

University of Alberta

Ecology and Management of White-tailed Deer (*Odocoileus virginianus*)
and Mule Deer (*O. hemionus*) of East-Central Alberta in Relation to
Chronic Wasting Disease

by

Thomas John Habib

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science

in

Ecology

Department of Biological Sciences

©Thomas John Habib

Fall 2010

Edmonton, Alberta

Permission is hereby granted to the University of Alberta Libraries to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only. Where the thesis is converted to, or otherwise made available in digital form, the University of Alberta will advise potential users of the thesis of these terms.

The author reserves all other publication and other rights in association with the copyright in the thesis and, except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatsoever without the author's prior written permission.

Examining Committee

Dr. Evelyn Merrill, Department of Biological Sciences

Dr. Robert Hudson, Department of Renewable Resources

Dr. Mark Lewis, Department of Mathematical and Statistical Sciences

ABSTRACT

Chronic wasting disease (CWD) is a fatal pathogen affecting white-tailed and mule deer in east-central Alberta, and I addressed two current limitations of CWD management. First, to improve precision and accuracy of density estimates obtained from aerial surveys, I evaluated alternative survey designs and developed a model to correct for undetected deer due to low snow cover, small group sizes, and deer inactivity. Surveys stratified by resource selection functions showed the greatest improvement in precision compared to currently employed designs. Second, I addressed how density and landscape features affect contact rates among deer, a major component of CWD transmission. Contact rates increased as a saturating function of density, and were highest in regions where deer habitat was limited. My results will allow managers to better plan and evaluate management actions such as herd reductions, and underscore the need for developing spatially-explicit models to understand CWD spread in heterogeneous environments.

ACKNOWLEDGEMENTS

I would like to thank a number of people and organizations without whose support and expertise this work could not have been completed. Throughout my degree, Evie provided immeasurable guidance on scientific research and writing, as well as how to put together excellent slide presentations, and I thank her for all of the time and effort she has put into my thesis research. My supervisory committee, Bob Hudson, Mark Lewis, and Jim Allen provided much advice and many helpful comments throughout my degree. I thank Margo Pybus, Dave Moore, Mark Ball, and everyone else with Alberta Fish & Wildlife for their guidance and project input, and for putting up with countless requests for data. The Merrill Lab was a constant source of support, academic and otherwise, in particular my office-mate, Stata guru, and vegetation sampling partner extraordinaire, Heather McPhee, and Barry Robinson, who was always able to supply me with desperately needed R code.

I especially thank everyone who helped out as part of a field crew, whether for weeks, months, or even a few years. Eric Brownrigg and Chris Garrett were the marathoners who stayed in the field collaring and tracking deer throughout the study, and I sincerely thank them for their incredibly hard work. Julia Wachowski, James Guindon, Axelle Dudouet, Chelsea Flaig, Barry Nobert, Wonnita Andrus, and Nabilah Rawji all assisted with deer captures and tracking. Ken Froggatt, Shane Mascarin, Pat Porter, Mary Edey, and Nate Webb contributed their time and expertise to help with sightability trials, for which I am extremely grateful. Thank you to all of the pilots I flew with over the years who always got me safely back on the ground with my lunch still firmly in place. I would also like to thank all of the landowners in my study area who allowed access to their land for all project activities; without their support, this project would not have been possible.

Many individuals at U of A helped me along the way. Jens Roland, who had the misfortune of having an office across the hall from mine, was an excellent de facto stats advisor who was always willing to lend a hand. Charlene Nielsen

provided invaluable support for programming in GIS, without which I might still be in the GIS lab babysitting the GUI. Perhaps most importantly, thank you to the many friends I met while at U of A; after-work beers, intramurals, folkfests, and backyard campfires made this experience worthwhile.

Lastly, I would like to thank my family for all of their support. Luke and Layla were always able to help guide me through the grad student experience in matters of academics and life in general, and were happy to provide a much-needed mountain getaway. The Neufeld clan was the best adoptive family I could ask for, and I especially thank Pat & Garry for many memorable Thanksgivings and Easters on the farm. Finally, thank you to my parents, who made so much possible and taught me the importance of putting care into my work. Throughout my childhood summers spent away at camp, on canoe trips, or at the cottage, they instilled in me an appreciation for wild places and a curiosity about nature that has led me here.

The following organizations provided project funding, personal funding, and/or in-kind support:

Alberta Prion Research Institute

Alberta Conservation Association

Natural Sciences and Engineering Research Council

Alberta Advanced Education and Technology Graduate Scholarship Program

Alberta Fish and Wildlife

Alberta Professional Outfitters Society

Alberta Public Lands

Alberta Cooperative Conservation Research Unit

Saskatchewan Environment

The Spatial Data Warehouse Ltd.

TABLE OF CONTENTS

Chapter 1: Introduction	1
1.1 Modelling Infectious Disease.....	1
1.2 Chronic Wasting Disease Modelling and Management.....	5
1.3 Thesis Organization.....	9
1.4 Literature Cited	12
Chapter 2: Evaluating Stratification for Aerial Surveys of Prairie Parkland Deer Using Empirical and Simulation Methods	19
2.1 Introduction.....	19
2.2 Study Area.....	21
2.3 Methods.....	21
2.3.1 <i>Deer sightability model</i>	21
2.3.2 <i>Simulated aerial surveys</i>	24
2.3.3 <i>Resource selection functions</i>	28
2.4 Results.....	29
2.4.1 <i>Sightability model</i>	29
2.4.2 <i>Resource selection functions</i>	29
2.4.3 <i>Survey design</i>	30
2.5 Discussion.....	32
2.5.1 <i>Sightability</i>	32
2.5.2 <i>Survey design</i>	33
2.6 Literature Cited	44
Chapter 3: Modelling the Effects of Density and Landscape on Contact Rates Among Deer	49
3.1 Introduction.....	49
3.2 Study Area.....	54
3.3 Methods.....	54
3.3.1 <i>Resource selection functions</i>	55
3.3.2 <i>Deer home ranges and pairwise contact rates</i>	56

3.3.3 <i>Deer densities and group sizes</i>	60
3.3.4 <i>Per capita total contact rate</i>	60
3.4 Results	63
3.4.1 <i>Resource selection functions</i>	63
3.4.2 <i>Deer home ranges and pairwise contact rates</i>	64
3.4.3 <i>Deer group sizes</i>	65
3.4.4 <i>Per capita total contact rate</i>	65
3.5 Discussion	66
3.6 Literature Cited	87
Chapter 4: Synthesis and Management Implications.....	94
4.1 Synopsis	94
4.2 Aerial Surveys in Alberta.....	94
4.3 CWD Management in Alberta.....	96
4.4 Future Directions.....	98
4.5 Literature Cited	102
Appendices.....	106

LIST OF TABLES

Table 2-1. Model selection results for a deer sightability model derived from 100 trials conducted in 2008-2009 on 46 mule deer and 54 white-tailed deer in the prairie parkland of east-central Alberta. Included are the model covariates, log-likelihood (LL), ΔAIC corrected for small sample size (ΔAIC_c), model weight (w_i), and the area under the receiver-operating characteristic curve (AUC).....36

Table 2-2. Top exponential models for species-specific resource selection functions for mule and white-tailed deer developed during winter (January-March) daylight hours (0900-1600h) using 55-709 relocations from 64 GPS-collared deer (31 white-tailed deer and 33 mule deer) in east-central Alberta from 2006-2008. Included are the model covariates, log-likelihood (LL), ΔAIC corrected for small sample size (ΔAIC_c), and model weight (w_i).....37

Table 2-3. Top models for a combined mule and white-tailed deer resource selection function developed during winter (January-March) daylight hours (0900-1600h) using 55-709 relocations from 64 GPS-collared deer (31 white-tailed deer and 33 mule deer) in the prairie parkland of east-central Alberta from 2006-2008. Included are the model covariates, log-likelihood (LL), ΔAIC corrected for small sample size (ΔAIC_c), and model weight (w_i).....38

Table 2-4. Median coefficients of variation (CV), 90% confidence intervals (CI) and accuracy of estimated number of mule deer from simulated aerial surveys under three stratification schemes, strata binning strategies, and allocation strategies. Each design was simulated 1000 times and the median values for the six most accurate or precise designs are reported, as well as for the traditional design (see Appendix 3 for full simulation results). CI is one side of the 90% CI width, reported as a percentage of the population estimate and accuracy is the absolute difference from the true population size, reported as a percentage of the true population size with a lower value indicating higher accuracy. In 2008, there were 885 mule deer observed in the survey, and in 2009 there were 1354 observed.....39

Table 2-5. Median coefficients of variation (CV), 90% confidence intervals (CI) and accuracy of estimated number of white-tailed deer from simulated aerial surveys under three stratification schemes, strata binning strategies, and allocation strategies. Each design was simulated 1000 times and the median values for the six most accurate or precise designs are reported, as well as for the traditional design (see Appendix 3 for full simulation results). CI is one side of the 90% CI width, reported as a percentage of the population estimate and accuracy is the absolute difference from the true population size, reported as a percentage of the true population size with a lower value indicating higher accuracy. In 2008, there were 1183 mule deer observed in the survey, and in 2009 there were 2142 observed.....40

Table 2-6. Population estimate (N), Coefficient of variation (CV) and 90% confidence intervals (CI) of white-tailed and mule deer population estimates for the original survey conducted in WMU 234 in 2003 based on the traditional survey design (see text), post-stratified by mule deer, white-tailed deer, and combined resource selection function (RSF) average for a survey unit.....41

Table 3-1. Selected exponential models for species-specific resource selection functions derived using logistic regression for winter (December-April) using 746-3192 relocations per deer from 31 GPS-collared white-tailed deer and 33 GPS-collared mule deer in east-central Alberta from 2006-2008. Included are the model covariates, log-likelihood (LL), Δ AIC corrected for small sample size (Δ AIC_c), and model weight (w_i).....71

Table 3-2. General linear models predicting the size of the 95% kernel winter range for 33 GPS- collared mule deer and 31 GPS-collared white-tailed deer radiocollared in east-central Alberta during 2006-2009. Included are the model covariates, log-likelihood (LL), Δ AIC corrected for small sample size (Δ AIC_c), and model weight (w_i).....72

Table 3-3. Coefficients (β) of the top models predicting the size of the 95% kernel winter range for 33 GPS-collared mule deer and 31 GPS-collared white-tailed deer radiocollared in east-central Alberta during 2006-2009.....73

Table 3-4. Top general linear models predicting the probability of direct contact at a point in time, defined as a simultaneous relocation within 25 m for 15 pairs of GPS-collared deer, developed from 33 mule deer and 31 white-tailed deer radiocollared in east-central Alberta between 2007-2009. VI is the volume of intersection of a pair’s utilization distributions (Millsaugh *et al.* 2004), an index of spatial overlap incorporating intensity of use. Included are the model covariates, log-likelihood (LL), Δ AIC corrected for small sample size (Δ AIC_c), and model weight (w_i).....74

Table 3-5. General linear mixed models predicting winter group size for white-tailed and mule deer, calculated within $n = 98$ survey units of 9 km² obtained from aerial surveys conducted in east-central Alberta in January 2008 and 2009. Group size and densities were ln-transformed to linearize the data prior to model-fitting, except where indicated with *. Included are the model covariates, log-likelihood (LL), Δ AIC corrected for small sample size (Δ AIC_c), and model weight (w_i).....75

Table 3-6. Coefficients (β) of the top models predicting winter group size for white-tailed and mule deer, calculated within $n = 98$ survey units of 9 km² obtained from aerial surveys conducted in east-central Alberta in January 2008 and 2009. Group size and densities were log-transformed to normalize the data prior to model-fitting.....76

Table 3-7. Summed home range overlap index (OI) per individual white-tailed or mule deer with all neighbouring deer, derived from simulated deer distributions in each of four landscapes representative of east-central Alberta. OI values are averaged across 20 iterations at all simulated levels of density (0-12 deer/km²), and standard errors are included.....77

Table 3-8. Expected mean home range size and group size in simulated distributions of white-tailed and mule deer in four landscapes representative of east-central Alberta. Group sizes are predicted at a representative density of 6 deer/km²78

Table 3-9. Estimated parameter values of k and q from Equation 3-1 used to model the total contact rate per individual, c_t , as a function of deer density in each of four different landscapes, under three different within-group contact rate inflation factors (I), in mule and white-tailed deer. All $P < 0.01$ for both parameters.....79

LIST OF FIGURES

- Figure 1-1.** Theoretical density-contact rate relationships giving rise to density-dependent transmission (long dash), frequency-dependent transmission (solid line), or various nonlinear density-transmission relationships.....11
- Figure 2-1.** Study area in east-central Alberta centred in Wildlife Management Unit 234. Areas where white-tailed and mule deer were captured and relocated from 2007-2009 are highlighted.....42
- Figure 2-2.** Effect of snow cover on white-tailed and mule deer sightability when deer are first observed standing (solid line) and bedded (dashed line), the two most common activity states. All other variables were held constant at their average (for continuous variables) or modal (for categorical variables) values. The sightability model was based on 100 trials of 46 mule and 54 white-tailed deer conducted from 2008-2009 in the prairie parkland of east-central Alberta...43
- Figure 3-1.** Per capita contact rate as a function of host population density, under different values of q from Equation 3-1. Adapted from Smith *et al.* (2009).....80
- Figure 3-2.** Organizational flow chart outlining data sources and methodology used to estimate total per capita contact rates among white-tailed and mule deer in east-central Alberta. Empirical data collected from 2006-2009 included a telemetry study of 64 GPS-collared deer (31 white-tailed deer and 33 mule deer) and aerial surveys. Items above the dashed line represent empirical data and/or relationships, and items below the dashed line were based on simulations developed using these empirical relationships.....81
- Figure 3-3.** Probability of direct contact between a pair of deer at a given point in time, defined as a simultaneous relocation within 25 m, summed across 15 pairs of GPS-collared deer (33 mule deer and 31 white-tailed deer) radiocollared in east-central Alberta between 2007-2009.....82
- Figure 3-4.** Mean white-tailed (open circles, dashed line) and mule deer (black circles, solid line) group size as a function of density within 9-km² survey blocks sampled in January 2008 and 2009 ($n = 114$ for white-tailed deer and $n = 133$ for white-tailed deer, because both species were not always present in the same block) in east-central Alberta. Log transformed group size were related to log transformed density for white-tailed ($r^2 = 0.48$; $P < 0.001$) and mule deer ($r^2 = 0.51$; $P < 0.001$).....83
- Figure 3-5.** Relative per capita total contact rate, c_i (deer encountered/unit time), in mule (black) and white-tailed deer (grey) derived as a function of conspecific density in landscapes of 12% (long dash), 26% (solid line), and 67% (short dash) woody cover with within-group contact rates derived with inflation factors (f) of

10, 20, and 50 presented from top to bottom. Results from the 53% cover landscape were similar to the 67% landscape and are not presented.....84

Figure 3-6. Relative per capita between-group contact rate, c_b (deer encountered/unit time), in mule deer as a function of density in each of four representative landscapes ranging from 12-67% forest cover, based on simulations developed for deer in aspen parkland communities of Alberta.....85

Figure 3-7. Relative per capita between-group contact rate, c_b (deer encountered/unit time), in white-tailed deer as a function of density in each of four representative landscapes ranging from 12-67% forest cover, based on simulations developed for deer in aspen parkland communities of Alberta.....86

CHAPTER 1

INTRODUCTION

1.1 Modelling Infectious Disease

The number and publicity of infectious wildlife diseases such as West Nile Virus, chronic wasting disease (CWD), Lyme disease, and foot-and-mouth disease have promoted recent public concern and scientific attention due implications for species conservation, economics, and public health (Dobson and Foufopoulos 2001; Williams *et al.* 2002; Wobeser 2002; Jones *et al.* 2008; Plowright *et al.* 2008). Disease control is most likely to be successful when vaccines that essentially reduce the number of susceptible hosts are available and can be administered cost-effectively to the diseased population (*e.g.* Rosatte *et al.* 2001); however, vaccines do not exist for most wildlife diseases. In the absence of vaccines, understanding disease transmission is key to effective management.

Epidemiological models provide a conceptual approach to understanding disease transmission and usually include a minimum of two terms: a term describing the rate at which susceptible hosts become infected, and a “loss” term describing the decrease in infected individuals over time due to recovery or mortality. Here, I only consider the former, in which the increase in the number of infected individuals (I) in a population over time typically includes the following components:

Equation 1-1

$$\frac{dI}{dt} = Scpv$$

where S represents the number of susceptible hosts, c is the contact rate or the number of other hosts encountered per individual per unit time, p is the probability that the contact occurs with an infected host, and v is the probability that a contact between an infected and susceptible host will successfully transmit disease (Begon *et al.* 2002). The product cpv is the rate at which susceptible hosts are converted to infected individuals, and is termed the “force of infection.” The

value of p usually is assumed to be the proportion of hosts in the population that is infected, which implicitly assumes that infected individuals are distributed homogeneously throughout the population. The v term is typically considered to be constant for a particular host-pathogen system. Under these assumptions about the nature of p and v , differences in transmission focus on the contact rate, c , or more precisely, how c is related to density (Begon *et al.* 2002). Two commonly-employed models are that c is linearly related to density, which gives rise to density-dependent (DD) transmission, or that c is constant, which leads to frequency-dependent (FD) transmission.

In DD transmission, the contact rate term is rewritten as $c = k(N/A)$, where k is a constant, N is the host population size, and A is the area inhabited by the host population. Thus, the rate of change in the number of infected hosts is rewritten as:

Equation 1-2

$$\frac{dI}{dt} = Scpv = Sk \left(\frac{N}{A} \right) \left(\frac{I}{N} \right) v = \beta S \left(\frac{I}{A} \right)$$

where β , termed the “transmission coefficient,” is the product of the constants k and v . DD transmission is typically assumed for directly-transmitted diseases where hosts mix randomly (Bartlett 1957; Anderson and May 1986). In FD transmission, because c is assumed to be constant, the rate of change in the number of infected hosts is rewritten as:

Equation 1-3

$$\frac{dI}{dt} = Scpv = Sc \left(\frac{I}{N} \right) v = \beta' S \left(\frac{I}{N} \right)$$

where β' is the transmission coefficient, although it has different units than β , which has been the source of some confusion (Begon *et al.* 2002). FD transmission is typically assumed for sexually-transmitted diseases where the number of mates per individual is assumed to be constant and unaffected by density (May and Anderson 1987; Hamede *et al.* 2008).

A common approach to determining how transmission relates to host density is to statistically derive the transmission-density relationship from prevalence time-series data (e.g. Greer *et al.* 2008; Smith *et al.* 2009, Wasserberg *et al.* 2009). However, this approach has several limitations. First, for many disease-host systems, it is infeasible to regularly collect prevalence data, especially over the long period of time necessary for a reliable estimate of this relationship (e.g. Wasserberg *et al.* 2009). Secondly, strict DD or FD transmission are likely unrealistic models, so imposing a linear or constant density-contact structure when attempting to model a host-pathogen system may not be helpful (McCallum *et al.* 2001). Rather, DD and FD transmission as illustrated in Figure 1-1 are likely two extremes along a continuum of transmission-density relationships. Indeed, there is little support in the literature for any disease following strictly DD or FD transmission (Lloyd-Smith *et al.* 2005), whereas intermediate forms (Figure 1-1) such as the transmission rate saturating with density have been demonstrated in many systems (Ramsey *et al.* 2002; Greer *et al.* 2008; Smith *et al.* 2009). Finally, when the contact rate (c) and the infection probability of a contact (v) are combined into the transmission coefficient β , it is impossible to distinguish the individual effects of these two components on the transmission rate (Equation 1-1). A data-fitting approach to estimating the transmission coefficient (β) under the common assumption that v is constant (Begon *et al.* 2002) presupposes that the only potential source of variability in transmission is density acting by increasing the contact rate. However, it is also possible for different values of v to exist for different types of contacts (e.g. mating may be more likely to transmit disease than grooming). As a result, transmission may depend on host structure as well as population density. Even if variable transmission (Klepac *et al.* 2009) or force of infection (Heisey *et al.* 2006) among host classes are included in a model, a data-fitting approach is unable to determine what mechanisms are responsible for variation in c and/or v that could lead to nonlinear density-transmission relationships. If environment or management actions influence c and v differently, this could lead to unexplained

outcomes of disease management. Therefore, a more mechanistic understanding of disease transmission is likely necessary to effectively manage wildlife diseases.

Several mechanisms have been proposed or demonstrated to lead to nonlinear density-contact rate relationships. White *et al.* (1995) and Ramsey *et al.* (2002) found that an inverse relationship between home range size and density led to contact rates saturating with host density in red foxes (*Vulpes vulpes*) and brushtail possums (*Trichosurus vulpecula*), respectively. If infectious contacts occurred only within social groups, then group sizes that increase nonlinearly with density would lead to a nonlinear density-contact relationship. Although group sizes in some species have been demonstrated to increase nonlinearly with density (McLellan *et al.* 2010), to my knowledge no studies exist linking nonlinear density-group size relationships to contact rates. Density-dependent resource selection is a process whereby hosts occupy sub-optimal habitats as density (and therefore intraspecific competition) increases in higher-quality habitats (*i.e.* Ideal Free Distribution; Fretwell and Lucas 1970). If a host species followed the Ideal Free Distribution, contact rates may rise quickly with density until high-quality habitats become crowded, but then rise more slowly as density continues to increase because additional hosts would begin occupying available lower-quality habitats. Density-dependent host selection of insect vectors has been examined in vector-borne diseases and found to be a plausible source of nonlinear density-transmission dynamics (Kelley and Thompson 2000; Basanez *et al.* 2007), although the same principle could apply to directly-transmitted pathogens of vertebrate hosts. Resource availability could also affect the density-contact relationship. For example, if home range size were governed by resource availability (*e.g.* Kie *et al.* 2002; Walter 2009), then landscape features could increase or decrease the rate at which spatial overlap among hosts, and therefore the contact rate, increases with density. In this thesis, I examine several mechanisms that may influence contact rates to explore their potential influence on the transmission of chronic wasting disease.

1.2 Chronic Wasting Disease Modelling and Management

Chronic wasting disease (hereafter CWD), is a fatal infectious prion disease of free-ranging cervids endemic to several regions of North America, first detected in north-central Colorado (Williams and Young 1980). It has been detected in white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*), although it is most common in the two deer species (Miller *et al.* 2000; Williams *et al.* 2002). Since its initial detection, CWD has spread to wild populations in several jurisdictions across North America, including major foci in Wyoming, Wisconsin, Illinois, New York, Saskatchewan, and Alberta (Williams *et al.* 2002; Joly *et al.* 2003; Bollinger *et al.* 2004; Alberta Sustainable Resources Development 2010). The first case of CWD in free-ranging deer in Canada was detected in a Saskatchewan mule deer in 2001. Although surveillance for CWD in farmed and wild cervids in Alberta began in 1996, no cases were found in this province until 2002, when an elk at one game farm and two white-tailed deer at a second game farm tested positive. Response programs to these cases found no other cases of CWD in any farmed cervids that had spent time at the affected farms in the previous three years. In 2005, the first wild case of CWD in Alberta was detected in a mule deer near Oyen in the south of the province along the Saskatchewan border. In 2006, a new focus of CWD infection in Alberta was detected near Chauvin, approximately 150 km north of Oyen (Alberta Sustainable Resource Development 2010).

CWD may be transmitted both directly between animals (Williams *et al.* 2002) and indirectly, with infectious agent being shed into the environment via carcasses (Miller *et al.* 2004) and excreta such as urine (Haley *et al.* 2009), saliva (Mathiason *et al.* 2006; Haley *et al.* 2009), blood (Mathiason *et al.* 2006), and feces (Tamguney *et al.* 2009). Indirect transmission may be of particular importance in regions with a long history of CWD where an environmental reservoir has had time to become established, or in facilities with captive cervids (*e.g.* Miller *et al.* 2006), but because CWD is relatively new to Alberta, direct transmission may be dominant. To date, only 75 cases of CWD have been confirmed, and they are distributed across a region stretching > 400 km along the

Saskatchewan border (Alberta Sustainable Resource Development 2010). As in other jurisdictions (Williams *et al.* 2002; Miller and Conner 2005; Gear *et al.* 2006; Osnas *et al.* 2009), Alberta cases of CWD have been documented more frequently in male deer, with 66% of all cases occurring in males (Alberta Sustainable Resource Development 2010). The vast majority (90%) of reported cases have occurred in mule deer, which is consistent with other sympatric populations of infected white-tailed and mule deer (Miller *et al.* 2000; Saskatchewan Environment 2010).

Early models developed to describe CWD transmission made an assumption of frequency-dependent transmission (Gross and Miller 2001), which were subsequently criticized because they accepted this assumption uncritically and did not attempt to compare prevalence data against other competing transmission models (Schauber and Woolf 2003). Subsequent modelling efforts examined the likelihood of DD versus FD transmission for CWD in white-tailed deer in Wisconsin, but both models had similar support (Wasserberg *et al.* 2009). Joly *et al.* (2006) observed higher CWD prevalence in regions with a greater extent of deer habitat and suggested this was a result of higher densities and contact rates in these areas, implying DD transmission. Farnsworth *et al.* (2005) also suggested that higher prevalence in areas of increased anthropogenic landscape use may be due to locally inflated deer densities resulting from animals crowding into smaller areas of undeveloped habitat. Schauber and Woolf (2003) argued that indirect CWD transmission through the environment could be a route to DD contact rates and therefore transmission, particularly when deer aggregate on winter range (Nixon *et al.* 1991; Dumont *et al.* 1998) and large numbers of deer could be exposed to exudates of infected individuals. In contrast, CWD appears to spread readily among members of a social group (Nakada 2009; Gear *et al. in press*), which is typically associated with a constant contact rate if deer only contact members of their own group, and therefore FD transmission (Altizer *et al.* 2003). Due to the potential for both density-dependent or density-independent contact rates, several authors have argued that the overall density-transmission relationship is likely to be nonlinear, falling somewhere between

strict DD or FD transmission (*e.g.* Schauber and Woolf 2003; Wasserberg *et al.* 2009).

A significant limitation on these models' ability to explain and predict CWD spread is that they did not include heterogeneity in disease transmission (c or ν) across species-sex classes or due to landscape heterogeneity within the areas of study, despite ample evidence of variation in CWD prevalence across species-sex groups (Miller *et al.* 2000; Williams *et al.* 2002) and landscapes (Farnsworth *et al.* 2005; Grear *et al.* 2006). Data-fitting is not capable of distinguishing between the separate influences of c and ν on transmission, nor can it identify the mechanisms responsible for variations in c and ν . Therefore, examining these components of transmission explicitly is a worthwhile endeavour for understanding CWD spread. Although there is some evidence of higher values of ν for environmental contacts due to the increased infectivity of prions bound to soil particles (Johnson *et al.* 2007), understanding variation in ν for different types of contacts requires more information than is currently available about CWD transmission pathways (Williams *et al.* 2002). In contrast, examining variation in contact rates can be accomplished through ecological studies.

Studies explicitly examining contact rates among deer have identified three major influences on contact rates, all of which could potentially interact with density and lead to nonlinear density-contact relationships: deer social structure, spatial overlap between individuals (Schauber *et al.* 2007) and resource selection (Kjær *et al.* 2008). Although group size is typically associated with constant contact rates, group size in many ungulates including deer increases with density (Borkowski 2000; McLellan *et al.* 2010), thereby introducing some element of density-dependence to contact rates (Begon *et al.* 2002). Spatial overlap can be influenced by home range size, which in turn may be related to deer density (Kilpatrick *et al.* 2001). Kjær *et al.* (2008) found that the majority of direct contacts between pairs of GPS-collared deer occurred under forest cover, an important resource for deer in agro-forested environments (Nixon *et al.* 1991). However, if deer exhibit density-dependent resource selection (*i.e.* Ideal Free Distribution), this could lead to a slower rate of increase in contact rates with

density at higher densities if deer distribution becomes dispersed. Additionally, resource selection and habitat can influence group size (Jepsen and Topping 2004) and home range size (Kie *et al.* 2002; Walter *et al.* 2009). Finally, these relationships could vary among species-sex classes; for example, male deer could use larger home ranges (Nixon *et al.* 1991), or mule deer may form larger groups (Lingle 2003), all of which could contribute to the observed differences in CWD prevalence among these classes. Thus, understanding the nature of these relationships in the present study region is a prerequisite to modelling contact rates among deer. In my thesis, I focus on direct contact rates between individuals as one component of transmission that can be incorporated into spatially-explicit disease spread models for use in planning CWD management.

To date, CWD management in Alberta has consisted of population reduction of white-tailed and mule deer in areas of CWD, with a target population density of ≤ 1 deer per km^2 of critical (*i.e.* winter) habitat (Bollinger *et al.* 2004). This management approach is based on the assumption that there is at least a DD component of CWD transmission, and that reducing density will limit the direct spread of disease in the short-term and reduce potential environmental contamination with infectious agent in the long-term (Bollinger *et al.* 2004; Langenberg *et al.* 2008). To date, as many as 3406 deer/year have been removed via ground- and helicopter-based sharpshooters (Alberta Sustainable Resource Development 2010). Although Alberta has been effective at removing large numbers of deer, determining how deer density and landscape patterns of deer habitat shape deer distribution and social structure is critical to understanding contact rates, which is a prerequisite for effective management of diseases including CWD.

I address two major themes: estimating deer densities and the potential effects of deer density and landscape patterns on contact rates. Despite efficient removal of deer, is it unclear whether the target density of 1 deer/ km^2 has been met. Therefore, an effective monitoring program for estimating deer densities is essential not only for assessing the effectiveness of herd reduction programs, but also for assessing the impact of CWD-associated mortality on deer populations

over time. Alberta Fish and Wildlife uses aerial surveys to obtain deer population estimates (Glasgow 2000). Indeed, this is the only practical method of directly assessing ungulate density over large areas (Caughley 1977; Potvin *et al.* 2002; Bender *et al.* 2003). Management actions that reduce deer density may not be equally effective in all areas, because the extent of deer habitat may concentrate deer and increase the potential for animal-to-animal contact and disease transmission, and this effect may change with both landscape patterns and deer density in a nonlinear fashion. Therefore, understanding how contact rates may change with deer density and landscape features is an important step in understanding disease spread and will add to more complete modelling efforts. By focussing on contact rates, this component of CWD transmission can either be implicated, at least in part, for the observed prevalence patterns, or ruled out altogether. In the former situation, the mechanisms that shape contact structure in deer could be incorporated into spatially-explicit disease spread models for use in planning CWD management; in contrast, the latter situation would suggest that more attention be placed on unravelling the relative importance of transmission pathways such as the intensity of contacts between different age-sex groups or environmental transmission.

1.3 Thesis Organization

In Chapter 2, I addressed two principal issues for improving aerial surveys of deer. The first problem is that surveys routinely underestimate the number of animals present due to poor detectability, or sightability bias (Samuel *et al.* 1987; Unsworth *et al.* 1999). Sightability is typically assumed to be high due to the openness of the prairie parkland environment studied here, but this has never been explicitly tested, therefore I developed a sightability model for deer in this region. The second problem is that due to their high cost, surveys are limited to covering only a sample of the region, so an appropriate sampling design is needed to maximize accuracy and precision (*e.g.* Smith *et al.* 1995; Prenzlou and Lovvorn 1997; Allen *et al.* 2008; Pearse *et al.* 2009). Traditionally, Alberta has stratified aerial surveys by qualitative assessments of deer habitat, but these

surveys often suffer from low precision (Glasgow 2000). Therefore, I also evaluated alternative stratified survey designs by conducting simulated aerial surveys based on empirical data. I assessed stratification schemes based on quantitative and traditional qualitative measures of deer habitat, as well as alternative strata-grouping schemes and effort allocation strategies, all of which can have a strong effect on precision and accuracy (Sinclair *et al.* 2006; Pearse *et al.* 2009).

In Chapter 3, I used data from aerial surveys and a telemetry study to test several hypotheses relating to contact structure in white-tailed and mule deer. Specifically, for both species I quantified habitat selection by developing resource selection functions (RSF; Johnson *et al.* 2006) and determined how home range size and group sizes were affected by density and important resources. I also examined how pairwise contact rates between pairs of GPS-collared deer were affected by joint space use and landscape features. I then used these relationships to simulate distributions of deer across a range of densities in varying landscapes. In each simulated distribution I estimated the per capita total contact rate and modelled how it changed with density and landscape conditions. The modelling provided insight into the potential mechanisms underlying the observed differences in CWD prevalence in this region, and consequently how CWD management in Alberta could be approached. Although this thesis focuses on CWD, its implications could also be applied to other pathogens of white-tailed and mule deer, and this mechanistic approach to examining how contacts shape disease spread could be employed for other disease-host systems as well.

In Chapter 4, I summarize my results and discuss the implications of my findings for CWD management in Alberta.

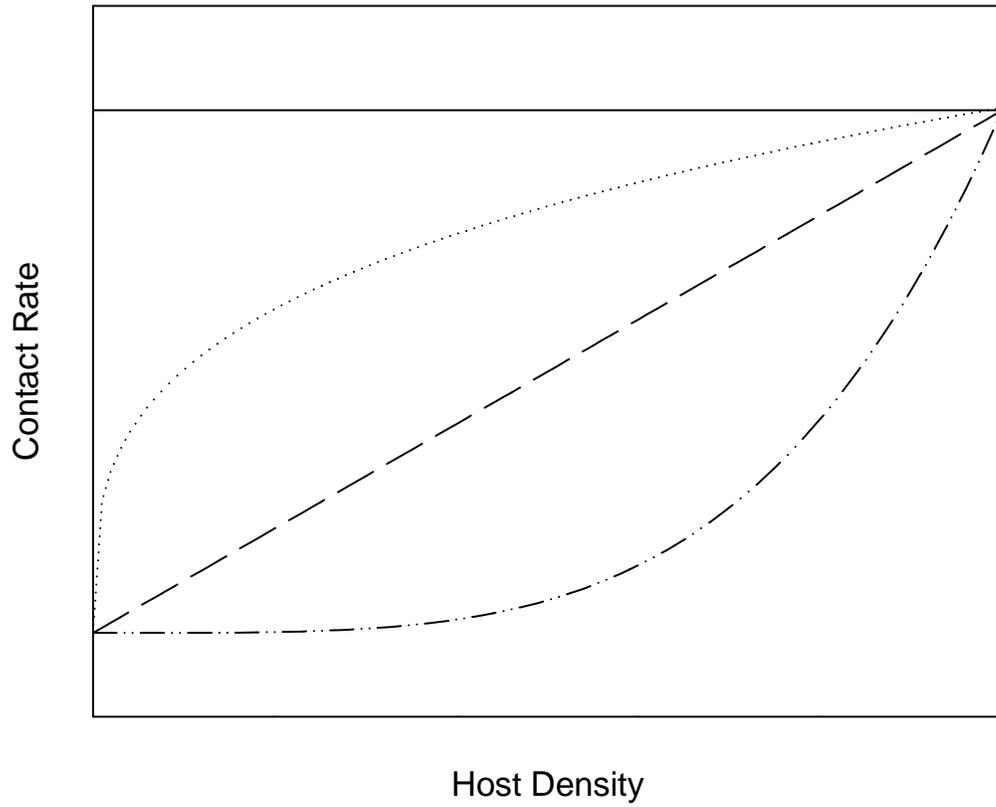


Figure 1-1. Theoretical density-contact rate relationships giving rise to density-dependent transmission (long dash), frequency-dependent transmission (solid line), or various nonlinear density-transmission relationships.

1.4 Literature Cited

- Alberta Sustainable Resource Development. 2010. Statistics: Chronic Wasting Disease in Wild Deer. URL www.srd.alberta.ca/BioDiversityStewardship/WildlifeDiseases/ChronicWastingDisease.aspx [accessed 20 March 2010]
- Allen, J. R., L. E. McInenly, E. H. Merrill, and M. S. Boyce. 2008. Using resource selection functions to improve estimation of elk population numbers. *Journal of Wildlife Management* 72:1798-1804.
- Altizer, S., C. L. Nunn, P. H. Thrall, J. L. Gittleman, J. Antonovics, A. A. Cunningham, A. P. Dobson, V. Ezenwa, K. E. Jones, A. B. Pedersen, M. Poss, and J. R. C. Pulliam. 2003. Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology Evolution and Systematics* 34:517-547.
- Anderson, R. M., and R. M. May. 1986. The invasion, persistence and spread of infectious-diseases within animal and plant-communities. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 314:533-570.
- Bartlett, M. S. 1957. Measles periodicity and community size. *Journal of the Royal Statistical Society Series A-General* 120:48-70.
- Basanez, M. G., K. Razali, A. Renz, and D. Kelly. 2007. Density-dependent host choice by disease vectors: epidemiological implications of the ideal free distribution. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 101:256-269.
- Begon, M., M. Bennett, R. G. Bowers, N. P. French, S. M. Hazel, and J. Turner. 2002. A clarification of transmission terms in host-microparasite models: numbers, densities and areas. *Epidemiology and Infection* 129:147-153.
- Bender, L. C., W. L. Myers, and W. R. Gould. 2003. Comparison of helicopter and ground surveys for North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus* population composition. *Wildlife Biology* 9:199-205.
- Bollinger, T., P. Caley, E. Merrill, F. Messier, M. W. Miller, M. D. Samuel, and E. Vanopdenbosch. 2004. Expert scientific panel on chronic wasting disease. Chronic wasting disease in Canadian wildlife: an expert opinion on the epidemiology and risks to wild deer. Prepared for Canadian Cooperative Wildlife Health Centre, University of Saskatchewan. URL <http://wildlife1.usask.ca/Publications/CWD%20Expert%20Report%20Final%20-%2020040804.pdf> [Accessed 15 August 2007]

- Borkowski, J. 2000. Influence of the density of a sika deer population on activity, habitat use, and group size. *Canadian Journal of Zoology* 78:1369-1374.
- Caughley, G. 1977. Sampling in aerial survey. *Journal of Wildlife Management* 41:605-615.
- Dobson, A., and J. Foufopoulos. 2001. Emerging infectious pathogens of wildlife. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 356:1001-1012.
- Dumont, A., J. P. Ouellet, M. Crete, and J. Huot. 1998. Characteristics of winter forest habitats of the white-tailed deer along the northern border of its distribution area. *Canadian Journal of Zoology* 76:1024-1036.
- Farnsworth, M. L., L. L. Wolfe, N. T. Hobbs, K. P. Burnham, E. S. Williams, D. M. Theobald, M. M. Conner, and M. W. Miller. 2005. Human land use influences chronic wasting disease prevalence in mule deer. *Ecological Applications* 15:119-126.
- Fretwell, S. D. and J. H. J. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16-36.
- Glasgow, W.M. 2000. White Area Ungulate Management Plan, 1997-98 to 1999-2000 Project Completion Report. Alberta Fish and Wildlife, Edmonton.
- Gear, D. A., M. D. Samuel, J. A. Langenberg, and D. Keane. 2006. Demographic patterns and harvest vulnerability of chronic wasting disease infected white-tailed deer in Wisconsin. *Journal of Wildlife Management* 70:546-553.
- Gear, D. A., M. D. Samuel, K. T. Scribner, B. V. Weckworth, and J. A. Langenberg. Influence of genetic relatedness and spatial proximity on chronic wasting disease infection among female white-tailed deer. *Journal of Applied Ecology* *in press*.
- Greer, A. L., C. J. Briggs, and J. P. Collins. 2008. Testing a key assumption of host-pathogen theory: density and disease transmission. *Oikos* 117:1667-1673.
- Gross, J. E., and M. W. Miller. 2001. Chronic wasting disease in mule deer: disease dynamics and control. *Journal of Wildlife Management* 65:205-215.
- Haley, N. J., D. M. Seelig, M. D. Zabel, G. C. Telling, and E. A. Hoover. 2009. Detection of CWD Prions in Urine and Saliva of Deer by Transgenic

Mouse Bioassay. PLoS One 4.

- Hamede, R. K., H. McCallum, and M. Jones. 2008. Seasonal, demographic and density-related patterns of contact between Tasmanian devils (*Sarcophilus harrisii*): Implications for transmission of devil facial tumour disease. *Austral Ecology* 33:614-622.
- Heisey, D. M., D. O. Joly, and F. Messier. 2006. The fitting of general force-of-infection models to wildlife disease prevalence data. *Ecology* 87:2356-2365.
- Jepsen, J. U., and C. J. Topping. 2004. Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: behavioural plasticity and choice of cover. *Canadian Journal of Zoology* 82:1528-1541.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347-357.
- Johnson, C. J., J. A. Pedersen, R. J. Chappell, D. McKenzie, and J. M. Aiken. 2007. Oral transmissibility of prion disease is enhanced by binding to soil particles. *PLoS Pathogens* 3:874-881.
- Joly, D. O., C. A. Ribic, J. A. Langenberg, K. Beheler, C. A. Batha, B. J. Dhuey, R. E. Rolley, G. Bartelt, T. R. Van Deelen, and M. D. Samuel. 2003. Chronic wasting disease in free-ranging Wisconsin White-tailed Deer. *Emerging Infectious Diseases* 9:599-601.
- Joly, D. O., M. D. Samuel, J. A. Langenberg, J. A. Blanchong, C. A. Batha, R. E. Rolley, D. P. Keane, and C. A. Ribic. 2006. Spatial epidemiology of chronic wasting disease in Wisconsin white-tailed deer. *Journal of Wildlife Diseases* 42:578-588.
- Jones, K. E., N. G. Patel, M. A. Levy, A. Storeygard, D. Balk, J. L. Gittleman, and P. Daszak. 2008. Global trends in emerging infectious diseases. *Nature* 451:990-U994.
- Kelly, D. W., and C. E. Thompson. 2000. Epidemiology and optimal foraging: modelling the ideal free distribution of insect vectors. *Parasitology* 120:319-327.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology* 83:530-544.

- Kilpatrick, H. J., S. M. Spohr, and K. K. Lima. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. *Canadian Journal of Zoology* 79:949-954.
- Kjær, L. J., E. M. Schaubert, and C. K. Nielsen. 2008. Spatial and temporal analysis of contact rates in female white-tailed deer. *Journal of Wildlife Management* 72:1819-1825.
- Klepac, P., L. W. Pomeroy, O. N. Bjornstad, T. Kuiken, A. Osterhaus, and J. M. Rijks. 2009. Stage-structured transmission of phocine distemper virus in the Dutch 2002 outbreak. *Proceedings of the Royal Society B-Biological Sciences* 276:2469-2476.
- Langenberg, J. A., M. W. Miller, and L. Creekmore. 2008. *Alberta Chronic Wasting Disease Management: Program Review Panel Report (Peer Review)*. URL http://srd.alberta.ca/BioDiversityStewardship/WildlifeDiseases/documents/CWD-ABreview_FINAL.pdf
- Lingle, S. 2003. Group composition and cohesion in sympatric white-tailed deer and mule deer. *Canadian Journal of Zoology* 81:1119-1130.
- Lloyd-Smith, J. O., P. C. Cross, C. J. Briggs, M. Daugherty, W. M. Getz, J. Latta, M. S. Sanchez, A. B. Smith, and A. Swei. 2005. Should we expect population thresholds for wildlife disease? *Trends in Ecology & Evolution* 20:511-519.
- Mathiason, C. K., J. G. Powers, S. J. Dahmes, D. A. Osborn, K. V. Miller, R. J. Warren, G. L. Mason, S. A. Hays, J. Hayes-Klug, D. M. Seelig, M. A. Wild, L. L. Wolfe, T. R. Spraker, M. W. Miller, C. J. Sigurdson, G. C. Telling, and E. A. Hoover. 2006. Infectious prions in the saliva and blood of deer with chronic wasting disease. *Science* 314:133-136.
- May, R. M., and R. M. Anderson. 1987. Transmission dynamics of HIV-infection. *Nature* 326:137-142.
- McCallum, H., N. Barlow, and J. Hone. 2001. How should pathogen transmission be modelled? *Trends in Ecology & Evolution* 16:295-300.
- McLellan, B. N., R. Serrouya, H. U. Wittmer, and S. Boutin. 2010. Predator-mediated Allee effects in multi-prey systems. *Ecology* 91:286-292.
- Miller, M. W., and M. M. Conner. 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: Spatial, temporal, and demographic influences on observed prevalence patterns. *Journal of Wildlife Diseases* 41:275-290.

- Miller, M. W., N. T. Hobbs, and S. J. Tavener. 2006. Dynamics of prion disease transmission in mule deer. *Ecological Applications* 16:2208-2214.
- Miller, M. W., E. S. Williams, N. T. Hobbs, and L. L. Wolfe. 2004. Environmental sources of prion transmission in mule deer. *Emerging Infectious Diseases* 10:1003-1006.
- Miller, M. W., E. S. Williams, C. W. McCarty, T. R. Spraker, T. J. Kreeger, C. T. Larsen, and E. T. Thorne. 2000. Epizootiology of chronic wasting disease in free-ranging cervids in Colorado and Wyoming. *Journal of Wildlife Diseases* 36:676-690.
- Nakada, S. 2009. Molecular Epidemiology of Chronic Wasting Disease in Free-Ranging Mule Deer (*Odocoileus hemionus*) of Western Canada. MSc thesis, University of Alberta.
- Nixon, C. M., L. P. Hansen, P. A. Brewer, and J. E. Chelsvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monographs* 118:3-77.
- Osnas, E. E., D. M. Heisey, R. E. Rolley, and M. D. Samuel. 2009. Spatial and temporal patterns of chronic wasting disease: fine-scale mapping of a wildlife epidemic in Wisconsin. *Ecological Applications* 19:1311-1322.
- Pearse, A. T., K. J. Reinecke, S. J. Dinsmore, and R. M. Kaminski. 2009. Using simulation to improve wildlife surveys: wintering mallards in Mississippi, USA. *Wildlife Research* 36:279-288.
- Plowright, R. K., S. H. Sokolow, M. E. Gorman, P. Daszak, and J. E. Foley. 2008. Causal inference in disease ecology: investigating ecological drivers of disease emergence. *Frontiers in Ecology and the Environment* 6:420-429.
- Potvin, F., L. Breton, and L. P. Rivest. 2002. Testing a double-count aerial survey technique for White-tailed Deer, *Odocoileus virginianus*, in Quebec. *Canadian Field-Naturalist* 116:488-496.
- Prenzlow, D. M., and J. R. Lovvorn. 1997. Design and results of a waterfowl breeding population survey for Wyoming. *Journal of Wildlife Management* 61:758-767.
- Ramsey, D., N. Spencer, P. Caley, M. Efford, K. Hansen, M. Lam, and D. Cooper. 2002. The effects of reducing population density on contact rates between brushtail possums: implications for transmission of bovine tuberculosis. *Journal of Applied Ecology* 39:806-818.
- Rosatte, R., D. Donovan, M. Allan, L. A. Howes, A. Silver, K. Bennett, C.

- MacInnes, C. Davies, A. Wandeler, and B. Radford. 2001. Emergency response to raccoon rabies introduction into Ontario. *Journal of Wildlife Diseases* 37:265-279.
- Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. *Journal of Wildlife Management* 51:622-630.
- Saskatchewan Environment. 2010. Chronic Wasting Disease (CWD). URL www.environment.gov.sk.ca/cwd [accessed 25 April 2010]
- Schauber, E. M., D. J. Storm, and C. K. Nielsen. 2007. Effects of joint space use and group membership on contact rates among white-tailed deer. *Journal of Wildlife Management* 71:155-163.
- Schauber, E. M., and A. Woolf. 2003. Chronic wasting disease in deer and elk: a critique of current models and their application. *Wildlife Society Bulletin* 31:610-616.
- Sinclair, A.R.E., J. M. Fryxell, and G. Caughley. 2006. *Wildlife Ecology, Conservation, and Management*, 2nd edn. Blackwell Publishing, Malden.
- Smith, D. R., M. J. Conroy, and D. H. Brakhage. 1995. Efficiency of adaptive cluster sampling for estimating density of wintering waterfowl. *Biometrics* 51:777-788.
- Smith, M. J., S. Telfer, E. R. Kallio, S. Burthe, A. R. Cook, X. Lambin, and M. Begon. 2009. Host-pathogen time series data in wildlife support a transmission function between density and frequency dependence. *Proceedings of the National Academy of Sciences of the United States of America* 106:7905-7909.
- Tamguney, G., M. W. Miller, L. L. Wolfe, T. M. Sirochman, D. V. Glidden, C. Palmer, A. Lemus, S. J. DeArmond, and S. B. Prusiner. 2009. Asymptomatic deer excrete infectious prions in faeces. *Nature* 461:529-U590.
- Unsworth, J.W., Leban, F.A., Garton, E.O., Leptich, D.J. and Zager, P. 1999. *Aerial Survey: User's Manual*, electronic edn. Idaho Department of Fish and Game, Boise.
- Walter, W. D., K. C. VerCauteren, H. Campa, W. R. Clark, J. W. Fischer, S. E. Hygnstrom, N. E. Mathews, C. K. Nielsen, E. M. Schaubert, T. R. Van Deelen, and S. R. Winterstein. 2009. Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. *Landscape Ecology* 24:1405-1420.

- Wasserberg, G., E. E. Osnas, R. E. Rolley, and M. D. Samuel. 2009. Host culling as an adaptive management tool for chronic wasting disease in white-tailed deer: a modelling study. *Journal of Applied Ecology* 46:457-466.
- White, P. C. L., S. Harris, and G. C. Smith. 1995. Fox contact behaviour and rabies spread: A model for the estimation of contact probabilities between urban foxes at different population densities and its implications for rabies control in Britain. *Journal of Applied Ecology* 32:693-706.
- Williams, E. S., M. W. Miller, T. J. Kreeger, R. H. Kahn, and E. T. Thorne. 2002. Chronic wasting disease of deer and elk: A review with recommendations for management. *Journal of Wildlife Management* 66:551-563.
- Williams, E. S., and S. Young. 1980. Chronic wasting disease of captive mule deer - spongiform encephalopathy. *Journal of Wildlife Diseases* 16:89-98.
- Wobeser, G. 2002. Disease management strategies for wildlife. *Revue Scientifique et Technique de l'Office International des Epizooties* 21:159-178.

CHAPTER 2

EVALUATING STRATIFICATION FOR AERIAL SURVEYS OF PRAIRIE PARKLAND DEER USING EMPIRICAL AND SIMULATION METHODS

2.1 Introduction

Accurate and precise estimates of wildlife population size are critical for sound management, whether the goal is conserving an endangered species (Guschanski *et al.* 2009), setting sustainable harvest limits for game species (Pettorelli *et al.* 2007), or controlling the spread of enzootic disease (Highfield *et al.* 2009). Aerial surveys are the primary tool for assessing the population size of large vertebrates such as ungulates, but they can yield inaccurate and imprecise population estimates for several major reasons (Caughley *et al.* 1976; Hone 2008). First, aerial surveys underestimate the number of animals due to poor detectability, or visibility bias (Samuel *et al.* 1987). However, sightability models that correct for this bias exist and are now commonly applied (Steinhorst and Samuel 1989; Unsworth *et al.* 1990; Anderson and Lindzey 1996; Anderson *et al.* 1998; Unsworth *et al.* 1999; McIntosh *et al.* 2009; Rice *et al.* 2009).

Second, high variability in animal density across a landscape can lead to low precision around population estimates. Appropriate survey design may improve precision by accounting for much of this variability (*e.g.* Smith *et al.* 1995; Prenzlów and Lovvorn 1997; Allen *et al.* 2008; Pearse *et al.* 2008). For example, adaptive cluster sampling (Thompson 1990) can be used to tailor the survey to aggregated distributions of the target species as the survey is being conducted by sampling a random subset of units and iteratively sampling adjacent units, so long as each sampled unit meets a specified density threshold. One unfavourable consequence of this procedure is that the sample size is not known in advance, which is undesirable for agencies with fixed monitoring budgets (Smith *et al.* 2004). Methods exist to limit the sample size, but these may introduce significant bias into the population estimates (Su and Quinn 2003; Mier and Picquelle 2008). Furthermore, adaptive cluster sampling can be less precise than stratified sampling designs, depending on the level of aggregation that exists

in the target species' distribution (Christman 2000; Mier and Picquelle 2008). Stratified random sampling (Thompson 2002) is among the most common approaches for improving wildlife survey estimates because it is relatively simple and cost-effective (Gasaway *et al.* 1986; Sinclair *et al.* 2006). In stratified random sampling, the survey area is partitioned into strata, sampled units are independently selected within strata, and variances of the estimators for each stratum are summed to obtain the total population variance (Thompson 2002).

Despite the popularity of stratified random designs, little emphasis has been placed on evaluating alternative stratification schemes and survey designs for aerial surveys in a given region (but see Allen *et al.* 2008; Pearse *et al.* 2009). In designing a stratified survey, three principal design options increase precision of the estimate. These include choosing a stratification criterion that corresponds to animal density, grouping survey units into strata in a way that minimizes the within-strata variation in animal density (strata binning), and allocating more sampling effort to strata with high variation so as to reduce within-stratum variability (Thompson 2002; Sinclair *et al.* 2006). Due to the high cost associated with aerial surveys, varying all three design options in a direct comparison is economically unfeasible. However, simulating surveys based on empirical data is a viable, cost-effective approach to evaluating alternative designs (Khaemba *et al.* 2001; Pearse *et al.* 2009). Furthermore, using simulations allows for the evaluation of survey accuracy as well as precision, in contrast to other methods such as post-stratification where the true number of animals present is unknown (Dressel and Norcross 2005; Allen *et al.* 2008).

In the present study, I developed sightability models for both white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) because they do not exist for the prairie parkland region. I also used data from winter aerial surveys of white-tailed and mule deer populations in prairie parkland from 2008 and 2009 to simulate surveys for evaluating alternative sampling designs to improve stratification for increasing survey precision and accuracy. Alberta Fish and Wildlife currently stratifies the landscape into three strata based on qualitative assessments of deer habitat quality derived from visually assessing aerial

photographs, assigns survey units to low, medium, and high quality strata in a 20:60:20 ratio, and allocates sampling effort equally among strata (Glasgow 2000), hereafter referred to as the traditional approach. This approach typically has produced population estimates with levels of precision such that the 90% confidence interval width is \pm 30-50% of the population estimate (Glasgow 2000; Moore 2003). I assessed the influence of alternative stratification criteria, strata-grouping schemes, and sample allocation options for this region.

2.2 Study Area

Data used in this study came from aerial surveys and sightability trials conducted in Wildlife Management Unit (WMU) 234, located in the aspen (*Populus tremuloides*) parkland environment of east-central Alberta along the Saskatchewan border (52°41 N 110°8 W; Figure 2-1). The approximately 2600 km² area is extremely heterogeneous, characterized by stands of aspen forest ranging in size from small patches (~10 m diameter) to large contiguous blocks up to several square kilometres, interspersed throughout native grasslands, agricultural fields, and wetlands (Bird 1961). Topography is generally flat with gentle hills, with the exceptions of the Battle River and its tributary, Ribstone Creek, which are significant drainage features with associated deep river valleys. The climate is relatively dry, with warm summers and cold winters, with yearly precipitation from 1971 to 2000 averaging 421 mm with a cumulative snowfall of 108 cm (Environment Canada 2009). Agriculture, both livestock and crops, is the principal land use in the region, but numerous small oil and gas development features are present as well. Elk (*Cervus elaphus*) and moose (*Alces alces*) are also present in the region, and coyotes (*Canis latrans*) are the only significant mammalian predator other than humans.

2.3 Methods

2.3.1 Deer sightability model

During the winters of 2007-2008 and 2008-2009, I conducted 100 “sightability trials” involving 54 different radiocollared white-tailed and 46 mule

deer using a procedure developed in previous studies (Samuel *et al.* 1987; Unsworth *et al.* 1999; Allen 2005). Sightability trials occurred in major five areas within WMU 234 and adjacent WMU 236 in eastern Alberta, which were selected to represent the range of landscapes present in the region where radiocollared deer of both species were present. Radiocollared deer were captured using Clover traps (Clover 1954) or by helicopter net-gunning (University of Alberta Animal Care Committee Protocol 494701).

Each sightability trial consisted of a fixed-wing aircraft (Cessna 182 or 185) locating a radiocollared deer via telemetry, calculating the coordinates of a randomly offset 1.6 x 1.6-km survey block containing the animal, and then surveying the block with a helicopter for deer and noting whether the collared deer was observed. I selected this survey block size to take advantage of the roads and fence lines spaced 1.6 km apart by the Dominion Land Survey which provided easily visible landmarks for navigation. The fixed-wing aircraft transmitted the coordinates of the survey block to a Bell 206B Jet Ranger helicopter equipped with a telemetry antenna. After receiving the block coordinates, the helicopter immediately surveyed the block following standard survey protocols for this region (Glasgow 2000). Personnel in the helicopter included a navigator seated next to the pilot and two observers in the rear of the aircraft. I ensured observers had at least 2 years of experience with ungulate surveys in the region, because observer experience has been demonstrated to affect sightability (Caughley *et al.* 1976). The helicopter followed protocols of Glasgow (2000) and flew at approximately 50 m above ground level and within a speed of 80-100 km/hr. Each survey unit was flown in transects 400 m apart, corresponding to complete coverage of the area, and only deer within 200 m on either side of the aircraft were recorded during each transect (Glasgow 2000). An onboard GPS recorded a continuous track log to ensure that the block was surveyed completely.

If the crew sighted the collared deer, I recorded nine variables that were found in past studies to influence sightability (Unsworth *et al.* 1999; Freddy *et al.* 2004, Allen 2005). These included the group size (deer within ~20 m of each

other), deer activity (bedded, standing, or moving), light intensity (flat or bright), percent tree cover (within 20 m), vegetation class (open, shrubland, or forest), percent snow cover (within 20 m), precipitation (present or absent), and temperature. If the collared deer was not observed during the trial, the helicopter crew immediately located the animal by telemetry and recorded the same variables. In all cases, I recorded these variables at the location where the radiocollared deer was first seen. Because snow cover was expected to be an important variable, I timed the trials to prioritize encountering a range of snow conditions, so trials were conducted across a range of dates within years (Appendix 1). A majority of male deer had dropped their antlers by the time of the trials, thereby precluding including group sex composition as an explanatory variable.

I used logistic regression to determine the probability, π , that a group of deer containing the radiocollared individual was sighted based on conditions at the group's location. The sightability model takes the form:

Equation 2-1

$$\pi = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)}$$

where $x_{1\dots k}$ represent habitat variables and $\beta_{0\dots k}$ are parameters of the model (Samuel *et al.* 1987). I used Akaike's Information Criterion corrected for small sample size (AIC_c) to select the best *a priori* model from several candidate models (Burnham and Anderson 2002). The area under the receiver operating characteristic (ROC) curve (AUC), which is a measure of a model's predictive success, was calculated for each model (Swets 1988; Fielding and Bell 1997; McPherson *et al.* 2004).

Because so few mule deer were not detected during trials (< 13%), I was unable to test for statistically meaningful species interaction effects to determine whether the recorded variables affected sightability differently across species. However, I compared the proportion of missed deer of each species using a G-test to determine whether mule or white-tailed deer were more likely to be undetected.

Additionally, I compared the observed values of all variables included in the final model between species, using G-tests for categorical variables and t-tests for continuous variables. These tests were performed only for variables related to deer activity and habitat and not abiotic factors such as light intensity, snow cover, and precipitation, which were products of the timing of the flights rather than due to differences between species.

2.3.2 Simulated aerial surveys

I conducted simulations for each of 27 survey designs that were developed by altering the three design options: stratification criteria, approaches to binning sample units into strata, and schemes for allocating sampling effort among strata. I overlaid a 3-minute latitude x 5-minute longitude (~5.6 x 5.6-km) grid over WMU 234, which divided the area into 87 survey units. This was the same grid size used by Alberta Fish and Wildlife in their traditional surveys. I obtained deer counts in two years for each survey unit from surveys of white-tailed and mule deer in WMU 234 conducted in January 2008 and 2009, and 1000 simulations were conducted with data from each year to determine how robust the results were across years. Each survey consisted of 25% coverage of the entire WMU by flying lines spaced 1600 m apart and counting all deer within 200 m on either side of the aircraft (Bell 206B Jet Ranger) and recording the location of all deer groups with an onboard GPS. There was 100% snow coverage across the area in both years. In 2008, 1183 white-tailed and 885 mule deer were observed, and in 2009 2142 white-tailed and 1354 mule deer were observed. Each simulated survey consisted of randomly sampling 16 units according to one of the 27 candidate designs and calculating a population estimate for both species as well as measures of their precision and accuracy. Sampling 16 units corresponds to the sampling effort of surveys conducted in WMU 234 by Alberta Fish and Wildlife.

I evaluated four stratification criteria: Alberta Fish and Wildlife's traditional stratification scheme, a scheme based on each unit's percent tree and shrub cover (woody cover) obtained from a GIS landcover map at a 30-m resolution (Agriculture and Agri-Food Canada 2009), and schemes based on

either white-tailed deer or mule deer resource selection function (RSF) values averaged across a survey unit. Traditional stratification has been based on a qualitative assessment of deer habitat, obtained by visually estimating the amount of woody cover present in a survey unit from aerial photographs (D. Moore, pers. comm.; Glasgow 2000). Survey units were classed as either low, medium, or high deer density based on assessed deer habitat quality. The second approach differs from the first in that it was based on a formal, quantitative assessment of percent woody cover obtained from a GIS landcover map. Both cover-based stratification schemes were included because deer tend to be associated with woody cover during winter in environments with a mixture of grassland, agriculture, and forest such as the region studied here (Nixon *et al.* 1991; Kjær *et al.* 2008). RSF value is a measure of the relative probability of an animal selecting a habitat (Johnson *et al.* 2006). As a result I expected deer distribution to be related to mean RSF value of a survey unit. Allen *et al.* (2008) found stratification by RSF improved precision of elk population estimates in western Alberta. I derived both mule deer and white-tailed deer RSFs to see if they differed, and if they did how stratification by each RSF influenced the precision of the population estimates.

I grouped survey units into strata in three ways: the 20:60:20 low:medium:high ratio used in the traditional stratification system (Glasgow 2000), equal sized strata, and dividing survey units and based on “natural breaks” in the stratification variable’s value. Natural breaks were calculated using ArcGIS 9.3.1 (ESRI, Redlands, CA, 2009) with a modified Jenks-Fisher optimization algorithm, or goodness-of-variance fit (Jenks 1967). The traditional stratification system is not based on a continuous habitat variable, but rather fixes units in a 20:60:20 ratio, so the latter two grouping options were evaluated for only cover- and RSF-based designs. The allocation of sampling effort was varied among strata in three ways: equal allocation, in which strata had the same number of units sampled regardless of their size; proportional allocation, in which the number of units sampled per stratum was proportional to the number of units in that stratum; and optimal allocation, in which the number of units sampled per

stratum increases with both stratum size and the standard deviation of deer densities among its units (Thompson 2002; Sinclair *et al.* 2006). Under optimal allocation, the number of units sampled in stratum h , n_h , is calculated as:

Equation 2-2

$$n_h = \frac{nN_h\sigma_h}{\sum N_h\sigma_h}$$

where n is the total number of units sampled, N_h is the number of units in stratum h , and σ_h is an estimate of the standard deviation in animal density in stratum h (Thompson 2002). I obtained estimates of strata standard deviations from previous surveys of WMU 234 (Moore 2003).

The density estimate for stratum h , D_h , was calculated using the ratio method for unequal-sized sampling units (Sinclair *et al.* 2006):

Equation 2-3

$$D_h = \frac{\sum y_h}{\sum a_h}$$

where y_h is the total number of deer observed in stratum h , and a_h is the sampled area of stratum h . I calculated the population estimate for stratum h , Y_h , using:

Equation 2-4

$$Y_h = D_h \cdot A_h$$

where A_h is the total area of stratum h . An unbiased estimator of the standard deviation around D_h was calculated as:

Equation 2-5

$$S(D_h) = \frac{n_h}{a_h} \cdot \sqrt{\frac{1}{n_h(n_h - 1)} \cdot \left(\sum y_{hi}^2 + D_h^2 \sum a_{hi}^2 - 2D_h \sum a_h y_h \right)} \cdot \sqrt{1 - \frac{a_h}{A_h}}$$

where n_h is the number of units sampled in stratum h , y_{hi} is the number of deer in the i^{th} survey unit in stratum h , and a_{hi} is the area of the i^{th} survey unit in stratum h

(Sinclair *et al.* 2006). An unbiased estimator of the variance around the stratum population estimate, $Var(Y_h)$, was calculated by:

Equation 2-6

$$Var(Y_h) = [A_h \cdot S(D_h)]^2$$

The total population estimate, Y , was calculated as the sum of the population estimates for each stratum. The total population variance, $Var(Y)$, was the sum of the variances for each stratum (Sinclair *et al.* 2006).

To evaluate the precision of each simulated survey, I calculated the width of the 90% confidence interval (CI) and the coefficient of variation (CV; Zar 1999). By convention, a $CV < 20\%$ is considered to be an acceptable level of variation for deer surveys in this jurisdiction (Glasgow 2000). To evaluate the accuracy of the population estimate, I calculated its absolute difference from the true number of deer observed in the entire WMU during data collection. The difference was expressed as a percentage of the true number of observed deer for ease of comparing accuracy across species and years. I also calculated the design effect (DEFF) of each design, which is the ratio of the variance under the stratified design in question to the variance that would be obtained under simple random sampling (Lehtonen and Pahkinen 2004). These measures of precision and accuracy were repeated for each of 1000 simulated surveys per candidate design per year, and I compared the median values. Rather than conducting null hypothesis tests (*e.g.* ANOVA) which would report even small differences in these metrics as statistically significant due to the large sample size, I focussed instead on the magnitude of improvement in these metrics (Nakagawa and Cuthill 2007).

To assess the improvement in the “best” survey approach on a second data set, I compared the original population estimate obtained from a stratified random survey of WMU 234 ($n = 16$) conducted in 2003 using the historical stratification approach (Moore 2003) to an estimate obtained by post-stratifying according to the design that performed best in the simulations. I used the same formulae described above to calculate the original population estimate and its CV and 90%

CI, but added an additional variance term for the post-stratified estimate following Dressel and Norcross (2005).

2.3.3 Resource selection functions

I calculated separate resource selection functions for 31 white-tailed deer and 33 mule deer fitted with Global Positioning System (GPS) collars (55-709 locations per deer) with fix rates varying from 1-6 hours. To ensure that the models would represent selection corresponding to times of year and day when aerial surveys occur, I used only locations taken during mid-winter in daylight hours (0900-1600 hours from January to March). Available points for each deer were selected from within the minimum convex polygon (MCP) of its winter home range. I used mixed-effects logistic regression with individual deer as a random effect (Gillies *et al.* 2006) to determine the covariates for 9 *a priori* RSF models for each species, and used AIC_c to select the best model (Burnham and Anderson 2002). Landscape covariates measured at a 30 x 30-m cell resolution included elevation (m) and terrain ruggedness index value (Riley *et al.* 1999) derived from a 30-m digital elevation model. Percent woody (tree and shrub) cover at a deer location was measured at five spatial scales (within 120, 240, 510, and 750 m radii), and road density, linear feature density, and well density were measured within a 500 m radius around each location. Distance to the nearest edge of woody cover, water bodies, roads, and linear features (roads, rail lines, seismic lines, and power lines), and oil and gas wellpads were derived in ArcGIS. Base layers for GIS analyses were obtained from Agriculture and Agri-Food Canada, Spatial Data Warehouse Ltd., and Saskatchewan Environment.

Because I was interested in improving surveys flown for mule deer and white-tailed deer simultaneously, I developed RSFs for both species and tested whether they were equivalent. To do this, I first developed species-specific RSF models to determine what variables most influenced each species. If similar variables influenced the selection of each species, I combined data from both species and tested for a species main effect and species*covariate interactions. Additionally, to determine whether both species select similar habitats, I used

mixed-effects regression to determine whether the density of white-tailed and mule deer were correlated, with the survey unit included as a random effect.

2.4 Results

2.4.1 Sightability model

In the 100 sightability trials, I detected collared deer 83 times and missed animals 17 times. The proportion of mule deer (13%) and white-tailed deer missed (20%) was not significantly different ($G = 0.960$; $df = 1$, $P = 0.33$). The average detection rate of 83% applies to the range of conditions under which I sampled, where deer were observed in group sizes that averaged 5.37 ± 5.78 SD, and white-tailed deer (31%) were more likely than mule deer (11%) to be bedded ($G = 6.48$, $df = 1$, $P = 0.011$, Appendices 1-2). The small number of undetected mule deer ($n = 6$) precluded any meaningful species-specific sightability model for mule deer, so I did not include a species main effect or interactions in the models. Precipitation did not occur during any of the trials, so this variable was also dropped from the analysis.

Group size and deer activity were the most consistent variables in the top models, with $\Delta AIC_c > 8$ for all models without both of these variables (Table 2-1). I selected the following model, which also included snow cover (Figure 2-2) and vegetation class, to correct for sightability bias in deer surveys:

Equation 2-7

$$\pi = \frac{\exp(15.603 + 0.665x_1 + 1.986x_2 + 2.320x_3 + 0.026x_4 - 18.917x_5 - 19.537x_6)}{1 + \exp(15.603 + 0.665x_1 + 1.986x_2 + 2.320x_3 + 0.026x_4 - 18.917x_5 - 19.537x_6)}$$

where π is the probability of detecting a group of deer, x_1 = group size, x_2 = standing (0 or 1), x_3 = moving (0 or 1), x_4 = snow cover (%), x_5 = shrubland (0 or 1), and x_6 = forest (0 or 1). The AUC of this model was 0.87.

2.4.2 Resource selection functions

The RSFs developed separately for white-tailed and mule deer with the lowest AIC_c included the same covariates, except that the white-tailed deer model

included well density and the mule deer RSF included distance to wells (Table 2-2). The best species-specific RSF models were:

Equation 2-8, Equation 2-9

$$w_{wtd} = \exp(2.4333X_1 + 0.0153X_2 + 0.0035X_3 + 0.00056X_4 + 0.00025X_5 - 0.1622X_6)$$

$$w_{mule} = \exp(1.6374X_1 + 0.1093X_2 + 0.0025X_3 + 0.00034X_4 + 0.00027X_5 - 0.00040X_7)$$

where X_1 was the percent cover within 120 m, X_2 was terrain ruggedness index value within a 30 x 30-m cell, X_3 was elevation (m) within a cell, X_4 was distance to water (m), X_5 was distance to roads (m), X_6 was well density within 500 m, and X_7 was distance to wells (m).

Because both species were influenced by the same variables, I pooled the species data and tested for a species main effect and species interactions with all environmental variables. The species main effect and all interaction effects of the combined RSF were significant ($P < 0.001$), indicating that the species-specific RSFs were not statistically equivalent. However, due to the similarity in resource selection in both species, I deemed the models sufficiently similar to develop a combined RSF (Table 2-3) to determine whether it would provide better overall precision across both species. Furthermore, mixed-effects linear regression indicated that white-tailed and mule deer density at the level of the survey unit were significantly correlated ($n = 87, p < 0.001$), suggesting that the two species have similar habitat requirements. The combined model with the lowest AIC_c value was:

Equation 2-10

$$w_{combined} = \exp(2.043X_1 + 0.0734X_2 + 0.00391X_3 + 0.000456X_4 + 0.000290X_5 - 0.0402X_6)$$

2.4.3 Survey design

Because there were more white-tailed deer than mule deer observed in the surveys, there was higher variability in mule deer population estimates (CV 28-46%) than white-tailed deer estimates (CV 21-34%). Survey designs that grouped survey units into strata by natural breaks in the stratification variable (percent cover or mean RSF value) using Jenks optimization consistently produced the most precise and accurate population estimates compared to other grouping

methods, using data from either 2008 or 2009 (Table 2-4, Table 2-5). It was not possible to alter the strata groupings and employ the Jenks procedure for the traditional stratification because this approach assigned units to strata qualitatively, so I used only natural breaks to define strata for cover or RSF-based designs. Compared to cover or RSF-based designs that also grouped strata in a 20:60:20 ratio, estimates developed using the historical stratification scheme were still less precise and accurate (Appendix 3).

The best overall design for estimating mule deer numbers was based on mule deer RSF value, with survey units grouped into strata by natural breaks in the RSF value calculated using Jenks optimization, and an equal allocation of sampling effort (Table 2-4). The most accurate and precise estimates for white-tailed deer also came from a design based on mule deer RSF with strata grouped by natural breaks, but using equal or optimal allocation of sampling effort yielded similarly precise and accurate estimates (Table 2-5). Stratification by combined RSF value yielded slightly less accurate and precise estimates than the best species-specific RSF, with CVs and accuracy values 0-2% larger for mule deer (Table 2-4) and 2-5% larger for white-tailed deer (Table 2-5). The best design based on cover, for both species, used natural breaks to group strata and either optimal allocation (for mule deer) or equal allocation (for white-tailed deer). The cover-based design yielded precision and accuracy values 2-4% larger for mule deer and 1-3% larger for white-tailed deer, depending on the measure and year (see Appendix 3 for full results). DEFF tended to follow the other measures of precision and accuracy (Table 2-4, Table 2-5), and all stratified designs were more efficient than a null design of simple random sampling.

Post-stratification of data from the 2003 survey of WMU 234 using combined RSF-based stratification and units assigned to strata by natural breaks resulted in 8 low stratum units, 6 medium stratum units, and 2 high stratum units being sampled. The 90% CI width and the CV were lower for both species of deer in the post-stratified design compared to the original design (Table 2-6) even though I accounted for the additional uncertainty related to post stratification (Dressel and Norcross 2005). I also post-stratified by species-specific RSFs with

similar results, although the amount of improvement gained varied among species depending on which RSF was used for post-stratification (Table 2-6).

2.5 Discussion

Efforts to improve survey design are likely to produce a more consistent improvement in deer population estimates than applying sightability models, because detection of deer was generally high in this region. Nonetheless, application of sightability model may improve population estimates when population densities are low or if snow conditions deteriorate during surveys.

2.5.1 Sightability

Deer were more likely to be detected when there was good snow cover, open canopy, if they were in large groups, and active rather than bedded, which is consistent with studies in other ecoregions (Unsworth *et al.* 1999; Freddy *et al.* 2004, Allen 2005). However, overall deer detection in sightability trials (83%) was generally high compared to the detection rates of 48-79% typically found in similar studies (Unsworth *et al.* 1999; McIntosh *et al.* 2009). Most past studies have been conducted in forests where the canopy closure of coniferous forest makes observations of ungulates difficult. In this region, an even higher percentage of deer may be detected during actual helicopter surveys than in the sightability trials, because surveys are typically conducted under complete snow cover, whereas during the trials snow cover ranged from 0 to 100% (Appendices 1-2). For example, if I assumed 100% snow cover during all trials, the model predicted that 90% of all deer would have been observed, but only 78% of deer would have been detected if snow cover dropped to 50% (Figure 2-2). More white-tailed than mule deer were recorded as bedded, so white-tailed deer may not respond as readily to helicopters flying in the area compared to mule deer. If true, underestimation of white-tailed deer may be more severe than for mule deer, and employing a sightability correction would be particularly helpful for surveys of white-tailed deer.

2.5.2 Survey design

In my simulations, I found that stratifying survey units by mean RSF value provided the most precise and accurate estimates compared to other available stratification variables. The improvement was consistent across both white-tailed and mule deer, and a similar improvement has been found for surveying elk in western Alberta (Allen *et al.* 2008). The improvement in precision gained by using RSF value to post-stratify the 2003 survey of WMU 234 further supports the use of RSFs as a stratification variable in future surveys of this region. Precision (CV) was improved by 10-26% over the traditional stratification approach, even though an additional variance term was added to account for the increase in variance expected from post-stratification compared to pre-stratification (Dressel and Norcross 2005). Even further improvement in precision would be expected in a pre-stratified survey, because I found that allocation of sampling effort among strata also affected precision, but selecting the effort allocation strategy was not possible with these previously collected data. In this case, precision of the estimates might have reached a $CV \leq 20\%$ for at least white-tailed deer, which typically is an acceptable level of precision for aerial surveys. At the same time, I also found that employing a simple stratification approach based on woody cover performed nearly as well as using the more detailed RSF (Table 2-4, Table 2-5). This was not unexpected, because woody cover was a major component of the RSF, and woody cover and RSF values were correlated (*e.g.* for combined RSF versus cover, $r^2 = 0.55$).

Survey precision and accuracy also were improved by grouping survey units by natural breaks in RSF value or percent woody cover using Jenks optimization. Jenks optimization minimizes variability in the value of the stratification variable within each stratum (Jenks 1967), thereby grouping the most similar survey units based on RSF into the same strata. My simulations indicate that Jenks optimization is preferable to arbitrarily setting strata sizes in a 20:60:20 ratio; the 20:60:20 ratio implicitly assumes that the majority of the area is of intermediate habitat quality (Glasgow 2000), whereas Jenks optimization seeks to define strata sizes based on an empirical assessment of the distribution of

resources or deer habitat. In many regions, strata consist of distinct habitat types (Dressel and Norcross 2005; Brown *et al.* 2007; Dorr *et al.* 2008), but in the present study area the landscape is heterogeneous at multiple spatial scales. Consequently, one cannot define distinct habitat types except at very small scales (< 10km²) at which sampling via aerial surveys would be inefficient. In other regions with similarly heterogeneous landscapes, defining strata by natural breaks should be considered.

Proportional allocation of sampling effort among strata consistently performed more poorly than optimal and equal allocation, as has been demonstrated in a variety of systems (Harbitz *et al.* 1998; Hata and Berkson 2004; Pearse *et al.* 2009). The ideal allocation system places the most effort in strata with the highest variability in animal density among its survey units, which usually increases linearly with population size for most species (Sinclair *et al.* 2006). In WMU 234, natural breaks in percent cover or mean RSF value always allocated a large number of survey units to the low-density stratum and very few to the high-density stratum. For this reason, proportional allocation placed the majority of sampling effort in the extensive, low-density stratum, which contained the fewest number of animals and had lower variability in densities. In contrast, very little sampling effort was allocated to the much smaller high-density stratum, which had relatively high levels of variability and contained up to 40% of the total population. Because optimal allocation takes into account relative strata sizes as well as an estimate of variability among strata, it is also susceptible to placing an inappropriate amount of effort in a very large low-density stratum, although not to the same degree as proportional allocation. Equal allocation generally performed better than optimal allocation in the present study because it tended to place more effort in the medium- and high-density strata, though the differences in precision and accuracy were not large.

In this prairie parkland environment, I found that stratification by natural breaks in RSF values provided the highest levels of precision and accuracy, and therefore suggest this as a strategy that should be considered in other jurisdictions. When an RSF or telemetry database is not available, I recommend using a

quantified estimate of woody cover that can be measured readily from available aerial photographs or GIS landcover layers to stratify survey units for deer in prairie parkland regions. Because of the need to survey for multiple species, I recommend using the combined RSF. This approach may not be appropriate for other multi-species systems if the species' distributions are not similar. In the prairie parklands, I found that densities of mule deer and white-tailed deer were correlated, and factors influencing their selection were the same but differed as to the magnitude of influence (*i.e.*, significant interactions in the combined RSF). Although some precision and accuracy may be sacrificed by using a combined rather than species-specific RSF, these differences generally were small.

Applying sightability models is becoming commonplace (Unsworth *et al.* 1999; Freddy *et al.* 2004; Rice *et al.* 2008), but not for mule deer or white-tailed deer. For the prairie parkland region, sightability is generally high in winter due to the openness of the deciduous forest, particularly under ideal snow conditions for surveys. Under current deer densities ($\sim 5\text{-}15/\text{km}^2$), I found it difficult to reliably record site characteristics for all groups in areas of high deer concentrations. Where deer densities are low, or when less ideal conditions necessitate sightability corrections, my models provide a means to adjust aerial survey population estimates for important biases.

Table 2-1. Model selection results for a deer sightability model derived from 100 trials conducted in 2008-2009 on 46 mule deer and 54 white-tailed deer in the prairie parkland of east-central Alberta. Included are the model covariates, log-likelihood (LL), ΔAIC_c corrected for small sample size (ΔAIC_c), model weight (w_i), and the area under the receiver-operating characteristic curve (AUC).

Model	LL	ΔAIC_c	w_i	AUC
Group, activity, snow, veg class	-29.94	0.00	0.20	0.872
Group, activity, snow	-32.50	0.45	0.16	0.844
Group, activity, snow, light	-31.47	0.69	0.14	0.852
Group, activity, snow, veg class, light, temp	-29.14	0.82	0.13	0.878
Group, activity, light	-32.84	1.13	0.11	0.830
Group, activity, snow, veg class, light	-29.64	1.81	0.08	0.875
Group, activity, snow, light, canopy	-30.85	1.82	0.08	0.864
Group, activity	-34.53	2.24	0.07	0.810
Group, activity, veg class	-33.40	4.56	0.02	0.826
Group, snow, light	-37.44	8.07	0.00	0.795
Group, snow	-38.57	8.09	0.00	0.788

Table 2-2. Top exponential models for species-specific resource selection functions for mule and white-tailed deer developed during winter (January-March) daylight hours (0900-1600h) using 55-709 relocations from 64 GPS-collared deer (31 white-tailed deer and 33 mule deer) in east-central Alberta from 2006-2008. Included are the model covariates, log-likelihood (LL), ΔAIC_c corrected for small sample size (ΔAIC_c), and model weight (w_i).

Species	Model	LL	ΔAIC_c	w_i
Mule Deer	Cover120, TRI, elev, dt_wat, dt_road, dt_well	-23551.76	47127.99	> 0.99
	Cover120, TRI, elev, dt_wat, dt_linear, dt_well	-23579.67	47183.82	< 0.01
	Cover120, TRI, elev, dt_wat, dt_road, well_500	-23621.18	47266.84	< 0.01
	Cover120, TRI, elev, dt_wat, well_500, line_500	-23693.39	47411.25	< 0.01
	Cover120, TRI, dt_wat	-23704.58	47422.16	< 0.01
	Cover120, TRI	-23791.71	47593.32	< 0.01
White-Tailed Deer	Cover120, TRI, elev, dt_wat, dt_road, well_500	-23286.08	0	> 0.99
	Cover120, TRI, elev, dt_wat, well_500, line_500	-23347.74	123.31	< 0.01
	Cover120, TRI, elev, dt_wat, dt_road, dt_well	-23424.48	272.56	< 0.01
	Cover120, TRI, elev, dt_wat, dt_linear, dt_well	-23459.75	343.10	< 0.01
	Cover120, TRI, dt_wat	-23590.58	597.53	< 0.01
	Cover120, TRI	-23820.52	1054.31	< 0.01

Cover120 = cover within 120m; TRI = Terrain Ruggedness Index value; elev = elevation (m); dt_wat = distance to water (m); dt_road = distance to roads (m); dt_well = distance to wells (m); line_500 = linear feature density within 500m; well_500 = well density within 500m.

Table 2-3. Top models for a combined mule and white-tailed deer resource selection function developed during winter (January-March) daylight hours (0900-1600h) using 55-709 relocations from 64 GPS-collared deer (31 white-tailed deer and 33 mule deer) in the prairie parkland of east-central Alberta from 2006-2008. Included are the model covariates, log-likelihood (LL), ΔAIC_c corrected for small sample size (ΔAIC_c), and model weight (w_i).

Model	LL	ΔAIC_c	w_i
Cover120, TRI, elev, dt_wat, dt_road, well_500	-47240.95	0.00	> 0.99
Cover120, TRI, elev, dt_wat, dt_road	-47287.38	90.15	< 0.01
Cover120, TRI, elev, dt_wat, dt_road, dt_well	-47287.15	92.41	< 0.01
Cover120, TRI, elev, dt_wat, dt_line, dt_well	-47372.63	151.17	< 0.01
Cover120, TRI, elev, dt_wat ,line_500, well_500	-47410.14	263.37	< 0.01
Cover120, TRI, elev, dt_wat	-47495.74	338.40	< 0.01
Cover120, TRI	-47819.31	504.25	< 0.01

Cover120 = cover within 120m; TRI = Terrain Ruggedness Index value; elev = elevation (m); dt_wat = distance to water (m); dt_road = distance to roads (m); dt_well = distance to wells (m); line_500 = linear feature density within 500m; well_500 = well density within 500m.

Table 2-4. Median coefficients of variation (CV), 90% confidence intervals (CI) and accuracy of estimated number of mule deer from simulated aerial surveys under three stratification schemes, strata binning strategies, and allocation strategies. Each design was simulated 1000 times and the median values for the six most accurate or precise designs are reported, as well as for the traditional design (see Appendix 3 for full simulation results). CI is one side of the 90% CI width, reported as a percentage of the population estimate and accuracy is the absolute difference from the true population size, reported as a percentage of the true population size with a lower value indicating higher accuracy. In 2008, there were 885 mule deer observed in the survey, and in 2009 there were 1354 observed.

Stratification	Strata Binning	Allocation of Effort	2008				2009			
			CI	CV	Accuracy	DEFF	CI	CV	Accuracy	DEFF
Mule RSF	Jenks	Equal	49%	27%	20%	0.07	50%	28%	22%	0.04
Combined RSF	Jenks	Equal	51%	29%	21%	0.07	50%	28%	22%	0.04
WTD RSF	Jenks	Equal	54%	30%	21%	0.08	53%	30%	22%	0.04
WTD RSF	20:60:20	Optimal	53%	30%	21%	0.09	56%	32%	23%	0.08
Cover	Jenks	Optimal	52%	29%	23%	0.07	53%	30%	26%	0.04
Cover	Equal	Optimal	54%	30%	20%	0.10	61%	34%	26%	0.10
*Historical	20:60:20	Equal	73%	41%	31%	0.33	81%	46%	32%	0.46

* Survey design traditionally used by Alberta Fish and Wildlife

Table 2-5. Median coefficients of variation (CV), 90% confidence intervals (CI) and accuracy of estimated number of white-tailed deer from simulated aerial surveys under three stratification schemes, strata binning strategies, and allocation strategies. Each design was simulated 1000 times and the median values for the six most accurate or precise designs are reported, as well as for the traditional design (see Appendix 3 for full simulation results). CI is one side of the 90% CI width, reported as a percentage of the population estimate and accuracy is the absolute difference from the true population size, reported as a percentage of the true population size with a lower value indicating higher accuracy. In 2008, there were 1183 mule deer observed in the survey, and in 2009 there were 2142 observed.

Stratification	Strata Binning	Allocation of Effort	2008				2009			
			CI	CV	Accuracy	DEFF	CI	CV	Accuracy	DEFF
Mule RSF	Jenks	Optimal	36%	20%	14%	0.12	41%	23%	18%	0.09
Mule RSF	Jenks	Equal	39%	22%	16%	0.15	38%	22%	17%	0.05
Mule RSF	Equal	Optimal	36%	20%	15%	0.13	43%	24%	19%	0.11
Cover	Jenks	Equal	38%	21%	17%	0.13	43%	24%	18%	0.07
WTD RSF	Equal	Optimal	40%	22%	16%	0.15	44%	25%	18%	0.12
Combined RSF	Jenks	Optimal	41%	23%	16%	0.24	44%	25%	20%	0.10
*Historical	20:60:20	Equal	54%	31%	21%	0.54	61%	34%	31%	0.58

* Survey design traditionally used by Alberta Fish & Wildlife

Table 2-6. Population estimate (N), Coefficient of variation (CV) and 90% confidence intervals (CI) of white-tailed and mule deer population estimates for the original survey conducted in WMU 234 in 2003 based on the traditional survey design (see text), post-stratified by mule deer, white-tailed deer, and combined resource selection function (RSF) average for a survey unit.

Design	White-tailed Deer			Mule Deer		
	N	CI	CV	N	CI	CV
Traditional	2639	67%	38%	2702	58%	33%
Post-stratified (Combined RSF)	2775	41%	23%	2476	48%	27%
Post-stratified (Mule deer RSF)	3428	38%	22%	2861	54%	31%
Post-stratified (White-tailed deer RSF)	2884	52%	25%	2569	56%	33%

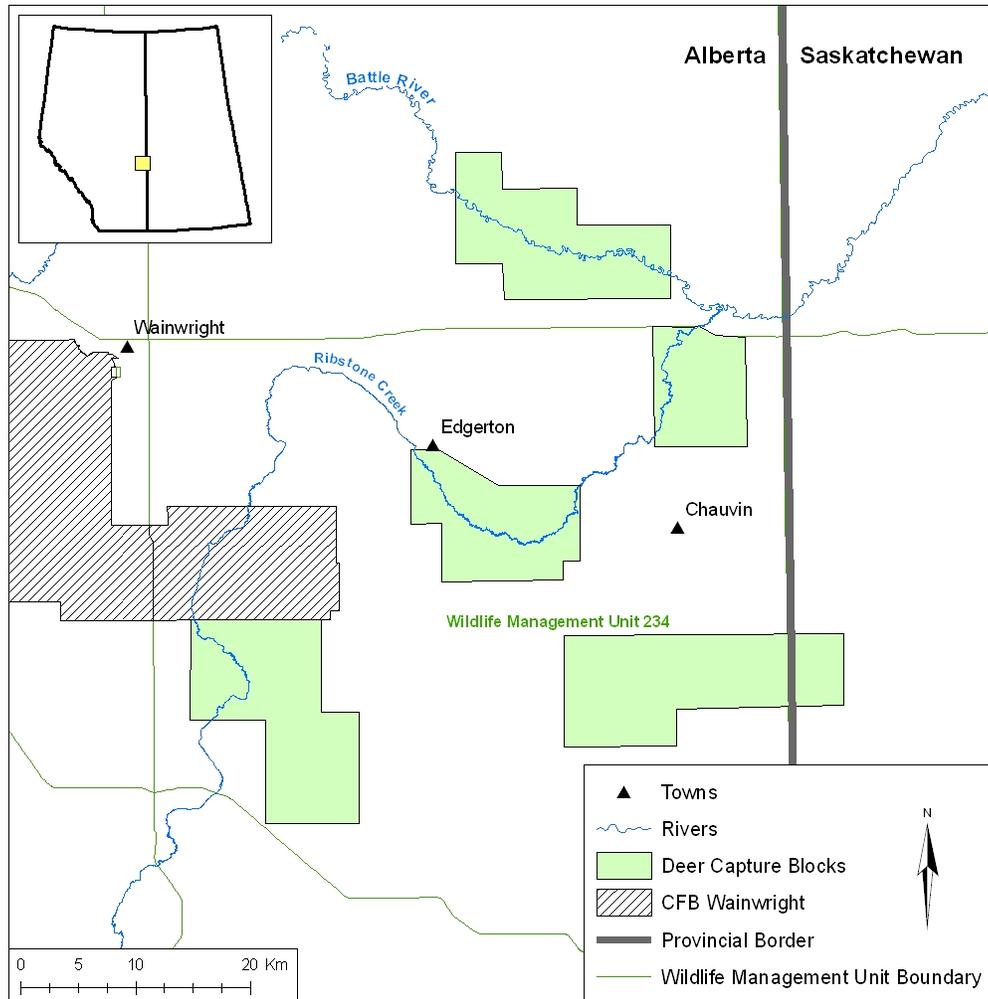


Figure 2-1. Study area in east-central Alberta centred in Wildlife Management Unit 234. Areas where white-tailed and mule deer were captured and relocated from 2007-2009 are highlighted.

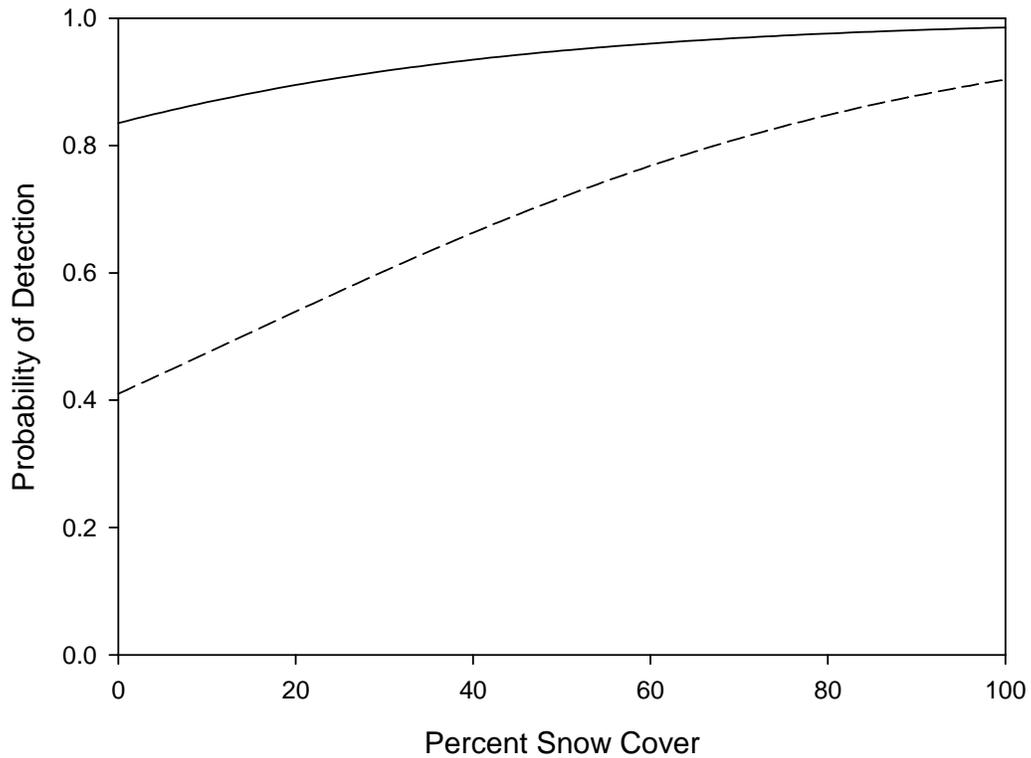


Figure 2-2. Effect of snow cover on white-tailed and mule deer sightability when deer are first observed standing (solid line) and bedded (dashed line), the two most common activity states. All other variables were held constant at their average (for continuous variables) or modal (for categorical variables) values. The sightability model was based on 100 trials of 46 mule and 54 white-tailed deer conducted from 2008-2009 in the prairie parkland of east-central Alberta.

2.6 Literature Cited

- Agriculture and Agri-Food Canada. 2009. *Circa 2000 Land Cover for Agricultural Regions of Canada*. Government of Canada, Ottawa, Canada. URL http://ftp://ftp.agr.gc.ca/pub/outgoing/nlwis-lc/LCV_CA_AAFC_30M_2000_V12/Mosaic [accessed 1 May 2009]
- Allen, J.R. 2005. Use of sightability models and resource selection functions to enhance aerial population surveys of elk (*Cervus elaphus*) in Alberta. MSc thesis, University of Alberta.
- Allen, J. R., L. E. McInenly, E. H. Merrill, and M. S. Boyce. 2008. Using resource selection functions to improve estimation of elk population numbers. *Journal of Wildlife Management* 72:1798-1804.
- Anderson, C. R., and F. G. Lindzey. 1996. Moose sightability model developed from helicopter surveys. *Wildlife Society Bulletin* 24:247-259.
- Bender, L. C., W. L. Myers, and W. R. Gould. 2003. Comparison of helicopter and ground surveys for North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus* population composition. *Wildlife Biology* 9:199-205.
- Anderson, C. R., D. S. Moody, B. L. Smith, F. G. Lindzey, and R. P. Lanka. 1998. Development and evaluation of sightability models for summer elk surveys. *Journal of Wildlife Management* 62:1055-1066.
- Bender, L.C., W.L. Myers, and W.R. Gould. 2003. Comparison of helicopter and ground surveys for North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus* population composition. *Wildlife Biology* 9:199-205.
- Bird, R.D. 1961. *Ecology of the Aspen Parkland of Western Canada in Relation to Land Use*. Canada Department of Agriculture, Ottawa.
- Brown, S., J. Bart, R. B. Lanctot, J. A. Johnson, S. Kendall, D. Payer, and J. Johnson. 2007. Shorebird abundance and distribution on the coastal plain of the Arctic National Wildlife Refuge. *Condor* 109:1-14.
- Burnham, K. P. and D. R. Anderson. 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*, 3rd edn. Springer Verlag, New York.
- Caughley, G., R. Sinclair, and D. Scott-Kemmis. 1976. Experiments in aerial survey. *Journal of Wildlife Management* 40:290-308.

- Christman, M. C. 2000. A review of quadrat-based sampling of rare, geographically clustered populations. *Journal of Agricultural Biological and Environmental Statistics* 5:168-201.
- Clover, M. R. 1954. A portable deer trap and catch-net. *California Fish and Game* 40:367-373.
- Dorr, B. S., L. W. Burger, and S. C. Barras. 2008. Evaluation of aerial cluster sampling of double-crested cormorants on aquaculture ponds in Mississippi. *Journal of Wildlife Management* 72:1634-1640.
- Dressel, S. C., and B. L. Norcross. 2005. Using poststratification to improve abundance estimates from multispecies surveys: a study of juvenile flatfishes. *Fishery Bulletin* 103:469-488.
- Environment Canada. 2009. *Canadian climate weather normals, 1971-2000*. Government of Canada, Ottawa. URL http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html [accessed 12 October 2009]
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38-49.
- Freddy, D. J., G. C. White, M. C. Kneeland, R. H. Kahn, J. W. Unsworth, W. J. deVergie, V. K. Graham, J. R. Ellenberger, and C. H. Wagner. 2004. How many mule deer are there? Challenges of credibility in Colorado. *Wildlife Society Bulletin* 32:916-927.
- Gasaway, W.C., S. D. DuBois, D. J. Reed, and S. J. Harbo. 1986. *Estimating Moose Population Parameters from Aerial Surveys*. Institute of Arctic Biology, University of Alaska, Fairbanks.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887-898.
- Glasgow, W. M. 2000. *White Area Ungulate Management Plan, 1997-98 to 1999-2000 Project Completion Report*. Alberta Fish and Wildlife, Edmonton.
- Guschanski, K., L. Vigilant, A. McNeilage, M. Gray, E. Kagoda, and M. M. Robbins. 2009. Counting elusive animals: Comparing field and genetic census of the entire mountain gorilla population of Bwindi Impenetrable National Park, Uganda. *Biological Conservation* 142:290-300.

- Harbitz, A., M. Aschan, and K. Sunnana. 1998. Optimal effort allocation in stratified, large area trawl surveys, with application to shrimp surveys in the Barents Sea. *Fisheries Research* 37:107-113.
- Hata, D., and J. Berkson. 2004. Factors affecting horseshoe crab *Limulus polyphemus* trawl survey design. *Transactions of the American Fisheries Society* 133:292-299.
- Highfield, L. D., M. P. Ward, S. W. Laffan, B. Norby, and G. Wagner. 2009. The impact of seasonal variability in wildlife populations on the predicted spread of foot and mouth disease. *Veterinary Research* 40:15.
- Hone, J. 2008. On bias, precision and accuracy in wildlife aerial surveys. *Wildlife Research* 35:253-257.
- Jenks, G. F. 1967. The data model concept in statistical mapping. *International Yearbook of Cartography* 7:186-190.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347-357.
- Johnson, C. J., and D. R. Seip. 2008. Relationship between resource selection, distribution, and abundance: a test with implications to theory and conservation. *Population Ecology* 50:145-157.
- Khaemba, W. M., A. Stein, D. Rasch, J. De Leeuw, and N. Georgiadis. 2001. Empirically simulated study to compare and validate sampling methods used in aerial surveys of wildlife populations. *African Journal of Ecology* 39:374-382.
- Kjær, L. J., E. M. Schaubert, and C. K. Nielsen. 2008. Spatial and temporal analysis of contact rates in female white-tailed deer. *Journal of Wildlife Management* 72:1819-1825.
- Lehtonen, R. and E. Pahkinen. 1994. *Practical Methods for Design and Analysis of Complex Surveys*. John Wiley and Sons, New York.
- McIntosh, T. E., R. C. Rosatte, J. Hamr, and D. L. Murray. 2009. Development of a sightability model for low-density elk populations in Ontario, Canada. *Journal of Wildlife Management* 73:580-585.
- McPherson, J. M., W. Jetz, and D. J. Rogers. 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology* 41:811-823.

- Mier, K. L., and S. J. Picquelle. 2008. Estimating abundance of spatially aggregated populations: Comparing adaptive sampling with survey designs. *Canadian Journal of Fisheries and Aquatic Sciences* 65:176-197.
- Moore, D. 2003. *WMU 234 Ungulate Survey: January 18-20, 2003*. Alberta Fish and Wildlife, Vermillion.
- Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* 82:591-605.
- Nixon, C. M., L. P. Hansen, P. A. Brewer, and J. E. Chelsvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife monographs* 18:1-77.
- Pearse, A. T., S. J. Dinsmore, R. M. Kaminski, and K. J. Reinecke. 2008. Evaluation of an aerial survey to estimate abundance of wintering ducks in Mississippi. *Journal of Wildlife Management* 72:1413-1419.
- Pearse, A. T., K. J. Reinecke, S. J. Dinsmore, and R. M. Kaminski. 2009. Using simulation to improve wildlife surveys: wintering mallards in Mississippi, USA. *Wildlife Research* 36:279-288.
- Pettorelli, N., S. D. Cote, A. Gingras, F. Potvin, and J. Huot. 2007. Aerial surveys vs hunting statistics to monitor deer density: the example of Anticosti Island, Quebec, Canada. *Wildlife Biology* 13:321-327.
- Potvin, F., L. Breton, and L.P. Rivest. 2002. Testing a double-count aerial survey technique for white-tailed deer, *Odocoileus virginianus*, in Quebec. *Canadian Field-Naturalist* 116:488-496.
- Prenzlow, D. M., and J. R. Lovvorn. 1997. Design and results of a waterfowl breeding population survey for Wyoming. *Journal of Wildlife Management* 61:758-767.
- Rabe, M. J., S. S. Rosenstock, and J. C. deVos. 2002. Review of big-game survey methods used by wildlife agencies of the western United States. *Wildlife Society Bulletin* 30:46-52.
- Rice, C. G., K. J. Jenkins, and W. Y. Chang. 2009. A sightability model for mountain goats. *Journal of Wildlife Management* 73:468-478.
- Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* 5:1-4.

- Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. *Journal of Wildlife Management* 51:622-630.
- Sinclair, A. R. E., J. M. Fryxell, and G. Caughley. 2006. *Wildlife Ecology, Conservation, and Management*, 2nd edn. Blackwell Publishing, Malden.
- Smith, D. R., J. A. Brown, and N. C. H. Lo. 2004. Applications of adaptive sampling to biological populations. *Sampling for Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters* (ed W. L. Thompson), pp. 77-122. Island Press, Washington.
- Smith, D. R., M. J. Conroy, and D. H. Brakhage. 1995. Efficiency of adaptive cluster sampling for estimating density of wintering waterfowl. *Biometrics* 51:777-788.
- Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. *Biometrics* 45:415-425.
- Su, Z. M., and T. J. Quinn. 2003. Estimator bias and efficiency for adaptive cluster sampling with order statistics and a stopping rule. *Environmental and Ecological Statistics* 10:17-41.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285-1293.
- Thompson, S. K. 1990. Adaptive cluster sampling. *Journal of the American Statistical Association* 85:1050-1059.
- Thompson, S. K. 2002. *Sampling*, 2nd edn. John Wiley and Sons, New York.
- Unsworth, J. W., L. Kuck, and E. O. Garton. 1990. Elk sightability model validation at the national-bison-range, Montana. *Wildlife Society Bulletin* 18:113-115.
- Unsworth, J. W., F. A. Leban, E. O. Garton, D. J. Leptich, and P. Zager. 1999. *Aerial Survey: User's Manual*, electronic edn. Idaho Department of Fish and Game, Boise.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th edn. Prentice Hall, New Jersey.

CHAPTER 3
MODELLING THE EFFECTS OF DENSITY AND LANDSCAPE ON
CONTACT RATES AMONG DEER

3.1 Introduction

Infectious wildlife diseases are of serious concern due to their economic, ecological, and human health consequences (Bengis *et al.* 2004), but predicting their consequences is extremely challenging for most diseases due limited knowledge of transmission dynamics. Two modes of transmission that typically form the basis of epidemiological models are density-dependent (DD) transmission and frequency-dependent (FD) transmission, which describe how the per capita contact rate, or the number of hosts encountered per individual per unit time, changes with density (Begon *et al.* 2002). In DD transmission, the contact rate increases linearly with host density, whereas in FD transmission the contact rate is constant. Assumptions underlying strictly DD or FD transmission are likely unrealistic descriptions of how hosts interact, so perhaps unsurprisingly neither mode of transmission is particularly well-supported by empirical studies (McCallum *et al.* 2001; Lloyd-Smith *et al.* 2005). More realistic models of contact rate may be represented by a general contact-density equation that allows for a wider range of relationships than simple linear dynamics (Smith *et al.* 2009):

Equation 3-1

$$c = k \left(\frac{N^{(1-q)}}{A} \right)$$

In this equation, c is the per capita contact rate, k and q are constants, N is the host population size, and A is the area inhabited by the host population. k represents an overall scaling constant particular to a host-pathogen system. Of particular consequence is q , a dimensionless scaling constant ≤ 1 that dictates the concavity of the density-contact rate relationship. DD and FD contact rates are obtained in the special cases where q is equal to 0 or 1, respectively, but other values of q yield nonlinear relationships (Figure 3-1).

Suggested mechanisms leading to nonlinear density-contact relationships include social structure (Altizer *et al.* 2003; Schaubert and Woolf 2003; Schaubert *et al.* 2007), heterogeneous mixing among hosts (Barlow 2000; Meyers *et al.* 2005), or changes in individual behaviour with density such as dispersal rates (Sandell *et al.* 1990) or home range size (White *et al.* 1995; Ramsey *et al.* 2002). Although studies of infectious disease transmission have traditionally focussed on how host density affects contact rates, recently there has been a greater appreciation of how landscape features may also shape disease transmission and prevalence (Ostfeld *et al.* 2005). Landscape heterogeneities may influence contact rates by altering host behaviour in a number of ways, such as influencing home range size (Kie *et al.* 2002; Walter *et al.* 2009), leading to aggregated host distributions (Highfield *et al.* 2009), or concentrating host use at particular types of resources (Greer and Collins 2008). In addition to fostering disease transmission in particular regions, these landscape mechanisms may also have an interacting effect on the density-contact relationship.

CWD is a fatal prion disease of free-ranging cervids (Williams and Young 1980), and the first wild case in Alberta was detected in a mule deer in 2005 near Oyen, in southeast Alberta along the Saskatchewan border. CWD was subsequently detected in a mule deer in Wildlife Management Unit (WMU) 234 near Chauvin, Alberta in 2006, approximately 150 km north of Oyen (Alberta Sustainable Resource Development 2010). The disease may be transmitted both directly between animals (Williams *et al.* 2002) and indirectly through the environment (Miller *et al.* 2004, Miller *et al.* 2006; Johnson *et al.* 2007). By 2010, only 75 cases of CWD were confirmed in Alberta (Alberta Sustainable Resource Development 2010), with the majority of cases (91%) occurring in mule deer and higher prevalence in males (67% of confirmed cases), although it is unclear why these differences exist. The overall low prevalence provides little opportunity to statistically model the factors influencing disease prevalence as has been attempted in other jurisdictions (Miller and Conner 2005; Grear *et al.* 2006; Osnas *et al.* 2009). Due to these low prevalence levels and short history, it is unlikely that a significant environmental reservoir of infectious agent has become

established, so direct transmission may be the dominant transmission pathway in this region (Bollinger *et al.* 2004; Langenberg *et al.* 2008); as such, the present study focus on direct transmission only.

Direct transmission is governed by two quantities in Equation 1-1: the contact rate c , which may change with density, and the probability of transmission associated with a given contact, v , which is usually viewed as a constant (Begon *et al.* 2002) but may vary with the type of contact in question (*e.g.* grooming behaviour versus mating). Previous attempts to model CWD transmission have been based on fitting time-series prevalence data to epidemiological models (Gross and Miller 2001; Wasserberg *et al.* 2009), but this approach has been unable to determine whether CWD follows DD or FD transmission, in part because a longer-term dataset was required. Furthermore, a data-fitting approach cannot tease apart the potentially separate influences of c and v . Therefore, estimating the contact rate-density relationship directly in this system is necessary given the data deficiencies, and also has the advantage of isolating the effect of contact rates on disease transmission, potentially uncovering the mechanisms driving the observed differences in prevalence rates across species and sexes. Alternatively, if contact rates are found not to differ between species-sex classes, then the relative importance of transmission pathways such as the intensity of contacts between different host classes may be implicated as responsible for the observed differences in CWD prevalence.

Previous efforts to directly estimate deer contact rates have deployed GPS-collars on a sample of deer to determine pairwise contact rates (Schauber *et al.* 2007). Such studies are limited to recording contacts only among a sample of radiocollared hosts, whereas the per capita total contact rate must incorporate contacts with all hosts neighbouring an individual. Although extrapolating to a per capita total contact may be possible for low-density populations of hosts with minimal movements (*e.g.* Ramsey *et al.* 2002), it is infeasible to effectively track the movements of a sufficient number of individuals in a large population of mobile hosts such as deer. Instead, it may be possible to determine through ecological studies how factors such as group size and home range size and

overlap affect pairwise contact rates and then model how those factors change with density to determine the overall density-contact rate relationship (e.g. White *et al.* 1995).

Schauber *et al.* (2007) found that group membership had a strong effect on pairwise contact rates in white-tailed deer in Illinois, but they did not examine how group sizes changed with density. Ungulate group size is often nonlinearly related to density (Borkowski 2000; McLellan *et al.* 2010), which could contribute to a nonlinear density-contact rate relationship, and it has also been demonstrated to be affected by landscape in some ungulates (Jepsen and Topping 2004). Furthermore, unlike Illinois, Alberta has both mule deer and white-tailed deer, and group sizes may differ between species (Lingle 2003). Spatial overlap is also an important determinant of pairwise contact rates, particularly for deer in different social groups (Schauber *et al.* 2007). Spatial overlap is intimately linked with home range sizes, which in these species may be affected by density (Kilpatrick *et al.* 2001) and different landscape features in the two species (Kie *et al.* 2002; Walter *et al.* 2009).

Landscape can also affect contact rates through deer resource selection. Kjær *et al.* (2008) found that the majority of contact rates among deer in an agro-forested landscape occurred under forest cover. Strong selection for a limiting resource may increase contact rates due to processes occurring at two spatial scales. First, at the landscape level, spatial overlap among hosts could be increased through aggregated host distributions in certain habitats (Dumont *et al.* 1998; Joly *et al.* 2006). Second, within-home range microhabitat choices may increase the likelihood of two hosts coming together in space and time (Greer and Collins 2008). Resource selection, home range size, and group size all likely change seasonally, so I focused my study in winter when deer within agro-forested environments tend to aggregate their distribution on winter range and group sizes are largest (Nixon *et al.* 1991; Lingle 2003), potentially leading to higher contact rates (Farnsworth *et al.* 2006). Differences between white-tailed and mule deer in resource selection (Sawyer *et al.* 2006; Jenkins *et al.* 2007) or social grouping behaviour (Lingle 2003) may lead to differences in species-

specific contact rates that may account, at least in part, for the vastly different CWD prevalence rates in these two species in Alberta.

In this Chapter, I used empirical data on white-tailed and mule deer obtained from a telemetry study and aerial surveys to quantify resource selection and estimate factors affecting pairwise contact rates, home range size, and group size. I subsequently combined these relationships to develop simulated deer distributions across a range of densities in landscapes with varying extents and arrangements of woody (tree and shrub) cover. In each simulated distribution, I estimated the relative per capita total contact rate based on an individual's pairwise contact rates with all neighbouring individuals to determine how deer contact rates are affected by density and landscape. I expected woody cover to be strongly selected, because deer tend to select for cover in agro-forested environments during winter, and often concentrate their distribution in this habitat (Chapter 2; Nixon *et al.* 1991). If true, landscapes with limited woody cover may see higher contact rates as deer would be more aggregated compared to evenly wooded landscapes where distribution may be dispersed. Furthermore, if more contacts occur under woody cover (Kjær *et al.* 2008), then contact rates should be increased when cover is limiting and deer are more likely to use this limiting resource simultaneously. I hypothesized that the extent and arrangement of woody cover would also influence deer home range size (Kie *et al.* 2002; Walter *et al.* 2009), which could in turn influence spatial overlap among deer. Finally, if group size increases nonlinearly with density (*e.g.* McLellan *et al.* 2010), this could confer a nonlinear shape to the density-contact rate relationship. Combining the above relationships into simulated distributions allows for estimating a per capita total contact rate, which would be unfeasible for a real population of deer due to sampling constraints. To quantify the shape of the resulting density-contact relationship, I fit the estimated per capita total contact rates from each simulated distribution to Equation 3-1 and compared the resulting curves across species for predetermined landscape configurations. I discuss the implications of my results for potentially explaining the differences in CWD

prevalence between species and sexes observed in this region and addressing the efficacy of alternative disease management strategies.

3.2 Study Area

Data on deer distribution and movements used in this study were collected in Wildlife Management Unit (WMU), a 2600 km² area in east-central Alberta along the Saskatchewan border (52°41 N 110°8 W; Figure 2-1). The area is located in the aspen (*Populus tremuloides*) parkland, where vegetation consists of a heterogeneous mix of aspen stands ranging in size from small patches (~0.01 ha) to large contiguous blocks up to several square kilometres, interspersed throughout native grasslands, agricultural fields, and wetlands (Bird 1961). Topography is generally flat with gentle hills, with the exceptions of the Battle River and its tributary, Ribstone Creek, which are significant drainage features with associated deep river valleys. The climate is relatively dry, with warm summers and cold winters, with yearly precipitation from 1971 to 2000 averaging 421 mm with a cumulative snowfall of 108 cm (Environment Canada 2009). Agriculture, including both crops and ranching, is the principal land use in the region, but numerous small oil and gas development features are present as well. In addition to white-tailed and mule deer, elk (*Cervus elaphus*) and moose (*Alces alces*) are present in the region. Coyotes (*Canis latrans*) are the only significant mammalian predator in the area other than humans.

3.3 Methods

I modelled relative pairwise contact rates in winter between any two randomly sampled deer as a function of home range overlap and extent of deer habitat, and I also modelled winter deer group size and home range size as functions of deer density and landscape features. These relationships were then used to develop simulated distributions of deer at varying levels of density and in different landscapes, and for each distribution I estimated the relative per capita total contact rate by estimating the pairwise contact rates between a target individual and all neighbouring deer (Figure 3-2). I developed species-specific

resource selection functions (RSF) following Johnson *et al.* (2006) to establish the initial deer distributions on the landscape and determine what resources may influence deer home ranges.

3.3.1 Resource selection functions

I derived separate exponential RSFs for white-tailed and mule deer for guiding the placement of deer home ranges on the landscape in the simulated deer distributions. RSFs were based on movements of 31 adult (23 females, 8 males) GPS-collared white-tailed deer and 33 adult mule deer (22 females, 11 males) relocated during 2006-2008 at 1-6 hour intervals. Deer were captured using Clover traps (Clover 1954) baited with hay and oats or by helicopter net-gunning, and adults were fitted with a GPS collar (Lotek 3300S or Lotek 4400S). I modified collars deployed on males by adding an expandable section of elastic surgical tubing to accommodate neck-swelling during the rut, although this section broke on several collars causing them to drop off prematurely. All capture and handling procedures followed protocols approved by the University of Alberta Animal Care Committee (UA Permit #494701). Positional accuracy of collars were based on fixes taken every hour for 8 days within different vegetation cover types on a stationary collar hung 1 m off the ground prior to deployment on deer, and had an average location error of 8 ± 6 m over 1143 fixes out of 1148 attempts across all vegetation types.

I used locations collected from December through April (746-3192 locations per deer), and drew 1000 available points for each individual deer from within the deer's minimum convex polygon (MCP) home range (7.6-583.6 points/km²). I used mixed-effects logistic regression with the individual deer as a random effect (Gillies *et al.* 2006) to determine the best model of 10 *a priori* RSF models for each species. I used AIC corrected for small sample size (AIC_c) to select the best model (Burnham and Anderson 2002). Landscape covariates were measured at a 30 x 30-m cell resolution and included elevation (m) and topographic ruggedness index (TRI; Riley *et al.* 1999) derived from a 30-m digital elevation model. Percent woody (tree and shrub) cover was delineated

from a landcover map derived from Landsat 5 TM and/or 7 ETM+ multi-spectral imagery at a 30-m resolution (Agriculture and Agri-Food Canada 2009) and was measured at each deer and random point locations at two spatial scales (within 240 and 510-m radii buffers). Road and linear feature (roads, rail lines, seismic lines, and power lines) density (km/km^2), and oil/gas well density ($\#/\text{km}^2$) were measured within a 500-m radius buffer around each location. I measured the distance (m) to the nearest edge of woody cover, water body (lake/pond $> 100 \text{ m}^2$, river, or stream), road, and linear feature, and oil/gas wellpads. All layers were derived in ArcGIS 9.3.1 (ESRI, Redlands, CA, 2009). GIS base layers were obtained from Agriculture and Agri-Food Canada, Spatial Data Warehouse Ltd, and Saskatchewan Environment.

I used the top RSF model for each species to predict the RSF values for each 30-m cell within the study region. I then calculated a new value for each 30-m cell based on the average RSF values within a 1500-m radius, reflecting the scale of an average deer home range ($6.9 \pm 4.2 \text{ km}^2$; $n = 33$ mule deer and 31 white-tailed deer) under current deer densities ($6.5 \pm 5.1 \text{ deer}/\text{km}^2$). I used the same home range size for mule deer and white-tailed deer in winter because they did not differ ($t = 0.063$, $df = 62$, $P = 0.950$). The resulting values were rescaled from 0-1 by dividing by the maximum RSF value, and each new cell value represented the probability, P_{HR} , of a cell being the centroid of a deer home range in my simulated deer distributions used to estimate the total per capita contact rate.

3.3.2 Deer home ranges and pairwise contact rates

Home ranges and pairwise contact rates among adult deer were based on movements of GPS-collared deer. Winter home ranges for each deer were derived from a 95% utilization distribution (kernel) using the plug-in method to determine the bandwidth value (Gitzen *et al.* 2006). For pairs of deer that exhibited some amount of home range overlap, I calculated two metrics of joint space use: the volume of intersection (VI) of their utilization distributions (Millspaugh *et al.* 2004; Schaubert *et al.* 2007), and a proportional metric of home

range overlap index (OI). VI is a three-dimensional index that incorporates the intensity of use, and has minimum and maximum values of 0 and 1, representing no overlap and identical space use patterns, respectively (Millsbaugh *et al.* 2004). OI is a two-dimensional index calculated as the area of intersection of the 95% kernel home ranges of two deer, divided by the summed area of both individual home ranges. OI ranges from 0 at no overlap to 0.5 at full overlap. Because VI incorporates intensity of use, it is a more detailed index and is preferable to the two-dimensional OI for predicting pairwise contact rates (Schauber *et al.* 2007). However, because I could not derive deer intensity of use *per se* for my simulated deer distributions, I used OI in my simulations to estimate spatial overlap between two deer. I found evidence that VI and OI were correlated for both white-tailed ($r^2 = 0.59, n = 6, P = 0.07$) and mule deer ($r^2 = 0.89, n = 6, P < 0.01$), suggesting that OI is a suitable surrogate for VI.

For each pair of deer of either species with overlapping home ranges (17 pairs from 64 collared deer), I enumerated occasions when two deer were simultaneously relocated within 25 m of each other, and defined these occasions as direct contacts. Although not every close encounter would result in an actual contact event, the true number of direct contacts should be proportional to these close-proximity approaches, and 25 m was deemed to be an appropriate distance threshold given the precision and frequency of GPS collar relocations (Schauber *et al.* 2007; Kjær *et al.* 2008). Because not all GPS collars had identical sampling frequencies, I used only the sampling times when both animals were simultaneously relocated to estimate contact rates (Schauber *et al.* 2007). I calculated a relative index of pairwise contact rate as:

Equation 3-2

$$P_c = \frac{c_{25m}}{N_s}$$

where P_c represents the probability that at any point in time the two deer are within in 25 m of each other, c_{25m} is the number of observations when the pair of deer was within 25 m simultaneously, and N_s is the total number observations

when both deer were sampled simultaneously. Therefore, P_c represents a relative index of contact rates rather than the actual number contacts per unit time. To address my assumption that the majority of contacts occur in winter (Farnsworth *et al.* 2006), I examined the monthly distribution of P_c values summed across all deer pairs.

I next modelled P_c as function of spatial overlap of home ranges, percent woody cover within the area of home range intersection, species, sex, and whether a pair was of the same or different species and sex, and used a model selection approach based on AIC_c to choose the best model (Burnham and Anderson 2002). Because VI is more detailed than OI, I used VI as the metric of spatial overlap in my candidate models to determine what other variables influence P_c .

After selecting the best candidate model using VI, I redeveloped the top model but substituted OI for VI to obtain a final model to be used for estimating contact rates in the simulated deer distributions. In two cases, I excluded pairs from this analysis because I believed them to be members of the same social group, and expected P_c between individuals in the same social group to be an order of magnitude higher than between groups (Schauber *et al.* 2007). I used two criteria to judge whether deer were in the same social group. First, I used the approach of Schaubert *et al.* (2007) and calculated the degree of correlation of movements between each pair of deer. For each deer I summed the Universal Transverse Mercator x- and y- coordinates (easting and northing), which are inherently orthogonal and measured on the same scale (Schauber *et al.* 2007). I then calculated the univariate correlation (Pearson's r) between these summed coordinate values for each pair's simultaneous locations. Pairs with $r \geq 0.6$ were considered to be in the same social group (Schauber *et al.* 2007). Second, I considered P_c values that were $\geq 10x$ those of other pairs to be outliers, and therefore having a tight social bond.

Finally, I determined the relationship between deer home range size and deer density as well as several habitat features previously found to influence home range size in white-tailed and mule deer (Kie *et al.* 2002, Lingle 2003, Walter *et al.* 2009). Local deer densities were obtained from aerial surveys in WMU 234

conducted between 21-22 January 2008 and 15-21 January 2009 by Alberta Fish and Wildlife. Surveys were conducted from a Bell 206B Jet Ranger helicopter with a pilot and navigator in the front and two observers in the rear of the aircraft. Surveys consisted of the helicopter flying linear transects 400 m apart at approximately 50 m above ground level at a speed of 80-100 km/hr (Glasgow 2000). The number and location of all deer within 200 m on either side of the aircraft were recorded with an onboard GPS. Sightability during these surveys was high (~90%) due to high snow cover (Chapter 2). I used conspecific density within a deer's home range centroid as a predictor variable. Habitat features included terrain ruggedness quantified as the mean topographic ruggedness index (TRI) value (Riley *et al.* 1999), and several metrics of woody cover arrangement. The metrics of woody cover included were mean patch area, patch area coefficient of variation, edge density, area-weighted shape index, mean nearest neighbour distance to another woody cover patch, and contagion index; all metrics were calculated using the computer program FRAGSTATS (McGarigal *et al.* 2002). The minimum patch size of woody cover considered was a 30 x 30-m pixel. Because several metrics are closely related, I tested for collinearity among all variables and in the case of two variables having a $r > 0.6$, I only used one in the same model. Metrics of woody cover were calculated within a 1500-m radius buffer of each deer's home range centroid (Kie *et al.* 2002), which corresponded to the scale of the mean home range size in this study ($6.9 \pm 4.2 \text{ km}^2$, yielding a mean radius of 1482 m). I developed candidate models for each species in three steps that focused on selecting the best variables for woody cover pattern and extent. First, I developed univariate models with each metric of woody cover arrangement, and used AIC_c to determine which metric(s) best explained home range size in each deer species. Second, I combined the best metric(s) of woody cover arrangement with the extent of woody cover in a home range when they were not correlated, because home range size may be influenced by the amount of habitat as well as its arrangement. After selecting the best model accounting for extent and arrangement of woody cover, I developed three additional models by adding mean TRI value, local density, or deer sex. Finally, I also evaluated a

global model including woody cover extent and arrangement, TRI, density, and sex.

3.3.3 Deer densities and group sizes

I obtained a distribution of deer group sizes from the aerial surveys described above. During the survey, a group was defined as conspecific individuals within 20 m of each other, although in general groups were highly aggregated and easily distinguishable. Implicit in this classification of groups is an assumption that aggregated deer constituted social groups, rather than transient congregations around resources. To evaluate the importance of this assumption, I compared the resulting group size distribution to a distribution obtained from ground observations of deer groups which were recorded opportunistically whenever deer were encountered during field activities. Sex composition of the groups could not be estimated reliably because the surveys were conducted in mid-winter after the majority of males had dropped their antlers.

I modelled group size for both white-tailed and mule deer based on conspecific density using the data obtained from aerial surveys and extent of woody cover using a general linear mixed model (GLMM, R, R-Project for Statistical Computing, 2010). The surveyed area was divided into 3 x 3-km grid cells, and the number of deer of each species within a cell was derived for each grid cell by plotting the centroids of the deer groups in ArcMap 9.3.1 (ESRI, Redlands, CA, 2010) and summing the number of deer across all groups of deer in the grid cell. I included the grid cell ID as a random effect to account for including data observed in the same grid cells in 2008 and 2009. I used AIC_c as the criterion to select the best candidate model for each species (Burnham and Anderson 2002).

3.3.4 Per capita total contact rate

I simulated deer distributions within 10 x 10-km landscapes to explore the effects of deer density and landscape patterns on the relative per capita total contact rate (c_i). I simulated deer distributions for densities ranging from 0-12

deer/km² (at intervals of 0.5 deer/km²) in landscapes with 4 different extents of woody cover (12, 26, 53, and 67%). I developed 20 simulated distributions for each species under each density-woody cover combination. For simplicity, all simulated distributions were single-species, because I assumed interspecific spatial overlap, and therefore contacts, were minimal. Deer distributions were simulated using the Geospatial Modelling Environment extension (Beyer 2010) for ArcGIS 9.3.1. An assumption of my model was that deer habitat selection did not change with density.

Each deer distribution was simulated in the following steps. First, for each level of density I estimated the expected mean deer group size based on its relationship with density and woody cover developed above. Second, I estimated the expected home range size based on the species-specific relationships with the extent and arrangement of woody cover developed above. FRAGSTATS metrics are highly influenced by the scale at which they are calculated (Wu *et al.* 2002), so I could not simply calculate them for the 100 km² landscape. Instead, for each landscape I calculated representative values of each metric at the scale of a 1500-m radius circle, which was the scale used in the above relationships predicting home range size. I randomly placed 9 circles of this size in each landscape, calculated the metrics for each circle, and used the mean value of each metric across these 9 samples to calculate the expected mean home range size for each landscape.

Next, I located the centroid of a home range for each deer group based on the landscape's RSF_{HR} raster by randomly selecting a cell and comparing its P_{HR} value to a random probability value (P_{random}). Centroids were rejected if $P_{HR} < P_{random}$, and this process was repeated until all groups for a specified density were located in the landscape according the RSF_{HR} raster. I assumed all home ranges were circular, deer in the same group used the same home ranges, and home ranges of groups could overlap. Each deer group was assigned a group size and home range size drawn from normal distributions centred around the expected mean values for the landscape-density combination of the simulation. Standard deviations for each normal distribution were calculated from the residual variation

in group size or home range size not accounted for by the density and/or landscape predictor variables.

In each simulated distribution, I calculated c_t for a single, randomly selected target individual. c_t was calculated as the sum of the target individual's between-group contact rate (c_b) and within-group contact rate (c_w). To estimate c_b , I first calculated the home range overlap index (OI) between the target individual and all home ranges that overlapped its own. Second, I predicted the probability of pairwise contact (P_c) between the target deer and one member of each overlapping deer group, based on the pair's OI and the amount of woody cover within the area of home range intersection. Third, each P_c was multiplied by the size of the group in the overlapping home range, because I assumed the target deer would have equal amounts of contact with all members of another social group. The resulting P_c values were summed across all deer groups with home ranges intersecting the target animal's home range to obtain c_b . Thus, c_b was calculated as:

Equation 3-3

$$c_b = \sum_{i=1}^g P_{ci} n_i$$

where g is the number of deer groups intersecting the target deer home range, P_{ci} is the pairwise relative contact rate index between the target individual and each member of the i^{th} group, and n_i is the number of deer in the i^{th} group.

To calculate the target individual's within-group contact rate, c_w , I needed to account for the higher contact rates among deer in the same social group (Schauber *et al.* 2007), even assuming complete spatial overlap between group members as I did here. Therefore, I calculated P_c for the target deer and another deer in its social group using the same formula as for between-group pairs, but multiplied it by an inflation factor. Because the present study had a small number ($n = 2$) of within-group pairs of collared deer, I based the inflation factor on work by Schauber *et al.* (2007). Schauber *et al.* (2007) found pairwise contact rates for within-group pairs of GPS-collared deer to be 5-22 times higher than expected

based on spatial overlap, depending on the proximity criterion (distance in m) used to classify occasions as direct contacts, which in their study ranged from 100 m to 10 m. Therefore, I multiplied P_c by a range of inflation factors, f , ($f = 10, 20, \text{ or } 50$) to obtain the within-group pairwise contact rate, P_{cw} . To extrapolate to c_w , I multiplied P_{cw} by the number of other deer in the target group, minus the target individual. In using this approach, I assumed all deer within the target deer's social group had equal interactions with each other. Thus, c_w was calculated as:

Equation 3-4

$$c_w = P_{cw}f(n_j - 1)$$

where, P_{cw} is the calculated relative pairwise contact rate index between any two members of the target deer group, f is the inflation factor of 10, 20, or 50, and n_j is the number of deer in the target individual's group. The total contact rate, c_t , was calculated as the sum of c_b and c_w .

Finally, for each of the four landscapes, I used nonlinear least-squares regression to fit the values of c_t derived for each density to Equation 3-1 and estimate the values of the parameters k and q . I assessed the value of q to determine the shape of the contact-density relationship for each of the four landscapes.

3.4 Results

3.4.1 Resource selection functions

The models for white-tailed and mule deer RSFs with the lowest AIC_c included similar covariates (Table 3-1). Models that did not include extent of woody cover performed considerably poorer than those with woody cover included in both mule deer ($\Delta AIC_c = 688$) and white-tailed deer ($\Delta AIC_c = 1209$). Mule deer RSFs without terrain ruggedness also performed poorly ($\Delta AIC_c = 1664$). Distance to well-sites was a more important metric than well-site density in mule deer ($\Delta AIC_c = 141.8$), while in white-tailed deer the reverse was true ($\Delta AIC_c = 249.1$). The best species-specific RSF models were:

Equation 3-5, Equation 3-6

$$w_{mule} = \exp(0.5166X_1 + 0.1268X_2 + 0.0045X_3 + 0.00010X_4 - 0.00019X_5 - 0.00033X_6)$$

$$w_{wtd} = \exp(0.9698X_1 + 0.01189X_2 + 0.0026X_3 + 0.00053X_4 + 0.00018X_5 - 0.07577X_7)$$

where X_1 was the percent cover within 240 m, X_2 was terrain ruggedness index value within a 30 x 30-m cell, X_3 was elevation (m) within a cell, X_4 was distance to water (m), X_5 was distance to roads (m), X_6 was distance to wells (m), and X_7 was well density within 500 m.

3.4.2 Deer home ranges and pairwise contact rates

Home range sizes averaged $6.9 \text{ km}^2 \pm 4.3$ for mule deer and $6.8 \text{ km}^2 \pm 4.2$ for white-tailed deer, and were not different between species (t-test, $df = 62$, $P = 0.95$). Home range size in both species was not influenced by density or deer sex but was influenced by landscape (Table 3-2). The landscape metric best predicting white-tailed deer home range size was the mean nearest-neighbour distance among patches of woody cover (NN) within a 1500-m radius buffer of a deer's home range centroid point ($\Delta\text{AIC}_c > 2$ for all other metrics). The top model included NN and percent woody cover, although there was some support for a model that additionally included terrain ruggedness ($\Delta\text{AIC}_c = 2.02$; Table 3-2, Table 3-3). Mean nearest neighbour distance, percent woody cover, and terrain ruggedness averaged $101.7 \text{ m} \pm 22.2$, $47.2\% \pm 9.6$, and 1.75 ± 0.94 , respectively. I used the most parsimonious model including only NN and percent woody cover in the simulated deer distributions.

The best landscape metric for predicting mule deer home range size was density of woody cover edge ($\Delta\text{AIC}_c > 2$ for all other metrics). Because edge density and percent woody cover were correlated ($r = 0.64$), I did not include both variables in any model. There was similar support ($\Delta\text{AIC}_c < 2$) for models including edge density or edge density and terrain ruggedness value (Table 3-2, Table 3-3). Edge density averaged $66.1 \text{ m/ha} \pm 23.4$ while terrain ruggedness averaged 1.75 ± 0.72 . I used a final model averaged by Akaike weight to predict the expected mean home range size in the simulated mule deer distributions.

Outside the rut, pairwise relative contact rates were 5.04 times higher during winter (December-April, 0.0178 ± 0.0089) than during spring/summer (May-October, 0.0035 ± 0.0040) (Mann-Whitney U-test, $U = 2.19$, $df = 7$, $P = 0.028$; Figure 3-3). VI in winter ranged from 0.066-0.575 in 6 mule deer pairs and 0.016-0.382 in 6 white-tailed deer pairs. The average index of pairwise contact, P_c , for mule deer with overlapping home ranges in winter was 0.011 ± 0.013 and for white-tailed deer was 0.010 ± 0.013 . The top model for predicting P_c in winter included VI and percent woody cover in the region of home range overlap (Table 3-4). P_c increased with spatial overlap and as the amount of woody cover in the region of home range overlap decreased. Although I tested for effects of species and sex, models including any of these variables had little support ($\Delta AIC > 2$).

Indices of OI and VI were highly correlated across species ($r^2 = 0.80$; $n = 15$; $P < 0.01$). Further, there was similar weight of evidence for a model predicting pairwise contact rates based on OI and percent woody cover ($\Delta AIC = 2.38$) as there was for VI. Therefore, although VI may be a better index of spatial overlap, I used the following model in the simulated distributions of deer to predict pairwise contact rates of a target deer with all other deer with overlapping home ranges:

Equation 3-7

$$P_c = 0.0841(OI) - 0.0552(\% \text{ Cover}) + 0.0264$$

3.4.3 Deer group sizes

Average group sizes in winter were 6.5 ± 6.0 for mule deer and 4.2 ± 3.1 for white-tailed deer and were significantly different between species (t-test, $df = 1319$, $P < 0.001$). Ground observations found group sizes of 5.1 ± 5.0 for mule deer, which was significantly smaller than the mean group size obtained from aerial observations (t-test, $df = 695$, $P = 0.002$), and 4.4 ± 4.0 for white-tailed deer, which was not different from aerial observations (t-test, $df = 1153$, $P = 0.604$). Further, ground observations also found that mule deer groups were significantly larger than white-tailed deer groups (t-test, $df = 529$, $P = 0.028$).

There was more support for a log-log than a linear relationship between group size and local conspecific density for both species ($\Delta AIC_c = 1802$ for mule deer and $\Delta AIC_c = 2583$ for white-tailed deer; Figure 3-4). The best model predicting white-tailed deer group size included the natural logarithm of white-tailed deer density and percent of woody cover within 3-km² (Table 3-5). The top model predicting mule deer group size included only the natural logarithm of mule deer density within 3-km² (Table 3-5). I used the top model for each species to predict mean group size for given density-woody cover extents in the simulated deer distributions within 10 x 10-km landscapes (Table 3-6).

3.4.4 Per capita total contact rate

The relative per capita total contact rate (c_t) increased with deer density, resulting in $0 < q < 1$ under all conditions modelled, although c_t was strongly influenced by species and woody cover extent (Figure 3-5). Values of c_t were higher in low-cover relative to high-cover landscapes due to two processes. First, home range overlap among groups increased as woody cover decreased (Table 3-7) due to larger home ranges in these landscapes, particularly in white-tailed deer (Table 3-8). Second, pairwise contact rates were higher in overlap areas in low-cover landscapes (Table 3-4). As a result, the between-group contact rate in both species was almost linearly related to density with a faster rate of increase in low-cover landscapes, especially for white-tailed deer (Figure 3-6, Figure 3-7). Within-group contact rates were governed principally by group size, because home range overlap was assumed to be complete for deer in the same social group. Group sizes were larger in mule deer than white-tailed deer in all landscapes (Table 3-8) and saturated with increasing density (Figure 3-4). Because c_t was the net effect of both within- and between-group contacts, white-tailed deer had higher values of c_t than mule deer when woody cover was low (Figure 3-5), due to their high between-group contact rate. In contrast, when woody cover was abundant and between-group contacts were low, the larger group sizes in mule deer led to higher values of c_t (Figure 3-5). Increasing cover or increasing the within-group contact rate inflation factor (f) both had the effect

of increasing the relative importance of within-group contacts on calculating c_i , leading to higher values of q (Table 3-9). At higher values of q , c_i increased faster at low densities, but its rate of increase began to slow at lower densities compared to when q was lower (Figure 3-5).

3.5 Discussion

My findings that per capita total contact rates in both white-tailed and mule deer increased as a saturating function of deer density support arguments that CWD transmission should be intermediate between strict DD or FD transmission (Schauber and Woolf 2003; Schauber *et al.* 2007; Wasserberg *et al.* 2009), although no study has yet explicitly demonstrated a nonlinear density-transmission or density-contact rate relationship. The observed nonlinearity in the present study was due to the social structure of deer, whereby group sizes reached an asymptote at some density (Figure 3-4). The density-contact relationship was relatively robust to changes in the within-group contact rate inflation factor (f). Although increasing f had a positive effect on q , for all values of f that I evaluated the value of q fell between 0 and 1 and thus the resulting density-contact relationship had a saturating shape (Figure 3-1); that is, altering f changed only the degree, rather than the type, of concavity. As might be expected for non-territorial species such as deer, increasing density did not have an effect on home range size in either species (*e.g.* Lesage *et al.* 2000). Therefore, increasing density increased the amount of spatial overlap among deer home ranges and consequently the between-group contact rate.

Deer in this region selected for woody cover, and this influenced contact rates at two spatial scales. First, at large spatial scales, deer home ranges were distributed around areas with high extents of cover (*e.g.* Dumont *et al.* 1998; Chapter 2), leading to a large degree of home range overlap in low-cover landscapes because home ranges were aggregated around the few areas of woody cover. An important model assumption was that deer still selected for woody cover when density and intraspecific competition were high. Although I did not test for an effect of density on habitat selection, there is little evidence for such

density-dependent habitat selection in these species (Kohlmann and Risenhoover 1997; Nicholson *et al.* 2006). If deer did follow the Ideal Free Distribution (IFD; Fretwell and Lucas 1970) and moved into less-wooded habitats as density increased, the rate of increase in contacts with density would slow at higher levels of density. Therefore, my conclusion of a contact rate that saturates with density is likely robust to the assumption of a non-IFD because density-dependent habitat selection would reinforce rather than counteract this pattern.

Second, at the smaller scale of the individual deer home range, pairwise contact rates were higher between two deer that had less woody cover in their home range overlap area. This increase in pairwise contact rates with lower woody cover may be the result of both species selecting strongly for woody cover within their home ranges during winter, which is consistent with previous studies (Nixon *et al.* 1991; McClure *et al.* 2005). While preferential use of limited habitat would be expected to lead to an increased probability that two deer will come together in space and time, this has not been explicitly demonstrated. For example, Kjær *et al.* (2008) found that contacts among pairs of white-tailed deer in a similar agro-forested environment in Illinois occurred disproportionately under forest cover, although they did not examine whether the overall extent of jointly available forest contributed to a pair's observed pairwise contact rate. Nevertheless, there is evidence that strong selection for a limiting resource can be associated with high disease prevalence in other systems. For example, Greer and Collins (2008) found higher prevalence of the *Ambystoma tigrinum* virus in *A. tigrinum* larvae inhabiting ponds with sparse emergent vegetation, an important resource for the larvae, compared to evenly vegetated ponds.

Pairwise contact rates were not different between white-tailed and mule deer in areas of home range overlap. However, differences in how home range size and group size changed with landscape and density resulted in different species-specific values of c_i in simulated deer distributions under different conditions. I did not find support for differences in mean home range sizes across species, which is consistent with comparisons in sympatric populations elsewhere (Brunjes *et al.* 2009), but home range sizes were influenced by different features

in the two species: mule deer were affected by woody cover edge density, and white-tailed deer by extent of woody cover and mean nearest-neighbour distance between patches of cover, which has also been found in other populations of these species (Kie *et al.* 2002; Walter *et al.* 2009). Because white-tailed deer home range size was strongly inversely related to extent of woody cover and mule deer home range size was not, in low-cover landscapes white-tailed deer had much larger home ranges and therefore greater home range overlap. I observed larger group sizes in mule deer, although there is some uncertainty as to whether the mule deer groups observed in aerial surveys were truly social groups rather than congregations around resources. Although ground observations found mule deer groups to have 1.4 fewer individuals than what was observed during aerial surveys, the ground observations nevertheless found that mule deer formed larger groups than white-tailed deer. Furthermore, Lingle (2003) also observed larger group sizes in mule deer relative to white-tailed deer in a nearby sympatric population, and also found that mule deer groups exhibited higher stability. Larger group sizes among mule deer led to higher within-group contact rates relative to white-tailed deer. Because mule deer have a much higher prevalence of CWD, the higher within-group contact rate observed in mule deer suggests that within-group transmission may be the dominant pathway of CWD transmission. Indeed, several studies have found that CWD is readily transmitted throughout members of the same social group (Nakada 2009; Gear *et al. in press*), but this is the first evidence comparing the relative importance of within- and between-group contact rates across species.

Although the larger group sizes I observed in mule deer may, at least partially, account for the higher CWD prevalence in this species, none of my results were consistent with different contact rates between sexes that could account for the higher CWD prevalence in male deer. Pairwise contact rates within regions of home range overlap were not found to differ between female-female and male-female pairs. However, due to a small sample of collared males because of expandable collar drop-offs, none of my sampled pairs were male-male so I could not examine potential differences in this pair type. Male-female

contacts may be expected to decrease in winter following the rut due to sexual segregation (Main 2008); however, in this environment mixed-sex groups are highest during winter (Lingle 2003) implying a low degree of sexual segregation, which is consistent with other populations in winter (Bowyer and Kie 2004). Furthermore, large groups of mule deer have been reported to be more stable than white-tailed deer groups in winter (Lingle 2003). Greater group stability in winter could lead to higher contact rates and CWD prevalence in mule deer compared to white-tailed deer, but stable mixed-sex groups are not consistent with different prevalence rates between sexes. I found only weak evidence for differences in winter home range size between sexes ($\Delta AIC_c = 2.11$ for mule deer and $\Delta AIC_c = 2.84$ for white-tailed deer; Table 3-2), which suggests that home range overlap with other deer groups would not differ between sexes. Therefore, the higher rates of CWD in males are likely due to a different mechanism.

Sex differences in prevalence may be due to direct contacts outside winter, such as within male groups in spring and summer, male promiscuity, or males visiting rubs/scrapes during the rut (Hirth 1977; Gear *et al.* 2006).

Environmental transmission through rubs and scrapes may be particularly important because prion infectivity is increased by binding to certain soil particles (Johnson *et al.* 2007). Due to the short history of CWD in Alberta, I do not expect that a major environmental reservoir of infectious agent yet exists here such that ordinary foraging behaviour could result in acquiring CWD; however, key rub or scrape sites visited by multiple males in succession could plausibly serve as focal points for CWD transmission. Although differences in CWD prevalence may result from differences in the probability of transmission among species-sex classes (v , Equation 1-1), the total per capita contact rate (c) and therefore transmission will still be dependent on group size and home range overlap. Thus, the understanding developed here of how group size, home range overlap, and total contact rate are affected by density and landscape structure remains a key component for understanding disease transmission and for devising CWD control strategies based on herd reductions.

Table 3-1. Selected exponential models for species-specific resource selection functions derived using logistic regression for winter (December-April) using 746-3192 relocations per deer from 31 GPS-collared white-tailed deer and 33 GPS-collared mule deer in east-central Alberta from 2006-2008. Included are the model covariates, log-likelihood (LL), ΔAIC_c corrected for small sample size (ΔAIC_c), and model weight (w_i).

Species	Model	LL	ΔAIC_c	w_i
Mule Deer	Cover240, terrain, elev, dt_water, dt_roads, dt_wells	-51269.2	0.00	> 0.99
	Cover240, terrain, dt_roads, dt_wells	-51361.43	173.77	< 0.01
	Terrain, elev, dt_water, dt_roads, dt_well	-51419.10	295.89	< 0.01
	tri elev dt_water	-51618.61	688.13	< 0.01
	Cover240, dt_roads, dt_wells	-52106.57	1664.05	< 0.01
White-tailed Deer	Cover240, terrain, elev, dt_water, dt_roads, well_500	-49512.1	0.00	0.91
	Cover240, elev, dt_water, dt_roads, well_500	-49516.4	4.63	0.09
	Cover240, terrain, elev, dt_water	-49770.01	508.13	< 0.01
	Cover240, dt_roads, well_500	-49884	732.76	< 0.01
	Terrain, elev dt_water dt_roads well_500	-50118.9	1209.65	< 0.01

Cover240 = cover within 240 m; Cover510 = cover within 510 m; terrain = Terrain ruggedness (Riley *et al.* 1999); elev = elevation (m); dt_water = distance to water (m); dt_roads = distance to roads (m); dt_well = distance to wells (m); well_500 = well density within 500 m (#/km²).

Table 3-2. General linear models predicting the size of the 95% kernel winter range for 33 GPS- collared mule deer and 31 GPS-collared white-tailed deer radiocollared in east-central Alberta during 2006-2009. Included are the model covariates, log-likelihood (LL), ΔAIC_c corrected for small sample size (ΔAIC_c), and model weight (w_i).

Species	Model Variables	LL	ΔAIC_c	w_i
Mule Deer	Edge	-88.19	0.00	0.43
	Edge + Terrain	-87.22	0.67	0.31
	Edge + Sex	-87.94	2.11	0.15
	Global model	-86.39	4.80	0.07
	% Cover	-93.36	10.34	0.04
White-tailed Deer	% Cover + NN	-83.00	0.00	0.49
	% Cover, NN, Terrain	-82.58	2.02	0.18
	% Cover + NN + Density	-82.85	2.57	0.14
	% Cover + NN + Sex	-82.99	2.84	0.12
	% Cover	-86.77	4.88	0.04
	NN	-87.16	5.68	0.03
	Global model	-82.33	8.00	0.01

Edge = edge density of woody cover (m/ha); Terrain = mean topographic ruggedness index value (Riley *et al.* 1999); NN = mean nearest neighbour distance between patches of woody cover; Global model includes Edge, Terrain, Sex, and Density for mule deer; and % Cover, NN, Terrain, Sex, and Density for white-tailed deer.

Table 3-3. Coefficients (β) of the top models predicting the size of the 95% kernel winter range for 33 GPS-collared mule deer and 31 GPS-collared white-tailed deer radiocollared in east-central Alberta during 2006-2009.

Species	Variable	β	<i>P</i>
Mule Deer (Model 1) (Model 2)	Woody cover edge density (m/ha)	-0.097	< 0.001
	Constant	13.281	< 0.001
	Woody cover edge density (m/ha)	-0.109	< 0.001
	Topographic ruggedness index	-0.727	0.179
	Constant	15.710	< 0.001
	<hr/>		
White-tailed Deer	% Cover	-21.491	0.003
	Mean nearest neighbour distance between woody cover patches (m)	-0.088	0.006
	Constant	26.020	< 0.001
	<hr/>		

Table 3-4. Top general linear models predicting the probability of direct contact at a point in time, defined as a simultaneous relocation within 25 m for 15 pairs of GPS-collared deer, developed from 33 mule deer and 31 white-tailed deer radiocollared in east-central Alberta between 2007-2009. VI is the volume of intersection of a pair's utilization distributions (Millsaugh *et al.* 2004), an index of spatial overlap incorporating intensity of use. Included are the model covariates, log-likelihood (LL), ΔAIC_c corrected for small sample size (ΔAIC_c), and model weight (w_i).

Model	LL	ΔAIC_c	w_i
VI, % cover	53.52	0	0.45
VI, % cover, mixed sex	54.51	2.69	0.12
VI	49.84	3.54	0.08
VI, % cover, WTD	54.05	3.61	0.07
VI, % cover, mule	53.77	4.18	0.06
VI, % cover, same species	53.60	4.52	0.05
VI, mixed sex	50.07	6.91	0.01
VI, mule	49.88	7.29	0.01
VI, % cover, mule, mixed sex	54.64	8.27	0.01
VI, mule, mixed sex,	50.08	11.56	0.00

Table 3-5. General linear mixed models predicting winter group size for white-tailed and mule deer, calculated within $n = 98$ survey units of 9 km^2 obtained from aerial surveys conducted in east-central Alberta in January 2008 and 2009. Group size and densities were ln-transformed to linearize the data prior to model-fitting, except where indicated with *. Included are the model covariates, log-likelihood (LL), ΔAIC_c corrected for small sample size (ΔAIC_c), and model weight (w_i).

Model Variables		LL	ΔAIC_c	w_i
Mule Deer	Mule deer density	-582.42	0.00	0.81
	Mule deer density, Woody cover	-582.80	2.94	0.19
	*Mule deer density	-1483.38	1801.91	< 0.001
White-tailed Deer	White-tailed deer density, Cover	-865.58	0.00	0.95
	White-tailed deer density	-869.57	5.82	0.05
	*White-tailed deer density	-2158.2	2583.09	< 0.001

Table 3-6. Coefficients (β) of the top models predicting winter group size for white-tailed and mule deer, calculated within $n = 98$ survey units of 9 km^2 obtained from aerial surveys conducted in east-central Alberta in January 2008 and 2009. Group size and densities were log-transformed to normalize the data prior to model-fitting.

Species	Variable	β	P
Mule Deer	Mule deer density	0.250	< 0.001
	Constant	1.206	< 0.001
White-tailed Deer	White-tailed deer density	0.277	< 0.001
	% Woody cover	-0.475	0.001
	Constant	1.081	< 0.001

Table 3-7. Summed home range overlap index (OI) per individual white-tailed or mule deer with all neighbouring deer, derived from simulated deer distributions in each of four landscapes representative of east-central Alberta. OI values are averaged across 20 iterations at all simulated levels of density (0-12 deer/km²), and standard errors are included.

Species	12% Cover	26% Cover	53% Cover	67% Cover
Mule Deer	4.89 ± 0.14	3.39 ± 0.10	2.84 ± 0.09	3.49 ± 0.10
White-tailed Deer	8.71 ± 0.25	8.05 ± 0.22	5.70 ± 0.18	3.15 ± 0.10

Table 3-8. Expected mean home range size and group size in simulated distributions of white-tailed and mule deer in four landscapes representative of east-central Alberta. Group sizes are predicted at a representative density of 6 deer/km².

Landscape	Mean Home Range Size (km²)		Mean Group Size	
	Mule Deer	White-tailed Deer	Mule Deer	White-tailed Deer
12% Cover	9.25	13.55	5.2	4.6
26% Cover	6.53	12.13	5.2	4.3
53% Cover	6.76	7.72	5.2	3.8
67% Cover	6.66	3.97	5.2	3.5

Table 3-9. Estimated parameter values of k and q from Equation 3-1 used to model the total contact rate per individual, c_t , as a function of deer density in each of four different landscapes, under three different within-group contact rate inflation factors (I), in mule and white-tailed deer. All $P < 0.01$ for both parameters.

Species	Landscape	$I = 10$			$I = 20$			$I = 50$		
		k	q	r^2	k	q	r^2	k	q	r^2
Mule Deer	12% Cover	6.14	0.25	0.92	17.10	0.37	0.93	80.46	0.53	0.92
	26% Cover	6.94	0.34	0.91	21.46	0.46	0.91	90.85	0.59	0.88
	53% Cover	4.58	0.38	0.79	14.18	0.49	0.81	52.04	0.58	0.81
	67% Cover	13.20	0.59	0.75	39.70	0.68	0.78	137.53	0.76	0.79
White-tailed Deer	12% Cover	5.97	0.20	0.91	15.58	0.32	0.92	80.76	0.52	0.91
	26% Cover	4.34	0.22	0.93	11.35	0.34	0.93	54.17	0.51	0.90
	53% Cover	5.16	0.41	0.80	16.37	0.53	0.81	71.98	0.66	0.80
	67% Cover	4.59	0.50	0.69	15.41	0.61	0.71	56.73	0.69	0.70

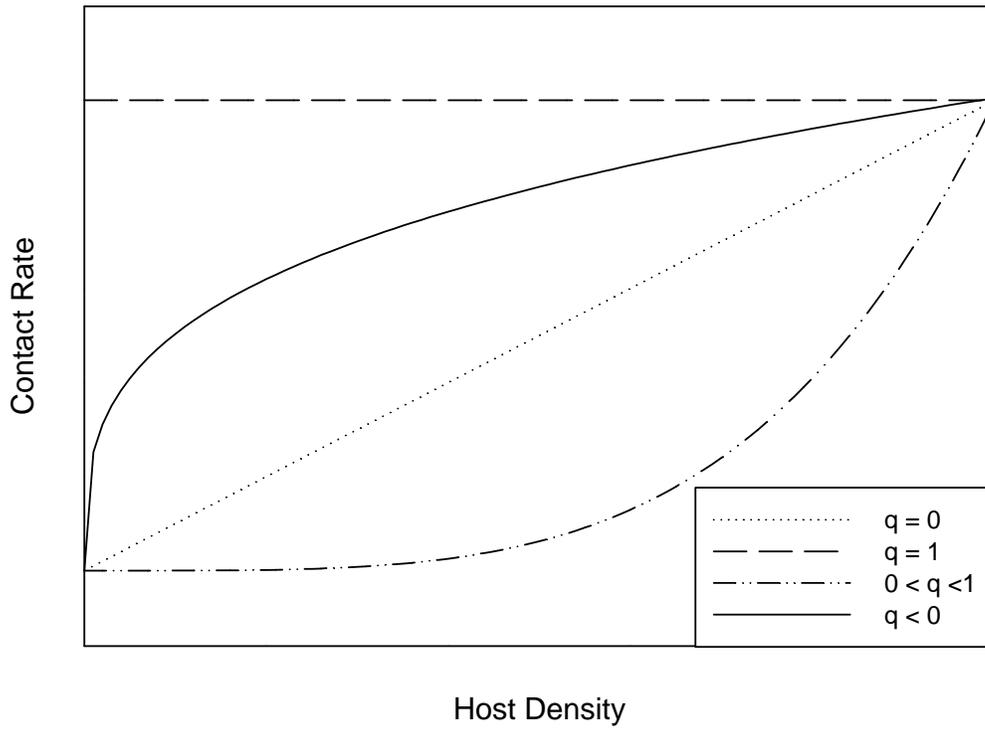


Figure 3-1. Per capita contact rate as a function of host population density, under different values of q from Equation 3-1. Adapted from Smith *et al.* (2009).

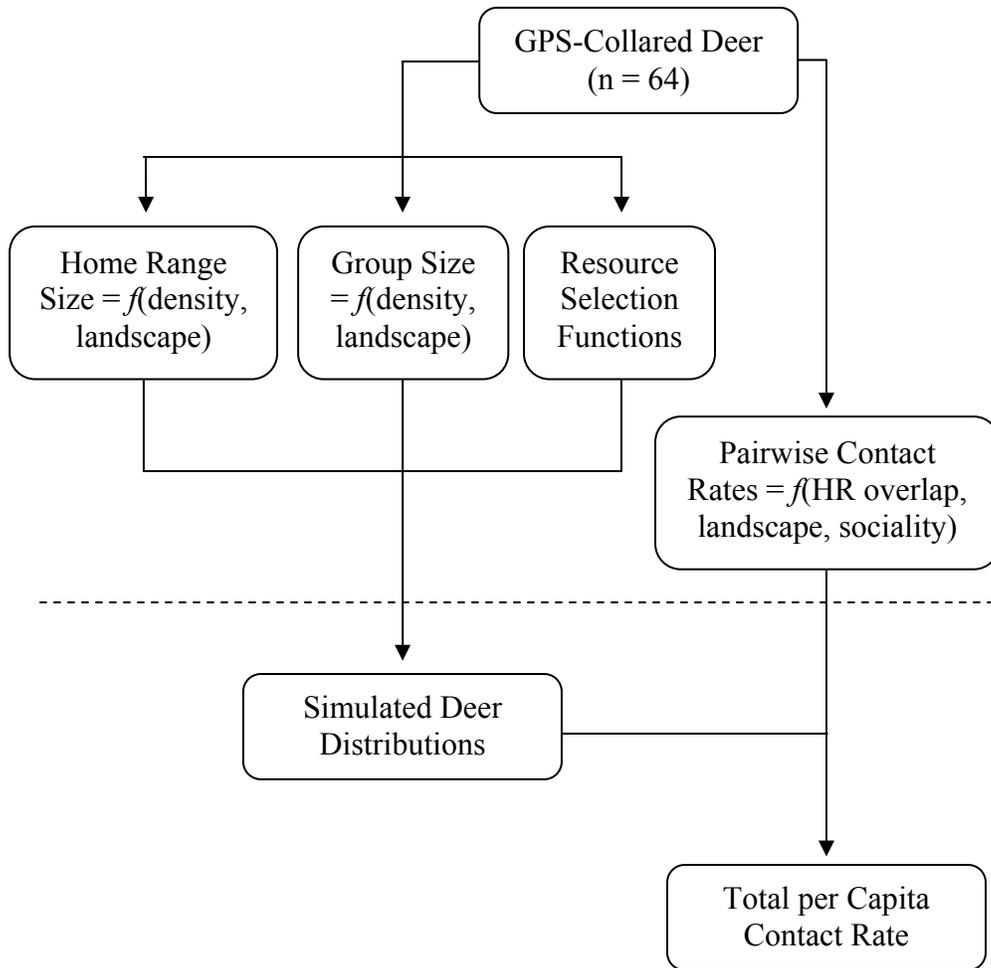


Figure 3-2. Organizational flow chart outlining data sources and methodology used to estimate total per capita contact rates among white-tailed and mule deer in east-central Alberta. Empirical data collected from 2006-2009 included a telemetry study of 64 GPS-collared deer (31 white-tailed deer and 33 mule deer) and aerial surveys. Items above the dashed line represent empirical data and/or relationships, and items below the dashed line were based on simulations developed using these empirical relationships.

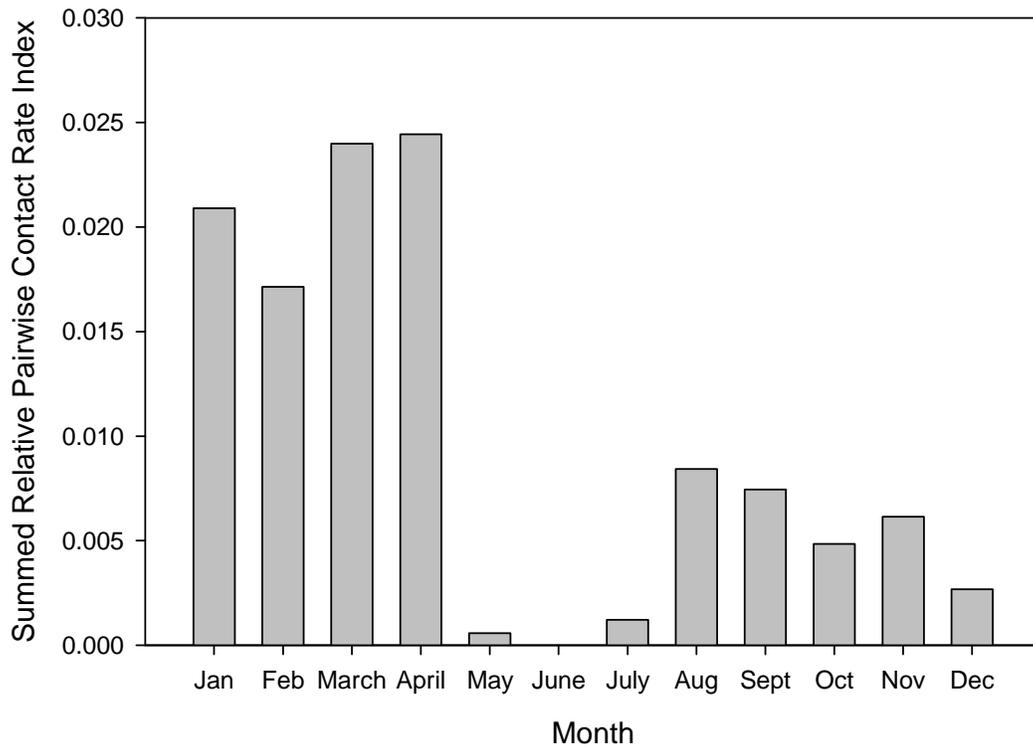


Figure 3-3. Probability of direct contact between a pair of deer at a given point in time, defined as a simultaneous relocation within 25 m, summed across 15 pairs of GPS-collared deer (33 mule deer and 31 white-tailed deer) radiocollared in east-central Alberta between 2007-2009.

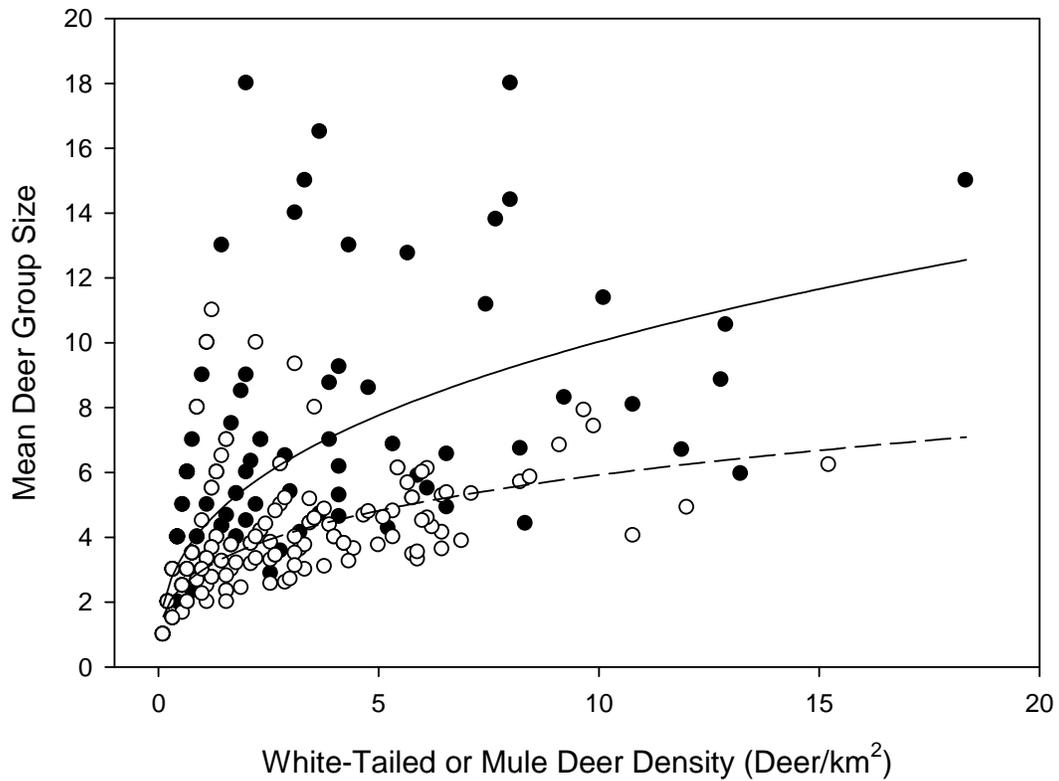


Figure 3-4. Mean white-tailed (open circles, dashed line) and mule deer (black circles, solid line) group size as a function of density within 9-km² survey blocks sampled in January 2008 and 2009 ($n = 114$ for white-tailed deer and $n = 133$ for white-tailed deer, because both species were not always present in the same block) in east-central Alberta. Log transformed group size were related to log transformed density for white-tailed ($r^2 = 0.48$; $P < 0.001$) and mule deer ($r^2 = 0.51$; $P < 0.001$).

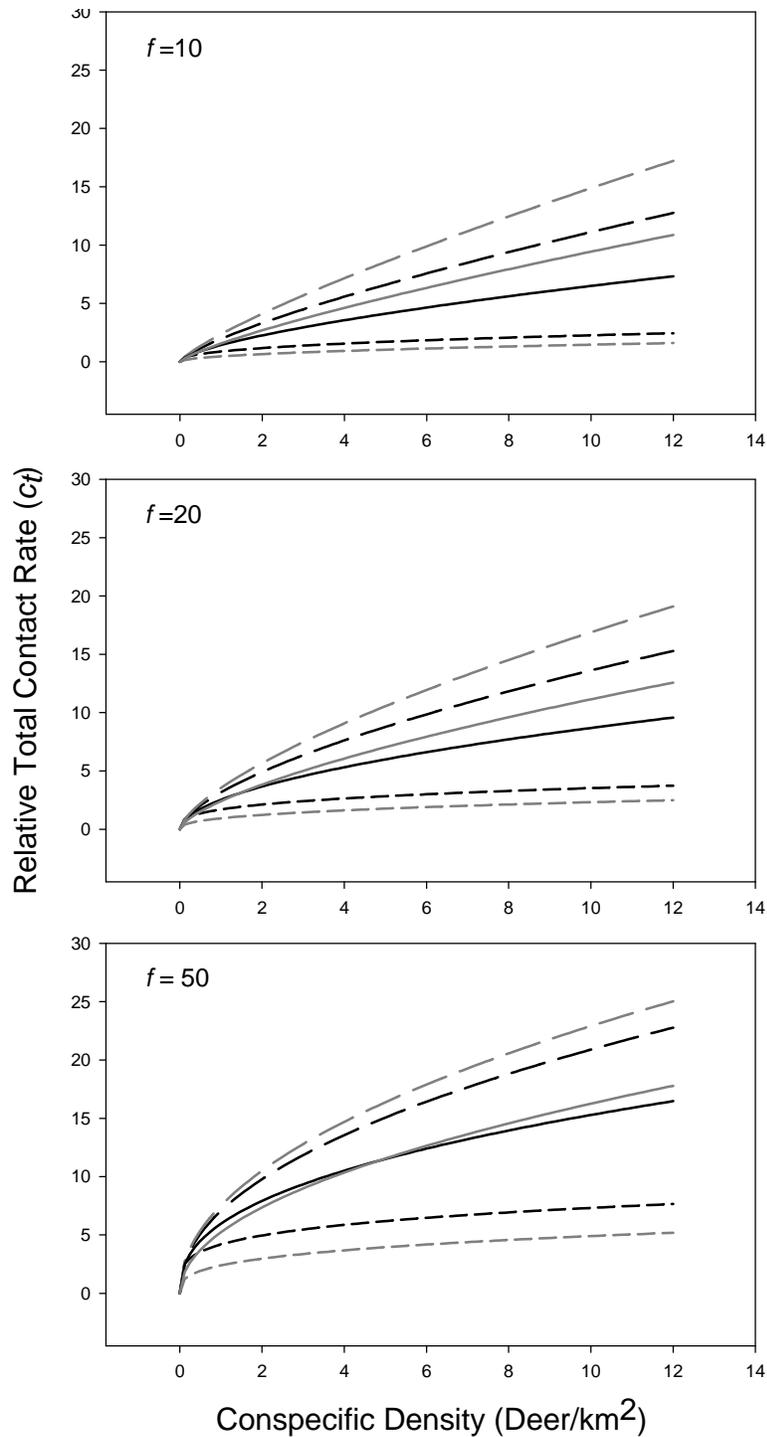


Figure 3-5. Relative per capita total contact rate, c_t (deer encountered/unit time), in mule (black) and white-tailed deer (grey) derived as a function of conspecific density in landscapes of 12% (long dash), 26% (solid line), and 67% (short dash) woody cover with within-group contact rates derived with inflation factors (f) of 10, 20, and 50 presented from top to bottom. Results from the 53% cover landscape were similar to the 67% landscape and are not presented.

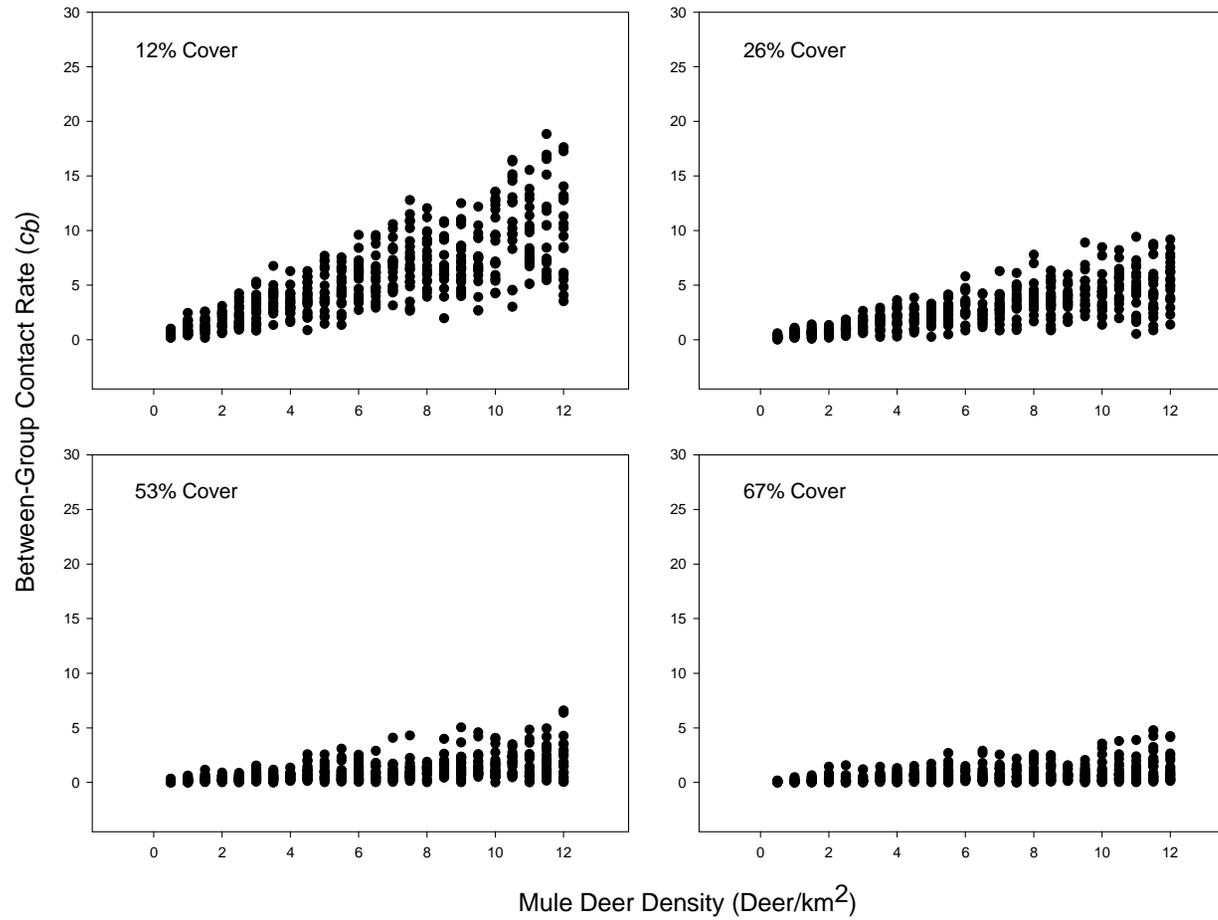


Figure 3-6. Relative per capita between-group contact rate, c_b (deer encountered/unit time), in mule deer as a function of density in each of four representative landscapes ranging from 12-67% forest cover, based on simulations developed for deer in aspen parkland communities of Alberta.

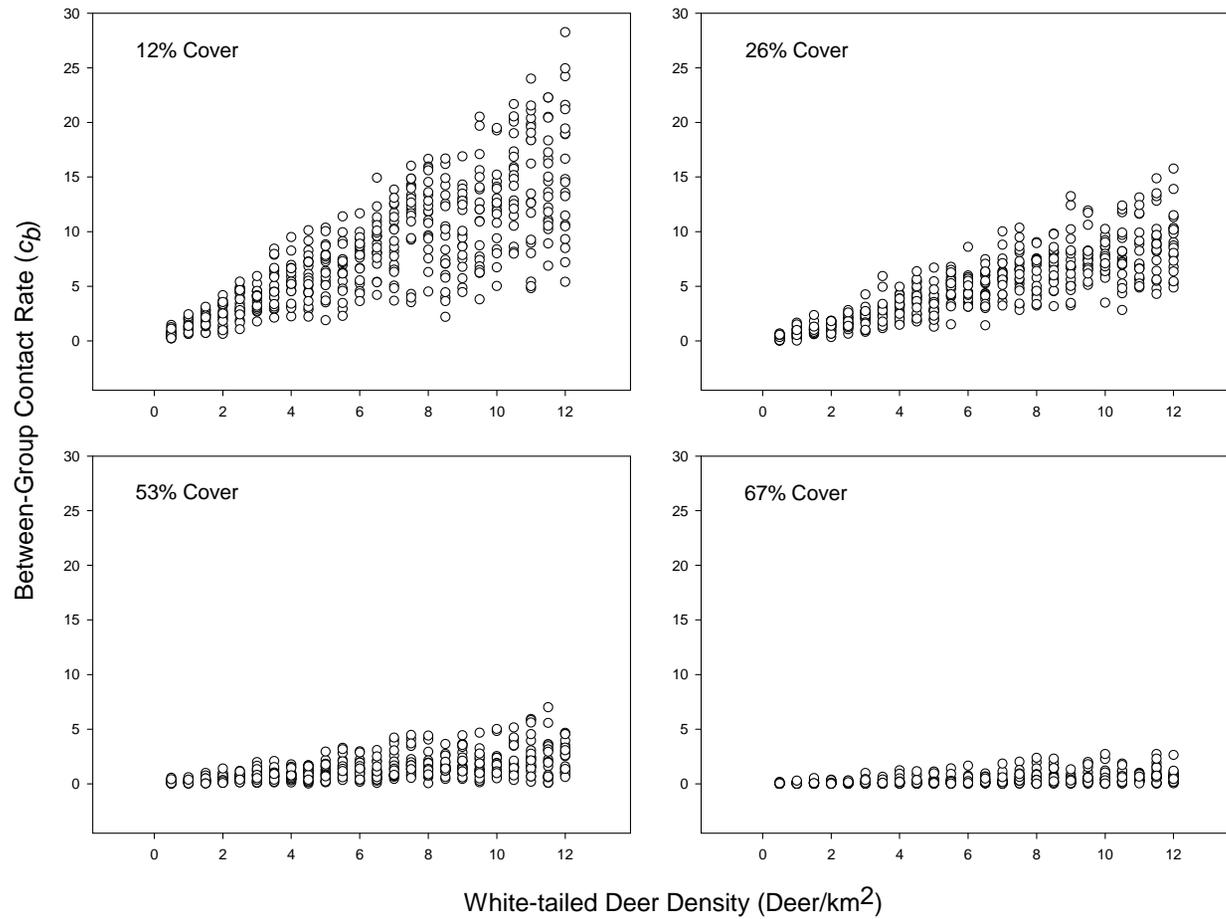


Figure 3-7. Relative per capita between-group contact rate, c_b (deer encountered/unit time), in white-tailed deer as a function of density in each of four representative landscapes ranging from 12-67% forest cover, based on simulations developed for deer in aspen parkland communities of Alberta.

3.6 Literature Cited

- Agriculture and Agri-Food Canada. 2009. *Circa 2000 Land Cover for Agricultural Regions of Canada*. Government of Canada, Ottawa, Canada. URL http://geodiscover.cgdi.ca/wes/RecordSummaryPage.do?uuid=F1E6A665-C15B-F64B-FC6D-4472BBA89F55&recordLocale=en_US&view=summary&entryPoint=jsMap&mode=unmapable [accessed 1 May 2009]
- Alberta Sustainable Resource Development. 2010. Statistics: Chronic Wasting Disease in Wild Deer. URL www.srd.alberta.ca/BioDiversityStewardship/WildlifeDiseases/ChronicWastingDisease.aspx [accessed 20 March 2010]
- Altizer, S., C. L. Nunn, P. H. Thrall, J. L. Gittleman, J. Antonovics, A. A. Cunningham, A. P. Dobson, V. Ezenwa, K. E. Jones, A. B. Pedersen, M. Poss, and J. R. C. Pulliam. 2003. Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology Evolution and Systematics* 34:517-547.
- Begon, M., M. Bennett, R. G. Bowers, N. P. French, S. M. Hazel, and J. Turner. 2002. A clarification of transmission terms in host-microparasite models: numbers, densities and areas. *Epidemiology and Infection* 129:147-153.
- Bengis, R. H., F. A. Leighton, J. R. Fischer, M. Artois, T. Morner, and C. M. Tate. 2004. The role of wildlife in emerging and re-emerging zoonoses. *Revue Scientifique et Technique de l'Office International des Epizooties* 23:497-511.
- Beyer, H. 2010. Geospatial Modelling Environment. ArcGIS Extension. URL www.spatial ecology.com
- Bird, R. D. 1961. *Ecology of the Aspen Parkland of Western Canada in Relation to Land Use*. Canada Department of Agriculture, Ottawa.
- Bollinger, T., P. Caley, E. Merrill, F. Messier, M. W. Miller, M. D. Samuel, and E. Vanopdenbosch. 2004. Expert scientific panel on chronic wasting disease. Chronic wasting disease in Canadian wildlife: an expert opinion on the epidemiology and risks to wild deer. Prepared for Canadian Cooperative Wildlife Health Centre, University of Saskatchewan. URL <http://wildlife1.usask.ca/Publications/CWD%20Expert%20Report%20Final%20-%2020040804.pdf> [Accessed 15 August 2007]
- Borkowski, J. 2000. Influence of the density of a sika deer population on activity, habitat use, and group size. *Canadian Journal of Zoology* 78:1369-1374.

- Bowyer, R. T., and J. G. Kie. 2004. Effects of foraging activity on sexual segregation in mule deer. *Journal of Mammalogy* 85:498-504.
- Burnham, K. P. and Anderson, D. R. 2002. *Model selection and inference: a practical information-theoretic approach*, 3rd ed. Springer Verlag.
- Clover, M. R. 1954. A portable deer trap and catch-net. *California Fish and Game*, 40, 367-373.
- Dumont, A., J. P. Ouellet, M. Crete, and J. Huot. 1998. Characteristics of winter forest habitats of the white-tailed deer along the northern border of its distribution area. *Canadian Journal of Zoology* 76:1024-1036.
- Environment Canada. 2009. *Canadian climate weather normals, 1971-2000*. Government of Canada, Ottawa. URL http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html [accessed 12 October 2009]
- Farnsworth, M. L., J. A. Hoeting, N. T. Hobbs, and M. W. Miller. 2006. Linking chronic wasting disease to mule deer movement scales: A hierarchical Bayesian approach. *Ecological Applications* 16:1026-1036.
- Fretwell, S. D. and J. H. J. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16-36.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887-898.
- Gitzen, R. A., J. J. Millspaugh, and B. J. Kernohan. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management* 70:1334-1344.
- Glasgow, W.M. 2000. *White Area Ungulate Management Plan, 1997-98 to 1999-2000 Project Completion Report*. Alberta Fish and Wildlife, Edmonton.
- Gear, D. A., M. D. Samuel, J. A. Langenberg, and D. Keane. 2006. Demographic patterns and harvest vulnerability of chronic wasting disease infected white-tailed deer in Wisconsin. *Journal of Wildlife Management* 70:546-553.
- Gear, D. A., M. D. Samuel, K. T. Scribner, B. V. Weckworth, and J. A. Langenberg. Influence of genetic relatedness and spatial proximity on chronic wasting disease infection among female white-tailed deer. *Journal of Applied Ecology* *in press*.

- Greer, A. L., and J. P. Collins. 2008. Habitat fragmentation as a result of biotic and abiotic factors controls pathogen transmission throughout a host population. *Journal of Animal Ecology* 77:364-369.
- Gross, J. E., and M. W. Miller. 2001. Chronic wasting disease in mule deer: disease dynamics and control. *Journal of Wildlife Management* 65:205-215.
- Highfield, L. D., M. P. Ward, S. W. Laffan, B. Norby, and G. Wagner. 2009. The impact of seasonal variability in wildlife populations on the predicted spread of foot and mouth disease. *Veterinary Research* 40:15.
- Hirth, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. *Wildlife Monographs* 53:3-55.
- Jenkins, D. A., J. A. Schaefer, R. Rosatte, T. Bellhouse, J. Hamr, and F. F. Mallory. 2007. Winter resource selection of reintroduced elk and sympatric white-tailed deer at multiple spatial scales. *Journal of Mammalogy* 88:614-624.
- Jepsen, J. U., and C. J. Topping. 2004. Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: behavioural plasticity and choice of cover. *Canadian Journal of Zoology* 82:1528-1541.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347-357.
- Johnson, C. J., J. A. Pedersen, R. J. Chappell, D. McKenzie, and J. M. Aiken. 2007. Oral transmissibility of prion disease is enhanced by binding to soil particles. *PLoS Pathogens* 3:874-881.
- Joly, D. O., M. D. Samuel, J. A. Langenberg, J. A. Blanchong, C. A. Batha, R. E. Rolley, D. P. Keane, and C. A. Ribic. 2006. Spatial epidemiology of chronic wasting disease in Wisconsin white-tailed deer. *Journal of Wildlife Diseases* 42:578-588.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology* 83:530-544.
- Kilpatrick, H. J., S. M. Spohr, and K. K. Lima. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. *Canadian Journal of Zoology* 79:949-954.

- Kjær, L. J., E. M. Schaubert, and C. K. Nielsen. 2008. Spatial and temporal analysis of contact rates in female white-tailed deer. *Journal of Wildlife Management* 72:1819-1825.
- Kohlmann, S. G., and K. L. Risenhoover. 1997. White-tailed deer in a patchy environment: A test of the ideal-free-distribution theory. *Journal of Mammalogy* 78:1261-1272.
- Langenberg, J. A., M. W. Miller, and L. Creekmore. 2008. *Alberta Chronic Wasting Disease Management: Program Review Panel Report (Peer Review)*. URL http://srd.alberta.ca/BioDiversityStewardship/WildlifeDiseases/documents/CWD-ABreview_FINAL.pdf
- Lesage, L., M. Crete, J. Huot, A. Dumont, and J. P. Ouellet. 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. *Canadian Journal of Zoology* 78:1930-1940.
- Lingle, S. 2003. Group composition and cohesion in sympatric white-tailed deer and mule deer. *Canadian Journal of Zoology* 81:1119-1130.
- Lloyd-Smith, J. O., P. C. Cross, C. J. Briggs, M. Daugherty, W. M. Getz, J. Latta, M. S. Sanchez, A. B. Smith, and A. Swei. 2005. Should we expect population thresholds for wildlife disease? *Trends in Ecology & Evolution* 20:511-519.
- Main, M. B. 2008. Reconciling competing ecological explanations for sexual segregation in ungulates. *Ecology* 89:693-704.
- McCallum, H., N. Barlow, and J. Hone. 2001. How should pathogen transmission be modelled? *Trends in Ecology & Evolution* 16:295-300.
- McClure, M. F., J. A. Bissonette, and M. R. Conover. 2005. Migratory strategies, fawn recruitment, and winter habitat use by urban and rural mule deer (*Odocoileus hemionus*). *European Journal of Wildlife Research* 51:170-177.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program, University of Massachusetts, Amherst. URL www.umass.edu/landeco/research/fragstats/fragstats.html
- McLellan, B. N., R. Serrouya, H. U. Wittmer, and S. Boutin. 2010. Predator-mediated Allee effects in multi-prey systems. *Ecology* 91:286-292.

- Meyers, L. A., B. Pourbohloul, M. E. J. Newman, D. M. Skowronski, and R. C. Brunham. 2005. Network theory and SARS: predicting outbreak diversity. *Journal of Theoretical Biology* 232:71-81.
- Miller, M. W., and M. M. Conner. 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: Spatial, temporal, and demographic influences on observed prevalence patterns. *Journal of Wildlife Diseases* 41:275-290.
- Miller, M. W., N. T. Hobbs, and S. J. Taverer. 2006. Dynamics of prion disease transmission in mule deer. *Ecological Applications* 16:2208-2214.
- Miller, M. W., E. S. Williams, N. T. Hobbs, and L. L. Wolfe. 2004. Environmental sources of prion transmission in mule deer. *Emerging Infectious Diseases* 10:1003-1006.
- Millsbaugh, J. S. J., R. A. Gitzen, B. J. Kernohan, J. A. Larson, and C. L. Clay. 2004. Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin* 32:148-157.
- Nakada, S. 2009. Molecular Epidemiology of Chronic Wasting Disease in Free-Ranging Mule Deer (*Odocoileus hemionus*) of Western Canada. MSc thesis, University of Alberta.
- Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 2006. Forage selection by mule deer: does niche breadth increase with population density? *Journal of Zoology* 269:39-49.
- Nixon, C. M., L. P. Hansen, P. A. Brewer, and J. E. Chelvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monographs* 118:3-77.
- Osnas, E. E., D. M. Heisey, R. E. Rolley, and M. D. Samuel. 2009. Spatial and temporal patterns of chronic wasting disease: fine-scale mapping of a wildlife epidemic in Wisconsin. *Ecological Applications* 19:1311-1322.
- Ostfeld, R. S., G. E. Glass, and F. Keesing. 2005. Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends in Ecology & Evolution* 20:328-336.
- Ramsey, D., N. Spencer, P. Caley, M. Efford, K. Hansen, M. Lam, and D. Cooper. 2002. The effects of reducing population density on contact rates between brushtail possums: implications for transmission of bovine tuberculosis. *Journal of Applied Ecology* 39:806-818.
- Riley, S.J., DeGloria, S.D. and Elliot, R. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*

5:1-4.

- Sandell, M., J. Agrell, S. Erlinge, and J. Nelson. 1990. Natal dispersal in relation to population-density and sex-ratio in the field vole, *Microtus agrestis*. *Oecologia* 83:145-149.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396-403.
- Schauber, E. M., D. J. Storm, and C. K. Nielsen. 2007. Effects of joint space use and group membership on contact rates among white-tailed deer. *Journal of Wildlife Management* 71:155-163.
- Schauber, E. M., and A. Woolf. 2003. Chronic wasting disease in deer and elk: a critique of current models and their application. *Wildlife Society Bulletin* 31:610-616.
- Smith, M. J., S. Telfer, E. R. Kallio, S. Burthe, A. R. Cook, X. Lambin, and M. Begon. 2009. Host-pathogen time series data in wildlife support a transmission function between density and frequency dependence. *Proceedings of the National Academy of Sciences of the United States of America* 106:7905-7909.
- Walter, W. D., K. C. VerCauteren, H. Campa, W. R. Clark, J. W. Fischer, S. E. Hygnstrom, N. E. Mathews, C. K. Nielsen, E. M. Schauber, T. R. Van Deelen, and S. R. Winterstein. 2009. Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. *Landscape Ecology* 24:1405-1420.
- Wasserberg, G., E. E. Osnas, R. E. Rolley, and M. D. Samuel. 2009. Host culling as an adaptive management tool for chronic wasting disease in white-tailed deer: a modelling study. *Journal of Applied Ecology* 46:457-466.
- White, P. C. L., S. Harris, and G. C. Smith. 1995. Fox contact behaviour and rabies spread: A model for the estimation of contact probabilities between urban foxes at different population densities and its implications for rabies control in Britain. *Journal of Applied Ecology* 32:693-706.
- Williams, E. S., M. W. Miller, T. J. Kreeger, R. H. Kahn, and E. T. Thorne. 2002. Chronic wasting disease of deer and elk: A review with recommendations for management. *Journal of Wildlife Management* 66:551-563.
- Williams, E. S., and S. Young. 1980. Chronic wasting disease of captive mule deer - spongiform encephalopathy. *Journal of Wildlife Diseases* 16:89-98.

Wu, J. G., W. J. Shen, W. Z. Sun, and P. T. Tueller. 2002. Empirical patterns of the effects of changing scale on landscape metrics. *Landscape Ecology* 17:761-782.

CHAPTER 4

SYNTHESIS AND MANAGEMENT IMPLICATIONS

4.1 Synopsis

In this thesis I addressed two current information needs for managing CWD in white-tailed and mule deer in east-central Alberta. First, I provided a sightability model for correcting for missed deer in aerial surveys in prairie parkland environments, and I provided recommendations for stratification of survey units by resource selection functions to improve the precision and accuracy of population estimates for deer in this region. Accurate and precise density estimates are necessary to evaluate the efficacy of CWD management and determine the effects of CWD-associated mortality on deer populations. Second, a better mechanistic understanding of how per capita contact rates may change with landscape patterns and grouping behaviour of deer under a range of population densities is an important step for modelling CWD spread. I extended past approaches for estimating pairwise contact rates (Schauber *et al.* 2007; Kjær *et al.* 2008) to obtain a per capita total contact rate. By simulating deer distributions for a range of deer densities and using empirical relationships between group sizes and home range sizes with density, I showed that if per capita contact rates of mule deer and white-tailed deer are important in disease transmission, a model intermediate between density- and frequency-dependent transmission (Begon *et al.* 2002) is likely most appropriate for CWD.

4.2 Aerial Surveys in Alberta

Developing sightability models has become relatively common for a number of species (Unsworth *et al.* 1999; Rice *et al.* 2008; McIntosh *et al.* 2009), but I present the first such model for deer in prairie parkland communities. Sightability was previously assumed to be high due to the open canopy of this environment, and I found this to be supported so long as snow cover was complete. Given my experience in the aerial surveys, I expect that the application of the sightability model to be problematic when deer densities are high ($> 5/\text{km}^2$)

because of the difficulty in reliably assessing and recording model variables for every deer group observed. In these situations, it may be advantageous to apply a population correction of at least 1.10 when survey conditions consist of full snow coverage, because my model predicted 90% sightability under full snow cover. When snow cover is spatially variable, it may be necessary to adjust this correction factor for local snow conditions. For example, if snow cover were 75% across the survey area, my model predicts the average sightability would drop to 84%, and a correction factor of 1.16 would be more appropriate.

Alberta Fish and Wildlife employs a stratified random sampling design, in which survey units are allocated to low, medium, or high deer density strata according to an arbitrary 20:60:20 ratio (Glasgow 2000). I found that stratification based on a natural breaks in resource selection function (RSF; Johnson *et al.* 2006) value calculated by Jenks optimization improved survey precision compared with the traditional stratification system in which units are allocated based on qualitative estimations of the amount of deer habitat present. Furthermore, RSF-based stratification has also been demonstrated to improve precision of elk surveys in western Alberta (Allen *et al.* 2008). While the RSF developed here would apply only to east-central Alberta or similar prairie parkland environments, the simulation approach I used is in itself a useful tool for evaluating alternative survey designs that could be employed in other jurisdictions. Simulations are particularly useful because the prohibitive costs of aerial surveys make it economically unfeasible to conduct multiple surveys to evaluate the efficiency of alternative designs.

The stated goal of CWD management programs in Alberta is to reduce deer density below 1 deer/km² of critical habitat (*i.e.* winter range) (Bollinger *et al.* 2004). More precise and accurate population estimates will allow managers to better assess whether this target density is being met, as well as how losses to CWD have impacted deer populations. Based on a post-stratified survey in east-central Alberta, the increase in precision using my recommended survey design will allow managers to detect with 90% confidence changes in deer density of 0.44 white-tailed deer/km² or 0.46 mule deer/km² compared to 0.68 and 0.60

deer/km² for white-tailed and mule deer, respectively, under the traditional survey design. This assessment of the improvement in precision is conservative, because post-stratification is limited by its inability to select how sampling effort is allocated and incorporates an additional variance term (Dressel and Norcross 2005). In fact, a pre-stratified survey would be capable of reliably detecting even smaller changes in deer density. In light of the results presented in Chapter 3, improved survey precision would be particularly important for low-density populations. My results suggest that contact rates in low-density populations could be highly sensitive to changes in deer density, and that changes < 1 deer/km² could have a strong effect on contact rates (Figure 3-5).

4.3 CWD Management in Alberta

Managing disease by reducing host density is based on the concept of a population threshold below which transmission will be reduced to the point where the disease will go extinct, although this phenomenon has not been well-documented (Lloyd-Smith *et al.* 2005). The existence of such a threshold would depend on CWD following density-dependent transmission. In contrast, early models assumed that CWD followed strict frequency-dependent transmission because of the aggregative behaviour of deer (Gross and Miller 2001). However, Gross and Miller (2001) did not critically evaluate this assumption of their model or weigh it against other possible models, so any conclusions that can be drawn from it are severely limited (Schauber and Woolf 2003). Wasserberg *et al.* (2009) attempted to address the density-transmission relationship in Wisconsin white-tailed deer by comparing time-series data on CWD prevalence to predictions generated from models assuming either density- or frequency-dependent transmission. However, Wasserberg *et al.* (2009) found nearly equivalent support for both models, although they suggested that culling could be employed in an adaptive management framework to distinguish between competing transmission models. Additionally, Wasserberg *et al.* (2009) conceded that CWD transmission is likely intermediate between the strictly density- and frequency-dependent

models they considered, and recommended that future modelling efforts consider nonlinear contact functions.

Several studies have identified spatial variation in CWD prevalence (Conner and Miller 2004; Farnsworth *et al.* 2006; Osnas *et al.* 2009) that may be attributed to the extent of deer habitat (Joly *et al.* 2006) or anthropogenic development (Farnsworth *et al.* 2005) and attempted to map risk factors for CWD. Previous efforts to model transmission (Gross and Miller 2001; Wasserberg *et al.* 2009) examined transmission at the level of the entire deer population, and did not incorporate how landscape features could influence the spread of CWD within a region. Using information from aerial surveys and radiocollared individuals, I detected mechanisms through which landscape features may influence the density-contact relationship and provide insight into the potential for spatially variable transmission within a single region. If, as my results suggest, the density-contact relationship varies considerably within a region due to landscape heterogeneity, this may explain why previous studies that pooled data across a large region may have been unable to distinguish between competing transmission models. If the density-contact relationships I obtained from simulated distributions approximate real-world processes, then management actions may have variable results even within one management region. Landscape influences on disease transmission underscore the need for spatially-explicit disease modelling to predict CWD spread in heterogeneous regions and subsequently plan management actions.

I found that deer contact rates exhibited a nonlinear relationship where the total per capita contact rate saturated as density increased, and in landscapes with a large amount of deer habitat the contact rate was lower and saturated at lower levels of density due to reduced home range size and overlap. Although others have suggested the likelihood of a nonlinear density-contact relationship for deer because of their social grouping behaviour (Schauber and Woolf 2003; Schauber *et al.* 2007; Wasserberg *et al.* 2009), my modelling is the first attempt to quantitatively explore mechanisms that may give rise to such a relationship. My results suggest that a saturating density-contact relationship may result from deer

group sizes that asymptote with density (Figure 3-4). If my finding of a nonlinear density-contact rate relationship in deer is true, it has important implications for CWD management in Alberta. For example, in areas where the local winter deer densities may be operating on the flat portion of the curve (Figure 3-5), a reduction in deer contact rate may not be accomplished without a dramatic reduction in deer density. This suggests that although the target of 1 deer/km² may be an appropriate objective, management that reduces density but falls short of this target may not achieve a meaningful effect on contact rates or CWD transmission. Failure to reduce contact rates through herd reductions is particularly likely for landscapes with a high proportion of woody cover in which I found the contact rate to saturate at the lowest densities. A local example of such a landscape is Canadian Forces Base Wainwright, a heavily wooded area adjacent to the current study area (Figure 2-1) with a large deer population. CWD was detected at CFB Wainwright in 2008 and 2009.

Because contacts within social groups appear to be an important mechanism for CWD spread (Gear *et al. in press*), eliminating entire social groups may be most effective management approach for limiting CWD transmission (Schauber *et al. 2007*). Ground- or helicopter-based sharpshooters are likely the most reliable method of eliminating entire social groups of deer. Herd reductions that only partially eliminate matrilineal social groups may lead to unrelated survivors forming new social groups (Williams *et al. 2008*). If such remaining members of a social group were infected with CWD, the infected survivors would very likely transmit CWD to members of a new social group, therefore a large-scale re-ordering of social structure could increase CWD prevalence. Alberta Fish and Wildlife's sharpshooting program was suspended in 2009, but neither sufficient population reduction nor elimination of entire deer social groups are feasible without this management tool.

4.4 Future Directions

Two prominent patterns of CWD prevalence in Alberta are that the vast majority of confirmed CWD cases (91%) have been in mule deer, and that 67%

have been in males of either species (Alberta Sustainable Resource Development 2010). Higher prevalence in mule deer has also been reported in other jurisdictions where the two species are sympatric, including Colorado/Wyoming (Miller *et al.* 2000) and Saskatchewan (Saskatchewan Environment 2010), and higher prevalence in males is also common (Williams *et al.* 2002; Miller and Conner 2005; Grear *et al.* 2006; Osnas *et al.* 2009). The present study explored the influence of deer habitat selection and grouping behaviours on density-dependent changes in direct contact rates during winter, and assessed whether these mechanisms could account for the observed variation in CWD prevalence among species-sex classes.

My results suggest that observed differences in contact structures between mule deer and white-tailed may at least partially explain the higher prevalence in mule deer. Mule deer had larger group sizes in winter across the range of deer densities found in my study area (Figure 3-4), which implies higher within-group contact rates. This could lead to the higher levels of CWD in mule deer if within-group transmission was the dominant pathway of CWD spread. In contrast, I did not find any evidence for different contact rates across sexes that could explain the higher prevalence among males. However, several components of transmission that have not been well-investigated may contribute to higher CWD prevalence in males. The major components of transmission not addressed in this thesis are variation among species-sex classes in the probability of transmission of a given contact (ν , Equation 1-1), indirect transmission through the environment, and transmission outside of winter, the latter due to a limited sample of GPS-collars being deployed on males during seasons other than winter.

Grear *et al.* (2006) proposed three mechanisms that could lead to higher prevalence rates in males. First, larger male home ranges could provide more opportunity for males to acquire CWD through the environment. Although I found no evidence for larger male home ranges in winter, this finding would not necessarily hold in other seasons (*e.g.* Nicholson *et al.* 1997). The second mechanism proposed by Grear *et al.* (2006) was that transmission could occur in male groups in spring and summer, contrasting with the dispersed distribution of

fawning does during those periods (Hirth 1977; Lingle 2003). Gear *et al.*'s (2006) third proposed mechanism was that altered male behaviour during the rut, including promiscuity and visiting rubs and scrapes (Hirth 1977), could increase transmission to males. These mechanisms could act either through increasing the contact rate, c , or through higher probabilities of disease transmission of a given contact, ν (Equation 1-1). Examples of the former include male groups exhibiting a greater number of contacts compared to female groups, or males experiencing more contacts through the environment via larger home ranges or visiting rubs and scrapes. Examples of the latter include interactions within male groups such as sparring (Hirth 1977) being more likely to transmit disease than interactions in female groups, and higher rates environmental transmission because of the increased infectivity of prions bound with soil particles (Johnson *et al.* 2007).

These two components, c and ν , of the overall force of infection likely differ among species-sex classes, potentially due to the mechanisms above, although this list is by no means exhaustive. Such differences would almost certainly shape the observed patterns of CWD prevalence, therefore knowledge of how c and ν differ between host classes is critical to future modelling efforts. Variable infection rates across host classes can be accounted for in a model by developing a matrix of transmission coefficients, with different values for transmission in either direction between each class, known as a WAIFW, or who-acquires-infection-from-whom, matrix (Anderson and May 1991; Dobson 1995; Klepac *et al.* 2007). Using this approach to model CWD transmission requires more knowledge of transmission pathways than is currently available, but it could provide more insight than current models that do not distinguish between host classes (*e.g.* Wasserberg *et al.* 2009).

Regardless of whether environmental transmission is responsible for differences in CWD prevalence among species-sex classes, it may be an important pathway of transmission. Indirect transmission is likely less influenced by social grouping than direct contacts, because it only requires spatial overlap, rather than the spatio-temporal coincidence required for direct contacts. Indeed, Schaub *et al.* (2007) found that the indirect contact rates between pairs of GPS-collared

white-tailed deer could be predicted by joint space use alone, regardless of whether the pair were in the same or different social groups. If true, indirect contact rates would likely be related to density and landscape in a similar manner as direct contacts between social groups (Figure 3-6, Figure 3-7), which were principally governed by spatial overlap and the amount of deer habitat (woody cover) in the region of overlap. If indirect contacts are linearly related to density, then including indirect contacts in the overall density-contact relationship would lead to increased density-dependence instead of the saturating relationship detected here.

This research was conducted to address CWD in deer, but my findings on contact structure would apply to other pathogens of deer as well, such as parasites, bovine tuberculosis (Schmitt *et al.* 1997), and foot-and-mouth disease (Highfield *et al.* 2008). Because my finding of a contact rate that saturates with density was obtained from simulated distributions rather than direct observation, this relationship can be viewed as a hypothesis to be tested explicitly. Due to the slow-spreading nature of CWD, evaluating this hypothesis directly would require years, or more likely, decades of data. Therefore, examining transmission rates of other directly-transmitted pathogens of free-ranging deer may be a viable approach to evaluating my findings.

4.5 Literature Cited

- Alberta Sustainable Resource Development. 2010. Statistics: Chronic Wasting Disease in Wild Deer. URL www.srd.alberta.ca/BioDiversityStewardship/WildlifeDiseases/ChronicWastingDisease.aspx [accessed 20 March 2010]
- Allen, J. R., L. E. McInenly, E. H. Merrill, and M. S. Boyce. 2008. Using resource selection functions to improve estimation of elk population numbers. *Journal of Wildlife Management* 72:1798-1804.
- Anderson, R. M. and R. M. May. 1991. *Infectious Diseases of Humans*, Oxford University Press.
- Begon, M., M. Bennett, R. G. Bowers, N. P. French, S. M. Hazel, and J. Turner. 2002. A clarification of transmission terms in host-microparasite models: numbers, densities and areas. *Epidemiology and Infection* 129:147-153.
- Conner, M. M., and M. W. Miller. 2004. Movement patterns and spatial epidemiology of a prion disease in mule deer population units. *Ecological Applications* 14:1870-1881.
- Dobson, A. 1995. The ecology and epidemiology of rinderpest virus in Serengeti and Ngorongoro conservation area. In *Serengeti II. Dynamics, Management and Conservation of an Ecosystem* (Sinclair, A.R.E. and P. Arcese, eds), pp. 485–505, University of Chicago Press.
- Dressel, S. C., and B. L. Norcross. 2005. Using poststratification to improve abundance estimates from multispecies surveys: a study of juvenile flatfishes. *Fishery Bulletin* 103:469-488.
- Farnsworth, M. L., J. A. Hoeting, N. T. Hobbs, and M. W. Miller. 2006. Linking chronic wasting disease to mule deer movement scales: A hierarchical Bayesian approach. *Ecological Applications* 16:1026-1036.
- Farnsworth, M. L., L. L. Wolfe, N. T. Hobbs, K. P. Burnham, E. S. Williams, D. M. Theobald, M. M. Conner, and M. W. Miller. 2005. Human land use influences chronic wasting disease prevalence in mule deer. *Ecological Applications* 15:119-126.
- Glasgow, W.M. 2000. *White Area Ungulate Management Plan, 1997-98 to 1999-2000 Project Completion Report*. Alberta Fish and Wildlife, Edmonton.
- Grear, D. A., M. D. Samuel, J. A. Langenberg, and D. Keane. 2006. Demographic patterns and harvest vulnerability of chronic wasting disease infected white-tailed deer in Wisconsin. *Journal of Wildlife Management* 70:546-

- Grear, D. A., M. D. Samuel, K. T. Scribner, B. V. Weckworth, and J. A. Langenberg. Influence of genetic relatedness and spatial proximity on chronic wasting disease infection among female white-tailed deer. *Journal of Applied Ecology* *in press*.
- Gross, J. E., and M. W. Miller. 2001. Chronic wasting disease in mule deer: disease dynamics and control. *Journal of Wildlife Management* 65:205-215.
- Hirth, D. H. 1977. Social behaviour of white-tailed deer in relation to habitat. *Wildlife Monographs* 53:3-55.
- Highfield, L., M. P. Ward, and S. Laffan. 2008. Representation of animal distributions in space: how geostatistical estimates impact simulation modeling of foot-and-mouth disease spread. *Veterinary Research* 39.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347-357.
- Johnson, C. J., J. A. Pedersen, R. J. Chappell, D. McKenzie, and J. M. Aiken. 2007. Oral transmissibility of prion disease is enhanced by binding to soil particles. *PLoS Pathogens* 3:874-881.
- Joly, D. O., M. D. Samuel, J. A. Langenberg, J. A. Blanchong, C. A. Batha, R. E. Rolley, D. P. Keane, and C. A. Ribic. 2006. Spatial epidemiology of chronic wasting disease in Wisconsin white-tailed deer. *Journal of Wildlife Diseases* 42:578-588.
- Klepac, P., L. W. Pomeroy, O. N. Bjornstad, T. Kuiken, A. Osterhaus, and J. M. Rijks. 2009. Stage-structured transmission of phocine distemper virus in the Dutch 2002 outbreak. *Proceedings of the Royal Society B-Biological Sciences* 276:2469-2476.
- Lingle, S. 2003. Group composition and cohesion in sympatric white-tailed deer and mule deer. *Canadian Journal of Zoology* 81:1119-1130.
- Lloyd-Smith, J. O., P. C. Cross, C. J. Briggs, M. Daugherty, W. M. Getz, J. Latta, M. S. Sanchez, A. B. Smith, and A. Swei. 2005. Should we expect population thresholds for wildlife disease? *Trends in Ecology & Evolution* 20:511-519.
- McIntosh, T. E., R. C. Rosatte, J. Hamr, and D. L. Murray. 2009. Development of

- a sightability model for low-density elk populations in Ontario, Canada. *Journal of Wildlife Management* 73:580-585.
- Miller, M. W., and M. M. Conner. 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: Spatial, temporal, and demographic influences on observed prevalence patterns. *Journal of Wildlife Diseases* 41:275-290.
- Miller, M. W., E. S. Williams, C. W. McCarty, T. R. Spraker, T. J. Kreeger, C. T. Larsen, and E. T. Thorne. 2000. Epizootiology of chronic wasting disease in free-ranging cervids in Colorado and Wyoming. *Journal of Wildlife Diseases* 36:676-690.
- Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: Tradeoffs associated with migration. *Journal of Mammalogy* 78:483-504.
- Osnas, E. E., D. M. Heisey, R. E. Rolley, and M. D. Samuel. 2009. Spatial and temporal patterns of chronic wasting disease: fine-scale mapping of a wildlife epidemic in Wisconsin. *Ecological Applications* 19:1311-1322.
- Rice, C. G., K. J. Jenkins, and W. Y. Chang. 2009. A sightability model for mountain goats. *Journal of Wildlife Management* 73:468-478.
- Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. *Journal of Wildlife Management* 51:622-630.
- Saskatchewan Environment. 2010. Chronic Wasting Disease (CWD). URL www.environment.gov.sk.ca/cwd [accessed 25 April 2010]
- Schauber, E. M., D. J. Storm, and C. K. Nielsen. 2007. Effects of joint space use and group membership on contact rates among white-tailed deer. *Journal of Wildlife Management* 71:155-163.
- Schauber, E. M., and A. Woolf. 2003. Chronic wasting disease in deer and elk: a critique of current models and their application. *Wildlife Society Bulletin* 31:610-616.
- Schmitt, S. M., S. D. Fitzgerald, T. M. Cooley, C. S. BruningFann, L. Sullivan, D. Berry, T. Carlson, R. B. Minnis, J. B. Payeur, and J. Sikarskie. 1997. Bovine tuberculosis in free-ranging white-tailed deer from Michigan. *Journal of Wildlife Diseases* 33:749-758.
- Unsworth, J.W., F. A. Leban, E. O. Garton, D. J. Leptich, and P. Zager. 1999. *Aerial Survey: User's Manual*, electronic edn. Idaho Department of Fish and Game, Boise.

- Wasserberg, G., E. E. Osnas, R. E. Rolley, and M. D. Samuel. 2009. Host culling as an adaptive management tool for chronic wasting disease in white-tailed deer: a modelling study. *Journal of Applied Ecology* 46:457-466.
- Williams, S. C., A. J. DeNicola, and I. M. Ortega. 2008. Behavioral responses of white-tailed deer subjected to lethal management. *Canadian Journal of Zoology* 86:1358-1366.
- Williams, E. S., M. W. Miller, T. J. Kreeger, R. H. Kahn, and E. T. Thorne. 2002. Chronic wasting disease of deer and elk: A review with recommendations for management. *Journal of Wildlife Management* 66:551-563.

APPENDICES

Appendix 1. Observed values of recorded variables in 100 sightability trials of 46 mule deer and 54 white-tailed deer in the prairie parklands of east-central Alberta conducted from January to April 2008-2009.

Deer ID	Date	Species	Sex	Time	Sighted	Group Size	Activity	Habitat	Canopy Cover (%)	Snow Cover (%)	Light	Temp
D407147	4/07/09	Mule	F	1021	1	7	Standing	Open	0	20	0	3
D507065	4/06/09	Mule	F	1022	1	2	Standing	Open	0	20	0	2
D609289	4/07/09	Mule	M	1441	1	4	Standing	Open	0	0	1	9
D609293	4/07/09	Mule	M	1508	1	8	Moving	Open	0	30	1	9
D609294	4/05/09	Mule	M	1110	1	6	Moving	Open	0	50	1	0
D609299	4/05/09	Mule	F	1207	1	5	Moving	Open	0	50	1	4
D407076	3/25/08	Mule	F	1530	1	3	Standing	Shrubs	15	50	1	1
D407183	3/25/08	Mule	F	1504	1	3	Moving	Shrubs	10	80	1	1
D407183	4/07/09	Mule	F	1034	1	2	Moving	Shrubs	15	0	0	3
D408218	4/07/09	Mule	F	1114	1	8	Moving	Shrubs	20	20	0	4
D408230	3/25/08	Mule	F	1511	1	5	Standing	Shrubs	10	50	1	1
D609288	4/07/09	Mule	M	1450	1	6	Standing	Shrubs	15	20	1	9
D609296	4/05/09	Mule	F	1405	1	6	Standing	Shrubs	10	50	1	6
D108257	3/25/08	Mule	M	1055	0	2	Bedded	Shrubs	40	100	1	-2
D308226	2/01/08	Mule	F	1114	0	1	Standing	Trees	30	100	0	-28
D408230	4/07/09	Mule	F	1052	0	4	Standing	Trees	25	40	0	4
D509317	4/06/09	Mule	F	1310	0	3	Moving	Trees	15	60	1	5
D609299	4/07/09	Mule	F	1239	0	3	Standing	Trees	15	30	0	7
D106021	1/31/08	Mule	F	1153	1	4	Standing	Trees	40	100	0	-28
D107056	3/25/08	Mule	F	1210	1	32	Standing	Trees	10	95	1	0

Appendix 1 Continued

Deer ID	Date	Species	Sex	Time	Sighted	Group Size	Activity	Habitat	Canopy Cover (%)	Snow Cover (%)	Light	Temp
D107163	1/31/08	Mule	F	1523	1	2	Standing	Trees	10	100	0	-30
D108221	1/31/08	Mule	F	1207	1	3	Standing	Trees	25	100	0	-28
D307109	2/01/08	Mule	F	1301	1	9	Standing	Trees	20	100	1	-26
D307115	2/01/08	Mule	M	1052	1	1	Standing	Trees	20	100	0	-28
D407083	2/01/08	Mule	F	1133	1	1	Standing	Trees	20	100	1	-27
D407147	2/01/08	Mule	F	1205	1	15	Standing	Trees	15	100	1	-27
D407147	3/25/08	Mule	F	1620	1	9	Standing	Trees	20	80	1	2
D407174	2/01/08	Mule	F	1021	1	6	Standing	Trees	18	100	0	-28
D407183	2/01/08	Mule	F	957	1	4	Standing	Trees	15	100	0	-28
D408220	2/01/08	Mule	F	952	1	7	Standing	Trees	10	100	0	-28
D507067	1/25/08	Mule	M	1345	1	2	Standing	Trees	20	100	0	-12
D507068	4/06/09	Mule	F	1245	1	9	Standing	Trees	20	40	1	5
D509318	4/06/09	Mule	F	1328	1	4	Standing	Trees	10	30	1	6
D509319	4/06/09	Mule	F	1332	1	15	Moving	Trees	15	35	1	6
D609287	4/05/09	Mule	M	1454	1	1	Moving	Trees	20	65	1	6
D609288	4/05/09	Mule	M	1413	1	1	Standing	Trees	80	90	1	6
D609289	4/05/09	Mule	M	1148	1	4	Moving	Trees	80	95	1	2
D609295	4/05/09	Mule	F	1125	1	3	Moving	Trees	15	70	1	0
D609295	4/07/09	Mule	F	1348	1	6	Standing	Trees	20	60	1	8
D609298	4/05/09	Mule	F	1443	1	4	Standing	Trees	10	35	1	6
D609298	4/07/09	Mule	F	1331	1	3	Standing	Trees	20	10	1	8
D609301	4/07/09	Mule	F	1220	1	4	Moving	Trees	25	60	0	7
D509316	4/06/09	Mule	M	1234	0	3	Bedded	Trees	50	50	0	2

Appendix 1 Continued

Deer ID	Date	Species	Sex	Time	Sighted	Group Size	Activity	Habitat	Canopy Cover (%)	Snow Cover (%)	Light	Temp
D407174	3/25/08	Mule	F	1627	1	5	Bedded	Trees	40	30	1	2
D508253	3/25/08	Mule	M	1000	1	15	Bedded	Trees	20	100	1	-2
D609290	4/05/09	Mule	M	1141	1	4	Bedded	Trees	20	85	1	0
D107060	1/31/08	WTD	F	1650	1	30	Standing	Trees	0	100	0	-30
D107169	1/31/08	WTD	F	1326	1	13	Standing	Trees	0	100	0	-29
D407184	3/25/08	WTD	F	1521	1	20	Standing	Trees	0	20	1	1
D407184	4/07/09	WTD	F	1101	1	3	Standing	Trees	10	15	0	4
D509320	4/06/09	WTD	F	955	1	3	Standing	Trees	20	40	0	2
D609303	4/07/09	WTD	F	1304	1	1	Moving	Trees	10	0	0	8
D107031	3/25/08	WTD	F	1255	0	3	Standing	Trees	5	65	1	0
D107030	1/31/08	WTD	F	1341	1	2	Standing	Trees	0	100	0	-30
D107031	4/06/09	WTD	F	1629	1	3	Standing	Trees	10	0	1	10
D107062	1/31/08	WTD	M	1300	1	3	Standing	Trees	0	100	0	-28
D408203	4/07/09	WTD	M	1006	1	5	Standing	Trees	5	15	0	3
D107033	1/31/08	WTD	F	1620	1	2	Bedded	Trees	10	100	0	-30
D108185	3/25/08	WTD	M	1121	1	11	Bedded	Trees	10	95	1	-3
D109307	4/06/09	WTD	M	1751	0	2	Moving	Trees	70	20	1	10
D109310	4/06/09	WTD	F	1810	0	4	Standing	Trees	20	15	1	10
D407079	2/01/08	WTD	F	1151	0	2	Standing	Trees	30	100	1	-27
D107031	1/31/08	WTD	F	1606	1	3	Standing	Trees	30	100	0	-30
D107052	3/25/08	WTD	F	1323	1	1	Moving	Trees	15	95	1	0
D107054	1/31/08	WTD	F	1241	1	2	Standing	Trees	30	100	0	-28
D107054	3/25/08	WTD	F	1311	1	6	Moving	Trees	40	90	1	0

Appendix 1 Continued

Deer ID	Date	Species	Sex	Time	Sighted	Group Size	Activity	Habitat	Canopy Cover (%)	Snow Cover (%)	Light	Temp
D107161	1/31/08	WTD	F	1249	1	5	Standing	Trees	40	100	1	-28
D107164	1/31/08	WTD	F	1311	1	4	Standing	Trees	15	100	0	-28
D107169	4/06/09	WTD	F	1610	1	2	Standing	Trees	55	25	1	10
D108189	1/31/08	WTD	F	1557	1	15	Standing	Trees	20	100	0	-30
D108217	1/31/08	WTD	F	1548	1	4	Standing	Trees	20	100	0	-30
D307057	4/05/09	WTD	F	1503	1	2	Standing	Trees	20	50	1	6
D307176	2/01/08	WTD	F	1038	1	2	Standing	Trees	10	100	0	-28
D407144	4/07/09	WTD	F	1014	1	3	Moving	Trees	10	60	0	3
D407179	2/01/08	WTD	F	1007	1	3	Standing	Trees	30	100	0	-28
D408206	3/25/08	WTD	M	1454	1	4	Standing	Trees	15	85	1	1
D408234	3/25/08	WTD	F	1443	1	3	Standing	Trees	15	95	1	1
D408245	4/07/09	WTD	F	959	1	4	Moving	Trees	25	50	0	3
D507066	3/25/08	WTD	F	1725	1	1	Standing	Trees	25	55	1	4
D507086	1/25/08	WTD	F	1410	1	4	Moving	Trees	25	100	0	-12
D507193	1/25/08	WTD	M	1435	1	3	Standing	Trees	30	100	1	-12
D507195	1/25/08	WTD	F	1440	1	1	Standing	Trees	55	100	0	-12
D508193	3/25/08	WTD	M	1021	1	5	Standing	Trees	10	100	1	-2
D609297	4/05/09	WTD	F	1513	1	6	Moving	Trees	15	55	0	6
D609304	4/05/09	WTD	F	1427	1	4	Standing	Trees	20	60	1	6
D106012	4/06/09	WTD	F	1600	0	3	Bedded	Trees	10	5	1	10
D107030	3/25/08	WTD	F	1232	0	2	Bedded	Trees	10	95	1	0
D108189	4/06/09	WTD	F	1732	0	6	Bedded	Trees	30	30	1	10
D109277	4/06/09	WTD	F	1434	0	2	Bedded	Trees	80	50	1	8

Appendix 1 Continued

Deer ID	Date	Species	Sex	Time	Sighted	Group Size	Activity	Habitat	Canopy Cover (%)	Snow Cover (%)	Light	Temp
D109327	4/06/09	WTD	M	1536	0	1	Bedded	Trees	15	5	1	10
D507107	1/25/08	WTD	F	1458	0	2	Bedded	Trees	65	100	0	-12
D609305	4/07/09	WTD	F	1520	0	2	Bedded	Trees	70	55	1	9
D107036	3/25/08	WTD	F	1109	1	15	Bedded	Trees	10	100	1	-3
D107158	1/31/08	WTD	F	1319	1	3	Bedded	Trees	30	100	0	-29
D107159	4/06/09	WTD	F	1709	1	6	Bedded	Trees	50	5	1	10
D107166	1/31/08	WTD	F	1535	1	3	Bedded	Trees	45	100	0	-30
D308228	2/01/08	WTD	F	1423	1	2	Bedded	Trees	15	100	0	-26
D508194	3/25/08	WTD	F	1028	1	8	Bedded	Trees	10	100	1	-2
D508259	3/25/08	WTD	F	1010	1	30	Bedded	Trees	25	100	1	-2
D609291	4/07/09	WTD	M	1255	1	4	Bedded	Trees	25	40	0	8

Group Size = Conspecific deer within 20 m of radiocollared individual; Canopy Cover = Percent of tree cover within 20 m of individual; Snow Cover = Percent of snow cover within 20 m of individual; Light = flat (0) or bright (1) reflection off snow; Temp = Temperature in °C. All variables were recorded for the time and location that the radiocollared deer was first seen.

Appendix 2a. Observed values of continuous variables in 100 sightability trials of 46 mule deer and 54 white-tailed deer in the prairie parklands of east-central Alberta

Variable	Mean	Median	Range
Group Size	5.37	4	1 – 32
Canopy Cover (%)	21.7	19	0 – 80
Snow Cover (%)	70	80	0 – 100
Temperature (°C)	-5.8	1	-30 – 10

Appendix 2b. Observed values of categorical variables in 100 sightability trials of 46 mule deer and 54 white-tailed deer in the prairie parklands of east-central Alberta

Variable	Values	<i>n</i>
Activity	Bedded	25
	Standing	57
	Moving	18
Habitat Class	Open	12
	Shrubs	15
	Trees	73
Light Intensity	Flat	43
	Bright	57

Appendix 3. Complete results of simulated surveys for white-tailed (WTD) and mule deer in Wildlife Management Unit 234 in east-central Alberta, based on data obtained from aerial surveys conducted in 2008 and 2009.

Stratification Criteria	Strata Binning	Allocation	White-tailed Deer 2008			White-tailed Deer 2009			Mule Deer 2008			Mule Deer 2009		
			CI	CV	Acc	CI	CV	Acc	CI	CV	Acc	CI	CV	Acc
Historical	20:60:20	Equal	54%	31%	21%	61%	34%	31%	73%	41%	31%	81%	46%	32%
Historical	20:60:20	Proportional	52%	30%	21%	61%	35%	29%	73%	41%	33%	81%	46%	38%
Historical	20:60:20	Optimal	49%	28%	20%	58%	33%	26%	67%	38%	27%	74%	42%	29%
Cover	20:60:20	Equal	43%	24%	22%	53%	30%	27%	60%	34%	34%	72%	41%	36%
Cover	20:60:20	Proportional	45%	25%	25%	56%	32%	31%	70%	40%	37%	80%	45%	44%
Cover	20:60:20	Optimal	41%	23%	21%	48%	27%	27%	57%	32%	34%	67%	38%	35%
Cover	Equal	Equal	44%	25%	17%	52%	29%	24%	69%	39%	30%	77%	44%	33%
Cover	Equal	Optimal	39%	22%	18%	44%	25%	18%	54%	30%	20%	61%	34%	26%
Cover	Jenks	Equal	38%	21%	17%	43%	24%	18%	57%	32%	24%	64%	36%	27%
Cover	Jenks	Proportional	42%	24%	16%	50%	28%	23%	67%	38%	29%	74%	42%	34%
Cover	Jenks	Optimal	44%	25%	19%	41%	23%	17%	52%	29%	23%	53%	30%	26%
Combined RSF	20:60:20	Equal	49%	28%	19%	53%	30%	26%	60%	34%	25%	68%	38%	29%
Combined RSF	20:60:20	Proportional	47%	27%	19%	56%	31%	26%	68%	39%	28%	76%	43%	32%
Combined RSF	20:60:20	Optimal	47%	27%	18%	52%	29%	23%	61%	35%	27%	67%	38%	31%
Combined RSF	Equal	Equal	42%	24%	17%	50%	28%	23%	70%	39%	30%	74%	42%	34%
Combined RSF	Equal	Optimal	41%	23%	16%	48%	27%	21%	67%	38%	28%	74%	42%	29%
Combined RSF	Jenks	Equal	39%	22%	19%	40%	22%	16%	50%	28%	19%	51%	29%	20%
Combined RSF	Jenks	Proportional	42%	24%	17%	48%	27%	21%	63%	36%	26%	75%	42%	28%
Combined RSF	Jenks	Optimal	39%	22%	15%	43%	24%	18%	57%	32%	23%	67%	38%	29%
Mule RSF	20:60:20	Equal	50%	28%	21%	53%	30%	26%	62%	35%	25%	69%	39%	28%
Mule RSF	20:60:20	Proportional	47%	26%	19%	55%	31%	27%	69%	39%	31%	79%	44%	37%

Appendix 3 Continued

Stratification Criteria	Strata Binning	Allocation	White-tailed Deer 2008			White-tailed Deer 2009			Mule Deer 2008			Mule Deer 2009		
			CI	CV	Acc	CI	CV	Acc	CI	CV	Acc	CI	CV	Acc
Mule RSF	20:60:20	Optimal	43%	24%	16%	48%	27%	21%	62%	35%	26%	68%	38%	31%
Mule RSF	Equal	Equal	41%	23%	16%	50%	29%	25%	69%	39%	30%	77%	43%	32%
Mule RSF	Equal	Optimal	36%	20%	15%	43%	24%	19%	61%	34%	23%	65%	37%	25%
Mule RSF	Jenks	Equal	39%	22%	16%	38%	22%	17%	49%	27%	20%	50%	28%	22%
Mule RSF	Jenks	Proportional	41%	23%	16%	47%	26%	21%	63%	35%	26%	73%	41%	28%
Mule RSF	Jenks	Optimal	36%	20%	14%	41%	23%	18%	55%	31%	22%	66%	37%	26%
WTD RSF	20:60:20	Equal	48%	27%	20%	51%	29%	25%	56%	32%	22%	63%	35%	25%
WTD RSF	20:60:20	Proportional	46%	26%	19%	54%	31%	27%	68%	39%	30%	72%	41%	34%
WTD RSF	20:60:20	Optimal	43%	24%	18%	47%	26%	21%	53%	30%	21%	56%	32%	23%
WTD RSF	Equal	Equal	45%	26%	19%	52%	29%	25%	69%	39%	31%	74%	42%	35%
WTD RSF	Equal	Optimal	40%	22%	16%	44%	25%	18%	58%	33%	23%	62%	35%	25%
WTD RSF	Jenks	Equal	46%	26%	20%	43%	24%	18%	54%	30%	21%	53%	30%	22%
WTD RSF	Jenks	Proportional	44%	25%	18%	49%	28%	20%	67%	38%	28%	74%	42%	30%
WTD RSF	Jenks	Optimal	43%	24%	17%	44%	25%	19%	60%	34%	25%	67%	38%	26%

CI = One-sided 90% confidence interval, expressed as a percentage of the population estimate; CV = Coefficient of Variation; Acc = Accuracy of population estimate, calculated as the absolute value of the difference between the estimate of the simulated survey and the true number of deer observed in the original survey, expressed as a percentage of the true number of deer observed.