs as individuals weigh the trade-offs to joining or leaving a group under different environmental conditions, such as habitat cover, forage availability, and level of predation risk (Krause and Ruxton 2002). Studies examining group size responses to these conditions are extensive in the literature, but often they examine changes in mean group size (*e.g.*, Lagory 1986, Chapman et al. 1995, White et al. 2012b, Marino and Baldi 2014) or typical group size (measuring the group size that the average individual experiences; *e.g.*, Heard 1992, Gower 2008, White et al. 2012a). Few studies, however, take a more complete look at the group size distribution to identify other, potentially stronger predictive relationships (Cade and Noon 2003; but see Valeix et al. 2012 for a study of factors affecting quantiles of lion group biomass). An analysis of this type may be particularly important for animals whose group size distributions are right-skewed and span several orders of magnitude, as occurs with many birds and mammals (*e.g.*, Jarman 1974, Reiczigel et al. 2008). For these animals, the upper quantiles of the group size distribution will be substantially larger than the centers and may have disproportionate effects on ecology or policy, in which case identifying

environmental conditions related to larger group sizes may be more important to conservation and management than studies of the mean. For other animals, however, the group size of interest may not be known *a priori* and therefore examining relationships with various quantiles may be important to consider.

For social ungulates, there is a lot of information on how various environmental conditions are related to mean group size. Typically, these studies examine relationships with habitat openness (*e.g.*, Hirth 1977, Mao 2003, Fortin et al. 2009), predation risk (*e.g.*, Gower 2008, Creel and Winnie 2005), population size (*e.g.*, Borkowski 2000, Hebblewhite and Pletscher 2002), and winter severity (*e.g.*, Gower 2008, Fortin et al. 2009, Proffitt et al. 2012). In some cases, land use (Proffitt et al. 2009), human hunting (Gude 2004, Proffitt et al. 2009), and human disturbance (Manor and Saltz 2003) are also examined as predictors of mean group size. Though less is known about how these variables are related to other parts of ungulate group size distributions (but see Proffitt et al. 2012 for relating elk population size to 0.99 quantile elk group size), several studies have focused on the typical group size to examine conditions important to the average individual. This measure may also be valuable for understanding large group sizes (as the typical group size will always be larger than the mean; Heard 1992), but few studies have conducted this analysis or examined other measures of large groups in populations where group sizes can reach into the thousands (but see Cross et al. 2009). This is an important information gap for many ungulates across the globe (such as blue wildebeest [*Connocheates taurinus*] in Africa, elk [*Cervus canadensis*] in North America, or the Mongolian gazelle [*Procapra gutturosa*] in Asia) who form large groups of more than

1000 and can occur on or near human settlements and agricultural land where they may be destructive to private property (*e.g.*, Haggerty and Travis 2006) or play a role in maintaining endemic infections of economically important diseases (*e.g.*, Stafford et al. 1991).

This is the case for elk populations across the Greater Yellowstone Area (GYA), who maintain endemic infections of *Brucella abortus* and have been implicated as the source of recent brucellosis outbreaks in cattle (Beja-Pereira et al. 2009). Because pathogen transmission rates can increase with group size (Côté and Poulin 1995, Altizer et al. 2003), increases in large elk groups may explain higher seroprevalence in certain elk populations and may increase the risk of transmission to cattle (Cross et al. 2010). These elk are also an important prey species for large predators such as wolves, in which case large groups could attract predators (Hebblewhite and Pletscher 2002) or potentially concentrate predators in areas close to domestic animals. Other research in the region, for example, showed that increases in wolf predation on livestock were related to increases in elk density near livestock grazing areas (Bradley and Pletscher 2005, Nelson 2011). Elk have also been known to aggregate on private land as refuge from human hunting that occurs on nearby public land (Burcham et al. 1999, Proffitt et al. 2009), or possibly because they are seeking out higher quality forage on irrigated pastures (as hypothesized by Wilmers and Levi 2013). Crops produced in these areas may be an important food source for elk, particularly in drought years when forage quality is low in other parts of their home range, and may be one explanation for growing resident elk populations that use irrigated pastures year round (Wilmers and Levi 2013). We studied the elk group size

distribution during the winter when elk aggregate on lower elevations nearer to human settlements and livestock.

We measured wintering elk group sizes across 10 elk management units (referred to as hunt areas) and three years (2010–2012), and examined the relationships between 0.10, 0.20, ..., 0.90 quantiles of the group size distribution and variables of land use (public, private, and irrigated), habitat, climate, and local wolf abundance. We hypothesized that quantiles of the group size distribution would be (1) larger on private land, (2) larger on irrigated land, (3) positively related to distance from maintained roads, habitat openness, population density, and wolf abundance, and (4) negatively related to slope of the landscape, habitat diversity, and winter severity. We also hypothesized that the magnitude of these relationships would be greater for the 0.90 quantiles (as a measure of the large groups) compared to the median (as a measure of groups in the center of the distribution, rather than the mean), but we compared all other quantiles to better understand changes in these magnitudes as quantiles increased. We also examined the interaction between the land type a group was located on (public or private land) and the proportion of public land available in each hunt area, and the interaction between wolf abundance in a hunt area and proportion of open habitat available in each hunt area.

Methods

Study Area

In the months of January through May (when snow is present at high elevation elk summer habitat) during 2010, 2011, and 2012, we measured elk group size and

environmental variables in 10 non-randomly selected elk hunt areas in western Wyoming (Figure 3.1). We selected these hunt areas because their annual elk densities of roughly 0.2 to 3.0 elk/km² (Wyoming Game and Fish Department [WGFD] 2011), wolf numbers of 0 to 18 wolves (US Fish and Wildlife Service [USFWS] et al. 2011), and brucellosis seroprevalence of roughly 0 to 25% (Cross et al. 2010, Scurlock and Edwards 2010) represented the typical range found in the region, and because they contained only unfed elk populations. Other hunt areas in western Wyoming contained feeding grounds where elk were supplementally fed during the winter, and thus, congregated in large, dense groups on the feedline. Our goal was to investigate how environmental variables were related to elk group size distributions on native winter range in areas where large groups may increase the risk of brucellosis transmission among elk (and potentially with livestock), without the influence of feeding grounds on group size.

The 10 hunt areas ranged from 350 to 2600 km² and included elk summer and winter range comprised of steep mountains, box canyons, wide mountain valleys, rolling foothills, badlands, riparian areas, and open agricultural lands. Elevations ranged from roughly 1200 to 4000 m and vegetation was predominately conifer forests (*Pinus contorta*, *Picea engelmannii*, *Psuedotsuga menziesii*, *Abies lasiocarpa*), willow (*Salix spp.*), aspen (*Populus tremuloides*), cottonwood (*Populus angustifolia*), shrubs (*Artemisia spp.*, *Amelanchier alnifolia*, *Atriplex spp.*, *Sarcobatus vermiculatus*), grass – forb/herb meadows, and irrigated hay meadows. Land ownership was primarily a mixture of private, state, Bureau of Land Management (BLM), and US Forest Service property, including two national forests and three wilderness areas. There were also four wildlife

habitat management areas (WHMAs) and one BLM elk winter range closure that were all closed to human traffic for most of the study period (closed from roughly December 1 through May 15).

Winters in the study area were characterized by heavy snowfall, cold temperatures, and high winds from early October through early June. During our study period, the Snow Telemetry (SNOTEL) stations nearest to the 10 hunt areas recorded a maximum snow water equivalent (SWE) of 58, 112, and 81 cm in 2010, 2011, and 2012, respectively.

Wolves recolonized the northern portion of our study area in 1999 and spread southward in subsequent years (USFWS et al. 2011). Since then, there have been roughly 21 packs recorded in and around our study area, with an average of 6 wolves per pack (USFWS et al. 2011). Elk are the preferred prey of wolves in the region (Gude 2004, Smith et al. 2004, Nelson 2011), but when these elk disperse or migrate to distant summer range, wolves may rely on other ungulates such as mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) (Nelson 2011). Elk may also be the preferred prey of mountain lion (*Puma concolor*) in other areas of the GYA (Bartnick et al. 2013, Elbroch et al. 2013), but to our knowledge there are no estimates of mountain lion densities in our study area. Other predators are black bear (*Ursus americanus*) and grizzly bear (*Ursus arctos horribilis*), but bears rarely hunt adult elk and they hibernate throughout a majority of the winter study period.

Human hunting of elk occurred on all 10 hunt areas from roughly the beginning of September to late-December (archery seasons occurred in September; rifle seasons

typically began in October). No hunts later than December were permitted in our study area during the study period. Hunting occurred predominately on public land, but there were several private ranches that participated in the WGFD Hunter Management Program (HMP) to allow hunters on their property during the regular hunting season. These ranches participated in the HMP all three years of the study.

Elk Group Size

Within all 10 hunt areas, we recorded elk group sizes from a fixed wing aircraft once a month from January through May for three years (2010–2012). We restricted the aerial surveys to elk winter range within each hunt area in order to reduce flying time and avoid areas with very few elk. We identified elk winter range using elk sightings recorded by the WGFD during the months of January through May, 2005–2009. These sightings included elk counted during trend and classification surveys, and any opportunistic sightings recorded by WGFD personnel from the air or ground.

For our aerial surveys, we flew transects set 2 km apart, for 1-km viewing widths from one side of the plane. We maintained these widths in flight using calibrated markers on the wing struts and a radar altimeter to hold our above ground level near 240 m, and on average we conducted flights at 150 km per hour. We assigned transects to be non-overlapping, to cover the full extent of each winter range, and to follow a north-south orientation, though in several cases transects were set to follow major landscape features such as a ridgeline or narrow valley. To increase our chances of seeing elk, we systematically selected four to seven transects that covered areas with a high probability of elk occurrence within each winter range, as determined by the WGFD elk sightings.

We also included three randomly selected transects per winter range, and we randomly selected the viewing direction (*e.g.*, looking east or west while flying north or south) for each random and non-random transect. The number of transects selected and length of transects varied by winter range, but summed to approximately 35% of each winter range. We used the same transects and viewing directions selected at the beginning of the study for all subsequent monthly flights.

Transects covered a range of elevations (roughly 1230 to 2800 m), topography (*e.g.*, mountain ridges, valleys, small drainages, and mesas), and habitat (*e.g.*, dense and open forests, grassland, sagebrush steppe, and badlands). The timing and order of our flights differed each month, as they required clear or overcast (high clouds) mornings (before noon), when winds aloft (at 2700 and 3600 m above sea level) were below 32 km per hour. From the airplane, we used a camera (D5000 [with 16 megapixels], Nikon, Tokyo, Japan), zoom lens (NIKKOR 70-300 mm, Nikon, Tokyo, Japan), and camera-GPS unit (GP-1, Nikon, Tokyo, Japan) to record elk group size and the GPS coordinates of our location (in Universal Transverse Mercator [UTM]). We examined the photos and coordinates, overlaid on 1-m resolution National Agriculture Imagery Program (NAIP) 2009 imagery data in a GIS to determine precise locations of elk groups (rather than using the location of the camera when the photo was taken). This process prevented any repeat counting of groups and was used to extract our explanatory variables from other GIS layers (described below).

We assessed sightability of elk using double-observer methods (Pollock and Kendall 1987). Briefly, two observers each flew in a different fixed wing aircraft, flying

in tandem over three winter ranges. We conducted these tandem counts in one winter range in March 2012 and two winter ranges in April 2012 to calculate the difference in total number of groups and total elk seen between the two observers, and to estimate the difference in our measures of group size.

Group-Scale Explanatory Variables

We used data layers in a GIS to obtain values of landscape and habitat variables at one of three scales ranging from fine to coarse (group, buffer, and hunt area-scale variables). The finest of these was the group scale, and refers to variables obtained from within a 30-m x 30-m pixel at the center of each elk group (0.0009 km²).

For these group-scale variables, we first used 2013 land ownership data provided by the BLM (*available online*²) to determine whether the center of each group was located on public or private land. We reassigned WHMAs in hunt area 67 as public land because they were managed for public access and hunting during the regular hunting season, even though they were closed to the public during a majority of our study period. These WHMAs covered 94 km² in hunt area 67. We also reassigned the private ranches that participated in the HMP as public land, because similar to WHMAs, they allowed hunter access during the hunting season but were closed to the public during our study period. These reassigned private ranches covered 23 km² in hunt area 50, 3.5 km² in hunt area 59, and 85 km² in hunt area 63.

² http://www.blm.gov/wy/st/en/resources/public_room/gis/datagis/state/state-own.html

We used irrigation data published in 2007 by the Wyoming Water Development Commission (*available online*³) to determine which groups were located on irrigated land. We confirmed this assignment (on or not on irrigated land) for each elk group using NAIP 2009 imagery data, and changed assignment where necessary (two groups were reassigned in this process). We also calculated the slope of the landscape using a 30-m digital elevation model of the study area and the linear distance of each group to the nearest maintained road from a map of road locations we obtained from the Wyoming Geographic Information Science Center. We selected these variables because elk may avoid steep terrain (Fortin et al. 2005) and human disturbance associated with roads (Millspaugh 1999, Rowland et al. 2000, Fortin et al. 2005).

Buffer-Scale Explanatory Variables

For the next scale, we obtained variables from a circular buffer with a 500-m radius around the center of each group (0.78 km²), including variables for land cover-class diversity and habitat openness. To do this we used the 2011 30-m National GAP Land Cover data (*available online*⁴) and reclassified the 97 GAP land cover classes occurring in our study area into 12 classes representing the major vegetation and habitat types. These included grassland (grassland meadows and forbland), sagebrush, scrubland (dominated by greasewood and saltbush), mixed forest (conifer and deciduous), agricultural land, badlands, mixed woodland-scrubland, alpine meadows (fell field and turf), riparian (mixed riparian woodland-shrubland), wetland, deciduous forest, and

³ <http://waterplan.state.wy.us/plan/statewide/gis/gis.html>

⁴ <http://gapanalysis.usgs.gov/gaplandcover/data/download/>

conifer forest. We also included the following three “other” classes: developed land, water, and rock (bedrock, scree, and cliff) for a total of 15 major land cover classes. With these 15 classes, we constructed an index of land cover-class diversity by summing the number of classes found in each buffer (similar to vegetation richness used by Boyce et al. 2003). We chose this variable because there is evidence that wintering elk select less diverse areas on the winter range (Boyce et al. 2003). We did not attempt to quantify a variable for fire, because it was not an important factor during our study period.

We further reclassified the 15 classes, into open, closed, and mixed habitat types, because elk group sizes have been related to habitat openness in previous studies (Creel and Winnie 2005, Mao 2003, Gower 2008, Proffitt et al. 2009, Proffitt et al. 2012, White et al. 2012a). Open habitats included grassland, sagebrush, and scrubland classes; closed habitats included conifer and deciduous forests; and mixed habitats included mixed woodland-scrubland and riparian areas. We constructed a measure of habitat openness by calculating the proportion of open habitat within each buffer (Boyce et al. 2003, Mao 2003).

Hunt Area-Scale Explanatory Variables

At the coarsest scale, that of the entire hunt area (average = 1107 km²), we considered covariates for winter severity, average winter elk density, and average wolf abundance. Using the shortest linear distance between each SNOTEL station and each hunt area boundary, we selected the SNOTEL station nearest to each hunt area. The distances between these SNOTEL stations and the nearest hunt area ranged from 0 (SNOTEL located within hunt area) to 27 km (average = 13 km). For each selected

SNOTEL station, we summed the daily SWE recorded from December 1 through June 30 as an index of annual winter severity. We did this each year for a total of 3 values of winter severity for each hunt area. This index incorporates snow depth and density, and has been shown to be a good predictor of snow effects on ungulate movement (Farnes et al. 1999), and allowed us to assess the broad scale relationship between group size and winter severity among years. Because our winter severity index varied annually, we did not include year as a categorical explanatory variable (Appendix B, Figure B1).

To examine the relationship of population density with group size, we calculated the average density of elk on the winter range by summing all elk counted each winter, and dividing by the transect area (ranged from 92 to 251 km²), then dividing by the number of monthly surveys conducted in a winter. This resulted in 30 values (three winters x 10 hunt areas) of average winter elk density.

Using wolf pack home range and pack size data collected by the USFWS, we calculated the average number of wolves using each hunt area from 2009 to 2011 (USFWS et al. 2011). We used wolf data from these years rather than 2010 to 2012 because final pack size estimates occurred in December, which immediately precedes our aerial surveys for elk groups (*e.g.*, wolf pack sizes were estimated in December 2009 and elk group sizes were recorded in January 2010). From these data, we calculated the percent of each wolf pack's home range that overlapped with each hunt area, we multiplied the percent overlap by the pack size, summed across all packs and years, and divided by three years to get average wolf abundance for each hunt area (total of 10 values). We used this measure of average wolf abundance rather than annual wolf

abundance to understand broad scale behavioral responses to cumulative predation risk.

We did not intend to assess how elk group sizes responded to wolf presence or absence at finer spatial and temporal scales.

Interactions

We expected the difference between elk group sizes found on public and private land to depend on how much public land was available in the hunt area. For example, when most of the available land is public and hunted, we expected group sizes to be larger on private land where they seek refuge from hunters compared to public land (Burcham et al. 1999, Proffitt et al. 2009). To investigate this interaction, we used the land use type a group was located on as previously determined, and we calculated the proportion of public land available in each hunt area from BLM-land ownership data² in a GIS. This interaction could not assess immediate behavioral responses of elk to hunting pressure, because elk hunting seasons in the region closed before the start of our aerial surveys, and elk may return to hunted areas relatively quick after hunting has ceased. However, we were interested in whether there were broad scale behavioral responses to cumulative hunting pressure, whereby elk are more likely to aggregate on private land even after hunting has ceased.

We also calculated the proportion of open habitat in each hunt area from our previously reclassified GAP Land Cover data (classified into open, closed and mixed habitat classes) in order to investigate the interaction between average wolf abundance and amount of open habitat available. We expected group size responses to predation risk would depend on how much open habitat was available to them. For example, elk have

been shown to decrease group size in response to the presence of wolves in habitats typified by relatively small open meadows embedded in a matrix of woodland (Creel and Winnie 2005).

Statistical Analysis

We constructed empirical group size distributions for each hunt area using all group size observations. We considered monthly surveys to be independent observations of group size because elk group membership is relatively fluid over the course of several days (Cross et al. 2013). Therefore, a group seen one month is not likely to contain the same individuals the following month. Using the empirical group size distributions, we compared 0.10, 0.20, ..., 0.90 quantile group sizes across hunt areas. We used median group sizes to measure central tendency rather than mean because the distributions were right skewed. To describe large groups we used 0.90 quantiles rather than the 0.99 quantile because we expected a great deal of sampling variation at this more extreme quantile (Cade and Noon 2003). We also compared those quantiles to Lloyd's crowding, to measure the group size a typical individual experiences (Lloyd 1967). We used Lloyd's crowding (measured by: $c = m + ([s^2/m] - 1)$, where m is the average group size and s is the standard deviation of the empirical group size distribution) simply to show that the typical individual experiences group sizes closer to the 0.90 quantile than to the median. We did not use Lloyd's crowding to describe relationships with large groups (we used 0.90 quantile) so we could use all group size observations in a quantile mixed model and compare the relationships across quantiles.

We used linear quantile mixed models to evaluate the relationships between each explanatory variable and conditional quantiles of the group size distribution (0.10, 0.20, ..., 0.90 quantiles), using all group size observations. In these models, we included all explanatory variables and we included hunt areas as random intercepts to account for dependence among group sizes recorded within the same hunt area. We examined models of 0.10 through 0.90 quantile group sizes to understand how relationships with our variables of interest differed across the group size distribution, but we focused our discussion on the median and 0.90 quantiles because our original aim was to understand how group sizes from the center of the distribution differed from larger group sizes. As this was our goal, we excluded interaction terms from the mixed models because we found little evidence for them when considering a relationship with empirical median or 0.90 quantile group sizes (Appendix B, Figure B2).

Prior to using the quantile mixed models, we centered all explanatory variables by subtracting the mean values. We also examined relationships between all explanatory variables using Pearson's correlation coefficient (r) and scatterplots to identify any apparent strong relationships. All analyses were conducted using the R environment for statistical computation (R Core Development Team 2013) with the *lqmm* package for linear quantile mixed models (Geraci 2014).

Results

Our flights consistently detected few elk in our hunt areas that were outside the delineated winter range. Therefore, elk groups that were missed because they were outside the winter range were probably rare and small, and would therefore have little effect on empirical estimates of median and upper quantile group sizes. We also expected small effects of observer error on these empirical estimates. In the double observer flights, the two observers recorded 33 and 32 elk groups, and 3084 and 3067 total elk, respectively. Observer one missed three of the groups recorded by observer two, and observer two missed four of the groups recorded by observer one. These missed groups were all small, ranging in size from three to 24 elk with an average of 11 elk. Median group sizes between the observers were 22 and 20 elk, respectively and empirical 0.90 quantile group sizes were 243 and 263 elk, respectively.

Over all hunt areas and years, we recorded 1243 elk groups ranging in size from 1 to 1952 elk and the distribution of group sizes was right skewed, as expected (Appendix B, Figure B3). Among hunt areas, the 0.90 quantiles appeared to be better measures of typical group sizes (Lloyd's crowding) than distribution centers (median; Figure 3.2). The empirical median and 0.90 quantile group sizes ranged from 6 to 52 elk and from 33 to 374 elk, respectively, with the largest groups occurring in hunt areas 63 and 67 (Figure 3.2). The winter range in both of these hunt areas was mostly private land, and while the largest groups in hunt area 63 occurred on this land use type, most of the largest groups in hunt area 67 occurred on public land (including WHMAs). See Appendix B, Figure B4 for further description of these two hunt areas and differences in hunt area-scale

explanatory variables across all hunt areas. As for the finer scale explanatory variables collected across all hunt areas, distance to nearest maintained road ranged from 15 m to 12 km, slope of landscape ranged from 0 to 38 degrees, number of major land cover types within the 0.78-km² buffers ranged from 1 to 12, and the proportion of open habitat in these buffers ranged from 0.01 to 1.0.

We recorded 818 elk groups on public land and 425 groups on private land, and there was little difference in empirical median and 0.90 quantile group sizes between these land types (median = 23 elk on private compared to 16 elk on public; 0.90 quantile = 160 elk on private compared to 168 on public). We recorded 18 elk groups on irrigated land, with most incidences occurring in hunt area 50 (seven groups) and none occurring in hunt areas 99, 67, and 63. Empirical median and 0.90 quantile group sizes were larger on irrigated land compared to non-agricultural lands (median = 18 elk on non-ag. land compared to 80 elk on irrigated land; 0.90 quantile = 153 elk on non-ag. land compared to 241 on irrigated land).

Quantile Mixed Models

Estimated collinearity among explanatory variables was relatively low (Pearson's correlation coefficients less than 0.40), except for the relationship estimated between land cover class diversity and open habitat ($r = -0.43$) and the relationship estimated between average wolf abundance and average winter elk density ($r = 0.52$; Appendix B, Table B1). There was also no evidence of strong nonlinear relationships among these variables (Appendix B, Figure B5).

Relationships described below were estimated while controlling for hunt area and holding all other variables constant. All conditional quantiles were greater on private and irrigated land; and negatively related to slope of the landscape, diversity of land cover types and winter severity; and positively related to proportion of open habitat in a 0.78-km² buffer (Figure 3.3). In general, these relationships increased in magnitude with increasing quantile, but this was not the case for distance to road and average wolf abundance. For these two variables, relationships with the conditional quantiles were mixed. For winter elk density, relationships with lower quantiles were positive, while relationships with the upper quantiles were negative (Figure 3.3). For all variables, there was also an abrupt increase in uncertainty at the 0.90 quantile, probably because there were fewer observations in the tails of these distributions (Figure 3.3; Cade and Noon 2003).

The estimated change in conditional median group size was greatest among groups found on irrigated land compared to groups on non-agricultural land (estimated increase of 58 elk [95% CI = 20, 96] when on irrigated land). By contrast, the estimated change in conditional median group size was small for every unit increase in each of the remaining variables of interest (Figures 3.3 and 3.4). For example, the conditional median group sizes were estimated to (1) decrease by 4 elk (-9, 0) for every 10 degree-increase in slope of the landscape, (2) decrease by 2 elk (-3, 0) for every increase of one land cover type within a 0.78-km² buffer, (3) increase by 2 elk (1, 3) for every 0.10 increase in the proportion of open habitat within a 0.78-km² buffer, (4) change by roughly zero elk (-2,

3) for every 1 elk/km² increase in winter elk density, and (5) change by roughly zero elk (-3, 2) for every 1 wolf increase in average wolf abundance (Figure 3.3).

As expected, the magnitude of these relationships was stronger for the 0.90 quantiles (Figures 3.3 and 3.4; except for the relationship with winter severity), though uncertainty was also greater at this quantile. Similar to median group sizes, the estimated change in conditional 0.90 quantiles was greatest among groups found on irrigated land compared to groups on non-agricultural land (estimated increase of 121 elk [95% CI = 25, 216] when on irrigated land), and the change in estimated 0.90 quantiles was much smaller for the other variables. For example, the conditional 0.90 quantiles were estimated to (1) decrease by 20 elk (-54, 15) elk for every 10 degree-increase in slope of the landscape, (2) decrease by 7 elk (-20, 6) for every increase of one land cover type within a 0.78-km² buffer, (3) increase by 10 elk (1, 19) for every 0.10 increase in the proportion of open habitat within a 0.78-km² buffer, (4) decrease by 5 elk (-22, 13) for every 1 elk/km² increase in winter elk density, and (5) decrease by 2 elk (-25, 22) for every 1 wolf increase in average wolf abundance (Figure 3.3).

Discussion

Considering relationships between environmental conditions and upper quantiles of the group size distribution rather than only measures of the center may be important to species management and conservation. For elk groups in the GYA, issues regarding disease transmission (Cross et al. 2010b), predator-prey relationships (Hebblewhite and Plestcher 2002), and destruction of private property (Haggerty and Travis 2006) are

particularly important for larger groups during the wintertime when elk aggregate near developed or cultivated land. In our study wintering elk group sizes ranged over several orders of magnitude, with most groups containing around 30 elk but most individuals occurring in groups of around 380 elk. We found that most quantiles of the group size distribution were related to land use and habitat openness, but that the magnitude of these relationships was generally greater for the 0.90 quantiles. Though the latter may be expected for right-skewed distributions, the practical implications of large elk groups getting larger in the GYA may be an increase in the frequency of conflicts with private landowners, increased intraspecific competition or competition with livestock, greater predator densities near human settlements, and a higher risk of disease transmission with livestock.

Estimated coefficients from our mixed quantile regression models suggest that irrigation had a stronger effect on the upper quantiles of the group size distribution compared to the median. After controlling for hunt area and all variables of interest, the conditional median group size was estimated to increase by 58 elk (95% CIs = 20, 96) on irrigated versus non-irrigated land, while the conditional 0.90 quantile group size was estimated to increase by 121 elk (25, 216) on irrigated versus non-irrigated land. Both of these are substantial increases in group size that could affect landowner tolerance of elk on private property and elk management. In particular, another study from the northern portion of our study area suggested that the use of irrigated land by a resident elk herd may actually explain higher growth rates compared to a migratory elk herd that winters in the same area (Wilmers and Levi 2013). Though we found that large group sizes were

larger on irrigated land, we only found one elk group located on an irrigated field within the winter range in question, and found few elk groups on irrigated land overall. These findings suggests that the effect of irrigation on wintering elk group size was not widespread, but each of these rare events may still have important consequences such as transmission of diseases or destruction of food crops. Additionally, we did not examine group sizes or group locations during the summer or fall and identifying whether irrigated fields are frequented by elk during these seasons may help managers understand the likelihood of effects on population dynamics and help identify additional high risk areas for disease transmission, livestock depredations (from predators also preying on elk groups), and landowner conflicts.

We also present evidence that all conditional quantile group sizes increased with increasing habitat openness. The effect of habitat openness on elk group size has been well studied (*e.g.*, Mao 2003, Gower 2008, Proffitt et al. 2012, White et al. 2012b), but to our knowledge we are the first to demonstrate that openness is more strongly related to elk group sizes in the tail of the distribution compared to the center. For example, after controlling for hunt area and our variables of interest, we estimated the conditional 0.90 quantile group sizes would increase by 10 elk (1, 19) for every 0.10 increase in the proportion of open habitat, while the conditional median group size would increase by only 2 elk (1, 3). Such large elk groups may occur in open areas because individuals connect visually as they search for similar grazing opportunities, and conversely, individuals may disaggregate when landscape features associated with topography or vegetation break the line of sight between individuals (Gerard et al. 2002). Elk may also

form large groups in open habitats as a way to reduce individual predation risk in areas where they are highly conspicuous and easily detected by predators (Hamilton 1971) or increase their ability to detect predators in these habitats (Pulliam 1973).

Studies that examine the effects of habitat openness *and* predation risk on mean elk group size have produced mixed results (Gude 2004, Creel and Winnie 2005, Mao 2003, Gower 2008, Proffitt et al. 2012), though some of these differences may be attributed to how predation risk was measured. For example, studies measuring predation risk at fine spatial and temporal scales (measured as wolf presence or absence during the time elk groups were recorded or measured as the distance to wolves within 8 hours since elk groups were recorded) found that elk aggregated in open habitats during times of low risk and disaggregated in times of high risk (Creel and Winnie 2005, Proffitt et al. 2009). On the other hand, studies measuring predation risk at coarser scales (measured as the number of wolves counted within 24 hours since counting elk groups and within the same drainage elk groups were located) found that elk aggregated in open habitat when predation risk was higher (Gower 2008).

In our study area, we found that the conditional 0.90 quantile group sizes were only weakly related to average wolf abundance, after controlling for hunt area and our variables of interest. We suspect this may be due in part to the small number of values used to measure cumulative predation risk (10 values of average wolf abundance), though it could also be due to the influence of both behavioral and demographic responses of elk to wolves. At the hunt area scale, for example, group sizes may increase in response to predation risk (Gower 2008), while simultaneously the population size may decrease

(with decreasing group sizes) due to direct predation and non-consumptive effects on elk survival and reproduction (Creel and Christianson 2008). It is also possible that elk group sizes were responding to other sources of predation risk, such as human hunting and mountain lions. Mean elk group size has been shown to increase in response to human hunting, but all hunting seasons were closed at least two weeks before we began surveying for elk groups. Group size responses to mountain lions are more likely to be a factor throughout our study period, but little is known about behavioral responses to mountain lions or about mountain lion densities in our study area. Future work should focus on the effects of other predators on elk grouping behavior.

Distance to road, slope of the landscape, land cover diversity, annual winter severity, and elk density were also only weakly related to the conditional median and 0.90 quantile group sizes after controlling for hunt area and all variables of interest. Overall, these findings suggest that when holding all other variables constant, individuals may seek out flatter terrain and less diverse habitats, probably for easier maneuverability and ability to escape as these areas may be wind swept with less snow. The weakly negative relationships with winter severity suggest that median and large group sizes may get smaller during winters with high levels of snow, which may be a result of a change in diet. In this case, snow could force elk to shift from grazing to browsing (Christianson and Creel 2007), thus favoring disaggregation to avoid competition for patchy resources. Other studies have shown that snow accumulation can affect ungulate movement and access to forage across regions with severe winters (Parker et al. 1984, Telfer and Kelsall 1984, Farnes et al. 1999, Bruggeman 2006), but the effects of snow on group size has

been mixed (Gower 2008, Proffitt et al. 2012, White et al. 2012b). Though we found a weak relationship between winter severity and all conditional quantile group sizes, median and larger group sizes may have stronger responses to snow accumulation at scales finer than the hunt area.

Overall, the estimated relationships and amount of uncertainty differed depending on the quantile examined. Therefore, it seems that the selection of any one quantile could be quite arbitrary, in which case future studies of grouping behavior should consider examining the group size distribution more completely. We also found that across the variables of interest there was an abrupt increase in uncertainty at the 0.90 quantiles (Figure 3.3). Though this probably occurred because there were fewer groups of this size compared to the other quantiles, even the rare occurrence of these large groups will be important to elk management. Therefore, for animals that form large groups such as elk, it is still important to understand the relationships between upper quantile group sizes and environmental conditions even if there is a high degree of uncertainty. However, we caution that because extreme quantiles are based on fewer data, these estimated relationships may be quite data-set dependent.

Finally, none of the interactions appeared to explain the variation in empirical median or 0.90 quantile group sizes (Figure A3). We expected to see group sizes increase on private land (where elk seek refuge from hunters; Burcham et al. 1999) when the proportion of public land available increased (where hunting is permitted). As previously mentioned, however, elk hunting seasons in the region closed before the start of our aerial surveys, and therefore some of the elk seeking refuge on private land during the hunting

season may have moved back to public land before our study began. It is also possible that elk did not need to leave public land to find refuge from hunters. Because the relationship between empirical median group size and availability of open space did not appear to depend on wolf abundance, we found little evidence for a broad scale pattern of group size trade-offs between predation risk and habitat type. An example of this trade off would be where elk disaggregate into smaller groups in order to reduce detection from predators in wooded areas with lower forage quality, or they aggregate to form large groups and run the risk of being detected by predators in open grasslands with high quality forage.

In conclusion, upper quantiles of the group size distribution may be of more interest to conservation and management than measures of the center such as mean or median group size, and quantile regression is a useful tool for investigating how larger groups are associated with covariates. We showed that for elk in our study area, group sizes were estimated to increase in size on irrigated land. We also showed that other habitat and climate variables were related to the upper quantiles of group size distribution. This dynamic could increase conflicts with private landowners, increase risk of interaction with cattle and facilitate disease transmission, because these elk groups occur in landscapes shared with humans and livestock. Lastly, we demonstrated that relationships between group size and environmental conditions may depend on which quantiles of the distribution are examined. Therefore, our study highlights the importance of focusing on more than one metric of the group size distribution to inform management and understand animal ecology.

Acknowledgements

We are grateful to Dave Stinson, Ken Overfield and Steve Ard for their piloting, and Carson Butler for his hard work as technician and second observer. We are grateful to Teton and Cody Interagency Dispatch for keeping track of our position in the air. This work was supported by the National Science Foundation and National Institutes of Health Ecology of Infectious Disease (grant number DEB-1067129) and the United States Geological Survey. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

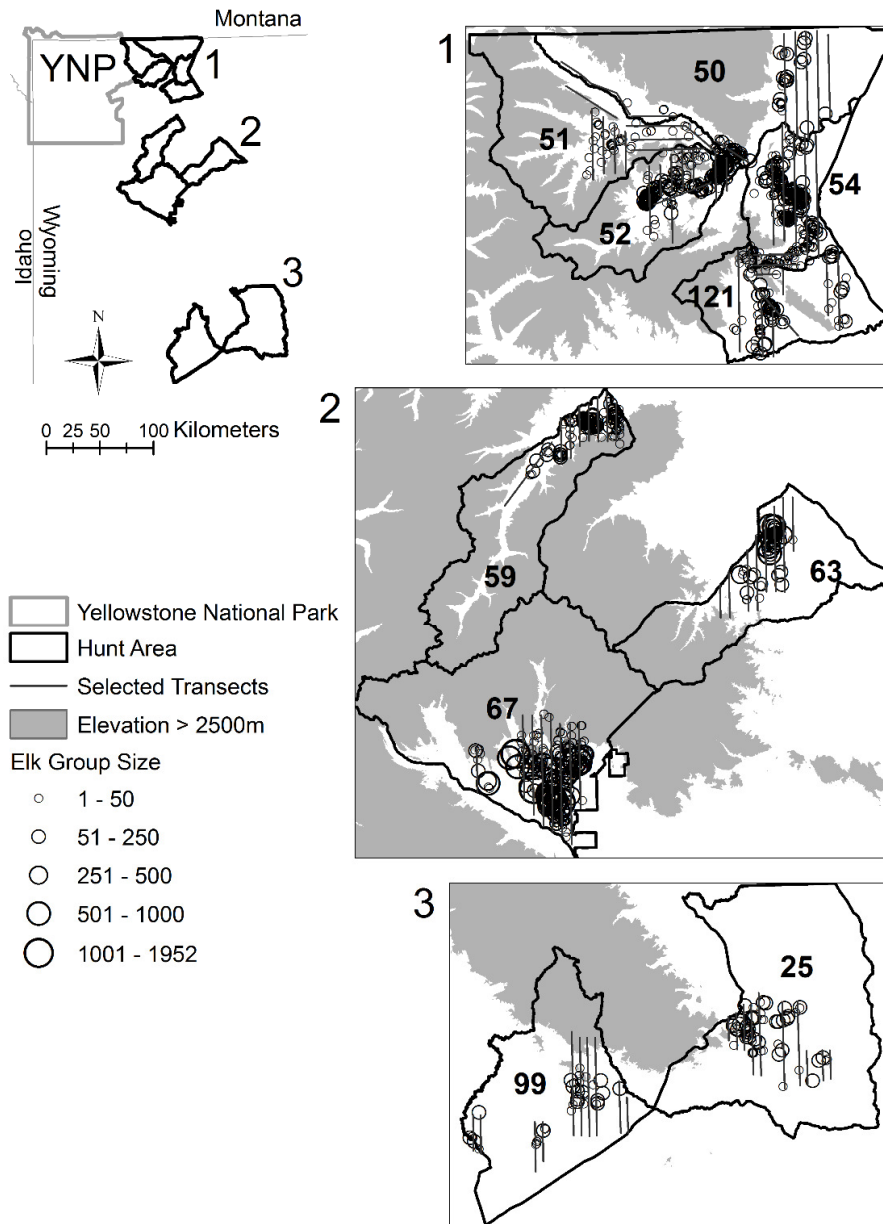


Figure 3.1. Map of the study area, including the 10 hunt areas of interest (labeled as 50, 51, 52, 54, 121, 59, 63, 67, 25, 99), transects used for locating elk groups from fixed-wing aircraft, and the elk groups (location and approximate size) that were recorded throughout the study (January through May, 2010–2012). Transects covered elk winter range delineated from Wyoming Game and Fish Department wintering elk observations.

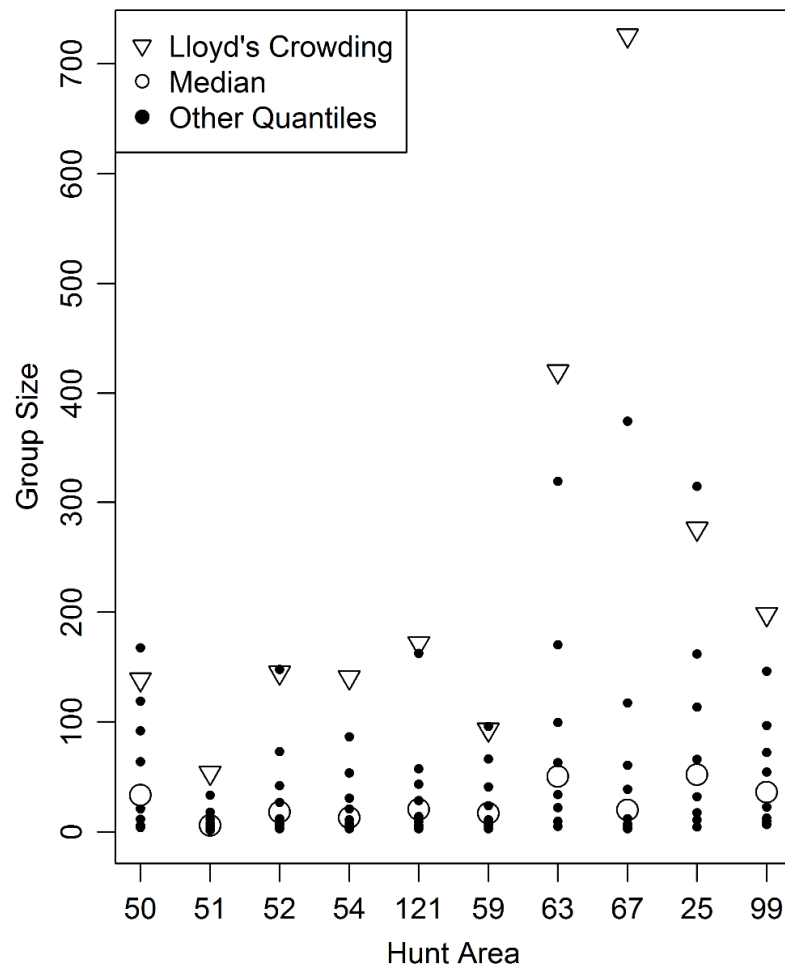


Figure 3.2. Elk group sizes by hunt area, including 0.10, 0.20,..., 0.90 quantiles and Lloyd's Crowding (measures the typical elk group size). Median group sizes are also identified with large open circle. From left to right, hunt areas are arranged from northernmost hunt area to southernmost hunt area (see Figure 3.1 for geographic distribution).

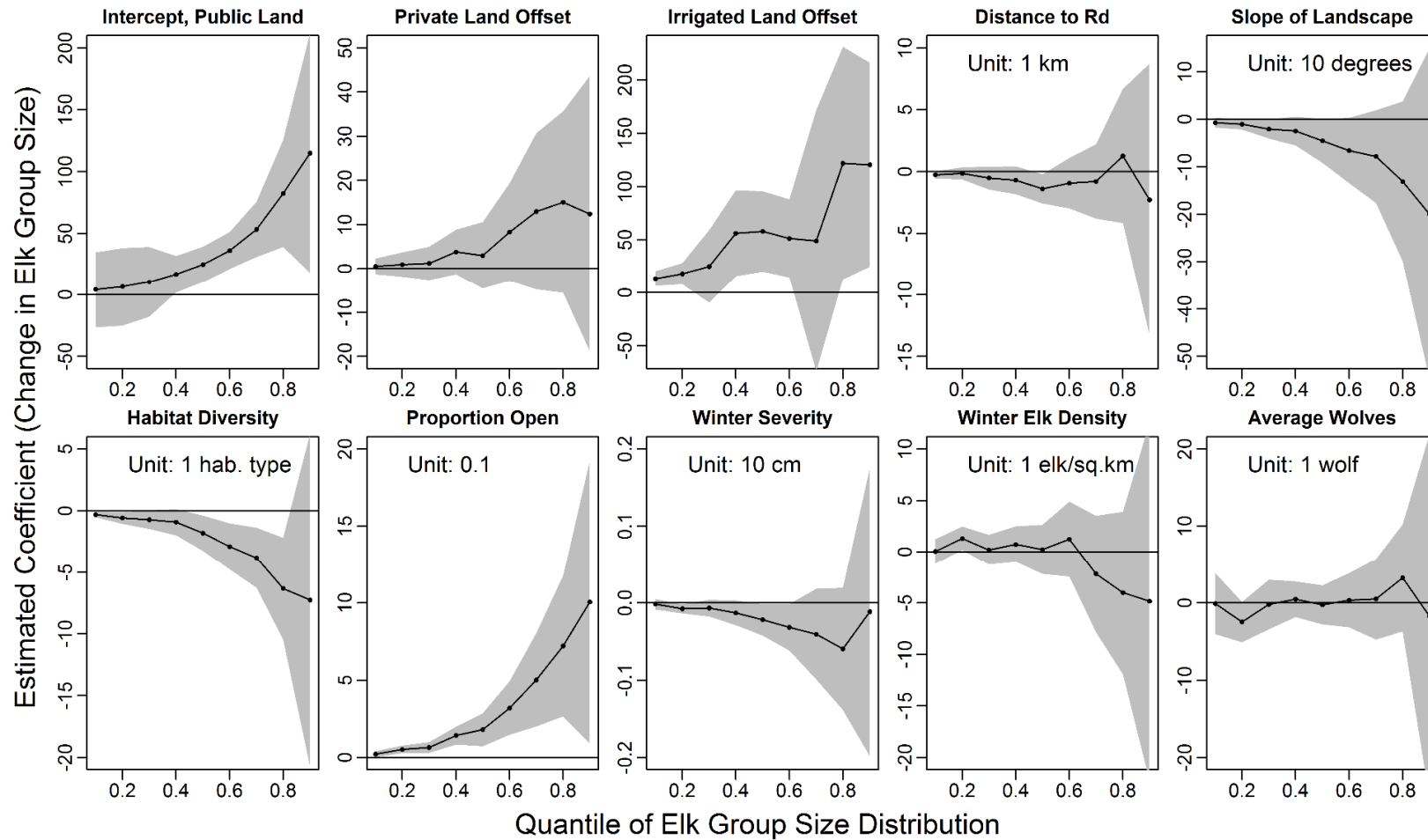


Figure 3.3. Estimated coefficients between the 0.10, 0.20, ..., 0.90 quantiles of the elk group size distribution and each of the explanatory variables of interest. Shaded area indicates bootstrapped 95% confidence intervals. Land use is a categorical variable, with public land as the intercept and private land as the intercept offset. See Methods for description of explanatory variables.

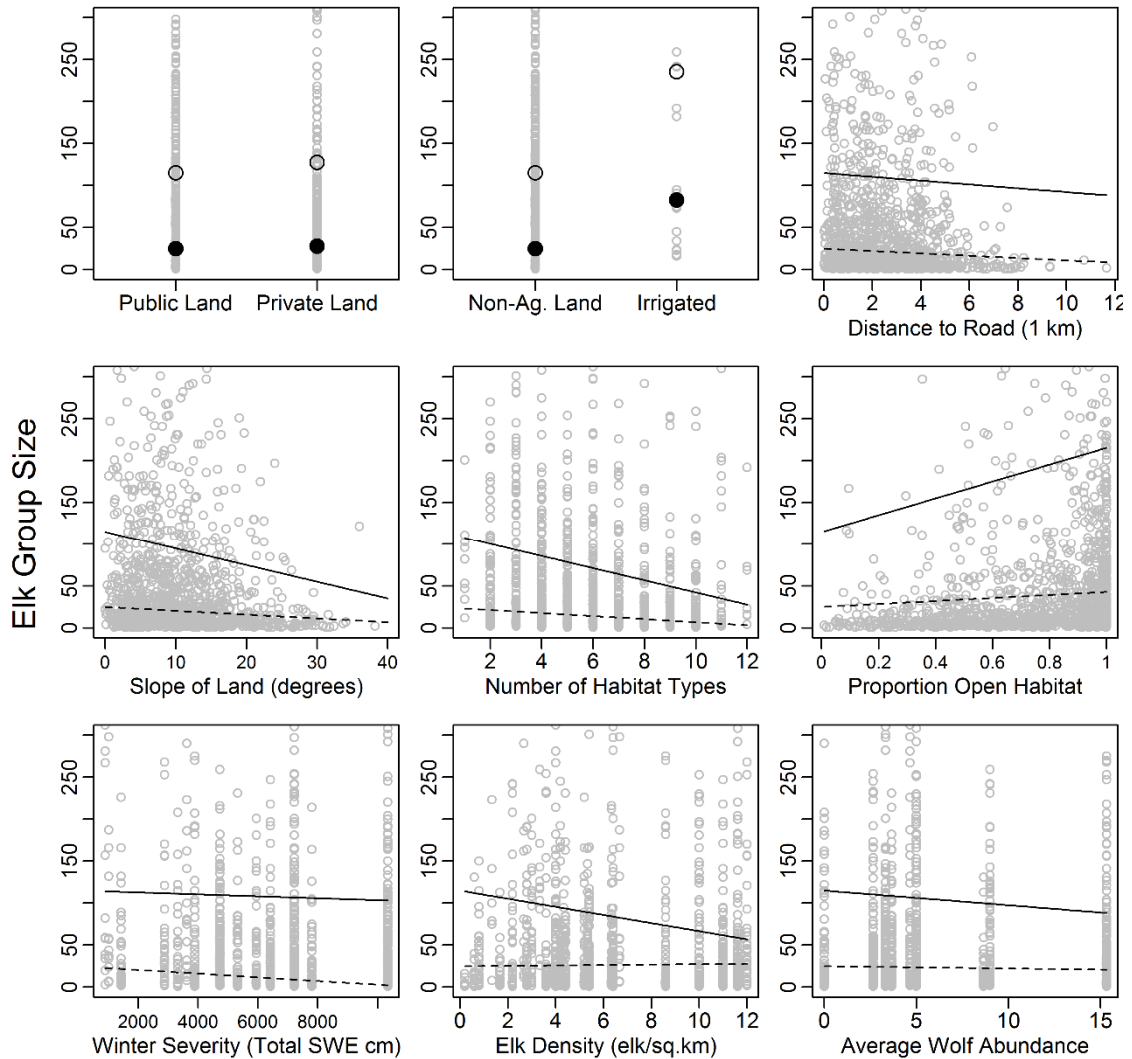


Figure 3.4. Scatterplots of elk group sizes (open grey dots) and each explanatory variable, with the y axis truncated at 300. The dotted black line is the relationship between median group sizes and the explanatory variables (while holding all other variables constant and controlling for hunt area) and the solid black line is the relationship between 0.90 quantile group sizes and the explanatory variables (while holding all other variables constant and controlling for hunt area). Non-Ag. Land is non-irrigated land, and Winter Severity is the sum of daily snow water equivalents from December 1 through June 31. See Methods for further description of explanatory variables.

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CHAPTER FOUR

INFERENCEAL CONSEQUENCES OF MODELING RATHER THAN MEASURING
SNOW ACCUMULATION IN STUDIES OF ANIMAL ECOLOGYContribution of Authors and Co-Authors

Manuscript in Chapter 4

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Contributions: Contributed personnel and equipment to conduct field work. Provided feedback on study design and comments on final draft of the manuscript.

Contribution of Authors and Co-authors Continued

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Manuscript Information Page

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Ecological Applications

Status of Manuscript

☐ Prepared for submission to a peer-reviewed journal

☐ Officially submitted to a peer-review journal

☐ Accepted by a peer-reviewed journal

☒ Published in a peer-reviewed journal

Ecological Society of America, 2013

Submitted June, 2012

Accepted October, 2012

Abstract

It is increasingly common for studies of animal ecology to use model-based predictions of environmental variables as explanatory or predictor variables, even though model prediction uncertainty is typically unknown. To demonstrate the potential for misleading inferences when model predictions with error are used in place of direct measurements, we compared snow water equivalent (SWE) and snow depth as predicted by the Snow Data Assimilation System (SNODAS) to field measurements of SWE and snow depth. We examined locations on elk (*Cervus canadensis*) winter ranges in western Wyoming, because modeled data such as SNODAS output are often used for inferences on elk ecology. Overall, SNODAS predictions tended to overestimate field measurements, prediction uncertainty was high, and the difference between SNODAS predictions and field measurements was greater in snow shadows for both snow variables compared to non-snow shadow areas. We used a simple simulation of snow effects on the probability of an elk being killed by a predator to show that, if SNODAS prediction uncertainty was ignored, we might have mistakenly concluded that SWE was not an important factor in where elk were killed in predatory attacks during the winter. In this simulation, we were interested in the effects of snow at finer scales ($< 1 \text{ km}^2$) than the resolution of SNODAS. If bias were to decrease when SNODAS predictions are averaged over coarser scales, SNODAS would be applicable to population-level ecology studies. In our study, however, averaging predictions over moderate to broad spatial scales (9 to 2200 km^2) did not reduce the differences between SNODAS predictions and field measurements. This study highlights the need to carefully evaluate two issues when using

model output as an explanatory variable in subsequent analysis: (1) the model's resolution relative to the scale of the ecological question of interest and (2) the implications of prediction uncertainty on inferences when using model predictions as explanatory or predictor variables.

Keywords: *Cervus canadensis*, climate variables, elk, elk winter range, prediction uncertainty, SNODAS, snowpack model, snow shadow.

Introduction

Statistical and mathematical models are often used to predict environmental variables where and when direct measurements are not collected (*e.g.*, PRISM, Daymet, and WorldClim climate variables). These models may vary in complexity, extent, and spatial and temporal resolution (see Watson et al. 2006 for comparison of snowpack models), but they commonly rely on interpolation among sparsely distributed direct measurements (Daly 2006, Fuentes et al. 2006) or downscaling to reach finer resolutions (Wilby and Wigley 1997, Wilby et al. 2004, Tabor and Williams 2010, Littell et al. 2011, Fordham et al. 2011). Model predictions may represent broad trends with little bias when averaged over large areas or time frames, while prediction error increases at finer scales (Daly 2006). At any scale, prediction uncertainty is rarely quantified or accounted for in the analysis or conclusions of ecological studies that use model predictions as explanatory or predictor variables. Given the number of such studies using model predictions in place of direct measurements (≥ 9 articles in *Ecology* and 19 in *Ecological*

Applications from January 2011 – February, 2012 [*e.g.*, Erb et al. 2011, Cord and Rödder 2011]), it is important to understand the inferential consequences of treating these predictions as if they were directly-measured data without error. We used predictions of snow accumulation generated from the Snow Data Assimilation System (SNODAS; data *available online*⁵) to demonstrate potential levels of model prediction error at scales relevant to wildlife ecology, and to examine the practical effects of using model predictions in place of direct measurements in a typical wildlife application.

Snow accumulation is strongly associated with the behavior and ecology of animals in cold climates (Nelson and Mech 1986, Hobbs 1989, Hupp and Braun 1989, Brodie and Post 2010, Beckmann et al. 2012), and therefore snowpack models such as SNODAS may appeal to wildlife researchers and managers who require snow data at times or places where field measurements cannot be collected (*e.g.*, daily measurements at multiple remote locations). Snow variables recorded at fine spatial (*e.g.*, $\leq 0.05 \text{ km}^2$) and moderate to fine temporal scales (*e.g.*, $\leq$ biweekly) can be important for understanding individual animal behavior (Christianson and Creel 2008), as snow can reduce access to forage patches (Craighead et al. 1973, Bruggeman 2006), decrease ability to escape predators, increase predator kill rate (Nelson and Mech 1986, Huggard 1993), change diet composition (Huggard 1993, Christianson and Creel 2007), or increase energy expenditure for thermoregulation, travel, and search for food (Telfer and Kelsall 1984, Parker et al. 1984). Cumulatively, these effects on individuals can result in population-level responses to snow accumulation, such as changes in recruitment,

⁵ <http://nsidc.org/data/g02158.html>

survival, or distribution. Analysis of these population-level effects typically requires data on snow variables collected at broad spatial (*e.g.*, $\geq 100 \text{ km}^2$ for large mammals) and temporal scales (*e.g.*, $\geq \text{year}$) (Garrott et al. 2003).

SNODAS has the potential for wide application to animal ecology studies because it predicts snow water equivalent (SWE) and snow depth at relatively fine spatial and temporal resolutions (*e.g.*, 1 km^2 , daily) and broad extents (*e.g.*, contiguous United States), from 2003 to the present. However, SNODAS was developed by the National Operational Hydrologic Remote Sensing Center (NOHRSC) to support basin-scale hydrologic models, not wildlife research. SNODAS predictions are generated from ingested Numerical Weather Prediction (NWP) model estimates of air temperature, relative humidity, wind speed, and precipitation that are downscaled from a 13 km^2 to a 1 km^2 resolution (Barrett 2003, Carroll et al. 2006). Multi-sensor snow data are then assimilated into the model in order to update model output. These data include SWE and snow depth provided by the National Weather Service (*e.g.*, weather stations and cooperatives), federal and state agencies (*e.g.*, Natural Resources Conservation Service's [NRCS] Snow Telemetry [SNOTEL] stations and snow course sites), and regional mesonets (*i.e.*, network of environmental monitoring stations); SWE obtained via the NOHRSC-operated airborne snow survey program; and satellite remote sensing data used to capture the extent of snow cover (*i.e.*, snow presence and absence). SNODAS also integrates digital elevation map (DEM)-derived slope and aspect, remotely sensed forest cover and type, and soils data (Barrett 2003, Carroll et al. 2006).

SNODAS relies on relatively few, sparsely-distributed direct field observations of snow to update model output, and therefore prediction uncertainty could be high at fine spatial scales. This problem is not unique to SNODAS, and prediction uncertainty has been discussed frequently in the contexts of other snowpack and rainfall-runoff models (*e.g.*, Chaplot et al. 2005, Franz et al. 2010, Kuczera et al. 2010, Renard et al. 2011), as well as downscaled Global Circulation Models (GCMs) (*e.g.*, Wilby 1997, Wilby and Wigley 1997, Wilby et al. 2004, Tabor and Williams 2010, Fordham et al. 2011, Littell et al. 2011). The effects of prediction uncertainty have also been explored, but generally in the contexts of using precipitation models to drive biogeochemical simulations (Fuentes et al. 2006) or using GCM predictions of temperature and precipitation to project natural resource dynamics (Littell et al. 2011) or species distributions under future climate scenarios (Tabor and Williams 2010, Fordham et al. 2011). Prediction uncertainty has not been addressed, however, in animal ecology studies that use model predictions of snow accumulation such as SNODAS output as explanatory variables. To examine the consequences of this problem in a wildlife ecology setting, we compared SNODAS-predicted SWE and snow depth to field measurements collected from elk winter ranges in western Wyoming to: 1) measure SNODAS SWE and snow depth prediction bias and uncertainty, 2) examine the potential consequences of SNODAS prediction uncertainty for inferences on the relationship between snow and animal ecology (using a simulation in elk ecology), and 3) determine whether SNODAS prediction bias decreases at broad spatial scales applicable to population-level studies of large mammals. Our goal was to highlight potential issues that may arise from using model predictions of snow in place of

direct measurements in a typical wildlife application, not to validate SNODAS as a metric of snow for other purposes (*e.g.*, hydrologic forecasting).

Methods

Study Area

Across our study area, which covered 15000 km² in western Wyoming (Figure 4.1), we compared SNODAS predicted SWE and snow depth to field measurements collected during the months of January through March 2009 and 2010 at sites where elk are supplementally fed in winter (*i.e.*, feedgrounds) and where elk winter off feedgrounds (*i.e.*, native winter range). These study sites were located along the western foothills of the Wind River Range, the Wyoming Range and its eastern foothills, the uplands of the Upper Green River Basin, the northern foothills of the Salt River Range, and the northern, southern and western foothills and valleys of the Gros Ventre Range (Figure 4.1). Site elevations ranged from roughly 1700 to 2750 m and the topography ranged from high mountain valleys and varying grades of mountain slopes, to open, rolling mountain foothills. Vegetation in the mountain valleys and foothills was characteristic of Rocky Mountain montane, subalpine or riparian habitats which includes closed conifer forests (*Pinus spp.*, *Picea spp.*, *Abies lasiocarpa*), willow (*Salix spp.*), aspen (*Populus tremuloides*), grass – forb/herb meadows, and shrubs (*Artemisia spp.*, *Amelanchier alnifolia*). High mountain slopes were dominated by rock and talus. Lowlands were dominated by sagebrush (*Artemisia spp.*), saltbrush (*Atriplex spp.*), greasewood (*Sarcobatus vermiculatus*), herbaceous species, and irrigated hay meadows.

Approximately 22,000 elk winter on feedgrounds and another 4,000 winter on native winter range in the study area (Wyoming Game and Fish Department [WGFD] 2006, Maichak et al. 2009).

The study area has long, often severe winters generally lasting from October through May, although it is not unusual for snow accumulation to begin in September and continue through mid-June. During the winters of 2008 to 2009 and 2009 to 2010 (*i.e.*, when snow accumulation > 0), the 18 SNOTEL stations in our study area (Figure 4.1) recorded a mean SWE of 29 and 21 cm, and mean snow depth of 101 and 90 cm, respectively. Parts of the Gros Ventre Range directly east of the Tetons are located in snow shadows (Hobbs et al. 2003), which are areas on the leeward side of mountain ranges that receive less snow than typical areas of comparable elevation.

Sampling Design

For our study sites, we selected 16 feedgrounds and three native winter ranges to cover the range of habitat, elevation, and topography used by wintering elk in western Wyoming. We used SNODAS grid cells (1-km² pixels) as our sampling units, simply to pair field measurements with SNODAS predictions (not to validate SNODAS at the pixel scale). On the feedgrounds, we randomly selected two SNODAS pixels within a circular area defined by a 2-km radius from the center of each feedground. For the native winter ranges, we used areas delineated as elk winter range by the WGFD and randomly selected five to seven SNODAS pixels within each of those areas.

Within each selected SNODAS pixel we measured SWE and snow depth along one 150-m transect with random starting location and azimuth, though adjustments were

made to the azimuth when necessary to ensure transects remained in the original pixel. Along each transect, we collected five snow cores (using a Mt. Rose Federal snow sampler) 30 m apart to measure SWE and snow depth, as well as four additional snow depth measurements 15 m from each snow core location in each of the cardinal directions. We estimated mean transect values for both snow variables, but to improve precision of mean transect estimates of SWE we used the ratio of SWE to snow depth from snow cores to estimate SWE where only snow depth was measured (Rovansek et al. 1993). Hereafter, we refer to mean transect values as field estimates of SWE or snow depth.

We randomly selected pixels and sampled new transects each winter (in 2009 and 2010) at 11 of the feedgrounds. At the remaining five feedgrounds and three winter ranges, we sampled transects only in 2010. Also in 2010, we randomly selected an additional 8 pixels across four of the feedgrounds (2 pixels per feedground) that had minimal constraints to access (due to elk management practices or private land restrictions) and repeatedly sampled one transect within each of those pixels at sampling intervals of 15 to 30 days. We used these repeated samples to assess whether or not SNODAS prediction accuracy changed throughout a winter.

The total area covered by each transect was 4500 m² (150 m in length, 15 m X 2 in width), which is obviously a small fraction of a 1-km² SNODAS pixel. However, our intention was not to validate SNODAS at the pixel scale. Rather, the goal was to quantify how well SNODAS predicts snow at the transect scale in areas used by wintering elk and to measure snow as it relates to elk ecology. Therefore, we used sampling methods

typical of studies of snow effects on ungulate ecology (Hoskinson and Tester 1980, Sweeney and Sweeney 1983, Anderson et al. 2005, Fortin et al. 2009), which are also similar to those used by the NRCS to measure snow accumulation at snow course sites. Since field estimates were obtained at a much finer scale than the SNODAS resolution, however, differences between SNODAS predictions and field estimates may be attributable to how well SNODAS estimates the average snow depth and SWE for a pixel, as well as the amount of variation within that pixel.

Analysis

As a result of our sampling design, our field estimates were clustered by site (19 total study sites: 16 feedgrounds plus 3 native winter ranges). Therefore, we conducted all analyses using linear mixed effects models with site as the random effect (*i.e.*, allowing the intercept to vary by site) to account for the correlation among field estimates from the same site. We used the R environment for statistical computation (R Code Development Team 2011) with the package lme4 (Bates et al. 2011). We examined the assumptions of linear regression, and all were reasonably met.

We calculated SNODAS bias, which we defined as the difference between SNODAS predictions and field estimates. We also aggregated the study sites into seven regions (Figure 4.1). We defined region *post hoc* as either a discrete elk native winter range or a set of feedgrounds closest to one another. Using linear models of SNODAS bias (response variable) on region (explanatory variable), we estimated the mean SNODAS bias and 95% confidence intervals (CIs) by region for both snow variables.

Retrospectively, we observed less snow on average at transects located in snow shadows of the Teton and Gros Ventre Ranges compared to other transect locations, even though transect elevations tended to be higher in snow shadows (Appendix C, Figure C1). We did not anticipate that SNODAS bias would be greater in snow shadows, but differences were revealed between these and other regions. To demonstrate the magnitude of the prediction bias in snow shadows, we compared the estimated mean SNODAS bias and 95% CIs for both snow variables in snow shadows to other regions. Our goal for this comparison was not to suggest that SNODAS bias is only a concern in snow shadows, but rather to highlight the effect of potentially unaccounted for local-scale atmosphere or land surface properties on prediction bias. Other study sites may be impacted by different physical processes potentially not captured by SNODAS.

We examined the linear relationship between SNODAS predictions (predictor variable) and field estimates (response variable) of SWE or snow depth and compared the estimated intercept, slope and 95% CIs to a 1:1 relationship (*i.e.*, slope = 1, intercept = 0). We repeated this analysis without snow shadow data to determine the effect of snow shadows on regression bias. Because the estimated linear relationship between SNODAS predictions and field estimates does not account for the scatter around the regression line, we quantified the effect of bias *and* variance on future field estimates predicted from new SNODAS values using 95% prediction intervals (PIs).

Finally, we examined whether or not SNODAS predictions matched field estimates more closely earlier in the winter when there may be less snow on the ground, compared to later in the winter. We plotted SNODAS bias for SWE over time for

transects measured repeatedly in 2010 to assess evidence for a time trend in SNODAS bias.

Testing Snow Effects in an Ecological Model

To demonstrate the potential consequences of using model predictions in place of field measurements, we prepared a hypothetical example relating SNODAS-predicted SWE to the (relative) probability of an elk being killed by a predator. This is based on a comparison of SWE at kill sites relative to SWE at “available” sites, which are generally defined as random sites within the nearby area (Hebblewhite et al. 2005). We used SWE because it incorporates snow depth and density, and has been identified as the best predictor of ungulate responses to snow in our study area (Farnes et al. 1999). Elk generally avoid areas that exceed 15 cm SWE, and are known to more commonly use winter ranges with less than 7 cm SWE (Farnes and Romme 1993). Our field estimates of SWE ranged roughly from 0 to 20 cm and SNODAS predictions ranged from 2 to 35 cm, which not only covers typical levels of SWE on an elk winter range, but also spans the levels of SWE detected in studies of snow effects on probability of an elk kill (Becker 2008).

We simulated random binary outcomes representing kill or no kill from a binomial distribution with probabilities obtained from a logistic regression model with our field estimates of SWE as the explanatory variable, an intercept = -0.9, and slope = 0.11. These hypothetical parameters were not empirically estimated, but represent reasonable approximations of how elk kills may be related to snowpack, while holding other variables constant. We fit two logistic regression models to our simulated binary

response variable. In the first model, we used field estimates of SWE (same data used to generate the response variable) as the explanatory variable, and in the second we used SNODAS-predicted SWE as the explanatory variable to represent a situation where an ecologist may use SNODAS predictions in place of direct observations. We conducted the simulation and analyses in R.

SNODAS Prediction at Multiple Spatial Scales

Our sampling was not designed to test SNODAS accuracy at scales coarser than the transect. However, if SNODAS did poorly at predicting SWE and snow depth at the transect level, we hypothesized that predictions might improve at coarser spatial scales applicable to population-level studies of large mammals. Therefore, we examined SNODAS predictions at the feedground and region scales ranging from 9 to 2200 km². At the feedground scale, we averaged all SNODAS pixels falling at least partially within a 2-km radius around the center of each feedground on dates field sampling occurred. The number of pixels included was not identical among feedgrounds, resulting in areas ranging from 9 to 14 km². For region-scale calculations, we generated a circular area having a diameter equal to the greatest distance between sample locations within a region and a centroid equal to the midpoint between those sample locations. The resulting region-scale areas ranged from 150 to 2200 km².

Within each feedground or region area, we averaged only those SNODAS pixel values occurring within the elevation range of elk feedgrounds and native winter ranges in the study area (1700 to 2750 m). Feedground and region-scale field estimates were the average of all field measurements along all transects (SWE or snow depth) contained in

each feedground or region, respectively. The number of field measurements of SWE ranged from 10 to 25 per feedground and from 25 to 100 per region. For snow depth, the number of field measurements ranged from 50 to 125 per feedground and from 125 to 500 per region.

We calculated SNODAS bias for both snow variables as the difference between the averaged SNODAS predictions and the averaged field measurements at the feedground or region scale. We use the term “SNODAS bias” because it is used throughout this document to describe the differences between SNODAS predictions and field estimates, but we acknowledge that differences calculated at the region scale may be due, in part, to the assignment of region after sampling occurred, or to the lack of random samples outside study sites (resulting in biased field estimates at the region scale). However, we argue that our field estimates are a better representation of the average SWE and snow depth across potential elk winter range in the study area than SNOTEL data, which are used to update SNODAS predictions and are frequently used in elk ecology studies to estimate snow conditions at spatial scales similar to our feedground and region scales (*e.g.*, Singer et al. 1997, Taper and Gogan 2002). Because SNOTEL stations are sparsely distributed, few stations are used to depict snow conditions at those scales, and they are typically located at elevations higher than the winter ranges of large herbivores.

We quantified the mean SNODAS bias at the transect scale using a linear random effects model (intercept only) with site (19 total study sites) as the random effect. To quantify mean SNODAS bias at each of the coarser scales, we used intercept-only simple

linear regression models of SNODAS bias. For both snow variables, we compared the estimated mean SNODAS bias and 95% CIs among scales, as well as SNODAS bias in snow shadows to other regions.

Results

SNODAS Prediction Accuracy and Precision

In total, we sampled 99 transects with 495 and 2475 measurements of SWE and snow depth, respectively, on 19 study sites. Of the 99 field estimates, we used 72 for our primary analyses (paired with 72 SNODAS predictions). The remaining 27 were repeated samples and only used for determining whether or not SNODAS bias increased through time. We did not see evidence of a temporal trend (Appendix C, Figure C2), but it revealed spatial clustering of SNODAS bias for SWE by site that validated our use of random intercept models by site.

Snow conditions on each transect appeared to be similar to the general snow conditions of its study site (*i.e.*, snow on a transect was not overly deep, shallow or crusted compared to other locations while traveling across a study site). Field estimates of SWE ranged from 0.1 to 20 cm, field estimates of snow depth ranged from 0.6 to 72.0 cm, mean snow density was 21% (typical of mountain-continental snowpacks), and mean snow density by region ranged from 17.2 to 25.3%. Estimated mean SNODAS bias varied within and among regions for both snow variables, but was greater in snow shadow regions (Figure 4.2). Among regions, estimated mean SNODAS bias for SWE ranged from 1.2 cm (95% CI = -6.7, 9.1) to 17.3 cm (95% CI = 11.5, 23.1) and for snow

depth ranged from 8.5 cm (95% CI = -24.4, 41.4) to 68.0 cm (95% CI = 44.1, 91.9).

Estimated mean SNODAS bias for SWE in snow shadow regions was 14.5 cm (95% CI = 10.8, 18.2), compared to 4.1 cm (95% CI = 2.1, 6.0) in non-snow shadow regions.

Estimated mean SNODAS bias for snow depth was 55.4 cm (95% CI = 39.6, 71.1) in snow shadows, compared to 15.8 cm (95% CI = 7.6, 24.0) in non-snow shadow regions.

Snow shadows also explained a portion of the relationship bias between SNODAS-predictions and field-estimates for both snow variables (Figure 4.3). This relationship bias, in addition to the substantial scatter around the regression lines, resulted in wide 95% PIs for both snow variables. New SNODAS predictions of 0 cm, 10 cm, and 20 cm corresponded to the following 95% PIs for SWE on the ground: 0 – 10 cm, 0 – 13 cm, and 1 – 16 cm, respectively. For snow depth, new SNODAS predictions of 0 cm, 50 cm, and 100 cm corresponded to 95% PIs of 0 – 46 cm, 0 – 58 cm, and 0 – 71 cm snow depth on the ground, respectively. Prediction intervals were left-truncated at zero.

Testing Snow Effects in an Ecological Model

Using SNODAS predictions in place of field estimates resulted in a higher estimated probability of kill at 0 cm SWE (0.36 for SNODAS compared to 0.16 for field estimates of SWE), slower increase in the probability of kill with increasing SWE, and a lower estimated probability of kill at a mid-value (15 cm) of SWE (0.48 for SNODAS compared to 0.85 for field-estimated SWE) (Figure 4.4). The estimated slope on the logit scale using field estimates of SWE as the explanatory variable was 0.22 (95% CIs = 0.09, 0.35; $p < 0.001$), compared to 0.03 (95% CIs = -0.03, 0.10; $p > 0.3$) using SNODAS-predicted SWE as the explanatory variable. These slope estimates correspond to a 24%

increase in the relative odds an elk was killed by a predator for every 1 cm increase in field-estimated SWE, and a 3% increase in the relative odds an elk was killed for every 1 cm increase in SNODAS-predicted SWE.

SNODAS Prediction at Multiple Spatial Scales

Estimated SNODAS bias for both snow variables did not improve at broader spatial scales, and SNODAS bias was greater in snow shadows compared to other regions at all three spatial scales (Figure 4.5). Estimated mean SNODAS bias for SWE was 6.9 cm (95% CI = 4.2, 9.6) at the transect scale, 7.2 cm (95% CI = -3.3, 11.0) at the feedground scale, and 10.6 cm (95% CI = 2.9, 18.3) at the region scale. Estimated mean SNODAS bias for snow depth was 26.4 cm (95% CI = 15.7, 37.1) at the transect scale, 27.6 cm (95% CI = 12.9, 42.4) at the feedground scale, and 39.1 cm (95% CI = 15.0, 63.1) at the region scale.

Discussion

Model predictions of environmental variables are attractive as explanatory or predictor variables for logistical reasons, but these predictions carry uncertainty that can affect our conclusions about the relationships between environmental conditions and animal ecology. Our study compared field measurements of snow accumulation to SNODAS predictions to demonstrate the potential implications of ignoring model prediction uncertainty. We showed that SNODAS bias for SWE and snow depth was variable across all sampled transects and it was greatest in snow shadow regions (Figures 4.2, 4.3, and 4.5). We did not anticipate that snow shadows would be a source of added

prediction bias. Therefore, field measurements were necessary to identify and estimate the magnitude of this effect, though it appears common that model output are used as explanatory variables without studying the relationship between model predictions and field-measurements. The identification of snow shadows as one source of prediction bias suggests a potential for other local topographical or climate factors that could affect SNODAS prediction accuracy. Moreover, our identification of substantial bias across all regions is evidence that it is not appropriate to treat SNODAS predictions as data without error.

The high levels of SNODAS bias points to some of the general limitations of weather and climate models, including model structure and methods (*e.g.*, algorithm, interpolation, downscaling), depiction of regional atmosphere–land fluxes and, in the case of relatively fine resolution snowpack models, depiction of local land surface properties that affect snow fall and accumulation (*e.g.*, topography, vegetation, and water bodies) (Wilby 1994, Wilby et al. 2004, Daly 2006, Fordham et al. 2011, Littell et al. 2011). Though models are meant to be simple representations of complex processes, the exclusion of real-world details can result in prediction uncertainty, and we demonstrated through a simple simulation that this uncertainty can affect our understanding of the relationship between SWE and ecological processes, such as the probability that a predatory attack will succeed. For animals and contexts where snow effects may be strong, as is the case of large mammals in the Rocky Mountains, the inability to discern differences in individual or population-level responses to snow accumulation could impact species management or conservation efforts. For example, some Rocky Mountain

elk populations face population declines or low calf recruitment (Creel et al. 2011), and effective management requires an understanding of how demographic rates are related to snow or other climate-related factors, predation, and hunting. Beyond our analysis, similar impacts of prediction uncertainty on management and conservation are important to consider when projecting shifts in species distributions in response to climate change. Global Circulation Models are less accurate at describing local climates, and species distribution models may be sensitive to this uncertainty (Tabor and Williams 2010, Fordham et al. 2011, Winterhalter et al. 2011).

Depending on the scale of the question of interest, prediction uncertainty may have little effect on inferences. For example, averaging many predictions across large areas or timeframes for broad scale questions may be less biased than individual predictions used for fine scale questions, if the physical processes defined in the model occur at coarser rather than finer scales. In other words, models may not capture fine scale variation because of few localized observations or a failure to account for important local physical processes (Wilby 1994, Wilby et al. 2004, Littell et al. 2011). In the case of SNODAS, it was developed for hydrologic modeling at basin-scales, not for applications at fine spatial or temporal scales relevant to individual animal behavior. Moreover, we were interested in how well SNODAS predicted snow at scales finer than the SNODAS pixel. Because SNODAS is not designed to account for within-pixel processes, it is understandable that SNODAS predictions did not match our field estimates, but this is a point often overlooked by ecologists looking for environmental data to explain fine scale ecological processes. Therefore, SNODAS, or models that make predictions at similar or

coarser resolutions, may be better suited for broad scale studies applicable to large mammal populations. Though our study did not show decreases in estimated mean SNODAS bias at moderate scales (9 to 14 km²) or broad scales (520 to 2200 km²), a future study with larger sample sizes could reveal greater prediction accuracy at these coarser spatial scales.

Our study focused on SNODAS and identified areas where it poorly predicted snow accumulation, but the goal of our study was not to broadly condemn the use of SNODAS or other model predictions as covariates. Rather, we focused on estimating potential levels of prediction uncertainty and examining how this uncertainty can impact our understanding of how snow relates to elk ecology. Our linear regressions of field estimates on SNODAS predictions depicted bias when compared to a 1:1 relationship, and revealed a high degree of variability around the regression line (Figure 4.3). Removal of snow shadows from these analyses decreased the relationship bias only slightly, and the scatter around the regression lines remained (Figure 4.3). As a consequence of the bias *and* variability, new SNODAS predictions corresponded to a wide range of SWE and snow depth on the ground. It was also evident that SNODAS substantially over-predicts at higher values of field-estimated SWE and snow depth (Figure 4.3).

As seen in our simulation, SNODAS prediction uncertainty could substantially affect inferences about the relationship between snow and animal ecology. Because field estimates of SWE were not excessively high (range of 0.1 to 20 cm was below the average SNOTEL SWE for 2009 and 2010 winters), the simulation more appropriately reflects responses in late-winter when elk physiological condition has been weakened

(Becker 2008) to a point where even low to moderate snow levels could become important to survival. Strong responses of elk to snow, however, typically occur during more severe winters (Singer et al. 1997, Garrott et al. 2003). Because SNODAS tended to over-predict with substantial uncertainty at all levels of SWE and snow depth (Figure 4.3), the importance of snow to elk ecology could be underestimated if using SNODAS in place of field measurements even during winters with above average snow accumulation.

Given the degree of variability among SNODAS predictions in our study, field measurements used as ground truth samples may not be enough to adjust SNODAS predictions to eliminate bias, though a thorough ground truth of SNODAS would include more transects or sample locations per pixel than was included in our study. Ground truth samples or reference data are often used to establish the relationship between model predictions (or remotely sensed observations) and field measurements, in order to remove bias from future model predictions (*e.g.*, Czaplewski and Catts 1992). However, this process does not affect the scatter of individual predictions around the regression line. As this scatter increases, so does the prediction uncertainty, regardless of whether intensive ground-truth sampling occurred or not. Unless ground-truth sampling reveals greater precision among individual predictions than found in our study, SNODAS is probably better suited to monitoring trends over time or comparing among broad regions, rather than making comparisons among transects. Further study of SNODAS prediction uncertainty over broad areas and timeframes is needed to know if prediction uncertainty improves at these scales.

Our field estimates were transect means and therefore also had error associated with them. The difference between error in our field estimates versus error in SNODAS predictions is our ability to quantify and model that error (Buonaccorsi 2010). With our sampling methods, for example, we were able to calculate standard errors of the mean, and these standard errors were very small relative to the difference between transect means and SNODAS predictions (Figure 4.3). SNODAS or other model predictions, on the other hand, are provided without estimates of error and are often used as explanatory variables without acknowledging the potential for error and the effects it may have on inferences. However, in the case of GCMs where many models exist, the variability among model output can be quantified to understand potential prediction uncertainty (Fuentes et al. 2006, Tabor and Williams 2010, Fordham et al. 2011, Littell et al. 2011).

Conclusions

Prediction uncertainty from snowpack and climate models is expected because predictions are generated by interpolation between sparsely distributed direct observations or downscaling models that do not account for local physical processes. However, prediction uncertainty is rarely quantified or accounted for in studies of animal ecology that use model predictions in place of direct measurements. Blindly using model predictions as predictor variables without error can impact inferences, as we demonstrated in our example using SNODAS-predicted SWE to explain the relative probability of an elk kill. While we only investigated SNODAS, the cautions with regard to inference are relevant when using other snowpack, weather or climate model

predictions. Even the most sophisticated and highly-regarded models are approximations, and the scale at which predictions are generated should not be ignored. Model predictions may be useful as indices for some questions of interest, but misleading when used at fine scales when prediction uncertainty is high.

Acknowledgments

We thank J. Rogerson, J. Henningsen, E. Maichak, and A. Williams at the Wyoming Game and Fish Department for their assistance accessing study sites and sampling snow on elk winter range. We also thank A. Barbknecht for her hard work in collecting snow data. This work was supported by the National Science Foundation and National Institutes of Health Ecology of Infectious Disease (grant number DEB-1067129) and the United States Geological Survey. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

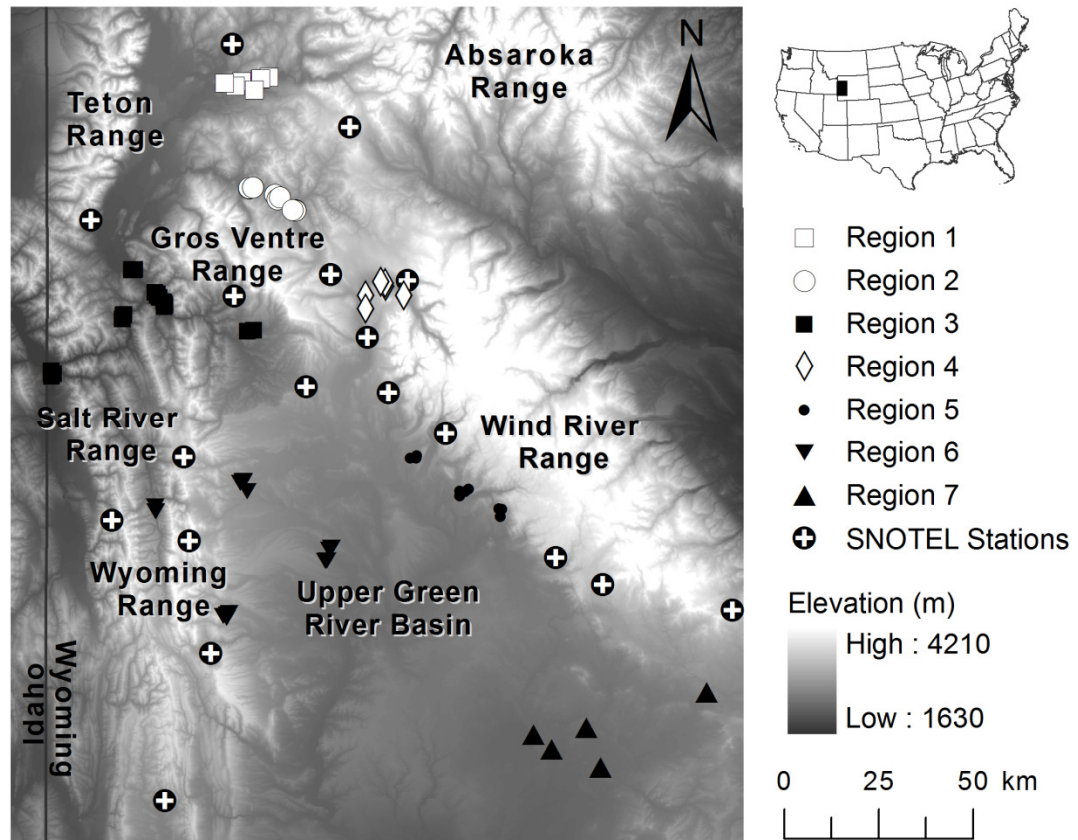


Figure 4.1. Map of study area, snow sampling transects within seven general regions, the 18 SNOTEL stations nearest to transect locations, WY cities (Jackson, Pinedale and Dubois), elevation (m), and relevant mountain ranges. White-filled region symbols are snow shadow regions.

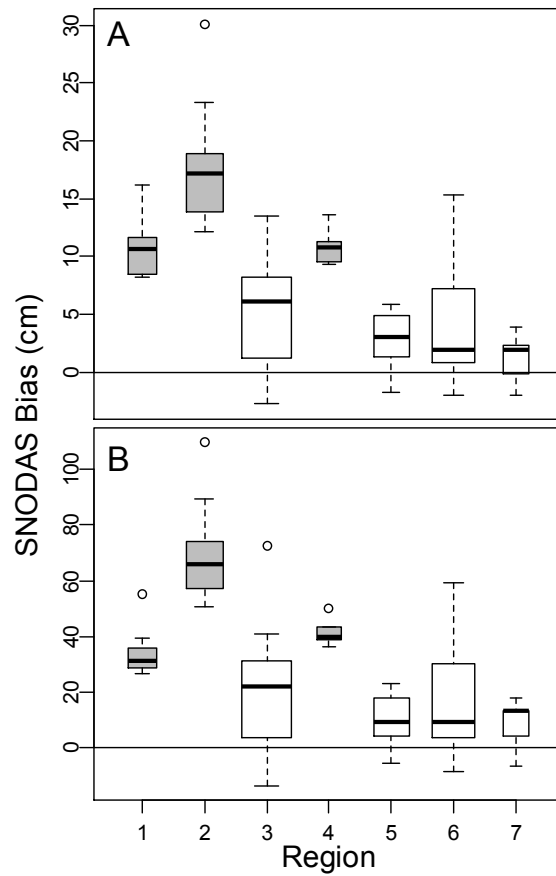


Figure 4.2. Boxplots of SNODAS bias (cm) for SWE (A) and snow depth (B). SNODAS bias is the difference between SNODAS predictions and field estimates (transect means). Boxes identify quartiles and medians, whiskers are 1.5 times the interquartile range, and points outside of boxes identify minimum and maximum data points. Box widths are proportional to number of observations within region. Regions are ordered from northernmost (1) to southernmost (7). Grey boxplots are regions in the snow shadow on the lee side of a major mountain range.

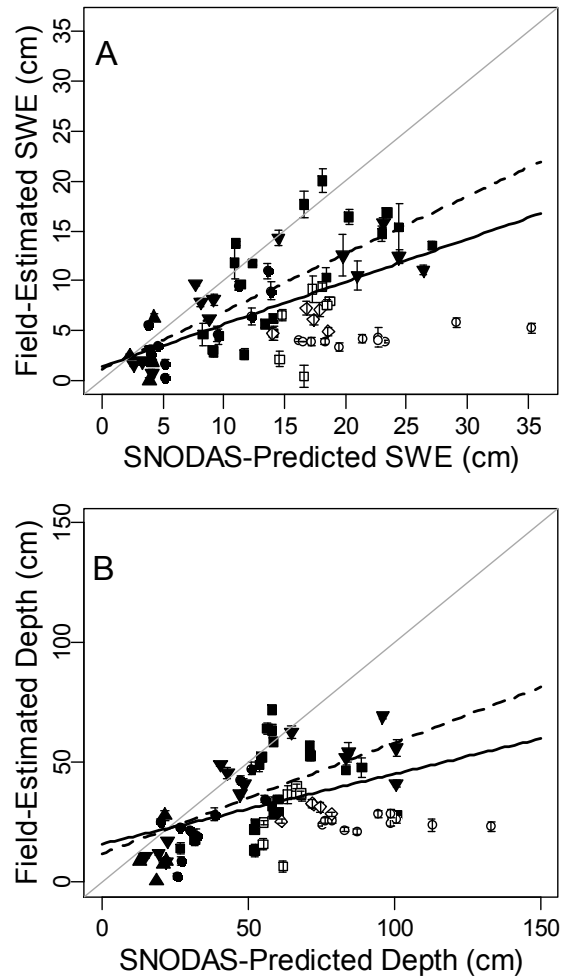


Figure 4.3. Linear regressions of field estimates (transect means) on SNODAS predictions of SWE (cm) (A) and snow depth (cm) (B) on elk feedgrounds and native winter ranges in western Wyoming. Different symbols indicate the seven regions of interest as depicted in Figure 4.1; open symbols are regions located in a snow shadow. The solid black line is the estimated linear relationship across all transects sampled ($n = 72$; SWE: intercept = 1.37 [95% CIs = -1.27, 4.00], slope = 0.43 [0.29, 0.56]; snow depth: intercept = 15.98 [4.51, 27.45], slope = 0.29 [0.14, 0.45]). The dashed black line is the estimated linear relationship across only non-snow shadow transects ($n = 56$; SWE: intercept = 1.17 [-1.00, 3.33], slope = 0.58 [0.44, 0.72]; snow depth: intercept = 11.94 [0.72, 23.17], slope = 0.46 [0.28, 0.64]). Error bars are standard errors of the transect mean and the grey line represents a 1:1 relationship between SNODAS predictions and field estimates. Linear models were mixed effects models with site as random effect. Site refers to the 19 total study sites (16 feedgrounds plus 3 native winter ranges).

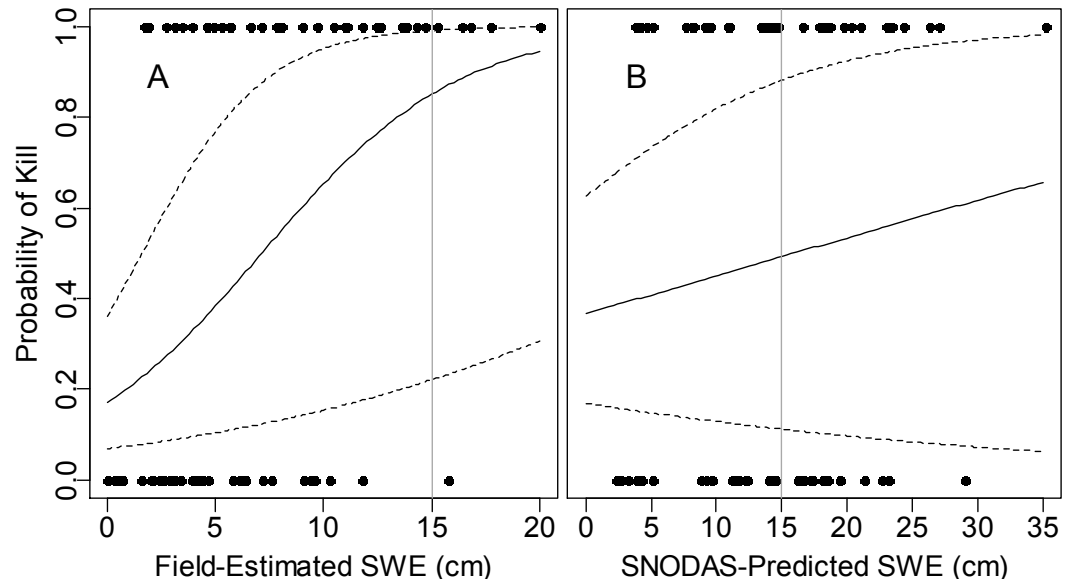


Figure 4.4. The fitted logistic relationship (solid black lines) between the probability that an elk is killed by a predator and field estimates of SWE (cm) (A) or SNODAS-predicted SWE (cm) (B). Dashed black lines are 95% CIs and grey lines identify estimated probability of kill and uncertainty at 15 cm SWE.

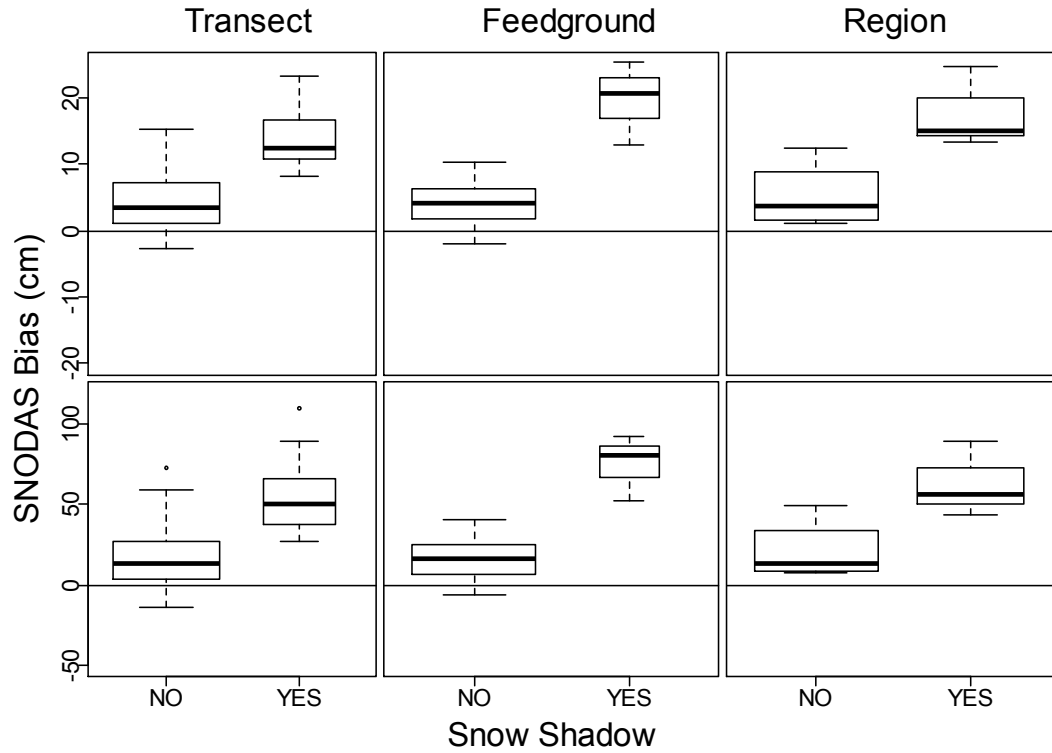


Figure 4.5. Boxplots of SNODAS bias for SWE (top row) and snow depth (bottom row) at three spatial scales: transect (4500 m²; n = 72), feedground (9 to 14 km²; n = 16), and region (150 to 2200 km², n = 7). SNODAS bias is the difference between SNODAS predictions and field estimates (transect means). Grouping is by being located in (YES) or not in (NO) a snow shadow. Boxes identify quartiles and medians, whiskers are 1.5 times the interquartile range, and points outside of boxes identify minimum and maximum data points. Box widths are proportional to number of observations.

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CHAPTER FIVE

TESTING AUTOMATED HOWLING DEVICES IN A WINTERTIME WOLF
SURVEY

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

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Contributions: Conceived, developed, and implemented hypotheses and study design. Collected and analyzed data. Wrote first draft and subsequent revisions of the manuscript.

Co-Author: Dr. Paul C. Cross

Contributions: Helped conceive hypotheses and study design. Provided funding and feedback on statistical analyses, presentation of findings, and all drafts of the manuscript.

Co-Author: David E. Ausband

Contributions: Helped conceive hypotheses and study design, and provided comments on all drafts of the manuscript.

Co-Author: Andrea Barbknecht

Contributions: Helped develop study design and provided comments on final draft of the manuscript.

Co-Author: Dr. Scott Creel

Contributions: Helped develop hypotheses and study design. Provided funding, feedback on statistical analyses, and comments on all drafts of the manuscript.

Manuscript Information Page

Angela Brennan, Paul C. Cross, David E. Ausband, Andrea Barbknecht, and Scott Creel
Wildlife Society Bulletin

Status of Manuscript: (Put an x in one of the options below)

☐ Prepared for submission to a peer-reviewed journal

☐ Officially submitted to a peer-review journal

☐ Accepted by a peer-reviewed journal

☒ Published in a peer-reviewed journal

The Wildlife Society, 2013

Submitted March, 2012

Accepted December, 2012

Abstract

Previous tests of the automated acoustic device, referred to as a howlbox, effectively identified the presence of wolves (*Canis lupus*) during the summer, near rendezvous sites. Howlboxes are self-contained devices that broadcast simulated wolf howls and record howls made in response, and are of interest in remote locations to document the presence of dispersing wolves and new wolf packs. It is unclear whether the howlbox can also detect wolves during the winter when wolves are more mobile. We tested the howlbox's ability to detect wolves in an area with approximately 3 wolves/100 km² and overlapping pack territories in western Wyoming, USA, during January–May 2011. Howlboxes detected wolves in only 1.1% ($n = 185$, 95% CI = 0.1–3.8%) of the surveys, but we recorded wolf tracks within 50 m of howlboxes 14.8% ($n = 54$, 95% CI = 6.6–27.1%) of the time. Though howlboxes seldom recorded wolf howls, our findings suggest the possibility that howlboxes may attract wolves in areas with overlapping pack territories during the winter.

Keywords: Abundance, *Canis lupus*, distribution, Greater Yellowstone Ecosystem, howling survey, noninvasive survey, snow-tracking, wolves, Wyoming.

Introduction

Employing multiple survey methods to monitor elusive, rare, or widely dispersing carnivores can reduce monitoring costs and increase precision or spatial coverage, though each method has different strengths and weaknesses in terms of data quality, logistical

difficulty, expense, and potential biases (Campbell et al. 2008). Noninvasive survey methods are attractive because they do not require animal capture, and many do not require a human presence (Long et al. 2008). They also can be used to apply consistent methodology among surveys and efficiently increase the number of surveys conducted in remote locations (Long et al. 2008). For example, genetic survey methods based on hair collection have been effective for grizzly bears (*Ursus arctos horribilis*; Kendall et al. 2008), and camera-trapping has been effective for tigers (*Panthera tigris*) and leopards (*P. pardus*; Karanth et al. 1998). Currently, radiotelemetry and a variety of noninvasive methods, including an automated acoustic survey device (hereafter, referred to as ‘howlbox’), are being used to monitor wolves (*Canis lupus*) in the Northern Rocky Mountain region of the United States (Ausband et al. 2009, Holyan et al. 2011).

Howlboxes are self-contained devices that broadcast a simulated wolf howl and record howls made in response. To date, the howlbox has successfully identified wolf packs at rendezvous sites in Idaho, USA (Ausband et al. 2009, Ausband et al. 2011), a context in which wolf movements are constrained while adults care for pups. To our knowledge, howlbox performance has not been tested during the wintertime when wolves are more mobile.

Following wolf reintroduction into Yellowstone National Park and central Idaho in 1995 and 1996, monitoring wolf recovery has relied heavily on radiocollaring ≥ 1 pack member and tracking locations of those individuals to estimate pack size and reproduction 2–4 times/month (USFWS et al. 2011). As the wolf population grew and expanded, however, the proportion of known packs that were collared declined from 77%

to 41%, and radiotelemetry became less effective at producing accurate total counts (USFWS et al. 2011). The logistical and financial challenges of radiocollaring new wolf packs are due, in part, to the expanding wolf population and the remoteness of wolf habitat (which includes much of the National Forests and Parks of central and northern ID, western MT, and northwestern WY, USA), except in Yellowstone National Park, where wolf packs and their home ranges are studied extensively (Figure 5.1).

Furthermore, it can be difficult to identify new wolf packs that contain few individuals or that move into new territory (e.g., OR and WA). Therefore, it is important to explore other methods of detecting wolves in remote terrain, and to test their feasibility and accuracy under a variety of settings and seasons. Our objective was to test the howlbox's ability to detect wolf presence during winter and to determine the factors associated with howlboxes that successfully record wolf howls.

Methods

Study Area

We tested howlboxes in a western Wyoming region used by an estimated 7 wolf packs, with a density of approximately 3 wolves/100 km² (USFWS et al. 2011). The study area covered approximately 2,100 km², extending northwest, west, and southwest of Cody, Wyoming, along the valleys and foothills of the Absaroka Mountains (Figure 5.1). Valley bottoms and foothills to the east were composed of private, Bureau of Land Management, and state-managed lands. Mountain foothills to the west were in the Shoshone National Forest. Dominant vegetation included closed conifer forests (*Pinus*

spp., *Picea* spp., *Abies lasiocarpa*), willow (*Salix* spp.), aspen (*Populus tremuloides*), grass–forb–herb meadows, shrubs (*Artemisia* spp., *Amelanchier alnifolia*), and irrigated hay fields. From January through May 2011, snow depth ranged from 0 cm to 54 cm and temperature ranged from -32° to 16° C (Natural Resources Conservation Service’s Snow Telemetry [SNOTEL] site no. 875; <http://www.wcc.nrcs.usda.gov/snotel/Wyoming/wyoming.html>; accessed 1 Jun 2011).

Howlbox and Sampling Design

We used previously described hardware and software to construct and operate 8 howlboxes (Ausband et al. 2011). The hardware is primarily composed of a netbook computer, microphone, and speaker, but we included a weather-tight plastic case and a 17-inch-high (43.2-cm-high) brace fixed on top of the case to lift the speaker and microphone above deep snow. We also tested 2 modified howlboxes that included a 12-V deep-cycle marine battery, a Pro-400W 400-Watt Power Inverter (Whistler, Bentonville, AK), a Home PCA2 Mini 2×40 -Watt Stereo Power Amplifier (Pyle Audio, Brooklyn, NY), and 2 PHSP4 6-inch Indoor/Outdoor 50-Watt PA Horn Speakers (Pyle Audio). The goal of the modified howlbox was to power 2 speakers, in order to broadcast more effectively in all directions for situations when the location of responding wolves could not be anticipated (Ausband et al. 2011). We used any successfully run broadcasts and recordings from both howlbox designs in the results.

We identified 8 sites where wolves were frequently observed (S. Becker, United States Fish and Wildlife Service, personal communication) to test howlboxes in areas with a relatively high probability of use by wolves. We also tested howlboxes at 30

randomly located sites that fit the following criteria: 1) could be accessed within 2 hours on foot, 2) located on non-wilderness public land, 3) >1.5 km from human-occupied private land (low end of the howlbox's max. broadcast range; Ausband et al. 2011), and, 4) within 2.4 km of an open road, closed road, or U.S. Forest Service trail. We used 2.4 km as the cutoff because the howlbox microphone's maximum distance for detecting human-simulated howls is 2.4 km (Ausband et al. 2011). We used sites near to, but not on, roads and trails because wolves have been shown to use linear corridors (James and Stuart-Smith 2000), but we also wanted to avoid human disturbance to howlbox devices.

Each howlbox deployment consisted of 1 survey/night (beginning at 1930 hr or 2000 hr) for 3 nights (Harrington and Mech 1982), except where there were electronic failures. We also included 1 survey/morning (beginning at 0530 hr or 0600 hr) for 3 mornings, but we eliminated morning surveys after February to prevent howlbox failures due to power loss. Each survey included 3 successive 48-second broadcasts of alternating flat and breaking howls and 90-second recordings (Harrington and Mech 1982). Though human-simulated howls have been shown to elicit more replies than recorded wolf howls (Theberge and Falls 1967) and have been used in previous howlbox tests (Ausband et al. 2011), we used a recorded lone wolf howl in a subset of deployments ($n = 20$) to assess effects of call type on reply rate. We used human-simulated howls for a majority of the deployments ($n = 165$; Ausband et al. 2011).

We tested howlboxes between 4 January and 19 May 2011, spaced deployments with overlapping dates ≥ 1.5 km apart, and staggered survey times by 30 minutes. At each site, we recorded percent snow cover, cover type (i.e., open or forested), and basic terrain

(i.e., flat or hilly). Wind speeds >12 km/hour can affect wolf reply rates to howling surveys (Harrington and Mech 1982); therefore, we recorded the wind speed (km/hr) for each deployment date and time from the nearest weather station (Figure 5.1). We compared these wind speeds with wind speeds recorded at 4 other weather stations to determine whether wind speeds in our study area were typical of the Northern Rocky Mountain wolf recovery area (<http://mesowest.utah.edu/index.html>).

Wolf Detection

We reviewed all howlbox recordings in RavenLite 1.0 software (Cornell Lab of Ornithology, Ithaca, NY; Ausband et al. 2011). We listened to raw and amplified recordings while simultaneously watching a display of the sonogram. Wolf howls were differentiated from coyote howls by their lower frequency and their longer call duration (D. E. Ausband, personal communication). We determined the ability of howlboxes to detect wolf presence as the percentage of surveys that recorded wolf replies, and we calculated exact 95% binomial confidence intervals (CI) using R (R Development Core Team 2011).

We tested whether howlboxes might attract wolves even when no howls were recorded by conducting track surveys near active howlboxes and inactive howlboxes (i.e., a howlbox with all electronics turned off). We examined inactive howlboxes to determine whether wolf attraction was due to the howlbox broadcast or human presence and equipment. We deployed inactive howlboxes for 3 nights during April and May at 11 randomly located sites following the same criteria as active howlbox site selection. Six of these sites were previously used by active howlboxes. We calculated the percentage of

inactive or active howlboxes with ≥ 1 set of wolf tracks within 50 m of the device and calculated exact 95% binomial CI.

We compared the howlbox results with the track surveys near active howlbox results by month (i.e., percentage of surveys in a month that detected a wolf by howl or track) to identify times when howlboxes were more successful at detecting wolves. Finally, we identified occasions when 3 wolves that were radiocollared with Global Positioning System (GPS) units (collared for other research purposes) were within 2.4 km of a howlbox during operation. The 2.4-km cutoff is the howlbox's maximum detection distance, as discussed previously.

Results

The howlbox experienced 2 complete failures (i.e., no broadcasts or recordings occurred) and 3 partial failures (i.e., a subset of broadcasts and recordings ran successfully), whereas the modified howlbox experienced 5 complete and 6 partial failures due to inverter errors (e.g., cracked wires or over-heating). We used the modified howlbox only between 4 January and 18 February for 63 successful surveys and pooled the results with the other howlbox surveys.

We performed 54 howlbox deployments at 38 unique sites, with a total of 20 morning surveys and 165 evening surveys. Sixty percent of the deployments were in an area where 3 wolf packs' territories overlapped or closely bordered one another (USFWS et al. 2011). Nineteen of the sites were in forested habitat, 19 were in open habitat, and 17 of the latter were on relatively flat terrain having good sound propagation. Wind speeds

during howlbox operation ranged from 0 km/hour to 52 km/hour ($\bar{x}$ = 17 km/hr) and monthly median wind speeds were often greater in the study area than at other locations around the Northern Rocky Mountains (Appendix D, Figure D1). However, 30% of the howlbox surveys occurred during wind speeds of <12 km/hour.

We received only 3 wolf replies. Two were recorded during the same survey on 25 January; one followed the first broadcast (2000 hr) and the other followed the third broadcast (2005 hr). Because these replies were recorded during the same survey, we view this as a single occurrence. The third reply followed the third broadcast (1935 hr) on 11 February. The percentage of surveys that recorded wolf replies was 1.1% (n = 185, 95% CI = 0.1–3.8%). The recorded replies occurred on the first night of deployment by the modified howlbox, following a human-simulated howl, at bench habitat sites with a wide view-scape. The wind speed was 0 km/hour and 17 km/hour during the first 2 replies and the third reply, respectively.

We recorded wolf tracks near 14.8% (n = 54, 95% CI = 6.6–27.1%) of the active howlboxes and near 9.1% (n = 11, 95% CI = 0.2–41.3%) of the inactive howlboxes. The percent of active howlboxes with wolf tracks within 50 m varied by month, but the majority of tracks were detected during January through March (Figure 5.2). There were 7 occasions when a radiocollared wolf was within 2.4 km of an operating howlbox and 8 occasions where a wolf was within 2.4 km of a howlbox within 1 hour after its operation. Of these 15 occasions, 11 were when wind speeds were <12 km/hour, 9 were in open habitat, and zero wolf replies were recorded.

Discussion

Combining multiple survey methods, including automated tools such as the howlbox, could make monitoring expanding carnivore populations more feasible. For monitoring wolves in the Northern Rocky Mountains, the howlbox is one of several noninvasive survey tools being applied in remote terrain (Ausband et al. 2010, Ausband et al. 2011). Our assessment of howlboxes during winter in a region with approximately 3 wolves/100 km² produced few wolf responses, with a roughly 1% successful recording rate. Though we did record wolf tracks near howlboxes about 15% of the time, we did not show strong evidence that the howlbox was an auditory attractant, rather than an olfactory (i.e., due to human scent around howlboxes) or visual attractant (i.e., due to howlbox equipment). However, in our study area, humans trapped wolves for research or lethally removed wolves for management (USFWS 2011). Therefore, it is not likely that wolves are habituated to humans, and the human scent should be more likely to cause wolves to retreat than approach (Karlsson et al. 2007). It is also not likely that the howlbox was a visual attractant, because visual cues may be less important than auditory or olfactory cues in forested environments (Harrington and Asa 2003), and half of the active howlboxes with wolf tracks occurred in forests. Moreover, to our knowledge there is no documented evidence that wolves are attracted to human equipment in the absence of an olfactory attractant.

Regardless of how wolves are drawn to the howlbox, if it is an attractant, howlboxes might be used after new snowfall to aid snow-tracking of wolves. Howlboxes could also be useful when combined with camera traps and scent lures, to increase the

probability of attracting wolves to a camera station. Camera traps can be important for studies of disease (e.g., mange) in wolves or studies of wolf presence–absence during times of the year when snow-tracking is not possible (Galaverni et al. 2012).

There are seasonal considerations for using howlboxes to document wolf presence. A howling survey conducted in northeastern Minnesota, USA, found that reply rates were greatest in mid-summer to early autumn, but that winter and spring reply rates peaked in March during the breeding season nearly to summer levels (Harrington and Mech 1982). Another survey conducted in northern Italy found similar broad seasonal differences without a peak during the breeding season (Gazzola et al. 2002). Although there were too few wolf replies in our study to determine any pattern, our detection of wolf tracks near active howlboxes declined from a high in January–March, to a few in April, and to none in May (Figure 5.2). However, 4 of the 10 active howlbox sites visited in May were snow-free, so diminishing snow levels in late spring may have contributed to the decline in track detection at that time.

Greater mid-summer reply rates to howling surveys correspond with seasonal aggregation of wolves at homesites for pup-rearing and may reflect a high rate of response by pups (Harrington and Mech 1978, 1982; Gazzola et al. 2002). Moreover, an adult may be more likely to respond when pups are present compared with times when the same adult is alone (Harrington and Mech 1979). Because focusing surveys on seasonal aggregations could increase monitoring efficiency, the first test of howlboxes occurred during the summer at homesites with known adult wolf and pup presence (Ausband et al. 2009). That study tested howlboxes at 15 active rendezvous sites of 9 wolf

packs in Idaho and produced responses 25% and 75% of the time for howlboxes used at distances of 1.0 km and 0.5 km, respectively (Ausband et al. 2009).

During the autumn and winter, wolves can be highly mobile within a territory and their locations can be unpredictable (Harrington and Mech 1978). Despite this unpredictability, we showed that wolves were within audible range on ≥ 15 occasions. Additionally, we found that wolves approached howlboxes much more often than they howled in response, which suggests that it may be advantageous for wolves in our study area and time-frame to remain quiet, and sometimes to investigate a howlbox broadcast. The territory boundaries of 3 wolf packs overlapped where we deployed a majority of the howlboxes, and the number of wolves among these packs totaled 24 (USFWS et al. 2011). One of these packs was new to the area and the other packs' territory boundaries have shifted since its arrival (USFWS et al. 2011). Because inter-pack conflict can occur as wolf numbers increase and territory boundaries change (Smith and Bangs 2009), wolves in our study area may not have responded to howlboxes in order to avoid or engage in aggressive encounters (Harrington and Mech 1979).

Management Implications

Howlboxes may not be effective tools for detecting wolves by recording howls during the winter, in areas where pack territories overlap. For detecting new wolf packs in remote areas of the Northern Rocky Mountains, howlboxes may be useful during the summer at habitats typical of rendezvous sites (Ausband et al. 2010) or if used to attract wolves after new snowfall to aid in snow-tracking. In areas where wolves are already

known to be present through direct observation or GPS radiocollars, however, howlboxes may not meaningfully extend our ability to survey wolf distribution and pack sizes.

Acknowledgments

We thank M. Jimenez and S. Becker with the U.S. Fish and Wildlife Service for reviewing the manuscript, providing information on wolf locations, and help identifying sites to test howlboxes. We thank A. Middleton of the Wyoming Cooperative Fish and Wildlife Research Unit for providing wolf GPS radiocollar data. We also thank S. Brennan for building the modified howlboxes and A. Roosa for help with their deployment. Finally, we thank 2 anonymous reviewers for their time and suggestions. This work was supported by the National Science Foundation and National Institutes of Health Ecology of Infectious Disease (grant no. DEB-1067129) and the U.S. Geological Survey. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

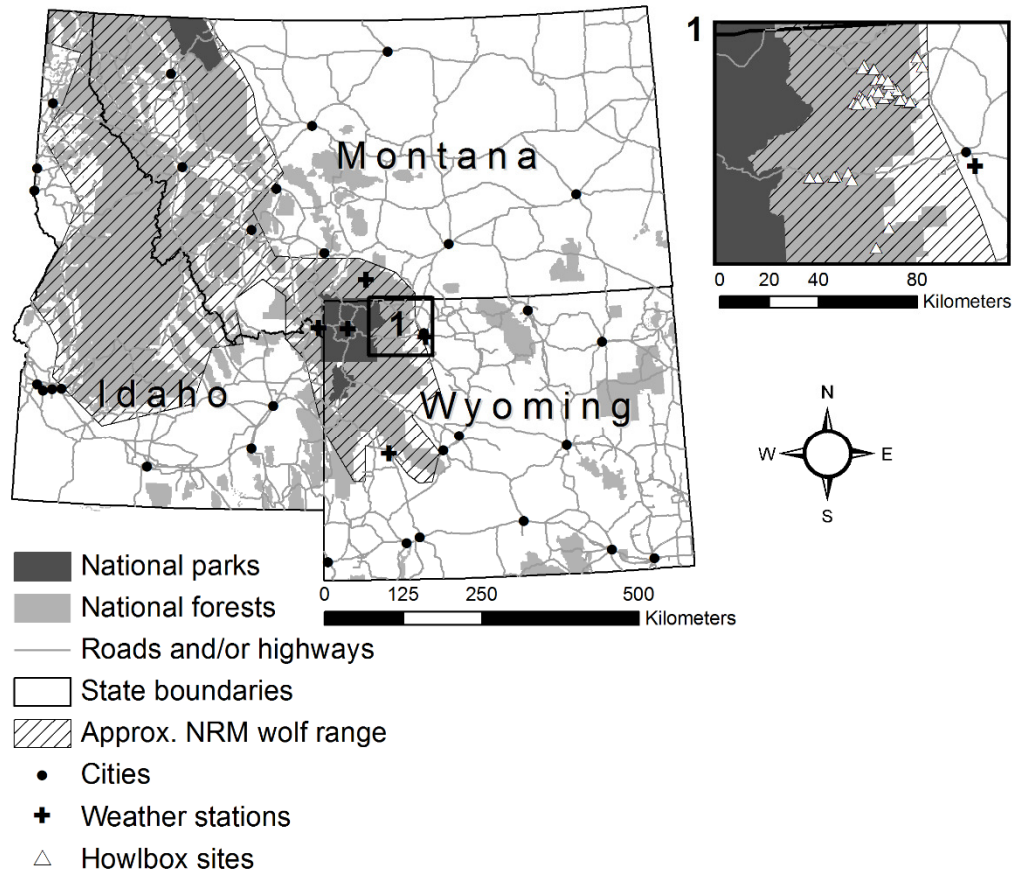


Figure 5.1. Map of approximate Northern Rocky Mountain wolf range in Montana, Idaho, and Wyoming, USA (based on wolf pack min. convex polygons or point locations shown in USFWS et al. [2011]), the study area (labeled 1 on large and close-up maps), howlbox sites (white triangle), and weather stations (black cross) where we compared wind speeds. Dates of data collection were from 4 January through 19 May 2011. Wolf range in Oregon and Washington is excluded.

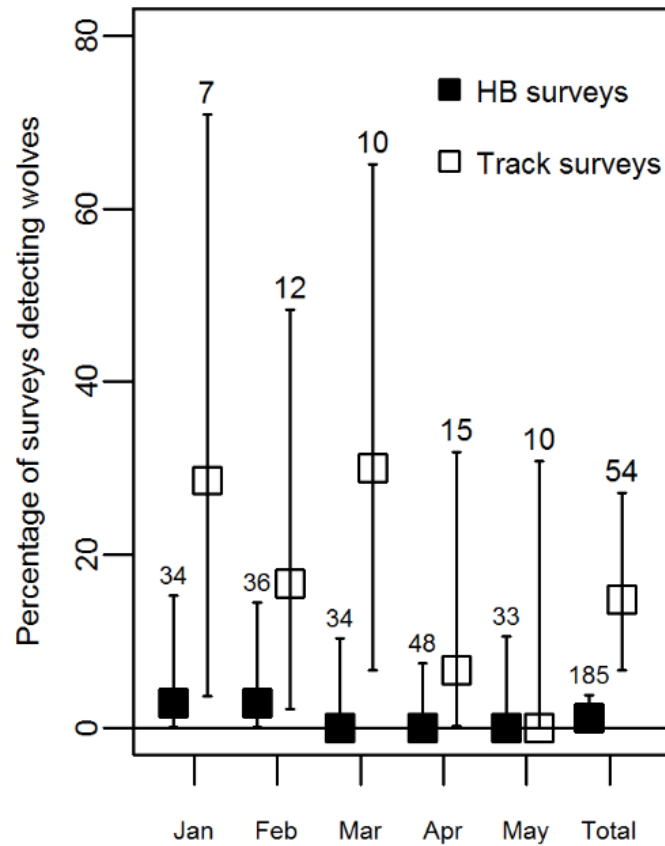


Figure 5.2. Monthly comparison of the percentage of howlbox surveys (HB surveys) in the Northern Rocky Mountain wolf range in Montana, Idaho, and Wyoming, USA, that recorded wolf howls and the percentage of track surveys near active howlboxes that detected ≥ 1 set of wolf tracks within 50 m (Tracks surveys). Dates of data collection were from 4 January through 19 May 2011. Error bars are exact 95% binomial confidence intervals. Above each upper error bar is the number of howlbox surveys and track surveys conducted each month and overall.

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CHAPTER SIX

CONCLUSION TO DISSERTATION

Overall Conclusions

Wildlife conservation and management issues will continue to occur where natural systems and human settlements overlap, and in these areas studies of disease may be particularly important because of the potential for transmission to livestock or from livestock to threatened and endangered wild populations (Gortázar et al. 2007). Our ability to understand disease dynamics in wildlife and to develop effective disease control strategies relies on our understanding of the relationship between host density and parasite transmission (Hudson et al. 2001), but this relationship is not well-studied for social species whose aggregation patterns vary across space and time. We studied this issue in Chapter Two by focusing on several elk populations in the Greater Yellowstone Area (GYA), where previous research suggests brucellosis is increasing and where the risk of transmission to cattle is high.

For this study, we examined elk aggregation patterns and increasing brucellosis and found that most reasonable measures of density and group size had similar utility in predicting brucellosis increases, suggesting the spread of *Brucella* may be driven by both within- and between-group transmission. These findings indicate that any one disease control strategy, aimed at either reducing population density or reducing the largest group sizes, may not effectively reduce transmission. This is important information for brucellosis management, but also for other studies assuming that transmission will be

better explained by group size than by population density (or vice versa). As many avian and mammalian species also have complex aggregation patterns, considering the multiple spatial and temporal scales in which animals aggregate could improve our understanding of complicated transmission dynamics.

Though grouping behavior and the occurrence of large animal groups, in particular, may certainly affect the spread of diseases (Altizer et al. 2003), large groups may also have disproportionate effects on other aspects of ecology or policy along the wildlife/livestock interface (e.g., Haggerty and Travis 2006, Stafford et al. 1991). In these contexts, understanding the relationships of environmental variables to the upper quantiles of the group size distribution may be more important for management and conservation than studies of mean or median group sizes. This distinction is particularly important when group size distributions are right skewed and span several orders of magnitude. In Chapter Three, we studied elk aggregation patterns for three years across the GYA, where issues regarding disease transmission, predator-prey relationships, and impacts to private property were particularly important.

We highlight the use of quantile regression models to examine variables related to upper quantiles of the group size distribution (Cade and Noon 2003), but we also discuss the importance of taking a more complete look at the group size distribution when it is not known *a priori* what quantiles are important. We found that groups were larger on irrigated land, and suggest examining elk use of these areas throughout the year if there are potential effects on reproduction or migratory behavior. We also found that upper quantile group sizes increased as the habitat got more flat, more open, and less diverse in

vegetation, and as snow levels decreased and predation risk increased. This dynamic is likely to increase conflicts with private landowners, increase risk of interaction with cattle, and facilitate disease transmission. This study highlights the importance of focusing on more than one metric of the group size distribution to inform management and understand animal ecology.

Two conditions important to elk grouping behavior, as well as to their survival and reproduction are snow accumulation (*e.g.*, Proffitt et al. 2012, White et al. 2012b) and predation risk (*e.g.*, Gower 2008, Creel and Winnie 2005). Because this is also the case for other animals living in temperate climates (*e.g.*, Heard 1992, White et al. 2012a), it is increasingly common for studies of animal ecology to use model-based predictions of environmental variables (in the case of snow accumulation) as explanatory or predictor variables, even though model prediction uncertainty is typically unknown. In Chapter Four, we demonstrated the potential for misleading inferences when model predictions with error are used in place of direct measurements. To do this, we compared snow water equivalent (SWE) and snow depth as predicted by the Snow Data Assimilation System (SNODAS) to field measurements of SWE and snow depth collected across elk winter ranges in western Wyoming.

Overall, SNODAS predictions tended to overestimate field measurements, prediction uncertainty was high, and relying on SNODAS predictions rather than direct measurements could affect our inferences regarding snow effects on elk ecology. This study highlights the need to carefully evaluate the model's resolution relative to the scale of the ecological question of interest and the implications of prediction uncertainty on

inferences. It is important to remember that all models are approximations, and the scale at which predictions are generated should not be ignored. Model predictions may be useful as indices for some questions of interest, but misleading when used at fine scales when prediction uncertainty is high.

Lastly, we examined automated howling devices to measure wolf presence and absence on an elk winter range in western Wyoming where the territory boundaries of 3 wolf packs overlapped (USFWS et al. 2011). Devices of this type may be useful for conducting noninvasive surveys of wolves during the summer or near rendezvous sites (Ausband et al. 2010), but in our study howlboxes detected wolves in only 1% of our surveys. Because inter-pack conflict may have been an issue in our study area, wolves may not have responded to howlboxes in order to avoid or engage in aggressive encounters (Harrington and Mech 1979). Despite the lack of responses to howlboxes, we did record wolf tracks within 50 m of howlboxes nearly 15% of the time, suggesting the possibility that howlboxes may attract wolves. In this case, howlboxes could be used to aid in snow-tracking of wolves, but in areas where wolves are already known to be present through direct observation or GPS radiocollars, howlboxes may not improve our ability to survey for wolves.

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APPENDICES

APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER TWO

Bayesian Model Description:

The following is a description of the model we used for estimating the rate of increase in brucellosis seroprevalence, on the logit scale, and for estimating the linear relationship between measures of elk aggregation and the estimated rates of increase in brucellosis seroprevalence.

$Y_{ij} \sim \text{Bin}(p_{ij})$	Let Y_{ij} be the exposure status determined by serology for individual elk i in region j (either herd unit 1, 2, ..., 5 or hunt area 1, 2, ..., 10). We modeled Y_{ij} as a binomially distributed response variable, where p_{ij} was the probability of testing positive.
$\text{logit}(p_{ij}) = \alpha + \beta_j * \text{year}_{ij}$	We used a logit link to relate p_{ij} to year (rescaled so that 1991 was zero), and we allowed the slope (β) to vary by region j (herd unit or hunt area).
$\alpha \sim N(0, 0.0001)$	We estimated a common intercept term (not forced through zero, but not allowed to vary by region j). We assumed the intercept came from a normal distribution with mean of zero and precision of 0.0001.
$B_j \sim N(\mu_j, \tau)$	We assumed the region-specific slopes came from a normal distribution with a mean (μ) estimated from the linear model below, and a standard deviation (τ). In the text of this article, we referred to these herd unit or hunt area-specific slopes as rates of increase in brucellosis seroprevalence, which measure the log odds of testing seropositive for each one-year increase in time.
$\mu_j = \delta + \psi * \text{agg}_j$	We hypothesized that the rates of increase in brucellosis seroprevalence were linearly related to measures of aggregation (agg = herd unit density, hunt area density, winter range density, cumulative density, mean group size, Lloyd's crowding, or Lloyd's crowding in May).
$\sigma \sim \text{Uniform}(0, 20)$	We assumed the standard deviation was uniformly distributed from 0 to 20 on the prior distribution.
$\tau = 1/\sigma$	
$\delta \sim N(0, 0.0001)$	We assumed the intercept term came from a normal distribution with mean of zero and precision of 0.0001.
$\psi \sim N(0, 0.0001)$	We assumed the slope term came from a normal distribution with mean of zero and precision of 0.0001.

Table A1. Herd Unit (HU) densities. See Figure 2.1 for the geographical distribution of herd units.

Herd Unit	HU Density (elk/km ²)
217	0.5
216	1.3
214	0.6
635	0.6
637	0.4

Table A2. Six measures of elk aggregation for the 10 hunt areas of interest. HA = hunt area, WR = winter range. See Figure 2.1 for the geographical distribution of the hunt areas.

Hunt Area	HA Density (elk/km ²)	WR Density (elk/km ²)	Cumulative Density (elk/km ²)	Mean Group Size	Lloyd's Crowding	May Lloyd's Crowding
50	0.3	0.8	35.8	109	175	87
51	0.5	1.3	8.7	19	70	28
52	2.9	4.5	127.4	101	261	339
54	2.7	3.1	74.7	69	207	150
121	1.7	2.1	51.7	79	236	100
59	1.0	3.1	53.9	68	151	34
63	1.0	2.9	66.7	235	554	184
67	3.0	7.7	134.5	201	840	214
25	0.3	1.5	34.6	125	286	38
99	0.2	0.4	12.0	91	198	0

Table A3. Comparison of estimated deviance information criteria (DIC) for the relationships between aggregation and rates of increase in brucellosis seroprevalence (measuring the log odds of testing seropositive for each one-year increase in time). The full dataset includes all years and hunt areas (2765 serologic results across 21 years and 10 hunt areas), while the truncated dataset includes only the eight hunt areas with two or more years of seropositive test results and excludes early years in the time series where brucellosis seroprevalence was zero (2245 serologic results across a number of years that vary by hunt area). Δ DIC = difference from the lowest DIC value (calculated among models fit to the full dataset, and again among models fit to the truncated dataset). HU = herd unit, HA = hunt area.

Measure of Aggregation	Full Dataset		Truncated Dataset	
	DIC	Δ DIC	DIC	Δ DIC
HA Density	1130.2	0	1082.8	1
WR Density	1132.0	1.8	1082.8	1
Cumulative Density	1131.3	1.1	1081.8	0
Mean Group Size	1131.4	1.2	1082.3	0.5
Lloyd's Crowding	1130.9	0.7	1083.2	1.4
May Lloyd's Crowding	1131.4	1.2	1082.3	0.5

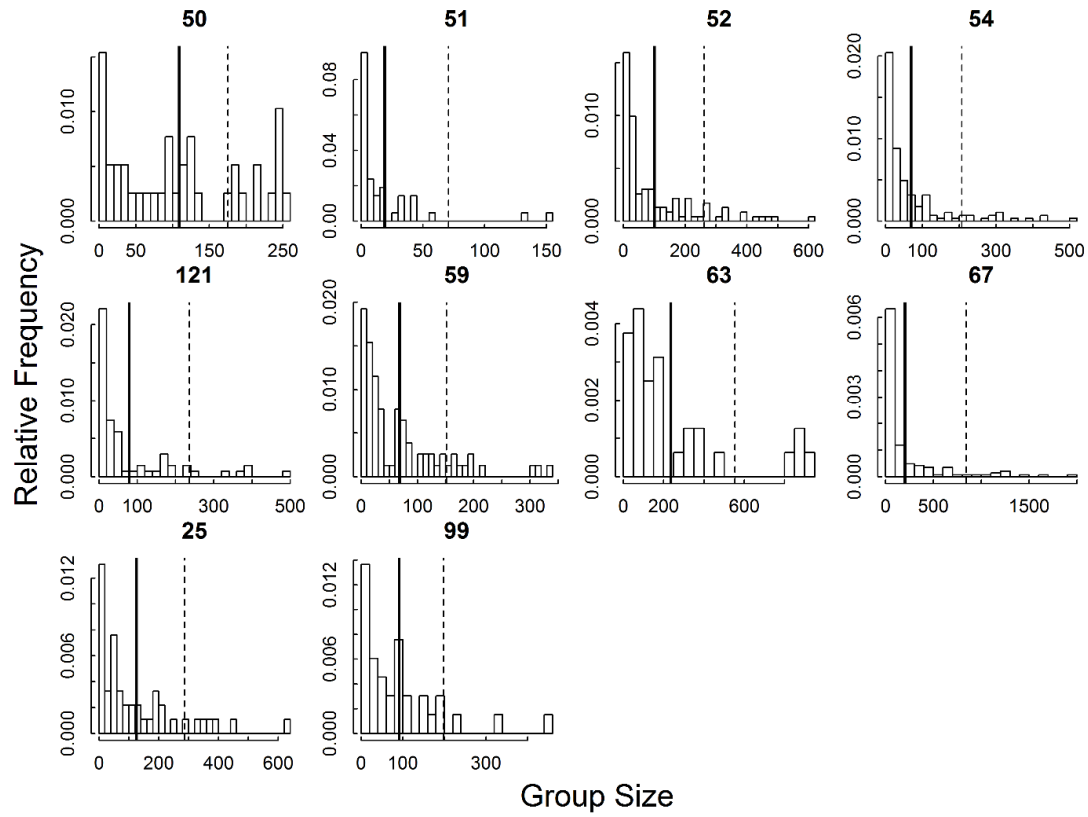


Figure A1. Elk group size distributions for the 10 hunt areas arranged from north (upper left) to south (lower middle). The distributions are plotted as relative frequencies, where each histogram has a total area equal to 1. Hunt area numbers are listed above each histogram (see Figure 2.1 for geographical distribution of hunt areas); solid black lines are mean group size and dotted lines are Lloyd's crowding.

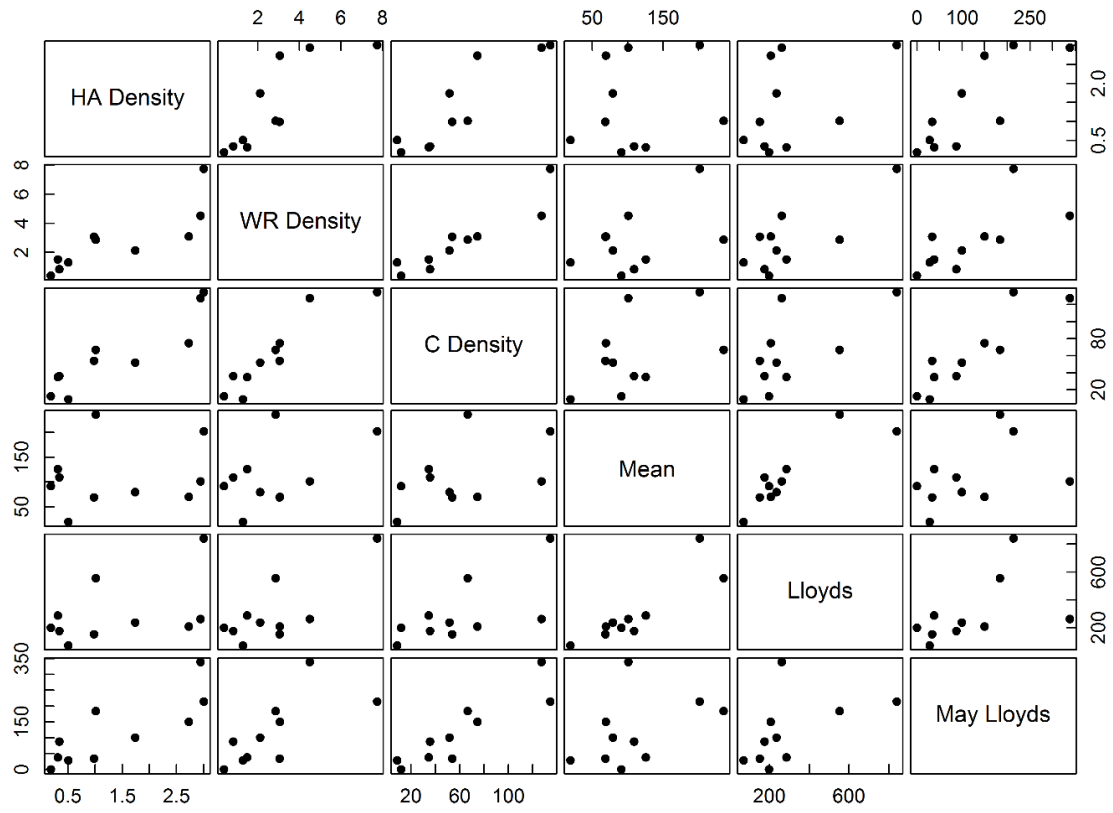


Figure A2. Scatterplot matrix of six elk aggregation measures. HA = hunt area density, WR = winter range density, C = cumulative density, Mean = mean group size, Lloyds = Lloyd's crowding, May Lloyds = Lloyd's crowding in May.

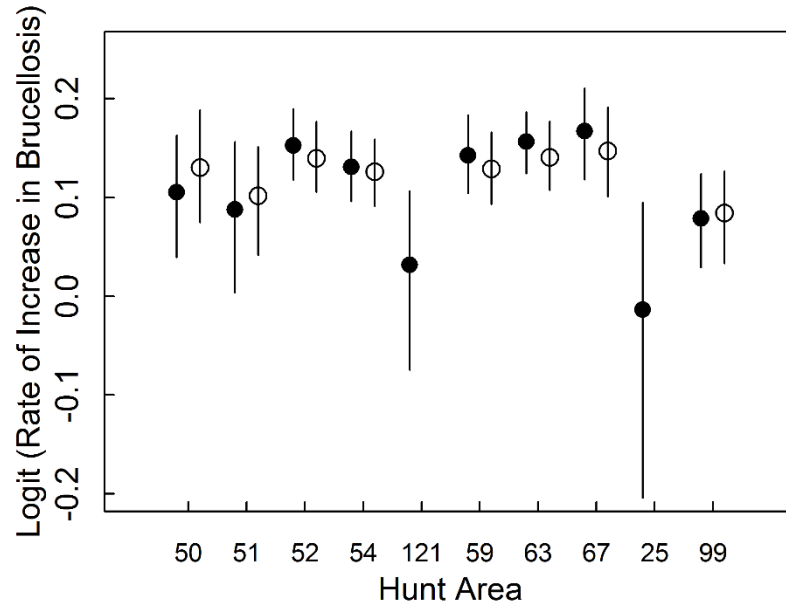


Figure A3. Comparison of the rates of increase in brucellosis seroprevalence (measuring the log odds of testing seropositive for each one-year increase in time) estimated by Bayesian hierarchical models. Closed symbols are posterior means of the rates of increase in brucellosis estimated from all 10 hunt areas and open symbols were estimated from the eight hunt areas where brucellosis was known to be present (which excluded initial years of zero seropositives, and excluded hunt areas 121 and 25). Bars are estimated 95% credible intervals.

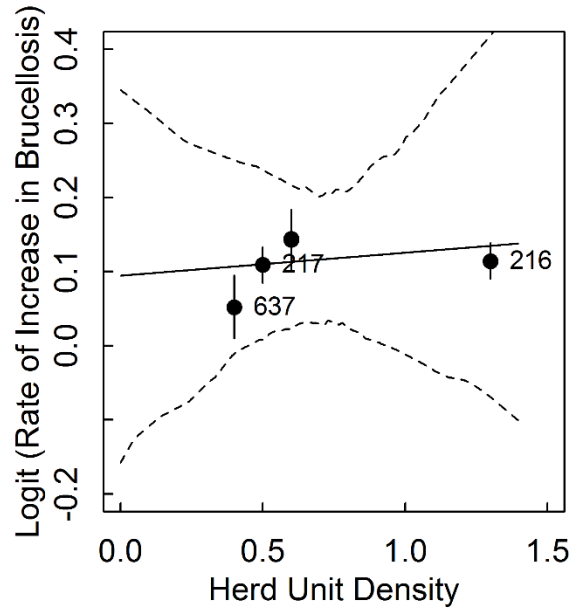


Figure A4. The linear relationship between herd unit density (broadest scale measure of density) and rates of increase in brucellosis seroprevalence (measuring the log odds of testing seropositive for each one-year increase in time), as estimated from a Bayesian hierarchical model. Points are labeled by several herd units for reference. See Figure 2.1 for the geographical distribution of herd units. Solid black line is the estimated relationship, and dotted line is the 95% credible intervals.

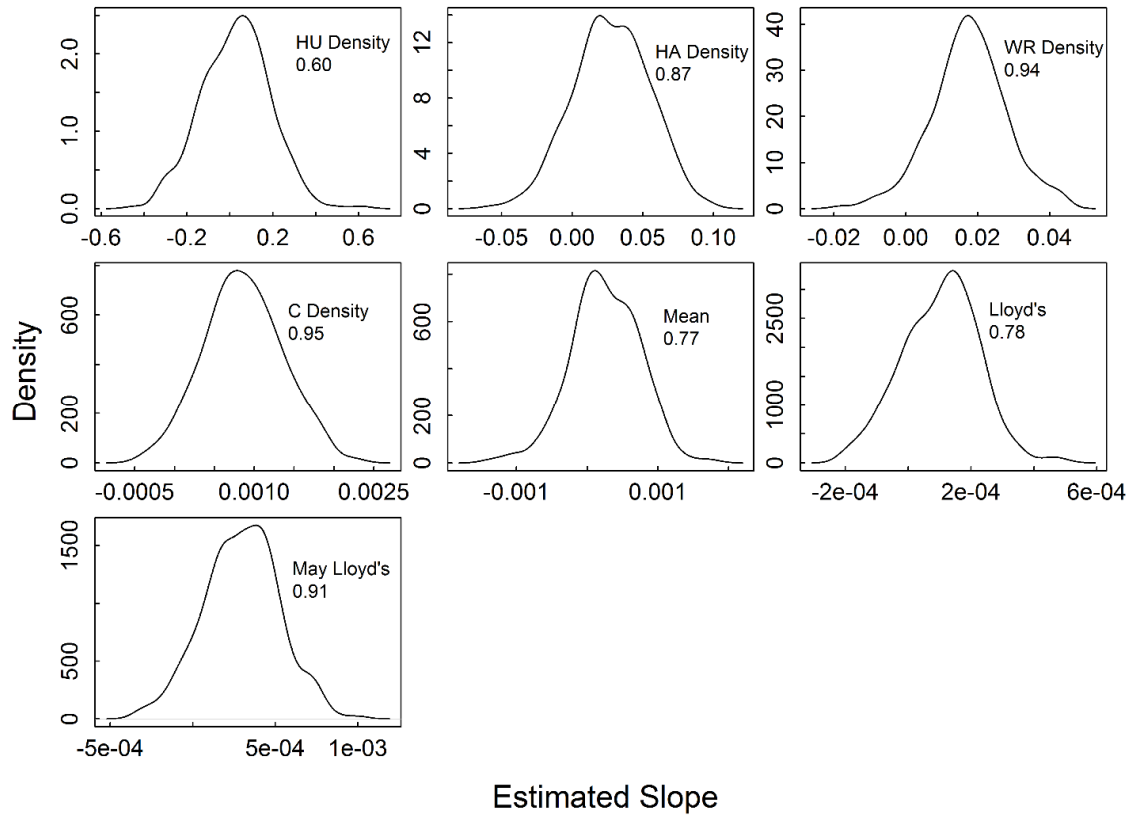


Figure A5. Posterior distributions of the slopes estimated for the relationship between aggregation and rates of increase in brucellosis seroprevalence (measuring the log odds of testing seropositive for each one-year increase in time). The upper left of each panel contains the aggregation measure and the probability that aggregation was positively related to rates of increase in brucellosis (where the estimated relationship greater than zero). HA = hunt area density, WR = winter range density, C = cumulative density, Mean = mean group size, Lloyds = Lloyd's crowding, May Lloyds = Lloyd's crowding in May.

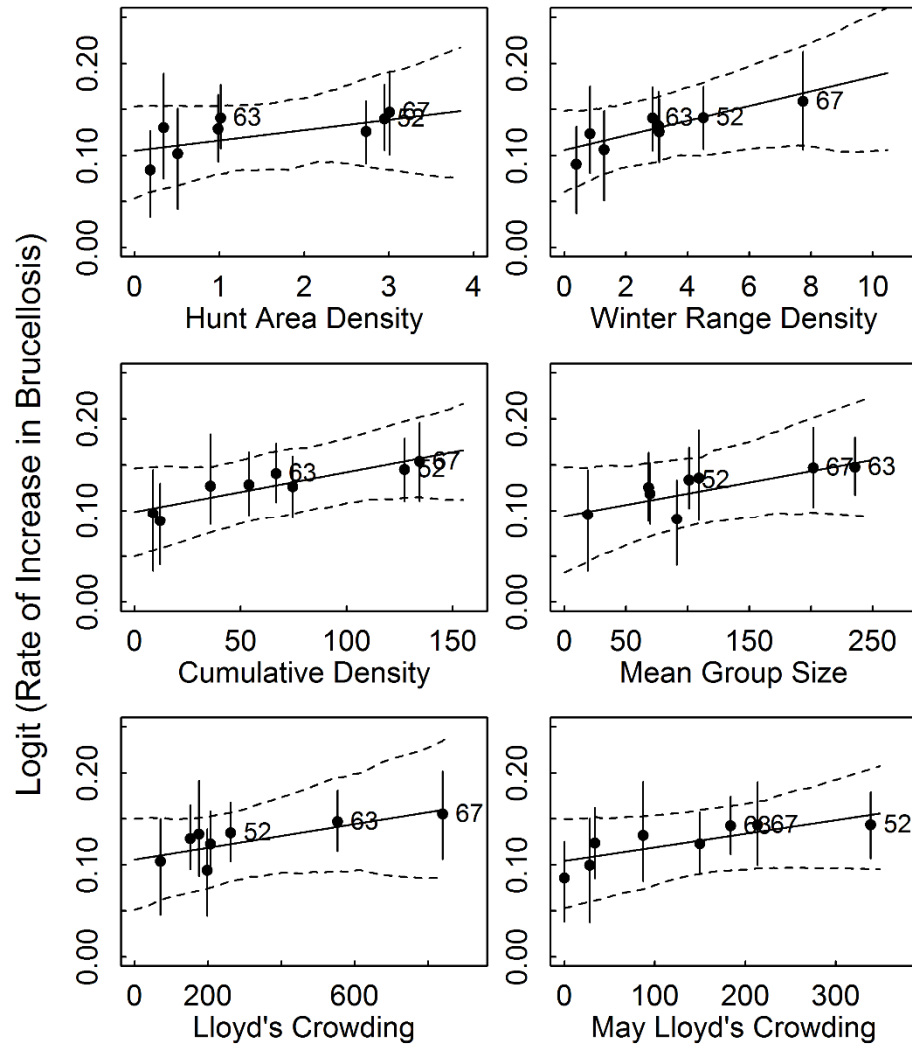


Figure A6. Shown are the linear relationships between elk aggregation and rates of increase in brucellosis seroprevalence (measuring the log odds of testing seropositive for each one-year increase in time), as estimated by Bayesian hierarchical models on the truncated dataset. This dataset included only the eight hunt areas with at least two years of seropositive test results and excluded early years in the time series when brucellosis seroprevalence was zero. Data labels are shown for three of the hunt areas for reference. See Figure 2.1 for geographic distribution of hunt areas. Solid black lines are the estimated relationship, and dotted lines display the 95% credible intervals.

APPENDIX B

SUPPORTING INFORMATION FOR CHAPTER THREE

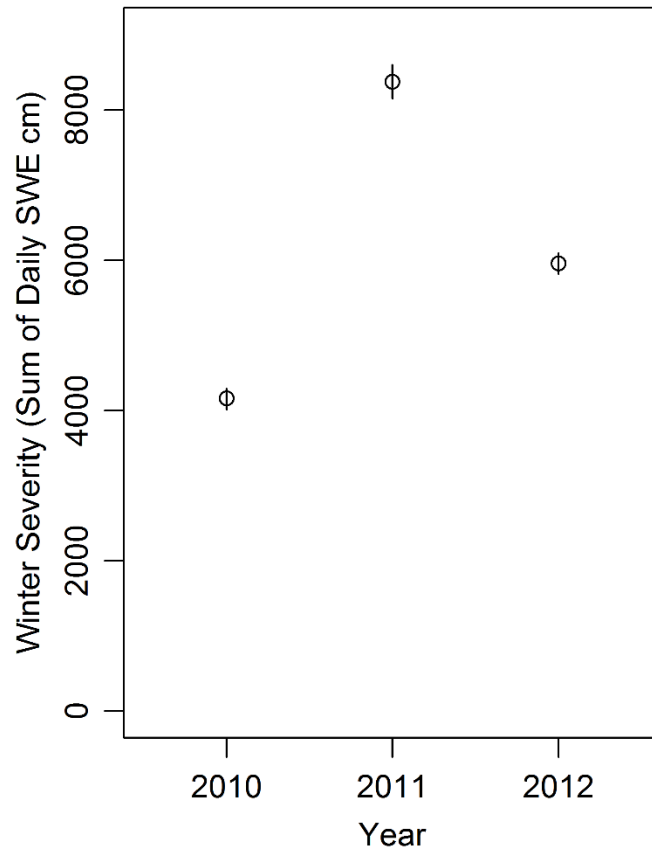


Figure B1. Annual winter severity: sum of daily snow water equivalents (SWE [cm]) recorded across the 10 SNOTEL stations nearest to the study area, from December 1 (of previous year) through June 30 (of year shown). Lines are 95% confidence intervals of the mean.

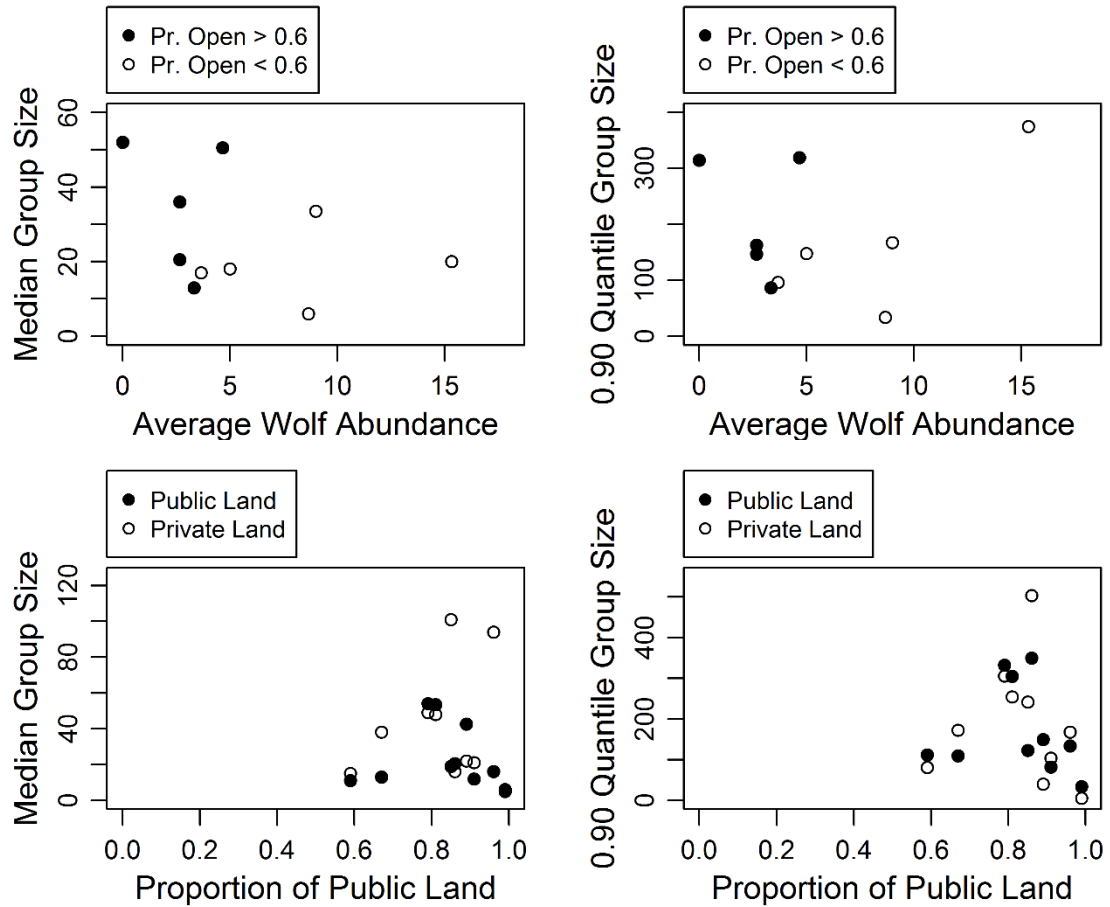


Figure B2. Interactions between average wolf abundance and proportion of open habitat available in a hunt area (Pr. Open; top row), and between proportion of public land available in a hunt area and the land use type a group was located on (public or private; bottom row). Y axes are empirical median or 0.90 quantile group sizes. Legends above each plot indicate how empirical group sizes are color-coded.

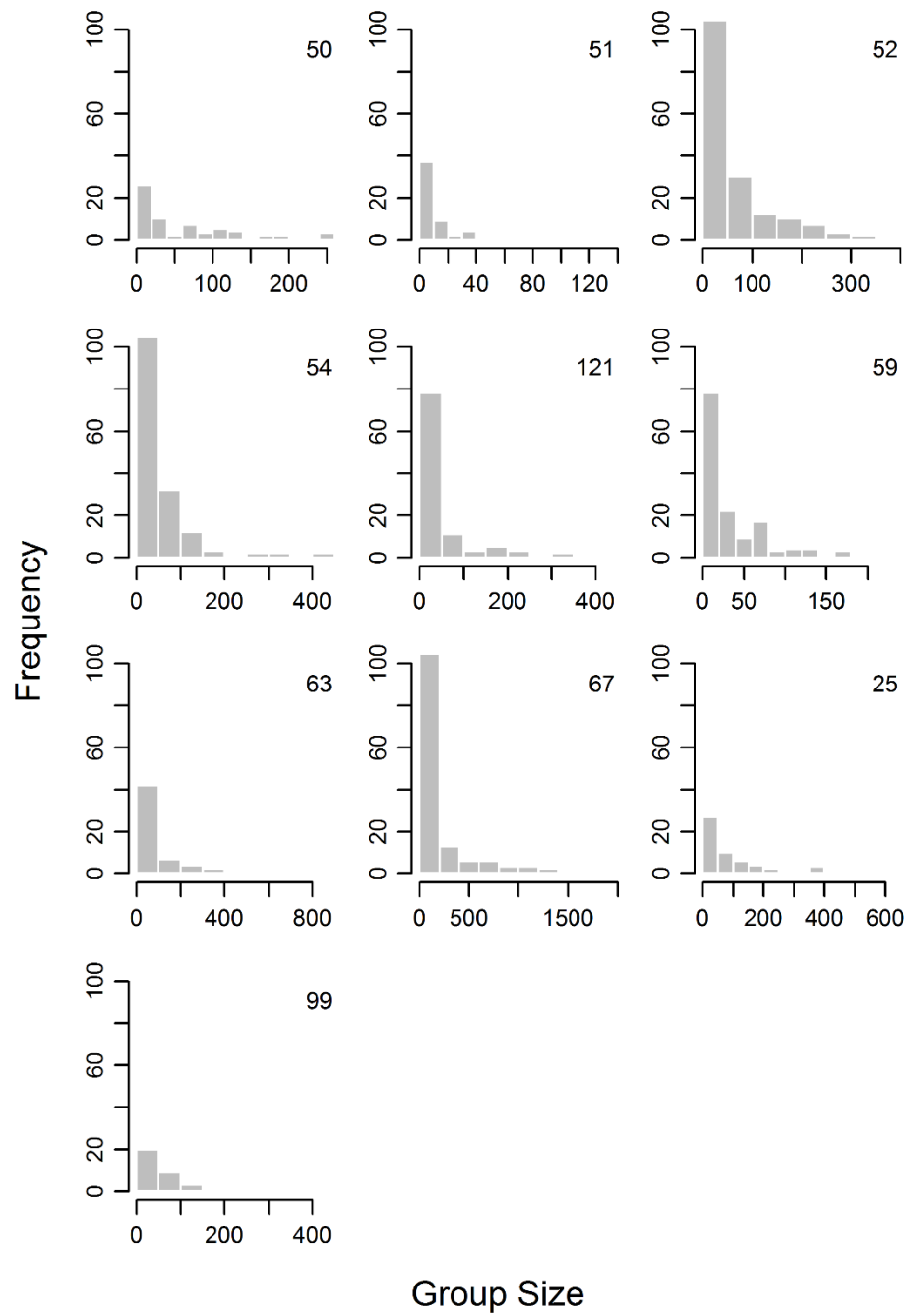


Figure B3. Frequency distributions of elk group sizes across the ten hunt areas. Hunt areas are shown in upper right of each plot.

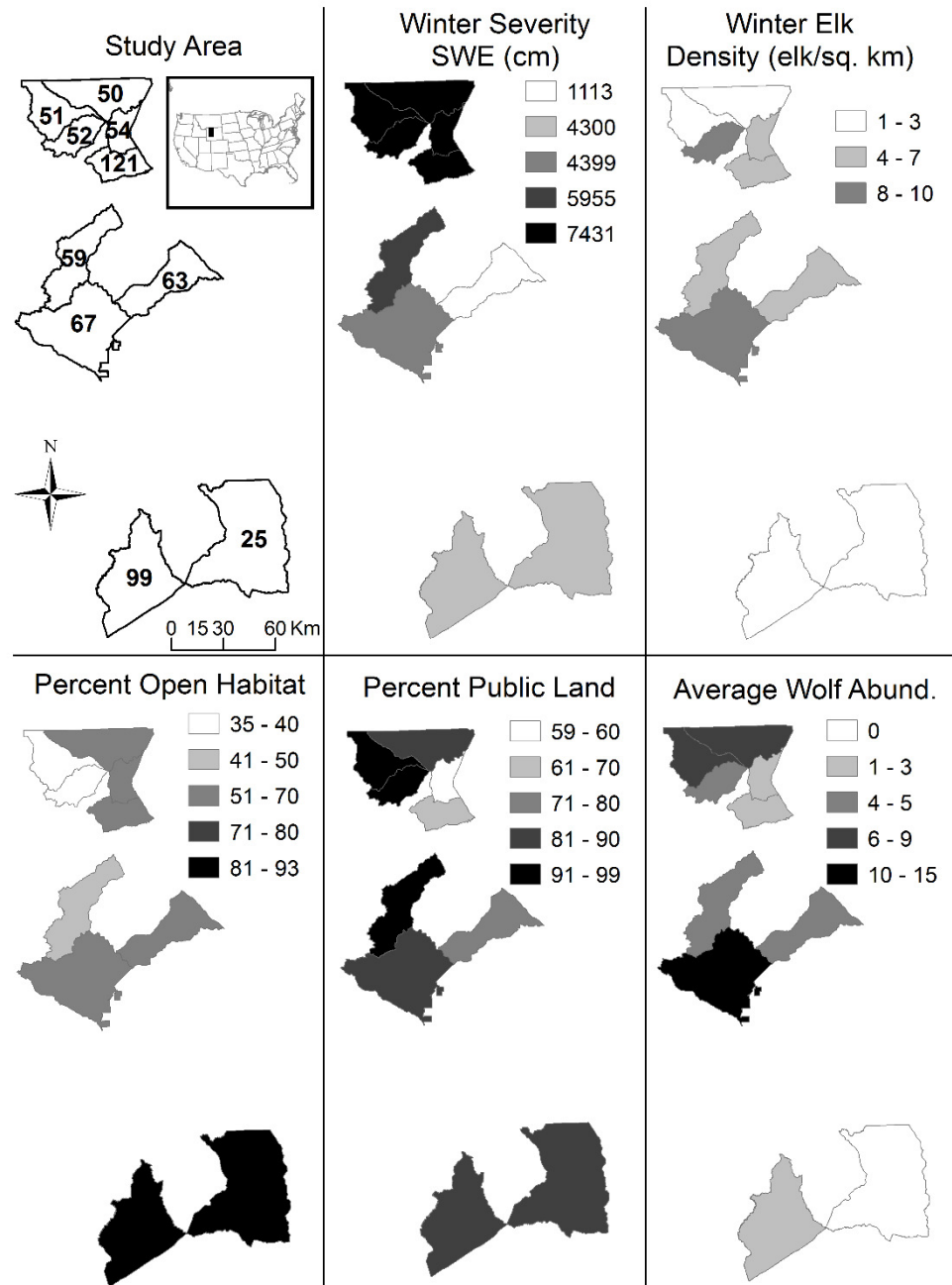


Figure B4. Hunt areas are shown in top left map, and five hunt area-scale explanatory variables are shown in remaining maps. Winter severity is the sum of snow water equivalents (SWE) recorded from Dec. through June, averaged across years (2010–2012). Winter elk density is the average of aerial survey elk density (total elk recorded in a hunt area divided by survey area, averaged across all 15 months of aerial surveys). Percent open habitat is the percent of the total hunt area that is open habitat, percent public land is the percent of the total hunt area that is public land, and average wolf abundance is the total number of wolves using a hunt area, averaged across years (2009 – 2011).

Table B1. Correlation matrix of explanatory variables used in the linear quantile mixed models. Estimated Pearson's correlation coefficients that are greater than 0.4 or less than -0.4 are in bold. Land refers to the categorical variable: public or private land; Irrigated refers to the categorical variable: irrigated or non-irrigated land; Road is the linear distance between the center of a group and nearest maintained road (m); Slope is the slope of the landscape (degrees) measured from the center of the group; Diversity is the number of land cover types within a 0.78-km² buffer around the center of each elk group; Open is the proportion of open habitat available within this buffer; Winter is the annual sum of snow water equivalents (from December through June); Density is the average winter elk density (elk/km²); Wolf is the average wolf abundance.

	Land	Irrigated	Road	Slope	Diversity	Open	Winter	Density	Wolf
Land	1.000	0.169	-0.124	-0.039	0.074	0.013	-0.054	-0.230	-0.326
Irrigated		1.000	-0.131	-0.120	0.165	-0.030	0.024	-0.082	-0.014
Road			1.000	0.082	-0.080	-0.075	-0.321	0.021	0.299
Slope				1.000	0.073	-0.215	0.124	0.092	-0.038
Diversity					1.000	-0.430	0.218	-0.012	-0.078
Open						1.000	-0.216	0.049	0.004
Winter							1.000	0.111	-0.208
Density								1.000	0.518
Wolf									1.000

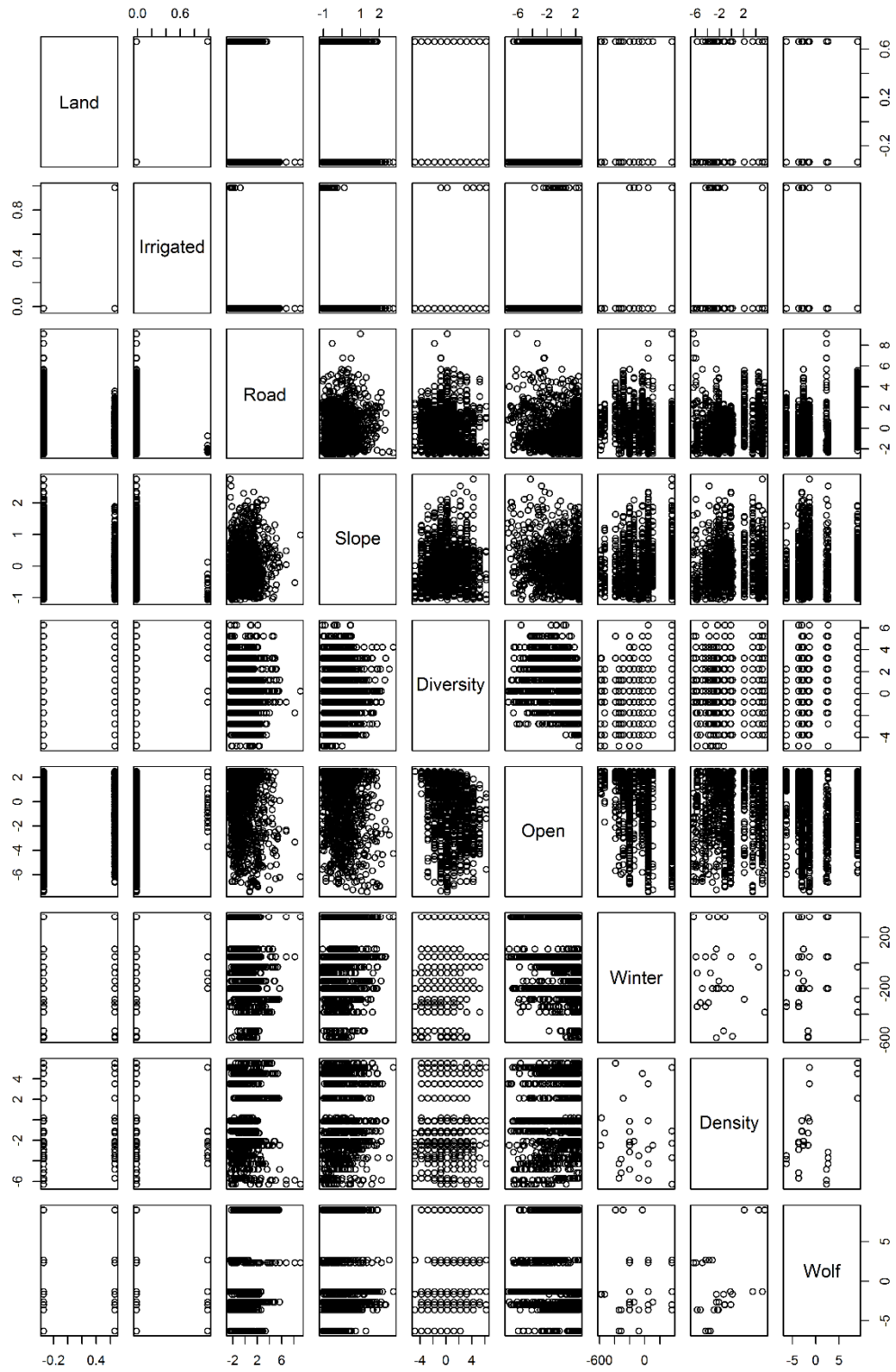


Figure B5. Scatterplot matrix of the explanatory variables used in the linear quantile mixed models, and as described in Table B1.

APPENDIX C

SUPPORTING INFORMATION FOR CHAPTER FOUR

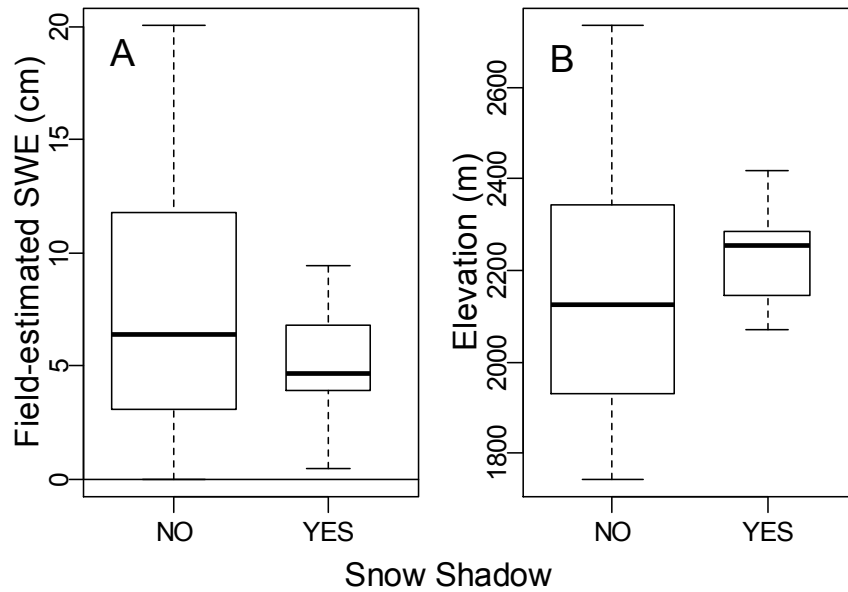


Figure C1. Comparison of A) field estimates of SWE (cm) in snow shadows (YES) to other regions (NO) and B) elevation (m) in snow shadows to other regions.

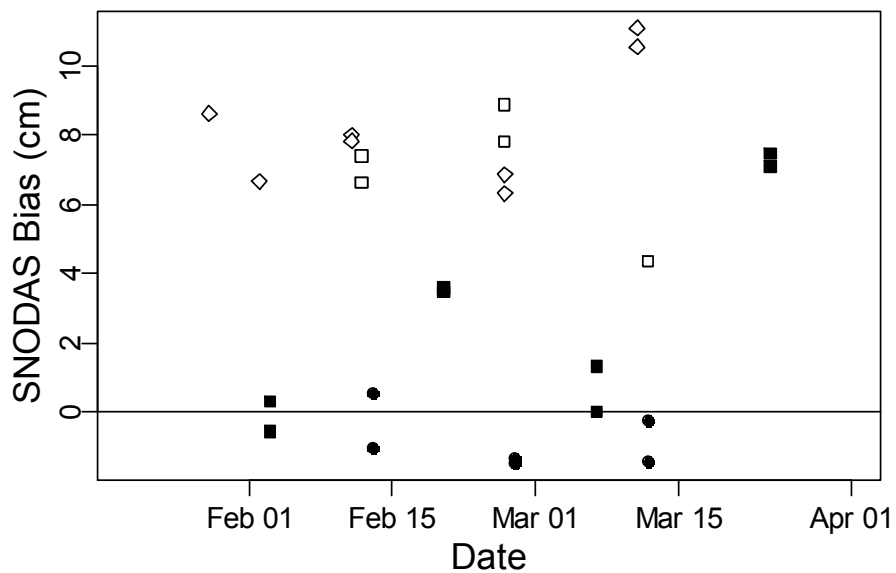


Figure C2. SNODAS bias (cm) for SWE at locations sampled repeatedly during the winter of 2010. SNODAS bias is the difference between SNODAS predictions and field estimates (transect means) of SWE. Symbols represent four different feedgrounds. Both square symbols are in region 3, the white diamond symbol is region 4 (a snow shadow region), and the black circle is region 5. See Figure 4.1 for location of regions.

APPENDIX D

SUPPORTING INFORMATION FOR CHAPTER FIVE

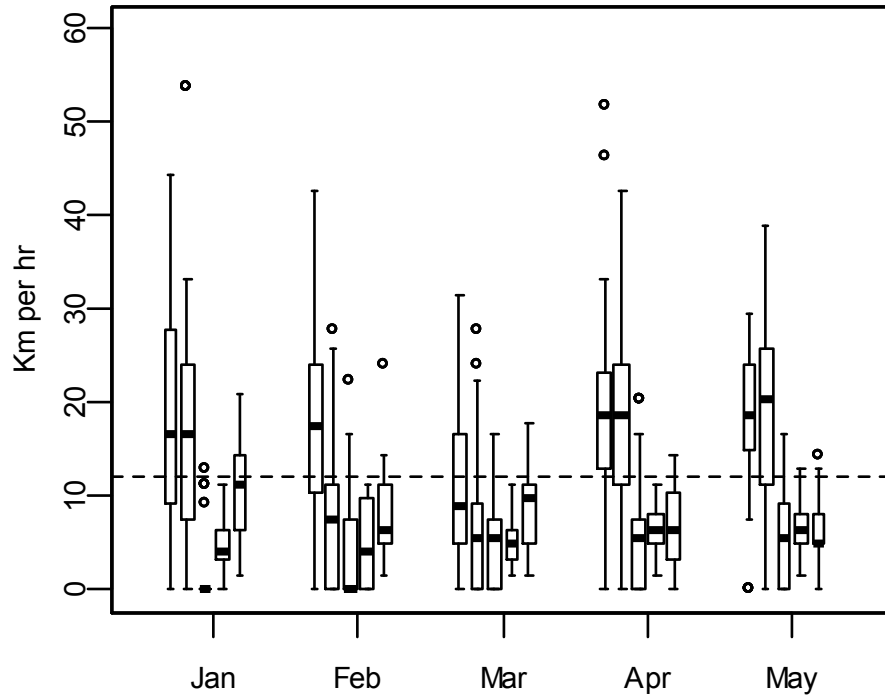


Figure D1. Boxplots of wind speeds (km/hr) recorded by five weather stations in or near the Northern Rocky Mountain wolf range in western Wyoming and southwestern Montana. From left to right the boxes correspond to weather stations near 1: Cody, Wyoming (nearest to study area), 2: Pinedale, Wyoming (southernmost station), 3: Yellowstone Lake (Yellowstone National Park), 4: Hebgen Lake (southwest Montana), and 5: Boulder River (north of Yellowstone National Park). Boxes identify quartiles and medians, whiskers are 1.5 times the interquartile range, and points outside of boxes identify minimum and maximum data points. The dotted line indicates 12 km/hr and winds exceeding this speed are thought to adversely affect howling surveys (Harrington and Mech 1982). Wind speeds were recorded on the dates and times that howlboxes were in operation.